

Gross production, respiration and biosphere CO₂ fluxes under global warming

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Abstract: Terrestrial gross primary production (GPP) has commonly been estimated as about 120 Gt C year⁻¹, based mainly on estimates from the International Biological Program (IBP, 1964-74, with 60 Gt C year⁻¹ for net primary production, NPP) and an assumption that autotrophic respiration (R_A) is about the same as NPP. This 2 x NPP assumption for GPP has been reinforced by some more recent studies that scaled up from short-term, temperate-zone site measurements using satellite data, with values of photosynthetic efficiency assumed to be constant. Analysis of the full IBP data-base suggests higher GPP and R_A site values, especially in the tropics, and higher values for terrestrial totals and the global R_A/GPP ratio. The CO₂ source-sink behavior of terrestrial vegetation is determined largely by this ratio, and a larger ratio implies possibly larger biospheric CO₂ sources under global warming but also possibly greater net CO₂ uptake by early-successional vegetation. On the other hand, the IBP data have been discredited by both improved methods for estimating respiration in the field and by better understanding of the nature and determinants of maintenance versus growth respiration. Examination of this new respiration paradigm, plus two studies by other authors, suggests that terrestrial GPP probably is higher than 120 Gt C year⁻¹, though not as high as the IBP data imply. The IBP data represent the largest, most geographically representative data-base available for stand metabolism, so it is perhaps useful to ask just how bad these data are, where and why, and whether they can be "rehabilitated" in any useful way. The largest uncertainty appears to be in the tropics, where landscape degradation is often severe and rehabilitation inherently difficult. Further study should focus on such critical needs, including better tropical metabolic data and methods for rehabilitating devastated tropical landscapes.

Resumen: Comúnmente se ha estimado que la producción primaria bruta terrestre (PPB) es de alrededor de 120 Gt C/año, sobre todo con base en estimaciones del Programa Biológico Internacional (PBI, 1964-74, con 60 Gt C/año para la producción primaria neta, PPN) y bajo la suposición de que la respiración autótrofa (R_A) es más o menos igual a la PPN. Este supuesto de que la PPB equivale al doble de la PPN ha sido reforzada por algunos estudios más recientes llevados a escalas superiores a partir de medidas de corto plazo para zonas templadas y usando datos satelitales, suponiendo que los valores de eficiencia fotosintética son constantes. El análisis de la base de datos completa del IBP sugiere valores mayores a nivel de sitio para la PPB y R_A, especialmente en los trópicos, y valores más altos para el total terrestre y el cociente global R_A/GPP. El comportamiento de la vegetación terrestre como fuente-resumidero de CO₂ está determinado en gran medida por este cociente, y un valor más alto implica que posiblemente hay fuentes más grandes de CO₂ de la biosfera debido al calentamiento global, pero también posiblemente una incorporación mayor de CO₂ neto en la vegetación sucesional temprana. Por otra parte, los datos del PBI han sido desacreditados tanto por métodos mejorados para estimar la respiración en el campo, como por una mejor comprensión de la naturaleza y los determinantes del mantenimiento versus respiración asociada al crecimiento. La revisión de este nuevo paradigma de la respiración, junto con dos estudios realizados por otros autores, sugiere que la PPB

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terrestre probablemente supere los 120 Gt C/año, si bien que no sea tan alta como lo sugieren los datos del IBP. Los datos del PBI constituyen la base de datos disponible más grande y más representativa geográficamente sobre metabolismo a nivel de rodal, de modo que quizá sería útil preguntarse qué tan malos son estos datos, dónde fallan y por qué, y si éstos pueden ser "rehabilitados" en alguna manera útil. La incertidumbre mayor parece estar en los trópicos, donde la degradación del paisaje es frecuentemente severa y la rehabilitación inherentemente difícil. Estudios futuros deberán enfocarse hacia estas necesidades críticas, incluyendo la obtención de mejores datos metabólicos para los trópicos y el desarrollo de métodos para rehabilitar paisajes tropicales devastados.

Resumo: A produção primária bruta terrestre (GPP) tem sido vulgarmente estimada em cerca de 120 Gt C/ano, principalmente com base nas estimativas do Programa Biológico Internacional (IBP, 1964-74 com 60 Gt C/ano para a produção primária líquida, NPP) e no pressuposto de que a respiração autotrófica (R_A) é aproximadamente a mesma que a NPP. Assim o pressuposto de 2 x NPP para a GPP foi reforçada por alguns estudos mais recentes que extrapolaram, a partir de medições de curto prazo usando medidas de satélite, e estações ecológicas de zonas temperadas, os valores da eficiência fotossintética consideradas constantes. A análise completa da base de dados do IBP sugere valores locais de GPP e R_A mais elevados, especialmente nos trópicos, e valores mais elevados para os totais terrestres e para o valor global do ratio R_A /GPP. O comportamento da fonte/sorvedouro do CO₂ da vegetação terrestre é largamente determinado por este ratio, e uma valor mais elevado implica, possivelmente, valores mais elevados de fontes de CO₂ bioesférico em situações de aquecimento global mas também, possivelmente, maior absorção líquida de CO₂ pela sucessão juvenil da vegetação. Por outro lado, os dados do IBP foram desacreditados quer pelos métodos melhorados de estimação da respiração no campo e por uma melhor compreensão quanto à natureza e os determinantes da manutenção versus respiração do crescimento. O exame deste novo paradigma da respiração, mais dois estudos de outros autores, sugere que o GPP terrestre é provavelmente mais elevado do que as 120 Gt C/ano, se bem que não tão alto como implícito nos dados do IBP. Os dados do IBP representam o maior e geograficamente a mais representativa base de dados disponível para o metabolismo das parcelas e, por isso, é provavelmente útil perguntar quão maus são estes dados, onde e porquê e se eles podem ser "reabilitados" de qualquer forma útil. A maior incerteza parece ocorrer nos trópicos onde a degradação da paisagem é por vezes bastante severa e a reabilitação inerentemente difícil. Estudos futuros devem debruçar-se sobre tais necessidades críticas, incluindo melhores dados do metabolismo nos trópicos e métodos para a reabilitação de paisagens tropicais devastadas.

Key words: Autotrophic respiration, biosphere-atmosphere CO₂ fluxes, data needs, global warming, gross primary production, International Biological Program, respiration paradigm, respiration-production ratio.

Introduction

The behavior of biosphere-atmosphere carbon fluxes depends not only on net primary production (NPP), as still emphasized by recent syntheses (e.g. IPCC 2001; Roy *et al.* 2001), but on its component processes gross primary production (GPP, i.e. photosynthesis) and autotrophic respiration (R_A):

$$NPP = GPP - R_A \quad (1)$$

NPP represents the balance of CO₂ fixation and respiratory release and appears as new biomass, the energy basis for all ecosystems. GPP and R_A , however, may respond quite differently to changing environmental conditions, and it is their ratio (or NPP/GPP) that largely determines biospheric CO₂ sources and sinks. Seasonal CO₂ fluxes in a stable, natural terrestrial biosphere were quantified (Box 1988) and largely reflect the

seasonal pattern in measurements of atmospheric CO₂ levels. The different responses by GPP and R_A in a changing atmosphere, however, suggest more permanent changes in CO₂ source/sink behavior and possible limitations on carbon sequestration in the terrestrial biosphere. Higher tropical temperatures and R_A/GPP ratios (at least in earlier data) suggest that accurate quantitative understanding of R_A and GPP in the tropics is especially important.

Attempts to estimate global primary productivity began in 1862 with Liebig's estimate of 230-240 Gt CO₂ year⁻¹ for total terrestrial NPP (Lieth 1975). All of these processes are difficult to measure, however, and the first major effort involved studies conducted under the International Biological Program (IBP, 1964-74). The first modeling attempts used these IBP data and yielded climate-based regression models such as the "Miami Model" for terrestrial NPP (Lieth & Box 1972; Lieth 1973). Quantifications of world maps based on such regressions converged on about 60 Gt C year⁻¹ for terrestrial NPP (Box 1975), a value which is still used (e.g. IPCC 2001; Wigley & Schimel 2000). A regression for GPP against NPP yielded a predictive map (Lieth & Box 1977) and an estimate of 132 Gt C year⁻¹ for terrestrial GPP (Box 1978). This left terrestrial R_A (by equation 1) at slightly over 50% of GPP. A value of 120 Gt C year⁻¹ for terrestrial GPP has been widely used since the early 1980s (e.g. Bolin & Fung 1992; Post *et al.* 1997; Trabalka 1985), often stated as being 2 x NPP (e.g. Schlesinger 1991), but usually without support (e.g. Houghton *et al.* 1985; IPCC 1995; Post *et al.* 1990).

Most analyses of the IBP data were done before all the tropical data were widely known (e.g. Cooper 1975; Edwards *et al.* 1981; Kira 1975; cf. UNESCO 1978). Some later estimates of R_A and GPP in tropical rainforests were higher, suggesting that terrestrial GPP may be higher than 120 Gt C year⁻¹ (and the R/GPP ratio higher than 50%). Newer studies using satellite data have also suggested higher totals. On the other hand, recent advances in understanding and measuring respiration in particular have suggested that the IBP data overestimated respiration (thus also GPP), due both to errors in methodology and to misunderstanding the quantitative importance of growth versus maintenance respiration (e.g. Ryan & Waring 1992; Ryan *et al.* 1994). Other recent work has

also suggested that maintenance respiration is less than once thought, is very closely linked to production through the chemistry of metabolism, and that both R_A and GPP are quite dependent on tissue nitrogen content (see summary by Cannell & Thornley 2000). At least one anonymous reviewer (of a different, earlier manuscript) believed that these new findings completely invalidate all earlier data and implications based on them.

Even though some CO₂ involved in metabolism is cycled quite locally (cf. Houghton *et al.* 1985), respiration and gross production are nevertheless key components of the changing global carbon budget (e.g. Gifford 1994; Saxe *et al.* 2001; Schoen 1997; Williams *et al.* 1997) and have implications for assumptions of constant NPP/GPP ratios and photosynthetic efficiency in global models. Those IBP studies that estimated all three production components (equation 1) thus become important, in spite of probable flaws, because they constitute a relatively large data-base with greater geographic coverage than newer studies and because the full data-base was never completely analyzed. Various authors have cited a need for "process models" for the components of NPP (e.g. Cramer *et al.* 2001; Ciais *et al.* 2001), but such models are complex and difficult to calibrate for global use. In the meantime, a statistical model for GPP provides some increased resolution for anticipating the response of carbon fluxes to climate change.

The purpose of this paper is, therefore, to:

(1) analyze the IBP data, derive a better statistical GPP model, and estimate its implied totals for terrestrial GPP and R_A, giving full weight to the later-arriving tropical data;

(2) consider implications of these mostly higher estimates (including higher R_A/GPP) for biospheric CO₂ sources and sinks;

(3) interpret these values in light of the newer findings on metabolism and the accuracy of earlier measurement methods; and

(4) suggest some remaining questions and needs, especially in the tropics, and the possibility of "rehabilitating" potentially useful older data.

If the IBP-based estimates of respiration are too large, as some later studies suggest, then these higher values can perhaps be understood as an upper limit on the true values. The largest differences appear to be in the tropics.

The IBP Data

The IBP emphasized primary productivity as a key to understanding ecosystem function. As a result, it supported many projects that estimated full stand metabolism, i.e. at least two components of equation 1 (thus also the third), both above and below ground, over the course of the whole year. IBP-era estimates were gathered from the literature, providing 56 studies of both mature and growing vegetation, from 22 study areas (on four continents), involving most terrestrial biome types. Since most of the (fewer) later studies have not attempted to estimate full stand metabolism, the IBP data represent the only full-metabolism database that is large enough to be geographically representative of the world's land areas. They also represent a discrete, roughly 20-year period with relatively constant atmospheric CO₂ and less CO₂ fertilization than now.

Almost every IBP study differed from the others in some aspects of method and biomass components actually measured. The metabolic estimates were, however, made largely according to standard methods documented by the IBP (Newbould 1967) and others (e.g. Shidei & Kira 1977; Whittaker & Marks 1975). Net production was usually estimated by some combination of harvest and allometric methods. Gross production was estimated both directly and indirectly (i.e. by estimating R_A and adding it to NPP). Strategies for direct estimation of GPP included gas-exchange (e.g. Odum & Pigeon 1970), micrometeorological (e.g. Kira 1978), and theoretical methods (e.g. photosynthesis models based on field measurements, Hozumi *et al.* 1969). Indirect GPP methods necessarily focused on estimation of autotrophic respiration, on which the accuracy of GPP values is thus heavily dependent.

Strategies for estimating respiration generally involved "enclosures" that trapped the CO₂ evolving from pieces of cut biomass placed inside. This method was pioneered by Boysen Jensen (1910, 1932), also used by Moeller (1945) on European beech forests, and expanded by Japanese teams working in both Southeast Asia and Japan (see Kira *et al.* 1964). The amount of CO₂ evolved was measured by analyzing air samples drawn from the chamber or by titration, usually with KOH (see Yoda 1978; cf Yoda 1967; Shidei & Kira 1977). In a few cases, respiration was estimated from surro-

gate respiration rates at other sites or extrapolated from base temperatures (using an assumed Q_{10} value and allometric biomass relationships) (e.g. Maruyama 1971; Tadaki 1965). It is the accuracy of these "enclosure" methods with detached biomass, used in most IBP-era studies, that has recently been questioned (Ryan 1990; Ryan *et al.* 1994).

The IBP data-base includes 31 stand estimates for broad-leaved forests, 16 for conifer forests, two at a tundra site, four for two disclimax tropical savanna-woodland stands, two for a substitute grassland in India, and one for a dry-climate (i.e. high-salinity) mangrove. Especially well represented are tropical rainforests of Southeast Asia (four locations in three countries), evergreen broad-leaved forests and montane conifer forests in Japan, and beech (*Fagus*) forests in Europe and Japan. All of the main terrestrial biomes are represented except deserts, lowland mediterranean climates, and temperate grasslands (though boreal conifer forests are represented only by subalpine analogs). The IBP data include 23 mature stands, 15 late-successional stands, 9 mid-successional stands, 3 early-successional stands, and the 6 disclimax stands.

Methodology

The IBP stands were first classified by biome, climate type and successional status, and the individual metabolic estimates by measurement method, standardized as far as possible. Ancillary biomass and other stand data were also collected, and site locations and climatic conditions were reconstructed. Potential evapotranspiration (PET) was estimated from air-temperature methods using a geographical balance designed to minimize regional errors (Box 1986). Actual evapotranspiration (AET) was then calculated using this PET basis and standard water-balance methodology (Mather 1974), giving the same global AET basis that has been used for various other models and maps of biosphere processes (e.g. Box 1988; Box *et al.* 1989). Since AET combines the availability of energy and water in one variable, it is a known index of many biosphere processes (cf Box & Meentemeyer 1991) and a useful single-variable representation of global climatic conditions. The IBP estimates of annual GPP, along with their respective measurement methods, are shown in

Fig. 1, plotted against annual AET. The scatter in values may reflect different estimation methods but also differences in stand maturity, different stands or vegetation types at the same general location, and the metabolism of the particular measurement year.

The data were next examined for extremes, outliers and suspicious values. Excluded, in particular, were a respiration-based GPP estimate of 14.4 kg of dry matter per m² of ground area annually (Yoda 1967, later retracted; cf Ogawa 1978) and five even higher respiration estimates in Oregon tall-conifer forests (Grier & Logan 1977, not

included in Fig. 1 or the 56 total). The highest remaining GPP estimates are 12.3 kg d.m. m⁻², based on titration for respiration (T in Fig. 1), and 12.2 kg d.m. m⁻² by a photosynthesis model (P), both in the Khao Chong rainforest in Thailand (Kira *et al.* 1967). Only slightly lower values were found in other SE Asian rainforests and by elaborate gas-exchange measurements in a lower-montane rainforest in Puerto Rico (Odum 1970). Lower values, however, were also reported: 8.2 kg (by titration) and 8.6 (by photosynthesis model) at Pasoh (Peninsular Malaysia, Kira 1978) and only 5.2 kg near Abidjan in West Africa (Müller & Nielsen 1965).

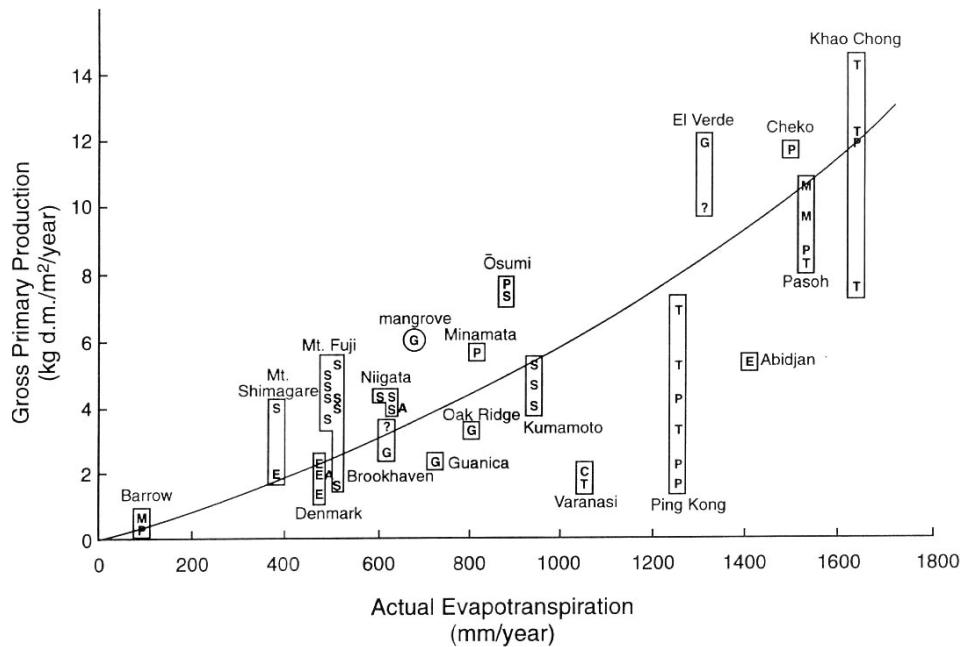


Fig. 1. IBP estimates of gross primary production, with measurement methods and general global trend. The IBP data for annual gross primary production (GPP), as shown here, were obtained from the published ecological literature. A few values that were aberrant or formally discredited, or for which the estimation method or site location could not be adequately understood, were excluded. GPP was estimated either directly or as respiration plus NPP (equation 1 in text). GPP is plotted here using the following symbolism to represent the estimation method: A = allometry (mainly for NPP, also respiration); C = "carbon assimilation" (incomplete description); E = enclosures (for respiration of cut vegetation); G = gas exchange of living vegetation (for GPP or respiration); M = micrometeorological estimates for GPP; P = photosynthesis models for GPP; S = surrogate respiration rates from other studies; T = titration (with KOH, for respiratory CO₂ in enclosures); ? = incompletely described method; the two entries (A) without a location indicated were at different elevations on Mt. Naeba in Japan. Actual evapotranspiration (AET) combines simultaneous climatic warmth and moisture availability and thus provides a good basis for examining global ecological trends; AET was estimated by standard water-budget methods involving locally appropriate soil water-holding capacities. The curve was hand-drawn to bisect the data and represent the general trend.

(This last “rainforest” had lower AET, a distinct dry season, a leaf area index of only 3.5 and should perhaps more properly be called a seasonal evergreen forest.) The multiple values at Pasoh represent different methods used on the same stand, with the sole titration-based value (T) as the lowest. The values at Khao Chong represent two nearby but different plots. Ping Kong (northern Thailand) has a strong dry season and involved three different, highly seasonal vegetation types (T and P for each type): dry monsoon forest (highest), monsoon forest/savanna ecotone, and savanna-woodland (lowest) (Yoda 1967; cf Kira *et al.* 1967; Ogawa 1978). Only at Ping Kong does the titration-based method (T) always give higher values than a direct GPP estimation method (P).

Scattergrams and regressions (SAS Institute 1989) for production and biomass showed decreasing NPP/GPP with more standing biomass (Fig. 2), suggesting that any statistical model for GPP should be based only on more stable later-successional and mature stands. NPP values from

these more mature stands showed values similar to earlier studies (with more data) and so did not suggest any need to revise earlier models or estimates of world totals. The data for gross production and respiration, however, showed more high (and higher) values than in the earlier data and suggested that world totals could be higher. Scattergrams and regressions of GPP against the climatic data, including formal relationships from earlier models, reinforced this impression by showing different coefficients and higher GPP trajectories.

A globally reliable geographic model to represent the GPP data was thus sought, using only the data from the 30 mature and late-successional stands. GPP and AET are both “throughput” processes, limited by simultaneous availability of warmth and wetness (cf Box & Meentemeyer 1991). This, Fig. 1, and residual analysis of regression results all suggested strongly that AET would be the best climatic basis for a global GPP model. The relationship be-

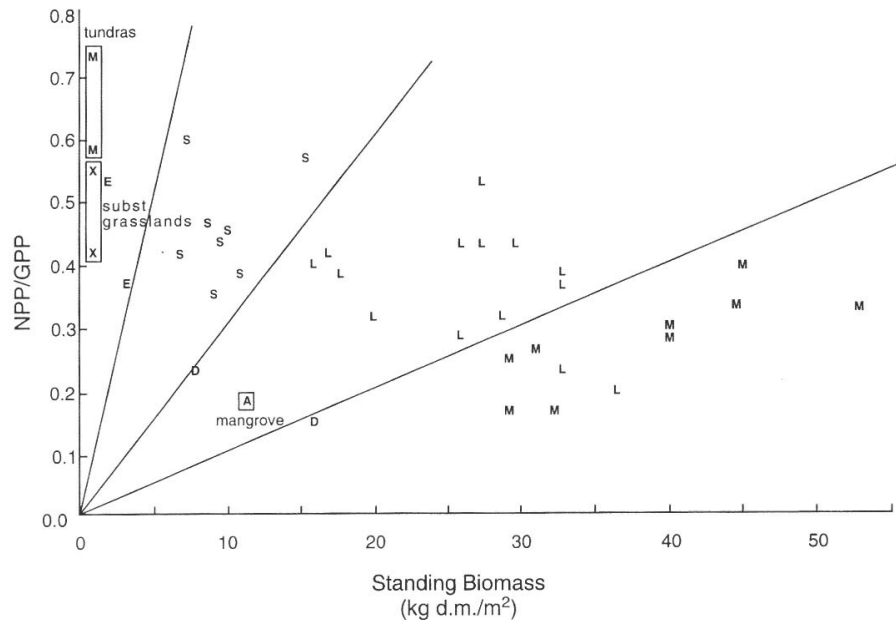


Fig. 2. NPP/GPP versus standing biomass, with symbolism for successional stage. The IBP stands were classified as representing one of four successional stages (plus some other situations), based on age, height, standing biomass, vegetation composition, and verbal description: E = early-successional, D = disclimax, A = aquatic (mangrove), S = mid-successional, X = substitute grassland, L = late-successional, M = mature; the vertical axis represents the ratio of annual net primary production (NPP) to gross primary production (GPP); for woody stands, these successional stages are separated rather well by the relationship between this NPP/GPP ratio and total standing biomass.

tween annual GPP and AET for the 30 mature sites is shown in Fig. 3. Although one may maintain that the data do not support anything more than a linear relationship, the tropical-rainforest sites (1) are somewhat above the general trend and suggest a slight GPP upswing in the humid tropics. Linear and exponential curve forms were fit, but each left the residuals strongly unbalanced (mostly on one or the other side of the curve). This is important for global application because it would result in a systematic over- or under-estimation of GPP across as much as 30-40% of the land area, primarily in the subtropics and tropics. As a result, a composite curve (shown in Fig. 3) was constructed that minimizes

this bias:

$$\begin{aligned} & 6.0147 (AET-20) \text{ if } AET \leq 1242 \text{ mm year}^{-1} \\ GPP = & 3040 [\exp ((AET-20)/1000)-1] \quad \dots(2) \\ & \text{if } AET > 1242 \text{ mm year}^{-1} \end{aligned}$$

with GPP in g dry matter $\text{m}^{-2} \text{year}^{-1}$ and AET in mm year^{-1} . The first equation describes a straight line from the zero-point (GPP=0 at AET=20mm) to the beginning of the upswing, near the transition from the subtropics into the humid tropics; the second equation is an exponential curve fit directly between the zero-point and the highest GPP value. The lines intersect at AET = 1242 mm year^{-1} , where GPP is estimated as 7350 g d.m., only 5% above the monsoon-forest value at Ping Kong. The correlation coefficient (r) of this composite formu-

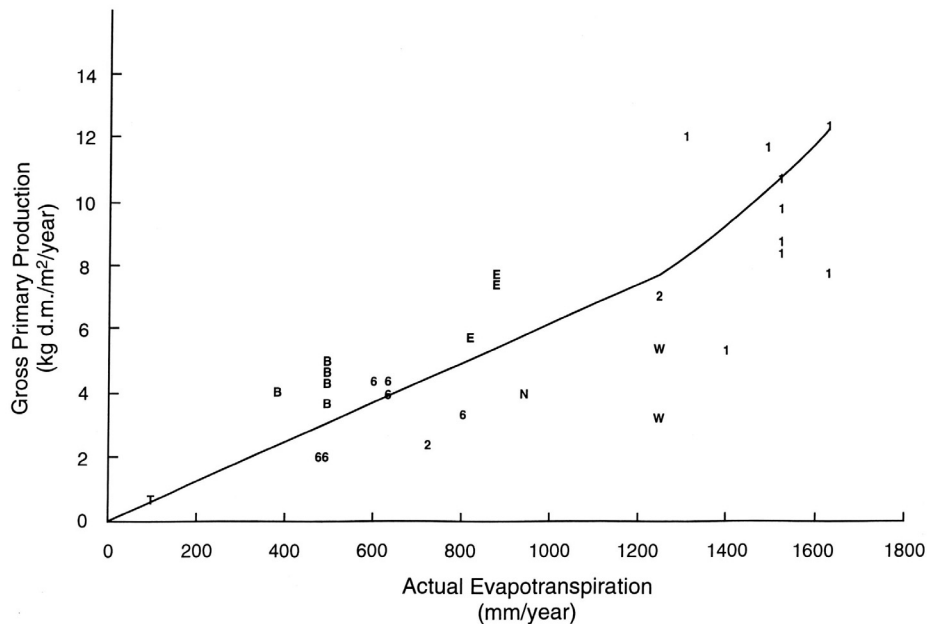


Fig. 3. Gross primary production of the mature IBP stands, versus actual evapotranspiration and AET-based model for global scaling. The estimates of annual gross primary production (GPP) for the 30 mature stands (two tundra stands superimposed) are plotted against annual actual evapotranspiration (AET), using symbolism for the biomes involved: 1 = tropical rainforest/montane forest, 2 = tropical deciduous forest, W = tropical deciduous woodland/savanna, E = warm-temperate evergreen broad-leaved forest, 6 = temperate deciduous forest, N = temperate conifer plantation, B = subalpine conifer forest, T = polar tundra. GPP values are in field units of $\text{g dry matter m}^{-2} \text{year}^{-1}$ and AET values are in millimeters per year. Annual AET essentially represents a geographic temperature gradient, since most data are from forest climates. GPP appears to increase quasi-linearly with increasing AET, over most of the range, but with a possible upswing in the humid tropics (AET above about 1200 mm year^{-1}). A single linear model would miss the high GPP values in the humid tropics, while a single exponential curve would underestimate GPP at intermediate levels. The composite curve shown here represents a compromise for geographically balanced global extrapolations based on the data.

lation is 0.89, almost exactly the same as that of a “best” linear regression.

About half the GPP data are predicted within 15% by equation (2), most accurately near the extremes (tropical rainforest and polar tundra). Deciduous forests were generally overpredicted and evergreen (broad-leaved and subalpine conifer) forests underpredicted. This result cannot be avoided, given the data, and may reflect seasonality effects (as discussed below). Large discrepancies occur only at sites that seem aberrant anyway. Equation (2) thus appears adequate (and slightly but arguably better than a straight line) to represent the GPP data in a geographically consistent way. Gross production by disclimax, disturbed, successional or other landscapes with relatively low leaf area will mostly be overpredicted by this model. Scaling GPP data to satellite data instead of climate may better estimate disturbed actual landscapes, but spectral methods still tend to underestimate metabolism systematically in some situations, especially evergreen forests with high leaf area.

Total terrestrial GPP was estimated by applying equation (2), as well as statistically best linear and exponential regression models, to a global AET data field (map) and quantifying the resulting map of predicted GPP. Total terrestrial autotrophic respiration was then inferred from equation

(1). Because the GPP model is based on climate, the estimates of total GPP and R_A both represent the potential totals for a natural vegetation cover near or approaching maturity. Finally, the effect of the R_A /GPP ratio on biospheric CO₂ fluxes under global warming is illustrated using current versus the IBP-implied values.

Results: Implications of the IBP data

Two implications of the IBP data have already been treated, namely the high values for GPP and R_A (but not NPP) in the humid tropics and the rather consistent relationship between NPP/GPP and standing biomass in forests. Three other results are treated here. All analyses were done in units of dry matter and then converted to carbon units using the relationship 2 g d.m. = 1 g C. The accuracy of all these results will be addressed in the next section.

Total terrestrial GPP

Quantification of the GPP map generated by applying equation (2) to the AET field yielded an estimate of 235 Gt C year⁻¹ for the total terrestrial GPP of a natural biosphere. A linear GPP-AET model yielded a similar value, slightly higher if the 20 mm AET offset is not kept. With NPP remaining at 60 Gt C year⁻¹, equation (1) implies that ter-

Table 1. Estimates of terrestrial gross primary productivity. Potential GPP represents estimates based on climatic relationships of natural vegetation, and actual GPP represents estimates based on current actual vegetation (some using satellite data).

*Potential (Gt C year ⁻¹)	Actual	Basis	Source
132		Global GPP map based on relationship to [climatically estimated] NPP	Box (1978)
	120	Assumption that GPP = 2 x NPP	Houghton <i>et al.</i> & Olson <i>et al.</i> , in Trabalka (1985)
	100-120	Global NPP estimate (48-60 Gt C) and ratio (GPP = 2 x NPP) at Brookhaven site	Houghton (1987)
	180	NDVI, derived PAR, and leaf-level "photosynthetic response"	Myneni <i>et al.</i> (1995)
	133	NDVI and photosynthetic efficiency from local calibration of daily CO ₂ fluxes to absorbed PPF	Ruimy <i>et al.</i> (1996)
235		Full IBP data-base of GPP field estimates (30 mature stands), scaled to AET	(herein)
135		Linear scaling (to AET) based on tropical GPP estimate by Ryan <i>et al.</i> (1994a)	(herein)

* 'Potential' and 'Actual' are two separate columns

GPP = gross primary productivity

NDVI = normalized-difference vegetation index

PPFD = photosynthetic photon flux density

NPP = net primary productivity

PAR = photosynthetically active radiation

AET = actual evapotranspiration

restrial R_A could be as high as 175 Gt C year⁻¹ (for vegetation near or at maturity). This and other estimates of terrestrial GPP are compared in Table 1, in which climate-based estimates are referred to as potential GPP (column 1) and estimates for actual vegetation, some based on satellite data, are referred to as actual GPP (column 2). The estimate of 132 Gt C was first thought to be too low because its Miami Model NPP basis was thought too low; Whittaker & Likens (1975) had suggested that GPP may be about 2.7 x NPP, implying a total of around 160 Gt C year⁻¹. Included also are later estimates of 133 Gt C (Ruimy *et al.* 1996) and 180 Gt C (Myneni *et al.* 1995), both based on NDVI satellite data, satellite-derived global imagery for photosynthetically active radiation (PAR), and values of a photosynthetic conversion efficiency calibrated from short-term photosynthetic CO₂ flux measurements.

The much higher IBP-based estimates are surprising but depend strongly on the accuracy of the high estimates for the humid tropical forests. These range from 5.2 to 12.3 kg d.m. m⁻² annually, largely from Southeast Asia but with one lower value there also. The highest GPP and R_A estimates did occur at the site (Khao Chong) with the highest AET. This means that scaling to an “average” GPP value for humid tropical forests, which would also have lower AET, could actually raise the values on the predictive GPP map and the terrestrial total, though probably not by very much either way. Scaling to much lower tropical values (but still with high AET) would reduce the implied terrestrial total but would contradict the data (from which higher values have already been excluded). On the other hand, some methods may systematically underestimate productivity, especially the continuing use of temperate-zone metabolic values with tropical-to-subpolar vegetation “types” defined mainly by ease of spectral recognition (e.g. “broad-leaved evergreen trees”, cf. Potter *et al.* 1993; Ruimy *et al.* 1996). This problem is compounded by the downward bias due to the darker, less reflective nature of evergreen leaves.

Geographic variation of the NPP/GPP ratio

Using 27 of the IBP estimates for GPP (but only two from the tropics), Kira (1975) showed that the NPP fraction of GPP ranged from 23% in the tropics to 68% or similar only in cooler high latitudes or high elevations. The NPP/GPP ratio for

the full set of mature and maturing IBP stands is plotted against the global AET gradient in Fig. 4. In this plot NPP/GPP appears to decrease rapidly from 74% in one tundra estimate to 17-20% in warmer tropical woodlands and one seasonal evergreen forest with much more standing biomass. This range is slightly wider than in Kira's analysis and means that respiration ranged from 26% of GPP in the tundra to as much as 80% in some wooded tropical stands (including Abidjan, the one with the lowest estimate for GPP).

For the stands in Fig. 4 the average NPP/GPP appears to be around 35%. Disclimax and other low-biomass stands (not plotted) generally had lower respiration values, but NPP/GPP in such stands was only slightly higher, since NPP and GPP could both be lower. NPP/GPP in the immature IBP stands (average about 40%) ranged from 15-24% in the disclimax tropical savanna-woodland stands to 42-54% in the substitute tropical grasslands and 35-60% in earlier-successional

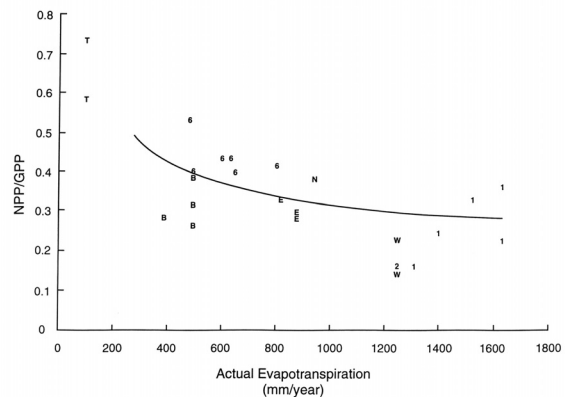


Fig. 4. NPP/GPP ratio in mature IBP stands, in various terrestrial biomes. The ratio of annual net (NPP) to gross (GPP) primary production is plotted against annual actual evapotranspiration (AET) for 29 of the 30 mature plus stable disclimax stands (some superimposed; one stand had no NPP estimate); symbolism and environmental gradient (AET) are the same as in Fig. 3. The data show NPP/GPP gradually decreasing with higher temperatures, from over 50% at two tundra sites, to 30-50% in cool-temperate and subalpine forests (AET around 400-650 mm), to 15%-35% in the tropical forests and woodlands (AET above about 1200 mm); early and mid-successional IBP stands generally showed somewhat higher NPP fractions, from 35% to 50% of GPP, with 60% in one young deciduous forest and 54% in a substitute tropical grassland.

temperate beech and conifer stands. If terrestrial NPP is 60 Gt C year⁻¹, an NPP/GPP average around 35% would imply a terrestrial GPP total of about 175 Gt C year⁻¹. On an area basis, however, average NPP/GPP could be somewhat less, since almost half the world's productive land area is in the warm tropics and subtropics, where NPP/GPP may be lower.

NPP/GPP and biospheric CO₂ fluxes under global warming

The CO₂ source/sink behavior of the terrestrial biosphere involves not only GPP and R_A but also CO₂ release by heterotrophic respiration (R_H), mainly detrital decomposition. The resulting net ecosystem production (NEP), or net carbon flux, was estimated monthly for a steady-state, natural terrestrial biosphere (Box 1988) but will probably

change significantly with changes in land use, degradation of actual landscapes, effects of global warming on respiration, and fertilization of photosynthesis by increased atmospheric CO₂ levels. For at least somewhat natural landscapes, however, the R_A/GPP fraction of living vegetation may be crucial to the behavior of CO₂ fluxes, as illustrated in Table 2.

Table 2 shows changes in terrestrial production, respiration and carbon balance, under two contrasting global-warming scenarios, implied by the 2 x NPP and the IBP estimates of gross production. The IBP estimate is probably too high but does bracket the range of probable values. Heterotrophic respiration (R_H) increases by 10% in both scenarios (though it may well increase more, due to oxidation of large amounts of soil carbon in the northern high latitudes). If GPP and R_A increase at similar rates (scenario 1, for example by 10%), a

Table 2. Carbon balance of a natural terrestrial biosphere, for GPP = 2 x NPP versus the higher IBP-based value, under different metabolic responses to global warming.

GPP estimate:	GPP=120 Gt C yr ⁻¹ (2 x NPP)		GPP=235 GtC yr ⁻¹ (IBP data)	
Recent Climate				
Gross Primary Production (GPP)	120		235	
Autotrophic Respiration (R _A)	- 60		- 175	
Net Primary Production (NPP)	60		60	
Heterotrophic Respiration (R _H)	- 60		- 60	
Balance (Net Ecosystem Production, NEP)	0		0	
1. Equal GPP and R _A increases				
GPP rises 10%	132		258.5	
R _A rises 10%	- 66		- 192.5	
NPP (= GPP - R)	66	(+6)	66	(+6)
R _H rises 10%	- 66		- 66	
Balance (= NPP - R _H)	0		0	
2. R _A increase > GPP increase				
GPP rises 10%	132		258.5	
R _A rises 15%	- 69		- 201.25	
NPP (= GPP - R)	63	(+3)	57.25	(-2.75)
R _H rises 10%	- 66		- 66	
Balance (= NPP - R _H)	- 3		- 8.75	

The balance (NEP) is calculated for the two estimates of terrestrial GPP (see main text), with the estimate of current NPP (60 Gt C year⁻¹) not in question. The scenarios for metabolic response to warming and increased atmospheric CO₂ (both with 10% increase in R_H) represent:

(1) equal percentage increases of GPP and R_A; and (2) greater percentage increase by R_A than by GPP. If GPP and R_A increase similarly (scenario 1), a balanced natural biosphere (R_H = NPP) would remain in balance, even with much higher R_A (column 2). If R_A increases more than does GPP (scenario 2), however, the biosphere becomes a CO₂ source (NEP becomes negative) in both cases, but moreso where R_A is a larger fraction of GPP (column 2).

balanced natural biosphere remains balanced in both cases, despite the much larger changes in GPP and R_A under the higher baseline estimates of both. If R_A increases at a higher rate than does GPP, however, for example by 15% to 10% (scenario 2), the overall balance (NEP) becomes negative in both cases, due to the consequent decrease in NPP. If GPP is 2 x NPP, terrestrial NPP does still increase by 3 Gt C year⁻¹ over the current 60 Gt C year⁻¹. Under the higher IBP estimates of GPP and R_A , however, R_A is a larger fraction of GPP. As a result, NPP absolutely decreases, by 2.75 Gt C year⁻¹ (4.6%), yielding a much larger potential CO₂ source of 8.75 Gt C year⁻¹. This suggests that changes in the global carbon budget, under expected atmospheric changes, could be more threatening if R_A /GPP is significantly higher than the 50% currently assumed.

Discussion: Implications of newer studies

The implications of the IBP data are disturbing but depend on the validity of the data. The upward trending GPP pattern shown in Figs. 1 & 2, rather than the asymptotic pattern shown by NPP data, is both interesting and suspicious. A linear relationship between gross production and AET seems reasonable, since stomatal behavior regulates both CO₂ intake for photosynthesis and water loss. An upswing in the humid tropics, however, where large evergrowing foliar canopies can be maintained, could represent elimination of the “down time” associated with seasonal foliation and defoliation. This is supported by the fact that the GPP values of evergreen broad-leaved forests often fall above the trend curve and those of deciduous forests below. On the other hand, this tropical upswing may signal overestimation of respiration and gross production. In the temperate zone, the GPP values for other evergreen stands (mostly subalpine conifer forests) are also generally above the general trend. This may reflect higher total leaf area of monopodial conifers, but a relationship between annual GPP and leaf-area duration has also been suggested (Kira 1975; Waring & Schlesinger 1985).

Beginning around 1990, new directions began to appear in the understanding and estimation of tree and stand metabolism, in particular the differences between maintenance and growth respira-

tion (as represented by the “functional model” of Ryan 1990). Also important for accurate measurement was better realization that:

- maintenance respiration in woody stems comes mainly from sapwood and is related to sapwood volume, not to stem surface area (Ryan 1990; Ryan & Waring 1992; Sprugel 1990); and that
- the CO₂ efflux from cut biomass includes some release of CO₂ stored in tissue and thus overestimates respiration by woody stems (e.g. Hari *et al.* 1991; Levy *et al.* 1999; Ryan *et al.* 1994).

This led to development of non-destructive methods for estimating wood respiration using chambers fixed outside the bark of living trunks and branches (e.g. Sprugel & Benecke 1991). New measurements of maintenance respiration in woody stems, based on such methods, suggested that maintenance respiration by woody stems may be a relatively small fraction of photosynthesis (as low as 10%), considerably lower than in the IBP data (based on CO₂ efflux from detached biomass), and that respiration (like photosynthesis) is closely related to tissue nitrogen content (Field & Mooney 1986; Ryan 1995). The one study that was done on tropical trees, at La Selva (Costa Rica), showed maintenance respiration by woody stems to be only 8-13% of photosynthesis, as compared with 23-50% in the IBP studies (Ryan *et al.* 1994). This study resulted in an annual estimate of 2700 g C m⁻² (5400 g d.m. m⁻²) for La Selva.

The lower values for maintenance respiration by accumulating woody biomass, improved understanding of growth respiration, and study of leaf area in stands of different ages led to the hypothesis that the NPP decline in older forest stands may result not so much from greater respiratory demands by greater biomass as from hydraulics, i.e. reduced photosynthetic capacity in taller boles with longer branches (Ryan & Waring 1992). At the same time, development of the eddy-covariance method was making it easier to estimate the photosynthesis of forests from gas-exchange measurements (e.g. Baldocchi *et al.* 1996; Grace *et al.* 1996).

Studying respiration in boreal forests, Ryan *et al.* (1997a) found that wood respiration rates were indeed temperature-sensitive and strongly seasonal (highest in summer) but that R_A and GPP appeared very strongly linked, resulting in offsetting changes and little variation in NPP/GPP with temperature. Dewar *et al.* (1999) suggested that

respiration is “effectively limited by the supply of carbohydrates fixed through photosynthesis” and provided a conceptual model that reconciles conflicting short-term and long-term responses of R_A/GPP to temperature changes, and implies that NPP/GPP may indeed be conservative under changing temperatures. Finally, Waring *et al.* (1998) compared the NPP/GPP ratio of mid-latitude forests, mainly coniferous, found NPP/GPP to be conservative, and suggested that NPP may even be “a constant fraction of gross primary production” and could be assumed so for modeling purposes.

So far, newer estimates of total terrestrial GPP (Myneni *et al.* 1995; Ruimy *et al.* 1996) have not made full use of the newer findings regarding respiration but rather have only extrapolated temperate-zone site measurements using satellite data instead of climate. These studies also assume constant “photosynthetic efficiency”, without reference to temperature or moisture constraints. Satellite data are necessary for assessing the metabolism of altered actual landscapes, but two common assumptions with satellite-based approaches still must be addressed:

- the NDVI does not represent “green leaf area” in most forest vegetation, since the AVHRR sensors saturate well below the leaf area of closed forests; and

- photosynthetic conversion efficiency may not be constant, since water and other environmental factors are ignored, as are seasonal effects such as leaf senescence (see discussion by Ruimy *et al.* 1996).

The study by Myneni *et al.* (1995) also assumed that:

- the GPP of tropical seasonal forests is higher than that of tropical rainforests;

- NPP/GPP is constant “over large space and long time scales”; and

- the tropical fraction of total NPP indicates the tropical fraction of total GPP (“consistent with reports on net primary productivity”).

The first assumption may come from the common practice (see above) of lumping all evergreen broad-leaved forests, from tropical to subpolar, together into a single “type” (e.g. Ruimy *et al.* 1996). The other two assumptions are not borne out by the large-area, long-term data needed to support them (or by the IBP data).

The IBP-based GPP estimate would clearly be too high for the current actual biosphere, even if the data were valid, since factors other than climate can also limit productivity and since much land is already degraded or totally unavailable for production. The commonly used value of 120 Gt C year⁻¹ (2 x NPP), however, implies a GPP average of only about 2 kg d.m. m⁻² annually by the world's non-desert land area, a level probably reached if not exceeded even by some cool-temperate forests and temperate grasslands, in which annual NPP may be near 1 kg d.m. m⁻². Many agricultural fields may also exceed this GPP level (e.g. Edwards *et al.* 1981), and tropical forests probably at least reach 6-8 kg d.m. m⁻². Agreement with the value 120 Gt C year⁻¹ would require recognizing a GPP maximum no higher than about 8 kg d.m. m⁻² (4 kg C m⁻²) annually -- but such a value would be consistent with the one newer tropical study, at La Selva, involving the new respiration paradigm (Ryan *et al.* 1994). A straight line drawn from the origin in Fig. 3 to this GPP estimate for the La Selva rainforest has a slope of 3.6635 (AET=1475 mm year⁻¹). If this linear model is applied to the global AET data-basis, quantification of the resulting map yields an estimate of 135 Gt C year⁻¹ for total terrestrial GPP, similar to other values in Table 1 but higher than 120 Gt C year⁻¹.

Conclusions

Analysis of the full IBP data-base suggested significant variation in NPP/GPP , both geographically and with changing biomass, a possible GPP upswing in the humid tropics, no significant change from earlier estimates of terrestrial NPP (60 Gt C year⁻¹), but distinctly higher estimates for terrestrial GPP (235 Gt C year⁻¹) and R_A (175 Gt C year⁻¹). These higher estimates result in a much higher R_A/GPP ratio of total terrestrial amounts, which translates into:

- larger CO₂ sinks now in successional vegetation with low standing biomass, but

- larger CO₂ sources in more mature vegetation under global warming.

The individual R_A/GPP data vary enough geographically that simply assuming a 50% global average would introduce significant bias in models and other estimates, especially when non-linear relationships are concerned. The IBP data suggest that an area-based global average for R_A/GPP , in

relatively mature vegetation, could be as high as 65-75%. Carbon-budget calculations with current actual land covers and estimates of natural and anthropogenic carbon fluxes suggested a “missing carbon sink” of now up to 2 Gt C (Saugier *et al.* 2001) that may involve the terrestrial biosphere (cf Denning *et al.* 1995; Tans *et al.* 1990; Williams *et al.* 1997). Nothing in the IBP data directly suggests that this sink has been “found”, but underestimated GPP coupled with low respiration in disturbed, managed, or other low-biomass landscapes could be consistent with a discrepancy of this magnitude.

On the other hand, these disturbing higher estimates depend heavily on the validity of the IBP data, especially the respiration estimates, which have been challenged. Newer methods and findings in the study of respiration have suggested the new paradigm that:

- Maintenance respiration was overestimated by earlier studies using detached biomass, and growth respiration is a larger fraction of the total but is limited by photosynthesis.

- NPP declines over succession are due to declines also in photosynthesis, such that NPP/GPP is in fact relatively constant with changes in standing biomass (Ryan & Waring 1992; Ryan *et al.* 1997b).

- R_A and GPP are closely linked physiologically, producing offsetting changes with changing temperature, such that NPP/GPP is also relatively constant and does not increase significantly with temperature (Ryan *et al.* 1997a; Saxe *et al.* 2001).

In particular, it has been shown that respiration in humid tropical forests is probably not as high as the IBP data suggested. It has even been suggested that NPP may be a constant fraction of GPP in forests and that this may be used to simplify forest growth models (Waring *et al.* 1998).

Even if R_A/GPP , and thus NPP/GPP, are fairly conservative over stand development and changing temperatures, this does not mean that they will be the same in all parts of the world, since different evolutionary histories may have produced different values in different climates. The attempt by Waring *et al.* (1998) to show a geographically constant NPP/GPP ratio in forests involved comparison at 12 mid-latitude sites only (31-41°S and 42-45°N latitude). There simply are not yet enough “acceptable” data to demonstrate a geographically constant R_A/GPP ratio. On the other hand, there are apparent differences, such as between conifers

and broad-leaved trees (cf Cannell & Thornley 2000). Moreover, even at the low temperatures in boreal forests, maintenance respiration was seen to increase with increasing biomass, and other changes in biomass and photosynthesis were also seen to occur (Ryan & Waring 1992).

Based on the above, some conclusions may be possible:

1. Some decrease in NPP/GPP with increasing biomass seems real, though not as much as the IBP data and other earlier data may suggest; in addition, geographic variation in NPP/GPP also seems real, despite relatively constant values in one study of temperate-zone sites.

2. There does not seem to be any need to revise the terrestrial NPP estimate of 60 Gt C year⁻¹; total GPP may be higher than the often stated 120 Gt C year⁻¹, however, and R_A/GPP higher than 50%, though not as high as the IBP data suggest. The higher IBP-based totals can be understood as possible upper limits on actual values and on the magnitude of variations in biotic CO₂ fluxes under global warming.

3. If both R_A and GPP change with temperature, even if apparently offsetting, it is dangerous to assume that their ratio will remain *exactly* constant. Small differences may still have significant consequences, since any increased R_A/GPP means greater CO₂ release, especially from the large warmer areas of the terrestrial biosphere, now and under global warming.

4. The GPP-AET relationship does appear to be roughly linear, though the IBP data suggest a slight upswing in the humid tropics. This upswing, and conflicting tropical estimates of GPP and respiration in general, need resolution by additional tropical studies, not only in tropical rainforests but also in tropical deciduous forests, scrub, and savannas.

Major questions remain. Regarding respiration data in particular, one might want to ask:

- To what extent might overestimates of maintenance respiration be offset by underestimates of growth respiration?

- Is there a geography to the errors? Are large respiration errors confined to the tropics? Are respiration and gross production really so much lower in all humid tropical forests?

- If R_A/GPP is conservative but not constant, how large is the variation: over succession? Geographically? With changing temperature?

In fact, given the need for a large, geographically representative data-base, it is perhaps not irreverent to ask just how “bad” these old data are (before discarding them completely) and whether enough information was given in the IBP publications to permit data “rehabilitation”, by reinterpreting valid measurements and recalculating final values using improved methods.

Finally, much of the uncertainty may be in mature tropical vegetation, which is rapidly disappearing. How relevant are the metabolic estimates made for quasi-natural vegetation to the actual and future landscapes dominated by disturbed and disclimax vegetation, perhaps especially in the tropics? Data for mature vegetation are not totally unrepresentative, since deforested tropical land is soon abandoned and may revert to relatively productive C₄ grassland, savanna or secondary forest. Respiration may increase in recovering landscapes as biomass accumulates and may be greater in stressed vegetation (a dry-climate mangrove site in Puerto Rico had the highest R_A/GPP in the entire IBP data-base). Higher temperatures under global warming may produce such stress. The R_A/GPP ratio was near or over 50% in most of the successional and disclimax IBP stands. Not quantified adequately, however, are factors such as:

- the rate at which the R_A/GPP fraction climbs in successional tropical vegetation;
 - the new potential biomass capacity of cleared areas of former tropical rainforest;
 - the areal extent to which poor soil and other non-climatic factors may limit the development and productivity of natural tropical rainforest.
- There are few if any data for successional stages in woody tropical vegetation, but in almost all vegetation GPP is largely proportional to leaf area and increases rapidly in early regrowth.

With land-use changes by humans as the most rapid of the various aspects of “global change” over the next few decades, data for successional, disturbed and other low-biomass vegetation are among the most needed. If accurate estimates for photosynthesis and respiration suggest any possibility of greater net CO₂ uptake by regrowing tropical vegetation, one must still consider the fact that this will NOT be possible unless the expanding degraded areas of former tropical rainforest can be fully rehabilitated to proceed beyond the stage of permanent disclimax grassland. For all the effort put into sophisticated and well financed

global modeling, it is unfortunate that more effort has not been directed at critical bottlenecks: improved metabolic estimates in the tropics and methods to rehabilitate tropical landscapes.

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