

Potential gross primary productivity of terrestrial vegetation from 1982 - 1990

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Abstract. Monthly mean global green leaf area and photosynthetically active radiation estimated from observations made from several geostationary and polar orbiting satellites were used to estimate potential, (i.e., unstressed) gross primary productivity of terrestrial vegetation from 1982 to 1990. Mean annual gross primary productivity was estimated to be about 179.9 ± 1.6 Pg C (1 Pg = 10^{15} g). Grasses and xerophytic vegetation on all continents exhibited high interannual variability. The evolution of monthly gross primary productivity anomalies was similar to atmospheric CO₂ growth rate during 1982-1990. This was observed both globally and for the 30° - 90° N latitudinal band, but not at other latitudes. From this, we may conclude that total ecosystem respiration and GPP respond similarly but disproportionately to climate, such that the difference between the two resembles the opposite of the observed atmospheric CO₂ growth rate.

Introduction

Gross primary production (GPP) denotes the amount of carbon photosynthesized by plants. Some of this carbon is respired, while the rest is invested in plant growth. This exchange of carbon between plants and the ambient involves vast quantities of gaseous carbon dioxide, which is an important green house gas. Seasonal and interannual variations in GPP of terrestrial vegetation are therefore of considerable interest. Results on monthly GPP estimated from monthly mean global green leaf area and photosynthetically active radiation derived from observations made from several geostationary and polar orbiting satellites for the years 1982 through 1990 are presented here.

Data and Methods

Satellite-sensed greenness is usually expressed as normalized difference vegetation index (NDVI), which is indicative of green vegetation amount, and therefore vicariously of photosynthetically active radiation absorption and associated physiological processes [Myneni *et al.*, 1995]. The archived Advanced Very High Resolution Radiometer data set is a maximum monthly value composite data set with a spatial resolution of 7.6 km [the Global Inventory Monitoring and Modeling Studies (GIMMS) data set]. The compositing procedure minimizes the effects of sun angle, view

angle, atmospheric gases, aerosols and clouds, all of which decrease NDVI [Holben, 1986]. The data were uniformly calibrated [Los, 1993] and corrected for missing values, residual bidirectional effects, and background effects [Los *et al.*, 1994]. The data were spatially aggregated to a resolution of $1^\circ \times 1^\circ$ from which a global data set of monthly leaf area index (green leaf area per unit ground area) was derived [Sellers *et al.*, 1994].

The utility of AVHRR data has been demonstrated previously in studies of global vegetation dynamics [Tucker *et al.*, 1985] and net primary productivity [Tucker *et al.*, 1986; Fung *et al.*, 1987]. The objective of this study is to investigate the interannual variability in the satellite-measured, spatially-continuous multi-year data set. However, normalized difference vegetation index (NDVI) and leaf area index (LAI) are both dimensionless quantities in space and time. Therefore, a conversion scheme is required, but this scheme should not introduce additional variance as this will likely degrade the value of the multi-year satellite data set.

The simplest conversion scheme involves estimation of GPP utilizing plant green leaf area, incident photosynthetically active radiation (PAR; $0.4-0.7 \mu\text{m}$) and the photosynthetic response of a leaf to incident PAR [Gutschick, 1991]. The canopy integration in this scheme is physically based [Myneni *et al.*, 1992], but requires coincident measurements of incident PAR which match the multi-year satellite LAI data set in terms of spatial and temporal resolution, and accuracy. PAR data sets satisfying these requirements were not available to us. Therefore we relied on a PAR climate data set, derived from the International Satellite Cloud Climatology Project [Schiffer and Rossow, 1985; Pinker and Lazlo, 1992]. Generic C3 and C4 leaf photosynthetic responses to PAR under optimal conditions of temperature and water status were used. Specifically, the nonrectangular hyperbolic form of the leaf light photosynthesis response function was employed with the following parameters - initial slope of 0.0524 [Evans and Farquhar, 1991], curvature parameter of 0.7 and asymptotic leaf photosynthesis of 20 (C3) and 35 (C4) $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ [Collatz *et al.*, 1991; 1992]. The choice of the latter parameters was based on trying to match, by trial and error, measured rates of daily photosynthesis of several C3 and C4 canopies reported in the literature [Boote and Loomis, 1991; Sellers *et al.*, 1992]. A map of the global distribution of C3 and C4 species [Collatz, 1992] was used in conjunction with the above response functions to calculate global GPP rates. This description of biospheric gross carbon assimilation ignores temperature and water dependencies; however, inhibition of photosynthesis at biome-specific low and high temperature is included. Thus, for instance, although northern

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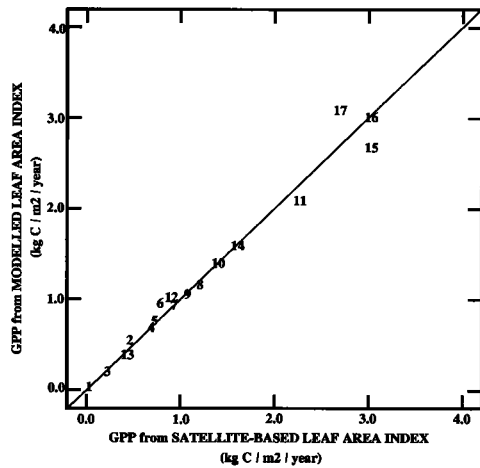


Figure 1. Biome gross photosynthetic rates estimated from hydrological equilibrium theory and the mean GPP estimated from multi-year satellite leaf area index data set. The numbers in the plot correspond to different land cover classes [Prentice et al., 1992] (also see Table 1).

MEAN ANNUAL GROSS PHOTOSYNTHESIS 1982-1990 (10-12 g C)

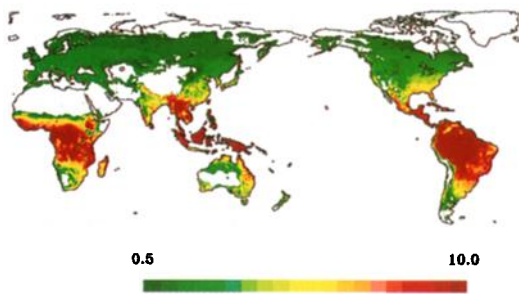


Figure 2. Mean annual gross primary production for the years 1982 through 1990.

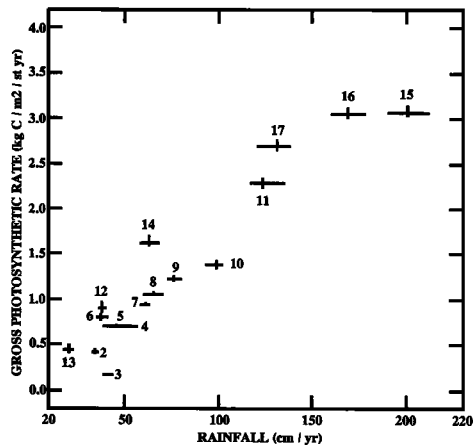


Figure 3. The dependence of biome gross primary production rate on rainfall. Mean and standard deviation of both variables during 1982-1989 are shown. The productivity rate is normalized to a standard year of 365 days with 12 hours of sunlight per day. The numbers in the plot correspond to different land cover classes [Prentice et al., 1992] (also see Table 1).

coniferous forests may be green during the boreal winter, carbon assimilation is turned off because of climatologically low air temperatures.

The advantages of this simple conversion scheme are that (a) it alleviates the need for measured temperature, precipitation and other data sets of comparable accuracy for the

Table 1. Mean and Standard Deviation of Biome GPP in Pg C/yr During 1982-1990

| Biome | Mean | Standard Deviation |
|----------------------------------|---------|--------------------|
| (1) Ice/Polar desert | 0.0607 | 0.0035 |
| (2) Semidesert | 2.3720 | 0.1156 |
| (3) Tundra | 2.2149 | 0.0150 |
| (4) Taiga | 7.7962 | 0.0204 |
| (5) Cold deciduous forest | 2.0017 | 0.0104 |
| (6) Cool grass/sgrub | 5.6423 | 0.1480 |
| (7) Cool conifer forest | 2.6424 | 0.1480 |
| (8) Cold mixed forest | 0.7932 | 0.0060 |
| (9) Cool mixed forest | 5.6987 | 0.0454 |
| (10) Temperate deciduous forest | 7.7283 | 0.1245 |
| (11) Evergreen/Warm mixed forest | 14.9989 | 0.2285 |
| (12) Warm grass/shrub | 8.9113 | 0.3037 |
| (13) Hot desert | 8.9016 | 0.4989 |
| (14) Xerophytic woods/shrub | 17.1024 | 0.2321 |
| (15) Tropical rain forest | 23.1533 | 0.1015 |
| (16) Tropical seasonal forest | 24.0256 | 0.1323 |
| (17) Tropical dry forest/savanna | 45.8432 | 0.3112 |

time period of calculation, and (b) no in situ empirical observations are used for tuning the model, thus avoiding the issue of scaling point measurements to areal values. The disadvantages are that (a) the method ignores water, temperature and nutrient functionalities, which is highly unrealistic, and (b) therefore results in GPP estimates that are suggestive of potential rather than actual photosynthesis. Detailed models that include temperature, water and nutrient stresses, and many other aspects exist [Running and Coughlan, 1988; McGuire et al., 1992; Potter et al., 1993; Warrant et al., 1994; Maisongrade et al., 1995]. Forcing one of these models with our multi-year LAI data set may likely produce realistic estimates of GPP, but assessing which of the interannual GPP variations are due to the multi-year satellite LAI data set will likely be difficult. These considerations explain our choice of the simple GPP model.

Results and Discussion

The amount of leaf area at a specific site can be estimated using the hydrological equilibrium theory, i.e., determining the leaf area required to balance potential evapotranspiration and precipitation. This was done globally, and monthly, using the BIOME-BGC model [Running and Coughlan, 1988] in conjunction with long-term climatology [Leemans and Cramer, 1990] and soil information [Zobler, 1986]. The resulting leaf area distribution is characteristic of global potential vegetation absent of stresses and human

COEFFICIENT OF VARIATION OF GROSS PHOTOSYNTHESIS (%) 1982-1990

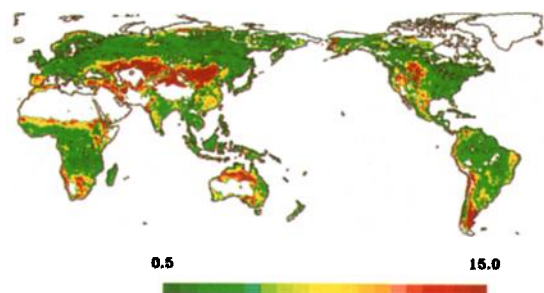


Figure 4. Coefficients of variation (standard deviation ÷ mean) of gross primary production from 1982-1990. Values for hot deserts [biome 13 of Prentice et al., 1992] are not shown because of low carbon assimilation rates.

influences. Biome gross photosynthetic rates estimated from this potential leaf area data set agreed well with those estimated from satellite leaf area (Figure 1). This comparison offers a measure of validity to the GPP results presented below. However, when the potential and satellite LAIs are compared, the correspondence is not good (results are not presented for brevity). This indicates that the GPP results are suggestive of potential rather than actual carbon assimilation estimates, because leaf area derived from the hydrological equilibrium theory is indicative of maximum possible leaf area at a site, but since GPP is a non-linear function of LAI, this difference does not translate into GPP and therefore the good correspondence observed in Figure 1.

Annual GPP of terrestrial vegetation varied from about 177.5 Pg C in 1982 to 181.9 Pg C in 1988, with a mean value of 179.9 Pg C (1 Pg = 10^{15} g). That is, the equivalent of 84 ppm of CO_2 , or about one quarter of the atmospheric CO_2 concentration, can potentially be photosynthesized by vegetation annually. The tropics contribute about 55% to the annual integral (Figure 2), which is consistent with reports on net primary productivity (NPP) [Melillo *et al.*, 1993]. July and February represent the extremes of photosynthetic activity with about 13% and 6% of the yearly total.

A global vegetation map was used in this study to stratify land cover [Prentice *et al.*, 1992]. The biomes tend to occupy distinct precipitation and temperature niches (Figure 3). Deserts (13) and tropical rain forests (15) inhabit the extremes of rainfall regime. The rate of carbon assimilation increases with rainfall upto about 150 cm/yr, after which it tends to an asymptotic value. Thus, tropical rain and seasonal forests (15 & 16) have comparable rates of carbon assimilation. When two or more biomes occupy the same rainfall niche, evergreen/warm mixed forest (11) and tropical dry forest/savanna (17) for example, biomes from a warmer region (17) have a higher assimilation rate than those from a cooler region (11). This temperature dependency is evident in Figure 2, with tundra (3), taiga (4), conifer and mixed forests (7, 8, 9, & 10) occupying the inner margin of the envelope, and xerophytes (14) and tropical forests (15, 16 & 17) occupying the outer margin.

Average annual GPP of the various biomes is given in Table 1. The tropical dry forest/savanna had the highest annual GPP (45.8 Pg C), followed by tropical seasonal (24 Pg C) and rain (23.2 Pg C) forests. The three biomes account for about 52% of the total annual carbon assimilation, which is consistent with recent NPP estimates [Melillo *et al.*, 1993]. Their productivity is also stable from year to year, with an interannual variability of 0.55 Pg C. In general, the regions with low coefficients of variation (standard deviation \div mean) are forested areas — tropical and temperate, evergreen and deciduous, broadleaf and needle (Figure 4). On the other hand, the biomes with high interannual variability are the hot and semi deserts, cool and warm grasses/shrubs, and xerophytic woods/shrubs. Their annual GPP is 43 ± 1.3 Pg C, or about 24% of the global total GPP. These biomes occupy marginally habitable niches with high precipitation variability. Therefore, they exhibit high coefficients of variation (> 10%), and include the grasslands of mid-west United States, the prairies and savannas of Argentina in South America, the Sahelian grasses and shrubs in Africa, the grasses and xerophytic woods east of Kalahari in Southern Africa, the Mediterranean shrublands, cool grasses/shrubs in the Anatolia plateau of Turkey, the Kazakh and Mongolian steppes in Asia, and the grasses and xerophytes in Australia (Figure 4).

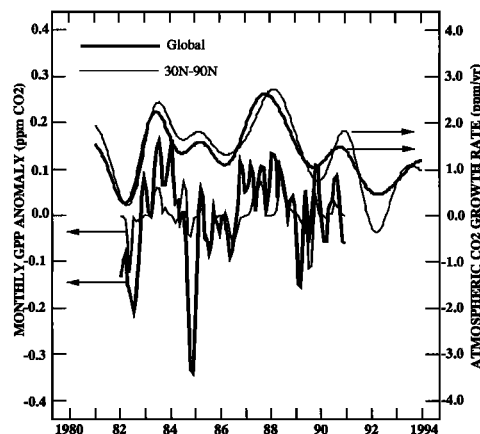


Figure 5. The progression of monthly gross primary productivity (GPP) anomalies and atmospheric CO_2 growth rate.

A caveat with respect to the previous result (Figure 4) needs to be addressed. It is well known that NDVI is a non-linear function of LAI and therefore, the ability of NDVI to respond to changes in LAI at the higher-end of the LAI domain ($LAI > 3$) decreases significantly. However, since canopy photosynthesis is also a non-linear function of LAI, one could argue that such changes in LAI do not appreciably affect canopy photosynthesis [Myneni *et al.*, 1992]. This is especially true of potential (i.e., unstressed) photosynthesis, where PAR is the only forcing variable. Therefore, the lack of appreciable interannual variability in the potential GPP of biomes with high LAI must not be construed as an artefact of the NDVI data set.

The interannual variability of GPP, ± 1.6 Pg C, is quite small compared to the mean annual GPP of about 180 Pg C. Interestingly, this is in good agreement with results on the interannual variability of atmospheric CO_2 increase [Conway *et al.*, 1994]. The largest year-to-year changes in atmospheric CO_2 increase, of the order 2-3 Pg C, occurred during 1982-83 and 1986-87 El Niño/Southern Oscillation events. Similar large year-to-year changes in GPP were also observed (4.3 and 2.3 Pg C, respectively). In fact, the evolution of monthly GPP anomalies was similar to atmospheric CO_2 growth rate during 1982-1990 (Figure 5). That is, periods of increasing atmospheric CO_2 growth were coincident with periods of higher-than-average biospheric GPP, and, vice versa. This was observed both globally and for the $30^\circ - 90^\circ$ N latitudinal band (Figure 5), but not for other latitudes ($0^\circ - 90^\circ$ N, $0^\circ - 30^\circ$ S & $30^\circ - 90^\circ$ S). If NPP is assumed to be a constant fraction of GPP, then heterotrophic respiration and biospheric NPP must respond similarly but disproportionately to climate in order to match the observed atmospheric CO_2 growth rate. This inability of heterotrophic respiration to balance biospheric NPP could be the likely mechanism by which the so-called missing carbon [Tans *et al.*, 1990] is being sequestered into soils ultimately via biospheric net fixation. But, this needs to be confirmed, although some evidence of carbon sequestration in tropical soils has recently been reported [Fisher *et al.*, 1994].

The assumption that NPP is a constant fraction of GPP is perhaps valid only over large space and long time scales [Prince *et al.*, 1994] and not interannually. In spite of this and the fact that our calculations are of potential photosynthesis, we may conclude that total ecosystem respiration and GPP respond similarly but disproportionately to climate, such that the difference between the two resembles

the opposite of the observed atmospheric CO₂ growth rate.

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