Terrestrial net primary productivity — A brief history and a new worldwide database

J.M.O. Scurlock and R.J. Olson

Abstract: Consistent data on terrestrial net primary productivity (NPP) are urgently needed to constrain model estimates of carbon fluxes and hence to refine our understanding of ecosystem responses to climate change. The NPP data have been collected in a coordinated manner for the past 30 years, but comprehensive summaries are rare. We report on the development and availability of a global NPP database that is suitable for modeling of the terrestrial carbon cycle at global and regional scales, for validation of remote sensing data, and for other applications. These data were obtained from the literature on ecophysiological field work and from detailed consultation with the scientific community. Data on NPP, biomass, and associated environmental variables are now publicly available for 53 detailed study sites, of which more than half have data for belowground biomass or biomass dynamics. Aboveground NPP ranges from 35 to 2320 g $m^{-2}a^{-1}$ (dry matter) and total NPP from 182 to 3538 g $m^{-2}a^{-1}$. Well-known but previously unobtainable compilations of data, such as the "Osnabrück Data Set" and the International Biological Program (IBP) Woodlands Data Set, are also incorporated in this database. Preliminary exploration of relationships between NPP and mean annual precipitation and temperature suggests that the new 53-site data collection, as well as the Osnabrück and IBP data, are all consistent with the historic "Miami" statistical model. These data are available from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) for biogeochemical dynamics (see http://www.daac.ornl.gov/NPP/).

Key words: net primary productivity, grasslands, forests, biogeochemical dynamics, global carbon cycle, model validation.

Résumé : Il est urgent de pouvoir disposer de données congrues sur la productivité terrestre primaire nette (NPP) afin de contraindre les modèles d'estimation des flux de carbone et raffiner ainsi notre compréhension des réactions des écosystèmes au changement climatique. Les données sur la NPP ont été récoltées de façon coordonnée au cours des dernières 30 années, mais les résumés globaux sont rares. Les auteurs font état du développement et de la disponibilité d'une base de données sur la NPP globale qui convient pour la modélisation du cycle terrestre du carbone, aux échelles globales et régionales, pour valider les données de télédétection et pour d'autres applications. Ces données ont été obtenues de la littérature provenant de travaux de terrain en écophysiologie, et de consultations détaillées auprès de la communauté scientifique. Les données sur la NPP, la biomasse et les variables environnementales associées sont maintenant publiquement disponibles pour 53 sites d'études détaillés, dont plus de la moitié comprennent des données sur la biomasse

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hypogée ou la dynamique de la biomasse. La NPP épigée va de 35 à 2320 g $m^{-2}an^{-1}$ (poids sec) et la NPP totale de 182 à 3538 g $m^{-2}an^{-1}$. Sont également incorporées dans cette base de données des compilations de données bien connues mais auparavant non-disponibles, telles que le « Osnabrück Data Set » et l'ensemble des données sur les milieux forestiers du Programme biologique international (IBP). Une exploration préliminaire des relations entre la NPP et la précipitation ainsi que la température annuelles moyennes suggère que la nouvelle collection de données sur les 53 sites, ainsi que les données d'Onasbrück et du IBP, sont toutes congrues avec le modèle statistique historique « Miami ». Ces données sont disponibles à partir du Oak Ridge National Laboratory/Distributed Active Archive Center (ORNL/DAAC) sur la dynamique biogéochimique, à partir du site web suivant : http ://www.daac.ornl.gov/NPP/

Mots clés : productivité primaire nette, prairies, forêts, dynamique biogéochimique, cycle global de carbone, validation des modèles.

[Traduit par la rédaction]

Introduction

Net primary productivity (NPP), a measure of plant growth, is a key ecosystem variable, which is the light-driven biosynthesis of vegetation that may be consumed by other organisms. Terrestrial NPP data are more widely available than other estimates of biosphere–atmosphere exchange of carbon such as gross primary productivity (GPP) and net ecosystem exchange (NEE), but there are significant problems with inconsistency in measurement techniques between NPP studies separated in space and time. Secondary users of these data need to beware of such inconsistencies and should obtain as much documentation as possible before performing their own analyses, model validation, etc. In the recent past, progress in developing predictive terrestrial biosphere models has been inhibited by the lack of a high-quality dataset based upon field observations (Scurlock et al. 1999).

The absence of a quality NPP data set became apparent when the International Geosphere–Biosphere Programme (IGBP) project on Global Analysis, Interpretation and Modeling (GAIM) held global NPP model intercomparison meetings in 1994 and 1995 in Potsdam, Germany (Hibbard and Sahagian 1998; Cramer et al. 1999). Furthermore, the Vegetation Ecosystem Modeling and Analysis Project (VEMAP) (Schimel et al. 1997) cited similar difficulties in comparing model predictions with currently available NPP estimates, and an analysis of terrestrial carbon sinks cited the need for additional data to refine model constraints (Fan et al. 1998). The mechanistic models developed in the 1980s and 1990s were not being served by the NPP data collected in the preceding decades.

Furthermore, NPP data are likely to play a role in the U.S. National Aeronautics and Space Administration (NASA) Earth Observing System (EOS) Validation program, since estimated NPP is one of the EOS satellite remote sensing products that requires validation against ground measurements (Justice et al. 2000). Ideally, NPP should be measured simultaneously with the satellite overpass, but historical NPP field data provide a range of values from diverse land cover types with which to compare satellite-based estimates. A global standard NPP product is also proposed as a primary goal of GT-Net, the Global Terrestrial Observing System (GTOS) System of Networks established in 1997 to better understand global and regional change. The GTOS is an integrated worldwide knowledge base established by four United Nations agencies together with the International Council of Scientific Unions (see http://www.fao.org/gtos/PAGES/gtnet.htm).

Most recently, a further IGBP–GAIM initiative has developed from the Potsdam meetings described above — the Ecosystem Model–Data Intercomparison (EMDI). A series of EMDI workshops are planned to formally compare terrestrial carbon cycle models with field data, enabling the refinement of both the models and the data sets and an improved understanding of environmental controls on carbon allocation and carbon fluxes at various scales (Hibbard 2000). This paper describes the generation of a "benchmark" NPP data set, comprising both intensively documented study sites and also more extensive pre-existing data collections, which together have become a key resource in the EMDI process. Some simple relationships between NPP and associated climatic data are explored, with reference to the historic “Miami” statistical NPP model (Lieth 1975*b*).

Definition — and a brief history of net primary productivity data

Regrettably, the usage of the term *net primary productivity* has still not been standardized in the literature. It has its origins in the concept of the ecosystem (Tansley 1935; Golley 1993), but despite efforts to clear up terminological confusion (e.g., Macfadyen 1949; Olson 1964) a precise definition did not really emerge until the International Biological Programme (e.g., Newbould 1967). Strictly speaking, net primary productivity refers to the rate process, i.e., the amount produced (net primary production) per unit time. Thus, NPP is the total photosynthetic gain of vegetation less respiratory losses per unit area of ground per unit of time (Long et al. 1989), i.e., the increase in plant mass plus losses: mortality, herbivory, etc.; summed for both above and belowground compartments; or in other words, the rate of supply of plant matter potentially available to consumer organisms. The NPP is clearly important also at the scale of planetary ecology: to quote Lieth (1975*a*), “primary productivity ... is of paramount importance (for humankind) ... it is by primary productivity that the life of the (Earth’s) vegetational mantle and thereby of man is maintained.”

Records of the productivity of vegetation (in the sense of production of economically valuable matter per unit time) began in earnest in the late 19th century for commercial goods such as crops, forage, and forest products (Olson 1964). Some of the long-term data sets on NPP originated from such commercial agricultural interests (e.g., the Park Grass experiment at Rothamstead, U.K. (Silvertown et al. 1994), rangeland forage production at the Central Plains Experimental Range, Colorado, U.S.A. (Lauenroth and Sala 1992)). However, long-term studies explicitly monitoring the productivity of natural vegetation did not begin until the 1950s; coordinated efforts since that time have included such well-known projects as the International Biological Program (IBP) and the U.S. Long-Term Ecological Research (LTER) program (Golley 1993; Franklin et al. 1990; Knapp and Smith 2001). Today, data from many study sites worldwide are scattered throughout the peer-reviewed literature as well as in government reports and other printed matter of limited circulation, and comprehensive summaries are rare. DeAngelis et al. (1981) and Cannell (1982) are notable exceptions; both of these publications were attempts to actually provide data that others could reanalyse in the future. Thus, the pressing need for more data sets to validate ecosystem models of NPP in response to increasing CO_2 and climate change, coupled with the recent growth of access to high-speed personal computers and data networks, has stimulated the formation of a detailed and reasonably representative world NPP data archive.

The NPP data described here were compiled for the Global Primary Production Data Initiative (GPPDI), a Focus 1 activity of the IGBP Data and Information System (Prince et al. 1995). One of the first steps of GPPDI was to identify existing NPP field data sets and the associated environmental data (climate, soils, etc.), which might be needed to drive or parameterize NPP models, and to make them available online through data centers such as the NASA-funded Distributed Active Archive Center (DAAC) at Oak Ridge National Laboratory (ORNL). Our data documentation and archiving standards were developed around NASA guidelines, existing data formats, and the needs of modelers, and we have also addressed the metadata guidelines proposed by the Ecological Society of America (Michener et al. 1997). Initial development of the database was aided by the existence of consistently formatted grassland data sets assembled under an earlier collaborative SCOPE Project (Breymeyer and Melillo 1991; Breymeyer et al. 1996). A SCOPE Grasslands Modeling Group previously synthesized detailed and long-term data from sites in both temperate and tropical grasslands, to further develop the CENTURY plant–soil ecosystem model and simulate response to climate change scenarios for grassland sites worldwide (Parton et al. 1993; Parton et al. 1995). Our GPPDI collaborators encouraged us to incorporate data from tropical and boreal forests, since these represent two extremes of tree-dominated biomes. Although syntheses of NPP data are known to exist for other biome types such as wetlands (e.g., Westlake et al. 1998), we had to concentrate our efforts on the more widespread biome–land cover types. We were also aware that the VEMAP group had not modeled NPP for wetlands because of difficulties in simulating edaphic conditions for this land cover type (Schimel et al. 1997).

Selecting, compiling, and checking the data

Since most previously available data were only partial estimates of NPP (Scurlock et al. 1999), our target was to compile enhanced NPP data for use by the global change research community, with a target of between 50 and 100 "intensively documented" study sites. The data compilation process involved (1) identifying and prioritizing existing study sites and sources of NPP data (in consultation with the ecophysiological field research community), (2) acquiring the data for the priority sites, together with accompanying descriptive material (documentation), (3) performing quality assurance checks, reformatting the data and documentation, and entering them into the database, and then (4) seeking review and authorization for these data before making them publicly available.

Criteria for selecting "intensive" study sites included the availability of complete and consistent information on NPP or at least partial NPP (components such as litterfall or biomass increment), together with biomass (standing crop of live matter). Site-description metadata, such as latitude, longitude, and elevation, were considered essential for linking the data to model-driving climate variables (which may be interpolated from actual measurement stations to the NPP study sites). Information on vegetation type (biome), soil type, and land-use history was also a prerequisite for inclusion of a study site in the compilation. At least one reference was required from the peer-reviewed literature, although exceptions were occasionally made where the data were well known in the research community (e.g., unpublished data from the Matador IBP grassland site, Canada).

Monthly climatological data for each study site for 5–100 years (precipitation, mean monthly maximum temperature, mean monthly minimum temperature) were also obtained, if possible, from the original literature or the original authors. Alternatively, we obtained these data from the nearest weather station ($<$10 km distant and at similar elevation) available from existing collections such as the National Climatic Data Center (Asheville, N.C., U.S.A.) or the Carbon Dioxide Information and Analysis Center (CDIAC, Oak Ridge, Tenn., U.S.A.).

Quality assurance included cross-checking the NPP records against other compilations of NPP data (e.g., DeAngelis et al. 1981; Cannell 1982), eliminating duplicates or documenting multiple treatments at one study site, plotting the points in geographical space to confirm they coincided with the relevant landforms, and checking data ranges for outlying values.

The NPP data have been provided or discovered in a variety of forms ranging from tabulated computer text files to graphs digitized from publications or theses. The penultimate step, data review and authorization, often involved locating and establishing communication with the original authors or their successors, first to get their attention and interest and then to agree on any corrections and permissions required. In some cases the original author had moved several times, retired, or even died, illustrating the principle of "data entropy" (Michener et al. 1997; Scurlock et al. 2002*b*). This task has taken an estimated 2–3 person-weeks per study site, often spread over a period of 6–12 months. As DeAngelis et al. (1981) found more than 15 years ago when compiling and publishing the IBP Woodlands Data Set, "... data did not always conform easily to the uniform format in which it is presented here. Repeated communications with members of ... projects were often employed before deciding on appropriate values."

However, we often found the original principal investigators (PIs) to be enthusiastic about finding new applications for data collected as much as 40 years ago. In some cases, our electronic tables have been carefully checked against the original field notes of the PIs and additional data have been resurrected from dusty personal archives. This process of data resynthesis adds value to the original published information from the literature, as well as simply providing a single point of access to data from many sites (Michener et al. 1997; Scurlock et al. 2002*b*).

Table 1. Distribution by vegetation classification of the intensive NPP study sites in the ORNL DAAC database. The number of sites falling within a particular category is given in parentheses. Note that certain classifications result in grassland sites, in particular, being placed in a nongrassland category.

Biome	Bailey ecoregions, simplified by the authors (after Bailey 1989)	Holdridge life zones (Holdridge 1947)	Matthews vegetation classes (Matthews 1983)	Olson world ecosystem complexes (Olson et al. 1982)
Grasslands	Savanna (6), humid savanna (5), humid temperate prairie (5), dry temperate steppe (8), cold desert steppe (5), others (5)	Steppe (10), tropical dry forest (7), temperate forest (5), others (12)	Grassland with shrubs (10), short grassland (5), temperate subpolar evergreen needleleaved forest (3), tropical/subtropical drought-deciduous forest (3), others (13)	Crop/settlement(18), grassland (7), others (9)
Boreal forest	Continental needleleaf taiga (3), continental mixed forest (1) forest/alpine meadow (1)	Boreal forest (3), forest tundra (1), temperate forest (1)	Temperate/subpolar evergreen needleleaf forest (4), arctic/alpine tundra (1)	Mixed forest (1), conifer forest (4)
Tropical forest	Constant humid evergreen forest (9), humid tropical montane forest (1), humid tropical forest/ montane savanna (3), forest-meadow-paramo (1)	Tropical rain forest (6), tropical dry seasonal forest (3), tropical dry forest (4), others (1)	Tropical evergreen rainforest (7), others (7)	Tropical/subtropical forest (3), forest/ field and dry evergreen broadleaf (2), others (9)

Table 2. Distribution of intensive terrestrial NPP study sites in the ORNL DAAC database, by region and country. Most parts of the world are included, of the 53 study sites, 46 fall in the northern hemisphere (highest latitude is 66.37°N) and 7 in the southern hemisphere (lowest latitude is 45.60°S). See also Fig. 1.

Region	Number of sites	Country	Number of sites
North America	12	U.S.A.	8
		Canada	2
		Mexico	2
South and Central America and Caribbean	13	Venezuela	3
		Argentina	2
		Costa Rica	2
		Panama	2
		Others	4
Europe	9	Russia	3
		Sweden	3
		Others	3
Asia	11	China	2
		India	2
		Kazakhstan	2
		Thailand	2
		Others	3
Africa	6	South Africa	2
		Others	4
Australia/Oceania	2	Australia	2
Total	53		53

Fig. 1. Map showing the geographical distribution of intensive terrestrial NPP study sites in the ORNL DAAC database. ▲ = boreal forest sites, ● = grassland sites, ■ = tropical forest sites. Some points may be indistinct because of their close proximity.

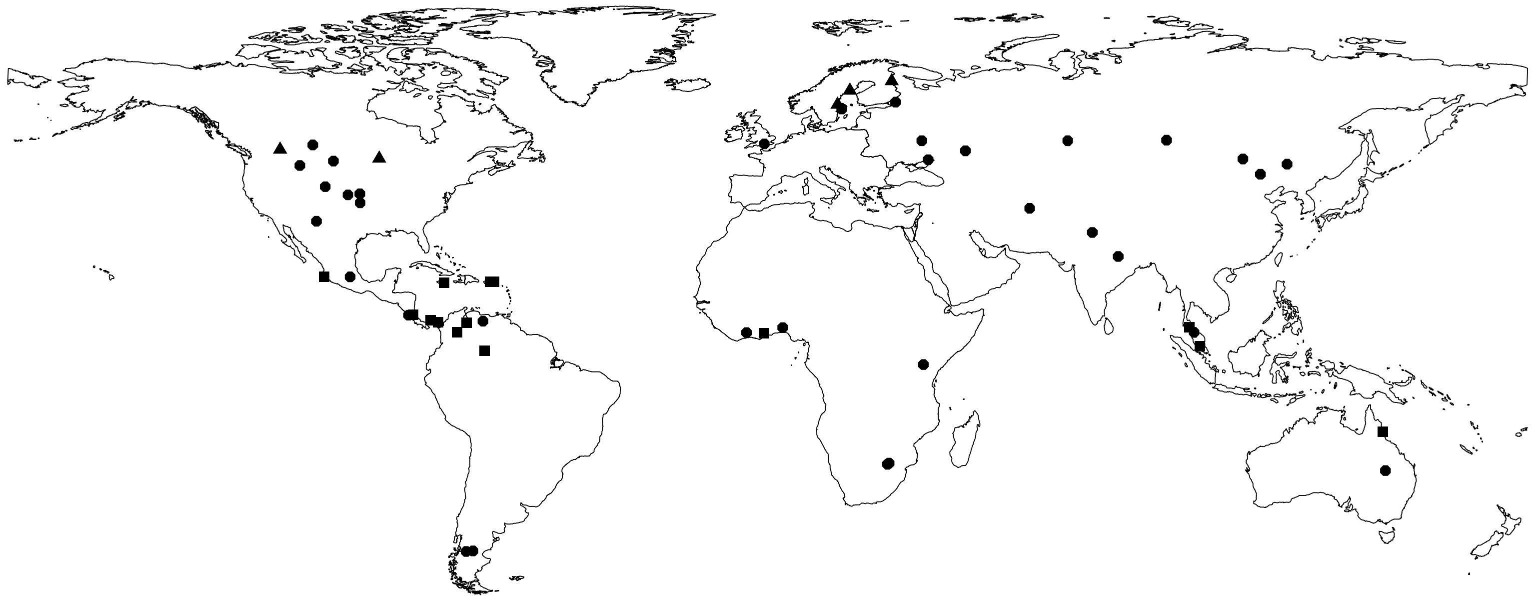


Table 3. Distribution by biome of the intensive NPP study sites in the ORNL DAAC database, and mean productivity of each biome as reported in the literature. Number of study sites in range is given thus (*n* = 7) where this is less than the total for the biome.

Biome	C_3grassland (including one shrub-steppe site)	C_4 grassland	Boreal forest	Tropical forest	Total
Number of sites	18	16	5	14	53
Mean ANPP ($g\ m^{-2}a^{-1}$, dry matter)	286	668	448	1254 (*n* = 13)	657 (*n* = 52)
Range ($g\ m^{-2}a^{-1}$, dry matter)	35–774	76–1706	198–727	682–2320	35–2320
Mean BNPP ($g\ m^{-2}a^{-1}$, dry matter)	887 (*n* = 7)	795 (*n* = 11)	275 (*n* = 4)	632 (*n* = 7)	706 (*n* = 29)
Range ($g\ m^{-2}a^{-1}$, dry matter)	60–1745	147–1832	20–500	260–1117	60–1832
Mean TNPP ($g\ m^{-2}a^{-1}$, dry matter)	1236 (*n* = 7)	1518 (*n* = 11)	696 (*n* = 4)	2061 (*n* = 8)	1484 (*n* = 30)
Range ($g\ m^{-2}a^{-1}$, dry matter)	182–2474	295–3538	291–1190	1497–2780	182–3538

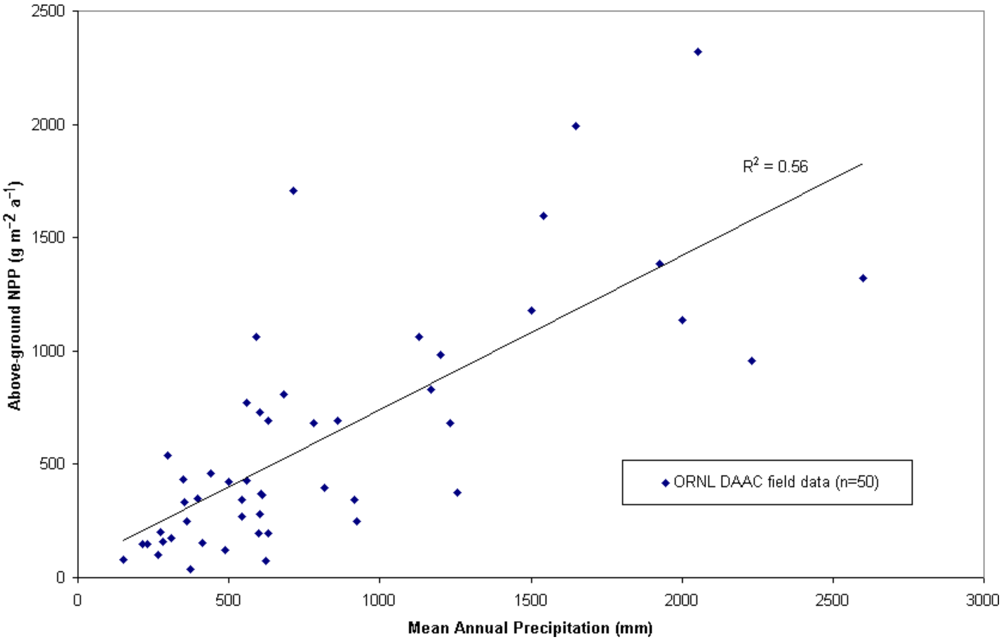
Notes: ANPP = aboveground net primary productivity, BNPP = belowground net primary productivity, TNPP = total net primary productivity.

In the course of our data selection we realized that the ecological research and modeling community would also benefit from access to quality-checked versions of existing compilations of “extensive” NPP data. Thus the authors worked on reformatting and quality checking of the *Osnabrück data set* of 720 records extracted from the literature, in collaboration with the originators of this data set (Esser 1991; Esser et al. 1997), and also digitized the *IBP Woodlands data set* of 117 forest research sites (DeAngelis et al. 1981). Other “extensive” or “multisite” NPP data sets include the *TEM data set* of 16 NPP study sites used to calibrate a well-known terrestrial ecosystem model (McGuire et al. 1992), the regional *OTTER NPP data set* of 6 study sites along a transect in Oregon, U.S.A. (Runyon et al. 1994), and a data set covering 17 forest types in China (Ni et al. 2001). Though adequately documented and peer reviewed these extensive data do not necessarily meet the more stringent criteria we used for selecting the “intensive” study sites (see above). For example, only summary climatology are available and information on soils and land-use history may be absent: we are also aware that the methodologies for NPP estimation may be inconsistent between these many sites.

Data consistency — spatial and temporal considerations

In common with many types of ecological and environmental data, our criteria for “consistency” included the use of common systems of names (e.g., species, vegetation classes), units of measure, and place names; conversion or translation was needed in many cases. Geographical coordinates were expressed as decimal degrees, although compass directions were retained instead of positive and negative coordinates (e.g., 34.85°N 101.32°W). With the increasing emphasis on scaling-up from study sites to landscapes or regions, and the use of GIS, digital elevation models and spatially explicit ecosystem–hydrology models, it is desirable to synthesize many kinds of field data in a geographical context (position, slope, aspect, and driving climate variables). In many cases, we had to reconstruct spatial coordinates (latitude, longitude, elevation) from maps, determining the location of an NPP study site from descriptions of its distance from the nearest town or other landmark. Contemporary guidelines on ecological data collection include the requirement to provide precise positional documentation (Michener

Fig. 2. An example of “data exploration” based upon the intensive NPP study sites in the ORNL DAAC database. Aboveground NPP is plotted against annual precipitation for 49 of the 53 NPP sites, where annual precipitation was less than 3000 mm.



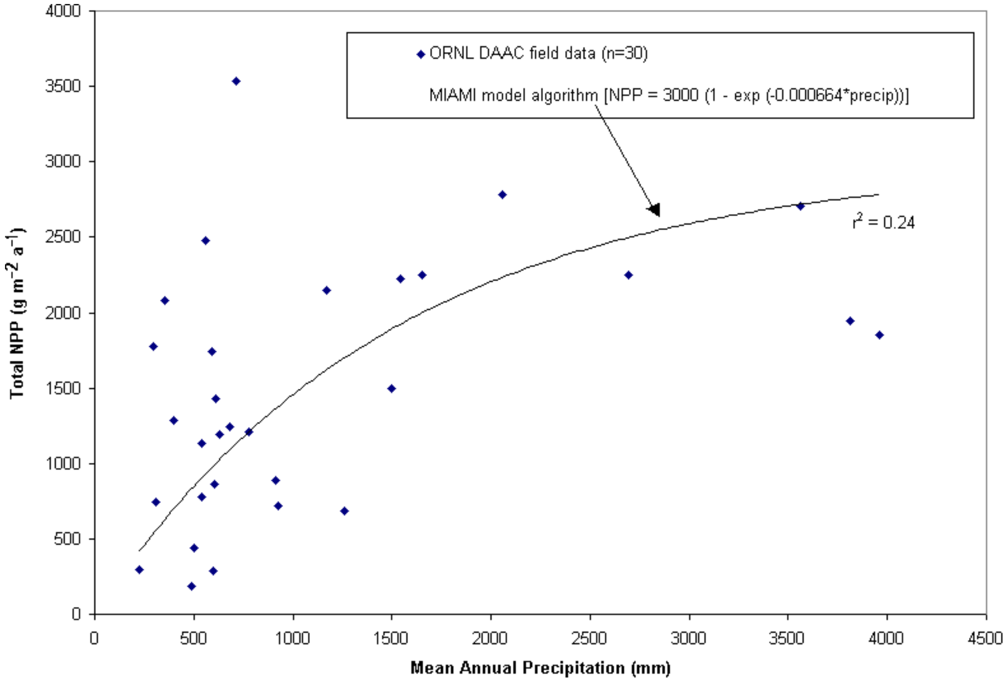
et al. 1997), and Global Positioning System (GPS) receivers can provide this cheaply for contemporary field work, but the accuracy of GPS (<1 m at best) is rarely matched by historical data in the literature, whose position may be known only to an accuracy of 5–10 km. Despite these spatial limitations of the NPP point data, we have attempted to provide some degree of geographical context by relating the study sites to “classic” vegetation and land cover classifications commonly used by modelers (Bailey 1989; Matthews 1983; Holdridge 1947; Olson et al. 1982). The information summarized in Table 1 is provided as a map-based interface to the NPP data at the ORNL DAAC Web site (see http://www.daac.ornl.gov/NPP/).

Temporal resolution is a further aspect of data consistency in ecological data. Exact dates of field sampling are rarely provided, although sampling intervals (weeks or months) may be specified for grasslands and year of measurement for forests. As far as possible, we assigned the NPP measurements to the date (day, month, year; or Julian date) as originally described or interpolated the date of measurement by digitizing published graphs. However, it must be realized by secondary users of these data that one “harvest interval” in the field may be spread out over several days of field work and that different components (such as shoots and roots) may be sampled on different dates.

Data characteristics

The NPP database at the ORNL DAAC presently contains detailed information from 53 individual study sites in grasslands, tropical forest, and boreal forest (Appendix: Table A1). Many of these sites have data for multiple treatments as well as ancillary information such as site photographs and pre-plotted graphs of biomass dynamics and climate. The scope of the data from the intensive study sites is shown here by country/region (Table 2, Fig. 1) and by biome (Table 3). Of the 53 sites, 29 have data for belowground biomass or biomass dynamics. The earliest NPP data are from 1939 and the most recent from 1996; the number of years of data for each site ranges from 1 to 51, and 18 sites have data for

Fig. 3. A second example of "data exploration", after Lieth (1975 *b*). Total NPP is plotted against annual precipitation for 30 of the intensive NPP sites (those for which an estimate of total NPP was available). The correlation between actual NPP and the Miami model precipitation algorithm is given by r^2 = 0.24.



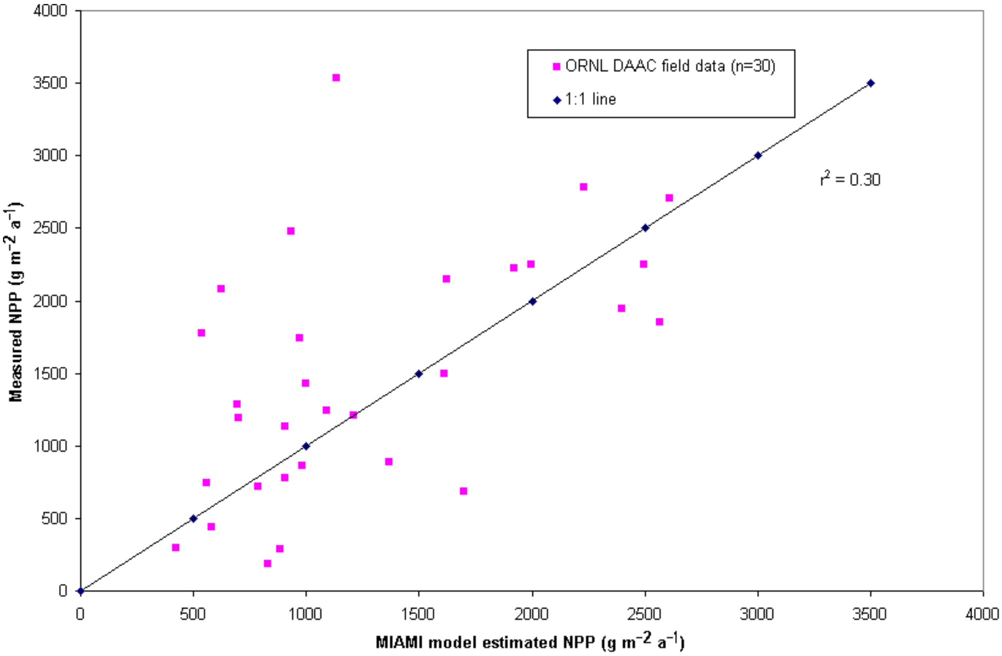
more than one "treatment" (fertilized or irrigated plots, different soil types, stand ages, etc.). The total number of site/treatment/year combinations is about 500.

Overall, aboveground NPP for the intensive sites ranges from 35 to 2320 g $m^{-2}a^{-1}$ (dry matter), belowground NPP from 60 to 1832 g $m^{-2}a^{-1}$ and total (aboveground + belowground) NPP from 182 to 3538 g $m^{-2}a^{-1}$ (Table 3). These statistics fall within the range of values reported for the 720 NPP records in the extensive Osnabrück data set (Esser et al. 1997) and are comparable to those for the IBP Woodlands Data Set (DeAngelis et al. 1981). It is also instructive to compare our present data compilation with the NPP ranges reported a generation ago by Lieth (1975*a*), commonly described as the "Lieth and Whittaker" synthesis (Lieth and Whittaker 1975), and still frequently cited. Whilst the numbers in Table 3 fall within Lieth's typical ranges (considered representative for 1950) it is noteworthy that the mean values reported here for total NPP of grasslands are more than twice as high. The possible underestimation of grassland NPP by the International Biological Program has been discussed previously (Long et al. 1989; Scurlock and Hall 1998).

Applications and exploration of the data

Some of these difficulties experienced today by secondary users of NPP data (e.g., poor documentation of measurement techniques) were foreseen at the time of data collection; others were not. For example, in the early 1970s Van Dyne and fellow coordinators of the US IBP Grassland Biome Program anticipated the synthesis and modeling of data on grassland dynamics from multiple study sites (Golley 1993). However, with the limited funding available in the post-IBP period of the late 1970s, this modeling capability developed more slowly and utilized only a fraction of the vast data resources that had been accumulated. It is only now, 25 years later, that both the models and the modeling capability

Fig. 4. Total NPP (TNPP) plotted againast Miami Model estimated TNPP for the subset of 30 intensive NPP sites.



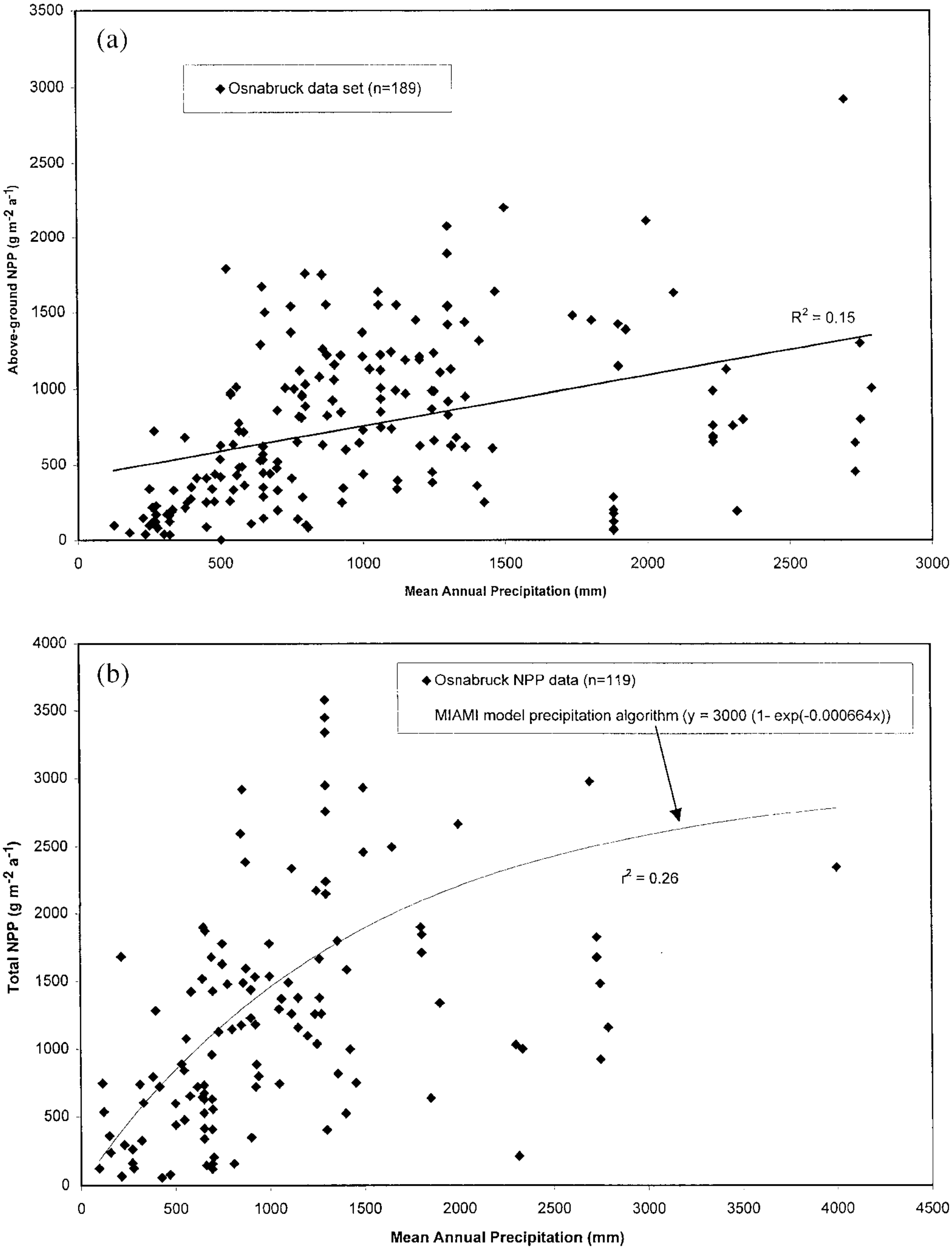
really exist to make use of these data. Again, in the words of Lieth (1975*a*, p. 212): "... (the) estimates I have given are representative for ca. 1950. The accelerating rate at which the world is being transformed and the biosphere is being affected by man hardly needs emphasis .... by 1980 or 1990 ... the primary production of the world will have altered. Approaches through environmental correlation and modeling ... may become more appropriate in representing the potential productivity of large areas ..."

This NPP database may be used for a variety of applications within the global carbon cycle research community; to re-examine worldwide patterns of NPP, to parameterize and evaluate global ecosystem models, and to calibrate and evaluate models driven by remotely sensed data. In addition, the NPP data may play a role in the NASA EOS Validation program (see above) and should also be suitable for addressing a variety of regional ecological problems.

Using these data, simple general relationships that may hold true across a wide range of biome types may be explored, such as the dependence of reported aboveground NPP (ANPP) upon annual precipitation where this is obviously a limiting factor. We found a good straight-line fit between ANPP and annual precipitation for 50 of the 53 NPP study sites worldwide for which mean annual precipitation was <3000 mm (r^2 = 0.56, Fig. 2). We chose to exclude the most humid climates from this simple analysis, as suggested by Lieth (1975*b*).

The statistical model of Lieth (1975*b*), commonly known as the "Miami Model," describes a similar relationship between total (aboveground + belowground) NPP and annual precipitation as a hyperbola (for cases where NPP is not limited by temperature). However, this approximates to a straight line for annual precipitation below about 1000 mm ("Walter's ratio", Lieth 1975*b*), and its "saturation curve" or hyperbolic asymptote only becomes significant at higher annual precipitation, about 3000 mm. A subset of 30 of the NPP study sites (for which total NPP was available) was compared with Lieth's NPP–precipitation algorithm. They were clearly distributed around the line of Lieth's algorithm, although the scatter of points was quite high (r^2 = 0.24, Fig. 3). However, NPP according to Lieth's Miami model actually comprises the minimum of this precipitation function and a temperature function, its assumption

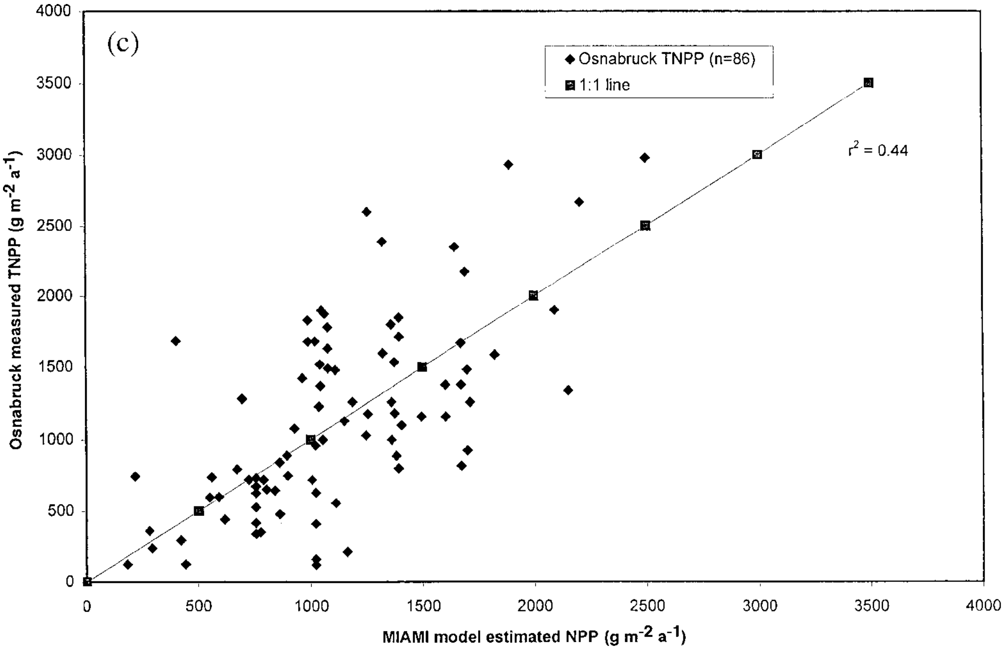
Fig. 5. Exploration of relationships in the Osnabrück data set. (*a*) ANPP vs. precipitation, (*b*) TNPP vs. precipitation, (*c*) TNPP vs. Miami Model estimated TNPP.



being that one of these two environmental factors is always limiting. Net primary productivity for several of our data points (e.g., boreal forests) is probably limited by temperature rather than precipitation. As expected, when we plotted NPP for these same 30 sites against Miami Model estimated NPP, which adjusts for temperature-limited sites, we found a better correlation (r^2 = 0.30, Fig. 4).

Although we have less confidence in the quality checking and consistency of the “extensive” NPP

Fig. 5. *Concluded.*



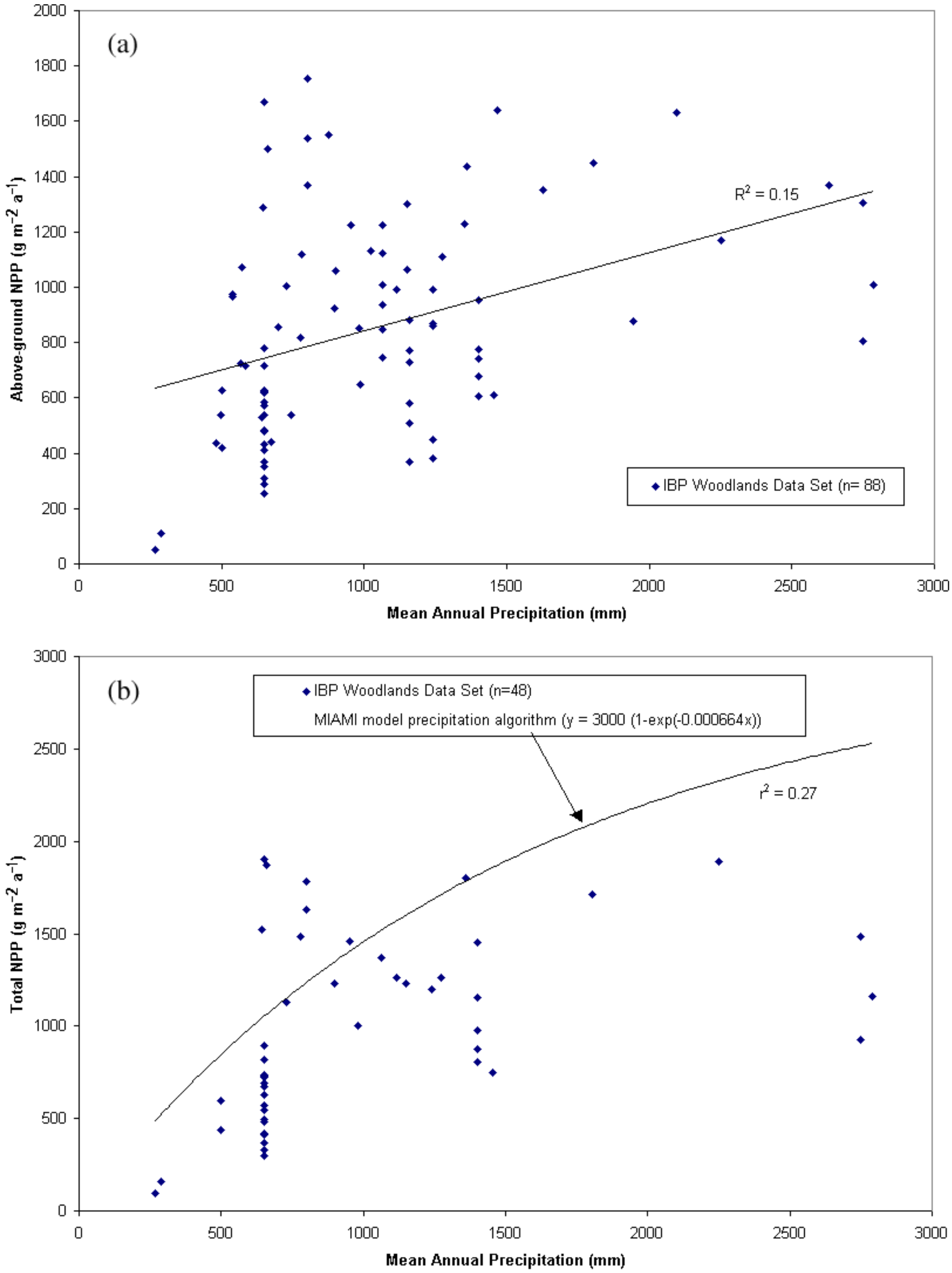
data, we performed a preliminary exploration of the same relationships for the Osnabrück data set and the IBP Woodlands data set (Figs. 5 *a–c*, Figs. 6 *a–c*). In each case, the number of points was restricted to those for which rainfall and temperature were available (189 and 119 out of 720 for the former, 88 and 48 out of 117 for the latter). The correlation between ANPP and precipitation was poor in each case, regardless of whether the regression line intercept was forced through the origin (we recognize that ANPP will be zero as precipitation approaches zero). The Osnabrück data set showed a reasonable fit to the Miami Model NPP–precipitation algorithm, but for the IBP Woodlands data set, the majority of data points fell below the Miami precipitation line (Fig. 6*b*). This suggests that temperature rather than precipitation is more limiting to NPP for many of these woodland sites. Further examination of these data showed indeed that the Miami Model predicts that temperature is limiting for 41 of the 48 points plotted, although there was no simple temperature threshold beyond which NPP is limited by precipitation (Lieth (1975 *b*), suggests that this threshold is a function of both temperature and precipitation). A similar "exploration" of the IBP Woodlands data set previously suggested that other factors may limit NPP at some of these sites (O'Neill and DeAngelis 1981). However, the overall fit between both the Osnabrück and the IBP Woodlands data sets and the Miami Model predicted NPP is remarkably good (r^2 = 0.44 and 0.36, respectively; Figs. 5*c* and 6*c*), suggesting that this simple statistical model is quite robust.

The more detailed biomass dynamics available in the NPP database are also suitable for more complex hypothesis testing, such as investigating the relationship between different algorithms for estimating NPP in grasslands (e.g., Singh et al. 1975; Scurlock et al. 2002*a*), or assessing interannual variation in ANPP across multiple study sites (Knapp and Smith 2001).

Conclusions

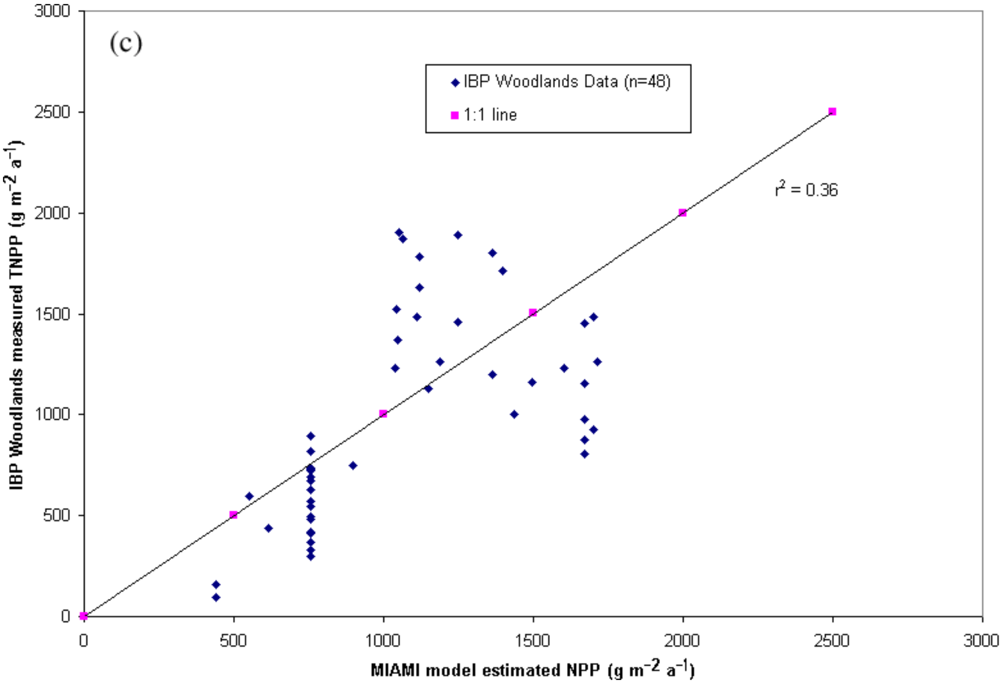
This global NPP database fills an important gap for modeling and validation at global and regional scales, especially for projects of the International Geosphere–Biosphere Program and others that address

Fig. 6. Exploration of relationships in the IBP Woodlands data set. (*a*) ANPP vs. precipitation, (*b*) TNPP vs. precipitation, (*c*) TNPP vs. Miami Model estimated TNPP.



global change issues. We anticipate that this database will grow further, both through the addition of new data and through feedback from secondary users of the data. The results of a series of NPP data synthesis workshops held under the GPPDI have already enhanced these data by providing methods for more

Fig. 6. *Concluded.*



complete and consistent NPP estimates (Clark et al. 2001*a*, 2001*b*; Gill et al. 2002; Gower et al. 2001) as well as techniques for scaling-up from field observations to landscape-level or regional-level estimates of NPP (Zheng et al. 2002). Some 30 years after the first coordinated studies of NPP, the data and the analysis–modeling tools are finally in place to enable a range of new data–data-, model–model-, and model–data-analyses and intercomparisons (e.g., Cramer et al. 1999; Alexandrov et al. 1999; Hibbard 2000; Knapp and Smith 2001). Thus, major global change questions may be addressed, such as testing simulated controls on and responses of the carbon budget, using enhanced field data together with other data sources (remote sensing, etc.) to constrain models of vegetation carbon fluxes.

Data availability

The NPP data are maintained and distributed by the ORNL DAAC for Biogeochemical Dynamics (http://www.daac.ornl.gov), which is part of the NASA Earth Observing System Data and Information System Project and an integral part of the NASA contribution to the U.S. Global Change Research Program. The ORNL DAAC provides information about the biogeochemical dynamics of the Earth to the global change research community, policy makers, educators, and the interested general public. For further information about this data set and others, contact the ORNL DAAC User Services staff (Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831-6407, U.S.A. Tel. +1 (865) 241-3952, Fax 574-4665, Email ornldaac@ornl.gov).

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References

Alexandrov, G.A., Oikawa T., and Esser, G. 1999. Estimating terrestrial NPP: what the data say and how they may be interpreted? Ecol. Model. **117**: 361–369.

Bailey, R.G. 1989. Explanatory supplement to ecoregions map of the continents. Environ. Conserv. **16**: 307–309.

Breymeyer, A.I., and Melillo, J.M. 1991. The effects of climate change on production and decomposition in coniferous forests and grasslands. Ecol. Appl. **1**: 111.

Breymeyer, A.I., Hall, D.O., Melillo J.M., and Ågren, G.I. (*Editors*). 1996. Global change: effects on coniferous forests and grasslands. SCOPE 56. John Wiley and Sons, Chichester, U.K., 459 p.

Cannell, M.G.R. 1982. World forest biomass and primary production data, Academic Press, London, U.K., 391 p.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., and Holland, E.A. 2001*a*. NPP in tropical forests: an evaluation and synthesis of existing field data. Ecol. Appl. **11**: 371–384.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson J.R., and Ni, J. 2001*b*. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. **11**: 356–370.

Cramer, W., Kicklighter, D.W., Fischer, A., Moore, B., III, Churkina, G., Ruimy A., and Schloss, A. 1999. Comparing global models of terrestrial net primary productivity (NPP): Overview and key results. Global Change Biol. **5**(Suppl. 1): 1–15.

DeAngelis, D.L., Gardner, R.H., and Shugart, H.H. 1981. Productivity of forest ecosystems studied during the IBP: the woodlands data set. *In* Dynamics of Forest Ecosystems. IBP 23. *Edited by* D.E. Reichle. Cambridge University Press, Cambridge, U.K., pp. 567–672.

Esser, G. 1991. Osnabrück Biosphere Model: structure, construction, results. *In* Modern ecology: basic and applied aspects. *Edited by* G. Esser and D. Overdieck. Elsevier, Amsterdam and London. pp. 679–709.

Esser, G., Lieth, H.F.H., Scurlock, J.M.O., and Olson, R.J. 1997. Worldwide estimates and bibliography of net primary productivity derived from pre-1982 publications, ORNL Technical Memorandum TM-13485, Oak Ridge National Laboratory, Oak Ridge, Tenn., U.S.A., 122 p.

Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi T., and Tans, P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science, **282**: 442–446.

Franklin, J.F., Bledsoe C.S., and Callahan, J.T. 1990. Contributions of the long-term ecological research program. Bioscience, **40**: 509–523.

Gill, R.A., Kelly, R.H., Parton, W.J., Day, K.A., Jackson, R.B., Morgan, J.A., Scurlock, J.M.O., Tieszen, L.L., Castle, J.V., Ojima D.S., and Zhang, X.S. 2002. Using simple environmental variables to estimate belowground productivity in grasslands. Glob. Ecol. Biogeogr. **11**: 79–86.

Golley, F.B. 1993. A history of the ecosystem concept in ecology, Yale University Press, London, U.K., 254 p.

Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder S., and Wang, C.K. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl. **11**: 1395–1411.

Hibbard, K. 2000. EMDI update. Research GAIM (Newsletter of the Global Analysis, Interpretation and Modeling task force). GAIM Project Office, University of New Hampshire, Durham, N.H., U.S.A., Vol. 4, No. 1.

Hibbard, K., and Sahagian, D. (*Editors*). 1998. Net primary productivity model intercomparison activity. IGBP/GAIM Report #5. University of New Hampshire, Durham, N.H., U.S.A., 41 p.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. Science, **105**: 367–368.

Justice C., Belward, A., Morisette, J., Lewis, P., Privette J., and Baret, F. 2000. Developments in the "validation" of satellite sensor products for the study of the land surface. Int. J. Remote Sens. **21**: 3383–3390.

Knapp, A.K., and Smith, M.D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science, **291**: 481–484.

Lauenroth, W.K., and Sala, O.E. 1992. Long-term forage production of North American shortgrass steppe. Ecol. Appl. **2**: 397–403.

Lieth, H.F.H. 1975*a*. Primary production of the major vegetation units of the world. *In* Primary productivity of the biosphere. *Edited by* H. Lieth and R.H. Whittaker. Ecological Studies 14. Springer-Verlag, New York and Berlin. pp. 203–215.

Lieth, H.F.H. 1975*b*. Modeling the primary productivity of the world. *In* Primary productivity of the biosphere. *Edited by* H. Lieth and R.H. Whittaker. Ecological Studies 14. Springer-Verlag, New York and Berlin. pp. 237–283.

Lieth, H, and Whittaker, R.H. (*Editors*). 1975. Primary productivity of the biosphere. Ecological Studies 14. Springer-Verlag, New York and Berlin, 339 p.

Long, S.P., Garcia Moya, E., Imbamba, S.K., Kamnalrut, A., Piedade, M.T.F., Scurlock, J.M.O., Shen Y.K., and Hall, D.O. 1989. Primary productivity of natural grass ecosystems of the tropics: a reassessment. Plant Soil **115**: 155–166.

Macfadyen, A. 1949. The meaning of productivity in biological systems. J. Anim. Ecol. **17**: 75–80.

Matthews, E. 1983. Global vegetation and land use: New high-resolution data bases for climate studies. J. Clim. Appl. Meteorol, **22**: 474–487.

McGuire, A.D., Melillo, J.M., Joyce, L.A., Kicklighter, D.W., Grace, A.L., Moore, B., III, and Vorosmarty, C.J. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem. Cycles, **6**: 101–124.

Michener, W.K., Brunt, J.W., Helly, J.J., Kirchner, T.B., and Stafford, S.G. 1997. Nongeospatial metadata for the ecological sciences. Ecol. Appl. **7**: 330–342.

Newbould, P.J. 1967. Methods for estimating the primary production of forests. IBP Handbook No. 2, International Biological Programme, Blackwell Scientific, Oxford, U.K.

Ni, J., Zhang, X.S., and Scurlock, J.M.O. 2001. Synthesis and analysis of biomass and net primary productivity in Chinese forests. Ann. For. Sci. **58**: 351–384.

Olson, J.S. 1964. Gross and net production of terrestrial vegetation. J. Ecol. **52**(suppl.): 99–118.

Olson, J.S., Watts J.A., and Allison, L.J. 1982. Carbon in live vegetation of major world ecosystems. ORNL-5862, Oak Ridge National Laboratory, Oak Ridge, Tenn., U.S.A.

O'Neill, R.V., and DeAngelis, D.L. 1981. Comparative productivity and biomass relations of forest ecosystems. *In* Dynamics of forest ecosystems. IBP 23. *Edited by* D.E. Reichle, Cambridge University Press, Cambridge, U.K., pp. 411–449.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J-C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., and Kinyamario, J.I. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem. Cycles, **7**: 785–809.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Schimel, D.S., Hall D.O., and SCOPEGRAM Group Members. 1995. Impact of climate change on grassland production and soil carbon worldwide. Global Change Biol. **1**: 13–22.

Prince, S.D., Olson, R.J., Dedieu, G., Esser, G., and Cramer, W. 1995. Global Primary Production Data Initiative Project Description. IGBP-DIS Working Paper No. 12, International Geosphere-Biosphere Programme Data and Information System, Toulouse, France. 38 p.

Runyon, J., Waring, R.H., Goward, S.N., and Welles, J.M. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecol. Appl. **4**: 226–237.

Schimel, D.S., Emanuel, W., Rizzo, B., Smith, T., Woodward, F.I., Fisher, H., Kittel, T.G.F., McKeown, R., Painter, T., Rosenbloom, N., Ojima, D.S., Parton, W.J., Kicklighter, D.W., McGuire, A.D., Melillo, J.M., Pan, Y., Haxeltine, A., Prentice, C., Sitch, S., Hibbard, K., Nemani, R., Pierce, L., Running, S., Borchers, J., Chaney, J., Neilson, R., and Braswell, B.H. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol. Monogr. **67**: 251–271.

Scurlock, J.M.O., and Hall, D.O. 1998. The global carbon sink: a grassland perspective. Global Change Biol. **4**: 229–233.

Scurlock, J.M.O., Cramer, W., Olson, R.J., Parton W.J., and Prince, S.D. 1999. Terrestrial NPP: towards a consistent data set for global model evaluation. Ecol. Appl. **9**(3): 913–919.

Scurlock, J.M.O., Johnson, K., and Olson, R.J. 2002*a*. Estimating net primary productivity from grassland biomass dynamics measurements. Global Change Biol. **8**: 1–18.

Scurlock, J.M.O., Olson, R.J., McCord R.A., and Michener, W.K. 2002*b*. Environmental data banks: archiving ecological data and information. *In* Encyclopedia of global environmental change. *Edited by* E. Munn. Vol. 2: The Earth system: biological and ecological dimensions of global environmental change, Ecosystems section. *Edited by* H. Mooney and J. Canadell. John Wiley, Chichester, Sussex, U.K., pp. 248–259.

Silvertown, J., Dodd, M., McConway, K., Potts, J., and Crawley, M. 1994. Rainfall, biomass variation, and community composition in the Park Grass Experiment. Ecology, **75**: 2430–2437.

Singh, J.S., Lauenroth W.K., and Sernhorst, R.K. 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. **41**: 181–232.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology, **16**: 284–307.

Westlake, D.F., Kvet, J., and Szczepanski, A. (*Editors*). 1998. The production ecology of wetlands: the IBP synthesis. Cambridge University Press, Cambridge, U.K., 568 p.

Zheng, D.L., Prince, S.D., and Wright, R. 2002. Terrestrial net primary production estimates for 0.5 degree grid cells from field observations – a contribution to global biogeochemical modelling. Global Change Biol. In press.

Appendix A:

Table A.1. Location, biome type, annual temperature and precipitation, and "best estimates" of NPP (aboveground, belowground, and total NPP, based upon numbers reported in the literature and the authors' own evaluation) for the 53 intensive terrestrial NPP study sites in the Oak Ridge National Laboratory Distributed Active Archive Center NPP database. See the ORNL DAAC Web pages for details of original references: http://www.daac.ornl.gov/NPP/.

Site name	Country	Latitude	Longitude	Biome type	Mean annual precipitation (mm)	Mean annual temperature (°C)	ANPP ($g\ m^{-2}a^{-1}$)	BNPP ($g\ m^{-2}a^{-1}$)	TNPP ($g/m^2/a$)
Badkhyz	Turkmenistan	35.68°N	62.00°E	C3 grassland	266	12.6	100	N/A	N/A
Bridger, MT	U.S.A.	45.78°N	110.78°W	C3 grassland	925	2.7	249	471	720
Charleville	Australia	26.40°S	146.27°E	C3 grassland	489	19.4	122	60	182
Dickinson, ND	U.S.A.	46.90°N	102.82°W	C3 grassland	397	4.8	351	932	1283
Kursk	Russia	51.67°N	36.50°E	C3 grassland	560	6.1	774	1700	2474
Dhzanybek	Kazakhstan	49.33°N	46.78°E	C3 grassland	274	5.0	201	N/A	N/A
Khomutov	Ukraine	47.17°N	38.00°E	C3 grassland	441	11.1	460	N/A	N/A
Media Luna	Argentina	45.60°S	71.42°W	C3 grassland	374	5.5	35	N/A	N/A
Matador	Canada	50.70°N	107.72°W	C3 grassland	350	3.0	431	N/A	N/A
Otradnoe	Russia	60.83°N	30.25°E	C3 grassland	543	8.6	306	650	956
Shortandy	Kazakhstan	51.67°N	71.00°E	C3 grassland	351	1.3	335	1745	2080
Tullgarnsnaset	Sweden	59.20°N	17.50°E	C3 grassland	560	2.5	430	N/A	N/A
Tumugi	China	46.10°N	123.00°E	C3 grassland	411	2.1	155	N/A	N/A
Tumentsogt	Mongolia	47.40°N	112.50°E	C3 grassland	280	1.7	160	N/A	N/A
Tuva	Russia	51.83°N	94.42°E	C3 grassland	214	−4.3	150	N/A	N/A
Xilingol	China	43.72°N	116.63°E	C3 grassland	360	−2.0	249	N/A	N/A
Pampa de Leman	Argentina	45.43°S	69.83°W	Shrub steppe	150	8.7	78	N/A	N/A
Canas	Costa Rica	10.40°N	85.10°W	C4 grassland	1926	28.0	1387	N/A	N/A
Calabozo	Venezuela	8.93°N	67.42°W	C4 grassland	1257	28.3	375	307	682
CPER/SGS, CO	U.S.A.	40.82°N	104.77°W	C4 grassland	310	9.9	172	568	740
Hays, KS	U.S.A.	38.87°N	99.38°W	C4 grassland	610	12.2	363	1062	1425
Jornada, NM	U.S.A.	32.60°N	106.85°W	C4 grassland	228	14.9	148	147	295
Klong Hoi Khong	Thailand	6.33°N	100.93°E	C4 grassland	1540	26.4	1595	625	2220
Konza, KS	U.S.A.	39.10°N	96.61°W	C4 grassland	818	12.6	394	N/A	N/A
Kurukshetra	India	29.97°N	76.85°E	C4 grassland	715	23.6	1706	1832	3538
Lamto	Cote Ivoire	6.22°N	5.03°W	C4 grassland	1170	28.8	830	1320	2150

Table A.1. *Concluded.*

Site name	Country	Latitude	Longitude	Biome type	Mean annual precipitation (mm)	Mean annual temperature (°C)	ANPP (g m^{-2}a^{-1})	BNPP (g m^{-2}a^{-1})	TNPP (g/m^2/a)
Montecillo	Mexico	19.46°N	98.91°W	C4 grassland	590	14.2	1063	678	1741
Nylsvley	South Africa	24.65°S	28.70°E	C4 grassland	623	17.1	76	N/A	N/A
Nairobi	Kenya	1.33°S	36.83°E	C4 grassland	680	19.7	811	431	1242
Olokemeji	Nigeria	7.42°N	3.55°E	C4 grassland	1232	26.8	680	N/A	N/A
Osage, OK	U.S.A.	36.95°N	96.55°W	C4 grassland	916	15.2	346	542	887
Towoomba	South Africa	24.90°S	28.35°E	C4 grassland	629	18.7	198	N/A	N/A
Vindhyan	India	24.30°N	83.00°E	C4 grassland	298	28.3	538	1237	1775
Canal Flats	Canada	50.20°N	115.50°W	Boreal forest	630	1.4	690	500	1190
Flakaliden	Sweden	64.12°N	19.45°E	Boreal forest	600	4.0	198	93	291
Jadraas	Sweden	60.82°N	16.50°E	Boreal forest	607	5.3	372	488	860
Superior Natl. For., MN	U.S.A.	48.07°N	92.04°W	Boreal forest	604	2.7	508	N/A	N/A
Atherton	Australia	17.30°S	145.60°E	Tropical forest	1200	20.0	984	N/A	N/A
Barro Colorado	Panama	9.15°N	79.85°W	Tropical forest	2600	27.4	1320	N/A	N/A
Cinnamon Bay	US Virgin Islands	18.33°N	64.80°W	Tropical forest	1130	26.6	1064	N/A	N/A
Darien	Panama	8.66°N	78.12°W	Tropical forest	2000	N/A	1137	N/A	N/A
Chamela	Mexico	19.50°N	105.05°W	Tropical forest	780	24.9	682	524	1206
Kade	Ghana	6.15°N	0.92°W	Tropical forest	1650	26.5	1990	260	2250
Khao Chong	Thailand	7.58°N	99.80°E	Tropical forest	2696	27.4	N/A	N/A	2250
Luquillo	Puerto Rico	18.32°N	65.82°W	Tropical forest	3810	23.0	1100	845	1945
Pasoh	Malaysia	2.98°N	102.31°E	Tropical forest	2054	26.5	2320	460	2780
San Carlos	Venezuela	1.93°N	67.05°W	Tropical forest	3563	27.4	1590	1117	2707
San Eusebio	Venezuela	8.62°N	71.35°W	Tropical forest	1500	12.6	1177	320	1497
La Selva	Costa Rica	10.43°N	83.98°W	Tropical forest	3962	26.3	950	900	1850
John Crow Ridge	Jamaica	18.08°N	76.65°W	Tropical forest	2230	17.6	956	N/A	N/A
Magdalena Valley	Colombia	6.39°N	73.56°W	Tropical forest	3000	27.8	1038	N/A	N/A