Ecological Applications, 11(2), 2001, pp. 371–384

NET PRIMARY PRODUCTION IN TROPICAL FORESTS: AN EVALUATION AND SYNTHESIS OF EXISTING FIELD DATA

Deborah A. Clark,[1] Sandra Brown,[2,8] David W. Kicklighter,[3] Jeffrey Q. Chambers,[4]
John R. Thomlinson,[5] Jian Ni,[6] and Elisabeth A. Holland[7]

[1]*Department of Biology, University of Missouri-St. Louis; Mailing address: INTERLINK-341,*
P.O. Box 02-5635, Miami, Florida 33102 USA
[2]*Department of Natural Resources and Environmental Sciences, University of Illinois,*
W503 Turner Hall, Urbana, Illinois 61801 USA
[3]*The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA*
[4]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara,*
735 State Street, Suite 300, Santa Barbara, California 93101-3351 USA
[5]*Institute for Tropical Ecosystem Studies, University of Puerto Rico, P.O. Box 363682,*
San Juan, Puerto Rico 00936-3682 USA
[6]*Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences,*
Xiangshan Nanxincun 20, 100093 Beijing, Peoples' Republic of China
[7]*Atmospheric Chemistry Division, National Center for Atmospheric Research, P.O. Box 3000,*
Boulder, Colorado 80307-3000 USA

Abstract. Information on net primary production in tropical forests is needed for the development of realistic global carbon budgets, for projecting how these ecosystems will be affected by climatic and atmospheric changes, and for evaluating eddy covariance measurements of tropical forest carbon flux. However, a review of the database commonly used to address these issues shows that it has serious flaws. In this paper we synthesize the data in the primary literature on NPP in old-growth tropical forests to produce a consistent data set on NPP for these forests. Studies in this biome have addressed only a few NPP components, all aboveground. Given the limited scope of the direct field measurements, we sought relationships in the existing data that allow estimation of unmeasured aspects of production from those that are more easily assessed. We found a predictive relationship between annual litterfall and aboveground biomass increment. For 39 diverse tropical forest sites, we then developed consistent, documented estimates of the upper and lower bounds around total NPP to serve as benchmarks for calibrating and validating biogeochemical models with respect to this biome. We developed these estimates based on existing field measurements, current understanding of aboveground consumption and biogenic volatile organic carbon emissions, and our judgment that belowground production is bounded by the range 0.2–1.2 × ANPP (aboveground NPP). Across this broad spectrum of tropical forests (dry to wet, lowland to montane, nutrient-rich to nutrient-poor soils), our estimates of lower and upper bounds on total NPP range from 1.7 to 11.8 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (lower bounds) and from 3.1 to 21.7 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (upper bounds). We also showed that two relationships that have been used for estimating NPP (the Bray-Gorham relationship based on leaf litterfall and the Miami model based on temperature or precipitation) are not valid for the tropical forest biome.

Key words: biomass increment; carbon budgets; forest inventory plots; litterfall; net primary production; tropical dry, moist, or montane forests.

Introduction

Tropical forests are disproportionately important in the world carbon budget, representing an estimated 59% of the global carbon pool in forests (Dixon et al. 1994). Although they are only 22% of potential vegetation by area (Melillo et al. 1993), tropical evergreen and deciduous forests have been estimated to account for 32% (Field et al. 1998) to 43% (Melillo et al. 1993) of the world's potential terrestrial net primary production (NPP). The net carbon flux between these forests and the atmosphere has been little studied and is currently controversial. Eddy covariance data (Fan et al. 1990, Grace et al. 1995*a, b*, Mahli et al. 1998, but see Keller et al. 1996) and long-term forest inventory records (Phillips et al. 1998) have suggested that mature tropical moist forests are carbon sinks. Other recent studies, however, indicate that reductions in NPP in these forests due to lowered soil moisture (Tian et al. 1998) or increased temperature (Kindermann et al. 1996; D. A. Clark, S. C. Piper, C. D. Keeling, and D. B. Clark, *unpublished manuscript*) may make them net carbon sources during some years.

Accurate characterization of NPP in this biome will

Manuscript received 24 February 1999; revised 16 March 2000; accepted 6 April 2000; final version received 1 May 2000.

[8] Present address: Winrock International, 1611 N. Kent Street, Suite 600, Arlington, Virginia 22209 USA.

be fundamental for realistic global and regional carbon budgets and for projecting how these will be affected by changing climate and atmospheric composition. Reliable field-derived NPP data from these ecosystems are needed for validating and calibrating global biogeochemical models. A recent comparison of existing models (Cramer et al. 1999, Kicklighter et al. 1999) showed that most models project the highest terrestrial NPP to occur in tropical evergreen forests. The models differ, however, in the predicted magnitude and seasonal timing of NPP within this biome, apparently due to contrasting assumptions related to forest structure (Bondeau et al. 1999, Ruimy et al. 1999) and the response of NPP to moisture, temperature, solar radiation, nutrients, and human disturbance (Churkina et al. 1999, Schloss et al. 1999). Field data on the relation of tropical forest NPP to these factors are needed to resolve these uncertainties. Such data will also be important for assessing the carbon-sequestering potential of these forests and as benchmarks for carbon offset agreements involving tropical countries. Finally, quantifying current and potential NPP will aid efforts toward sustainable management of tropical forests for timber and other products.

For this paper we evaluated in depth the current state of knowledge of NPP for old-growth tropical forests. We show that the characterization of these ecosystems in current regional and global carbon models may be considerably in error, as was recently found for estimates of NPP in the grassland biome (Scurlock and Hall 1998). For this assessment we first identified the field measurements required to produce an estimate of total forest NPP (Clark et al. 2001). Then we reviewed the primary literature on tropical forest NPP and found that: production studies in this biome have been conducted in relatively few sites; direct measurements have addressed only a few aspects of NPP, all aboveground; a number of the field methods used in past studies are problematic and/or insufficiently documented; and numerous tropical NPP estimates have involved errors due to lack of conceptual clarity regarding net production.

Based on this analysis, in this paper we synthesize the existing knowledge base with respect to NPP for the diverse forest types of the tropics: dry to wet, lowland to montane, seasonal to aseasonal, and on nutrient-rich to nutrient-poor soils. Because of the paucity of direct field measurements in old-growth tropical forests, we then seek relationships in the existing data that enable prediction of unmeasured aspects of production from those that are more easily assessed. We use these relationships to develop a consistent, documented set of current estimates of total NPP for 39 tropical forest sites. These NPP estimates should be useful as benchmarks for calibrating and validating biogeochemical models with respect to this biome. We conclude the paper with a research agenda for quantifying NPP in tropical forests.

FIELD ASSESSMENT OF FOREST NPP

Net primary production is the difference between total photosynthesis (Gross Primary Production) and total plant respiration in an ecosystem. In the field, however, NPP cannot be assessed in terms of this difference. An alternative definition of NPP is the total organic matter produced over a given interval. Although this production cannot be directly measured because of transformations such as consumption and decomposition during the measurement interval, it can be estimated based on a suite of diverse measurements and underlying assumptions. It is conceptually useful, therefore, to define the quantity NPP* as the field-measurement-based, operational estimate of actual NPP (Clark et al. 2001). NPP* comprises all materials that together represent: (1) the amount of new organic matter that is retained by live plants at the end of the interval, and (2) the amount of organic matter that was both produced and lost by the plants during the same interval. In forests, these materials are: aboveground biomass increment, fine litterfall, aboveground losses to consumers, emissions of biogenic volatile organic compounds (BVOCs), aboveground losses of leached organic compounds, net increments in biomass of coarse and fine roots, dead coarse and fine roots, root losses to consumers, root exudates, carbohydrates exported by plants to their mycorrhizal or nodule symbionts, and any net increases in stores of nonstructural carbohydrates. Clark et al. (2001) discuss each of these components of forest NPP* and the methods for their measurement in the field.

In addition to the difficulties in any forest for measuring many of these components, tropical forests present some particular challenges (also see Clark et al. 2001). Because ‘‘fine litterfall’’ in these ecosystems can include very large items, special methods are required for litter collection in order to avoid strong underestimation (cf. Villela and Proctor 1999). Precollection decomposition, leaching, and herbivory can all be intense in the tropics, particularly in the wetter forests. Estimating aboveground biomass increment is made particularly difficult by the diversity of tree species, wood densities, tree architectures, and life forms (lianas, hemiepiphytes, palms) in any tropical forest. Root production can occur year-round. Fine roots can be distributed far down the soil profile (e.g., to 18 m in a tropical moist forest, Nepstad et al. 1994) and can show great spatial variability. Given these factors (see Plate 1), and the logistical difficulties commonly encountered in the tropics, it is not surprising that tropical forest NPP remains poorly understood.

THE EXISTING DATA RELATED TO TROPICAL FOREST NPP

To synthesize research findings to date, we intensively reviewed the primary literature. We evaluated the NPP data from >70 tropical forest sites, including

PLATE 1. Several of the special challenges for estimating NPP in tropical forests are seen at this gap-edge site in an old-growth lowland rain forest in La Selva (Costa Rica). Due to protuberances on the bole at breast height, ladders are required to measure many trees. The tree at the center is being measured by two people on 3-m ladders. The diameter tape must be placed under vines, epiphytes, or arthropod structures on the bole (e.g., nests, termite trails), because fine litter can include very large items such as 2-m palm leaves. Growth forms of lianas and other non-tree woody life forms necessitate specially designed traps for estimating biomass. Only some of the copious woody litterfall (~1 m deep in this gap) should be included in NNP* components. Photograph by David B. Clark.

those cited in several past reviews (e.g., Bray and Gorham 1964, Lugo 1974, Murphy 1975, De Angelis et al. 1981, Brown and Lugo 1982, Raich et al. 1991, Vogt et al. 1996, Esser et al. 1997). We also included some data from recent, unpublished studies. In each case, we evaluated the data and methods presented in the primary sources in light of current understanding of the total set of components of forest NPP* and the appropriate methods for measuring them in the field (cf. Clark et al. 2001).

We established the following criteria for sites and studies to include in our analysis. Study sites were restricted to forest stands (no woodlands or savanna) at latitudes 23.5° N–23.5° S. We also exclusively focused on sites that could be considered old growth in structural/functional terms (sensu Clark 1996). We included sites that were described in the NPP literature with terms such as ''primary,'' or ''virgin,'' as well as sites that we were personally familiar with and judged to be at the old-growth end of the structure continuum (e.g., with a high basal area, wide range of tree diameters, large lianas, and a small-gap disturbance cycle [Clark 1996]). We eliminated forests aged ≤100 yr. We also eliminated a few specialized forest types (mangroves, and dune forest). We further restricted the sites to those for which there was an estimate of aboveground biomass and of at least one component of NPP*, measured over at least a full year, and with the biomass and NPP* components measured contemporaneously. These criteria were met for 39 sites (Tables 1 and 2).

The annotated data set from this review is available online.[9]

Aboveground biomass

In most studies, aboveground biomass was estimated by measuring the diameter of all woody stems above some minimum size (usually 3–10 cm in diameter) and calculating each stem's biomass based on allometric relations from trees harvested nearby or in previous studies elsewhere. The area of the measured study plot(s) was quite small. In 32 of the 39 studies, the total plot area assessed was ≤1 ha (median = 0.25 ha). In a few studies (9 of 39) aboveground biomass estimates for a site were based on locally harvested plots; in six of these cases the plots were extremely small (0.04–0.16 ha). Given these small areas, it is likely that the aboveground biomass estimates from many of these studies (Table 1) are overestimates due to plot biases

---

[9] URL: ⟨http://daac.ornl.gov/NPP/htmldocs/nceas des.html⟩

TABLE 1. Reported (in bold) and estimated (in parentheses) components of above- and belowground NPP* for 39 old-growth tropical forest sites with data for both aboveground biomass and at least one NPP* component.

		Components of aboveground NPP*				
Site	Aboveground biomass	Aboveground biomass increment	Fine litterfall	Losses to consumers	Volatile organic compounds	Estimated aboveground NPP
Ivory Coast: L'Anguédédou Forest	**151.5**	**3.8**	(9.3)	(1.1)	(0.2)	(14.3)
Thailand: Khaochong	**167.0**	**3.0**	(5.9)	(0.7)	(0.3)	(9.9)
Colombia: Magdalena terrace	**89.9**	(2.6)	**6.0**	(0.7)	(0.3)	(9.6)
Ivory Coast: Banco	**256.5**	(2.6)	**5.9**	(0.7)	(0.3)	(9.5)
Malaysia: Pasoh	**215.5**	**2.7**	**5.3**	(0.6)	(0.2)	(8.8)
Ivory Coast: Yapo (Plateau)	**216.5**	(2.3)	**4.8**	(0.6)	(0.2)	(7.9)
USA: Hawaii (Puu Kolekole)	**68.5**	**2.6**	**4.4**	(0.5)	(0.2)	(7.6)
Brazil: Fazenda Gaviao (BDFF)†	**151.0**	**2.5**	(4.3)	(0.5)	(0.3)	(7.6)
Colombia: Magdalena slope	**162.9**	(2.2)	**4.4**	(0.5)	(0.3)	(7.5)
Brazil: Fazenda Dimona (BDFF)†	**178.0**	**2.2**	**4.2**	(0.5)	(0.3)	(7.2)
Puerto Rico: palm floodplain forest	**114.5**	(2.2)	**4.3**	(0.5)	(0.2)	(7.2)
French Guiana: Piste de Saint-Elie	**294.8**	(2.1)	**3.8**	(0.5)	(0.3)	(6.7)
Brazil: Paragominas	**62.5**	**1.3**	**4.6**	(0.6)	(0.2)	(6.7)
Brazil: Egler Reserve	**203.0**	(2.0)	**3.7**	(0.4)	(0.2)	(6.4)
Brazil: Fazenda Cabo Frio (BDFF)†	**157.5**	**2.1**	(3.4)	(0.4)	(0.3)	(6.2)
Papua New Guinea: Mt. Kerigomma	**147.5**	(2.0)	**3.6**	(0.4)	(0.2)	(6.1)
Venezuela: San Eusebio	**174.0**	(2.0)	**3.5**	(0.4)	(0.2)	(6.1)
Jamaica-Blue Mtn. Mor Ridge	**114.5**	(1.9)	**3.3**	(0.4)	(0.2)	(5.8)
Venezuela: San Carlos (Oxisol)	**132.0**	**2.2**	**2.9**	(0.3)	(0.3)	(5.8)
Puerto Rico: Colorado Forest Perm. plots	**84.8**	(2.0)	**3.4**	(0.1)	(0.2)	(5.6)
Jamaica: Blue Mt. Gap Forest	**119.0**	(1.9)	**3.2**	(0.4)	(0.2)	(5.6)
Brazil: Fazenda Porto Alegre (BDFF)†	**200.5**	**1.9**	(3.0)	(0.4)	(0.3)	(5.6)
USA: Hawaii (Laupahoehoe)	**133.0**	**2.1**	**2.7**	(0.3)	(0.2)	(5.3)
Venezuela: San Carlos tall caatinga	**118.7**	(1.7)	**2.8**	(0.3)	(0.3)	(5.2)
USA: Hawaii (Kohala)	**72.5**	**1.4**	**3.2**	(0.4)	(0.2)	(5.1)
Jamaica: Blue Mt. Mull Ridge	**156.0**	(1.7)	**2.8**	(0.3)	(0.2)	(5.0)
Jamaica: Blue Mt. Wet Slope Forest	**115.0**	(1.7)	**2.8**	(0.3)	(0.2)	(5.0)
Puerto Rico: Guanica	**22.5**	(1.6)	**2.4**	(0.3)	(0.2)	(4.5)
USA: Hawaii (Kokee)	**103.0**	**1.9**	**2.1**	(0.2)	(0.2)	(4.4)
Mexico: Chamela lower plot	**40.0**	**1.5**	**2.1**	(0.3)	(0.2)	(4.0)
India: Bannadpare	**227.0**	(1.4)	**2.0**	(0.2)	(0.3)	(4.0)
India: Agumbe	**210.0**	(1.4)	**2.1**	(0.3)	(0.2)	(3.9)
India: Kagneri	**230.0**	(1.3)	**2.0**	(0.2)	(0.3)	(3.9)
Mexico: Chamela middle plot	**40.0**	**1.2**	**1.6**	(0.4)	(0.2)	(3.3)
India: S. Bhadra	**324.5**	(1.2)	**1.7**	(0.2)	(0.2)	(3.3)
Mexico: Chamela upper plot	**40.0**	**1.0**	**1.7**	(0.4)	(0.2)	(3.2)
Puerto Rico: Pico del Este	**23.8**	(1.1)	**1.6**	(0.1)	(0.2)	(2.9)
USA: Hawaii, Site 6 (3400 yr, 1660 m)	**40.5**	**0.5**	**1.1**	(0.1)	(0.2)	(1.8)
USA: Hawaii, Site 5 (3400 yr, 700 m)	**61.5**	**0.3**	**0.9**	(0.1)	(0.2)	(1.4)

Notes: See *Estimating missing NPP* components for tropical forests.* All units are megagrams of carbon per hectare per year except for aboveground biomass (Mg C/ha) in the first column (conversions from biomass data were based on the assumption that dry biomass is 50% carbon). Sites are ranked from high to low with respect to total estimated NPP. Site data and sources are given in Table 2.

† BDFF = Biological Dynamics of Forest Fragments Project.

and the influence of large trees (cf. Brown and Lugo 1992, Brown et al. 1995).

Aboveground biomass increment

This NPP* component was assessed at 33 of the 39 sites in a variety of ways, many of which we considered unacceptable for this analysis because of evident methodological problems (see Clark et al. 2001) or lack of methods documentation. We found 17 studies where aboveground increment was based on measurement of all trees in a plot at two censuses, with biomass estimated from empirical allometric relationships, and where the biomass increment appeared to have been ''accounted'' correctly (cf. Clark et al. 2001). The range of these values was 0.3 (a Hawaiian forest on 3400-yr-old lava at 700 m elevation [Raich et al. 1997]) to 3.8 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (a lowland moist forest in Ivory Coast [Müller and Nielsen 1965]).

The total plot area measured in most of these studies, however, was on the order of those used in the aboveground biomass studies. When based on such small plots, biomass increment data are likely to be unrepresentative due to the same problems of plot bias and the influence of big trees that affect tropical forest bio-

TABLE 1. Extended.

Estimated belowground NPP		Estimated total NPP	
Low (0.2 × ANPP)	High (1.2 × ANPP)	Low	High
(2.9)	(17.2)	(17.2)	(31.5)
(2.0)	(11.8)	(11.8)	(21.7)
(1.9)	(11.5)	(11.5)	(21.2)
(1.9)	(11.4)	(11.4)	(20.9)
(1.8)	(10.6)	(10.6)	(19.4)
(1.6)	(9.5)	(9.5)	(17.4)
(1.5)	(9.2)	(9.2)	(16.8)
(1.5)	(9.2)	(9.2)	(16.8)
(1.5)	(9.0)	(9.0)	(16.5)
(1.4)	(8.7)	(8.7)	(15.9)
(1.4)	(8.6)	(8.6)	(15.8)
(1.3)	(8.0)	(8.0)	(14.7)
(1.3)	(8.0)	(8.0)	(14.7)
(1.3)	(7.7)	(7.7)	(14.1)
(1.2)	(7.4)	(7.4)	(13.6)
(1.2)	(7.4)	(7.4)	(13.5)
(1.2)	(7.3)	(7.3)	(13.3)
(1.2)	(6.9)	(6.9)	(12.7)
(1.2)	(6.9)	(6.9)	(12.7)
(1.1)	(6.7)	(6.7)	(12.4)
(1.1)	(6.7)	(6.7)	(12.4)
(1.1)	(6.7)	(6.7)	(12.2)
(1.1)	(6.4)	(6.4)	(11.7)
(1.0)	(6.3)	(6.3)	(11.5)
(1.0)	(6.1)	(6.1)	(11.2)
(1.0)	(6.0)	(6.0)	(11.0)
(1.0)	(6.0)	(6.0)	(11.0)
(0.9)	(5.3)	(5.3)	(9.8)
(0.9)	(5.3)	(5.3)	(9.7)
(0.8)	(4.8)	(4.8)	(8.8)
(0.8)	(4.8)	(4.8)	(8.7)
(0.8)	(4.7)	(4.7)	(8.6)
(0.8)	(4.7)	(4.7)	(8.6)
(0.7)	(4.0)	(4.0)	(7.3)
(0.7)	(3.9)	(3.9)	(7.2)
(0.6)	(3.9)	(3.9)	(7.1)
(0.6)	(3.5)	(3.5)	(6.3)
(0.4)	(2.2)	(2.2)	(4.0)
(0.3)	(1.7)	(1.7)	(3.1)

mass studies (see Clark et al. 2001). It is probable that this bias is usually toward higher biomass increment due to an overrepresentation of big trees.

Fine litterfall

By far the most frequently measured NPP* component in tropical forests has been fine litterfall. As found by Proctor (1983, 1984), however, incomplete documentation and variation in the types of material collected make data interpretation problematic. In 21% of the 34 studies in our sample with litterfall data, the investigators do not state what was collected as ''litterfall.'' When the woody component was defined (15 studies), five different criteria had been used: pieces $\leq$10, $\leq$3.5, $\leq$1, and $\leq$0.5 cm in diameter, and all-sized wood. These intersite methods differences are likely to have affected the relative values for litterfall.

Another issue is the high spatial variance in litterfall in any tropical forest. For example, in a lowland Costa Rican forest, variance analysis of the data from two sets of 10 0.25-m^2 littertraps indicated that nearly 50 traps would be needed per 0.5-ha plot to measure litterfall within ± 20% (D. A. Clark, *unpublished data*). We found only three studies that reported confidence limits around the litterfall data. It is to be expected, however, that most published litterfall numbers for tropical forests are highly uncertain because of low numbers of traps.

For this compilation, we selected the litterfall data that were based on collections from at least six littertraps sampled at least monthly through a full year. In the case of the one study where wood was quantified by size class, we excluded the mass of pieces $\geq$1 cm in diameter from the reported litterfall value. In 12 studies, mass was given for woody litterfall with no size specified (''branches,'' ''wood,'' or ''woody material''), and in three studies only a broader size class was reported ($\leq$3.5 and 10 cm diameter); for these 15 cases the woody component averaged 19% of the reported litterfall (range: 4–33%). From a broad survey of litterfall data (W. Post, E. Matthews, E. Holland, and J. Sultzman, *unpublished data*) the mean value for the ''small wood'' component when it was specified separately ($N = 63$) was 21% of the mean of fine litterfall values from 126 tropical forest studies. Based on this comparison, we tentatively conclude that most of the woody material was appropriate in the 15 studies, and we therefore used the reported values for total litterfall. In most studies, however, no breakdown was given of litterfall components and we could not judge the quality of the data. The patterns we find in these data should be interpreted in this light.

The range of values for measured annual litterfall from these old-growth tropical forests was 0.9–6.0 Mg $\text{C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. The data are from sites that cover a broad range of rainfall, temperature, and elevation (Fig. 1). Given the edaphic variation among these forests (highly infertile spodosols to relatively fertile andosols) and the varied litterfall definitions, it is not surprising that litterfall values show a broad spread at any point along these environmental axes. Nevertheless, these data suggest that, for a wide spectrum of tropical forests, fine litterfall peaks at intermediate levels of precipitation and does not change systematically with temperature or elevation.

Two important caveats, however, affect interpretation of these patterns. One is that these data are uncorrected for precollection decomposition and thus may be underestimates, particularly for the litterfall measured in lowland wet forests (see Clark et al. 2001). A second caveat is that none of these studies reported using special collection methods for the large items, such as large palm leaves. Villela and Proctor (1999) showed for forests in Amazonian Brazil that fine litterfall can be underestimated by $>$2 Mg $\text{C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$

TABLE 2. Site data and references for the sites in Table 1.

Site	References	Latitude	Longitude	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Brazil: Egler Reserve	Klinge and Rodrigues (1968*a,b*, 1973), Klinge (1973, 1976, 1978), Klinge et al. (1975)	···	···	···	27.2	1171
Brazil: Fazenda Cabo Frio (BDFF)	Chambers (1998)	2.50° S	60° W	···	26.7	2300
Brazil: Fazenda Dimona (BDFF)	Sizer (1992), Chambers (1998)	2.50° S	60° W	···	26.7	2300
Brazil: Fazenda Gaviao (BDFF)	Chambers (1998)	2.50° S	60° W	···	26.7	2300
Brazil: Fazenda Porto Alegre (BDFF)	Chambers (1998)	2.50° S	60° W	···	26.7	2300
Brazil: Paragominas	Trumbore et al. (1995), J. Chambers and D. Nepstad (*personal communication*)	2.98° S	47.52° W	···	···	1750
Colombia: Magdalena terrace	Folster and de las Salas (1976), Folster et al. (1976)	6.50° N	73.8° W	···	27.5	3150
Colombia: Magdalena slope	Folster and de las Salas (1976), Folster et al. (1976)	6.50° N	73.8° W	···	27.5	3150
French Guiana: Piste de Saint-Elie	Lescure et al. (1983), Puig and DeLobelle (1988)	5.25° N	55.75° W	···	26.0	3450
India: Agumbe	Rai and Proctor (1986*a,b*)	13.50° N	75.10° E	575	22.2	7670
India: Bannadpare	Rai and Proctor (1986*a,b*)	12.08° N	75.70° E	200	27.0	5310
India: Kagneri	Rai and Proctor (1986*a,b*)	12.82° N	75.60° E	500	28.6	6100
India: S. Bhadra	Rai and Proctor (1986*a,b*)	13.25° N	75.25° E	800	···	6520
Ivory Coast: L'Anguédédou Forest	Muller and Nielsen (1965)	5.33° N	4.17° W	50	26.9	1900
Ivory Coast: Yapo (Plateau)	Bernhard (1970), Bernhard-Reversat et al. (1972, 1978), Huttel (1975)	5.70° N	4.10° W	70	···	1739
Ivory Coast: Banco	Bernhard (1970), Bernhard-Reversat et al. (1972, 1978), Huttel (1975)	5.38° N	4.03° W	100	26.2	2095
Jamaica: Blue Mt., Mor Ridge	Tanner (1977, 1980*a,b*, 1985)	18° N	77° W	1615	15.8	2230
Jamaica: Blue Mt., Mull Ridge	Tanner (1977, 1980*a,b*, 1985)	18° N	77° W	1600	15.5	2230
Jamaica: Blue Mt., Gap Forest	Tanner (1977, 1980*a,b*, 1985)	18° N	77° W	1590	15.5	2230
Jamaica: Blue Mt., Wet Slope Forest	Tanner (1977, 1980*a,b*, 1985)	18° N	77° W	1570	15.3	2230
Malaysia: Pasoh	Kira (1978)	~2.98° N	~102.3° E	···	25.0	1807
Mexico: Chamela, lower plot	Martinez-Yrizar et al. (1992), Martinez-Yrizar et al. (1996)	19.50° N	105.05° W	70–150	24.9	707
Mexico: Chamela, middle plot	Martinez-Yrizar et al. (1992), Martinez-Yrizar et al. (1996)	19.50° N	105.05° W	70–150	24.9	707
Mexico: Chamela, upper plot	Martinez-Yrizar et al. (1992), Martinez-Yrizar et al. (1996)	19.50° N	105.05° W	70–150	24.9	707
Papua New Guinea: Mt. Keri-gomma	Edwards (1977), Edwards and Grubb (1977)	6.00° S	145.18° E	2400–2500	13.0	3985
Puerto Rico: Colorado Forest, permanent plots	Weaver and Murphy (1990)	···	···	725	···	3725
Puerto Rico: Guanica	Lugo and Murphy (1986), Murphy and Lugo (1986)	18.00° N	66.92° W	175	25.1	860
Puerto Rico: palm forest	Frangi and Lugo (1985)	18.42° N	66° W	750	19.7	3725
Puerto Rico: Pico del Este	Weaver et al. (1986)	···	···	1000	~19	~5000
Thailand: Khaochong	Kira et al. (1967)	7.58° N	~100° E	···	27.2	2696
USA: Hawaii (Kohala)	Crews et al. (1995), D. A. Herbert and J. H. Fownes (*personal communication*)	20.05° N	155.9° W	1122	16.0	2500
USA: Hawaii (Kokee)	Crews et al. (1995), D. A. Herbert and J. H. Fownes (*personal communication*)	22.05° N	159.5° W	1134	16.0	2500
USA: Hawaii (Laupahoehoe)	Crews et al. (1995), D. A. Herbert and J. H. Fownes (*personal communication*)	19.95° N	155.3° W	1170	16.0	2500

TABLE 2. Continued.

Site	References	Latitude	Longitude	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)
USA: Hawaii (Puu Kolekole)	Crews et al. (1995), D. A. Herbert and J. H. Fownes (*personal communication*)	21.15° N	156.8° W	1210	16.0	2500
USA: Hawaii, Site 5 (3400 yr, 700 m)	Raich et al. (1997)	19.75° N	155.25° W	700	19.3	5800
USA: Hawaii, Site 6 (3400 yr, 1660 m)	Raich et al. (1997)	19.75° N	155.25° W	1660	13.0	2600
Venezuela: San Carlos, Site 4	Jordan and Escalante (1980), Uhl and Jordan (1984), Jordan (1989)	1.90° N	67.05° W	119	26.0	3550
Venezuela: San Carlos, tall caatinga	Herrera and Jordan (1981), Klinge and Herrera (1983)	1.93° N	67.05° W	100	26.2	3500
Venezuela: San Eusebio	Fassbender and Grimm (1981), Grimm and Fassbender (1981)	8.62° N	71.35° E	2000–2500	12.6–15	1500

when only the small standard litterfall traps are used. The variation of ''true litterfall'' across the environmental gradients of tropical forests may thus differ considerably, both in absolute and relative terms, from that seen in Fig. 1.

*Other components of NPP**

From our sample of 39 tropical forest sites, there were almost no data on the other aboveground NPP* components. Leaf herbivory was quantified at five sites. No measurements of BVOCs, organic leachates, or losses to other aboveground consumers (seed/fruit predators, sap-suckers/nectar-feeders) were reported.

None of the 39 studies had adequate data for belowground NPP* components. Coarse root increment and mortality were not estimated by direct measurements anywhere, and coarse root biomass was measured at a very few sites and only by excavating a few trees or digging a few monoliths. Fine roots were measured in a few sites, but with inadequate methods for estimating either net increment or losses (cf. Santantonio and Grace 1987, Fahey et al. 1999, Clark et al. 2001).

For seven tropical forests we found concurrent data for soil respiration and litterfall. These can be used to calculate total belowground carbon allocation, the sum of root respiration and belowground NPP (BNPP), using the C Balance Method of Raich and Nadelhoffer (1989). The resulting estimates (in megagrams per hectare per year) are: 5.7, 6.3, 8.7, 6.8 (four Hawaiian *Meterosideros* forests at 1134–1210 m elevation [D. A. Herbert and J. H. Fownes, *personal communication*]); 8.8, 9.1 (data given in Raich and Nadelhoffer [1989] for Brazilian terra firme forest [Egler Reserve], and Malaysian dipterocarp forest [Pasoh], respectively), and 17.0 Mg C·ha^{-1}·yr^{-1} (Brazilian terra firme forest [Paragominas] [Trumbore et al. 1995]). As discussed by Clark et al. (2001), a number of unmeasured processes (changes in soil organic carbon [SOC] pools, leaching of carbon out of the soil profile, other significant aboveground C inputs besides fine litterfall, or net biomass changes in either fine or coarse roots), could cause the C balance calculation to under- or overestimate true belowground allocation. For example, tropical forests may be responding to global warming with net losses from SOC pools (cf. Trumbore et al. 1996). Secondly, without independent on-site measurements of root respiration, belowground NPP cannot be estimated with the C balance method, because this method produces a joint estimate of root respiration plus BNPP. We found no studies in tropical forest where respiration of fine and coarse roots was quantified on a stand-level basis (cf. methods used in a pine plantation by Ryan et al. [1996]).

Relative contributions of NPP components*

In Table 3 we summarize these data on NPP* in old-growth tropical forests. Among aboveground components of NPP*, fine litterfall clearly dominates, even though these values may be substantial underestimates (see *Aboveground biomass increment* and *Fine litterfall*). Aboveground biomass increment is also important but is usually much smaller; for the 13 sites where both variables were measured, aboveground biomass increment averaged only 58% the value of litterfall (range 28–94%). For belowground components, the only available estimates are for total belowground C allocation, based on the C balance method. These estimates, which are confounded by including root respiration, by the steady-state assumptions for SOC and roots, and by the unknown effects of other unmeasured processes, nevertheless suggest that some BNPP components in tropical forest are sizable and must be evaluated.

ESTIMATING MISSING NPP* COMPONENTS FOR TROPICAL FORESTS

Given the limited data available on NPP* components for this biome, we examined our quality-con-

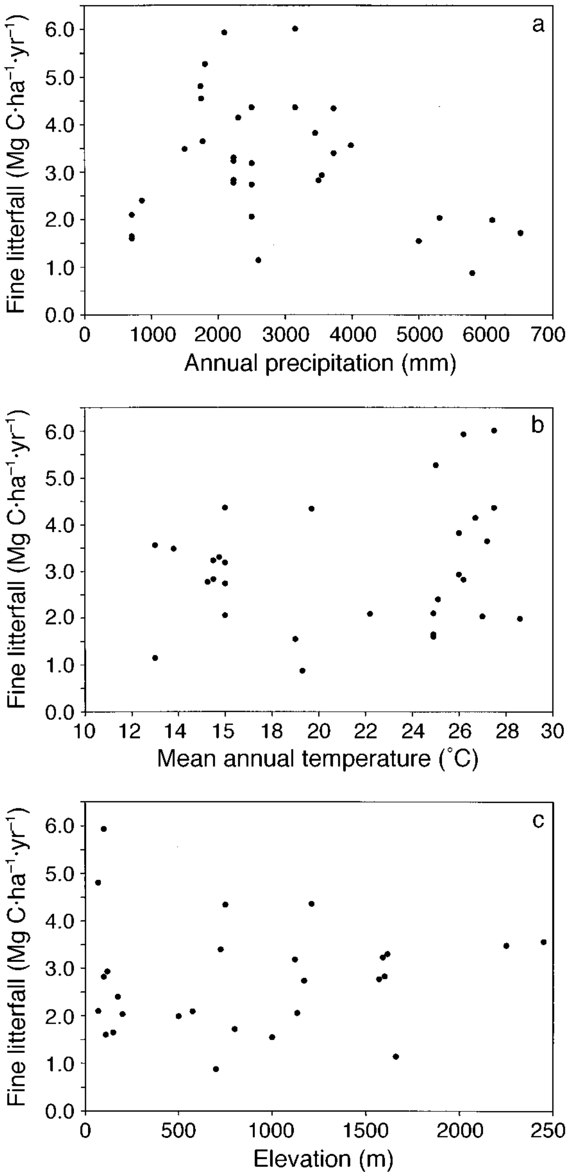

FIG. 1. The relation between annual litterfall in tropical forests and (a) annual precipitation, (b) annual mean temperature, and (c) elevation.

trolled database for relationships that could be used to estimate an unmeasured component from a measured one. We found two such relationships.

Using the 13 mature forest sites with acceptable data for both litterfall and aboveground biomass increment, we found a significant logarithmic relationship between these two components of NPP* (Fig. 2). This relationship provides a way to estimate aboveground biomass increment, a much more challenging quantity to measure than litterfall. The relatively high r^2 of this relationship (0.69) also increases confidence in the allometric methods used for estimating the 13 sites' aboveground biomass increment and indicates consistency in the litterfall data.

A second significant relationship is between aboveground biomass increment and aboveground biomass (Fig. 3). As perhaps might have been expected, the data suggest the existence of an asymptote for aboveground biomass increment at higher biomass (i.e., in those forest types where old-growth stands have high biomass). The data also suggest that, in old-growth tropical forests, aboveground biomass increment is ~1–2% of aboveground biomass. We did not, however, find reliable biomass increment data for sites with biomass >215 Mg/ha. Thus, it remains unknown how aboveground biomass increment behaves at the high end of tropical forest biomass (Table 1).

ESTIMATED TROPICAL FOREST NPP

Previous approaches

Prior estimates of total NPP for tropical forests have been based on direct measurement of only one or a very few NPP* components (Appendix). One frequently applied method (e.g., studies cited in Murphy 1975) has been to estimate annual aboveground NPP as three times annual leaf litterfall and total NPP as 3.3 times annual leaf litterfall. These relationships are based on the tropical forest data in Bray and Gorham's (1964) review of the relationship of leaf litterfall to estimated NPP. In fact, the tropical studies in that review were for only two sites (Bartholomew et al. 1953, Nye 1961), both were secondary forest, and in neither were any belowground components of NPP* measured. (BNPP was estimated as 0.2 ANPP.) For the 13 sites in our database with measurements of both aboveground biomass increment and litterfall, we have estimated ANPP (Table 1) as the sum [aboveground biomass increment + litterfall + estimated losses to consumers + estimated BVOC emissions] (see *Updated estimates of tropical forest NPP*). When we used the Bray and Gorham formula to estimate ANPP as 3 × leaf litterfall (which we estimated as 0.75 × total litterfall), the "Bray and Gorham" ANPP estimate was higher than our estimate in all 13 cases (mean = 26% higher; 31–55% higher for six sites), even though our ANPP estimate was based on additional NPP* components. Given the scanty basis for the Bray and Gorham index, this approach should not be used for tropical forests.

Other studies (e.g., Raich et al. 1991) have estimated total NPP for tropical forests by assuming that coarse root increment is proportional to aboveground increment and that fine root production is equal to fine litterfall. The existing data on biomass and production of both coarse and fine roots are few and flawed for tropical forests, as discussed earlier. Recent reviews of root biomass (Cairns et al. 1997, Jackson et al. 1997) have reported root-to-shoot ratios in mature tropical forests that range from 0.14 to 0.34, with coarse roots making up 30–97% of the total estimated root biomass. Further, several components of belowground NPP* (coarse root mortality, root losses to consumers, root exudates, car-

TABLE 3. Estimated ranges (likely upper and lower bounds) of the components of NPP* for old-growth tropical forests, and the basis for these estimates.

NPP* component	Estimated range (Mg C·ha^{-1}·yr^{-1})	Basis
Fine litterfall (aboveground)	0.9–6.0	Measured values, Table 1 (likely to be underestimates; not corrected for precollection decomposition)
Aboveground losses to consumers	0.1–0.7	Leaf herbivory estimated as [0.136 × (0.75 × Litterfall)]; then increased by 20% to account for precollection seed and fruit consumption and feeding by sapsucking insects and nectar-feeders
Tree biomass increment	0.3–3.8	Measured values, Table 1
Other aboveground biomass increment (understory, vines, palms)	0.03–0.4	Estimated as 10% of the tree biomass increment, based on relative biomass of these groups
Biogenic volatile organic compounds (isoprenoids, terpenes, etc.)†	0.15–0.31 (0.93)	Isoprenes + monoterpenes + other reactive VOCs; model estimates, with high uncertainty
Aboveground organic leachates	???	(No usable data)
Coarse root increment	???	(No usable data)
Fine root increment	???	(No usable data)
Fine root mortality	??? [⋘5.7–17.0]‡	(No usable direct measurements)
Root losses to belowground consumers	??? [⋘5.7–17.0]‡	(No usable direct measurements)
Root exudates, + CHO export to symbionts (mycorrhizae, nodules)	??? [⋘5.7–17.0]‡	(No usable direct measurements)

† The range of estimates of Guenther et al. (1995) for total BVOCs in different tropical forest types (in parentheses, 3 × the high value is the [minimum] uncertainty they cite for these estimates).

‡ The range of available tropical forest values for Raich and Nadelhoffer's (1989) ''Total Belowground Allocation,'' which also includes root respiration.

bohydrates exported to root symbionts) have never been measured in any tropical forest. It is thus not yet possible to validate estimates of belowground production based on aboveground measurements in these systems.

Updated estimates of tropical forest NPP

In spite of the limitations in the underlying database, there are pressing needs for estimates of total NPP for tropical forests. We developed such estimates for 39 tropical forests (Table 1), based on the most reliable NPP* measurements we found in the literature. These forests cover a broad range of elevation, temperature, and precipitation (Table 2).

We estimated unmeasured components of ANPP* for these sites (indicated in Table 1) by the following rules. When data existed either for litterfall or for aboveground biomass increment, we used the relationship shown in Fig. 2 (or its converse) to estimate the missing parameter. For five sites, leaf production losses to herbivory had been estimated on site (0.1–0.4 Mg C·ha^{-1}·yr^{-1}) based on tracking area loss from marked leaves; for the remaining sites, we estimated these losses as [0.10 × litterfall], on the assumption that litterfall averages ~75% leaves, and that there is

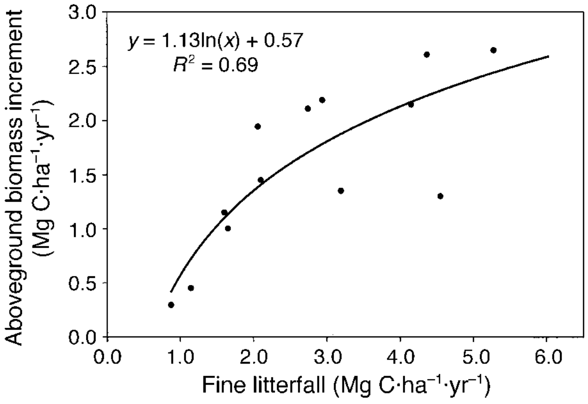

FIG. 2. The relation between measured annual litterfall and annual aboveground biomass increment for 13 tropical forest sites.

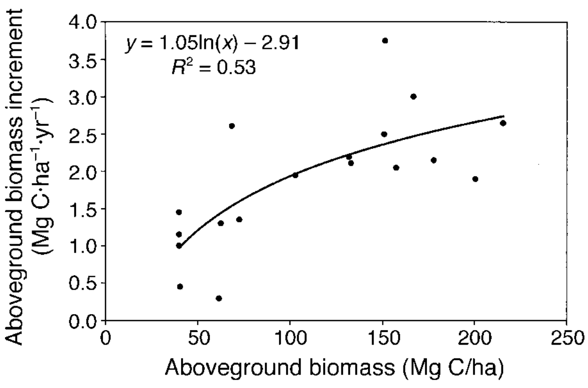

FIG. 3. The relation between annual aboveground biomass increment and aboveground biomass for 18 tropical forest sites.

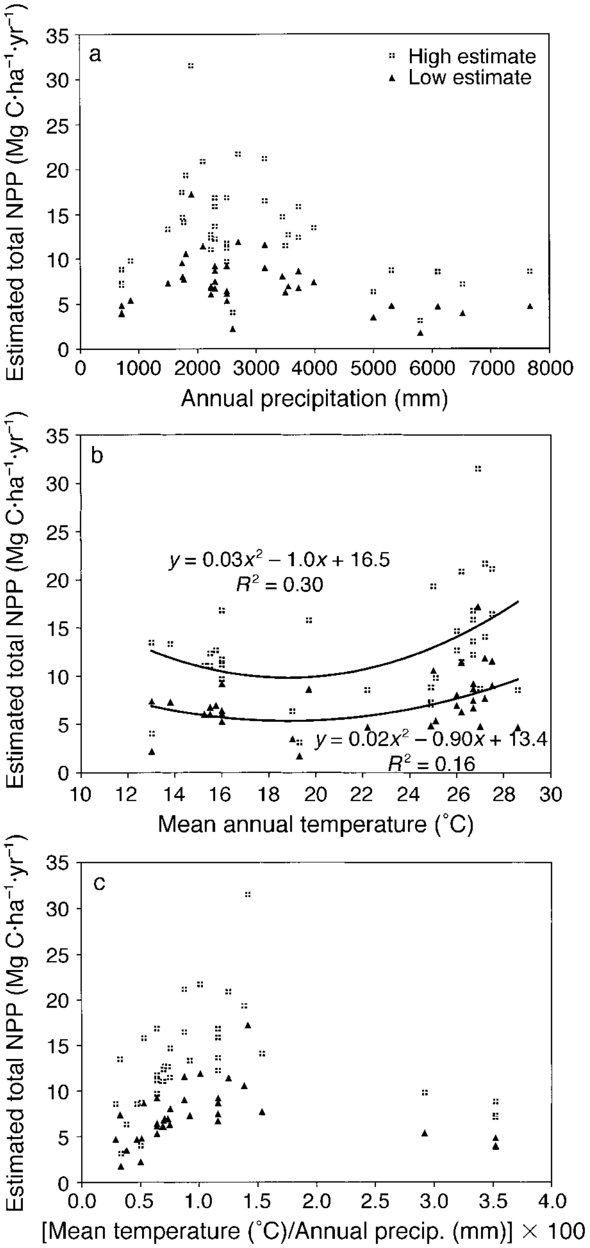

FIG. 4. The relationships between our low and high estimates of NPP for the 39 study sites and (a) annual precipitation (*P*), (b) mean annual temperature (*T*), and (c) the ratio *T*/*P* × 100.

a 12% herbivory loss from this material. We then estimated total losses to aboveground consumers as 1.2 × leaf herbivory, to account for the additional losses through fruit and seed consumption, phloem-feeding by sap-sucking insects, and nectar-feeding by vertebrates and insects. We based our estimates of BVOC emissions on the estimates of Guenther et al. (1995: 0.31, 0.15, and 0.21 Mg C·ha^{-1}·yr^{-1} for tropical rain forests, tropical montane forests, and tropical seasonal forests, respectively); we classified our sites as follows: ‘‘tropical montane forests,’’ elevation >500 m; ‘‘tropical rain forests,’’ elevation ≤500 m, annual rainfall >2000 mm; ‘‘tropical seasonal forests,’’ elevation ≤500 m, annual rainfall ≤2000 mm.

Given that direct measures of belowground NPP* components are lacking for tropical forests, we judged there was no direct empirical basis for setting bounds on BNPP. We therefore estimated a ‘‘confidence interval’’ of possible values. Our lower limit estimate for BNPP is calculated as [0.2 × estimated ANPP], based on our judgment that it is unlikely that the several components of belowground production (see *Estimated tropical forest NPP: Previous approaches*) sum to < 20% of ANPP. We set our upper bound for BNPP to [1.2 × estimated ANPP]. Total NPP has frequently been estimated by assuming that BNPP equals ANPP (e.g., Esser et al. 1997); we therefore used a somewhat higher ceiling. We then combined these BNPP estimates with our estimate of ANPP to generate upper and lower bounds for total NPP for these sites.

The diverse forests in the data set show a very wide range of estimated NPP. The ‘‘High’’ estimates range between 3.1 and 31.5 Mg C·ha^{-1}·yr^{-1} (Table 1). The site with the highest estimated NPP (L’Anguédédou Forest, Ivory Coast), however, is a clear outlier; its estimated total NPP is 45% higher than the next highest value in our dataset. This site lacked a direct measurement for litterfall. Because the aboveground increment data underlying our predictive relationship (0.3–2.7 Mg C·ha^{-1}·yr $^{-1}$; Fig. 2) fell far short of this site’s record value (3.8 Mg C·ha^{-1}·yr $^{-1}$), the very high extrapolated litterfall value for this site (9.3 Mg C·ha^{-1}·yr^{-1}) is suspect, as are the resulting estimates for total NPP. With this site excluded, our range of upper bounds for NPP is 3.1–21.7 Mg C·ha^{-1}·yr^{-1}. The lower bound estimates (with the outlier site excluded) similarly indicate a broad range of total NPP across these diverse types of tropical old-growth forest: 1.7–11.8 Mg C·ha^{-1}·yr^{-1}.

Relationships between estimated NPP and precipitation (Fig. 4a) and temperature (Fig. 4b) are similar to those found for litterfall by itself (Fig. 1a, b). This is not surprising, given that many of the NPP* components were estimated from litterfall. Similarly, the relationship between our NPP estimates for these forests and the index [*T*/*P* × 100], an indicator of potential water availability (Fig. 4c), resembles that found for tropical litterfall values and [*T*/*P* × 100] by Brown and Lugo in their 1982 review of tropical forest production data. A caution for interpreting Fig. 4, however, is that our estimated upper and lower bounds for total NPP are based on arbitrary relationships (BNPP = 0.2 ANPP and 1.2 ANPP, respectively) that are held constant over the broad environmental gradients spanned by these tropical forests. If the relation between ANPP and BNPP changes along these gradients, the resulting relationships between NPP and environmental factors could differ substantially from those depicted in Fig. 4.

In spite of these uncertainties, these NPP data and estimates suggest that the frequently used Miami model (cf. Dai and Fung 1993), which predicts NPP as a simple increasing function of temperature or precipitation, is inappropriate for the tropical forest biome. Secondly, these analyses highlight the pitfalls inherent in lumping tropical forests into one or very few categories and assigning them the same value for NPP when carrying out global simulations.

A crude independent check can be made of our upper bounds for tropical forest NPP using a simple model (Landsberg et al. 1996) based on forest radiation utilization efficiency (ϵ), the ratio of grams of dry mass of production to absorbed photosynthetically active radiation (APAR, in megajoules). Although empirical estimates of this ratio are few for forests, the values summarized in Landsberg et al.'s 1996 review are in the range 1–2 g/MJ, with mature stands closer to the lower bound (a much lower value was estimated for one Amazonian forest [Saldarriaga and Luxmoore 1991], but this estimate was based on NPP* measurements that did not account for most belowground and multiple aboveground components). As a first approximation, we estimate ϵ for old-growth tropical forests to be 1.2 g/MJ. Saldarriaga and Luxmoore (1991) calculated mean APAR in the older stands in an upper Amazonian site to average 2.73 $\mathrm{GJ \cdot m^{-2} \cdot yr^{-1}}$ over a 15-yr period. If we take this as an approximation of APAR in tropical evergreen forest, we can use it in the radiation utilization efficiency model to estimate a rough upper bound for NPP for tropical forests overall. This estimated upper bound is 16.4 $\mathrm{Mg\ C \cdot ha^{-1} \cdot yr^{-1}}$ (based on the assumption that dry biomass is 50% carbon). After exclusion of the one outlier site, our highest ''high'' estimate for total NPP (Table 1) is 21.7 $\mathrm{Mg\ C \cdot ha^{-1} \cdot yr^{-1}}$. This rough check, although admittedly based on very limited data, suggests that our ''high'' NPP estimates are unreasonable for some sites, but quite plausible for other sites in this biome.

Conclusions and Recommendations

The available data on net primary production in tropical forests are extremely limited, and even our best estimates for this biome can only be thought of as rough approximations within wide bounds. Nevertheless, this study has provided a basis for evaluating the quality and utility of the NPP* data and primary production estimates that have been reported in the literature for tropical forests. It also has underlined the strong variation in NPP to be expected across the diverse forest types that occur in the tropics—from rain forests to highly seasonal dry forests, and from the hot lowlands to the much cooler montane areas. Although in a sense our analysis is very discouraging for those seeking validation tools for global and regional modeling, it is important to recognize the limitations of the current data and the areas that urgently need better research.

The most important knowledge gap concerns the belowground components of NPP* in these ecosystems. It is also clear that many of the previous NPP studies in this biome have involved methodological problems and poor documentation. It is critical that future studies be designed and reported so as to avoid these pitfalls. A third issue that needs to be addressed is that of sampling bias and the lack of replication in either time or space. Given the small and generally subjectively located plots that are the basis for most of the existing data, the existing understanding of NPP processes in tropical forests may be highly skewed toward the highest biomass patches (flat sites with large trees, no gaps) and thus unrepresentative of larger tropical forest landscapes.

There is a great need for well-designed field studies of NPP in sites spanning the broad climatic and edaphic gradients covered by tropical forests. Of particular importance at this stage will be more studies of old-growth stands of these diverse forest types. While successional and human-impacted tropical forests are clearly ecologically and economically important, NPP processes in them are highly variable due to successional processes and the varied degrees and qualities of human impacts on them. It thus seems more productive to first concentrate on broadening our base of understanding of the more predictable processes in old-growth stands, which are the basis of many global modeling efforts and which also will be the more interpretable guides to how tropical forest ecosystems are responding to global climatic and atmospheric change.

Before confidence can be placed in scaled-up estimates of NPP for the tropical sector of the world's terrestrial ecosystems, improved data on NPP are needed from all tropical forest types. Estimating tropical forest NPP with ground-based techniques, as laid out in this paper, has by no means been made obsolete by the new eddy covariance methods for assessing whole-forest carbon exchange with the atmosphere (e.g., Grace et al. 1995*a, b*). Rather, the validation of these new methods will partially depend on obtaining independent field data on the components of NPP* (see discussion in Clark et al., 2001). Resolving whether or not tropical forests are currently carbon sinks or sources, where within these systems current carbon accumulation or loss is actually taking place, and how these processes relate to changing climate and atmospheric composition, will all require high-quality ground-based measurements. Given the urgent needs for such information, a major expansion of research into NPP processes in the world's tropical forests should be mounted as soon as possible.

Acknowledgments

This work resulted from a workshop conducted at the National Center for Ecological Analysis and Synthesis, a Center funded by the U.S. National Science Foundation (Grant No. DEB-9421535), the University of California at Santa Barbara, and the State of California. We thank D. B. Clark for extensive critical input during the writing of this paper, M. Lerdau, P.

Matson, and K. Nadelhoffer for commenting on the manuscript, and J. H. Fownes, D. A. Herbert, and D. Nepstad for unpublished data. During preparation of this paper, D. A. Clark was supported by grants from the Department of Energy (Grant No. DE-FG02-96ER62289), the National Science Foundation (Grant No. DEB-9629245), and the Andrew W. Mellon Foundation.

LITERATURE CITED

Bartholomew, W. V., J. Meyer, and H. Laudelot. 1953. Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. Publications de l'Institut National pour l'Etude Agronomique du Congo Belge, Serie Scientifique **57**.

Bernhard, F. 1970. Etude de la litiere et de sa contribution au cycle des elements mineraux en forets ombrophile de Cote d'Ivoire. Oecologia Plantarum **5**:247–266.

Bernhard-Reversat, F., C. Huttel, and G. Lemée. 1978. Structure and functioning of evergreen rain forest ecosystems of the Ivory Coast. Pages 557–574 *in* Tropical forest ecosystems: a state-of-the-knowledge report. UNESCO, Paris, France.

Bernhard-Reversat, F., L. Huttel, and G. Lemée. 1972. Some aspects of the seasonal ecologic periodicity and plant activity in an evergreen rain forest of the Ivory Coast. Pages 217–234 *in* P. M. Golley and F. B. Golley, editors. Papers from a symposium on tropical ecology with an emphasis on organic productivity. University of Georgia, Athens, Georgia, USA.

Bondeau, A., D. W. Kicklighter, J. Kaduk, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. Global Change Biology **5**:35–45.

Bray, J. R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research **2**:101–157.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. Forest Ecology and Management **75**: 175–189.

Brown, S., and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica **14**:161–187.

Brown, S., and A. E. Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia **17**:8–18.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia **111**:1–11.

Chambers, J. Q. 1998. The role of large wood in the carbon cycle of central Amazon rain forest. Dissertation. University of California, Santa Barbara, California, USA.

Churkina, G., S. W. Running, A. L. Schloss, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. Global Change Biology **5**:46–55.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, S. T. Gower, J. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: a synthesis of current concepts and field methods. Ecological Applications **11**: 0000–0000.

Clark, D. B. 1996. Abolishing virginity. Journal of Tropical Ecology **12**:735–739.

Cramer, W., D. W. Kicklighter, A. Bondeau, B. Moore III, G. Churkina, B. Nemry, A. Ruimy, A. L. Schloss, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. Global Change Biology **5**:1–15.

Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Mueller-Dombois, and P. M. Vitousek. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology **76**:1407–1424.

Dai, A., and I. Y. Fung. 1993. Can climate variability contribute to the ''missing'' CO_2 sink? Global Biogeochemical Cycles **7**:599–609.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science **263**:185–190.

Edwards, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. II. Production and disappearance of litter. Journal of Ecology **65**:971–992.

Edwards, P. J., and P. J. Grubb. 1977. Studies of mineral cycling in a montane rain forest in New Guinea: 1. The distribution of organic matter in the vegetation and soil. Journal of Ecology **5**:943–969.

Esser, G., H. F. H. Lieth, J. M. O. Scurlock, and R. J. Olson. 1997. Worldwide estimates and bibliography of net primary productivity derived from pre-1982 publications. ORNL/TM-13485. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Fahey, T. J., C. S. Bledsoe, F. P. Day, R. W. Ruess, and A. J. M. Smucker. 1999. Fine root production and demography. Pages 437–455 *in* G. P. Robertson, C. S. Bledsoe, D. C. Coleman, and P. Sollins, editors. Soils methods for long-term ecological research. Oxford University Press, New York, New York, USA.

Fan, S.-M., S. C. Wofsy, P. S. Bakwin, and D. J. Jacob. 1990. Atmosphere–biosphere exchange of CO_2 and O3 in the Central Amazon forest. Journal of Geophysical Research **95**:16851–16864.

Fassbender, H. W., and U Grimm. 1981. Ciclos bioquimicas en un ecosystema forestal de los Andes Occidentales de Venezuela. II. Producción y descomposición de los residuos vegetales. Turrialba **31**:39–47.

Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science **281**: 237–240.

Fölster, A., and G. de las Salas. 1976. Litter fall and mineralization in three tropical evergreen forest stands. Columbia. Acta Científica Venezolana **21**:196–202.

Fölster, A., G. de las Salas, and P. Khanna. 1976. A tropical evergreen forest site with perched water table, Magdalena Valley, Colombia: biomass and bioelement inventory of primary and secondary vegetation. Oecologia Plantarum **11**:297–320.

Frangi, J. L., and A. E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. Ecological Monographs **55**: 351–369.

Grace, J., J. LLoyd, J. McIntyre, A. Miranda, P. Meir, H. Miranda, J. Moncrieff, J. Massheder, I. Wright, and J. Gash. 1995*a*. Fluxes of carbon dioxide and water vapour over an undisturbed tropical forest in south-west Amazonia. Global Change Biology **1**:1–12.

Grace, J., J. LLoyd, J. McIntyre, A. C. Miranda, P. Meir, H. S. Miranda, C. Nobre, J. Moncrieff, J. Massheder, Y. Malhi, et al. 1995*b*. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. Science **270**:778–780.

Grimm, U., and H. W. Fassbender. 1981. Ciclos bioquimicas en un ecosistema forestal de los Andes Occidentales de Venezuela. I. Inventario de las reservas orgánicas y minerales (N, P, K, Ca, Mg, Fe, Al, Na). Turrialba **31**:27–37.

Guenther, A. C. Hewitt, D. Erickson, R. Fall, C. Geron, T. Graedel, P. Harley, L. Klinger, M. Lerdau, W. McKay, T. Pierce, B. Scholes, R. Steinbrecher, R. Tallamraju, J. Taylor, and P. Zimmerman. 1995. A global model of natural volatile organic compound emissions. Journal of Geophysical Research **100(D)**:8873–8892.

Herrera, R., and C. F. Jordan. 1981. Nitrogen cycle in a tropical Amazonian rain forest: the caatinga of low mineral nutrient status. *In* F. E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles. Ecological Bulletins-NFR **33**: 493–505.

Huttel, C. 1975. Root distribution and biomass in three Ivory Coast rain forest plots. *In* F. B. Golley and E. Medina, editors. Tropical ecological systems: trends in terrestrial and aquatic research. Ecological Studies **11**:123–130.

Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of the National Academy of Sciences (USA) **94**:7362–7366.

Jordan, C. F. 1989. An Amazonian rain forest: the structure and function of a nutrient stressed ecosystem and the impact of slash-and-burn agriculture. Parthenon, Park Ridge, New Jersey, USA.

Jordan, C. F., and G. Escalante. 1980. Root productivity in an Amazonian rain forest. Ecology **61**:14–18.

Keller, M., D. A. Clark, D. B. Clark, A. M. Weitz, and E. Veldkamp. 1996. If a tree falls in the forest. . . Science **273**:201.

Kicklighter, D. W., A. Bondeau, A. L. Schloss, J. Kaduk, A. D. McGuire, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes. Global Change Biology **5**:16–24.

Kindermann, J., G. Wurth, and G. H. Kohlmaier. 1996. Interannual variation of carbon exchange fluxes in terrestrial ecosystems. Global Biogeochemical Cycles **10**:737–755.

Kira, T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. Pages 561–590 *in* P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge University Press, New York, New York, USA.

Kira, T., H. Ogawa, K. Yoda, and K. Ogino. 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production, with special reference to the Khao Chong rain forest. Nature and Life in Southeast Asia **5**:149–174.

Klinge, H. 1973. Root mass estimation in lowland tropical rain forests of Central Amazon, Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. Tropical Ecology **14**:29–38.

Klinge, H. 1976. Bilanzierung von Hauptnährstoffen im Ökosystem tropischer Regenwald (Manaus)—vorläufige Daten. Biogeographica **7**:59–77.

Klinge, H. 1978. Litter production in tropical ecosystems. Malayan Nature Journal **30**:415–442.

Klinge, H., and R. Herrera. 1983. Phytomass structure of natural plant communities on spodosols in southern Venezuela: the tall Amazon Caatinga forest. Vegetatio **53**:65–84.

Klinge, H., and W. A. Rodrigues. 1968*a*. Litter production in an area of Amazonian terra firme forest. Part I. Litterfall, organic carbon and total nitrogen contents of litter. Amazoniana **I**:87–302.

Klinge, H., and W. A. Rodrigues. 1968*b*. Litter production in an area of Amazonian terra firme forest. Part II. Mineral nutrient content of the litter. Amazoniana **I**:303–310.

Klinge, H., and W. A. Rodrigues. 1973. Biomass estimation in a central Amazonian rain forest. Acta Cientifica Venezolana **24**:225–337.

Klinge, H., W. A. Rodrigues, E. Brunig, and E. J. Fittkau. 1975. Biomass and structure in a Central Amazonian rain forest. Pages 115–122 *in* F. B. Golley and E. Medina, editors. Tropical ecological systems. Trends in terrestrial and aquatic research. Springer-Verlag, New York, New York, USA.

Landsberg, J. J., S. D. Prince, P. G. Jarvis, R. E. McMurtrie, R. Luxmoore, and B. E. Medlyn. 1996. Energy conversion and use in forests: an analysis of forest production in terms of radiation utilisation efficiency (e). Pages 273–298 *in* H. L. Gholz, K. Nakane, and H. Shimoda, editors. The use of remote sensing in the modeling of forest productivity. Kluwer Academic, Dordrecht, The Netherlands.

Lescure, J. P., H. Puig, B. Riera, D. Leclerc, A. Beekman, and A. Beneteau. 1983. La phytomasse épigée d'une forêt dense en Guyane française. Acta Oecologica (Oecologia Generalis) **4**:237–251.

Lugo, A. 1974. Tropical ecosystem structure and function. Pages 67–111 *in* E. G. Farnsworth and F. B. Golley, editors. Fragile ecosystems: evaluation of research and applications in the Neotropics. Springer-Verlag, New York, New York, USA.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs **62**:1–41.

Lugo, A. E., and P. G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. Journal of Tropical Ecology **2**:55–72.

Martínez-Yrizar, A., J. M. Maass, L. A. Pérez-Jiménez, and J. Sarukhán. 1996. Net primary productivity of a tropical deciduous forest ecosystem in western Mexico. Journal of Tropical Ecology **12**:169–175.

Martínez-Yrizar, A., J. Sarukhán, A. Pérez-Jiménez, E. Rincón, J. M. Maass, A. Solís-Magallanes, and L. Cervantes. 1992. Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México. Journal of Tropical Ecology **8**:87–96.

Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. Nature **363**:234–240.

Müller, D., and J. Nielsen. 1965. Production brute, pertes par respiration et production nette dans la foret ombrophile tropicale. Forstlige Forsoegsvaesen (Denmark) **29**:69–160.

Murphy, P. G. 1975. Net primary productivity in tropical terrestrial ecosystems. Pages 222–231 *in* H. Lieth and R. H. Whittaker, editors. Primary productivity of the biosphere. Springer-Verlag, New York, New York, USA.

Murphy, P. G., and A. E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica **18**: 89–96.

Nepstad, D. C., C. R. de Carvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. da Silva, T. A. Stone, S. E. Trumbore, and S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature **372**:666–669.

Nye, P. H. 1961. Organic matter and nutrient cycles under moist tropical forest. Plant and Soil **13**:333–346.

Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. V.

Núñez, R. M. Vásquez, S. G. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science **282**:439–442.

Proctor, J. 1983. Tropical forest litterfall. I. Problems of data comparison. Pages 267–273 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest: ecology and management. Blackwell Scientific, Oxford, UK.

Proctor, J. 1984. Tropical forest litterfall II: the data set. Pages 83–113 *in* A. C. Chadwick and S. L. Sutton, editors. Tropical rain forest: the Leeds symposium. Leeds Philosophical and Literary Society, Leeds, UK.

Puig, H., and J.-P. Delobelle. 1988. Production de litière, nécromasse, apports minéraux au sol par la litière en forêt guyanaise. Revue de Ecologie (Terre et Vie) **43**:3–22.

Rai, S. N., and J. Proctor. 1986*a*. Ecological studies on four rainforests in Karnataka, India. I. Environment, structure, floristics and biomass. Journal of Ecology **74**:439–454.

Rai, S. N., and J. Proctor. 1986*b*. Ecological studies on four rainforests in Karnataka, India. II. Litterfall. Journal of Ecology **74**:455–463.

Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology **70**:1346–1354.

Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson, A. L. Grace, B. Moore III, and C. J. Vörösmarty. 1991. Potential net primary productivity in South America: application of a global model. Ecological Applications **1**:399–429.

Raich, J. W., A. E. Russell, and P. M. Vitousek. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. Ecology **78**:707–721.

Ruimy, A., L. Kergoat, A. Bondeau, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. Global Change Biology **5**:56–64.

Ryan, M. G., R. M. Hubbard, S. Pongracic, R. J. Raison, and R. E. McMurtrie. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiology **16**:333–343.

Saldarriaga, J. G., and R. J. Luxmoore. 1991. Solar energy conversion efficiencies during succession of a tropical rain forest in Amazonia. Journal of Tropical Ecology **7**:233–242.

Santantonio, D., and J. C. Grace. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Canadian Journal of Forest Research **17**:900–908.

Schloss, A. L., D. W. Kicklighter, J. Kaduk, U. Wittenberg, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index (NDVI). Global Change Biology **5**:25–34.

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

Sizer, N. 1992. The impact of edge formation on regeneration and litterfall in a tropical rain forest fragment in Amazonia. Dissertation. Cambridge University, Cambridge, UK.

Tanner, E. V. J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. Journal of Ecology **65**:883–918.

Tanner, E. V. J. 1980*a*. Litterfall in montane rain forests of Jamaica and its relation to climate. Journal of Ecology **68**: 833–848.

Tanner, E. V. J. 1980*b*. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. Journal of Ecology **68**:573–588.

Tanner, E. V. J. 1985. Jamaican montane forests: nutrient capital and cost of growth. Journal of Ecology **73**:553–568.

Tian, H., J. M. Melillo, D. W. Kicklighter, A. D. McGuire, J. V. K. I. Helfrich, B. Moore III, and C. J. Vörösmarty. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. Nature **396**:664–667.

Trumbore, S. E., O. A. Chadwick, and R. Amundson. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science **272**: 393–396.

Trumbore, S. E., E. A. Davidson, P. Barbosa de Camargo, D. C. Nepstad, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles **9**:515–528.

Uhl, C., and C. F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology **65**:1476–1490.

Villela, D. M., and J. Proctor. 1999. Litterfall mass, chemistry, and nutrient retranslocation in a monodominant forest on Maraca Island, Roraima, Brazil. Biotropica **31**:198–211.

Vogt, K. A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil **187**:159–219.

Weaver, P. L., E. Medina, D. Pool, K. Dugger, J. Gonzales-Liboy, and E. Cuevas. 1986. Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. Biotropica **18**:79–85.

Weaver, P. L., and P. G. Murphy. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica **22**:69–82.

Weck, J. 1956. Uber die grössenordnung der substanzerzeugung in baumbestanden verschiedener vegetationsgebiete. Allegemeine Forst-und Jagdzeitung **127**:76–80.

APPENDIX

A compilation of the published estimates of net primary productivity in tropical forests, with documentation of the methods used to derive these estimates, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-006.