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The above-ground coarse wood productivity of 104 Neotropical forest plots

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Abstract

The net primary production of tropical forests and its partitioning between long-lived carbon pools (wood) and shorter-lived pools (leaves, fine roots) are of considerable importance in the global carbon cycle. However, these terms have only been studied at a handful of field sites, and with no consistent calculation methodology. Here we calculate above-ground coarse wood carbon productivity for 104 forest plots in lowland New World humid tropical forests, using a consistent calculation methodology that incorporates corrections for spatial variations in tree-size distributions and wood density, and for census interval length. Mean wood density is found to be lower in more productive forests. We estimate that above-ground coarse wood productivity varies by more than a factor of three (between 1.5 and 5.5 $Mg\,C\,ha^{-1}\,a^{-1}$) across the Neotropical plots, with a mean value of 3.1 $Mg\,C\,ha^{-1}\,a^{-1}$. There appear to be no obvious relationships between wood productivity and rainfall, dry season length or sunshine, but there is some hint of increased productivity at lower temperatures. There is, however, also strong evidence for a positive relationship between wood productivity and soil fertility. Fertile soils tend to become more common towards the Andes and at slightly higher than average elevations, so the apparent temperature/productivity relationship is probably not a direct one. Coarse wood productivity accounts for only a fraction of overall tropical forest net primary productivity, but the available data indicate that it is approximately proportional to total above-ground productivity. We speculate that the large variation in wood productivity is unlikely to directly imply an equivalent variation in gross primary production. Instead a shifting balance in carbon allocation between respiration, wood carbon and fine root production seems the more likely explanation.

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Introduction

The net primary productivity (NPP) of an ecosystem is the net amount of carbon that is fixed from the atmosphere into new organic matter per unit time (Roy *et al*., 2001). In terrestrial ecosystems this is composed of a number of components, including leaf production, above-ground wood productivity, volatile hydrocarbon formation, below-ground wood productivity, fine root production, production of root exudates and the direct export of carbohydrate to symbionts and parasites. Understanding the relative magnitude and spatial and temporal variation of these component processes is a subject of considerable interest, for testing our understanding of the functioning of ecosystems, the role of the biosphere in global biogeochemical cycles, and the response of ecosystems to local and global perturbations.

While the quantification of below-ground NPP is still in its infancy, considerable work has been undertaken on the assessment of the main above-ground components of NPP (leaf, flower, fruit and wood production) for many ecosystems and over many years. In tropical forests and savannas, however, both these terms are still poorly quantified and their relationship to environmental factors not well understood (Clark *et al*., 2001a). This is despite the fact that tropical forests alone may account for up to one-third of global terrestrial NPP, and tropical savannas and grasslands for a further quarter (Saugier *et al*., 2001).

In this paper we concentrate on assessing one component of NPP: the *above-ground coarse wood carbon productivity in stems and branches*. We define this as the rate at which carbon is fixed into above-ground coarse woody biomass structures. These include boles, limbs and branches, but excludes small twig turnover. The latter, we include as part of litter production; viz. the production of leaves, flowers, fruit and sap, and of woody structures (e.g. twigs) with short mean residence times. For brevity we hereafter refer to the above-ground coarse wood carbon productivity in stems and branches as the *coarse wood productivity*; implicit in this shortened form is the exclusion of the productivity of twigs and below-ground coarse wood.

Although coarse wood productivity is only a small fraction of the total NPP (see Results), stems themselves constitute the most long-lived above-ground carbon fraction. The production of stem carbon therefore dominates the above-ground carbon storage dynamics of forest ecosystems (Lloyd & Farquhar, 1996; Chambers *et al*., 2001a). Hence identifying the key determinants of coarse wood productivity is important to understanding the carbon dynamics of tropical forests, their potential modulation by climate change, and their influence on the global carbon cycle.

There are few assessments of the wood productivity of tropical forests, and these have used a variety of methodologies. In the most comprehensive and methodologically consistent study to date, Clark *et al*. (2001a) presented a review of methodological problems in NPP assessment (including coarse wood productivity). They estimated NPP (including coarse wood productivity) for 39 tropical forest sites, 15 of which were from the lowland Neotropics (Clark *et al*., 2001b).

We here attempt to provide methodologically consistent estimates of coarse wood productivity for 104 old-growth forest plots in the lowland Neotropics, with the aim of providing sufficient data to untangle, which environmental factors determine the magnitude of coarse wood productivity. Many of these data were collected as part of the RAINFOR project (Malhi *et al*., 2002; details available at http://www.geog.leeds/projects/rainfor). The large-scale aims of the RAINFOR project are to understand the spatial variation of forest structure, biomass and composition across the Neotropics. These are investigated by censusing pre-existing old-growth forest plots, and collecting complimentary data on canopy and soil properties.

The basic approach we have adopted for the determination of wood productivity is to use multiple censuses of permanent forest plots to determine the growth rate of existing trees and the rate of recruitment of new trees, converting these measurements into estimates of coarse wood productivity using allometric equations that relate tree diameter to biomass. We have introduced two additional features into our calculations: (i) a correction that accounts for the varying time intervals between censuses, and (ii) a correction for variations of tree size distribution and mean wood density between plots. Both these features substantially influence our estimates of coarse wood productivity.

Methodology

We concentrate on two partially overlapping subsets of the plots: 50 plots where data on tree taxonomy are also

available (thus enabling a wood density correction), and 50 plots where three or more censuses are available (enabling a direct census interval correction). Empirical relationships derived from these core groups are used to estimate coarse wood productivity in a wider set of plots where more limited information is available.

Field methodology

Estimates of coarse wood productivity are vulnerable to errors introduced by inadequate field measurement protocols. Moreover, the analysis of existing datasets can be hampered by poor documentation of these protocols as well as by variations between researchers in the actual protocol used. For all plots sampled within the RAINFOR project, we use a standard measurement protocol, and for other datasets we attempt to quality control where possible, although not all sites can be equally assured. The RAINFOR field protocols are available at http://www.geog.leeds.ac.uk/ projects/ rainfor/rainforfield manual.doc

One noteworthy issue is the protocol for trees with buttress roots. A significant proportion of tropical trees can have buttress roots or other bole irregularities at the standard measurement height (1.30 m). If the tree diameters were measured around, rather than above, buttress roots, the vertical growth of the roots ('buttress creep') has the potential to artificially inflate estimates of tree growth (Clark 2002, but see Phillips *et al*., 2002). In the RAINFOR recensuses, the point of measurement (POM) of the tree is taken at 1.30 m height where possible. Where bole irregularities are present at 1.30 m, the POM is then taken at 2 cm below the irregularity (Condit *et al*., 1998). Likewise, if the tree has buttress roots at 1.30 m, the POM is taken 0.50 m above the highest point of the buttresses. For a few trees where it is not possible to get above the buttresses, an optical method (either relaskop or digital camera) is used. In all irregular cases the POM height is always recorded.

Many of the study plots were first censused in the 1980s, and it is not always certain that the same protocols were used in earlier censuses. Approaches for postcorrection of these data are outlined in the RAINFOR field protocol and in Baker *et al*. (2004b). In almost all plots these biases affected only a small fraction of trees and the overall effect on calculations of coarse wood productivity is minor.

Correction for census interval

As a first estimate, the total coarse wood production between two censuses is the sum of two directly calculable terms: the wood growth of trees that survived from the first census to the second census, plus the biomass of trees that appeared only in the second census. However, this direct estimate misses at least two factors: (i) the coarse wood productivity of trees that appeared after the first census, but died before the second census (i.e. that were never recorded); and (ii) the stem production in trees that grew for some time after the first census, but died prior to the second census. Hence our direct calculation will underestimate coarse wood productivity, and the magnitude of this underestimation will increase with increasing time interval between censuses, and will also be greater in more dynamic forests.

In Appendix 1 we develop an approach to correct for this effect. We first examine the phenomenon in detail for a few plots with many censuses, confirming that the correction increases linearly with census interval. We then directly calculate this correction for all plots with three or more censuses, and use these results to derive a general correction function that can be applied to plots with only two censuses.

As, averaged across many trees, small increases in basal area (BA) are linearly proportional to increases in biomass (Baker *et al*., 2004b), we calculate census interval corrections in more directly measured units of BA growth rate per unit area ($m^2\,ha^{-1}\,a^{-1}$) rather than as coarse wood productivity, which is calculated later. BA growth rate is defined as the sum of the BA increments (per unit time) of all individual trees in the study plot (ground area basis), not subtracting out any losses as a consequence of tree mortality.

Conversion from BA growth rate to coarse wood productivity

The relationship between BA growth rate and the rate of coarse wood production per unit ground area should be approximately linear, but is affected by three factors that may vary between study plots: (i) mean wood density of the trees; (ii) the distribution of the BA between different tree size classes; (iii) the relationship between tree diameter and tree height.

Where the individual tree data (including taxonomy) are available, we use the approach outlined by Baker *et al*. (2004a) to directly estimate the above-ground biomass at every census. This approach is anchored on a relationship between tree biomass and diameter derived from direct harvesting of 315 trees near the Bionte site near Manaus, central Amazonia (Higuchi *et al*., 1994; Chambers *et al*., 2001b). Baker *et al*. (2004a) compared this model with an alternative (Chave *et al*., 2001) and found significant differences. This difference may be because Chambers' equation is based on randomly selected trees and incorporates terms that empirically model tree damage, preventing overestimation of the biomass of the largest individuals. Baker

et al. (2004a) concluded that the best estimates of tree biomass in the plots that they were studying were provided by the Chambers *et al.* (2001b) relationship.

Baker *et al.* then modified this equation to allow for variations in wood density, by compiling wood density data for 584 species that occur in Amazonian forest from published sources, and taking mean genus or family wood densities for species without wood density data. Variation in wood density (σ) was then incorporated as a simple multiplication factor, σ/σ_m, where σ_m is the mean wood density of the trees harvested to create the Chambers *et al.* (2001b) biomass equation. This density σ_m was estimated to be $0.67\,g\,cm^{-3}$, the mean stand-level value for the central Amazon plots in that study. Hence, for each tree of diameter D greater than 10 cm, including palms, the above-ground living dry biomass (AGB, $kg\,ha^{-1}$), was calculated as (Baker *et al.*, 2004a):

$$\mathrm{AGB} = \frac{\sigma_i}{0.67}\exp(0.33[\ln D] + 0.933[\ln D]^2 - 0.122[\ln D]^3 - 0.37). \quad (1)$$

Following Baker *et al.* (2004b), we then estimated the biomass production between censuses by applying this equation to all trees that persisted between the first and second censuses and taking the difference, and also to all recruits that appear in the second census.

The overall effect of the wood density correction was assessed by comparing the ratio between wood-density corrected and non-wood-density corrected estimates of biomass production, and subsequently deriving a simple multiplicative factor for the correction. As this correction was relatively small and quasi-linear, this correction could be directly combined with the census interval correction (see Correction for census interval). Results from the detailed inventory data were used to derive a more general relationship between stand-level BA production and stand-level biomass production, as outlined in the Results section.

Consistent with Clark *et al.* (2001a) and Roy *et al.* (2001), the carbon fraction in dry wood is taken to be 0.5. The wood carbon fraction may, however, exhibit some small regional variation even when wood density is taken into account (Elias & Potvin, 2003), as faster growing trees may have fewer of the more reduced and stable carbon compounds (e.g. lignin) than do slower growing ones.

Missing factors

The approach for calculation of coarse wood productivity outlined in this paper explicitly includes spatial variation in the distribution and dynamics of different tree size classes, and spatial variation in mean wood density, and in doing so probably captures the most important corrections to estimates of coarse wood productivity. There are still a number of terms that are not included in this analysis, which we consider in turn below:

(i) *Productivity of small trees*. In our analysis we consider only trees with diameter greater than 10 cm. Thus when new trees 'appear' in a later census, they are unlikely to have grown from zero in the preceding interval, but from a previously existing tree that had a diameter of less than 10 cm at the previous census. Hence simply adding the biomass of the 'new' tree overestimates the coarse wood productivity *of that tree* in that census interval. Clark *et al.* (2001a) suggest that this effect be conservatively corrected for by subtracting the biomass of a 10 cm diameter tree for each new tree that appears, i.e. assume that each new tree grew from 10 cm dbh. However, as our aim here is to estimate total coarse wood productivity (and not the coarse wood productivity of trees >10 cm dbh only), this is not an appropriate correction to apply. The overestimate of coarse wood productivity produced by assuming that the 'new' trees in the census grew from zero would be exactly offset by the underestimate caused by not counting the new trees that do grow from zero but remain <10 cm dbh at the later census (assuming that the population of trees <10 cm dbh is more or less in equilibrium). Hence, not applying any correction provides a better approximation of total coarse wood productivity for our purposes.

Note that one term still missed in our calculation is the coarse wood productivity of trees and shrubs that grow from zero after the first census, remain below 10 cm dbh, and die before the second census, i.e. the turnover of trees below 10 cm diameter. This term is likely to be small but it is beyond the scope of the available datasets to quantify this term.

(ii) *Branch turnover.* The productivity of large branches is an 'in-between' term that is only partially captured by our definition of coarse wood productivity. The definition captures the net gain or loss of branches as tree form changes with size, but excludes branch turnover, i.e. the extent to which new branches replace fallen branches on the same tree, and therefore slightly underestimates total coarse wood productivity. Estimates of branch fall (wood >1 cm in diameter) in 10 tropical forest sites ranged from 0.1 to $2.9\,Mg\,C\,ha^{-1}\,a^{-1}$ (Clark *et al.*, 2001b). However, it is not clear to what extent branch fall rates represent an additional wood productivity term. If branch fall is replaced by new branch growth, branch fall represents an additional

productivity term (Chambers *et al.*, 2001b). On the other hand, if the loss of branches is a permanent feature that reflects the changing allometry of larger trees, it is a structural parameter already encompassed in the direct biomass measurements that led to the allometric relationship between tree diameter and biomass employed here (Eqn (1)), and therefore should not be double-counted as branch fall. The truth probably lies somewhere in between, and hence this factor is another potential source of underestimation of coarse wood productivity.

(iii) *Palm productivity.* Palms >10 cm diameter are included in our analysis of wood productivity, but, apart from factoring in their low wood density, they are not distinguished from other trees in the allometric calculations. In contrast to dicotyledons, mature palms increase biomass by apical growth with little secondary (diameter) growth and hence diameter measurements underestimate wood productivity. On the other hand, the lack of branches on palms means that application of our standard allometric equation (which includes branches) overestimates palm biomass and hence palm biomass recruitment rates. Overall, the small contribution of palms to stand BA (usually less than 10%) and their very low wood density mean that both these missing terms are a few percent in magnitude, and tend to cancel each other.

(iv) *Spatial variation in wood carbon fraction, diameter–height relationships or tree form.* In this analysis we assume these factors are spatially invariant, but there are few data available to assess this assumption. Current limited analyses (T. R. Baker *et al.*, unpublished data) show no consistent variation in tree diameter–height relationships across the Amazon basin. Variation in diameter–height relationships between plots could be a marginally significant factor, but is not explored in this analysis.

From hydraulic considerations it would be expected that, for a given basal area, tree height would decrease with increasing water stress. Hence, application of allometric relations from the moderately seasonal central Amazon may slightly overestimate coarse wood productivity at the dry margins, and underestimate it in the wettest regions.

Field sites

Site descriptions and classification

The study plots used in this analysis are described in Table A1. All are located in the mainland Neotropics (all but two in South America), at an elevation of less than 1000 m. All plots were mixed-age old-growth humid forests with no evidence of major human-induced disturbance (e.g. logging, clearance) for at least a century. In most cases the forests are unlikely to have ever experienced a major anthropogenic disturbance. Each plot has been assigned a unique plot code. Ninety-two of these plots are directly involved in the RAINFOR network; the information on the remaining

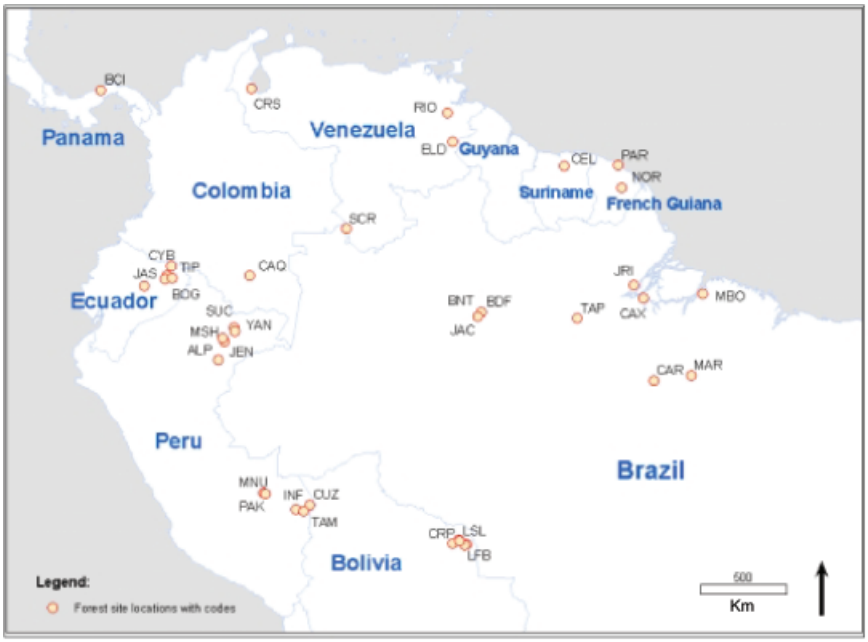

Fig. 1 Distribution of the study sites. Point labels refer to the plot codes in Table A1.

few is derived from the published literature. The plots are spread through nine countries in the Neotropics (Fig. 1). There is good coverage of Amazonia, and in particular of the southern and western fringes that have not been well covered by the Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA). The tree diversity of these forests is very high and correlates approximately with length of dry season, ranging from 100 tree species ($\geq$10 cm) ha^{-1} at the dry fringes in Bolivia, Panama and southern Brazilian Amazonia, to about 300 tree species ha^{-1} in the aseasonal climate of northern Peru and Ecuador.

The elevation of each plot was determined from local measurements where possible, or else determined from the US Geological Service 1 km Digital Elevation Model. Climatic data cover the period 1960–1998 and have been derived from the 0.5° resolution University of East Anglia Observational Climatology (New *et al.*, 1999), which has the advantage of covering a standardized period and therefore avoids the effects of interannual variability and net trends that can complicate comparisons (Malhi & Wright, 2004). For a few sites near the Andes the global climatology does not adequately capture the strong local rainfall gradients, and local field station meteorological data were favoured instead. The mean temperature estimates were corrected for elevation by comparing the plot elevation with the mean elevation of the 0.5° × 0.5° grid square, and applying a temperature lapse rate correction of 0.005 °C m^{-1}. The temperature correction was typically less that 0.5 °C, but ranged between −1 °C and + 2 °C. The dry season length was calculated as the average number of months per year with a rainfall of less than 100 mm.

The plots were divided into five categories (last column of Table A1), depending on the level of data available. The three questions relevant to assigning a category were:

1. Were tree growth measurements available, or did we only have published stem turnover data available from which to infer tree growth?
2. Had there been three or more censuses at the plot, enabling a direct estimation of the census interval correction effect, or did the census interval correction need to be inferred from the tree growth rate?
3. Could a wood density correction be applied based on the tree species composition of the study plot, or did this correction have to be inferred from tree dynamics data?

Based on answers to these three questions, the plots were assigned to one of five categories, as summarized in Table 1.

Soil classifications

The assignment to soil class here has been based on our own field descriptions where available, or else inferred from the landform and descriptions and geographical context provided by Sombroek (2000). Soils were divided into seven broad categories:

1. Heavily leached white sand soils (spodosols and spodic psamments in US Soil Taxonomy), which predominate in the upper Rio Negro region (category *Pa* in Sombroek, 2000).
2. Heavily weathered, ancient oxisols, which predominate in the eastern Amazon lowlands, either as Belterra clays of the original Amazon planalto (inland sea or lake sediments from the Cretaceous or early Tertiary), or fluvatile sediments derived from reworking and resedimentation of these old clays (categories *A* and *Uf* in Sombroek, 2000).
3. Less ancient oxisols, in younger soils or in areas close to active weathering regions (e.g. the Brazilian and Guyana crystalline shield) – category *Uc* in Sombroek (2000).
4. Less infertile lowland soils (ultisols and entisols), which particularly predominate in the western Amazonian lowlands, on sediments derived from the Andean cordillera by fluvatile deposition in the Pleistocene or earlier (category *Ua* in Sombroek, 2000).
5. Alluvial deposits from the Holocene (less that 11 500 years old), including very recent deposition (category *Fa* in Sombroek, 2000).
6. Young, submontane soils, perhaps fertilized by volcano-aeolian deposition (particularly sites in Ecuador, category *Uae* in Sombroek, 2000).
7. Seasonally flooded riverine soils, still in active deposition (tropaquepts), but perhaps occasionally experiencing anaerobic conditions.
8. Poorly drained swamp sites (probably histosols).

These soil categories are necessarily crude and it cannot be guaranteed that every plot has been correctly ascribed. A forthcoming paper will present our own detailed soil analyses from many of these sites. Nevertheless, even such a broad categorization does provide useful insights (see later).

Results and discussion

Census interval corrections

The application of the census interval correction for each plot is described in detail in Appendix A1. For a subset of 50 plots that has been censused three or more times (those of category 1 or 3, in bold type in Table

Table 1 Summary of the criteria used to assign forest plots to one of the five analysis categories

Analysis category	No. of plots	Total no. of hectares	Stem growth	Census interval correction	Density/structure correction
1	32	34.2	Measured	Calculated	Calculated
2	18	27.6	Measured	Inferred	Calculated
3	18	26.5	Measured	Calculated	Inferred
4	22	96.8	Measured	Inferred	Inferred
5	14	17.6	Inferred	Inferred	Inferred

A1), it was possible to calculate the census interval correction directly (Fig. A1b). In most cases this correction is small but significant. From this specific correction it was possible to derive a more generally applicable census interval correction (Fig. A2) that could be applied to a further 40 plots where only a single estimate of BA growth rate was available (i.e. where there had been only two censuses). These are shown in normal type (categories 2 and 4) in Table A2. The correction for all plots in categories 1–4 had a median value of 4.8% with a minimum of 0.3% and a maximum of 30%. On an annual basis, the median value of the correction is 0.67% per census interval year (minimum 0.04%, maximum 1.39%); the large corrections come from sites spanning 20–30 years between first and last census.

Finally, using an approximately linear relationship between stem turnover and BA growth rate (Fig. A3), BA growth rate was estimated for the remaining 14 plots where only stem turnover data were available (category 5 in Table A2), with a proviso that the uncertainties on the magnitudes of these estimates are higher. This crude estimation does, however, provide some insights into the likely productivity in some regions (e.g. Caqueta, Colombia and CELOS, Suriname) where no other data are currently available.

Conversion from BA growth rate to coarse wood productivity

Using the approach outlined in the Methods section, the coarse wood productivity (without census interval correction) was directly calculated for the 50 plots where individual tree taxonomic data were available (plots of categories 1 and 2). This calculation incorporates plot-to-plot variation in size-class distribution and wood density.

The results are shown in Table A3 (plots in bold type). Also shown are the effects of the census interval correction (repeated from Table A2). The two corrections were then combined into a single percentage correction that could be applied to the non-density corrected, non-census interval corrected estimate of above-ground wood carbon production.

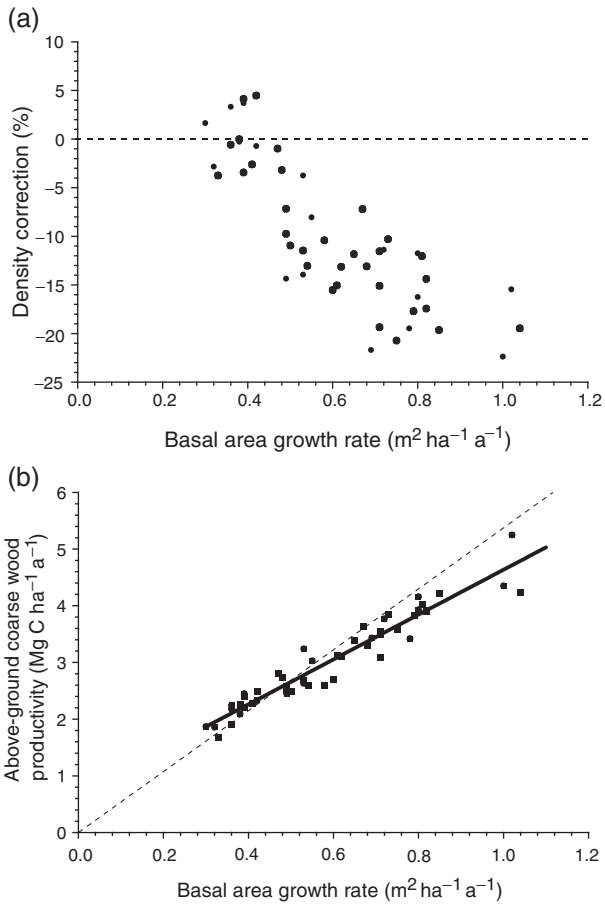

Fig. 2 (a) The relationship between the wood density correction and the basal area growth rate. The correction is relative to plots in the central Amazon (BNT-01, BNT-02, BNT-04). More dynamic plots have lower mean wood density. (b) The relationship between coarse wood productivity and census interval corrected basal area growth rate. Symbol coding is according to analysis category in Table A1 (solid circle = 1, solid square = 2, solid triangle = 3, open diamond = 4). The thin solid line goes the through the origin and the reference Bionte plots and represents the effect of applying the relationship between biomass carbon production and wood carbon production derived from the central Amazon uniformly to all sites; see text for details.

The relationship between the wood density correction and (census interval corrected) BA growth rate (in BA units) is shown in Fig. 2a. Faster growing forests

clearly have a lower mean wood density (Baker *et al*., 2004a). When applied with Eqn (1) the wood density correction alters the estimate of wood carbon production by between −22.4% and +4.5%, with a median value of −11.4%. The overall effect is negative because the reference Manaus plots that formed the basis of the original equation used by Chambers *et al*. (2001b) are among the slowest growing and highest wood density plots in our dataset. This correction works in the opposite direction to the census interval correction, and the two corrections can often approximately offset each other (more dynamic forests tend to have both a lower wood density and a larger census interval bias).

Figure 2b shows the relationship between our best estimate of coarse wood productivity in units of $Mg\,C\,ha^{-1}\,a^{-1}$ and the BA growth rate. Also shown is a line (thin dashed line) going through the origin and the reference Bionte plots, representing the effect of applying the relationship between biomass carbon production and wood carbon production derived from the central Amazon uniformly to all plots. The data deviate from this line, predominantly because of the wood density effect, but because this deviation is itself linearly related to BA growth rate, a modified linear fit (heavy dashed line) matches the data well ($r^2 = 0.96$, $P < 0.0001$).

The general empirical relationship is:

$$\text{Coarse wood productivity}\,(Mg\,C\,ha^{-1}\,a^{-1}) = (3.954 \pm 0.166\,\text{SE}) \times \text{basal area growth rate}\,(m^2\,ha^{-1}\,a^{-1}) + (0.693 \pm 0.104\,\text{SE}),$$

where $0.3\,m^2\,ha^{-1}\,a^{-1} < \text{BA growth rate} < 1.1\,m^2\,ha^{-1}\,a^{-1}$.

This provides a general relationship from which we can predict coarse wood productivity from BA growth rate for all our Neotropical plots, and perhaps for equivalent tropical forests worldwide. In Table A3 (plots in normal and italic type) this relationship is used to estimate coarse wood productivity for the 54 plots in categories 3, 4 and 5.

The variation of coarse wood productivity across Neotropical forests

The procedure outlined above has resulted in estimates of coarse wood productivity for 104 plots in the Neotropics (Table A3). For 90 plots this is derived directly from the tree growth measurements; for a further 14 plots it is estimated solely from stem turnover rates with an associated lower degree of confidence. Figure 3 shows the variation of above-ground coarse wood productivity across the study plots, varying by a factor of more than three (between 1.5 and $5.5\,Mg\,C\,ha^{-1}\,a^{-1}$) with a mean value of $3.1\,Mg\,C\,ha^{-1}\,a^{-1}$. Broad regional patterns in production are apparent. In particular, all the plots in lowland central and eastern Amazonia (BDF, BNT, JAC, TAP, CAX, JRI, SCR) have a relatively low productivity, with this region appearing to stretch as far west as San Carlos de Rio Negro (SCR) in Venezuela, and perhaps to Caqueta (CAQ-01) in Colombia. The lowest productivity is found on the *caatinga* forest on a spodic psamment (SCR-03). Generally intermediate productivities are found to the north and south, on sites on or close to the Guyana and Brazilian crystalline shields (MAR, CAR in Brazil, NOR in French Guyana, CEL in Suriname, RIO, ELD and CRS in Venezuela, and LFB, LSL, CRP, CHO in Bolivia), and at BCI in Panama. The highest productivities occur in western Amazonia (ALP, SUC, MSH, YAN in north Peru, CUZ, TAM, PAK and MNU in south Peru, and JAS, CYB, ANN, TIP and BOG in Ecuador), although a few plots there show intermediate productivities. The variation between site clusters is generally greater than that within clusters, suggesting that broad regional environmental factors drive wood productivity, rather than local landscape or individual plot dynamics.

Again assuming that the forests are in quasi-equilibrium, the mean residence time of carbon in wood biomass (penultimate column in Table A3) can be calculated as stem biomass pool divided by coarse wood productivity (for plots categories 1 and 2), or alternatively as BA/BA productivity (from Table A2, for plots categories 3 and 4). Figure 4 shows how residence time varies with wood carbon production. Mean biomass residence time (how long carbon stays fixed in above-ground live wood biomass of trees >10 cm diameter) varies between only 20 years in the high production regions to about 100 years in the slowest growing forests. The *caatinga* forest at San Carlos de Rio Negro appears to have a residence time of 150 years. The median residence time in this dataset is 49 years and the mean is 55 years. Points that fall significantly below the general curve (the liana forest CHO-01, and the seasonally inundated forests LSL-01, LSL-01) may indicate plots that are aggrading at a significant rate and not in quasi-equilibrium. This calculation ignores the residence time of trees <10 cm dbh, and is not equivalent to mean tree lifetime.

The relationship between coarse wood productivity and environmental variables

Coarse wood productivity shows strong regional patterns (Fig. 3), hinting that one or several environmental variables may be strongly influential in determining its overall magnitude. In the following section we therefore present an initial exploration of possible

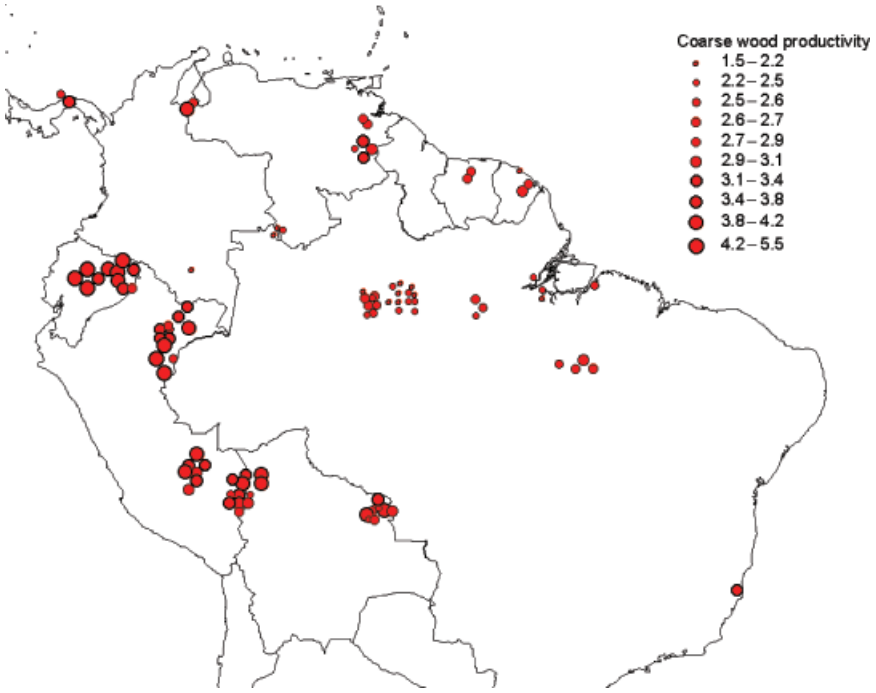

Fig. 3 Spatial variability in coarse wood productivity for 104 forest plots in the Neotropics. Circle diameter corresponds to calculated coarse wood productivity. The positions of some plots within clusters have been adjusted slightly to enable visibility, and do not correspond to exact geographic location.

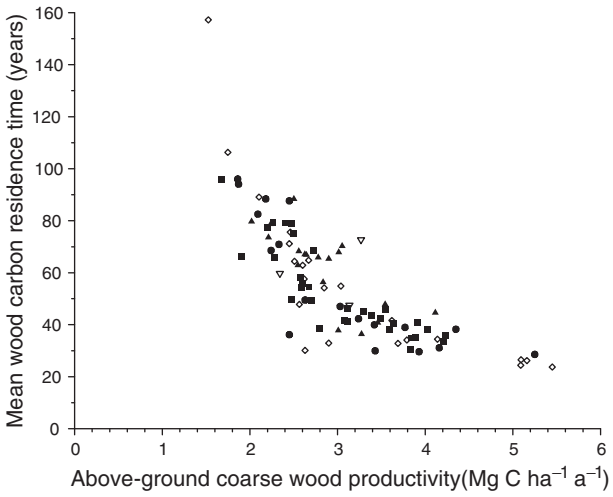

Fig. 4 The relationship between coarse wood productivity and the mean residence time of carbon in above-ground wood biomass. Symbols are coded according to analysis category as in Table A1 (solid circle = 1, solid square = 2, solid triangle = 3, open diamond = 4, inverted open triangle = 5).

environmental drivers; a more complete multivariate analysis will be presented in a future paper.

A correlation matrix was calculated for coarse-wood productivity against a variety of environmental variables using both unweighted and weighted regressions (Table 2). For the latter, weightings of 1.0, 0.7, 0.7, 0.4 and 0.2 were assigned to plots of data analysis categories 1 to 5, respectively, reflecting varying degrees of confidence in the calculation. The criteria used to define the five data analysis categories were listed in Table 1. Figure 5 shows coarse wood productivity plotted against the average annual air temperature (5a), average total annual precipitation (5b), average length of dry season (5c) and the average annual incoming solar radiation (5d). The fitted lines refer to the weighted regressions. It can be seen that the available data set spans a broad range of precipitation regimes from aseasonal to extremely seasonal, but only a relatively small range in temperature and solar radiation.

There appears to be little direct relationship between wood productivity and either annual precipitation or the average length of the dry season. Although the highest productivities are found in wet regions (north Peru, Ecuador), sites in south Peru and Brazil both experience moderately seasonal precipitation regimes yet the south Peruvian sites exhibit much higher productivities. Similarly, the sites in northern Bolivia experience more severe dry seasons than do those in lowland eastern Brazil, yet have higher productivities. There also appears to be no obvious relationship with solar radiation.

Table 2 Correlation matrix of regressions between climatic variables, elevation and coarse wood productivity, using both unweighted and weighted regressions for coarse wood productivity. For the latter, weightings of 1.0, 0.7, 0.7, 0.4 and 0.2 were assigned to plots of categories 1 to 5, respectively (Table 1), reflecting varying degrees of confidence in the calculation of coarse wood productivity

	Elevation	Precipitation	Dry season length	Temperature	Solar radiation	Stem productivity (unweighted)	Stem productivity (weighted)
Elevation	1.000						
Precipitation	0.219	1.000					
Dry season length	−0.080	−0.881	1.000				
Temperature	−0.843	−0.401	0.151	1.000			
Solar radiation	0.261	−0.130	0.354	−0.344	1.000		
Stem productivity (unweighted)	0.457	0.277	−0.277	−0.424	0.070	1.000	
Stem productivity (weighted)	**0.513**	**0.353**	**−0.300**	**−0.527**	**0.161**		1.000

There is, however, a significant correlation between coarse wood productivity and mean annual air temperature. However, because the Amazon basin tilts gently to the east, the sites in western Amazonia are typically found at elevations of 2–300 m, whereas those in the east are typically at elevations of 0–100 m and are therefore a few degrees warmer. In particular the plots at Jatun Sacha, at the foothills of the Andes (JAS: elevation 450 m) show some of the highest productivities. Hence, any possible relationship with temperature may be complicated by variations in another parameter: soil fertility. As outlined above, the poorest soils tend to be found in central and eastern Amazonia, and richer soils in the west. Moreover, more of our plots in the west are located on relatively recent alluvial terraces. Figure 6 therefore shows how coarse wood productivity clusters according to the eight soil categories listed in Table A1. These categories are necessarily broad, but there is some evidence of a soil fertility effect.

The data from the spodic psamment or spodosol plots are contradictory: SCR-03 shows the lowest productivity in our dataset as would perhaps be expected, but ALP-21 shows values more typical of neighbouring ultisol plots. The distinction between heavily weathered oxisols (eastern Amazon lowlands) and more recent oxisols (crystalline shield regions) appears significant, with the latter supporting 24% higher wood production on average. Further up the coarse wood productivity ranking, there appears little distinction in coarse wood productivity between the older (pre-Holocene) sediments and the Holocene alluvial deposits, both having average growth rates about 50% higher wood than the older oxisols. The younger submontane soils appear to be the most productive (75% more than the old oxisols), but show a wide variability in coarse wood productivities. Here a useful distinction can be made between plots in Bolivia (Huanchaca, Cerro Pelao), which support lower coarse wood productivity than plots in Ecuador (Jatun Sacha, Bogi, Tiputini, Cuyabeno). These Bolivian plots have very shallow soils (often <1 m), which may inhibit rooting depth and water supply, whereas in the Ecuadorean plots the soils are generally deeper and fertility may also have been enhanced by volcanic ash deposits. These Ecuadorean plots support production rates twice as high as the mean for the old oxisols.

The seasonally flooded fluvial plots show a wide range of coarse wood productivities, with Jenaro (northern Peru) showing among the highest productivities in our dataset. Tiputini (Ecuador) shows intermediate values and Las Londras (Bolivia) the lowest. This variation may be related to sediment load and the duration of flooding and waterlogging. Jenaro and Tiputini are on 'white-water' rivers originating in the Andes, whereas Las Londras is on a 'clear-water' river originating in the Brazilian crystalline shield. The swamp plots (both in southern Peru) do not show significantly lower wood productivity than the equivalent *terra firme* plots in the same region.

Given the strong correlations between the various climatic and edaphic variables a multivariate Generalized Linear Model (GLIM) was employed using observation weights (1.0, 0.7, 0.7, 0.4 and 0.2 for categories 1 to 5, respectively) and with eight indicator variables for the different soil types. This model, fitted via fast Givens transformations (Gentleman, 1974), gave an adjusted r^2 (r_a^2) of 0.54, with the inclusion of dry season length as an additional explanatory variable giving a marginal improvement in the model fit ($r_a^2 = 0.57$). These correlation coefficients are much greater than that for temperature when considered on its own ($r_a^2 = 0.27$). This suggests that the relationship with temperature in Fig. 5a is mostly correlative (as

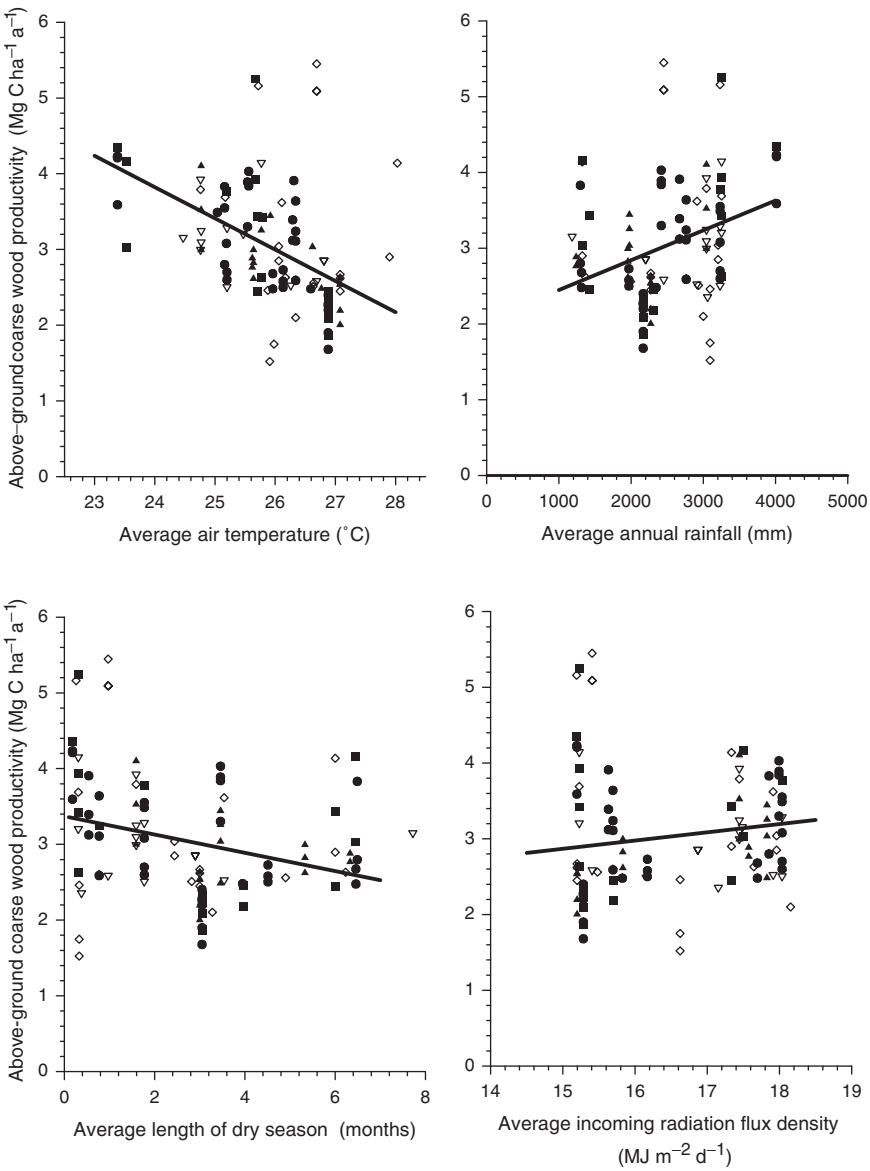

Fig. 5 The relationship between coarse wood productivity for all 104 plots (a) mean annual temperature; (b) total annual precipitation; (c) mean length of dry season (number of months with <100 mm rainfall; and (d) average annual incoming radiation flux. Temperature and precipitation data are from the University of East Anglia observational climatology. Symbol coding is according to analysis category as in Table A1 (solid circle = 1, solid square = 2, solid triangle = 3, open diamond = 4, inverted open triangle = 5). Also shown are weighted linear regressions as described in the text.

opposed to causative), arising from the tendency for higher fertility soils to be located towards the west where elevations are higher (Fig. 3). This conclusion is supported by the observation that the inclusion of air temperature as an independent term in addition to soil type into the multivariate GLIM (either with or without dry season length as an additional variable) did not improve the overall model fit ($P > 0.001$).

It thus seems that soil factors may be important in determining coarse wood productivity at the Basin wide scale, but the analysis shown here does not determine, which soil factors (soil texture, N, P, pH, Ca or other cations) could be important. To determine this and to fully tease apart the nature of the apparent correlation with temperature, a more rigorous and complete analysis will require a direct quantification of soil properties, rather than division into approximate soil classes as we have done here. The RAINFOR project (Malhi *et al.*, 2002) has already collected soils data from over 40 of the study plots listed in Table A1, and will collect further data in 2004. A multi-factorial analysis of these data has the potential to reveal the

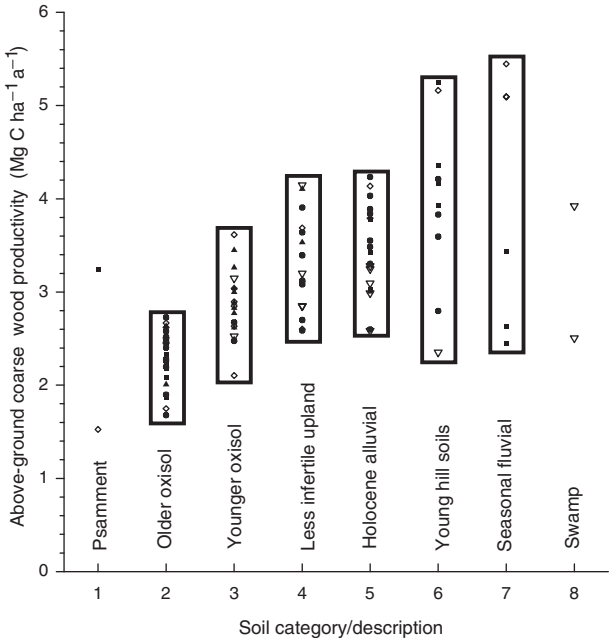

Fig. 6 The relationship between coarse wood productivity and soil type. The soil classification is described in the text. The bars encompass the upper and lower limits of the range. Symbol coding is according to analysis category as in Table A1 (solid circle = 1, solid square = 2, solid triangle = 3, open diamond = 4, inverted open triangle = 5).

Table 3 Values of coarse wood productivity and litterfall for eight plots in our dataset (bold type), and for 11 tropical sites reported in Clark *et al.* (2001a); normal type

Site name	Plot code (this study)	Stem growth rate (Mg C ha^{-1} a^{-1})	Total soft litterfall (Mg C ha^{-1} a^{-1})	Reference
BCI Plateau, Panamá	BCI-50	3.62	6.07	Foster (1982), cited in Leigh (1999)
San Carlos terra firme	SCR-01	1.76	2.93	Jordan (1989, p. 74), ignore branchfall
San Carlos caatinga	SCR-03	1.53	2.81	Cuevas and Medina (1986)
Bionte, Brazil	BNT-01,02,04	2.60	3.70	Luizão *et al*
BDFFP Fazenda Dimona	BDF-01	2.40	4.20	cited in Clark *et al.* (2001a)
Tapajos, Brazil	TAP-01,02,03	2.60	3.93	Nepstad *et al.* (2002)
Caxiuaná, Brazil	CAX-01,02	2.32	4.83	S. Almeida (unpublished)
Mocambo, Brazil	MBO-01	2.53	4.95	Cited in Clark *et al.* (2001a)
Sites from Clark et al. (2001a)				
Pasoh, Malaysia		2.7	5.3	Cited in Clark *et al.* (2001a)
Puu Kolekole, Hawaii		2.6	4.4	Cited in Clark *et al.* (2001a)
Paragominas, Brazil		1.3	4.6	Cited in Clark *et al.* (2001a)
Laupahoehoe, Hawaii		2.1	2.7	Cited in Clark *et al.* (2001a)
Kohala, Hawaii		1.4	3.2	Cited in Clark *et al.* (2001a)
Kokee, Hawaii		1.9	2.1	Cited in Clark *et al.* (2001a)
Chamela lower, Mexico		1.5	2.1	Cited in Clark *et al.* (2001a)
Chamela middle, Mexico		1.2	1.6	Cited in Clark *et al.* (2001a)
Chamela upper, Mexico		1	1.7	Cited in Clark *et al.* (2001a)
Hawaii 6		0.5	1.1	Cited in Clark *et al.* (2001a)
Hawaii 5		0.3	0.9	Cited in Clark *et al.* (2001a)

critical factors determining coarse wood productivity, and will be presented in a subsequent paper. Obvious candidates for critical soil factors affecting coarse wood productivity include both readily available phosphorous concentrations and soil cation status (Jordan & Herrera, 1981; Vitousek, 1984).

The relationship between coarse wood productivity and above-ground NPP

Apart from coarse wood production, the other major component of above-ground NPP is leaf, twig, flower and fruit production ('soft' productivity). For a quasi-equilibrium system (i.e. one that is particularly not gaining in leaf biomass over the measurement period), this can be estimated as being equivalent to the loss of leaf, flower and fruit through litterfall and herbivory. Litterfall collection tends to underestimate soft productivity, because of *in situ* consumption by leaf herbivores, seed and fruit feed feeders, sap-sucking insects and nectar feeders, and *in situ* decomposition in the canopy crown prior to drop. Clark *et al.* (2001a) estimate this consumption term to average 12% of measured litterfall, but it is likely to show considerable site-to-site and year-to-year variation. There are also a number of methodological difficulties with litterfall measurements (outlined in Clark *et al.*, 2001a), such as spatial sampling issues, and the uncertain distinction between fine litter (material that turns over on a roughly annual basis) and large branch fall.

Bearing the above uncertainties in mind, Table 3 presents data from the eight *terra firme* sites within our dataset where litterfall data (with no correction for herbivory) are available, alongside our current estimate of coarse wood productivity for the same sites (data from seasonally flooded sites have been excluded, as these are more difficult to interpret). Also shown are data on coarse wood productivity and litterfall reported from a further 11 sites by Clark *et al.* (2001b). Three other sites reported by Clark *et al.* (2001b), viz. BDF-01, SCR-01 and SCR-03, are also in our dataset and in these cases the values of coarse wood productivity as calculated in this study have been used. Most of the Clark *et al.* data come from montane forests in Hawaii (six plots) and Mexico (three plots), which would not necessarily be expected to have similar wood/leaf allocation relationships to lowland tropical sites. There does seem to be a linear relationship between coarse wood productivity and litterfall (Fig. 7), and the relationship appears to be almost identical in the two independent datasets (this study: $y = 1.719x$, $n = 8$, $r^2 = 0.76$; for the Clark *et al.* (2001b) dataset: $y = 1.739x$, $n = 11$, $r^2 = 0.57$; for a combined dataset: $y = 1.727x$, $n = 19$, $r^2 = 0.72$; relationship constrained to pass through the origin in all cases).

However, the data shown in Fig. 7 span the lower range of fertilities encountered in our dataset, with only one relatively fertile plot (BCI-50) included, and this proportionality may not hold for higher fertilities. A strong test of the generality of this relationship would be multiple site litterfall data from the high wood productivity sites in western Amazonia.

In Fig. 7, the ratio between leaf/twig production and coarse wood productivity is 1.72 : 1. If we assume that *in situ* consumption accounts for a further 12% of soft above-ground NPP (Clark *et al.*, 2001a), the ratio rises to 1.93 : 1. There is no *a priori* reason why this balance between leaf/twig production and stem growth should be constant: leaf production in most cases should be a higher priority for plants than stem production. Given that leaf biomass shows no large trends across the region (Patiño *et al.*, in preparation), this suggests that that the leaves of trees growing on infertile soils are longer lived (mean leaf lifetime = leaf biomass/leaf productivity), as is the case for stems, perhaps through reduced herbivory and increased investment in chemical defences. Reich *et al.* (1991) reported for 23 species at San Carlos de Rio Negro that leaves with lower leaf nitrogen and phosphorus concentrations were tougher, had longer leaf life spans and lower specific leaf areas (i.e. were thicker).

Two other components of NPP are biogenic volatile organic compounds (BVOCs) emissions and the loss of organic compounds that are leached from leaves by rainwater. Volatile emissions may account for 0.1–0.3 Mg C ha^{-1} yr^{-1} (Guenther *et al.*, 1995); the leachate flux may be of similar magnitude but has not been quantified (Clark *et al.*, 2001a).

If the relationship between wood and litterfall shown in Fig. 7 is a general one (and we emphasize that this is an untested assumption, in particular for the high-fertility sites), a reasonable estimate for above-ground NPP (coarse wood productivity + soft production) would be 2.93 times the coarse wood productivity. Including a further 0.2 Mg C ha^{-1} a^{-1} for BVOC and leachate produc-

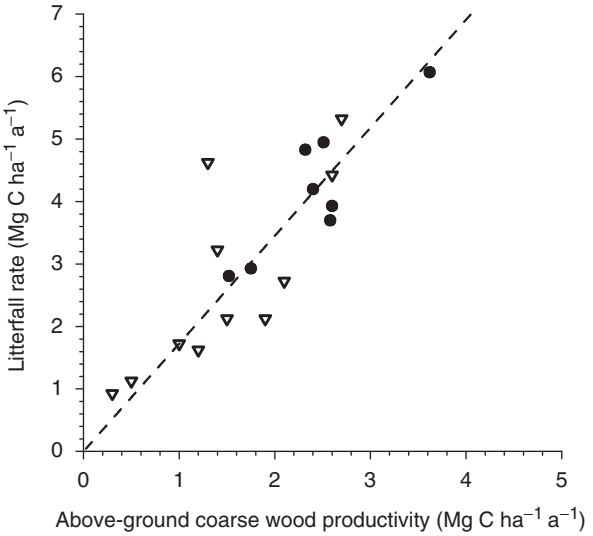

Fig. 7 The relationship between litterfall (leaves, fruit, flowers, small twigs, but excluding branchfall) and above-ground wood carbon production, for the eight *terra firme* plots in the current dataset where litterfall data are available (closed circles). Also shown for comparative purposes (open triangles) are data from the study of Clark *et al.* (2001a) Data values are given in Table 3.

tion, this would imply that, across the humid Amazonian forest, above-ground NPP varies between 4.7 and 16.2 Mg C ha^{-1} a^{-1} (last column of Table A3; mean of all plots 9.1 Mg C ha^{-1} a^{-1}). If we place a cap on litterfall rates rising no higher than the highest values shown in Fig. 7, the upper limit of this range reduces to 12.6 Mg C ha^{-1} a^{-1} (mean of all plots 8.8 Mg C ha^{-1} a^{-1}).

What drives the variation in productivity across the forest plots?

A remarkable feature of the results is the indication that spatial variation in above-ground NPP within Neotropical forests is driven not by climate, but rather by soil fertility. This contrasts with tree biodiversity, which correlates more with length of dry season (ter Steege *et al*., 2003), and hence suggests that tree biodiversity and above-ground NPP in tropical forests are largely determined by different environmental variables and are not closely linked.

This large variation in coarse wood productivity (and, more indirectly, above-ground NPP) across the region must reflect one or a combination of: (i) a variation in gross primary productivity (GPP); (ii) differences in plant respiratory costs relative to GPP, perhaps driven by temperature or soil nutrient status; or (iii) a variation in allocation of assimilated carbon between above-ground stems and other unmeasured below-ground components (in particular, fine root turnover, exudation and export of carbohydrate to mycorrhizae). We consider each of these possibilities in turn.

GPP should be mainly a function of leaf photosynthetic capacity, photosynthetic photon flux densities and leaf area index (light interception). The leaf area indices of these forests are already high (between 4 and 6) and preliminary data suggest that they are not higher at the more productive sites (Patiño *et al*., in preparation). Mean annual solar radiation varies by only about 20% across Neotropical forest regions, generally increasing with latitude as one heads to the seasonally dry subtropics, and in any case does not appear to be correlated with coarse wood productivity (Fig. 5d). Hence only large variations in leaf photosynthetic capacity (related to active rubisco content or electron transport capacity) could be driving large geographical variations in GPP. This has yet to be tested for, but recent canopy nitrogen measurements for over 30 sites in the data set used here (Patiño *et al*., in preparation) suggests canopy photosynthetic capacity is unlikely to vary by the factor of three necessary to explain the observed variation in above-ground NPP.

An alternative hypothesis is that GPP is relatively invariant, but plant respiration rates are higher in the less productive sites (and hence NPP is lower), either because they are at lower elevation and hence warmer (Fig. 5a), or perhaps because respiratory costs are higher for slower growing plants in less fertile soils (Lambers *et al*., 1998; Chambers *et al*., 2003).

The final option is that GPP, total autotrophic respiration and NPP are all relatively invariant, but that the allocation to below-ground NPP varies substantially between plots. One possible explanation would be variations in fine root activity. On infertile soils, it is likely that plants will invest more carbon in root production, exudation and symbiotic relationships with mycorrhizae. In addition, root lifetime may be substantially reduced on acid soils, thus accelerating turnover rates (Priess *et al*., 1999; Fölster *et al*., 2001).

Although some variation in GPP with soil fertility is possible, this is unlikely to be sufficient to explain the observed variation in coarse-wood productivity (without also incorporating shifts in allocation) given the few indications of variations in canopy leaf area index, nitrogen content and the annual total incoming radiation flux discussed above. Variations in allocation to respiration or fine root turnover seem more plausible, and hence much of the variation in coarse wood productivity may well simply reflect differences in below-ground carbon allocation. This could potentially be directly tested by examining variation in soil respiration rates, the ratio between production and respiration in stems and leaves, and the ratio of soil respiration to litterfall (Davidson *et al*., 2002). Furthermore, measurements of leaf nitrogen and phosphorus concentrations and canopy leaf area indices (already undertaken at over 30 RAINFOR plots) will help constrain potential variations in GPP.

A relatively simple measurement of the relationship between productivity (wood and litterfall) and soil respiration may be able to distinguish between the above hypotheses. In an analysis of the relationship between litterfall and soil respiration in a variety of forest ecosystems, Davidson *et al.* (2002) found that annual soil respiration increased linearly with litterfall. Strict adherence to this relationship would leave little space for variability in above- vs. below-ground allocation for any given NPP. However, Davidson *et al.* (2002) also reported that for their tropical sites the annual soil respiration varied by a factor of two for little variation in litterfall. Intriguingly, soil respiration rates (and implicitly below-ground allocation) were higher on Brazilian oxisol sites (Paragominas 20 Mg C ha^{-1} a^{-1}, Tapajos 17 Mg C ha^{-1} a^{-1}), than on an ultisol site (14.8 Mg C ha^{-1} a^{-1}) and an inceptisol site (10.5 Mg C ha^{-1} a^{-1}) at La Selva, Costa Rica, whereas litterfall rates were fairly similar across sites, varying between 3.6 and 4.8 Mg C ha^{-1} a^{-1}). This is, indeed, exactly the pattern that would be expected if below-ground allocation reduces in response to increased soil fertility but GPP stays relatively constant.

Distinguishing between the above hypotheses has implications for model-based estimates of the productivity, carbon stores and carbon sink of tropical forests. Most model studies of the NPP of tropical forest regions assume that allocation to live wood is a fixed proportion of total GPP, and hence spatial variations in wood productivity largely track spatial variation in sunshine and drought stress (e.g. Potter *et al*., 1998, 2001). This is clearly contradicted by the results presented here. Any substantial spatial variation in allocation to either respiration or fine root turnover decouples this simple relationship between wood productivity and GPP, and requires that allocation and its relation to environmental variables such as soil fertility be explicitly modelled.

Conclusions

In this paper, we have compiled a large dataset of coarse wood productivity estimates for mature forests in the Neotropics. Taken together, this shows variation in the values of coarse wood productivity between forest plots by a factor of three, with this variation more related to soil properties than to climatic conditions.

Several questions remain outstanding, all of which could be tested by directed future fieldwork:

1. Is there a simple relationship between coarse wood productivity and litterfall rates? In particular, does the linear relationship suggested in Fig. 7 extend to the higher wood productivity sites? If so, the observed variation in wood productivity reflects a proportionate variation in above-ground NPP. This could be directly tested by the collection of annual litterfall rates from one or more of the high-fertility sites.
2. Does the observed variation reflect different levels of gross primary production, autotrophic respiration or allocation to fine root activity? This could be directly tested by comparing the ratios of production to respiration in stems and leaves, and comparing the ratio of above-ground production to soil respiration at sites at the extremes of the gradient. Some basic ecophysiological measurements (litterfall and soil respiration) are lacking for forests growing on higher fertility Neotropical soils in western Amazonia. Indeed, in contrast to Eastern Amazonia, these forests represent one of the last ecophysiological frontiers. Collection of the appropriate simple data in the right locations could therefore provide substantial insights into the fundamental functioning of tropical forests.
3. Finally, perhaps the most obvious question is: is the observed spatial variation indeed driven by soil properties, and, if so, which soil factor (or factors) drives this variation? Soils data have been collected from a number of these sites, and this question is now a specific focus of the RAINFOR consortium.

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Table A1 The 104 study plots and their environmental parameters

Plot name and description	Plot code	Country	Long. (deg.)	Lat. (deg.)	Plot size (ha)	Elevation (m)	Forest type	First census date	Last census date	No. of censuses	Annual precipitation (mm)	Dry season length (months)	Mean temperature corrected (°C)	Soil type	Soil class	Analysis category
Allpahuayo A, poorly drained	ALP-11	Peru	−73.43	−3.95	0.44	114	Terra firme	1990.87	2001.03	3	2763	0.77	26.34	entisol (typic endoaquent)	4	1
Allpahuayo A, well drained	ALP-12	Peru	−73.43	−3.95	0.40	114	Terra firme	1990.87	2001.03	3	2763	0.77	26.34	ultisol (typic paleudult)	1	2
Allpahuayo B, sandy	ALP-21	Peru	−73.43	−3.95	0.48	114	Terra firme	1990.87	2001.04	3	2763	0.77	26.34	entisol (spodic udipsamment)	4	1
Allpahuayo B, clayed	ALP-22	Peru	−73.43	−3.95	0.44	114	Terra firme	1990.87	2001.04	3	2763	0.77	26.34	ultisol (typic hapludult)	4	1
Añangu, A1*	ANN-01	Ecuador	−76.43	−0.53	1	250	Seasonally flooded	1982.48	1990.98	2	3252	0.31	25.77	ultisol	4	5
Añangu, A2*	ANN-02	Ecuador	−76.43	−0.53	1	310	Terra firme	1982.48	1990.98	2	3252	0.31	25.47	ultisol	4	5
Añangu, A3*	ANN-03	Ecuador	−76.43	−0.53	1	370	Terra firme	1986.04	1990.96	2	3252	0.31	25.17	ultisol	4	4
BCI Putz & Milton	BCI-01	Panama	−79.85	9.17	2	100	Terra firme	1975.50	1980.50		2912	3.54	26.26	ultisol	3	5
BCI 50 ha	BCI-50	Panama	−79.85	9.17	50	130	Terra firme	1985.50	1995.50		2912	3.54	26.11	ultisol	3	4
BDFFP, 2303 Faz. Dimona 4–6	BDF-01	Brazil	−60.00	−2.40	2	100	Terra firme	1985.29	1997.71	4	2167	3.05	26.88	older oxisol	2	1
BDFFP, 1101 Gavião	BDF-03	Brazil	−59.90	−2.40	1	100	Terra firme	1981.13	1999.29	4	2167	3.05	26.88	older oxisol	2	1
BDFFP, 1102 Gavião	BDF-04	Brazil	−59.90	−2.40	1	100	Terra firme	1981.13	1999.29	4	2167	3.05	26.88	older oxisol	2	1
BDFFP, 1103 Gavião	BDF-05	Brazil	−59.90	−2.40	1	100	Terra firme	1981.21	1999.29	4	2167	3.05	26.88	older oxisol	2	2
BDFFP, 1201 Gavião	BDF-06	Brazil	−59.90	−2.40	3	100	Terra firme	1981.29	1999.29	4	2167	3.05	26.88	older oxisol	2	1
BDFFP, 1109 Gavião	BDF-08	Brazil	−59.90	−2.40	1	100	Terra firme	1981.63	1999.46	4	2167	3.05	26.88	older oxisol	2	1
BDFFP, 1113 Florestal	BDF-09	Brazil	−59.90	−2.40	1	100	Terra firme	1987.04	1997.29	3	2167	3.05	26.88	older oxisol	2	3
BDFFP, Florestal 1 = 1301.1	BDF-10	Brazil	−59.90	−2.40	1	100	Terra firme	1983.46	1997.13	3	2167	3.05	26.88	older oxisol	2	2
BDFFP, 1301 Florestal 2 = plots 1301.4,5,6	BDF-11	Brazil	−59.90	−2.40	3	100	Terra firme	1983.46	1997.13	3	2167	3.05	26.88	older oxisol	2	2
BDFFP, 1301 Florestal 3 = plots 1301.7,8	BDF-12	Brazil	−59.90	−2.40	2	100	Terra firme	1983.46	1997.13	3	2167	3.05	26.88	older oxisol	2	2
BDFFP, 3402 Cabo Frio	BDF-13	Brazil	−60.00	−2.40	9	100	Terra firme	1985.86	1998.88	4	2167	3.05	26.88	older oxisol	2	2
BDFFP, 3304 Porto Alegre	BDF-14	Brazil	−60.00	−2.40	2	100	Terra firme	1984.21	1998.38	5	2167	3.05	26.88	older oxisol	2	1
Bionte 1	BNT-01	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1999.50	11	2272	3.00	27.08	older oxisol	2	3
Bionte 2	BNT-02	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1999.50	11	2272	3.00	27.08	older oxisol	2	3
Bionte 4	BNT-04	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1999.50	10	2272	3.00	27.08	older oxisol	2	3

(continued)

Table A1 (Contd.)

Plot name and description	Plot code	Country	Long. (deg.)	Lat. (deg.)	Plot size (ha)	Elevation (m)	Forest type	First census date	Last census date	No. of censuses	Annual precipitation (mm)	Dry season length (months)	Mean temperature corrected (°C)	Soil type	Soil class	Analysis category
Bionte T4 B2 SB1	BNT-05	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1993.50	5	2272	3.00	27.08	older oxisol	2	4
Bionte T4 B1 SB3	BNT-06	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1993.50	5	2272	3.00	27.08	older oxisol	2	4
Bionte T4 B4 SB4	BNT-07	Brazil	−60.17	−2.63	1	73	Terra firme	1986.50	1993.50	5	2272	3.00	27.08	older oxisol	2	4
Bogi 1	BOG-01	Ecuador	−76.48	−0.70	1	271	Terra firme	1996.29	2002.13	2	3252	0.31	25.67	inceptisol	6	2
Bogi 2	BOG-02	Ecuador	−76.47	−0.70	1	270	Terra firme	1996.29	2002.13	2	3252	0.31	25.67	inceptisol	6	2
Caqueta	CAQ-01	Colombia	−72.10	−0.53	1	200	Terra firme	1989.50	1999.50	4	3059	0.38	26.88	ultisol	6	5
Carajás	CAR-01	Brazil	−50.50	−6.00	1	170	Terra firme	1986.38	1988.88	2	1993	4.90	25.64	younger oxisol	3	4
Caxiuaná 1	CAX-01	Brazil	−51.53	−1.70	1	15	Terra firme	1994.50	1999.50	2	2314	3.97	26.88	older oxisol	2	2
Caxiuaná 2	CAX-02	Brazil	−51.53	−1.70	1	15	Terra firme	1995.50	1999.50	2	2314	3.97	26.88	older oxisol	2	2
CELOS 67/9A plot8[†]	CEL-08	Suriname	−55.67	5.22	0.64	66	Terra firme	1967.50	1995.50		2201	2.90	26.81	ultisol	4	5
CELOS 67/9A plot15[†]	CEL-15	Suriname	−55.67	5.22	0.64	66	Terra firme	1967.50	1995.50		2201	2.90	26.81	ultisol	4	5
Chore 1	CHO-01	Bolivia	−61.16	−14.35	1	170	Liana forest	1996.53	2001.44	2	1357	6.23	26.17	younger oxisol (xanthic eutrustox)	3	4
Cerro Pelao 1	CRP-01	Bolivia	−61.48	−14.54	1	350	Rock outcrop	1994.21	2001.45	3	1297	6.49	25.16	inceptisol	6	1
Cerro Pelao 2	CRP-02	Bolivia	−61.48	−14.53	1	350	Rock outcrop	1994.27	2001.46	3	1297	6.49	25.16	inceptisol	6	1
Cano Rosalba 1[‡]	CRS-01	Venezuela	−72.00	9.25	1	60	Terra firme	1970.68	1972.70	2	1324	6.00	27.90	younger oxisol	3	4
Cano Rosalba 2[‡]	CRS-02	Venezuela	−72.00	9.25	1	35	Terra firme	1970.71	1972.70	2	1324	6.00	28.03	Pleistocene alluvial	5	4
Cuzco Amazonico, CUZAM1E	CUZ-01	Peru	−68.95	−12.50	1	200	Terra firme	1989.39	1998.77	3	2417	3.46	25.54	Holocene alluvial (inceptisol)	5	1
Cuzco Amazonico, CUZAM1U	CUZ-02	Peru	−68.95	−12.50	1	200	Terra firme	1989.42	1998.77	3	2417	3.46	25.54	Holocene alluvial (inceptisol)	5	1
Cuzco Amazonico, CUZAM2E	CUZ-03	Peru	−69.11	−12.49	1	200	Terra firme	1989.40	1998.77	3	2417	3.46	25.56	Holocene alluvial (inceptisol)	5	1
Cuzco Amazonico, CUZAM2U	CUZ-04	Peru	−69.11	−12.49	1	200	Terra firme	1989.44	1998.78	3	2417	3.46	25.56	Holocene alluvial (typic eutrudept)	5	1
Cuyabeno	CYB-01	Ecuador	−76.20	0.00	1	265	Terra firme	1988.40	1990.94	2	3232	0.26	25.72	inceptisol	6	4
El Dorado, km 91, plotG1[‡]	ELD-01	Venezuela	−61.50	6.50	0.25	210	Terra firme	1971.55	1994.44	15	1977	3.46	26.62	younger oxisol	3	3
El Dorado, km 91, plotG2[‡]	ELD-02	Venezuela	−61.50	6.50	0.25	180	Terra firme	1971.55	1994.44	15	1977	3.46	26.77	younger oxisol	3	3
El Dorado, km 98, plotG3[‡]	ELD-03	Venezuela	−61.50	6.50	0.25	380	Terra firme	1971.56	1981.19	11	1977	3.46	25.77	younger oxisol	3	3
El Dorado, km 98, plot G4[‡]	ELD-04	Venezuela	−61.50	6.50	0.25	350	Terra firme	1971.56	1981.19	11	1977	3.46	25.92	younger oxisol	3	3
Huanchaca Dos, plot 1	HCC-21	Bolivia	−60.75	−14.56	1	615	Gallery forest	1996.52	2001.43	2	1332	6.44	23.53	inceptisol	6	2

Huanchaca Dos, plot 2	HCC-22	Bolivia	−60.74	−14.57	1	615	Gallery forest	1996.54	2001.43	2	1332	6.44	23.53	inceptisol	6	2
Infierno	INF-01	Peru	−69.70	−12.73	1	226	Terra firme	1988.88	1995.96	2	3232	1.77	25.20	Holocene alluvial	5	5
Jacaranda 1	JAC-01	Brazil	−60.17	−2.63	5	73	Terra firme/ swampy valleys	1996.50	2002.50	3	2272	3.00	27.08	older oxisol & fluvent	2	3
Jacaranda 2	JAC-02	Brazil	−60.17	−2.63	5	73	Terra firme/ swampy valleys	1996.50	2002.50	3	2272	3.00	27.08	older oxisol & fluvent	2	3
Jatun Sacha 2	JAS-02	Ecuador	−77.60	−1.07	1	450	Terra firme	1987.63	2002.04	4	4013	0.18	23.38	inceptisol/ oxisol	6	1
Jatun Sacha 3	JAS-03	Ecuador	−77.67	−1.07	1	450	Terra firme	1988.88	2002.04	4	4013	0.18	23.38	ultisol/ inceptisol	6	1
Jatun Sacha 4	JAS-04	Ecuador	−77.67	−1.07	1	450	Terra firme	1994.54	2002.04	2	4013	0.18	23.38	inceptisol	6	2
Jatun Sacha 5	JAS-05	Ecuador	−77.67	−1.07	0.92	450	Terra firme	1989.38	2002.04	4	4013	0.18	23.38	Holocene alluvial	5	1
Jenaro High Restinga Plot 3§	JEN-03	Peru	−73.73	−4.92	1	116	Seasonally flooded (1 mo)	1993.71	1997.75	4	2715	0.97	26.69	entisol	7	4
Jenaro Low Restinga, plot 6§	JEN-06	Peru	−73.73	−4.92	1	116	seasonally flooded (2 month)	1993.71	1997.58	4	2715	0.97	26.69	entisol	7	4
Jenaro Tahuampa plot 9§	JEN-09	Peru	−73.73	−4.92	1	116	Seasonally flooded (4 months)	1993.71	1997.75	4	2715	0.97	26.69	entisol	7	4
Jenaro Herrera: Spichiger	JEN-10	Peru	−73.73	−4.92	1	116	Terra firme	1976.50	1981.50	1	2715	0.97	26.69	ultisol	5	5
Jari 1	JRI-01	Brazil	−52.05	−1.00	1	82	Terra firme	1985.50	1996.00	6	2346	3.95	26.59	older oxisol	2	1
Los Fierros Bosque I	LFB-01	Bolivia	−60.87	−14.61	1	225	Terra firme	1993.62	2001.40	3	1313	6.46	25.96	younger oxisol	3	1
Los Fierros Bosque II	LFB-02	Bolivia	−60.85	−14.60	1	225	Terra firme	1993.65	2001.40	3	1313	6.46	25.96	younger oxisol	3	1
Linhares	LIN-01	Brazil	−40.03	−19.20	2.5	43	Terra firme	1980.50	1995.50	6	1183	7.72	24.47	younger oxisol	3	5
Las Londras, plot 1	LSL-01	Bolivia	−61.13	−14.40	1	170	Seasonally flooded	1996.53	2001.48	2	1424	6.00	25.70	ultisol (oxyaquic kandiudult)	7	2
Las Londras, plot 2	LSL-02	Bolivia	−61.13	−14.40	1	170	Seasonally flooded	1996.53	2001.48	2	1424	6.00	25.70	ultisol (oxyaquic kandiudult)	7	2
Marabá, plot 1	MAR-01	Brazil	−49.05	−5.73	2	90	Terra firme	1988.46	1995.958	4	1956	5.33	26.64	younger oxisol	3	3
Marabá, plot 2	MAR-02	Brazil	−49.03	−5.70	2	90	Terra firme	1988.46	1995.958	4	1956	5.33	26.64	younger oxisol	3	3
Marabá, plot 3	MAR-03	Brazil	−49.00	−5.70	2	90	Terra firme	1988.46	1995.958	4	1956	5.33	26.64	younger oxisol	3	3
Mocambo¶	MBO-01	Brazil	−48.45	−1.45	2	24	Terra firme	1956.50	1971.50	2	2933	2.82	26.63	older oxisol	2	4
Manu, M1	MNU-01	Peru	−71.35	−11.88	0.97	312	Rarely flooded	1975.00	2000.75	6	3043	1.59	24.77	Holocene alluvial	5	3
Manu, M3	MNU-03	Peru	−71.35	−11.88	2	312	Terra firme	1991.75	2001.75	3	3043	1.59	24.77	Pleistocene alluvial	4	3
Manu, M4	MNU-04	Peru	−71.35	−11.88	2	312	Terra firme	1991.75	2001.75	3	3043	1.59	24.77	Pleistocene alluvial	4	3
Manu, Cocha Cashu Trail 12	MNU-05	Peru	−71.35	−11.88	2	312	Rarely flooded	1989.99	1999.99	3	3043	1.59	24.77	Holocene alluvial	5	5
Manu, Cocha Cashu Trail 2 & 13	MNU-06	Peru	−71.35	−11.88	2.25	312	Rarely flooded	1989.80	1999.80	3	3043	1.59	24.77	Holocene alluvial	5	5

(continued)

Table A1 (Contd.)

Plot name and description	Plot code	Country	Long. (deg.)	Lat. (deg.)	Plot size (ha)	Elevation (m)	Forest type	First census date	Last census date	No. of censuses	Annual precipitation (mm)	Dry season length (months)	Mean temperature corrected (°C)	Soil type	Soil class	Analysis category
Mishana	MSH-01	Peru	−73.50	−3.78	1	114	Terra firme	1983.04	1990.70	2	2763	0.77	26.34	Pleistocene alluvial	4	4
Nouragues PP	NOR-01	French Guiana	−52.67	4.08	12	110	Terra firme	1992.50		2	3205	2.44	26.06	younger oxisol	3	4
Nouragues GP	NOR-02	French Guiana	−52.67	4.08	10	110	Terra firme			2	3205	2.44	26.06	younger oxisol	3	4
Pakitza, plot1	PAK-01	Peru	−71.25	−11.93	1	313	Terra firme	1987.50	1991.50	2	3043	1.59	24.76	Holocene alluvial	5	4
Pakitza, Manu River, plot2	PAK-02	Peru	−71.25	−11.93	1	313	Terra firme	1987.50	1991.50	2	3043	1.59	24.76	Holocene alluvial	5	5
Pakitza, Manu river, swamp	PAK-03	Peru	−71.25	−11.93	1	313	Swamp	1987.50	1991.50	2	3043	1.59	24.76	waterlogged (histosol)	8	5
Paracou	PAR	French Guiana	−52.83	5.25	6.25	19	Terra firme	1984.50	1995.50		3000	3.28	26.34	younger oxisol	3	4
Rio Grande, plotDA1, RG	RIO-01	Venezuela	−61.75	8.00	0.25	270	Terra firme	1971.58	1994.46	16	1239	6.33	25.62	younger oxisol	3	3
Rio Grande, plotDA2, RG	RIO-02	Venezuela	−61.75	8.00	0.25	270	Terra firme	1971.58	1994.46	16	1239	6.33	25.62	younger oxisol	3	3
San Carlos de Rio Negro, SC1, Uhl ‖	SCR-01	Venezuela	−67.05	1.93	0.25	122	Terra firme	1975.71	1986.42	2	3093	0.33	25.98	older oxisol	2	4
San Carlos de Rio Negro, Veillon RN1-4, SC2	SCR-02	Venezuela	−67.00	1.75	2	122	Terra firme	1978.14	1982.15	2	3093	0.33	25.88	older oxisol	2	4
San Carlos de Rio Negro, SC3, MAB site	SCR-03	Venezuela	−67.00	1.75	0.25	117	Terra firme	1975.50	1979.50	2	3093	0.33	25.91	spodosol	1	4
Sucusari A	SUC-01	Peru	−72.90	−3.23	1	107	Terra firme	1992.13	2001.06	3	2671	0.54	26.29	ultisol	4	1
Sucusari B	SUC-02	Peru	−72.90	−3.23	1	107	Terra firme	1992.13	2001.07	3	2671	0.54	26.29	ultisol	4	1
Tambopata plot zero	TAM-01	Peru	−69.28	−12.85	1	239	Terra firme	1983.78	2000.59	6	2417	3.46	25.04	Holocene alluvial (typic dystrudept)	5	1
Tambopata plot one	TAM-02	Peru	−69.28	−12.83	1	207	Terra firme	1979.87	2000.58	8	2417	3.46	25.20	Holocene alluvial (oxaquic dystrudept)	5	1
Tambopata plot two swamp	TAM-03	Peru	−69.28	−12.83	0.58	207	Swamp	1983.79	1998.75	4	2417	3.46	25.20	Holocene alluvial (histosol)	8	5
Tambopata plot two swamp edge	TAM-04	Peru	−69.28	−12.83	0.42	207	Terra firme	1983.79	1998.75	4	2417	3.46	25.20	Holocene alluvial (oxaquic dystrudept)	5	2
Tambopata plot three	TAM-05	Peru	−69.28	−12.83	1	207	Terra firme	1983.70	2000.56	6	2417	3.46	25.20	Pleistocene alluvial (kandiustult)	4	1

Tambopata plot four	TAM-06	Peru	−69.30	−12.83	0.96	214	Terra firme	1983.71	2000.55	5	2417	3.46	25.16	Holocene alluvial (aquic durudept)	5	1
Tambopata plot six	TAM-07	Peru	−69.27	−12.83	1	209	Terra firme	1983.76	1998.73	5	2417	3.46	25.19	Pleistocene alluvial (xanthic hapludox)	4	1
Tapajos, RP014, 1–4	TAP-01	Brazil	−55.00	−2.75	1	100	Terra firme	1983.50	1995.50	4	1968	4.51	26.13	older oxisol	2	1
Tapajos, RP014, 5–8	TAP-02	Brazil	−55.00	−2.75	1	100	Terra firme	1983.50	1995.50	4	1968	4.51	26.13	older oxisol	2	1
Tapajos, RP014, 9–12	TAP-03	Brazil	−55.00	−2.75	1	100	Terra firme	1983.50	1995.50	4	1968	4.51	26.13	older oxisol	2	1
Tiputini 2	TIP-02	Ecuador	−76.14	−0.63	0.8	246	Terra firme	1997.71	2002.13	2	3252	0.31	25.79	younger oxisol	5	2
Tiputini 3	TIP-03	Ecuador	−76.15	−0.64	1	248	Seasonally flooded	1998.13	2002.13	2	3252	0.31	25.78	Holocene alluvial	7	2
Yanamono A	YAN-01	Peru	−72.85	−3.43	1	104	Terra firme	1983.46	2001.05	6	2671	0.54	26.31	ultisol	4	1

The allocation of analysis category and soil category for each plot is described in the text. Sources for published data are listed in the footnotes. Plot data are the best available at the time of final analyses, but are subject to future revision as a result of additional censuses and continued error-checking. The date of final analysis for this paper was 1 April 2003. Data with superscripts are from published sources:

*Korning (1992).

†de Graaf *et al.* (1999).

‡Veillon (1985).

§Nebel *et al.* (2001a, b).

¶Prance & Elias (1977).

‖Uhl & Murphy (1981), Uhl *et al.* (1988).

Table A2 Summary of census interval corrections for plots where possible. In plots in bold type they are calculated directly, in plots in normal type they are inferred from the measured coarse wood productivity, in plots in italic type they are estimated from stem turnover rates

Plot code	Analysis category	Basal area (latest census) ($m^2\,ha^{-1}$)	Stem turnover rate (%)	Basal area growth rate (uncorrected) ($m^2\,ha^{-1}\,a^{-1}$)	Basal area growth rate (corrected) ($m^2\,ha^{-1}\,a^{-1}$)	Correction slope ($\times10^{-3}$) ($m^2\,ha^{-1}\,a^{-2}$)	Percentage correction (%)
ALP-11	**1**	**27.6**	**2.99**	**0.54**	**0.58**	**3.39**	**6.4**
ALP-21	**1**	**27.3**	**2.72**	**0.63**	**0.67**	**6.23**	**6.8**
ALP-22	**1**	**26.8**	**2.55**	**0.56**	**0.62**	**4.16**	**11.3**
BDF-01	**1**	**30.3**	**1.47**	**0.38**	**0.39**	**1.22**	**4.1**
BDF-03	**1**	**29.5**	**1.45**	**0.36**	**0.39**	**1.50**	**7.6**
BDF-04	**1**	**22.5**	**3.34**	**0.33**	**0.36**	**1.42**	**7.7**
BDF-06	**1**	**26.0**	**1.68**	**0.36**	**0.41**	**2.30**	**11.4**
BDF-08	**1**	**28.1**	**2.04**	**0.31**	**0.33**	**0.79**	**4.5**
BDF-14	**1**	**30.7**	**1.57**	**0.37**	**0.38**	**1.22**	**4.3**
CRP-01	**1**	**19.9**	**3.03**	**0.46**	**0.47**	**1.46**	**2.3**
CRP-02	**1**	**24.8**	**3.13**	**0.75**	**0.79**	**5.15**	**4.8**
CUZ-01	**1**	**28.2**	**2.55**	**0.66**	**0.68**	**1.66**	**3.2**
CUZ-02	**1**	**28.1**	**2.15**	**0.73**	**0.82**	**10.23**	**12.8**
CUZ-03	**1**	**25.2**	**2.91**	**0.70**	**0.73**	**2.68**	**3.8**
CUZ-04	**1**	**29.3**	**2.81**	**0.73**	**0.81**	**6.89**	**9.9**
JAS-02	**1**	**29.8**	**2.43**	**0.67**	**0.75**	**5.91**	**12.7**
JAS-03	**1**	**30.6**	**2.46**	**0.79**	**0.85**	**4.19**	**8.1**
JAS-05	**1**	**35.3**	**2.83**	**0.92**	**1.04**	**8.31**	**12.3**
JRI-01	**1**	**33.1**	**1.67**	**0.41**	**0.42**	**1.31**	**3.7**
LFB-01	**1**	**25.0**	**3.66**	**0.49**	**0.50**	**1.76**	**2.8**
LFB-02	**1**	**29.0**	**3.28**	**0.53**	**0.53**	**0.29**	**0.3**
SUC-01	**1**	**27.9**	**2.25**	**0.56**	**0.61**	**6.12**	**9.8**
SUC-02	**1**	**27.8**	**2.85**	**0.59**	**0.65**	**6.24**	**9.5**
TAM-01	**1**	**28.9**	**2.92**	**0.62**	**0.71**	**5.35**	**15.1**
TAM-02	**1**	**30.0**	**2.31**	**0.48**	**0.54**	**3.02**	**14.0**
TAM-05	**1**	**26.6**	**3.08**	**0.58**	**0.60**	**1.14**	**3.3**
TAM-06	**1**	**36.1**	**2.81**	**0.64**	**0.71**	**3.17**	**10.6**
TAM-07	**1**	**29.0**	**3.17**	**0.63**	**0.71**	**4.98**	**11.6**
TAP-01	**1**	**26.9**	**1.38**	**0.45**	**0.49**	**2.79**	**7.4**
TAP-02	**1**	**31.3**	**1.37**	**0.47**	**0.48**	**1.13**	**2.9**
TAP-03	**1**	**34.4**	**1.42**	**0.48**	**0.49**	**0.94**	**2.4**
YAN-01	**1**	**32.4**	**3.09**	**0.68**	**0.82**	**8.05**	**21.2**
ALP-12	2	24.4	2.48	0.50	0.53		6.2
BDF-05	2	25.7	1.41	0.34	0.37		8.2
BDF-10	2	28.3	1.78	0.39	0.42		6.9
BDF-11	2	30.3	0.8	0.31	0.33		5.5
BDF-12	2	29.4	0.74	0.29	0.30		5.1
BDF-13	2	28.5	1.4	0.36	0.38		6.0
BOG-01	2	30.8	2.86	0.96	1.02		6.5
BOG-02	2	26.0	4.04	0.76	0.80		5.1
CAX-01	2	34.9	1	0.38	0.39		2.3
CAX-02	2	32.3	1.61	0.36	0.37		1.7
HCC-21	2	24.9	2.96	0.77	0.80		4.2
HCC-22	2	27.0	1.68	0.54	0.55		3.0
JAS-04	2	37.0	2.49	0.92	1.00		8.3
LSL-01	2	18.0	2.51	0.48	0.49		2.7
LSL-02	2	23.0	1.39	0.67	0.69		3.7
TAM-04	2	30.0	2.81	0.64	0.72		12.8
TIP-02	2	28.0	2.48	0.75	0.78		3.7
TIP-03	2	24.2	2.97	0.52	0.53		2.4
BDF-09	**3**	**29.8**	**1.16**	**0.38**	**0.39**	**1.48**	**4.0**

(continued)

Table A2 (Contd.)

Plot code	Analysis category	Basal area (latest census) ($m^2\,ha^{-1}$)	Stem turnover rate (%)	Basal area growth rate (uncorrected) ($m^2\,ha^{-1}\,a^{-1}$)	Basal area growth rate (corrected) ($m^2\,ha^{-1}\,a^{-1}$)	Correction slope ($\times10^{-3}$) ($m^2\,ha^{-1}\,a^{-2}$)	Percentage correction (%)
BNT-01	**3**	**31.2**	**1.21**	**0.45**	**0.47**	**2.58**	**4.5**
BNT-02	**3**	**33.0**	**0.78**	**0.49**	**0.50**	**0.68**	**1.1**
BNT-04	**3**	**29.0**	**1.4**	**0.46**	**0.47**	**1.70**	**3.0**
ELD-01	**3**	**32.7**	**1.23**	**0.46**	**0.60**	**4.49**	**29.8**
ELD-02	**3**	**36.3**	**0.82**	**0.41**	**0.46**	**3.69**	**12.6**
ELD-03	**3**	**23.3**	**2.66**	**0.63**	**0.66**	**5.16**	**3.6**
ELD-04	**3**	**27.6**	**1.34**	**0.67**	**0.70**	**4.87**	**5.0**
JAC-01	**3**	**27.3**	**1.53**	**0.37**	**0.39**	**2.91**	**4.7**
JAC-02	**3**	**26.4**	**1.41**	**0.33**	**0.34**	**1.24**	**2.3**
MAR-01	**3**	**20.4**	**2.31**	**0.53**	**0.59**	**7.34**	**10.4**
MAR-02	**3**	**28.5**	**1.70**	**0.50**	**0.54**	**6.11**	**8.4**
MAR-03	**3**	**31.2**	**1.86**	**0.46**	**0.49**	**4.39**	**6.4**
MNU-01	**3**	**31.4**	**2.93**	**0.46**	**0.59**	**5.07**	**28.5**
MNU-03	**3**	**31.3**	**3.96**	**0.65**	**0.72**	**7.45**	**11.5**
MNU-04	**3**	**34.4**	**2.64**	**0.76**	**0.87**	**10.53**	**13.8**
RIO-01	**3**	**31.6**	**1.32**	**0.48**	**0.56**	**4.78**	**16.5**
RIO-02	**3**	**31.4**	**1.96**	**0.47**	**0.53**	**2.30**	**12.4**
ANN-03	4	24.0	2.09	0.73	0.76		4.1
BCI-50	4	28.6	2.96	0.69	0.74		8.4
BNT-05	4	27.3	1.89	0.47	0.49		3.9
BNT-06	4	30.8	1.54	0.43	0.45		3.6
BNT-07	4	31.4	1.31	0.48	0.50		4.0
CAR-01	4	22.5	1.68	0.47	0.48		1.2
CHO-01	4	14.5	2.84	0.48	0.49		2.7
CRS-01	4	18.2	1.51	0.55	0.56		1.2
CRS-02	4	29.6	1.73	0.86	0.88		1.8
CYB-01	4	28.9	2.20	1.10	1.13		3.0
JEN-03	4	26.0	4.33	1.07	1.12		4.8
JEN-06	4	27.2	3.21	1.15	1.21		4.9
JEN-09	4	28.2	3.06	1.07	1.12		4.8
MBO-01	4	27.7	1.43	0.43	0.47		8.4
MSH-01	4	29.4	1.75	0.47	0.49		4.3
NOR-01	4	31.0	1.58	0.56	0.60		6.1
NOR-02	4	28.2	1.94	0.52	0.55		5.6
PAK-01	4	26.0	2.38	0.76	0.79		3.4
PAR-01	4	30.8	1.14	0.35	0.36		4.8
SCR-01	4	27.8	1.56	0.26	0.27		3.7
SCR-02	4	33.4	0.66	0.44	0.45		2.0
SCR-03	4	33.0	1.77	0.21	0.21		1.1
ANN-01	*5*		*3.66*		*0.87*		
ANN-02	*5*		*2.23*		*0.63*		
BCI-01	*5*		*1.21*		*0.46*		
CAQ-01	*5*	*30.3*	*0.95*		*0.42*		
CEL-08	*5*		*1.70*		*0.54*		
CEL-15	*5*		*1.70*		*0.54*		
INF-01	*5*	*38.9*	*2.35*		*0.65*		
JEN-10	*5*		*1.30*		*0.48*		
LIN-01	*5*	*29.2*	*2.15*		*0.62*		
MNU-05	*5*		*2.07*		*0.61*		
MNU-06	*5*		*2.30*		*0.64*		
PAK-02	*5*		*1.91*		*0.58*		
PAK-03	*5*		*3.32*		*0.81*		
TAM-03	*5*		*1.18*		*0.46*		

Table A3 Summary of census interval and wood density corrections, and estimates of stem production rates, biomass residence times and above-ground net primary productivity. The exact analysis pathway differs according to the analysis category of the plot, as detailed in the text. Plots in bold type: density and structure correction calculated directly from individual tree data; plots in normal type: density and structure correction inferred from measured basal area growth rate; plots in italics: basal area growth rate inferred from stem turnover rates

Plot code	Analysis category	Stem growth (uncorrected) ($Mg\,C\,ha^{-1}\,a^{-1}$)	Stem growth density (corrected) ($Mg\,C\,ha^{-1}\,a^{-1}$)	Density correction (%)	BA growth (uncorrected) ($m^2\,ha^{-1}\,a^{-1}$)	BA growth interval (corrected) ($m^2\,ha^{-1}\,a^{-1}$)	Census interval (correction) ($m^2\,ha^{-1}\,a^{-1}$)	Total correction (%)	Wood productivity combined correction ($Mg\,C\,ha^{-1}\,a^{-1}$)	Biomass residence time (years)
ALP-11	**1**	**2.72**	**2.43**	**−10.41**	**0.54**	**0.58**	**6.36**	**−4.71**	**2.59**	**54**
ALP-21	**1**	**3.67**	**3.41**	**−7.20**	**0.63**	**0.67**	**6.80**	**−0.89**	**3.64**	**42**
ALP-22	**1**	**3.22**	**2.79**	**−13.14**	**0.56**	**0.62**	**11.34**	**−3.30**	**3.11**	**40**
BDF-01	**1**	**2.22**	**2.31**	**4.13**	**0.38**	**0.39**	**4.06**	**8.35**	**2.40**	**41**
BDF-03	**1**	**2.11**	**2.04**	**−3.43**	**0.36**	**0.39**	**7.56**	**3.87**	**2.20**	**79**
BDF-04	**1**	**1.77**	**1.76**	**−0.58**	**0.33**	**0.36**	**7.73**	**7.11**	**1.90**	**77**
BDF-06	**1**	**2.10**	**2.05**	**−2.60**	**0.36**	**0.41**	**11.36**	**8.46**	**2.28**	**66**
BDF-08	**1**	**1.67**	**1.61**	**−3.75**	**0.31**	**0.33**	**4.50**	**0.59**	**1.68**	**69**
BDF-14	**1**	**2.17**	**2.17**	**−0.01**	**0.37**	**0.38**	**4.32**	**4.31**	**2.26**	**66**
CRP-01	**1**	**2.76**	**2.73**	**−0.97**	**0.46**	**0.47**	**2.30**	**1.31**	**2.80**	**96**
CRP-02	**1**	**4.44**	**3.66**	**−17.70**	**0.75**	**0.79**	**4.81**	**−13.74**	**3.83**	**71**
CUZ-01	**1**	**3.68**	**3.20**	**−13.09**	**0.66**	**0.68**	**3.17**	**−10.34**	**3.30**	**96**
CUZ-02	**1**	**4.03**	**3.45**	**−14.38**	**0.73**	**0.82**	**12.81**	**−3.41**	**3.89**	**94**
CUZ-03	**1**	**4.13**	**3.70**	**−10.29**	**0.70**	**0.73**	**3.78**	**−6.90**	**3.84**	**83**
CUZ-04	**1**	**4.17**	**3.67**	**−12.04**	**0.73**	**0.81**	**9.91**	**−3.32**	**4.03**	**79**
JAS-02	**1**	**4.02**	**3.19**	**−20.73**	**0.67**	**0.75**	**12.67**	**−10.69**	**3.59**	**29**
JAS-03	**1**	**4.85**	**3.89**	**−19.65**	**0.79**	**0.85**	**8.15**	**−13.10**	**4.21**	**30**
JAS-05	**1**	**4.68**	**3.77**	**−19.47**	**0.92**	**1.04**	**12.30**	**−9.57**	**4.23**	**88**
JRI-01	**1**	**2.29**	**2.39**	**4.48**	**0.41**	**0.42**	**3.70**	**8.35**	**2.48**	**88**
LFB-01	**1**	**2.71**	**2.41**	**−10.95**	**0.49**	**0.50**	**2.79**	**−8.47**	**2.48**	**38**
LFB-02	**1**	**3.01**	**2.67**	**−11.46**	**0.53**	**0.53**	**0.32**	**−11.18**	**2.68**	**31**
SUC-01	**1**	**3.35**	**2.85**	**−15.05**	**0.56**	**0.61**	**9.77**	**−6.75**	**3.12**	**45**
SUC-02	**1**	**3.52**	**3.10**	**−11.84**	**0.59**	**0.65**	**9.47**	**−3.49**	**3.39**	**35**
TAM-01	**1**	**3.57**	**3.03**	**−15.10**	**0.62**	**0.71**	**15.14**	**−2.24**	**3.49**	**35**
TAM-02	**1**	**2.62**	**2.28**	**−13.04**	**0.48**	**0.54**	**13.99**	**−0.87**	**2.60**	**38**
TAM-05	**1**	**3.09**	**2.61**	**−15.53**	**0.58**	**0.60**	**3.31**	**−12.74**	**2.70**	**31**
TAM-06	**1**	**3.63**	**3.21**	**−11.54**	**0.64**	**0.71**	**10.58**	**−2.18**	**3.55**	**47**
TAM-07	**1**	**3.43**	**2.76**	**−19.35**	**0.63**	**0.71**	**11.56**	**−10.02**	**3.08**	**38**
TAP-01	**1**	**2.66**	**2.40**	**−9.74**	**0.45**	**0.49**	**7.36**	**−3.09**	**2.58**	**34**
TAP-02	**1**	**2.74**	**2.65**	**−3.18**	**0.47**	**0.48**	**2.89**	**−0.38**	**2.73**	**38**
TAP-03	**1**	**2.64**	**2.45**	**−7.17**	**0.48**	**0.49**	**2.35**	**−4.99**	**2.50**	**36**
YAN-01	**1**	**3.90**	**3.22**	**−17.44**	**0.68**	**0.82**	**21.22**	**0.07**	**3.91**	**79**
ALP-12	**2**	**3.19**	**3.07**	**−3.74**	**0.50**	*0.53*	**5.57**	**1.63**	**3.24**	**50**
BDF-05	**2**	**2.12**	**2.10**	**−0.67**	**0.34**	*0.37*	**6.47**	**5.75**	**2.24**	**54**
BDF-10	**2**	**2.22**	**2.20**	**−0.71**	**0.39**	*0.42*	**5.70**	**4.95**	**2.33**	**36**

BDF-11	**2**	**1.84**	**1.79**	**−2.82**	**0.31**	0.33	**4.15**	**1.21**	**1.86**	**30**
BDF-12	**2**	**1.77**	**1.80**	**1.65**	**0.29**	0.30	**3.74**	**5.45**	**1.87**	**46**
BDF-13	**2**	**2.00**	**1.99**	**−0.26**	**0.36**	0.38	**4.79**	**4.51**	**2.09**	**43**
BOG-01	**2**	**5.82**	**4.92**	**−15.45**	**0.96**	1.02	**6.65**	**−9.83**	**5.25**	**42**
BOG-02	**2**	**4.47**	**3.74**	**−16.24**	**0.76**	0.80	**5.01**	**−12.05**	**3.93**	**56**
CAX-01	**2**	**2.32**	**2.41**	**3.70**	**0.38**	0.39	**1.87**	**5.64**	**2.45**	**39**
CAX-02	**2**	**2.08**	**2.15**	**3.33**	**0.36**	0.37	**1.37**	**4.75**	**2.18**	**49**
HCC-21	**2**	**4.53**	**3.99**	**−11.74**	**0.77**	0.80	**4.20**	**−8.03**	**4.16**	**46**
HCC-22	**2**	**3.21**	**2.95**	**−8.04**	**0.54**	0.55	**2.74**	**−5.52**	**3.03**	**42**
JAS-04	**2**	**5.17**	**4.01**	**−22.37**	**0.92**	1.00	**8.49**	**−15.78**	**4.35**	**58**
LSL-01	**2**	**2.79**	**2.39**	**−14.36**	**0.48**	0.49	**2.41**	**−12.30**	**2.45**	**69**
LSL-02	**2**	**4.23**	**3.31**	**−21.69**	**0.67**	0.69	**3.58**	**−18.88**	**3.43**	**75**
TAM-04	**2**	**3.79**	**3.36**	**−11.38**	**0.64**	0.72	**12.31**	**−0.46**	**3.77**	**40**
TIP-02	**2**	**4.10**	**3.30**	**−19.47**	**0.75**	0.78	**3.66**	**−16.53**	**3.42**	**49**
TIP-03	**2**	**3.00**	**2.58**	**−13.94**	**0.52**	0.53	**2.13**	**−12.10**	**2.63**	**41**
BDF-09	3				0.38	0.39	4.0		2.24	79
BNT-01	3				0.45	0.47	4.5		2.56	69
BNT-02	3				0.49	0.50	1.1		2.64	67
BNT-04	3				0.46	0.47	3.0		2.55	63
ELD-01	3				0.46	0.60	29.8		3.05	71
ELD-02	3				0.41	0.46	12.6		2.50	89
ELD-03	3				0.63	0.66	3.6		3.27	37
ELD-04	3				0.67	0.70	5.0		3.46	41
JAC-01	3				0.37	0.39	4.7		2.21	74
JAC-02	3				0.33	0.34	2.3		2.02	80
MAR-01	3				0.53	0.59	10.4		3.01	38
MAR-02	3				0.50	0.54	8.4		2.84	57
MAR-03	3				0.46	0.49	6.4		2.63	68
MNU-01	3				0.46	0.59	28.5		3.01	68
MNU-03	3				0.65	0.72	11.5		3.54	48
MNU-04	3				0.76	0.87	13.8		4.12	45
RIO-01	3				0.48	0.56	16.5		2.90	66
RIO-02	3				0.47	0.53	12.4		2.78	66
ANN-03	4				0.73	0.76	4.1		3.69	33
BCI-50	4				0.69	0.74	8.4		3.62	42
BNT-05	4				0.47	0.49	3.9		2.63	58
BNT-06	4				0.43	0.45	3.6		2.46	71
BNT-07	4				0.48	0.50	4.0		2.68	65
CAR-01	4				0.47	0.48	1.2		2.56	48
CHO-01	4				0.48	0.49	2.7		2.64	30
CRS-01	4				0.55	0.56	1.2		2.90	33
CRS-02	4				0.86	0.88	1.8		4.14	34

(continued)

Table A3 (Contd.)

Plot code	Analysis category	Stem growth (uncorrected) ($Mg\,C\,ha^{-1}\,a^{-1}$)	Stem growth density (corrected) ($Mg\,C\,ha^{-1}\,a^{-1}$)	Density correction (%)	BA growth (uncorrected) ($m^2\,ha^{-1}\,a^{-1}$)	BA growth interval (corrected) ($m^2\,ha^{-1}\,a^{-1}$)	Census interval (correction) ($m^2\,ha^{-1}\,a^{-1}$)	Total correction (%)	Wood productivity combined correction ($Mg\,C\,ha^{-1}\,a^{-1}$)	Biomass residence time (years)
CYB-01	4				1.10	1.13	3.0		5.16	26
JEN-03	4				1.07	1.12	4.8		5.09	24
JEN-06	4				1.15	1.21	4.9		5.43	24
JEN-09	4				1.07	1.12	4.8		5.09	27
MBO-01	4				0.43	0.47	8.4		2.53	64
MSH-01	4				0.47	0.49	4.3		2.61	63
NOR-01	4				0.56	0.60	6.1		3.05	55
NOR-02	4				0.52	0.55	5.6		2.86	54
PAK-01	4				0.76	0.79	3.4		3.79	34
PAR-01	4				0.35	0.36	4.8		2.12	89
SCR-01	4				0.26	0.27	3.7		1.76	106
SCR-02	4				0.44	0.45	2.0		2.47	76
SCR-03	4				0.21	0.21	1.1		1.53	157
ANN-01	*5*					*0.87*			*4.12*	
ANN-02	*5*					*0.63*			*3.18*	
BCI-01	*5*					*0.46*			*2.51*	
CAQ-01	*5*					*0.26*			*1.71*	*72*
CEL-08	*5*					*0.54*			*2.83*	
CEL-15	*5*					*0.54*			*2.83*	
INF-01	*5*					*0.65*			*3.26*	*59*
JEN-10	*5*					*0.48*			*2.57*	
LIN-01	*5*					*0.62*			*3.13*	*47*
MNU-05	*5*					*0.61*			*3.07*	
MNU-06	*5*					*0.64*			*3.23*	
PAK-02	*5*					*0.58*			*2.97*	
PAK-03	*5*					*0.81*			*3.90*	
TAM-03	*5*					*0.46*			*2.49*	

Appendix A1: Plot data tables (Tables A1–A3)

An effect of census interval is clear in forest plot data where multiple censuses have been conducted. Figure A1a shows the effect of increasing census length for the plots BNT-01, BNT-02 and BNT-04 in central Amazonia (Higuchi *et al.*, 1994). These plots have annual census data available for the period 1989–1997, enabling a partitioning of the dataset into equidistant census intervals of 1, 2, 4 and 8 years. The effect of census interval duration is approximately linear but relatively small (Fig. A1a). The zero-intercept defines the true or 'zero census interval' BA growth rate, and for a census interval of 8 years at these plots, BA growth rate would therefore have been underestimated by between 1.1% and 4.3%. Even an annual census underestimates BA growth rate by between 0.1% and 0.6%.

Assuming the linearity observed in Fig. A1a is generally applicable, we have directly estimated the magnitude of this census interval effect for all 50 plots in our dataset with three or more censuses (categories 1 and 3 in Table A1). For each plot the total census period was partitioned into smaller census periods and the BA growth rate calculated. Censuses were not always equidistant and so, where necessary, a mean census interval length was calculated by averaging. For example, if a plot was censused in 1990, 1994 and 1997, the total census period is 7 years, the subperiods are 4 and 3 years and the mean census period is taken as 3.5 years. This averaging is acceptable because of the linearity of the correction, but in general extremes in averaging were avoided (e.g. combining a 6 years interval with a 1 year interval to give a mean census interval of 3.5 years). In the above example, we could then compare the BA growth rate measured with a census interval of 7 years, with that measured when the mean census interval is 3.5 years. The subintervals were always summed to the same total census period for each particular plot (e.g. 1989–1997 in Fig. A1a). This ensured that interannual variations or long-term trends in BA growth rate did not cause the benchmark 'true' BA growth rate to vary.

The results for all plots are shown in Fig. A1b. In most cases the census interval effect is small but

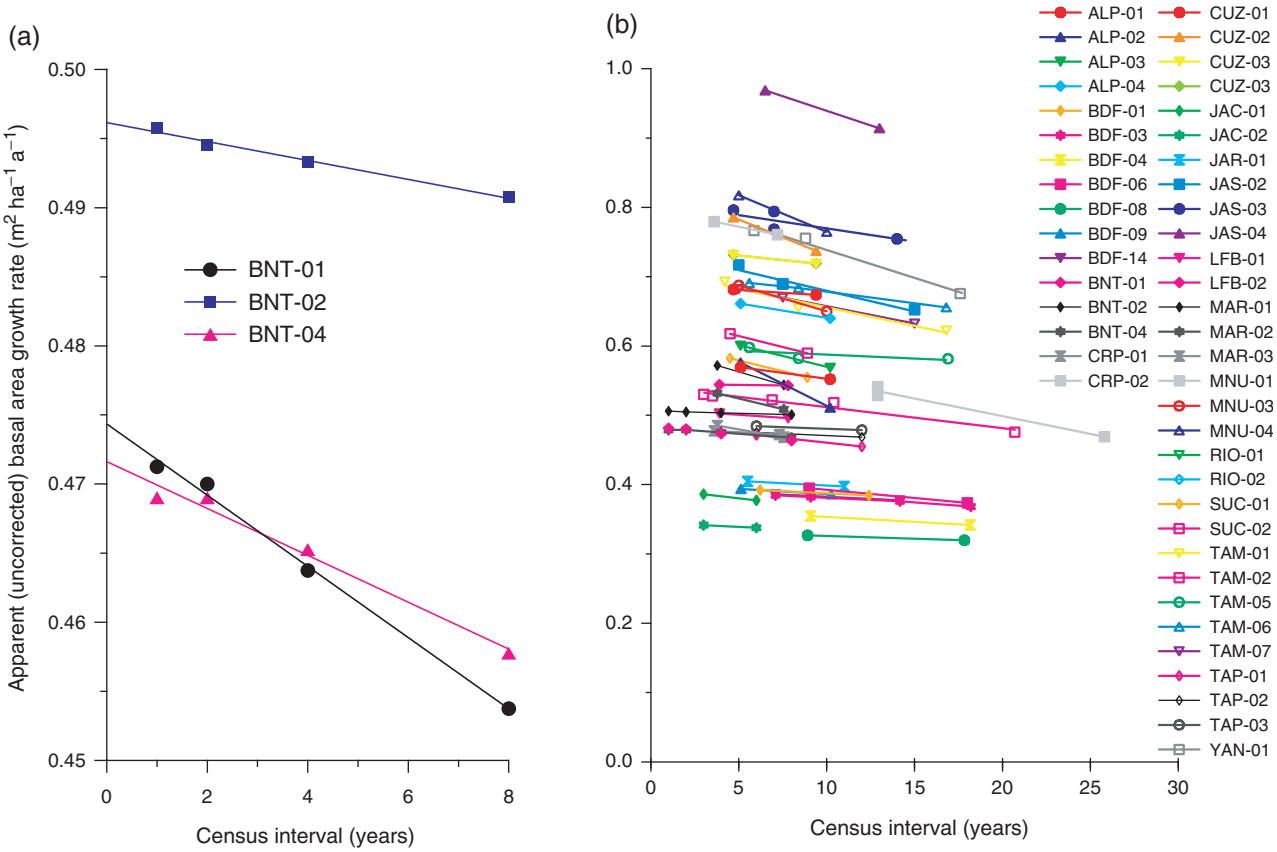

Fig. A1 (a) Demonstration of the census interval effect: a decrease of the measured annual basal area growth rate with increasing time interval between censuses. Results are shown for the plots BNT-01, BNT-02, BNT-04, for the period 1989–1997, where annual census data are available. (b) The census interval effect for all 50 plots with data for three or more censuses. The apparent basal area growth rate declines with increasing census interval at every plot.

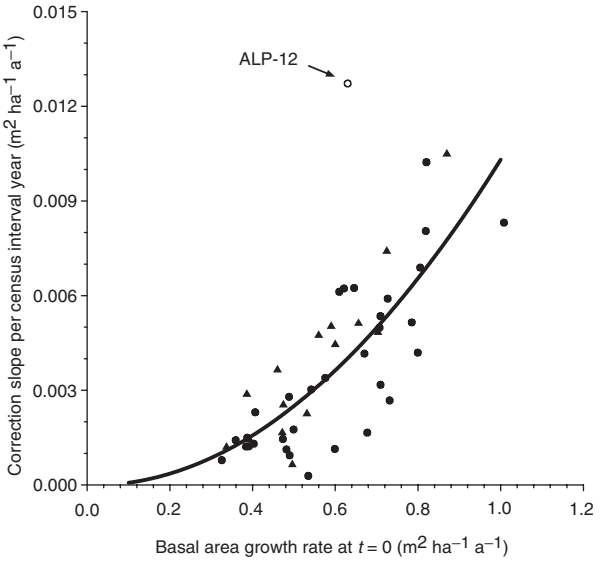

Fig. A2 The relationship between the gradient of the census interval effect (the slope of the lines in Fig. A1b, and the corrected basal area productivity (the intercept of the lines in Fig. A1b). The line is a quadratic fit, excluding the one outlier (ALP-12), with the equation $y = 0.0946x^2 - 0.000729x$ ($r^2 = 0.65$), where y is the gradient of the census interval effect, x is the basal area growth rate. The symbols are coded according to the analysis category in Table A1 (solid circle = 1, solid triangle = 3).

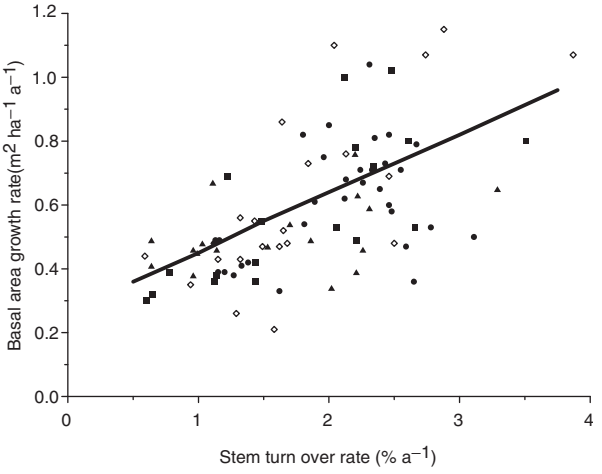

Fig. A3 The relationship between stem turnover rate and basal area growth rate. Symbol coding is according to analysis category in Table A1 (solid circle = 1, solid square = 2, solid triangle = 3, open diamond = 4).

significant. For plots where more than three censuses had been conducted, it is also apparent, as for the plots shown in Fig. A1a, that the correction is effectively linear. As would be expected, the slope of the correction appears greater at more productive plots (see Fig. A2). The zero-census interval BA growth rate was taken as the zero-intercept of the trend line and the magnitude of each correction is shown in Table A2 (plots in bold type: categories 1 and 3). For these plots the median of the correction slope is 0.0031 m^2 BA per census interval year (maximum = 0.0102, minimum = 0.0003).

The magnitude of the correction slope should be proportional to the product of the BA growth rate and the rate of fractional loss of BA through mortality. For a mature forest in quasi-equilibrium, BA growth ≈ BA mortality, and therefore the correction slope will vary approximately as the square of BA growth rate. Figure A2 plots the gradient of the correction (the slopes of the regression lines in Fig. 2b) against the corrected BA growth rate (the intercepts of the regression lines in Fig. 2b). With the exception of one outlier (ALP-12), there is a good relationship between these two variables. Excluding ALP-12, and assuming that the relationship should pass through the origin, the quadratic fit is

$$\text{Correction slope} = 0.00946\,(\text{BA growth rate})^2 - 0.000729\,(\text{BA growth rate}) \quad (r^2 = 0.59).$$

The linear term is relatively small compared with the quadratic one and significantly improves the relationship. It is thus kept for empirical reasons. This relationship provides the basis for a more generally applicable census interval correction for plots where only a single estimate of BA growth rate was available (i.e. there had been only two censuses). For such situations, the steps applied were as follows:

1. Calculation of the BA growth rate from original data.
2. Taking this value as an initial estimate of the corrected BA growth rate, use the relationship in Fig. A2 to estimate the correction slope.
3. Multiplication of the correction slope by the census interval and adding this to the original BA growth rate measurement to derive a census-interval corrected estimate of BA growth rate.
4. Using this revised estimate of BA growth rate to calculate a new estimate of the correction slope (step 2), and iteration of steps 2–4 until the estimates of BA growth rate stabilized to the required precision. Typically three iterations were sufficient for a precision of $< 0.001\ m^2\ ha^{-1}$.

For the 40 plots in normal type in Table A2 (plots of categories 2 and 4), the census interval corrected BA gain has been estimated using this approach. The correction for all plots in categories 1–4 has a median value of 4.8%, with a minimum of 0.3% and a

maximum of 29.8%. On an annual basis, the median value of the correction is 0.67% per census interval year (minimum 0.04%, maximum 1.39%).

The relationship between stem turnover (the average of the rate of recruitment and mortality of tree stems) and BA growth rate is shown in Fig. A3. As more dynamic plots have higher stem turnover and higher BA growth rate, there is a correlation between the two factors, although the significance of linear fit is relatively low ($y = (0.1678 \pm 0.0257\,\mathrm{SE})\ x + (0.2578 \pm 0.0506\,\mathrm{SE})$; $r^2 = 0.37$, $P < 0.01$). There is no improvement if only *terra firme* forests are considered ($y = 0.1459x + 0.2869$; $r^2 = 0.32$). The relationship for all forests has therefore been applied to estimate BA growth rate for 14 further plots for which only stem turnover data were available (italic type in Table A2; plots of category 5), with a proviso that the uncertainties on the magnitudes of these estimates are higher.