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# The global relationship between forest productivity and biomass

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## ABSTRACT

**Aim** We aim to determine the empirical relationship between above-ground forest productivity and biomass. There are theoretical reasons to assume a relationship between forest structure and function, as both may be influenced by similar ecological factors such as moisture supply. Also, dynamic global vegetation model simulations imply that any increase in forest productivity driven by climate change will result in increases in biomass and therefore carbon storage. However, few studies have explored the strength and form of the relationship between forest productivity and biomass, whether in space or time.

**Location** Global scale.

**Methods** We collated a large data set of above-ground biomass (AGB) and above-ground net primary productivity (ANPP) and tested the extent to which spatial variation in forest biomass across the Earth can be predicted from forest productivity.

**Results** The global ANPP–AGB relationship differs fundamentally from the strongly positive, linear relationship reported in earlier analyses, which mostly lacked tropical sites. AGB begins to peak at *c.* 15–20 Mg ha<sup>-1</sup> year<sup>-1</sup> ANPP, plateaus at ANPP > 20–25 Mg ha<sup>-1</sup> year<sup>-1</sup>, and may actually decline at higher levels of production.

**Main conclusions** High turnover rates in high-productivity forests may limit AGB by promoting the dominance of species with a low wood density. Predicted increases in ANPP will not necessarily favour increases in forest carbon storage, especially if changes in productivity are accompanied by compositional shifts.

## Keywords

**Biomass, carbon storage, dynamic global vegetation models (DGVMs), global data set, global forests, net primary productivity.**

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## INTRODUCTION

Forests represent an important carbon store, containing an estimated 638 Gt C (1 Gt = 1 billion tonnes) in their ecosystem as a whole, with 283 Gt C in biomass alone (FAO, 2005). Consequently, changes in the forest carbon store have an impact on global climate change. Even potentially small increases in carbon sequestration in forest biomass and soil may help buffer the impact of anthropogenic carbon dioxide (CO<sub>2</sub>) emissions, regulating the rate of climate change (Cao & Woodward, 1998a; Phillips *et al.*, 1998; Jastrow *et al.*, 2005). Whether or not forests will be able to continue to sequester additional carbon is a key concern as atmospheric CO<sub>2</sub> concentrations continue to rise. Most dynamic global vegetation model (DGVM) simulations

suggest that rising concentrations of CO<sub>2</sub> and increasing temperatures will stimulate tree growth across most of the Earth's surface, so increasing globally averaged productivity and potential vegetation biomass stores through to at least the mid-21st century (Cao & Woodward, 1998b; Cox *et al.*, 2000; Gerber *et al.*, 2004).

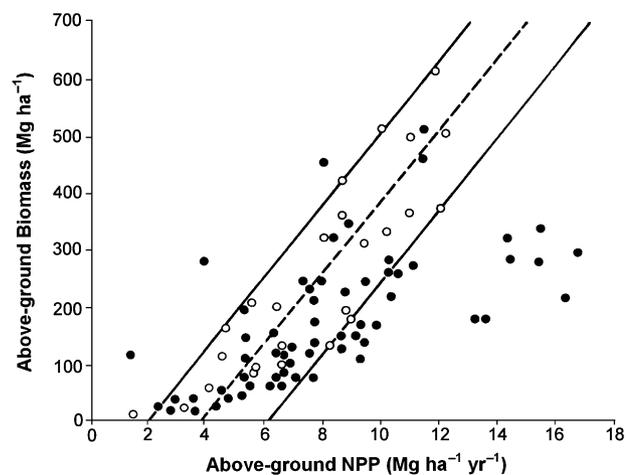
DGVMs incorporate both ecophysiological and biophysical processes in order to simulate ecosystem functions, through delineating climate, vegetation and soils and modelling fluxes in carbon, water, and in some cases nutrients, between vegetation, soils and the atmosphere (Cramer *et al.*, 1999). DGVMs can therefore be used to model forest carbon production and subsequent carbon storage, with applications including estimation of the present-day geographical distribution of forest carbon (Bonan *et al.*, 2003), past reconstructions (Joos *et al.*, 2004) and

modelling future scenarios, simulating the effect of climate change on global ecosystems, and ecosystem feedbacks on climate change (Cramer *et al.*, 2001).

Process-based representations of photosynthesis, respiration, carbon allocation, disturbance and mortality are used in DGVMs to calculate ecosystem carbon storage, with vegetation biomass annually updated using the sum of annual net primary productivity, less reproduction costs and losses to biomass turnover for each plant functional group (Bonan *et al.*, 2003). The resulting forest biomass outputs tend to respond positively to rising productivity, with a corresponding increase in carbon storage.

There are strong theoretical reasons to assume a relationship between productivity and biomass. Biomass is a direct function of productivity, and both are limited by similar ecological factors, such as moisture availability (Knapp & Smith, 2001; Ryan *et al.*, 2006), temperature (Raich *et al.*, 2006) and nutrient availability (Laurance *et al.*, 1999; Malhi *et al.*, 2004). It seems intuitively unlikely, however, that biomass should simply increase monotonically with increasing productivity, whether in space when comparing forests of the world, or in time when simulating future high-productivity ecosystems. The prediction is obviously inconsistent with the observation that whereas the highest productivity levels are found in tropical regions (Saugier *et al.*, 2001), the most massive forests are found in some temperate climates, such as the redwood forests of northern California [e.g. *Sequoia sempervirens* (D. Don) Endl.; Busing & Fujimori, 2005]. Additionally, it is evident that factors other than growth rates also determine biomass levels. For example, disturbance regimes clearly influence the ability of forests to accumulate carbon (Pregitzer & Euskirchen, 2004). Current DGVMs do include some mechanisms that may modify the increase in biomass storage with increasing productivity, principally fire disturbance (Thonicke *et al.*, 2001) and hydraulic limitations (Gerten *et al.*, 2005).

Given that it is both a basic property of the biosphere and essential for the development of vegetation models, it is surprising how poorly characterized the empirical relationship between forest productivity and biomass is. Indeed, the only really large-scale empirical evaluations of the relationship pre-date the advent of computer models of the biosphere. Whittaker and Likens (1973) found a positive linear relationship between the above-ground net primary productivity (ANPP) and the above-ground biomass (AGB) of 25 forest stands in the continental United States. However, since the study was restricted to temperate forests it lacked high-productivity sites. A more globally extensive forest data set collated by the International Biological Program (IBP) (O'Neill & De Angelis, 1981) appeared to verify Whittaker and Likens' (1973) relationship (Fig. 1), but this study, despite incorporating data from 117 forests, also contained few natural high-productivity sites, reflecting our poor knowledge base for tropical forest ecosystem processes in the late 20th century. A recent study of moist tropical forests also appeared to support Whittaker and Likens' positive linear relationship (Raich *et al.*, 2006), but with an ANPP range from 2 to 19 Mg ha<sup>-1</sup> year<sup>-1</sup> (Mg = megagrams), still does not represent truly high-productivity forests.



**Figure 1** Relationship between forest above-ground net primary productivity (NPP) and above-ground biomass. Relationship based on the data of Whittaker and Likens (1973) (data represented by open circles); regression fit shown by dashed line ( $y = 0.625x - 250$ ), with solid lines representing extremes of the original data. Solid circles represent the IBP woodland data set (O'Neill & De Angelis, 1981). Graph from O'Neill & De Angelis (1981).

We attempt here a more comprehensive analysis: (1) to specifically test whether the productivity–biomass relationship hypothesised by Whittaker and Likens holds for high-productivity forests; and (2) to provide a global-scale empirical relationship to aid in constructing and testing mechanistic models such as DGVMs. Forest biomass and productivity research has mostly focused on above-ground components due to the difficulty of accurately estimating below-ground components, and where below-ground biomass or NPP are considered these values are often only approximations based on a theoretical proportion of above-ground levels (Clark *et al.*, 2001). Consequently, we confine our analysis to AGB and ANPP.

## METHODS

In order to represent forest structure and function across each biome we collated a global data set of forest productivity and biomass to span as wide a spectrum of forest climates and biogeographical regions as possible. A thorough literature search identified studies where both stand-level AGB and ANPP had been calculated using forest inventories. Sites were allocated to biome according to climatic classifications, based on the Köppen system (Köppen, 1923): tropical humid forests (TrH) with mean monthly temperature > 18 °C and mean monthly precipitation > 100 mm; tropical seasonal (TrS) with mean monthly temperature > 18 °C and mean monthly precipitation < 100 mm for ≥ 2 months; tropical montane (TrM) with mean temperature of the coldest month < 18 °C due to altitude; temperate (Te) with mean temperature of the coldest month < 18 °C but > -3 °C; boreal (B) with mean temperature of the coldest month < -3 °C; montane (M) with mean temperature of the coldest month < -3 °C due to altitude. Only forests described as 'old growth' or 'mature' were included,

i.e. those with no human intervention or large-scale disturbance for at least 100 years. The original investigators of each study calculated AGB and ANPP using the following methods.

### Biomass (AGB)

'Biomass' refers to living organic matter, expressed as dry mass ( $\text{Mg ha}^{-1}$ ). Appropriate allometric models were used based on representative destructively harvested samples, in which individual tree structural attributes [e.g. diameter at breast height (d.b.h.), height, wood density] are used to estimate mass (Brown, 1997; Ketterings *et al.*, 2001). The only exception to this method was for samples for which appropriate allometric equations were unavailable, including *S. sempervirens* (coastal redwood). In these cases, stem wood mass was estimated using parabolic wood volume, multiplied by taper corrections and wood density, with empirical ratios used to predict bark, branch and foliage mass (e.g. Westman & Whittaker, 1975).

Understorey vegetation, epiphytes and climbers also contribute to total above-ground forest biomass. Within tropical forests, overstorey trees strongly dominate stand-level AGB (Clark *et al.*, 2001), with low light levels in the understorey limiting biomass to generally < 3% of total AGB (Brown, 1997). Consequently, non-tree components are often excluded from tropical AGB estimates. Eighty per cent of tropical lowland estimates are based on measurements of trees  $\geq 10$  cm d.b.h., with 67% of tropical montane estimates based on trees  $\geq 4.8$  or 5 cm d.b.h. and 33% on trees  $\geq 10$  cm d.b.h. In temperate and boreal forests, more open canopies mean that understorey layers may contribute more significantly to stand-level biomass. In the majority of temperate, boreal and montane sites in our study (92%), either the understorey vegetation is included in estimates, or the components measured are not detailed, with minimum diameter thresholds for tree measurements usually ranging from 1 to 5 cm. Shrub biomass is estimated using appropriate allometric equations, and ground vegetation through harvesting representative quadrats (e.g. Arthur & Fahey, 1992).

### Productivity (ANPP)

ANPP was calculated as the sum of biomass increment and litterfall. Biomass increment was estimated through repeated stand-level measurements (Chambers *et al.*, 2001) or, where reliable annual rings were available, growth cores with radial increments converted to biomass increments via allometric relationships (Clark *et al.*, 2001). For species lacking appropriate allometric models, biomass increment values were estimated using stem volume increments and appropriate empirical ratios for bark, branches and foliage (e.g. Westman & Whittaker, 1975). Non-tree production is excluded in the majority of tropical estimates, with understorey vegetation providing negligible productivity relative to the overstorey component (Clark *et al.*, 2001). In temperate and boreal forests, more open canopies permit understorey vegetation to contribute significantly to overall production (Clark *et al.*, 2001). In the majority of temperate, boreal and montane sites in our study (92%), understorey

vegetation production has been estimated, or the components measured are not detailed.

In addition to the ANPP invested in biomass increment, a large fraction of above-ground production is lost as litterfall, including leaves, woody debris and reproductive parts (Clark *et al.*, 2001). Within some studies, annual litterfall production was estimated using litter traps. However, not all studies incorporate an estimate of litterfall, and where it has been measured the components included (i.e. foliage, woody debris, fruit and flowers) often vary.

### Estimation of unmeasured ANPP components

We needed to standardize ANPP values where litterfall estimates were lacking or had missing components. Where tropical lowland forests lacked litterfall estimates, the relationship between above-ground coarse woody productivity (AGWP) and litterfall proposed by Malhi *et al.* (2004) was used to predict this component. For other biomes we used estimates from other studies of the same species in similar locations as an approximation (for details see Table 1 and Appendix S1 in Supplementary Material).

All ANPP estimates were also systematically standardized to reduce likely biome-related biases. Firstly, in warm, humid climates, rapid rates of decomposition mean that some litterfall is lost through decay and is consequently unaccounted for in productivity measurements (Clark *et al.*, 2001). Tropical forest ANPP values may therefore be significantly underestimated, to a much greater extent than in temperate and boreal climates. Tropical litterfall traps are typically emptied twice monthly to reduce this loss, but litter trapped in the canopy may decompose completely. Small woody litter in tropical forests has been observed to lose an average of  $38 \pm 2\%$  of its mass before falling into traps (Edwards, 1977), with equivalent losses found from leaves trapped in the canopy (Frangi & Lugo, 1985). Therefore, we estimated the litterfall lost through decomposition by assuming that the litterfall remaining was 62% of the original total, so multiplying the litterfall estimate (litterfall measured in the study, plus any estimated components) by 1.613 to derive the total litter production.

Secondly, we needed to account for losses of above-ground production to herbivory. Leaf herbivory, seed and fruit predation, and sap consumption are rarely measured in productivity studies, but can be considerable and are likely to vary between biomes. Again, greater losses are expected in tropical forests due to the greater insect biomass and activity in warm, moist environments (Coley & Aide, 1991; Clark *et al.*, 2001). Therefore, we adjusted ANPP values to take both insect and mammal herbivory into account, using biome-specific studies (Table 1, Appendix S1). The herbivory estimates applied are greatest in tropical forests, both for insects ( $0.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ) and vertebrates ( $0.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ) (Chave *et al.*, 2003). Within temperate, montane and boreal forests, insect herbivory was estimated as a percentage of either needle biomass (0.7%) (Larsson & Tenow, 1980), needle production (2.5%) (Larsson & Tenow, 1980) or broad leaf production (1.59%) (Reichle & Crossley, 1967; Nielsen, 1978), and vertebrate herbivory estimated as 0.056

**Table 1** Standardisation factors for above-ground net primary productivity (ANPP) data.

Factor	Tropical	Temperate	Montane	Boreal
Estimated litterfall (components: foliage, woody and reproductive parts)	Lowland forests: interpolated from estimated relationship between above-ground woody productivity and litterfall (source 1). Other: missing components derived from average of similar studies (source 2)	Missing components derived from average of similar studies (sources 2–5)	Missing components derived from average of similar studies (source 6)	Missing components derived from average of similar studies (sources 2, 4)
Potential litterfall lost to decomposition (tropical only)	(Litterfall/62) × 38 (sources 7, 8)	—	—	—
Biogenic volatile organic compounds (Mg ha <sup>-1</sup> year <sup>-1</sup> )	Rain forest, 0.653; seasonal, 0.442; montane, 0.316 (source 9)	Coniferous, 0.211; deciduous, 0.105; mixed, 0.147; mediterranean, 0.063; snow/rain conifer, 0.316 (source 9)	Snow/rain conifer, 0.316; snowy conifer, 0.063; snowy deciduous, 0.042 (source 9)	Conifer, 0.042 (source 9)
Losses to herbivory	Insect: 0.5 Mg ha <sup>-1</sup> year <sup>-1</sup> (source 10)	*Insect. Coniferous: 0.7% total needle biomass or 2.5% needle production (source 11). Deciduous: 1.59% ANPP (mean, <i>n</i> = 2, range 0.75–1.5%) (sources 12, 13)		
	Vertebrate: 0.3 Mg ha <sup>-1</sup> year <sup>-1</sup> (source 10)	*Vertebrate. Deciduous: 0.056 Mg ha <sup>-1</sup> year <sup>-1</sup> (source 14). Coniferous: 0.0298 Mg ha <sup>-1</sup> year <sup>-1</sup> (mean, <i>n</i> = 4, range 0.0001–0.058 Mg ha <sup>-1</sup> year <sup>-1</sup> ) (source 15)		

Sources: 1, Malhi *et al.* (2004); 2, Cannell (1982); 3, Law *et al.* (2001); 4, De Angelis *et al.* (1981); 5, Archibold (1995); 6, Arthur & Fahey (1992); 7, Edwards (1977); 8, Frangi & Lugo (1985); 9, Guenther *et al.* (1995); 10, Chave *et al.* (2003); 11, Larsson & Tenow (1980); 12, Reichle & Crossley (1967); 13, Nielsen (1978); 14, Bobek *et al.* (1979); 15, McInnes *et al.* (1992). \*applies to temperate, montane and boreal forests.

**Table 2** Confidence index scoring protocol.

	Score			
	1	2	3	4
AGB sample area	No information/< 0.25 ha	$0.25 \geq x < 0.5$ ha	$0.5 \geq x < 1$ ha	$\geq 1$ ha +
AGB repetitions*	No information/1	2	3	4+
ANPP repetitions*	No information/1	2	3	4+
Allometric equation	No information	Appropriate for species	Appropriate for species and location	Site and species specific
Litterfall estimates†	No estimate	One component	Two components	Three components

AGB, above-ground biomass; ANPP, above-ground net primary productivity.

\*Number of censuses (AGB) or census periods (ANPP) on which the estimate was based.

†Litterfall components are foliage, woody debris and reproductive parts (e.g. fruit and flowers).

Mg ha<sup>-1</sup> year<sup>-1</sup> for deciduous sites (Bobek *et al.*, 1979) and 0.0298 Mg ha<sup>-1</sup> year<sup>-1</sup> for coniferous sites (McInnes *et al.*, 1992).

Finally, a fraction of above-ground forest production is lost through volatile emissions of biogenic volatile organic compounds (BVOCs). Although this is difficult to quantify with certainty, it is known that BVOC emissions increase with temperature (Clark *et al.*, 2001), so tropical forests can be expected to suffer the greatest losses. For each biome, we used predicted BVOC emissions following Guenther *et al.* (1995) to adjust the forest ANPP estimates (Table 1). It has recently been suggested (Keppler *et al.*, 2006) that plants also emit methane, possibly in proportion to productivity. However, as the quantities of carbon involved are likely to be small and the process not yet shown outside laboratory studies, we ignore it here.

### 'Confidence index'

Compilation from various data sources, involving different investigators often applying slightly different methods, leads to varying confidence in the reliability of estimates. Consequently, the reliability of each ANPP and AGB estimate was rated according to a priori criteria, defined to produce a composite site-based 'confidence index', which accounts for methodological issues that have been highlighted as important possible sources of error. This is necessarily a rather crude exercise but is preferable to treating all sites equally, and allows us to explore how using data of potentially different quality could affect the perceived relationship between ANPP and AGB.

The first issue considered was the sample area used to estimate biomass, with this ranging from 0.05 to 50 hectares between studies. Small sample areas are particularly prone to produce biased landscape-scale biomass estimates. The presence of an exceptionally large tree within the plot, for example, may lead to an over-estimate of stand-level biomass. Although areas > 0.25–0.5 ha have been shown to provide a sufficient degree of reliability for stand-level AGB estimates (Clark & Clark, 2000; Chave *et al.*, 2004), in eastern Amazonia, sample areas > 5 ha were necessary to attain 95% confidence of estimating landscape-scale biomass to within  $\pm 10\%$  of the mean (Keller *et al.*, 2001). While this potential small-plot bias cannot be simply removed (there are only two published AGB and ANPP studies based on sample areas of

> 5 ha), it needs to be accounted for (Table 2). The sample area used to estimate ANPP is less of an issue because production is controlled by horizontally diffused variables, such as canopy-incident light (Williams *et al.*, 1997), rather than concentrated in the few biggest trees, and is therefore not considered.

The second and third factors accounted for in the confidence index are the number of repetitions of AGB and ANPP estimation. Forest structure and dynamics during and after an unusually dry or wet period are potentially unrepresentative of longer-term values (Adams & Kolb, 2005). Therefore, we assessed the number of censuses (AGB) and inventory periods (ANPP) that estimates were based upon (Table 2).

Fourthly, the quality and suitability of the allometric equation used affects confidence in the estimate. Allometric equations are approximations of the relationship between structural variables and AGB based on 'best fit' models, and therefore the quality of this model is important (Ketterings *et al.*, 2001). Ideally, allometric models should be applied based on comprehensive species-specific destructive sampling from the study location in order to produce the most accurate AGB estimates. However, time constraints and high species diversity (especially in tropical forests) usually necessitate the use of more general equations (Clark *et al.*, 2001; Ketterings *et al.*, 2001). Therefore, studies that used site- and species-specific regressions were differentiated from those applying published equations based on different locations, or different species (Table 2).

Finally, where litterfall estimates were lacking or incomplete, estimated components (with associated error) were used to standardize ANPP estimates. Therefore, the ANPP estimate was also rated according to the degree by which litterfall was based on actual site-specific measurements (Table 2).

All factors within the confidence index were weighted equally, with each based on a score from 1 to 4. One point was given where information was not available concerning these factors. Potentially, values for the index therefore range between 5 (least confidence) and 20 (greatest confidence).

### Empirical model selection

We compared three statistical models to select the most appropriate fit to the data. Following Whittaker and Likens (1973) we

tested linear regression models. Scatter plots also highlighted quadratic and asymptotic models as potential fits. Linear, quadratic and asymptotic models were therefore fitted and compared for: (1) the full data set; (2) the full data set after excluding extreme outliers (defined as outlying values consistently having standardized residual error  $> 2$ ); and (3) a 'core' data set including only data with a confidence index greater than or equal to the median score of 9. The Michaelis–Menten asymptotic model was fitted iteratively using SPSS version 13.0 (SPSS Inc, Chicago, IL, USA). The Akaike information criterion (AIC) (Akaike, 1974) was calculated to help select the best statistical model for each data set. Where little difference is found between the AIC of models, the probability that the correct model has been chosen can be calculated using the equation:

$$\text{Probability} = \frac{e^{-0.5\Delta\text{AIC}}}{1 + e^{-0.5\Delta\text{AIC}}}$$

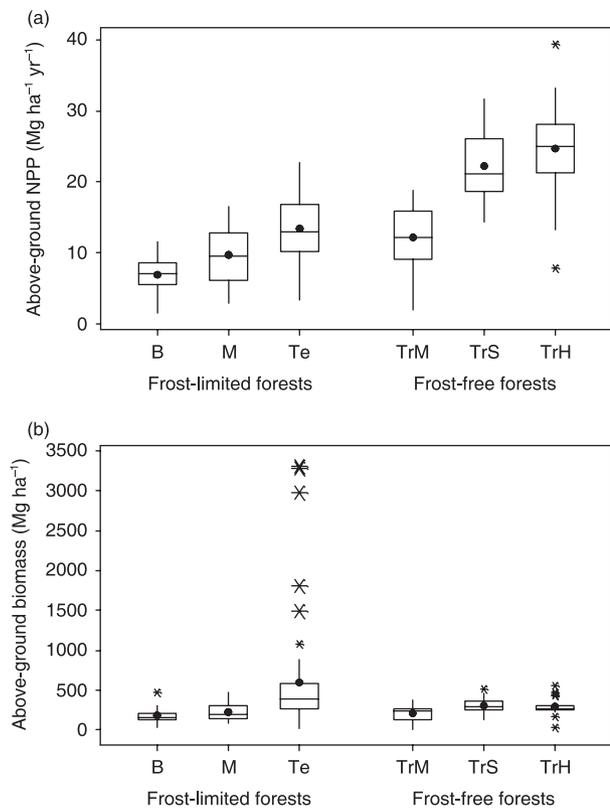
where  $\Delta\text{AIC}$  is the difference between AIC scores (Motulsky & Christopoulos, 2004).

In parametric statistical analyses it is assumed that the error associated with the response variable is constant. However, due to the varying reliability in this data set (cf. confidence index), constant error cannot be assumed. Therefore, in a subset of our analyses, we used weighted regression to account for this, with greater weight attributed to more reliable estimates. To determine how important the uneven level of confidence in plot data might be in driving our results, we weighted the data according to confidence index scores, with scores of 5 and 6 weighted as 0.2, 7 and 8 weighted as 0.4, 9 and 10 weighted as 0.6, 11 and 12 weighted as 0.8, and 13, 14 and 15 weighted as 1.0.

Finally, the estimated ANPP components, of which litterfall is the greatest, may themselves contribute some error to the overall ANPP estimate. To account for this potential error, two additional analyses of the relationship between ANPP and AGB were undertaken. Firstly, we truncated the data set by only including those sites that measured total litterfall *in situ*, and used the 'unstandardized' ANPP estimates from the original study. Secondly, we incorporated all sites, including all unmeasured ANPP component estimates, but where tropical lowland litterfall has been estimated based on the proposed relationship with AGWP (Malhi *et al.*, 2004), a cap was placed on this litterfall estimate to rise no higher than the highest measured value (12.8 Mg ha<sup>-1</sup> year<sup>-1</sup> from BCI Plateau, Panama; Foster, 1982). The resulting relationships found using these data sets could therefore be compared with those gained using the full, 'standardized' data set.

## RESULTS

Our global data set includes 191 mature forest sites, including 96 tropical, 55 temperate and 41 boreal and montane forests, in North and South America, Europe, Africa and Asia (see Appendices S1, S2 and S3 in Supplementary Material). No appropriate data were available for Australasia. The confidence index for each study ranged from 5 to 15, with a median of 9 for the whole data set. The tropical biome had the highest median score (11); temperate, montane and boreal biomes all had median scores of 7.



**Figure 2** Box plots of forest: (a) above-ground net primary productivity (NPP) (Mg ha<sup>-1</sup> year<sup>-1</sup>); (b) above-ground biomass (Mg ha<sup>-1</sup>); for different biome types: B, boreal ( $n = 27$ ); M, montane ( $n = 14$ ); Te, temperate ( $n = 54$ ); TrM, tropical montane ( $n = 28$ ); TrS, tropical seasonal ( $n = 40$ ); TrH, tropical humid ( $n = 28$ ). Box plots show 25% quartile, median and 75% quartile of the distributions (horizontal lines); vertical lines extend a further 1.5 times the interquartile (25–75%) range; ● denotes mean; \* denotes outlier; ✕ denotes extreme outlier (standardized residual error consistently  $> 2$ ).

The greatest ANPP is found in tropical regions, but the highest-biomass forests are located in temperate climates (Fig. 2a,b). The greatest range of AGB values is also found in temperate forests, with five extreme outliers representing forests from the Pacific Northwest of the United States: four *S. sempervirens* forests in northern California and one *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest in Oregon. These forests have AGB values from 1492 to 3300 Mg ha<sup>-1</sup>, much greater than those for tropical lowland biomass (mean  $\pm$  SE: 294.1  $\pm$  10.1 Mg ha<sup>-1</sup>). Even after excluding these five sites, temperate forest biomass (387.3  $\pm$  33.9 Mg ha<sup>-1</sup>) is still significantly greater than tropical lowland biomass (Mann–Whitney test,  $P = 0.035$ ). These five sites are consistently associated with substantial residual error during model fitting ( $> 2$ ) and represent the 'outliers' referred to throughout this analysis.

The ANPP–AGB relationship was represented most appropriately by the quadratic regression model, for all three data sets (the full global data set, excluding only the five outliers, and the core data set of data with confidence index scores  $\geq 9$ ) (Table 3). The

**Table 3** Comparison of empirical regression models for relationship between global forest above-ground net primary productivity (ANPP) and above-ground biomass (AGB).

Model	$r^2$	Adjusted $r^{2*}$	$P$ value	AIC†	Probability‡
<b>All data (<math>n = 191</math>)</b>					
Linear					
AGB = 221.13 + 7.83 ANPP	0.02	0.02	0.049	2305.5	
Quadratic					
AGB = -109.10 + 56.27 ANPP - 1.410 ANPP <sup>2</sup>	0.07	0.06	0.001	2296.8	95.9%
Asymptotic					
AGB = 563.459 ANPP/(ANPP + 8.268)	0.04	0.04	< 0.001	2303.1	4.1%
<b>Outliers excluded (<math>n = 186</math>)</b>					
Linear					
AGB = 184.69 + 6.33 ANPP	0.09	0.09	< 0.001	1880.0	
Quadratic					
AGB = 6.45 + 32.61 ANPP - 0.764 ANPP <sup>2</sup>	0.20	0.19	< 0.001	1859.3	99.2%
Asymptotic					
AGB = 443.887 ANPP/(ANPP + 7.266)	0.15	0.15	< 0.001	1868.9	0.8%
<b>Core data§ (<math>n = 106</math>)</b>					
Linear					
AGB = 136.55 + 6.28 ANPP	0.24	0.23	< 0.001	965.2	
Quadratic					
AGB = 22.69 + 22.73 ANPP - 0.463 ANPP <sup>2</sup>	0.36	0.35	< 0.001	949.4	91.3%
Asymptotic					
AGB = 401.811 ANPP/(ANPP + 9.089)	0.33	0.32	< 0.001	954.1	8.7%
<b>Weighted quadratic models:</b>					
All data					
AGB = -36.54 + 39.76 ANPP - 0.956ANPP <sup>2</sup>	0.08	0.07	< 0.001		
Outliers excluded					
AGB = 17.09 + 28.45 ANPP - 0.648 ANPP <sup>2</sup>	0.23	0.22	< 0.001		
Core data§					
AGB = 15.42 + 22.96 ANPP - 0.498 ANPP <sup>2</sup>	0.38	0.37	< 0.001		

\*Adjusted  $r^2$ : adjusted to account for the number of terms in the model.

†AIC: Akaike information criterion for model comparison.

‡Probability: probability that the correct model has been chosen when comparing two AIC values.

§Core data set: all sites with a confidence index of  $\geq 9$ .

asymptotic model also provided a reasonable approximation, with little difference in the  $r^2$ , AIC and residual plots between the quadratic and asymptotic models. However, the quadratic model had the highest probability of being correct for the full data set, the data set excluding outliers, and the core data set (95.9%, 99.2% and 91.3%, respectively).

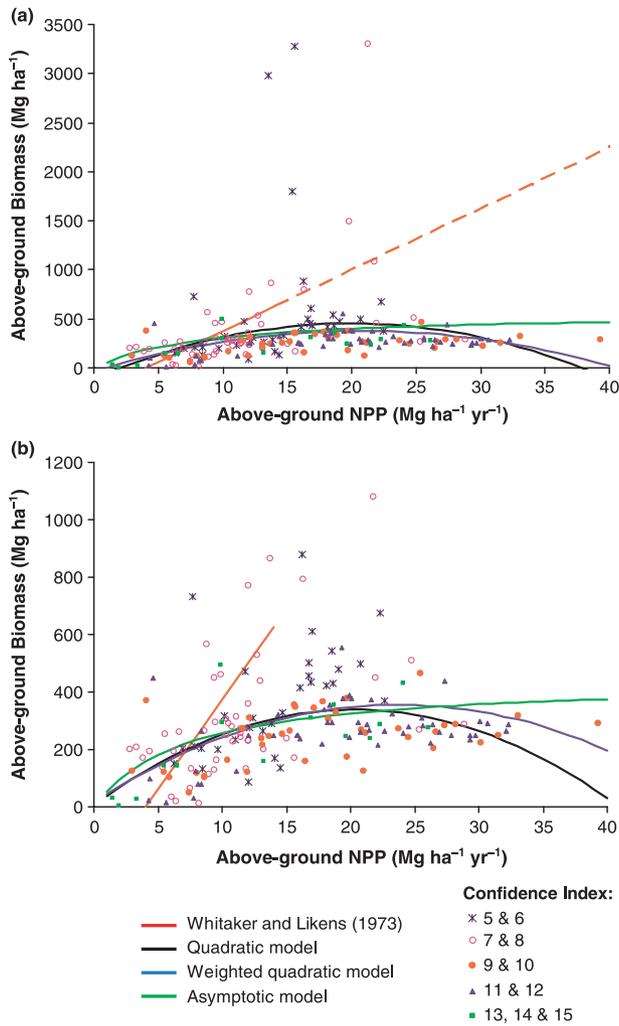
Although all models tested are statistically significant, the ANPP–AGB relationship is extremely weak in the full data set (quadratic regression model:  $r^2 = 0.07$ ,  $P = 0.001$ ) (Fig. 3a). Excluding the five outlying values improves the strength of the relationship (quadratic model:  $r^2 = 0.20$ ,  $P < 0.001$ ) (Fig. 3b). The core data set yields a much stronger relationship between AGB and ANPP (quadratic model:  $r^2 = 0.36$ ,  $P < 0.001$ ) (Fig. 4a,b). Weighted quadratic regression improves the strength of all relationships slightly (all data:  $r^2 = 0.08$ ; outliers excluded:  $r^2 = 0.23$ ; core data set:  $r^2 = 0.38$ ), but does not substantially change the resulting model (Table 3, Figs 3a,b & 4a).

The analyses using alternative data sets, undertaken for comparison with the ‘standardized’ data set, showed similar results. Restricting the analysis to ANPP values based purely on biomass

increment and litterfall estimates measured *in situ* limited the study to sites with ANPP  $< 20 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , so excluding the majority of tropical lowland forests from the relationship. Although model selection was consequently more difficult (between linear, quadratic and asymptotic), the gradient of all models was much shallower than that proposed by Whittaker and Likens (1973), with the quadratic model being slightly stronger ( $n = 63$ ,  $r^2 = 0.35$ ,  $P < 0.001$ , 56.2% probability of being correct compared with the linear model) (Fig. 5a). The second alternative analysis, using all sites with standardized ANPP values but with the cap on litterfall estimate, also shows the quadratic model to be strongest (core data only:  $n = 106$ ,  $r^2 = 0.36$ ,  $P < 0.001$ , 94.8% probability of being correct compared with the asymptotic model) with AGB beginning to plateau at ANPP 15–20  $\text{Mg ha}^{-1} \text{ year}^{-1}$  (Fig. 5b).

## DISCUSSION

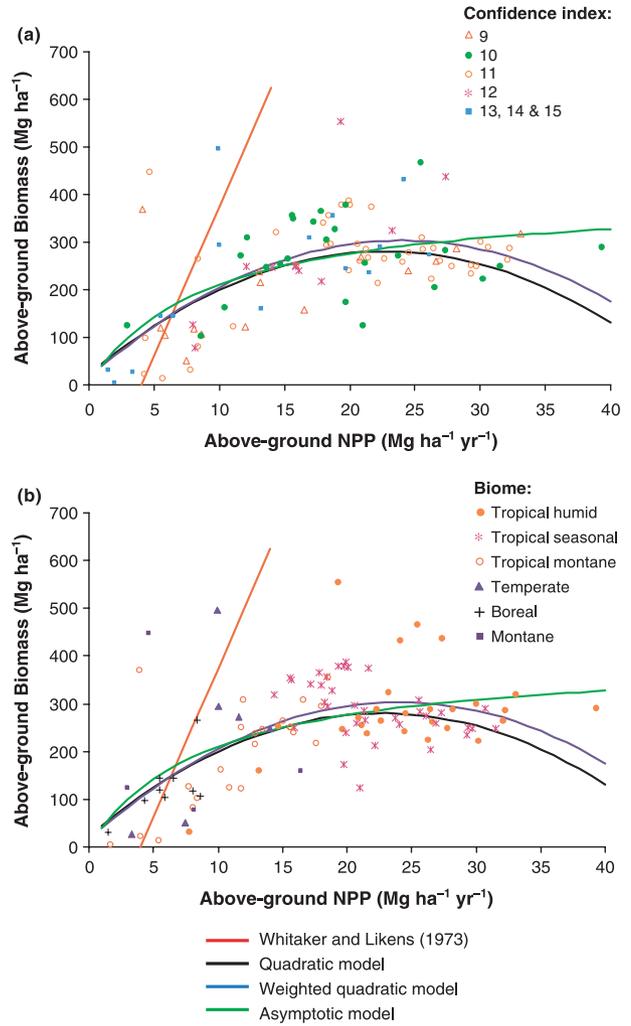
This analysis expands considerably upon previous studies of productivity–biomass relationships, by using a much larger and



**Figure 3** Regression models for the global relationship between above-ground net primary productivity (NPP) and above-ground biomass of mature forests, showing the degree of confidence in each estimate [scale: 5 (least) to 15 (most)]. Whittaker and Likens' (1973) linear model, and its extrapolation to high-productivity sites, is also shown ( $y = 0.625x - 250$ ). (a) All data ( $n = 193$ ); (b) outliers excluded ( $n = 188$ ).

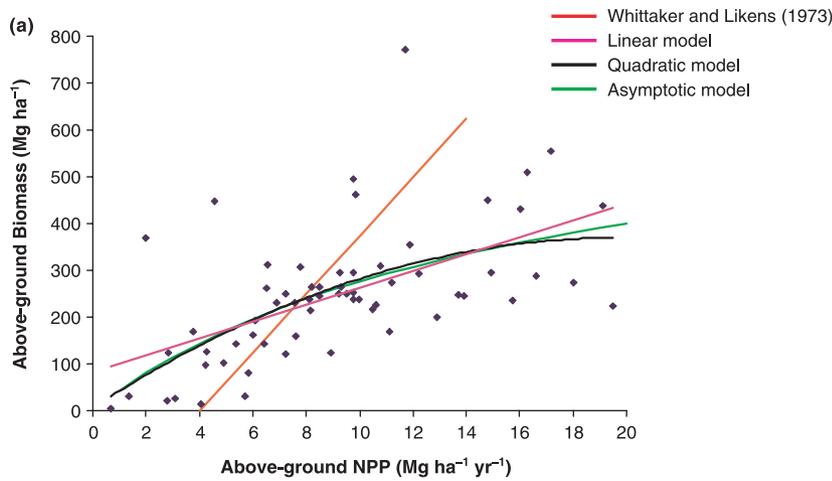
more comprehensive data set than was available to Whittaker and Likens (1973) and the IBP (O'Neill & De Angelis, 1981), and in particular by including a much improved representation of high-productivity tropical forests. We clearly demonstrate that the linear relationship previously assumed between forest above-ground productivity and biomass is incorrect. While a positive relationship exists between ANPP and AGB for low-productivity sites, it weakens at mid-productivity sites and biomass levels saturate completely in high-productivity forests.

In low-productivity sites, biomass is low. Climatic constraints, such as low temperatures and short growing seasons, limit productivity, and therefore biomass, in boreal and montane sites (Archibold, 1995). In these ecosystems, increasing temperatures are likely to enhance total annual production and may permit greater accumulation of biomass. In areas with mid-range ANPP

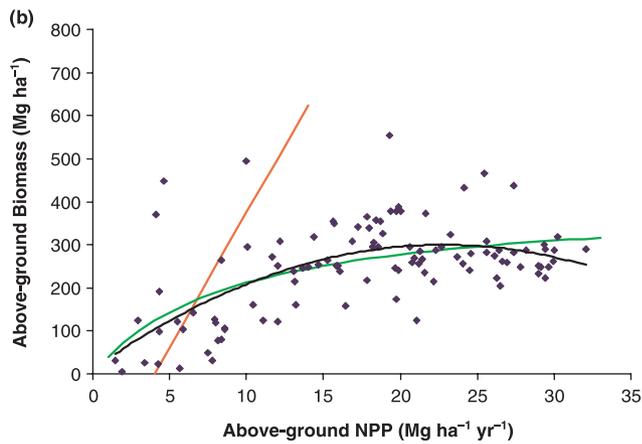


**Figure 4** Regression models for the global relationship between above-ground net primary productivity (NPP) and above-ground biomass of mature forests for the 'core' data set (data with a confidence index score  $\geq 9$ ,  $n = 106$ ). Whittaker and Likens' (1973) linear model ( $y = 0.625x - 250$ ) is also shown. (a) Core data set, showing confidence scores; (b) core data set, showing biomes.

(approximately  $10\text{--}20 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ), including most temperate sites, the positive relationship between above-ground production and biomass begins to break down, with high variation due to several extremely high biomass reports. Eighty-nine per cent of temperate estimates in the data set had a confidence index below the median value (9), and 42% of temperate studies scored the minimum index value of 5. The low confidence in these temperate sites is driven by generally small sample areas, a frequent lack of litterfall measurements and, simply, little available information on methods used, so it is conceivable that methodological problems such as small sample units may have inflated AGB estimates. However, excluding these low-confidence sites also eliminates the majority of temperate sites, and therefore may mask real effects unique to temperate forests. For example, the very large biomass found within northern Californian *Sequoia* forests



Data from original studies	$r^2$	$r_a^2$	$P$ value	AIC	Probability
<i>Linear model</i>					
AGB = 81.75 + 18.06 ANPP	0.33	0.32	< 0.001	602.0	43.8%
<i>Quadratic model</i>					
AGB = 6.45 + 36.91 ANPP – 0.938 ANPP <sup>2</sup>	0.35	0.33	< 0.001	601.5	56.2%
<i>Asymptotic model</i>					
AGB = 717.923 ANPP / (ANPP + 15.991)	0.35	0.34	< 0.001	602.1	



Cap on predicted tropical lowland litterfall	$r^2$	$r_a^2$	$P$ value	AIC	Probability
<i>Quadratic model</i>					
AGB = 11.00 + 25.33 ANPP – 0.555 ANPP <sup>2</sup>	0.36	0.35	< 0.001	948.3	94.8%
<i>Asymptotic model</i>					
AGB = 403.577 ANPP / (ANPP + 9.076)	0.33	0.32	< 0.001	954.1	5.2%

**Figure 5** Relationship between global forest above-ground net primary productivity (ANPP) and above-ground biomass (AGB) for alternative data sets. (a) Data from original studies, without standardization, including only sites with total litterfall measured *in situ* ( $n = 63$ ). (b) ‘Standardized’ ANPP data, with tropical lowland litterfall estimates capped to the maximum measured value. The analysis uses the ‘core’ data set of sites with a confidence index of  $\geq 9$  ( $n = 106$ ).  $r_a^2 = r^2$  adjusted to account for the number of terms in the model; AIC, Akaike information criterion for model comparison; ‘Probability’ is the probability that the correct model has been chosen when comparing two AIC values.

cannot be explained simply by sampling bias. Trees are known to grow exceptionally tall and massive here (Busing & Fujimori, 2005); this has been attributed to factors such as longevity, due to very low disturbance levels and deep well-drained soils promoting good anchorage, and year-round moist conditions allowing a

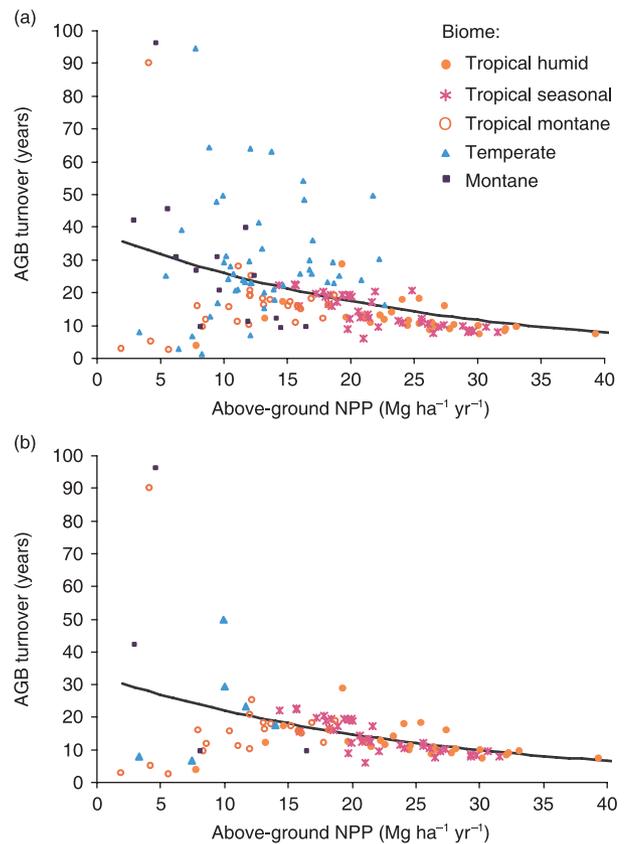
long growing season without exceptional heat or drought (Busing & Fujimori, 2005). Factors other than productivity *per se*, such as the floristic composition, disturbance regime, rooting depth and hydraulic limits on tree height, may then become the primary factors limiting AGB, all modifying the ANPP–AGB relationship.

At high ANPP values ( $> 20 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , predominantly tropical forests) AGB plateaus at around  $300 \text{ Mg ha}^{-1}$ , showing that biomass accumulation is limited by factors other than productivity. Within our data set, the largest tropical AGB ( $437\text{--}554 \text{ Mg ha}^{-1}$ ) is found on the lower slopes of Mount Kinabalu, Malaysian Borneo (estimates based on 1-ha plots) (Kitayama & Aiba, 2002). Other Southeast Asian studies also report AGB levels in excess of  $400 \text{ Mg ha}^{-1}$  (based on plots  $\geq 1 \text{ ha}$ ) (e.g. Hoshizaki *et al.*, 2004). This may suggest a tendency for forests to grow very large in this region, perhaps due to the dominance of large-stature species (particularly dipterocarps; Whitmore, 1984) or possibly a publication bias towards the largest biomass sites. Either way, the majority of global tropical sites do not exceed biomass levels of  $350 \text{ Mg ha}^{-1}$ .

Simplistically, forest biomass (both above and below ground) reflects the balance between the rate of mass gain (productivity), mass longevity and mass loss (mortality). Mature forests are close to biomass equilibrium, with levels of wood production more or less balanced by tree damage and mortality (Stephenson & van Mantgem, 2005). Productivity and stem turnover rate are positively correlated both in the tropics and globally (Phillips *et al.*, 1994; Stephenson & van Mantgem, 2005). Correspondingly, a significant negative correlation between ANPP and biomass turnover time (calculated as  $\text{AGB}/\text{ANPP}$ ) is observed in this study (outliers and boreal sites excluded: Pearson's correlation:  $-0.39$ ,  $P < 0.001$ ; core data set, boreal sites excluded:  $-0.39$ ,  $P < 0.001$ ) (Fig. 6). Boreal sites were excluded from this analysis, as frequent fire disturbance may prevent these forests in particular from reaching 'equilibrium', even after 100 years (Larsen, 1980).

Whether production drives mortality or mortality drives production is unclear, however. For example, high productivity may enhance mortality by intensifying competition, placing a premium on allocation to growth rather than to defence and structural integrity, or mortality may enhance productivity by ridding the forest of 'over-mature' trees, with their high maintenance respiration costs, and by accelerating nutrient cycling. Whether productivity, mortality or both, are the drivers, the resulting high turnover rates should influence the species composition of a forest. Frequent creation of gaps allows light-demanding, fast-growing species with low wood density to gain a competitive advantage over slow-growing, shade-tolerant species with a higher wood density. Species with low wood density are able to support greater xylem activity, due to higher hydraulic conductivity (Roderick & Berry, 2001) and consequently more rapid photosynthetic rates (Santiago *et al.*, 2004). Thus, while high turnover rates promote species with lower wood density, and may support faster rates of production, the lower carbon densities limit biomass levels.

These patterns are clearly observed within Amazonia. Here, the dynamic forests in western and southern regions have greater ANPP and turnover rates than forests in the centre and east (Malhi *et al.*, 2004; Phillips *et al.*, 2004), patterns that are reflected in floristic gradients, with species having low wood density more abundant in western Amazonia, and species with high wood density dominating in central and eastern regions (Baker *et al.*, 2004). This variation in wood density strongly



**Figure 6** Relationship between above-ground net primary productivity (ANPP) and above-ground biomass (AGB) turnover time (calculated as  $\text{AGB}/\text{ANPP}$ ), showing biomes. (a) Full data set, excluding outliers and boreal forests ( $n = 159$ ); regression line  $y = 38.8e^{-0.040x}$  ( $r^2 = 0.16$ ,  $P < 0.001$ ). (b) Core data set, excluding boreal forests ( $n = 97$ ); regression line  $y = 32.9e^{-0.041x}$  ( $r^2 = 0.15$ ,  $P < 0.001$ ).

influences the spatial patterns in AGB within Amazonia (Baker *et al.*, 2004). Consequently, high stem turnover does appear to limit biomass in many high-productivity forests.

There is some indication that the true relationship between ANPP and AGB is not asymptotic, but rather quadratic, beginning to turn negative for very high-productivity sites ( $\geq 30 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ). The above-ground biomass turnover time in very high-productivity forests (mean  $\pm$  SE:  $9.9 \pm 0.5$  years) is significantly faster than in lower-productivity sites ( $27.3 \pm 2.3$  years) (Mann–Whitney  $U$ -test,  $P < 0.001$ ). These forests may support communities that are adapted to highly dynamic processes, with low wood density species strongly dominating. These very high-productivity forests include sites in northern, western and southern Amazonia, Central America and Southeast Asia ( $n = 26$ ). At present, however, there is insufficient evidence to confirm that biomass always declines at very high levels of productivity, because such forests are rare (or under-sampled). If confirmed, however, this may have implications for global carbon storage, given that turnover has been increasing in tropical forests since before 1980 (Phillips *et al.*, 2004).

Another factor that may limit AGB in mature high-productivity forests is an increased proportion of production allocated elsewhere, such as below ground for structural support. This is a difficult hypothesis to test, however, as knowledge of below-ground biomass is limited (Cairns *et al.*, 1997; Mokany *et al.*, 2006). If high-productivity forests were allocating a greater proportion of biomass below ground, the root:shoot ratio of tropical forests would be expected to be greater than those of temperate and boreal forests, but this is not the case (Vogt *et al.*, 1996; Cairns *et al.*, 1997). Alternatively, there may be increased allocation above ground to leaves, rather than wood. However, we found no relationship between ANPP and the proportion of ANPP allocated to total litterfall ( $n = 63$ , Pearson's correlation 0.07,  $P = 0.585$ ).

When we repeated our analyses to take account of uncertainties with litterfall estimates and other estimated unmeasured ANPP components, results were remarkably similar to those attained using our 'standardized' ANPP, which assumes a linear increase of litterfall with ANPP. This implies that the proposed ANPP–AGB relationship is not driven by uncertainties in ANPP component estimation. There is substantial 'noise', however; for example, the core data set model  $r^2$  is only 0.36. To an extent this may reflect error within the data set, but is also likely to indicate that other factors control AGB storage, such as edaphic factors and disturbance (Laurance *et al.*, 1999; Pregitzer & Euskirchen, 2004).

In any event, the relationship between ANPP and AGB that we find contrasts strongly with the one proposed by Whittaker and Likens (1973) and the IBP study (O'Neill & De Angelis, 1981) (Fig. 3) in two key respects. Firstly, when comparing the quadratic model with that proposed by Whittaker and Likens the difference in the gradient is striking. The linear model is based on a small sample size, and is strongly influenced by a number of mid-productivity, high-biomass sites, leading to a very steep increase in AGB with ANPP. In our larger data set, the mid-productivity and high-biomass sites now appear rather atypical, and in our core analysis of more reliable data, many sites that best fit the Whittaker and Likens pattern have been excluded due to low reliability (cf. Fig. 3c,b). As discussed above, the extent to which these high-biomass estimates faithfully represent inherent high variation in biomass in temperate regions, or are methodological artefacts, is unclear. Interestingly, it can be observed that the results of the IBP study are not wholly consistent with Whittaker and Likens' hypothesis (Fig. 1), with most data points being consistent with a much slower rate of increase in AGB with ANPP. In particular, IBP sites with ANPP between 13 and 18 Mg ha<sup>-1</sup> year<sup>-1</sup> fall significantly below Whittaker and Likens' proposed line, but are dismissed by O'Neill and De Angelis as managed beech forests and evergreen plantations.

Secondly, whereas Whittaker and Likens propose a positive linear relationship, in our study AGB plateaus at mid to high levels of ANPP. As previously noted, Whittaker and Likens' study focused on temperate sites, and the IBP data set lacks any natural, high-productivity sites. Lowland tropical humid forests account for c. 39% of global forests (FAO, 2001), so the earlier analyses exclude a large fraction of the world's forests.

Our confidence index provided an a priori method to assess the reliability of data and to account for it analytically. Sites with higher

confidence index values were predominantly tropical (Fig. 3d), although still representing a range of ANPP levels due to limitations such as moisture supply (seasonal tropics) or temperature (tropical montane). It would be useful to repeat the analysis if more temperate and boreal sites could be located with more reliable estimates. However, we note that if the lower-confidence temperate sites are included, the nonlinear trend is still evident (Fig. 3b), and the regression fits for Figs 3(b) and 4(a) both begin to asymptote at approximately the same level of productivity.

The results of this study have implications for DGVM simulations of the current global biosphere, implying that biomass levels may be overestimated in high-productivity forests. Very high biomass values have been estimated by DGVMs for tropical sites; for example, the land surface model (LSM)–DGVM simulated 608.2 Mg ha<sup>-1</sup> AGB for a Brazilian tropical forest with estimated total NPP of 33.4 Mg ha<sup>-1</sup> year<sup>-1</sup> (Bonan *et al.* 2003), greatly exceeding the range of measured AGB values for Brazil in this data set (250.7–378.7 Mg ha<sup>-1</sup>). There may also be repercussions for projections of the impact of atmospheric change on ecosystems. As climates change and productivity increases, our results suggest that increased vegetation biomass and carbon storage may be possible in some regions, such as boreal forests, but elsewhere biomass accumulation may be limited by other factors. Increasing productivity is already contributing to enhanced turnover (growth and mortality) in high-productivity sites (Lewis *et al.*, 2004; Phillips *et al.*, 2004) and our results here provide empirical support for earlier predictions that the recent biomass sink in mature Amazon forests will prove to be only transient (Phillips *et al.*, 1998; Körner, 2004). Additionally, with enhanced turnover, increased carbon inputs into the soil will undoubtedly affect below-ground processes, with likely impacts on soil organic matter storage and respiration (Jastrow *et al.*, 2005). Therefore, increased biomass turnover, combined with the demonstrated limits to biomass storage in high-productivity forests, may significantly alter modelled and real-world biosphere carbon storage outcomes. Other factors, such as changing exogenous disturbance regimes, are also likely to play a role in determining the extent of biomass accumulation.

In conclusion, the simple linear relationship between AGB and ANPP reported previously is clearly an incorrect representation of global forest behaviour. Our findings suggest that increases in carbon storage by vegetation may not track the productivity increases anticipated for this century. Further analysis of which factors limit biomass accumulation is needed to better understand the processes involved.

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## REFERENCES

Adams, H.D. & Kolb, T.E. (2005) Tree growth response to drought and temperature in a mountain landscape in

- northern Arizona, USA. *Journal of Biogeography*, **32**, 1629–1640.
- Akaike, H. (1974) A new look at statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.
- Archibold, O.W. (1995) *Ecology of world vegetation*. Chapman & Hall, London.
- Arthur, M.A. & Fahey, T.J. (1992) Biomass and nutrients in an Engelmann spruce — subalpine fir forest in north central Colorado: pools, annual production, and internal cycling. *Canadian Journal of Forest Research*, **22**, 315–325.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, J.N.M. & Martinez, R.V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.
- Bobek, B., Perzanowski, K., Siwanowicz, J. & Zielinski, J. (1979) Deer pressure on forage in a deciduous forest. *Oikos*, **32**, 373–380.
- Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M. & Oleson, K.W. (2003) A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biology*, **9**, 1543–1566.
- Brown, S. (1997) *Estimating biomass and biomass change of tropical forests*. FAO, Rome.
- Busing, R.T. & Fujimori, T. (2005) Biomass, production and woody detritus in an old coast redwood (*Sequoia sempervirens*) forest. *Plant Ecology*, **177**, 177–188.
- Cairns, M.A., Brown, S., Helmer, E.H. & Baumgardner, G.A. (1997) Root biomass allocation in the world's upland forests. *Oecologia*, **111**, 1–11.
- Cannell, M.G.R. (1982) *World forest biomass and primary production data*. Academic Press, London.
- Cao, M.K. & Woodward, F.I. (1998a) Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology*, **4**, 185–198.
- Cao, M.K. & Woodward, F.I. (1998b) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Chambers, J.Q., dos Santos, J., Ribeiro, R.J. & Higuchi, N. (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management*, **152**, 73–84.
- Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B. & Hubbell, S.P. (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology*, **91**, 240–252.
- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 409–420.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R. & Ni, J. (2001) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Clark, D.B. & Clark, D.A. (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, **137**, 185–198.
- Coley, P.D. & Aide, T.M. (1991) Comparison of herbivory and plant defences in temperate and tropical broad-leaved forests. *Plant–animal interactions* (ed. by P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson), pp. 25–49. Wiley Interscience, New York.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, B., Churkina, C., Nemry, B., Ruimy, A. & Schloss, A.L. (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology*, **5**, 1–15.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- De Angelis, D.L., Gardner, R.H. & Shugart, H.H. (1981) Productivity of forest ecosystems studied during the IBP: the woodland dataset. *Dynamic properties of forest ecosystems* (ed. by D.E. Reichle), pp. 567–672. Cambridge University Press, Cambridge.
- Edwards, P.J. (1977) Studies of mineral cycling in a montane rainforest in New Guinea. II Production and disappearance of litter. *Journal of Ecology*, **56**, 971–992.
- FAO (2001) *State of the world's forests*. FAO, Rome.
- FAO (2005) *Global forest resource assessment: progress towards sustainable forest management*. FAO Forestry Paper 147. FAO, Rome.
- Foster, R.B. (1982) Famine on Barro Colorado Island. *The ecology of a tropical forest* (ed. by E.G. Leigh, A.S. Rand and D.M. Windsor), pp. 201–212. Smithsonian Institution Press, Washington, DC.
- Frangi, J.L. & Lugo, A.E. (1985) Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs*, **55**, 351–369.
- Gerber, S., Joos, F. & Prentice, I.C. (2004) Sensitivity of a dynamic global vegetation model to climate and atmospheric CO<sub>2</sub>. *Global Change Biology*, **10**, 1223–1239.
- Gerten, D., Lucht, W., Schaphoff, S., Cramer, W., Hickler, T. & Wagner, W. (2005) Hydrologic resilience of the terrestrial biosphere. *Geophysical Research Letters*, **32**, L21408, doi:10.1029/2005GL024247.
- Guenther, A., Hewitt, C.N., Erickson, D., Fall, R., Geron, C., Graedel, T., Harley, P., Klinger, L., Lerdau, M., McKay, W.A., Pierce, T., Scholes, B., Steinbrecher, R., Tallamraju, J., Taylor, J. & Zimmerman, P. (1995) A global model of natural volatile organic compound emissions. *Journal of Geophysical Research*, **100**, 8873–8892.
- Hoshizaki, K., Niiyama, K., Kimura, K., Yamashita, T., Bekku, Y., Okuda, T., Quah, E.S. & Noor, N.S.M. (2004) Temporal and spatial variation of forest biomass in relation to stand dynamics in a mature, lowland tropical rainforest, Malaysia. *Ecological Research*, **19**, 357–363.

- Jastrow, J.D., Michael Miller, R., Matamala, R., Norby, R.J., Boutton, T.W., Rice, C.W. & Owensby, C.E. (2005) Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology*, **11**, 2057–2064.
- Joos, F., Gerber, S., Prentice, I.C., Otto-Bliesner, B.L. & Valdes, P.J. (2004) Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum. *Global Biogeochemical Cycles*, **18**, doi: 10.1029/2003GB002156.
- Keller, M., Palace, M. & Hurtt, G. (2001) Biomass estimation in the Tapajos National Forest, Brazil. Examination of sampling and allometric uncertainties. *Forest Ecology and Management*, **154**, 371–382.
- Kepler, F., Hamilton, J.T.G., Brass, M. & Rockmann, T. (2006) Methane emissions from terrestrial plants under aerobic conditions. *Nature*, **439**, 187–191.
- Ketterings, Q.M., Coe, R., van Noordwijk, M., Ambagau, Y. & Palm, C.A. (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management*, **146**, 199–209.
- Kitayama, K. & Aiba, S.I. (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology*, **90**, 37–51.
- Knapp, A.K. & Smith, M.D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481–484.
- Köppen, W. (1923) *Die climate de erde: grundriss der klimakunde*. De Gruyter, Berlin.
- Körner, C. (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 493–498.
- Larsen, J.A. (1980) *The boreal ecosystem*. Academic Press, London.
- Larsson, S. & Tenow, O. (1980) Needle eating insects and grazing dynamics in a mature Scots pine forest in Central Sweden. *Structure and function of northern coniferous forests: an ecosystem study* (ed. by T. Persson), pp. 269–306. Berlings, Sweden.
- Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin-de Merona, J.M., Chambers, J.Q. & Gascon, C. (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127–138.
- Law, B.E., Van Tuyl, S., Cescatti, A. & Baldocchi, D.D. (2001) Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. *Agricultural and Forest Meteorology*, **108**, 1–14.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D., Silva, N., Terborgh, J., Lezama, A.T., Martinez, R.V., Brown, S., Chave, J., Kuebler, C., Nunez, P. and Vinceti, B. (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 421–436.
- Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitmans, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B. & Lloyd, J. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 1–29.
- McInnes, P.F., Naiman, R.J., Pastor, J. & Cohen, Y. (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, **73**, 2059–2075.
- Mokany, K., Raison, R.J. & Prokushkin, A.S. (2006) Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology*, **12**, 84–96.
- Motulsky, H. & Christopoulos, A. (2004) *Fitting models to biological data using linear and nonlinear regression*. Oxford University Press, Oxford.
- Nielsen, B.O. (1978) Aboveground food resources and herbivory in a beech forest ecosystem. *Oikos*, **31**, 273–279.
- O'Neill, R.V. & De Angelis, D.L. (1981) Comparative productivity and biomass relations of forest ecosystems. *Dynamic properties of forest ecosystems* (ed. by D.E. Reichle), pp. 411–449. Cambridge University Press, Cambridge.
- Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Martinez, R.V. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences USA*, **91**, 2805–2809.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Martinez, R.V., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S. & Grace, J. (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, **282**, 439–442.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N.M., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patino, S., Pitman, N.C.A., Quesada, C.A., Salidas, M., Lezama, A.T. & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 381–407.
- Pregitzer, K.S. & Euskirchen, E.S. (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology*, **10**, 2052–2077.
- Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J. & Vitousek, P.M. (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology*, **87**, 76–87.
- Reichle, D.E. & Crossley, D.A. (1967) Investigation on heterotrophic productivity in forest insect communities. *Secondary productivity of terrestrial ecosystems (principles and methods)* (ed. by K. Petrusewicz), pp. 563–587. Panstwowe Wydawnictwo Naukowe, Warsaw.
- Roderick, M.L. & Berry, S.L. (2001) Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. *New Phytologist*, **149**, 473–485.

- Ryan, M.G., Phillips, N., & Bond, B.J. (2006) The hydraulic limitation hypothesis revisited. *Plant Cell and Environment*, **29**, 367–381.
- Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**, 543–550.
- Saugier, B., Roy, J. & Mooney, H.A. (2001) Estimations of global terrestrial productivity: converging toward a single number? *Terrestrial global productivity* (ed. by J. Roy, B. Saugier and H.A. Mooney), pp. 543–557. Academic Press, San Diego, CA.
- Stephenson, N.L. & van Mantgem, P.J. (2005) Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters*, **8**, 524–531.
- Thonicke, K., Venevsky, S., Stich, S. & Cramer, W. (2001) The role of fire disturbance for global vegetation dynamics: coupling fire into a dynamic global vegetation model. *Global Ecology and Biogeography* **10**, 661–677.
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., Ohara, J. & Asbjornsen, H. (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil*, **187**, 159–219.
- Westman, W.E. & Whittaker, R.H. (1975) The pygmy forest region of northern California: studies on biomass and primary productivity. *Journal of Ecology*, **63**, 493–520.
- Whitmore, T.C. (1984) *Tropical rain forests of the Far East, with a chapter on soils by C.P. Burnham*. Clarendon, Oxford.
- Whittaker, R.H. & Likens, G.E. (1973) Carbon in the biota. *Carbon and the biosphere: proceedings of the 24th Brookhaven Symposium in Biology, Upton, N.Y., May 16–18, 1972* (ed. by G.M. Woodwell and E.V. Pecan), pp. 281–302. Technical Information Center, US Atomic Energy Commission, Washington, DC.
- Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Shaver, G.R. & Johnson, L.C. (1997) Predicting gross primary productivity in terrestrial ecosystems. *Ecological Applications*, **7**, 882–894.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Global forest data set, including original data, standardization factors and confidence index scores.

**Appendix S2** Global forest data set, including site information.

**Appendix S3** Sources for Appendices S1 and S2.

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