Tropical forest wood production: a cross-continental comparison

Lindsay Banin[1,2]*, Simon L. Lewis[2,3], Gabriela Lopez-Gonzalez[2], Timothy R. Baker[2], Carlos A. Quesada[4], Kuo-Jung Chao[5], David F. R. P. Burslem[6], Reuben Nilus[7], Kamariah Abu Salim[8], Helen C. Keeling[2], Sylvester Tan[9], Stuart J. Davies[10], Abel Monteagudo Mendoza[11], Rodolfo Vásquez[11], Jon Lloyd[12], David A. Neill[13], Nigel Pitman[14,15] and Oliver L. Phillips[2]

[1]*Centre for Ecology and Hydrology, Bush Estate, Penicuik Midlothian EH26 0QB, UK;* [2]*School of Geography, University of Leeds, Leeds, West Yorkshire LS2 9JT, UK;* [3]*Department of Geography, University College London, London WC1E 6BT, UK;* [4]*Instituto Nacional de Pesquisas da Amazônia, Avenida André Araújo, 2936, Aleixo, CEP 69060-001 Manaus, AM, Brazil;* [5]*International Master Program of Agriculture, College of Agriculture and Natural Resources, National Chung Hsing University, Taichung 40227, Taiwan;* [6]*School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK;* [7]*Forest Research Centre, Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia;* [8]*Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Tungku Link Road BE 1410, Brunei Darussalam;* [9]*Sarawak Forestry Corporation, Lot 218, KCLD, Jalan Tapang, Kota Sentosa, 93250 Kuching, Sarawak, Malaysia;* [10]*Center for Tropical Forest Science, Smithsonian Tropical Research Institute, PO Box 37012, Washington, DC 20013-7012, USA;* [11]*Jardín Botánico de Missouri, Oxapampa 19231, Pasco, Peru;* [12]*Faculty of Natural Sciences, Department of Life Sciences, Imperial College London, South Kensington Campus, London SW7 2AZ, UK;* [13]*Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador;* [14]*Science and Education, The Field Museum, 1400 South Lake Shore Drive, Chicago, IL 60605, USA;* and [15]*Nicholas School of the Environment, Duke University, Durham, NC 27708-0381, USA*

Summary

1. Tropical forest above-ground wood production (AGWP) varies substantially along environmental gradients. Some evidence suggests that AGWP may vary between regions and specifically that Asian forests have particularly high AGWP. However, comparisons across biogeographic regions using standardized methods are lacking, limiting our assessment of pan-tropical variation in AGWP and potential causes.

2. We sampled AGWP in NW Amazon (17 long-term forest plots) and N Borneo (11 plots), both with abundant year-round precipitation. Within each region, forests growing on a broad range of edaphic conditions were sampled using standardized soil and forest measurement techniques.

3. Plot-level AGWP was 49% greater in Borneo than in Amazonia (9.73 ± 0.56 vs. 6.53 ± 0.34 Mg dry mass ha^{-1} a^{-1}, respectively; regional mean $\pm$ 1 SE). AGWP was positively associated with soil fertility (PCA axes, sum of bases and total P). After controlling for the edaphic environment, AGWP remained significantly higher in Bornean plots. Differences in AGWP were largely attributable to differing height–diameter allometry in the two regions and the abundance of large trees in Borneo. This may be explained, in part, by the greater solar radiation in Borneo compared with NW Amazonia.

4. Trees belonging to the dominant SE Asian family, Dipterocarpaceae, gained woody biomass faster than otherwise equivalent, neighbouring non-dipterocarps, implying that the exceptional production of Bornean forests may be driven by floristic elements. This dominant SE Asian family may partition biomass differently or be more efficient at harvesting resources and in converting them to woody biomass.

5. *Synthesis.* N Bornean forests have much greater AGWP rates than those in NW Amazon when soil conditions and rainfall are controlled for. Greater resource availability and the highly productive dipterocarps may, in combination, explain why Asian forests produce wood half as fast again as comparable forests in the Amazon. Our results also suggest that taxonomic groups differ in their fundamental ability to capture carbon and that different tropical regions may therefore have different carbon uptake capacities due to biogeographic history.

Key-words: Amazon, Asia, carbon, Dipterocarpaceae, dynamics, growth, plant–soil interactions, productivity, soil nutrients, tropical forest

*Correspondence author. E-mail: Lindsay.banin@gmail.com

Introduction

Tropical forests are a vital component of the global carbon cycle (Malhi & Grace 2000; Pan *et al.* 2011). Whilst tropical moist forests only constitute ca. 10% of terrestrial land cover (Mayaux *et al.* 2005), they cycle large quantities of carbon, contributing an estimated 34% of global, terrestrial gross primary production (GPP) (Beer *et al.* 2010) and about half the terrestrial carbon sink (Pan *et al.* 2011). Thus, it is critical to understand how tropical moist forest production varies over landscapes, between the major forest regions, and how environmental properties and species assemblages contribute to this variation (Clark *et al.* 2001; Keeling & Phillips 2007; Aragao *et al.* 2009). An earlier synthesis of study sites across the lowland and montane tropics reported variation in above-ground wood biomass production (AGWP) from 0.6 to 7.6 Mg ha^{-1} a^{-1} (Clark *et al.* 2001), but subsequent studies suggested higher maximum AGWP rates, reaching 11.0 Mg ha^{-1} a^{-1} in Amazonia (Malhi *et al.* 2004) and up to 23.6 Mg ha^{-1} a^{-1} in Asia (Paoli & Curran 2007), implying both some uncertainty and possible regional differences in AGWP. Reducing the uncertainty of carbon stocks and fluxes is a key focus of ecological research, and quantifying the spatial variation in production capacities of tropical forests holds important practical implications for carbon modelling, accounting and forest management (Keith, Mackey & Lindenmayer 2009).

Much of our current knowledge on carbon stocks and dynamics in humid tropical forests comes from work in Central and South America; comparative data from Asia are sparse (Pan *et al.* 2011). The few Asian sites used to study wood production suggest a range of AGWP from 5.6 to 23.6 Mg ha^{-1} a^{-1} (Kitayama & Aiba 2002; Miyamoto *et al.* 2007; Paoli & Curran 2007; Chave *et al.* 2008; Hertel *et al.* 2009). However, these studies may not provide representative AGWP estimates for the lowland tropical moist forests of Asia, due to their premontane elevation (Hertel *et al.* 2009), short monitoring periods or small plot sizes (Paoli & Curran 2007). If production rates are indeed higher in Southeast Asia, is this difference related to environmental conditions (i.e. the availability of growth resources) or is it determined by the floristic assemblages and their relative ability to access and use resources efficiently?

The abiotic environment is an important source of variation in forest growth and production rates. Temperature does not typically limit the growing season in the tropics, and thus, growth is most likely to be limited by one or more of the key plant resources: nutrients, water and photosynthetically active radiation (PAR) (Baker, Swaine & Burslem 2003). Recent work has indicated that edaphic conditions are important determinants of plant growth and AGWP both in Amazonia (Malhi *et al.* 2004; Aragao *et al.* 2009; Quesada *et al.* 2012) and in Asia (Kitayama & Aiba 2002; Paoli & Curran 2007). Tropical ecosystems are widely held to be comparatively rich in nitrogen (N) and depauperate in strongly weathered nutrients, in particular phosphorus (P) (Vitousek & Sanford 1986; Tanner, Vitousek & Cuevas 1998; Hedin *et al.* 2009). For example, a 62-site synthesis showed that fine litterfall was significantly correlated with soil P, but not nitrogen (N) (Vitousek 1984). Similarly, McGroddy, Daufresne & Hedin (2004) showed that, in tropical forests, litter tends to have higher N/P ratios than foliage, indicating the resorption of P which tends to occur where P-supply is limited. Across Amazonia, total P in soil is the single best predictor of forest growth rates (Quesada *et al.* 2012). Base cations [calcium (Ca), potassium (K), magnesium (Mg)] have also been shown to be important in determining growth and production rates (Tripler *et al.* 2006; Kaspari *et al.* 2008; Wright *et al.* 2011; Baribault, Kobe & Finley 2012). Since spatial variation in the edaphic environment appears to drive variation in growth and production rates, it should be carefully controlled for in regional comparisons.

Climatic factors are also key determinants of plant productivity. Tree growth tends to increase with water availability and decrease in areas susceptible to drought stress (e.g. Murphy & Lugo 1986). In regions where the growing season is rarely limited by rainfall, as in the aseasonal tropics, production may instead be limited by incoming solar radiation due to cloud cover (Churkina & Running 1998; Nemani *et al.* 2003), particularly during the rainy season (Graham *et al.* 2003). Variation in incoming solar radiation may be expected to influence patterns in tropical AGWP, at least in the wettest parts of the equatorial belt.

Alongside variation in the abiotic environment, differences in growth and production rates may be driven by the extant floristic assemblage and its functional attributes. A number of studies have examined differences in diameter growth rates between species (e.g. King *et al.* 2005; Baribault, Kobe & Finley 2012), and differences between species can be explained by life-history strategies, differences in allocation and particularly trade-offs between fast growth rates (for competition with neighbouring trees) and high wood density (for enhanced survival rates) (e.g. Poorter *et al.* 2010; Rüger *et al.* 2012). Species composition may also affect AGWP, but differences in wood production rates between taxonomic groups are not well understood presently. Thus, it is unclear how interspecific differences translate to ecosystem-level processes such as AGWP. Baker *et al.* (2009) used a resampling approach to examine the effects of the east-to-west gradient in soil fertility on wood production across the Amazon, concluding that environmental conditions had a much greater impact than the functional composition of the forest. In the NW Amazon, Keeling *et al.* (2008) found some evidence for greater dry mass AGWP from denser-wooded trees than from tree species with less-dense wood within the same forests, once local light environment (crown illumination) was controlled for, implying a potential role for species and functional composition in among-site AGWP variation. Spatial differences in functional composition may also be related to, and exacerbated by, differences in disturbance rates, since light-wooded species are associated with more dynamic forests (Baker *et al.* 2004b).

Considering the effects of floristic composition may be even more important when comparing different biogeographic regions. High AGWP rates in Asia have been associated with

Fig. 1. Map indicating locations of forest inventory plots; 18 plots in north-western Amazonia and 11 in northern Borneo.

frequency of large (> 60 cm dbh) trees (e.g. Paoli & Curran 2007), which are more abundant in the family Dipterocarpaceae (Slik *et al.* 2010). It is not yet known how the dipterocarps attain these large sizes; it could be due to faster growth, lower mortality, greater allocation to wood and/or greater resource-use efficiency. Several authors have suggested that the dominance of the family Dipterocarpaceae itself may be the putative cause of high AGWP rates in Asian forests (Mirmanto *et al.* 1999; Paoli & Curran 2007; Hertel *et al.* 2009). However, despite some data showing faster diameter growth of Dipterocarpaceae (Mirmanto *et al.* 1999), the 'dipterocarp effect' on wood production remains untested without first accounting for differences in wood density. Likewise, it remains unknown how faster production rates may be achieved by some taxonomic groups given a limited level of resources available for growth.

To date, there are no reported attempts to compare forest production among continents using identical forest and soil measurement techniques. The aim of this study is to test the putative hypothesis that Asian forests are more productive than those in the Amazon and then to understand why this may be the case. We compare two lowland, aseasonal regions – North-western Amazonia and Northern Borneo. We chose to sample in two areas that are biogeographically highly distinct but climatically similar to remove, as far as possible, confounding effects of temperature and rainfall (water availability). Sites were located across a wide range of substrates to maximize the variation in soil fertility within each region, from nutrient-poor white sand soils to nutrient-rich alluvial substrates, to enable us to statistically control for soil nutrient availability on AGWP.

We use two levels of analysis to identify differences and ascertain possible causes for differences in AGWP between regions. Firstly, we use plot-level analyses to determine regional differences and to relate these to environmental variables (i.e. resource availability). Secondly, we use individual tree-level analyses to examine growth responses of different size classes, and functional groups (as determined by wood density) and taxonomic groups (Dipterocarpaceae versus non-

dipterocarps) to identify whether or not regional differences are driven by specific plant groups (i.e. the ability of plants to access resources and convert them to biomass).

Materials and methods

STUDY SITES

We censused a total of 28 permanent sample plots in the lowland, aseasonal tropics – 17 in north-western Amazonia (RAINFOR; Lopez-Gonzalez *et al.* 2011) and 11 in northern Borneo (Banin 2010; Table S1 in Supporting Information; Fig. 1). Plots were selected to avoid known anthropogenic disturbance and restrict variation in climate; on average, rainfall is non-limiting in both regions year-round, that is, ≥ 100 mm in every month, and plots are lowland, that is, < 1000 m.a.s.l. (Table S1). The north-west Amazon sites were not impacted by recent droughts (2005 and 2007) that affected some other parts of Amazonia (Phillips *et al.* 2009). Forest plots in both regions deliberately encompass a broad range of edaphic conditions. Plots in close proximity (cf. Table S1) were located on contrasting soil types to avoid confounding spatial and soil fertility effects. As far as possible, we used data from similar calendar years in both regions to avoid the possibility of confounding our analysis with possible large-scale temporal trends in productivity. Forest inventory data were curated in the ForestPlots.net data base (Lopez-Gonzalez *et al.* 2009, 2011).

Climatic (temperature and precipitation) data for each plot were extracted from WorldClim data sets at 2.5-min spatial resolution (Hijmans *et al.* 2005; Table S1). Mean annual solar radiation data, as calculated from interpolated station data of sunshine hours and cloud cover, were extracted from the Climatic Research Unit data set at 0.5 degree resolution (New, Hulme & Jones 1999). All plots are c. 1 ha in area to avoid potential biases associated with small or inconsistent plot size. In the case of the two Lambir plots (LAM-06 & 07) and three Sepilok plots (SEP-01 to 03), 1-ha subplots were randomly selected from within larger plots and within regions of relatively homogenous soil type. Four analytical units in Amazonia were less than 1 ha in area (ALP-11, 12, 21 and 22; minimum 0.4 ha) to split the 20 × 500 m transect plots into strongly distinctive edaphic units.

Detailed descriptions of soil sampling and analysis protocols are provided elsewhere (Quesada *et al.* 2010; Banin 2010). The measured chemical properties of topsoil (depth 0–30 cm) were as follows:

pH (H_2O extracted), exchangeable bases (Ca, K, Mg and Na, extracted with silver thiourea, cmol kg^{-1}) and sum of exchangeable bases (Σ_B) (cmol kg^{-1}), total P (mg kg^{-1}) and total C and N % (Table S1). Physical properties of the soil were depicted by particle fractions (sand, silt and clay %). Since chemical and physical soil attributes are often highly correlated, principal component analysis (PCA) was used to reduce the soil data set to a smaller set of independent axes that can be incorporated into analyses to simultaneously account for variability in soil conditions. Soil data were not available for three plots in NW Amazonia (SUC 03-05), and thus, these plots were removed from analyses using this information.

ESTIMATION OF GROWTH AND AGWP

In each plot, the diameter of all free-standing trees ≥ 10 cm diameter at breast height (dbh) was measured at least twice (census dates are given in Table S1), using standard protocols (Baker *et al.* 2004b). Tree diameter growth was checked for all stems, and outliers were treated following methods described by Baker *et al.* (2004a) and Phillips *et al.* (2009). Tree height was measured for c. 50 trees per hectare, using a standardized stratified-random sampling approach whereby 10 trees were randomly selected from four size classes (10–20, 20–30, 30–40 and > 40 cm diameter) plus 10 additional large trees (detailed further in Banin *et al.* 2012). Tree height was measured using the 'tangent approach' (cf. Larjavaara & Muller-Landau 2013) with either a hypsometer or clinometer.

Plot-level basal area (BA) growth was calculated as the sum of BA increment for all stems surviving from the previous census to the subsequent census, plus the basal area of recruited stems, *sensu* Malhi *et al.* (2004). Annualized plot-level BA growth was calculated for each consecutive census interval for each plot. Since Bornean plots had longer intervals, on average, than Amazonian plots (mean, 7.6 and 4.4 years, respectively; Table S3), and longer interval bias rates derived from heterogeneous populations downwards (Sheil & May 1996; Lewis *et al.* 2004), we applied a correction for census interval length following the procedure described in Malhi *et al.* (2004) and Appendix S2. Both census-interval corrected and uncorrected data are presented in Table S2.

We followed an identical procedure for AGWP. However, since above-ground biomass (AGB) increments cannot be directly measured, AGB must be estimated by applying allometric relationships relating stem diameter, height and wood density to AGB. For each census, individual above-ground tree biomass (the biomass of the tree bole, limbs and branches in kg) was estimated using the moist forest equation (eqn 1) presented by Chave *et al.* (2005),

$$AGB_{tree} = 0.0509 \times \rho D^2 H \qquad \text{eqn 1}$$

where ρ is wood density, D is diameter (cm) at breast height and H is total tree height (m). This equation was selected as it is based on the largest pan-tropical sample of harvested trees and best represents the study regions presented here.

Height–diameter relationships differ significantly between sites and regions (Banin *et al.* 2012). Plot-specific curve parameters, based on concurrent height and diameter measurements, were estimated using nonlinear mixed-effects (NLME) models, where 'plot' was specified as a random effect (see Pinheiro and Bates 2000; analytical protocols detailed in Banin *et al.* 2012). The height of every tree in the plot was then estimated using the plot-specific height–diameter function (Fig. S1) and applied to eqn 1. The resulting AGWP values from this approach are referred to in this paper as 'AGWP with height'. For means of comparison, biomass increment was also calculated using

the equation presented by Chave *et al.* (2005), which excludes a height term (eqn 2). AGWP calculations using eqn 2 are referred to from here as 'AGWP without height'.

$$AGB_{tree} = \rho.\exp(-1.499 + 2.148\ln(D) + 0.207(\ln(D))^2 \\ - 0.0281(\ln(D))^3) \qquad \text{eqn 2}$$

Data on wood mass density (wood dry mass divided by wood fresh volume; termed 'wood density') were taken from the global wood density data base (Chave *et al.* 2009; Zanne *et al.* 2009) for each tree within the studied plots. For incompletely identified species, the appropriate genus- or family wood density value was attributed, with plot-level mean wood density applied in the cases of unidentified stems. In the plot-level data set (individual-level data set) in this study, 52.3% (55.3) of stems used a species-level average, 40.1% (38.9) a genus-level average, 5.8% (5.1) a family-level average and 1.8% (0.7) a plot-level average.

For the analyses of individual trees, both diameter growth and AGWP were calculated using the census interval (i) that was > 5 year to reduce noise associated with inter-annual differences and (ii) that minimized the difference from the median date for all censuses (2001.6). Individual diameter rates do not require interval correction, as the principal bias arises from combining heterogeneous populations of trees. Seven stems were removed from the individual analysis due to large (≥ 5 mm $year^{-1}$) negative growth rates.

DATA ANALYSIS

Plot-level analyses

Analyses of covariance (ANCOVAS) were used to model relationships between three response variables (plot-level BA growth, AGWP with and without height) and environmental covariates (soil parameters, key climatic variables and solar radiation) and to test for differences in the intercepts and slopes of these relationships for Amazonian and Bornean plots. In the case of each response variable, a maximal model was produced, which included mean annual precipitation, mean annual temperature, solar radiation and three independent PCA axes to represent soil characteristics, as well as a factor variable 'continent', where significant interactions between continent and the covariates were also tested. A further two maximal models were produced for each response variable that included either total P or sum of bases to test for their effect specifically on growth and production; they were not included as covariates together in the same model due to their collinearity, which can yield spurious results. To arrive at the best model, an automated stepwise approach in both directions was used to sequentially test for the improvement in AIC. All analyses were performed using R software, version 2.13.1 (http://www.R-project.org/, R Development Core Team 2008).

Individual-level analyses

We used a mixed-effects modelling approach to examine differences in individual tree diameter growth and AGWP between (i) Amazon and Borneo and (ii) dipterocarps and non-dipterocarps, to test the hypotheses that the Dipterocarpaceae have intrinsically faster diameter growth rates (Mirmanto *et al.* 1999) and wood production rates. Initial tree size (D), wood density (WD) and soil fertility ($PCA1$) were incorporated as fixed-effect covariates, and we accounted for the non-independence of growth and production rates of trees within the same plot through a random 'plot' effect (α_{plot}). In the individual analyses,

we consider only AGWP with height as it provides the most accurate estimate of AGWP. Diameter growth (gr) in mm a^{-1} and AGWP with height (pr) in Mg a^{-1} were ln-transformed to improve adherence to model assumptions, after a constant had been added to remove negative and zero values. Response variables were initially modelled, respectively, as eqns 3 and 4. Initial diameter (D) was also ln-transformed, since diameter and biomass have a multiplicative relationship.

$$\ln(gr + 5) = \mu + \alpha_{cat} \times [\beta_1(\ln D) + \beta_2(WD) + \beta_3(PCA1)] + \alpha_{plot} + \varepsilon$$
$$\text{eqn 3}$$

$$\ln(pr + 1.04) = \mu + \alpha_{cat} \times [\beta_1(\ln D) + \beta_2(WD) + \beta_3(PCA1)] + \alpha_{plot} + \varepsilon$$
$$\text{eqn 4}$$

In eqns 3 and 4, μ is the intercept and α_{cat} is a fixed-effect categorical term (i.e. Amazon/Borneo and dipterocarp/non-dipterocarp), which is able to interact with fixed-effect covariates. Errors (ε) are assumed to have a mean 0 and variance σ^2. The maximum likelihood (ML) method was applied initially to allow comparisons of nested models for simplification by comparing AIC values; the final model was rerun using restricted maximum likelihood (REML) method for improved parameter estimation. Residuals were assessed, and a quadratic polynomial term for the effect of tree size $(\ln D)^2$ was included in the final models. This removed nonlinearity in residuals and significantly improved all models.

Results

REGIONAL DIFFERENCES IN THE PHYSICAL ENVIRONMENT

Average rainfall and temperature conditions were similar in the two regions (Table 1). Solar radiation was significantly different between regions, averaging c. 18% greater in the Bornean sites (Table S1; Mann–Whitney U test, $P \leq 0.0001$), but varied little within region, ranging from 10.6 to 11.4 MJ m^{-2} day^{-1} in Amazonian sites and 13.3 to 13.6 MJ m^{-2} day^{-1} among Bornean sites (Fig. S2).

Table 1. Regional mean (standard deviation) for environmental conditions for plots in NW Amazonia and N Borneo. Climatic data were extracted from WorldClim (Hijmans *et al.* 2005) and Climatic Research Unit (New, Hulme & Jones 1999). Soil data are from Quesada *et al.* (2010) and Banin (2010). Data are available for individual plots in Appendix S1

Region	Amazon	Borneo
No. plots	17	11
Climate		
Mean annual rainfall (mm)	3003 (395)	3234 (308)
Mean annual temperature (°C)	25.7 (1.0)	26.5 (0.6)
Solar radiation (MJ m^2 day^{-1})	11.2 (0.3)	13.5 (0.1)
Soil		
Sum of bases (cmol kg^{-1})	2.6 (3.2)	0.8 (0.9)
C/N	10.4 (2.0)	16.2 (8.7)
Total P (mg kg^{-1})	255.1 (182.8)	101.2 (93.2)

A broad range of soil conditions were captured in each region (Table S1 and Fig. S3), though average conditions differed due to the inclusion of more nutrient-rich sites in NW Amazonia. Sum of bases ($\sum_B$) and total P were typically higher among Amazonian plots than among Bornean plots sampled (Table 1). Correspondingly, soil C/N ratios (where high values are associated with lower fertility) were on average greater for Bornean plots.

The soil variables were well correlated; soils high in base cations also tended to be high in total P and have a low C/N ratio. Soils with high percentage of sand were associated with low fertility. The first three axes of the PCA explained 80.6% of variation in the soil data set (Table S2). Loading values indicated that PCA1 was positively associated with sum of bases and total P and negatively with C/N and sand content. High values in PCA2 represent high Al and K and low C. PCA3 was positively associated with N, C and clay content and negatively with Mg.

REGIONAL DIFFERENCES IN STRUCTURE, GROWTH AND WOOD PRODUCTION

Mean (± 1 SE) stem density was almost identical in Borneo (587 stems $ha^{-1} \pm 35.3$) and Amazonia (589 stems $ha^{-1} \pm 16.1$). However, mean BA was substantially higher in Borneo (37.5 m^2 $ha^{-1} \pm 2.62$) than in Amazonia (28.1 m^2 $ha^{-1} \pm 0.71$). Thus, mean tree diameter was greater across the Bornean plots (28.6 cm) compared with Amazon plots (24.7 cm). The density of large trees was substantially higher in the Bornean plots; on average, per hectare, there were 56 stems ≥ 40 cm diameter in Borneo, and 45 stems ≥ 40 cm diameter in Amazonia. The NLME analysis determined that average maximum height of trees in the plots in Borneo was significantly greater than that in the Amazon plots (60.3 m ± 2.87 and 34.2 m ± 1.03, respectively; Fig. S1). Mean (by stem) wood density was calculated for each plot; when averaged across plots, both regions had the same mean wood density value of 0.599 g cm^3. The higher the BA, greater frequency of large diameter trees and taller trees together contributed to much greater AGB values (as calculated using eqn 1) in Borneo compared with the Amazon (median of 525.2 vs. 253.0 Mg ha^{-1}; Mann–Whitney U test P-value < 0.0001).

Plot-level BA growth rate did not differ significantly between regions, with mean (median in brackets) census-interval corrected BA growth rates of 0.67 (0.69) m^2 ha^{-1} a^{-1} and 0.65 (0.68) m^2 ha^{-1} a^{-1} for Bornean and Amazonian plots, respectively (Mann–Whitney U test P-value = 0.853; Fig. 2a). When AGWP was calculated without including the height term (eqn 2), mean (median) values were slightly higher for Bornean plots at 8.63 (8.66) Mg ha^{-1} a^{-1} than for Amazonian plots at 8.43 (8.27) Mg ha^{-1} a^{-1}, but this difference was not significant (P-value = 0.578; Fig. 2b). By contrast, AGWP including the height term was significantly greater in Bornean than in Amazonian plots, with mean (median) values of 9.73 (9.70) Mg ha^{-1} a^{-1} and 6.53 (6.42) Mg ha^{-1} a^{-1}, respectively (P-value = 0.00014; Fig. 2c). AGWP with height ranged from 4.54 to 9.07 Mg ha^{-1} a^{-1} across Amazonian plots, and from 6.33 to 13.25 Mg ha^{-1} a^{-1} in Bornean plots.
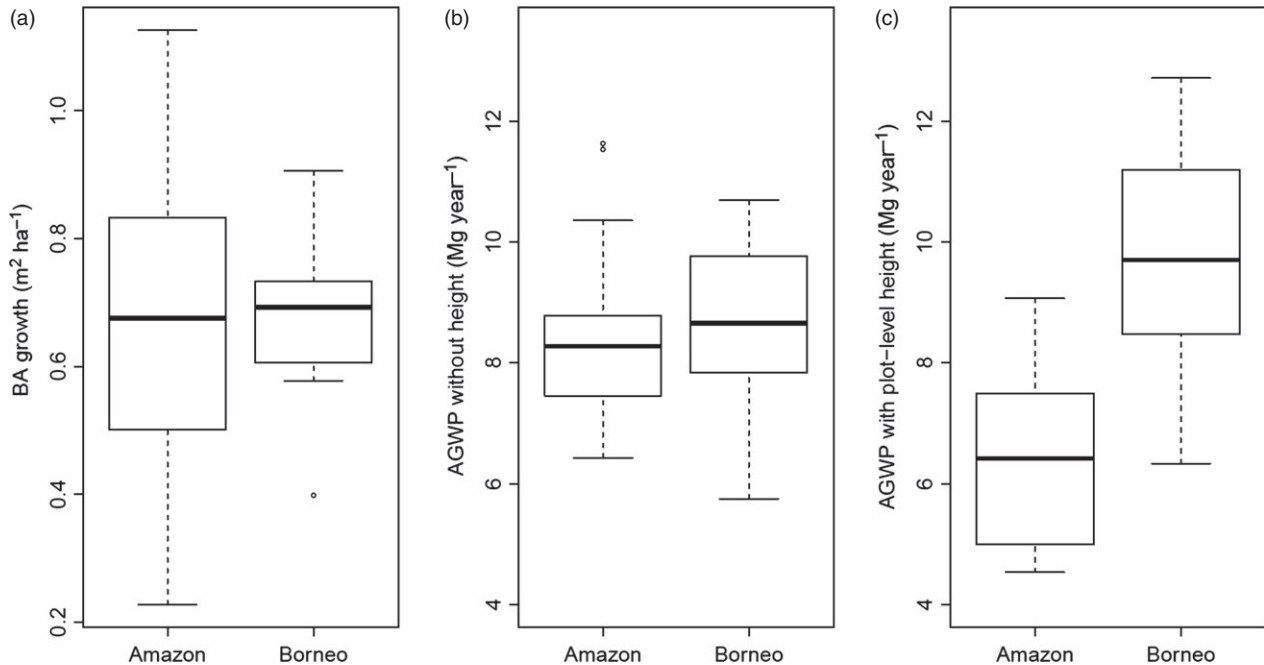
Fig. 2. Boxplots showing regional differences in plot-level (a) basal area (BA) growth; (b) above-ground wood production (AGWB) calculated without a height term (AGWP without height); and (c) AGWP with height, where a height term was included in the estimation.

RELATIONSHIPS BETWEEN ENVIRONMENTAL CONDITIONS AND PLOT-LEVEL GROWTH AND AGWP

We considered the effect of soil and climate parameters, plus the factor term 'continent', on BA growth and AGWP. Soil fertility had a significant positive effect on BA growth and AGWP in all models (Table 2 and Fig. 3). BA growth was positively related to PCA1 (itself positively associated with sum of bases and total P and negatively associated with C/N and sand content) and negatively related to PCA2 (Al, K, Mg). The slopes of these relationships were statistically indistinguishable between the two regions, but the intercept was significantly higher for Borneo than for Amazon, showing that BA growth has the same relationship with soil fertility in both regions and that when soil conditions are controlled for, BA growth is substantially higher in Borneo. The models that replaced PCA axes with (i) sum of bases and (ii) total P had lower explanatory powers (adjusted R^2 = 0.525 and 0.443, respectively) than the model containing the PCA axes (adjusted R^2 = 0.647, P < 0.0001), but all measures of soil fertility were positively related to BA growth. In both of the latter models, the continent term became non-significant and mean annual precipitation became significant.

Above-ground wood production (AGWP) without height was also positively related to PCA1 (Table 2); no other terms were significant in this model, neither the intercept nor the slope of the relationship were significantly different between the two regions, and this model had low explanatory power (adjusted R^2 = 0.280). However, when PCA axes were replaced in the model by (i) sum of bases and (ii) total P, the intercept was significantly greater in Borneo than in Amazon. AGWP with height was also positively related to PCA1, and

whilst the slope of this relationship was not significantly different between regions, the intercept was significantly higher for Borneo, and no other terms were significant. Similarly, sum of bases and total P had the same positive effect on AGWP with height in both regions, but the intercept remained significantly higher in Borneo than in Amazon. Overall, the results show that when soil conditions were controlled for, AGWP was significantly higher in the Bornean than in the Amazonian plots.

DIFFERENCES IN INDIVIDUAL TREE GROWTH AND PRODUCTION BETWEEN REGIONS AND TAXONOMIC GROUPS

Analysis of individual trees in all plots showed that individual tree growth rate (mm year^{-1}; eqn 3) was significantly positively related to tree size and soil fertility (PCA1) and negatively related to wood density (Table 3). The continent factor term was also significant; whilst the intercept was greater for Amazonian trees, the slope of the relationship between tree size and growth was significantly greater in Borneo. As a result, when tree size, wood density and PCA1 were standardized, individual diameter growth was marginally greater in NW Amazonia than in Borneo (mean difference, 0.6 mm year^{-1}; Table S4). Individual AGWP with height (eqn 4) was significantly positively related to tree size and PCA1. In contrast to the individual diameter growth results, wood density was positively related to AGWP in both regions. The intercept was greater in Borneo than in Amazonia, but in the best model, there was no difference in slopes of the covariates between regions. Thus, AGWP with height was greater in Bornean stems than in Amazonian stems
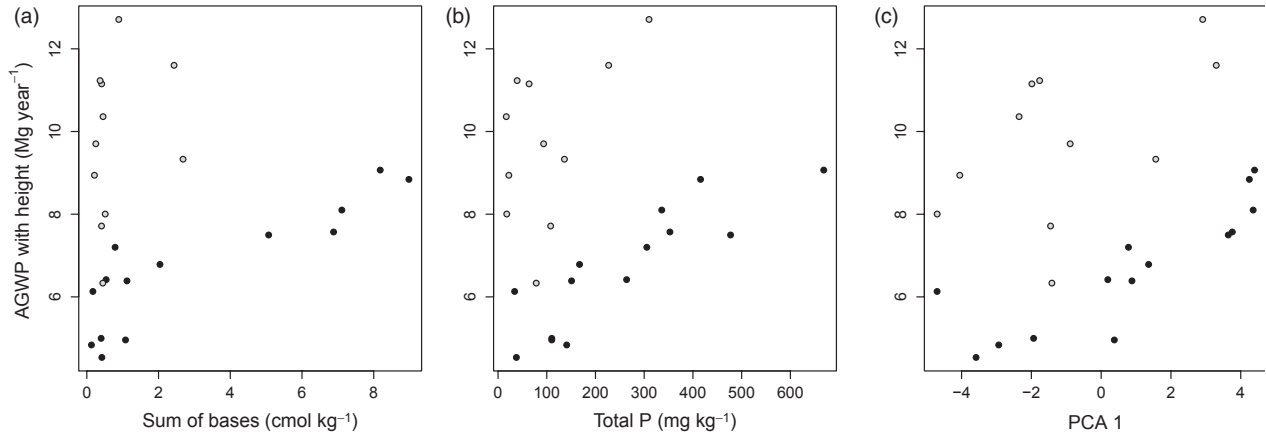
Fig. 3. Relationships between environmental conditions - sum of bases (a), total P (b) and principal component axis 1 (c) - with plot-level above-ground wood production (AGWP with height) in Amazonia (solid circles) and Asia (open circles). Fit-lines are shown for significant relationships.

Table 2. Best linear regression models for forest dynamics response variables [plot-level basal area growth (m^2 ha^{-1} $year^{-1}$), above-ground wood production (AGWP), with and without height (Mg ha^{-1} $year^{-1}$)]. Explanatory variables in maximal models were mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), mean solar radiation (SR, MJ m^{-2} day^{-1}) and either (1) soil component axes (PCA 1, 2 and 3) or key soil explanatory variables (2) sum of bases $\sum_B$ (cmol kg^{-1}) or (3) total P (mg kg^{-1}), and 'region' as a fixed factor. Model fit is indicated by adjusted R^2. Residuals met regression model assumptions

Y (Model number)	Region	Model	Adjusted R^2	P-value
Basal area growth				
(1)	Amazonia	$0.537 + 0.059$ (PCA 1) $- 0.100$ (PCA 2)	0.647	< 0.0001
	Borneo	$0.824 + 0.059$ (PCA 1) $- 0.100$ (PCA 2)		
(2)		$-0.229 + 0.0462$ ($\sum_B$) $+ (2.54 \times 10^{-4}$.MAP)	0.525	0.0001
(3)		$-0.227 + (6.80 \times 10^{-4}$.Total P) $+ (2.44 \times 10^{-4}$.MAP)	0.443	0.0006
AGWP without height				
(1)		$8.635 + 0.284$ (PCA1)	0.280	0.0038
(2)	Amazonia	$7.403 + 0.404$ ($\sum_B$)	0.410	0.0012
	Borneo	$8.291 + 0.404$ ($\sum_B$)		
(3)	Amazonia	$6.976 + 0.007$ (Total P)	0.348	0.0035
	Borneo	$7.964 + 0.007$ (Total P)		
AGWP with height				
(1)	Amazonia	$6.357 + 0.400$ (PCA 1)	0.699	< 0.0001
	Borneo	$10.128 + 0.400$ (PCA 1)		
(2)	Amazonia	$5.473 + 0.389$ ($\sum_B$)	0.633	< 0.0001
	Borneo	$9.413 + 0.389$ ($\sum_B$)		
(3)	Amazonia	$4.725 + 0.008$ (Total P)	0.693	< 0.0001
	Borneo	$8.964 + 0.008$ (Total P)		

(Table S4). The mean AGWP of stems > 40 cm diameter gained, on average, 49% more AGWP in Borneo than in Amazonia (Fig. S5).

Within the Borneo sample, trees of the family Dipterocarpaceae gained diameter faster, on average, than those from the other families combined into a contrasting non-dipterocarp group (Fig. 4). Tree diameter growth was negatively related to wood density and positively related to tree size for both dipterocarps and non-dipterocarps (Table 3). PCA1 was positively associated with growth rate in dipterocarps and slightly negatively so for non-dipterocarps. Whilst the intercept of non-dipterocarps was higher, the positive relationship between tree size and growth was stronger in dipterocarps than in non-dipterocarps. For trees of a standardized size, wood density

and soil fertility, diameter growth was faster in dipterocarps than in non-dipterocarps and particularly so at larger diameters (Table S4). The AGWP with height of both taxonomic groups was positively related to tree size, wood density and PCA1, and the positive effects of tree size and PCA1 were stronger in dipterocarps than in non-dipterocarps. When comparing standardized size, wood density and soil values, dipterocarps had faster AGWP rates (Fig. 4 and Table S6).

Discussion

The results reveal that rain forests in two climatically similar regions, N Borneo and NW Amazonia, despite being virtually identical in terms of stem density and wood density, differ

Table 3. Best individual-level mixed-effects models for tree growth (*gr*) and wood production (*pr*). Full models included ln-diameter (ln*D*) as a quadratic term, wood density (*WD*) and soil fertility (PCA1) as fixed effects, 'continent' or 'dipterocarp' as fixed factors and 'plot' as a random effect. Model simplification is described in the Methods text. Estimated coefficients are presented to 3 significant figures

| Model; response	Factor level	Function
Eqn 3; ln(*gr* + 5)	NW Amazon	$4.03 - 0.945.\ln D + 0.108.(\ln D)^2 - 0.203.WD + 0.00445.PCA1$
	N Borneo	$1.46 + 0.0296.\ln D + 0.0150.(\ln D)^2 - 0.203.WD + 0.00445.PCA1$
Eqn 4; ln(*pr* + 1.04)	NW Amazon	$0.920 - 0.355.\ln D + 0.0356.(\ln D)^2 + 0.00718.WD + 0.000725.PCA1$
	N Borneo	$0.922 - 0.355.\ln D + 0.0356.(\ln D)^2 + 0.00718.WD + 0.000725.PCA1$
Eqn 3; ln(*gr* + 5)	Dipterocarp	$-0.737 + 0.862.\ln D - 0.0570.(\ln D)^2 - 0.346.WD + 0.00942.PCA1$
	Non-dipterocarp	$1.07 + 0.199.\ln D - 0.00413.(\ln D)^2 - 0.188.WD - 0.0035.PCA1$
Eqn 4; ln(*pr* + 1.04)	Dipterocarp	$0.987 - 0.384.\ln D + 0.0389.(\ln D)^2 + 0.0125.WD + 0.00279.PCA1$
	Non-dipterocarp	$0.566 - 0.219.\ln D + 0.0225.(\ln D)^2 + 0.0125.WD + 0.000265.PCA1$
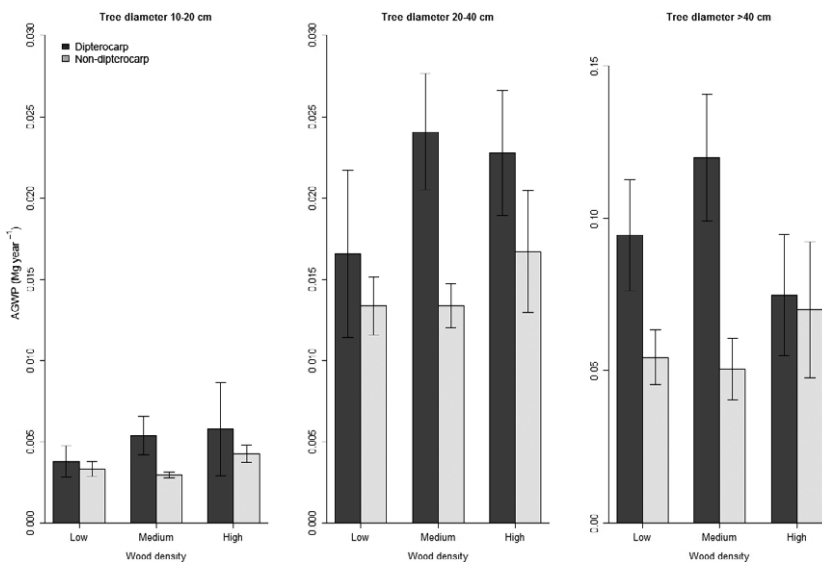
Fig. 4. Mean (± 2 SE) individual above-ground wood production for diameter and wood density classes for dipterocarps (dark grey) and non-dipterocarps (light grey) in Bornean plots.

significantly and very substantially (49%) in AGWP, with median values of 9.70 and 6.53 Mg ha^{-1} year^{-1}, respectively, when local height–diameter allometries were accounted for (Fig. 3). The sites from NW Amazonia are among the most productive recorded within the Amazon basin, in terms of woody biomass (Malhi *et al.* 2004), so the comparison here shows that these tropical forests of Borneo attain greater wood production rates than most or all Amazonian forests. Nevertheless, the Bornean AGWPs reported here are not as high as those estimated by Paoli & Curran (2007) where rates of up to 23.6 Mg ha^{-1} year^{-1} were reported. The authors themselves stress that these high values are likely due to very small (0.07 ha) plots, located non-randomly to avoid large canopy gaps and monitored for only 1 year, and so their results are presumably not representative of larger forest areas. The Borneo AGWP rates presented here are close to those reported by Kitayama & Aiba (2002) and the SE Asian sites in Chave *et al.* (2008). Combining the published AGWP values (Table 4) and the 11 plots reported here gives a mean value of 8.74 Mg ha^{-1} year^{-1} for Asia (ranging from 5.6 to 12.7, calculated using a mean value for plots from Paoli & Curran 2007), compared with the published Amazon mean of

6.2 (ranging from 3.0 to 11.0) Mg ha^{-1} year^{-1} (Malhi *et al.* 2004). Whilst most previous studies do not include local height–diameter allometry, data from the literature, together with our results, suggest that wood production rates are ~40% greater in Asian forests than in the rain forests of Amazonia.

Accounting for local height–diameter allometries was critical in revealing the regional differences in AGWP. AGWP, even when calculated without the inclusion of local height–diameter relationships, was significantly higher in Borneo when soil conditions were controlled for, but the between-region difference in AGWP estimates was especially marked once height allometry was accounted for. Differences in vertical structure are known to underpin substantial variation in tree biomass (Chave *et al.* 2005; Banin *et al.* 2012; Feldpausch *et al.* 2012). Our result suggests that it is also critical to account for allometric differences when assessing woody productivity and carbon dynamics.

Above-ground wood production represents one part of an ecosystem's net primary production (NPP). Whether the between-region differences in AGWP reflect differences in NPP depends on the proportional allocation to other components of NPP, such as leaf and root production. Whilst most

Table 4. Asian tropical moist forest sites with above-ground wood production (AGWP) data available from the literature. All sites < 1000 m.a.s.l. altitude except for Lore Lindu, at 1050 m.a.s.l

Site	Substrate	Area, ha (sub-plot size)	Observation period	AGWP ($Mg\ ha^{-2}\ year^{-1}$)	Reference
Gunung Palung (Kalimantan, Indonesia)	Alluvium, sedimentary, igneous granite	2.1 (0.07)	1999–2001	5.8–23.6 (mean 12.0)	Paoli & Curran (2007)
Central Kalimantan (P1) (Kalimantan, Indonesia)	White sand	1	1998–1999	6.60	Miyamoto *et al.* (2007)
Central Kalimantan (P4) (Kalimantan, Indonesia)	White sand	1	1998–2000	7.95	Miyamoto *et al.* (2007)
Pasoh (Peninsular Malaysia)	Sedimentary	50	1986–2000	6.96	Chave *et al.* (2008)
Mount Kinabalu (Sabah, Malaysia)	Sedimentary	1	1996–1997	8.03	Kitayama & Aiba (2002)
Mount Kinabalu (Sabah, Malaysia)	Ultrabasic	1	1996–1997	6.02	Kitayama & Aiba (2002)
Lambir (Sarawak, Malaysia)	Sedimentary	52	1992–2003	7.13	Chave *et al.* (2008)
Sinharaja (Sri Lanka)	Metamorphic	25	1993–1998	7.40	Chave *et al.* (2008)
Lore Lindu (Sulawesi, Indonesia)	Metamorphic	0.96 (0.16)	2007–2008	5.62	Hertel *et al.* (2009)

studies of tropical forests indicate that leaf production is positively related to stem production (Clark *et al.* 2001; Paoli & Curran 2007), the relationship was not strongly supported in another Amazonian study (Aragao *et al.* 2009). Significant differences in allocation between the regions are not inconceivable, particularly if different resources are limiting in differing locations and plants shift allocation to improve acquisition of the most limiting resource, for example, to roots when water or nutrients are limiting (Gleeson & Tilman 1992). Unfortunately, comparable stem, root, leaf, fruit and flower production data are rare (Malhi, Doughty & Galbraith 2011). Chave *et al.* (2009) recorded a mean annual litterfall production of 8.6 (range, 5.2–12.5) $Mg\ ha^{-1}$ from Amazonia; four studies in Asian forests report similar litterfall values of 7.7 $Mg\ ha^{-1}$ (Paoli & Curran 2007), 11.1 $Mg\ ha^{-1}$ (Kitayama & Aiba 2002), 5.7–7.7 $Mg\ ha^{-1}$ (Dent *et al.* 2006) and 7.5 $Mg\ ha^{-1}$ (Hertel *et al.* 2009). From these limited data, it does not appear that differences in AGWP are compensated for by production of canopy plant parts. Using data from multiple sites, compiled from the literature, Malhi, Doughty & Galbraith (2011) also found there to be little variation in canopy production, but that the observed inter-site variation was caused by shifting allocation between woody NPP and fine-root NPP. On average, sites in Asia tended towards higher woody allocation and lower allocation to roots compared with Amazonian sites; however, this data set included only eight Asian sites, predominantly from India and China where climatic conditions differ substantially from Borneo (Malhi, Doughty & Galbraith 2011). Another key difference between Bornean and Amazonian forests is in the timing of reproduction – the dipterocarp forests in Borneo have super-annual mass flowering and fruiting events, which could result in lower carbon allocation to reproduction. A pan-Amazonian study reported mean allocation to reproductive organs of 0.69 ± 0.40 $Mg\ ha^{-1}\ year^{-1}$ and 9% of total litterfall (Chave *et al.* 2010). Two studies in Borneo reported reproductive litter of 0.05 $Mg\ ha^{-1}\ year^{-1}$ (0.4% of total litter; Dent *et al.*, 2006) and 0.4 $Mg\ ha^{-1}\ year^{-1}$ (5% of total litter; Paoli & Curran 2007), each measured over a 2-year period. However, for a true comparison, litterfall needs to be monitored for much longer in Asian forests to account for mast fruiting events which occur rarely in association with drought events (Sakai *et al.* 2006). Other contributions to NPP, notably the growth of stems smaller than 10 cm diameter, palms and lianas (which together may constitute an estimated additional ~10% of AGB; DeWalt & Chave 2004), as well as below-ground growth, are rarely reported. Until standardized measurements of most components of ecosystem production are available from across the tropics, it is likely to remain uncertain whether the marked continental differences in AGWP reported here reflect large differences in NPP.

Above-ground wood production was positively correlated with soil fertility, as represented by PCA axes, in both Amazonia and Borneo (Fig. 3) though the observed gradient in fertility (sum of bases, total P) was longer in Amazonia. The positive relationship is consistent with results from other tropical moist forest studies (Kitayama & Aiba 2002; Paoli & Curran 2007; Aragao *et al.* 2009; Cleveland *et al.* 2011; Quesada *et al.* 2012). The positive relationship between AGWP and total P is consistent with suggestions that soil P limits tree growth in much of the tropics (Vitousek 1984; Quesada *et al.* 2012). Since soil attributes are highly correlated, it is difficult to identify the extent to which each nutrient may be limiting: both *in situ* nutrient addition experiments (e.g. Tanner, Vitousek & Cuevas 1998; Kaspari *et al.* 2008; Wright *et al.* 2011) and physiological studies (e.g. Meir, Grace & Miranda 2001) will be required to better understand the basis of nutrient limitation in tropical forests.

Notwithstanding the above, our results demonstrate that soil nutrient status alone cannot explain the observed inter-continental differences in plot-level AGWP. At comparable levels of soil fertility, Bornean forests achieve higher rates of wood production than Amazonian forests do. This is the first time, to our knowledge, in which standardized methodologies have been applied to estimate forest growth, AGWP and soil chemical composition across more than one tropical continent. Since soil parameters are highly sensitive to the methods and laboratories used, such standardized approaches are critical to being able to draw robust conclusions (Quesada *et al.* 2012). Assuming that the ~49% inter-regional difference in AGWP reported here is not fully counterbalanced by large differences in allocation to other components of NPP, the findings suggest that either (i) significant additional growth resources are available to trees growing in Asia or (ii) the species growing in Asian forests are better equipped to convert the resources available into assimilated carbon, or both processes are occurring. Each possibility is discussed here.

Photosynthetically active radiation is a fundamental growth resource. Mean solar radiation, as calculated from interpolated station data of sunshine hours and cloud cover (New, Hulme & Jones 1999), was significantly higher (18%) across the Bornean sites than the Amazonian sites. This difference can be attributed to differing diurnal patterns in precipitation; Southeast Asian forests are reported to have relatively less cloudy skies during the day and receive the majority of precipitation at night as a result of the more maritime climate (Richards 1996). It is reasonable to infer that this might affect tree growth and AGWP, as experiments, modelling approaches and satellite data have suggested that radiation can limit canopy tree growth in parts of the humid tropics (Churkina & Running 1998; Graham *et al.* 2003; Nemani *et al.* 2003). Furthermore, temporal variation in tree growth in four tropical forest sites has also been found to correlate with temporal variation in light availability derived from satellite data (Dong *et al.* 2012). Whilst the effect of solar radiation was included in our maximal models, it was not significant in explaining variation in our data set; this is because there was very little within-region variation in solar radiation (Fig. S2), and as such, the model was unable to partition variation in growth and AGWP in relation to radiation. Improved localized radiation data would help improve our understanding of the role of PAR as a limiting resource, its effect in determining differences between regions and thus the likely impact of future changes in cloud cover associated with climatic change.

The sites in this study do not differ substantially in terms of the mean annual rainfall they receive (Tables 1 and S1) and do not have dry seasons in most years, so water supply *per se* does not determine the large cross-continental differences in woody productivity. Nevertheless, forests in Asia are subject to occasional, severe El Niño droughts (e.g. the widespread droughts in 1982/3 and 1997/8). Western Amazonia additionally is subject to occasional short-term drying associated with warming of the tropical north Atlantic (Marengo *et al.* 2011). In the context of this study, we would expect drought to first increase tree mortality and perhaps reduce NPP through water limitation (Nakagawa *et al.* 2000; Potts 2003; Cao *et al.* 2004; Phillips *et al.* 2010). After the drought event, growth rates of surviving trees may increase due to a release of growth resources, for example light and nutrients. The net long-term effect on productivity is poorly known, but the disproportionate loss of large trees during drought events (Slik 2004; Phillips *et al.* 2010) and the greater contribution of large trees to plot-level productivity (Stephenson *et al.* 2014) would suggest an overall negative effect of drought on productivity. Stem turnover rates in western Amazonia over recent monitored time periods are at least as great as those in N Borneo (Lewis *et al.* 2004; Phillips *et al.* 2010; Galbraith *et al.* 2013), whilst AGB is currently much higher in the Bornean sites than in NW Amazonia (this study), suggesting that extra drought disturbance in Borneo is very unlikely to be driving the differences in wood production.

More generally, we sampled only in areas without known major anthropogenic disturbance. Whilst it is not possible to formally exclude the potential subtle effects of past disturbances, it is improbable that such events could generate sufficient additional resources for growth to explain the magnitude of long-term continental differences that we measured. Further, the differences in AGWP are particularly apparent once the differing height–diameter allometry is accounted for, yet greater disturbance would be expected to result in smaller, not taller, trees (e.g. Banin *et al.* 2012).

Whilst soil available nutrients were standardized, atmospheric deposition of nutrients has not been measured in this study and may be acting as a fertilizer in some parts of the tropics (Lewis, Malhi & Phillips 2004; Lewis 2006). There have been long-term N inputs impacting upon tropical vegetation, as evidenced by increasing N concentration in leaves in a forest in Panama (Hietz *et al.* 2011), though this does not indicate a growth effect. Substantial regional variation in N deposition has been reported, and total N deposition is higher in Asia than in South America (Galloway & Cowling 2002; Hietz *et al.* 2011). Whilst this might help reduce N limitation in Asian forests, it is generally accepted that tropical forest growth is not limited by N except in the most depauperate soils (Jordan & Herrera 1981; Vitousek 1984), so it is as yet unclear how deposition of N affects ecosystem processes such as productivity. Furthermore, N deposition may make soils more acidic, thus decreasing the availability of some nutrients rather than increasing them (Lewis *et al.* 2009). Atmospheric inputs have been noted as an important source of P in the Amazon basin (DeLonge, D'Odorico & Lawrence 2008). Mahowald *et al.* (2005) report that *c.* 23% of P flux in the Amazon is due to biomass burning and human disturbance. Nutrient additions resulting from biomass burning may be equivalent, if not larger, in N Borneo as they tend to be closer to areas of widespread deforestation than the plots in NW Amazonia. Further understanding of the local, spatial distribution of atmospheric deposition of nutrients, the impacts on terrestrial nutrient cycling and forest growth is required.

The capacity for trees of different species to be able to utilize resources more, or less, efficiently is not well understood. As with plot-level comparisons, differences may exist between

species in terms of allocation to different plant parts; thus, whilst AGWP differs, NPP may not, and this warrants testing. The composition of the understorey in the forests of Amazonia and Asia also differs: juveniles of canopy species dominate the understorey in Asian forests, whilst in parts of Amazonia, understorey specialists often prevail (LaFrankie *et al.* 2006). Understorey species may have inherently slower wood production rates as they do not need to attain a super-canopy position in order to reproduce. These contrasting species assemblages may therefore affect the stand-level capacity for wood production.

We found that the Dipterocarpaceae produce wood more quickly than trees belonging to other families in Borneo (Fig. 4). There are several mechanisms by which dipterocarps could achieve this. Dipterocarp trees may be able to more efficiently make use of nutrients because they form ectomycorrhizal symbioses. Ectomycorrhizal associations are rare in tropical trees species; most tropical species form associations with arbuscular mycorrhiza (Brearley 2012). Ectomycorrhizal relations are also more common in species forming dominant stands, indicating that they may provide a competitive advantage (Henkel, Terborgh & Vilgalys 2002) although evidence is mixed (Peh, Lewis & Lloyd 2011). In particular, ectomycorrhizae may help trees to access soil P at greater rates and overcome P limitation (Henkel, Terborgh & Vilgalys 2002; Brearley 2012). In our study, the effect of soil fertility on growth and production was greater in dipterocarps than in non-dipterocarps, and this could indicate that dipterocarps receive a greater growth advantage per unit increase in fertility. Another possibility is that their tall stature allows Dipterocarpaceae to escape competition not only from other trees but also from lianas, which appear to be less abundant in Bornean forests than in Amazonian forests (Gentry & Emmons 1987). This liana-escape hypothesis would predict lower liana leaf production in dipterocarp-dominated forests than elsewhere. These hypotheses are not mutually exclusive, and indeed, dipterocarps may gain a competitive advantage through a combination of these means. The role of the dipterocarps in increasing stand-level AGWP highlights that particular floristic elements can be important in driving production rates in forests. Evidently, forest restoration efforts should consider restoring floristic assemblages, as well as tree cover, where possible.

Conclusion

We found that plot-level AGWP is significantly and substantially greater in N Borneo than in NW Amazonia. At the plot level, the difference in Amazon and Bornean production is associated with (i) taller trees for a given diameter and (ii) a greater number of the larger trees that tend to be absolutely the most productive. The differences are not caused by differences in wood density or the number of stems per hectare. Neither are they due to soil nutrient availability, even though as expected soil fertility was an important determinant of AGWP within regions. We show for the first time that trees in the family Dipterocarpaceae produce wood faster than coexisting taxa when soil, tree size and wood density are all controlled for. Our working hypotheses to explain the higher AGWP rates in N Borneo are (i) the apparent greater availability of incoming solar radia-

tion compared to NW Amazonia and (ii) that floristic elements in Asia (namely the Dipterocarpaceae) are able to make use of resources more efficiently to achieve fast AGWP rates. The results identify a need for further inter-continental comparative research of all ecosystem production components and key environmental variables, including solar radiation using standardized measurements. A key question remains – How do different tree taxa achieve different production rates in similar environments?

The differences observed have implications for quantifying and modelling carbon stocks and fluxes for better understanding of consequences of land-use change and climate change mitigation, and for forest management for the purposes of REDD+. The relatively high capacity of dipterocarp trees to take up carbon into long-lived woody tissues presents a special opportunity for carbon sequestration in the restoration of Southeast Asia's heavily degraded forests.

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Data accessibility

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Study site conditions.

Appendix S2. Census interval corrections.

Appendix S3. Individual tree growth.

Figure S1. Height-diameter relationships in N Borneo and NW Amazon.

Figure S2. Map of solar radiation.

Figure S3. Topsoil properties (base cations, total P and C:N) by inventory plot.

Figure S4. Plot-level census interval correction slope.

Figure S5. Mean ($\pm$ 2 SE) individual above-ground wood production for diameter and wood density classes in Amazonia and Borneo.

Table S1. Description of study plots.

Table S2. Table of Principal Components Analysis (PCA) on plot-level soil variables.

Table S3. Details of plot censuses, corrected and uncorrected values.

Table S4. Model-estimated individual tree growth and wood production for standardised size, wood density and soil conditions.