Tree height integrated into pan-tropical forest biomass estimates

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Abstract

Above-ground tropical tree biomass and carbon storage estimates commonly ignore tree height. We estimate the effect of incorporating height (*H*) on forest biomass estimates using 37,625 concomitant *H* and diameter measurements (n=327 plots) and 1816 harvested trees (n=21 plots) tropics-wide to answer the following questions:

1) For trees of known biomass (from destructive harvests) which *H*-model form and geographic scale (plot, region, and continent) most reduces biomass estimate uncertainty?
2) How much does including *H* relationship estimates derived in (1) reduce uncertainty in biomass estimates across 327 plots spanning four continents?
3) What effect does the inclusion of *H* in biomass estimates have on plot- and continental-scale forest biomass estimates?

The mean relative error in biomass estimates of the destructively harvested trees was half (mean 0.06) when including *H*, compared to excluding *H* (mean 0.13). The power- and Weibull-*H* asymptotic model provided the greatest reduction in uncertainty, with the regional Weibull-*H* model preferred because it reduces uncertainty in smaller-diameter classes that contain the bulk of biomass per hectare in most forests. Propagating the relationships from destructively harvested tree biomass to each of the 327 plots from across the tropics shows errors are reduced from 41.8 Mg ha^{-1} (range 6.6 to 112.4) to 8.0 Mg ha^{-1} (-2.5 to 23.0) when including *H*. For all plots, above-ground live biomass was 52.2 ± 17.3 Mg ha^{-1} lower when including *H* estimates (13%), with the greatest reductions in estimated biomass in Brazilian Shield forests and relatively no change in the Guyana Shield, central Africa and southeast Asia. We show fundamentally different stand structure across the four forested tropical continents, which affects biomass reductions due to *H*. African forests store a greater portion of total biomass in large-diameter trees and trees are on average larger in diameter. This contrasts to forests on all other continents where smaller-diameter trees contain the greatest fractions of total biomass. After accounting for variation in *H*, total biomass per hectare is greatest in Australia, the Guyana Shield, and Asia and lowest in W. Africa, W. Amazonia, and the Brazilian Shield (descending order). Thus, if closed canopy tropical forests span 1668 million km^2 and store 285 Pg C, then the overestimate is 35 Pg C if *H* is ignored, and the sampled plots are an unbiased statistical representation of all tropical forest in terms of biomass and height factors. Our results show that tree *H* is an important allometric factor that needs to be included in future forest biomass estimates to reduce error in estimates of pantropical carbon stocks and emissions due to deforestation.

1 Introduction

Accurate estimates of tropical tree biomass are essential to determine geographic patterns in carbon stocks, the magnitudes of fluxes due to land-use change, and to quantify how much carbon has not been emitted via mechanisms such as REDD+ (Reducing Emissions from Deforestation and forest Degradation). Global estimates of tree carbon in tropical forests vary between 40 to 50% of the total carbon in terrestrial vegetation (Watson et al., 2000; Kindermann et al., 2008), indicating considerable uncertainty. Such uncertainty is consequent on the complex process that links individual tree measurements to large-scale patterns of carbon distribution, as well as definition as to what constitutes “forest.” The accurate estimation of tree-, plot-level or regional global mass of tropical trees requires first harvesting and weighing trees (Fittkau and Klinge, 1973), and subsequently estimating biomass on a larger population by measuring tree stem diameter (*D*) and converting *D* to biomass based on allometric equations developed using the destructive harvest data (Brown et al., 1989; Overman et al., 1994; Ogawa et al., 1965).

Biomass can also be estimated using active (e.g. radar) and passive (e.g. Landsat) remote sensing-based methods (e.g. Drake et al., 2003; Steininger, 2000; Mitchard et al., 2011). Nevertheless, these all require plot-based biomass estimates derived from stem diameter measurements and allometric equations (either calibrated “on-site” or from the literature to “ground-truth” data (e.g. Lucas et al., 2002; Mitchard et al., 2009)) and have large uncertainty. For example, carbon stock estimates for Amazonia based on spatial interpolations of direct measurements, relationships to climatic variables, and remote sensing data vary by a factor of two (Houghton et al., 2001) due to allometric models and different representations of the spatial extent of forest type and associated biomass.

The most widely used allometric equation for tropical forest biomass estimates are based on ~1300 harvested and weighed moist forest trees (Chave et al., 2005; Chambers et al., 2001), and with no biomass data from Africa included. The small sample size and geographical limits of this dataset are due to the tremendous efforts required to work in remote forests dissecting and determining mass of trees, some of which may weigh over 20 Mg. Such a lack of calibration data may bias estimates of carbon stocks in tropical forests (Houghton et al., 2000; Malhi et al., 2004). One major uncertainty in carbon stock estimates is related to architectural differences in tropical trees. For example, across plots, regions and continents there is significant and systematic variation in tropical forest tree height (*H*) for a given diameter (Feldpausch et al., 2011). This applies both to multispecies equations and to those restricted to individual species (Nogueira et al., 2008b). Hence, accounting for *H*:*D* allometry may reduce uncertainty associated with tropical forest biomass estimates from plot to pan-tropical scales.

Improving the accuracy of such estimates is important as almost all tropical forest regions of the world are currently undergoing major changes which must inevitably involve changes in their biomass and carbon stocks. For example, it is now apparent that many remaining intact tropical forests are not at carbon equilibrium, but rather are accumulating biomass (Lewis et al., 2009; Phillips et al., 1998), but an accurate quantification of this pantropical sink hinges on, amongst other factors, unbiased biomass estimates for individual trees. Similarly, quantifying changes in global carbon stocks and emissions where much of the active deforestation occurs (e.g. arc of deforestation in Brazil, INPE, 2009) can be overestimated when ignoring the effect of tree *H* in biomass estimates, because trees tend to be shorter trees for a given *H* in transitional forests where the most active deforestation fronts often occur (Nogueira et al., 2008b). As a result, carbon emissions from tropical deforestation (INPE, 2009) may be biased. More generally, incorporation of *H* in biomass estimates may help to account for variation in carbon stocks and could represent potential changes in calculated carbon emissions under deforestation (INPE, 2009), selective logging (Pinard and Putz, 1996; Feldpausch et al., 2005), sinks caused by forest regrowth (Uhl and Jordan, 1984; Feldpausch et al., 2004) and carbon valuation under Reducing Emissions from Deforestation and Degradation (REDD) (Aragao and Shimabukuro, 2010; Asner et al., 2010; Gibbs et al., 2007).

Along with wood specific gravity (ρ_W) (Baker et al., 2004b), tree *H* has already been incorporated into some regional and pantropical forest biomass models (Brown et al., 1989; Chave et al., 2005). Biomass estimation is then based on a four-step process:

i) measure individual tree *D*;
ii) estimate ρ_W at the finest taxonomic level available from ρ_W databases (Chave et al., 2009; Fearnside, 1997);

iii) measure or estimate H from allometric models based on the relationship between H and D alone (Brown et al., 1989) or with additional forest structure and climate variables to parameterise H estimates (Feldpausch et al., 2011);

iv) use these data to calculate biomass for individual trees from allometric equations based on D, ρ_W, and H.

Wood specific gravity is highly variable across regions and is a key determinant of larger-scale tree biomass spatial patterns (Baker et al., 2004b; Chave et al., 2006), and therefore accounting for it holds a central role in reducing uncertainty in biomass estimates. Despite the early recognition of the importance of H in biomass estimates (Crow, 1978; Ogawa et al., 1965), in practice H has less frequently been accounted for in pantropical biomass estimates due to lack of data.

Nevertheless, where data have been available inclusion of H has been shown to appreciably reduce errors in the estimation of destructively sampled biomass. For example, the standard error in estimating stand biomass for a destructively sampled dataset of trees $\geq$ 10 mm D was 12.5% if an equation including H was used, but 20% if an equation ignoring H (but calibrated on the same dataset) was applied (Chave et al., 2005). This same study showed that H was more important than a precipitation-based forest categorisation (dry, moist, wet) in more accurately estimating biomass.

Thus, allometric model choice, rather than sampling error or plot size, may be the most important source of error in estimating biomass (Chave et al., 2004). With the pantropical destructive biomass dataset sample size restricted by sampling cost and effort, H estimates from regional or continental-scale H:D models may provide a simple way to improve aboveground biomass estimates. Selection of the "*best*" model form to represent H in biomass models is, however, not straightforward with numerous statistical forms, geographical and environmental parameterisations, separations by growth form (etc) having been tested (e.g., Fang and Bailey, 1998; Feldpausch et al., 2011; Rich et al., 1986; Thomas and Bazzaz, 1999; Banin et al., 2012). In a global tropical analysis using multi-level models to examine the relationship between H and diameter, Feldpausch et al. (2011) found that after taking into account the effects of environment (annual precipitation coefficient of variation, dry season length, and mean annual air temperature) and forest basal area, there to be two main regional groups differing in their *H*:*D* relationships. Forests in Asia, Africa and the Guyana Shield are all similar in their *H:D* allometry, but with trees in the forests of much of the Amazon Basin and tropical Australia typically being shorter at any given diameter. Using an overlapping but different dataset, Banin et al, (2012) showed significantly different *H*:*D* allometry on all four continents, after accounting for differences in environment, forest structure and wood specific gravity. These results suggest that either continental, or sub-continental geographic *H:D* patterns may, in addition to model form, be important in reducing error in biomass estimates.

Here, using the largest available dataset of tree *H*, destructive biomass data (i.e. actual tree biomass is known) and pantropical permanent plot data (where information on *H* and *D* is known, but not the true biomass of a plot), we provide a first pantropical evaluation of the effects of *H* on biomass estimates, including by geographical location (plot, region, and continent). Specifically, we address the following questions:

1) Which is the best *H*-model form and geographic scale for inclusion in biomass models to significantly reduce site-level uncertainty in estimates of *destructive* biomass?
2) What is the reduction in uncertainty in plot-level biomass estimates based on census data from *permanent plots* across the tropics?
3) How does inclusion of *H* in biomass estimation protocols modify plot- and continental-level biomass estimates across the tropics?

2 Methods

We developed above-ground forest biomass estimates and evaluated biases using tree diameter (*D*), wood specific gravity (ρ_W) and *H* based on destructive sampling and permanent-plot census data. This assessment was based on the following steps, (1) compiled pantropical destructive biomass, tree *H*, and permanent sample plot census data, (2) computed new pantropical biomass models that include or exclude tree *H*, (3) develop *H* models, (4) used the destructive data to evaluate the effect of inclusion or exclusion of actual or simulated *H* in biomass estimates, (5) apply the new biomass models and error estimate from destructive biomass estimates to pantropical plot-based tree census data to (6) determine how biomass estimates change when including *H*, (7) determine the error associated with biomass estimates for pantropical permanent plots, (8) assess regional and continental changes in biomass estimates due to *H* integration in biomass estimates.

Destructive biomass data was compiled from published and non-published data from 21 plots in 10 countries (described below). *H* and *D* measurements are identical to those in Feldpausch et al. (2011). The tree census data reported here (Figure 1; SI Table S1) are from permanent sample plots primarily from the RAINFOR (Peacock et al., 2007; Baker et al., 2004a; Phillips et al., 2009) and AfriTRON (Lewis et al., 2009) networks across South America and Africa respectively, the TROBIT network of forest-savanna transition sites (Torello-Raventos et al., in review), the CSIRO network in Australia (Graham, 2006), and data from Asia (Banin, 2010) curated in the www.forestplots.net data repository (Lopez-Gonzalez et al., 2011). In addition, for each plot, mean annual precipitation, annual precipitation coefficient of variation, and dry season length were obtained from WorldClim global coverage at 2.5 minute resolution based on meteorological station data from 1950-2000 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

[Figure 1]

2.1 The destructive dataset

To determine the efficacy of biomass models to predict biomass, we assembled a destructively sampled tree biomass dataset (*n*=1816 trees) based on actual cut and weighed tropical forest trees (Chave et al., 2005; Nogueira et al., 2008a; Hozumi et al., 1969; Araújo et al., 1999; Mackensen et al., 2000; Brown et al., 1995; Lescure et al., 1983; Yamakura et al., 1986; Djomo et al., 2010; Henry et al., 2010; Deans et al., 1996; Ebuy et al., 2011; Samalca, 2007). We hereafter refer to this as the "destructive data." The destructive data are pantropical but with relatively few samples from Africa (*n*=116). The main differences between the dataset used by Chave et al. (2005) are that we excluded mangrove and subtropical biomass data from Chave *et al*. (2005) from our analysis; and, we included new destructive biomass datasets from Africa (Ghana, the Democratic Republic of Congo, and Cameroon) (Djomo et al., 2010; Henry et al., 2010; Deans et al., 1996; Ebuy et al., 2011), Kalimantan, Indonesia (Samalca, 2007) and Brazil (Nogueira et al., 2008a). To classify sites, climate data for the destructive dataset were extracted from the WorldClim data based on plot coordinates. For the destructive site data, mean annual precipitation ranged from 1520 to 2873 mm, dry season length 0 to 6 months, *D* from 1.2 to 1800 mm, and *H* from 1.9 to 70.7 m.

2.2 Tree height measurements

Tree height (*H*) had been previously measured at many of the permanent census plots from each of the four continents. Methodology and sites are specified in Feldpausch et al. (2011). To summarise the methods, in general a minimum of 50 trees per plot were sampled for *H* (total tree *H* above the ground) from 100 mm binned diameter classes (*i.e.*, 100 to 200, >200 to 300, > 300 to 400 mm, and > 400 mm). For some plots every tree was measured for *H*. Tree *H* was measured using Vertex hypsometers (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf Sweden), laser range-finders (*e.g.* LaserAce 300, LaserAce Hypsometer, Leica Disto-5), mechanical clinometers, physically climbing the tree with a tape measure, or by destructive methods. To examine how tree architectural properties related to stem *D*, independent of external factors such as trees damaged by treefalls, trees known to be broken or with substantial crown damage were excluded from analyses.

2.3 Biomass calculations

Above-ground biomass of trees for each destructively sampled site or permanent sample plot was calculated from a combination of variables. Wood specific gravity, ρ_W, was extracted from a global database ((Zanne et al., 2010); data dryad database). Where species-specific values were unavailable, we applied genus-level values. Likewise when genus-level values were missing, we applied family level values. Where tree identification was lacking, we applied the mean ρ_W from all stems in the plot. Based on the moist forest biomass model form proposed by Chave et al. (2005), we developed bootstrapped biomass model (1) as described below to estimate biomass based on either just the measured diameter and estimated ρ_W (i.e., excluding tree *H*) using the model form:

$$B = \exp(a + b\ln(D) + c(\ln(\mathrm{D}))^2 - d(\ln(D))^3 + e\ln(\rho_W)), \qquad (1)$$

Alternatively, using a range of *H*:*D* allometric models developed by Feldpausch *et al*. (2011) we inferred *H* and then used that inferred value in a bootstrapped biomass model (2) based on the form proposed by Chave et al. (2005) as described below. The model parameterisation, which includes *H* in addition to diameter and ρ_W is:

$$B = \exp(a + b\ln(\rho_W D^2 H)) \quad (2)$$

2.4 Biomass error estimation with and without height

From the destructive dataset, we evaluated the ability of a range of models to estimate biomass (kg) from a combination of D and ρ_W, or D, ρ_W and H, also examining error distributions across diameter classes and sites. To develop the H:D allometric relationships for inclusion in biomass models we used H measurements for individual trees made in 283 plots in 22 countries representing 39,955 individual concurrent H and D measurements. Because the global destructive tree biomass dataset is small compared to this and with the distribution of trees in the destructive dataset is not necessarily similar to biomass/size distribution of a natural forest, we applied a three-step approach to scale biomass estimates and their associated errors from the destructive dataset to permanent plots and landscape.

(i) When biomass models included H, we recomputed the regional and continental H models of Feldpausch et al. (2011) to test for their efficacy to reduce error in biomass estimates. These H models were either a non-linear 3-parameter exponential (Fang and Bailey, 1998) *viz*:

$$H = a\text{-}b(\exp(-cD)), \quad (3)$$

or, a model where H scales with D according to a simple power function as in:

$$H = aD^b, \quad (4)$$

or, alternatively a Weibull function, which takes the form of (Bailey, 1979):

$$H = a(1-\exp(-bD^c), \quad (5)$$

As there is good evidence of a large difference between different geographical areas in H:D allometry (Feldpausch et al., 2011), we derived region- and continent-specific parameterisations for each H:D equation and report the residual standard error and Akaike Information Criterion for the selected models (Akaike, 1974). We then tested how these parameterisations of H increased or decreased biomass estimates.

(ii) To test the effect of the inclusion of H estimates on biomass estimates, we computed a biomass model of all sites with destructively harvested trees, except the site which we wished to estimate. We then estimated the biomass of the trees in the site that was excluded from the model. We them repeated dropping a different single site each time. For each dropped site, the mean relative error in estimated biomass was calculated for a site, where relative error was represented as: $(B_{\mathrm{P}} - B_{\mathrm{M}})/B_{\mathrm{M}}$, where B_{P} is the predicted biomass of a tree (with or without H model) and B_{M} is the biomass measured by destructive sampling of individual trees.

(iii) To evaluate how the error from the destructive dataset relate to the distribution of trees found in pantropical forests, we estimated biomass for 327 plots from the forest permanent-plot database as described above by locale for tree-diameter classes, providing a biomass distribution by diameter class for each geographic locale (note that the destructive data come from “sites”—sample areas that may not have defined boundaries—while the permanent plot data come from defined-area sample “plots”). We then propagated error from (ii) from the destructive dataset to each diameter bin by geographical location and report the mean relative error for each region. The log-transformation of tree D and biomass data produces a bias in final biomass estimation so that uncorrected biomass estimates are theoretically expected to underestimate the real value (Sprugel, 1983; Baskerville, 1972). This effect can be corrected by multiplying the estimate by a correction factor:

$$C_F = \exp(\frac{RSE^2}{2}) \qquad (6)$$

which is always a number greater than 1, and where RSE is the residual standard error of the regression model.

2.5 **Permanent plot tree census data**

To determine how *H* integration alters biomass estimates and affects error in biomass estimates, we compiled a pantropical dataset of permanent sample plots (Supplemental Information Table S1). All plots occur in intact (minimal recent direct anthropogenic influence) forest, with a minimum plot size of 0.2 ha (mean = 0.95; max = 9 ha), area using standardised sampling methodologies across all sites. Diameters of all live trees and palms (≥ 100 mm diameter at breast height *(D)*) were measured to the nearest 1 mm at 1.3 m above the ground or 0.5 m above any buttresses or stilt-roots following international standards of permanent sampling plot protocol (Phillips et al., 2010). Trees were identified by a local botanist. For unknown species, vouchers were collected, later identified and archived. Plots were only included if some tree *H* information was available. This ranges from every tree to just 4% of trees in a plot measured for *H*.

2.5.1 Africa

Censused permanent sample plots were grouped into three geographical regions: Western, Eastern and Central Africa. Measurements were made in West Africa in Ghana and Liberia (Lewis et al. 2009). Central African sites were sampled in central and southern Cameroon, and Gabon (Lewis et al. 2009). Eastern African sites were established in the Eastern Arc Mountains of Tanzania (Marshall et al., in review). The number of months with precipitation < 100 mm per month, the estimated average monthly evapotranspiration of a tropical forest (Shuttleworth, 1988) and a widely used index of dry season length (Malhi and Wright, 2004), varies from 1 to 7 months across all sites.

2.5.2 Asia

We classified forests in Asia as one region for this study, with the division between Asian and Australasian plots according to Lydekker’s line (Lohman et al., 2011). Wet and moist forests were sampled in Brunei and Malaysian Borneo (Banin, 2010; Banin et al., 2012). These sites have zero months with mean precipitation < 100 mm per month.

2.5.3 Australasia

Trees were sampled in tropical forest permanent plots in northern Australia (Graham, 2006; Torello-Raventos et al., in review). Precipitation varies over very short distance from coastal to inland sites, with the dry season ranging from 4 to 10 months.

2.5.4 South America

Tree censuses conducted in South America are here grouped into four regions based on geography and substrate origin: Western Amazonia (Colombia, Ecuador and Peru), with soils mostly originating from recently weathered Andean deposits (Quesada et al., 2009); Southern Amazonia encompassing the Brazilian shield (Bolivia and Brazil); on the opposite side of the Basin to the north the Guyana shield (Guyana, French Guiana, Venezuela), and Eastern-Central Amazonia (Brazil) which is mostly comprised of old sedimentary substrates derived from the other three regions. The number of months with precipitation < 100 mm per month ranges from 0 to 9 months.

2.6 Patterns and revision of biomass and carbon stocks

Spatial patterns in plot-level biomass estimates with and without *H* were examined by region and continent. Plot-level biomass estimates with and without *H* were averaged by each region. Based on the regional tropical forest area estimates of broadleaf deciduous open and closed and evergreen tree cover classification from GLC2000 (Global Land Cover Map 2000)(Bartholomé and Belward, 2005) reclassified in ArcGIS® (ESRI, 2010), we scaled regional biomass estimates tropics-wide. Our estimates of tropical forest are lower than those reported by Mayaux et al. (2005) since we excluded the more open vegetation classes. Biomass was converted to carbon values using a conversion factor of 0.5 (Chave et al., 2005). Statistical analyses were conducted using the `R` statistical platform (R Development Core Team 2011). Biomass and *H* models were developed using the `lme` and `nlme` functions of R (Pinheiro et al., 2011).

3 Results

Using our expanded pantropical destructive biomass dataset (Figure 2a), we first examine how estimates of real (destructive) biomass data using boot-strapped biomass models (Table

1) are affected by different *H* model forms and regional or continental parameterisations by examining the relative error by diameter bin (Figure 2b) and overall bias in biomass estimates by destructively sampled site (Table 2). We next examine how the selected *H* models (Table 3) affect biomass estimates (Figure 3) and uncertainty (Figure 4) as a result of regional variation in forest structure (SI Table S2) and distribution of biomass among diameter classes for trees measured in pantropical permanent sample plots (SI Table S1), and finally extrapolating our results to assess the influence of incorporating variations in *H*:*D* allometry on regional/continental and global biomass estimates (Table 4 and 5).

3.1 How much does the inclusion of height reduce uncertainty in destructive biomass estimates?

The distribution of destructively sampled above-ground tree dry mass from the available pantropical dataset was roughly equally sampled across the 50 mm increment diameter classes from 250 mm < $D \leq$ 500 mm but, although involving many more individual trees, somewhat less for $D <$ 250 mm (Figure 2a). Although relatively few trees had been sampled for large diameter classes (*e.g.* 17 trees ≥ 1000 mm diameter), these larger trees clearly accounted for a significant proportion of the total biomass to be simulated within the dataset. The biomass in Figure 2a represents the nearly 1500 Mg of biomass destructively sampled to date in moist tropical forest which we use to assess the effect of *H* in biomass estimates. Some of these data have been used in the parameterisation of currently used pantropical biomass models (e.g. Chave et al., 2005), but with newly published data from Africa, Asia, and Brazil included in our analysis.

[Figure 2]

3.1.1 Measured heights

The effect of the inclusion of *H* using the biomass model forms of Chave et al. (2005) as applied to our dataset are presented in Table 1, where our allometric equations both with and without *H* included (i.e. Eq. 1 and Eq. 2) are compared. This shows that applying Eq. 1 (which excludes *H*) resulted in a considerably higher residual standard error (RSE) and Akaike information criteria (AIC) estimates than for when *H* was included (Eq. 2).

3.1.2 Simulated heights

The effects of substituting estimates of *H* from Eqs. 3-5 into Eq. 2 are shown in Table 2. The inclusion of *H* improved site-level estimates of aboveground biomass, bringing them closer to the known destructive harvest values, with a relative error of, *e.g.* 0.06 for both the Weibull-*H* region and continent-specific *H* models (Table 2). Excluding *H* tended to produce overestimated aboveground biomass estimates, with a relative error of 0.13. Regionally derived *H* estimates were non-significantly better than continental scale-derived *H* estimates at predicting site-level biomass (table 2) Overall, the Weibull model outperformed the other two function forms of *H*:*D* relationships (Table 2). Thus the best performance was obtained by including Weibull regional-specific *H* models (Table 2).

[Table 2]

Specifically, the Weibull-*H* (Eq. 5) (Table 3) consistently reduced the relative error in biomass estimates over all diameter classes as compared to the non-*H* estimates. This contrasted with the power-*H* model (Eq. 4) which, although reducing error even further in some diameter classes, had greater error for other diameter classes, even than those derived from Eq. 1 which excludes *H* (Figure 2b), The power model also had greater error for small diameter classes.

[Table 3]

3.2 Improving biomass estimates from permanent sample plots

3.2.1 Effect of including height in biomass estimates

Integration of the region-specific Weibull-*H*, on average, reduced estimated biomass per plot ($\hat{B}$) relative to excluding *H* in biomass estimates, on average by -52.2±17.3 Mg dry mass ha^{-1} (Figure 1b; Figure 3; Table 4). As shown by the cumulative biomass curves in Figure 3, including *H* in biomass estimates did not affect all regions equally. For South America, including *H* reduced biomass estimates for all regions except the Guyana Shield (by -55.9, -

66.6, and -47.9 Mg ha^{-1} for the Brazilian Shield, east-central Amazonia and western Amazonia, respectively). East and West Africa, and Northern Australia also had lower biomass estimates when including *H* (-13.5, -107.9, -116.5 Mg ha-1, respectively) Southeast Asia and central Africa showed no change in biomass estimates when including *H*. No region had significantly higher biomass estimates after including *H* (see Supplemental Information, Table S1, for Δbiomass estimates for all 327 plots).

3.2.2 Global differences in biomass distribution and tropical forest structure

There were appreciable differences in the biomass distribution among diameter classes reflecting strong regional and continental patterns (Figure 3). On average, biomass was found to be concentrated in the smaller diameter-classes for South America, Australia and, to some extent in Asia, than was the case the forests in Africa, which show a distinct biomass distribution. Specifically the latter have a greater contribution to biomass from larger diameter trees, as shown by the linear cumulative biomass curves in Figure 3. Regions that have the largest average diameter trees also have the lowest stem density (SI Table S2); however, it is not always the case that regions with on average larger diameter trees have higher biomass per hectare. The largest plot-level mean tree diameter for Africa (246 mm) was larger than for the other continents (216 to 236 mm); stem density, however, was higher on other continents compared to Africa (SI Table S2).

[Table 4]

[Figure 3]

It is because of the skewed biomass distributions of Figure 3 with a concentration of biomass in smaller diameter classes that in Sect 3.1 we chose of the Weibull-*H* model, which has lower relative error in small diameter classes (in contrast to the power-*H* model and three-parameter exponential model), and therefore has the greatest plot-level effect in reducing uncertainty. After accounting for regional tree *H* differences, total biomass per hectare is thus estimated to be greatest in Australia, the Guyana Shield, and Asia and lowest in W. Africa, W. Amazonia, and the Brazilian Shield (descending order) (Table 5).

3.2.3 Estimating effects of *H* on errors in permanent sample plot biomass estimates

To estimate error in permanent plots due to error in destructive measurements, we multiplied the relative error from the diameter bin from the small sample of destructive measurements for the Weibull-*H* model (Eqs. 2 and 5) as shown in Figure 2b by the biomass of the equivalent size-class in each pantropical permanent plots. This relative error in pantropical field-based plots was greater when the same procedure was undertaken for the 'no-*H*' Eq. 1 (Figure 4). Specifically, by including *H*, the error in estimates is reduced in small diameter-classes, but not large diameter-classes. This is because of the increasing absolute errors of the Weibull-*H* model for the larger trees. The mean error in biomass estimates for all regions when including Weibull-*H* in biomass estimates was an overestimate of 8.0 Mg ha^{-1}; a value considerably less than the calculated overestimate of 41.8 Mg ha^{-1} when *H* was excluded (Figure 4). The alternative two *H* models of Eqs. 3 and 4 were also tested and found to underestimate biomass by -8.2 and -5.5 Mg ha^{-1}, respectively. Overall, inclusion of Weibull-*H* (Eq. 5) in biomass estimates for tropical forest plots resulted in a smaller mean bias in biomass estimates compared to when *H* was omitted. Specifically the bias with *H* included ranged from 6 to 9.5 Mg ha^{-1} (South America), 10.1 to 10.6 Mg ha^{-1} (Asia and Australia), and 5.3 to 7.3 Mg ha^{-1} (Africa), as compared to estimation without *H*, which had biases of 28.6 to 47.2 Mg ha^{-1} (South America), 48.9 to 63.2 Mg ha^{-1} (Asia and Australia), and 40.5 to 49.4 Mg ha^{-1} (Africa) (Figure 4).

[Figure 4]

3.3 Effect on global carbon estimates

Based on published estimates of tropical forest area (GLC2000), and biomass and carbon estimated in our permanent plot networks, we have calculated the change in regional and continental above-ground live tree carbon stocks due to integration of *H* in biomass models. Using GLC2000 (Bartholomé and Belward, 2005) tropical forest categories and mean carbon storage in each region from the plot data, the tropical Americas had the largest relative reduction (-0.14) in estimated carbon storage due to *H*, and with Asia (-0.02) the smallest. Inclusion of region-specific *H* models to estimate carbon reduced tropics-wide estimates of total carbon in tropical forests from 320 to 285 Pg C, a reduction of 35.2 PgC, or 13%, relative to when *H* was included (Table 5).

[Table 5]

4 Discussion

We show that (1) including *H* significantly improves the accuracy of estimation of tropical forest aboveground biomass, (2) failing to include *H* usually causes an overestimate of biomass, (3) such overestimates can have globally significant implications, with one estimate being that carbon storage in tropical forests may be overestimated by 13%, and; finally (4) we recommend continental or regional-specific asymptotic Weibull *H*:*D* functions to be included in future estimates of biomass to reduce uncertainty in aboveground biomass estimates in tropical forests. Below, we discuss some of the sources of variability in biomass and *H* estimates, limitations of these models and implications for pantropical scaling and carbon valuation under REDD.

4.1 Compensating for imperfect biomass models

4.1.1 Representing height in biomass estimates

In this study we selected the *H* model based on the region-specific parameterisation of the Weibull-*H* (Eq. 5) model because it reduced error in estimating biomass for the smaller diameter classes (Figure 2b), and with these classes constituting the bulk of the plot-level biomass (Figure 3). Although the Weibull-*H* form is less than ideal for trees 800-1000 mm diameter, the three-parameter exponential (Eq. 3) and power-*H* models (Eq 4) were not significantly better biomass estimators for the largest trees (Fig. 2b). This may be because the parameterisation of the Weibull-*H* model should theoretically account for some of the asymptotic nature of tree growth more than the power or 3-parameter-exponential-*H* model (Banin et al. 2012). In general, however, asymptotic *H* is not as universal as may expected among species growing in tropical forest (Poorter et al., 2006; Chave et al., 2003; Davies et al., 1998; Thomas, 1996; Iida et al., 2011), where only one-fourth of species in sites sampled in Bolivia did reach an asymptote (Poorter et al., 2006). Unlike the power model, the 3-parameter-exponential-*H* and Weibull function for tree *H* have an additional biologically meaningful parameter, with a term for maximum tree height (*hmax*) here being applied at the plot, regional, or continental (as opposed to species) level, and it is for this reason the *hmax* should be interpreted carefully. For example, in the study here, the Weibull-*H* model converged on a *hmax* of >200 m for the Brazilian Shield of Amazonia, an unrealistic tree *H*. This model, however, gives an estimate of 11 and 47 m for trees of 100 and 1600 mm diameter, respectively, demonstrating that although the model provides realistic values, use of *hmax* alone to describe stand properties could give spurious interpretations. For some forests, the power-*H* model provides a better fit for large-diameter trees (Feldpausch et al., 2011) and in the current study the power model resulted in a lower mean error in estimating destructive tree biomass (SI Table S1). With a goal of reducing error in stand biomass estimates, the asymptotic model form—which reduces error in small-diameter trees—outperforms the power model because of the skewed distribution of stand-level biomass found in smaller-diameter trees, and was, therefore, chosen (Figure 3).

Independent of *H* model form, no current large-scale *H* models are parameterised to account for successional variation of tropical forest trees. Secondary forest trees are frequently taller for a given *D* (Montgomery and Chazdon, 2001). Mechanical effects can also modify small patches of forest over large areas, where, for example, bamboo can modify *H*:*D* relationships (Griscom and Ashton, 2006) and wind may alter forest structure (Laurance and Curran, 2008). Our *H* models were developed from the most comprehensive dataset to date, which includes a range of forest types including bamboo and liana forests. Developing site- or forest-specific *H* models is one alternative to account for localised variations in forest structure, but requires substantial cost and field time to develop.

4.1.2 Modelling destructive biomass data

Examination of Figure 2b raises two questions: “Why does exclusion of *H* in biomass estimates largely overestimate true biomass?” and “Why are biomass models unable to reduce error in large trees?” Chave et al. (2005) had previously noted that pantropical biomass models overestimate biomass in large trees. Some of this error was attributed to the lack of sampling in large trees (Chave et al. 2004); however, close inspection of Figure 4 in Chave et al. (2005) shows that biomass of the smallest trees (e.g., <100 mm diameter) is also underestimated (with these trees having the largest sample size). This suggests a different biomass model formulation may be necessary to remove the positive bias of trees $\geq$ 100 mm diameter either with or without including *H*. Other studies have confirmed that the model parameterisation we use (Eqs. 1 and 2) provides a better fit than other parameterisations (e.g. Vieilledent et al., 2011 (preprint)).

The challenge to reduce uncertainty in biomass estimates of large-diameter trees (e.g. $\geq$ 800 mm diameter) can be understood by examining the destructively sampled trees. Trees from this diameter class have an enormous variation in mass, from 4.6 to 70.2 Mg (mean 15.3 Mg) and similarly, a wide range of wood specific gravity, 0.26 to 0.9 g cm^3 (mean 0.56), and vary in *H* from 32 to 71 m (mean 46). These differences may represent the substantial variation in life-strategies among "emergent" canopy species, where large diameter low-density light demanding trees coexist with shade tolerant species. Thus, not only larger sample sizes of large size trees are needed, but in the future perhaps two differing equation, for differing life history strategies will be required (e.g. see Henry et al. 2011, for some data analysed in this way).

Clearly, greater collaboration is required to unify the many destructively sampled tree datasets (e.g. Araújo et al., 1999; Chambers et al., 2001; Nogueira et al., 2008a; Carvalho et al., 1998; Chave et al., 2005; Deans et al., 1996; Brown, 1997; Overman et al., 1994; Higuchi et al., 1998; Henry et al., 2010; Djomo et al., 2010; Alvarez et al., 2012); into one database to improve regional or pan-tropical biomass equations with inclusion of *H*. Our study provides a first step in dissecting one component of this vegetation-specific variation (regional *H*:*D* relationships) to adjust large-scale tropical biomass estimates: *e.g.* we show that African forests differ strikingly in their distribution of biomass among *D* class compared to other regions (Figure 3), and that as a result, effects of inclusion of *H* estimates on predicted biomass values vary strongly from region to region (Table 5)

4.1.3 Regional and continental differences

Forest biomass, after taking *H* into account was highest in Australian forests. Biomass was also higher in the Guyana Shield than SE Asian forests. Previous studies have suggested that aboveground biomass storage is higher in Southeast Asia (e.g. Slik et al., 2010). Regional adjustments in biomass estimates due to elevation and tree *H* may be necessary for some areas. For example, tree *H* varies with elevation in Tanzania, with the tallest trees at mid-elevation (Marshall et al., in review).

We found fundamentally different biomass distribution among diameter classes and stand structure across the four forested tropical continents. African forests store a greater portion of total biomass in large-diameter trees and trees are on average larger in diameter, while stem density is lower. This is as opposed to forests in Asia, Australia and South America where smaller-diameter trees store the greatest percentage of total biomass, where stem density is higher. These regional differences in stem density were previously shown for a smaller pan-tropical height:diameter dataset (Feldpausch et al. 2011). The most obvious causes for difference in forest structure between African and other forests is the large herbivore fauna, specifically, gorillas and elephants. These may reduce smaller stems in forests, compared particularly to South America, where humans have substantially modified the fauna with their arrival 12,000 years ago. Alternatives include the input of nutrients from 'Harmattan winds' and average higher soil fertility than South America (e.g. Sanchez (1976)). Larger sample sizes are needed to assess if these biomass distributions differences are consistent when expanded beyond the regional clusters in West Africa, East Africa, and Central Africa. Our results indicate that the greater error in African large diameter trees is diluted by the small tail in biomass distribution by diameter class found in those forests (Figure 3).

Feldpausch et al. (2011) showed a group of tall-stature forests (African, Asia and Guyana Shield) and other lower-statured forests (Amazon and Australia), and Banin et al. (2012) reported differences in *H*:*D* allometry between African forests and those of South America. Intriguingly, the biomass distribution results follow a continental split, not a forest stature split, with the Guyana shield forests grouping with the rest of South America and not African forests. The reasons for this are unclear. Their study also showed that *H*:*D* relationships were modified by stem density, with forests with higher stem density having shorter trees for a given diameter. Trees of the Guyana Shield, for example, have the lowest stem density for plots in South America, and also are on average taller and have the highest biomass stocks for the continent (Table 4; SI Table S2). Our current results indicate that the inclusion of *H* in biomass estimates for the Guyana Shield, Asia and Central Africa do not substantially modify estimates compared to estimates based on the no-*H* Eq. 1, but that including *H* in biomass estimates for those regions reduces the bias in destructive estimates relative to excluding *H*

(Table 2). These results showing substantial variation in biomass distribution and forest structure among regions and continents indicate that future biomass models based on continents and regions may prove more robust than pantropical models.

4.1.4 Climate and biogeography

Furthermore, the patterns that emerge in tree *H* variation as a function of region, climate and, forest structure suggest alternative structuring is needed for pantropical *Biomass*:*Diameter* tree allometric models rather than basing them solely on forest moisture class (e.g., dry, moist, wet). For example, *H*:*D* relationships vary not only according to climate (e.g., taller trees in moist climates), but also by forest structure (e.g. taller trees in higher basal area forests), soil quality, and geography (e.g. taller trees for a given diameter in the Guyana Shield, Africa and Asia than in the rest of South America and Australia; Feldpausch et al., 2011). *Biomass*:*Diameter* allometry for most published large-scale biomass models, however, is fixed by region (e.g. Amazonia, Chambers et al. 2001) or is pan-tropical (e.g., Chave et al., 2005), or is based on broad classifications of forest moisture (e.g., dry, moist, wet forest: Chave et al. 2005) or vegetation (e.g., diptercarp, secondary forest (Basuki et al., 2009; Nelson et al., 1999)). These models therefore lack parameters to account for climate-driven or biogeographic variation in *Biomass*:*Diameter* relationships. However, the clear biogeographical differences amongst SE Asian and forests on other continents (dominance by the Dipterocarpaceae) were not the proximate reason for differences in *H*:*D* allometry in Asia versus elsewhere (Banin et al. 2012). Formation of region-specific *H* models provides a first step in parameterising regional biomass estimates based on reported variation in tree *H* allometry (Nogueira et al., 2008b; Feldpausch et al., 2011).

4.1.5 Crown biomass variation

Current pantropical biomass models are unable to cope with regional or forest-specific variation in crown diameter, where wider crowns may impart greater biomass for a given diameter. Based on high-resolution remote-sensing data, Barbier et al. (2010) indicated that crown size increases by ~20% from the wetter to the more-seasonal regions of Amazonia. The regional *H* patterns showing shorter trees in southern Amazonia (Nogueira et al., 2008b; Feldpausch et al., 2011) that would result in reduced biomass stocks, may be partially offset by wider crowns that contain more mass for a given diameter. Such possible effects remain to be tested with field data.

4.1.6 Intra-species, diameter-specific and regional wood density variation

Tree wood specific gravity (ρ_W) variation is another parameter that biomass models may inadequately represent. Current biomass calculations use ρ_W databases to assign the finest taxonomic value to an individual (e.g., species-specific ρ_W) independent of stem diameter. Data from Barro Colorado Island, Panama showed significantly lower ρ_W in large-diameter trees than in smaller trees (Chave et al., 2004), while Patiño et al. (2009) showed, using branch wood density, that there is considerable plot-to-plot variation in wood specific gravity. Additionally, tree ρ_W is significantly lower in some regions of Amazonia (Nogueira et al., 2007). In addition, engineering theory suggests that trees with low density wood have an advantage in both H growth and in mechanical stability as compared to high-wood-density trees (Anten and Schieving, 2010; Iida et al., 2012); in contrast to vertical growth, high-density wood imparts greater efficiency for horizontal expansion. Together, these results suggest that biomass models may benefit from greater parameterisation.

Variation in the wood carbon fraction is another source of uncertainty in estimating regional and pantropical carbon stocks. Many studies, as in the current study, take the wood carbon fraction as 0.5 to convert estimated biomass to carbon (e.g. Lewis et al., 2009; Malhi et al., 2004; Clark et al., 2001). However, carbon content varies regionally (Elias and Potvin, 2003), where, for example, a forest in Panama has mean carbon values of 0.474 ± 0.025, which would result in an overestimate of 4.1-6.8 Mg C ha^{-1} if the assumed 0.5 carbon content were used (Martin and Thomas, 2011). Accounting for such variation may play an important role in refining future pantropical carbon estimates.

4.1.7 Limited spatial extent

A further concern is the use of spatially limited destructively sampled biomass data forming the base of biomass models used to estimate biomass for trees in other regions. Until only recently, destructive data were unavailable for Africa, so that large-scale biomass estimates for this continent were based on data from elsewhere. Even regional equations may yield site-specific bias. For example, the Chambers et al. (2001) equation, which is based on data from a small area north of Manaus, Brazil, yet by necessity has been used to estimate biomass across the Amazon Basin (Baker et al., 2004a; Malhi et al., 2004; Malhi et al., 2006), an area with important variation in tree architecture (Nogueira et al., 2008b; Feldpausch et al., 2011), taxonomy (Pitman et al., 1999) and wood density (Baker et al., 2004b). Application of this model to southern Amazonia requires down-scaling biomass estimates for shorter, less dense trees (Nogueira et al., 2008b; Nogueira et al., 2007). Country-level assessments of biomass model-effects on estimates indicate that application of generic pantropical biomass models (e.g. Brown et al., 1989; Chave et al., 2005) should be evaluated prior to application, especially those that lack *H* parameterisation (Alvarez et al., 2012; Vieilledent et al., 2011 (preprint); Marshall et al., in review). Our current results showed tropics-wide geographical variation in biomass distribution among *D* classes in permanent plots, which, together with tropics-wide variation in *H*:*D* relationships (Feldpausch et al., 2011), may not be represented when forming small regional subsets or pooling pantropical destructive data without accounting for *H*.

4.2 Consequences for remote sensing

Observed tropical forest *H*:*D* allometry differences in ground-based studies (Feldpausch et al., 2011; Nogueira et al., 2008b; Banin et al., 2012) and their associated regional effects on biomass estimates shown here will be important for improving retrieval of biomass estimates from light detection and ranging (LiDAR e.g. Drake et al., 2002; Lefsky et al., 2005; Asner et al., 2010), a technique that either estimates a canopy *H*, or is used to estimate forest structure (full waveforem LiDAR), either of which is then translated into a biomass estimate. Transforming variation in tropics-wide biomass estimates due to *H* into reliable biomass estimates via remote sensing, however, has not, yet been fully addressed. For example, a recent attempt using Geoscience Laser Altimeter System (GLAS) and Moderate Resolution Imaging Spectroradiometer (MODIS), a method dependent on tree *H* did not explain if/how *H* was incorporated into biomass estimates (Baccini et al., 2012). A second recent study relies on a large compilation of GLAS-estimated Lorey's *H* (basal-area weighted *H*) to estimate biomass in tropical forest (Saatchi et al., 2011). This study estimates biomass based on equations that were developed using height data collected from temperate forests from North America and tropical forests (Lefsky, 2010) rather than exclusively primarily tropical forest, which may introduce a bias in regional tropical estimates. Future remote sensing biomass estimates that address regional variations in *H* should therefore assist in evaluating potential bias and be able to provide tropical biomass estimates of a greatly improved accuracy.

4.3 Implications for carbon sink and estimates of nutrient turnover

Permanent plot data indicate that mature tropical forests are not in biomass equilibrium, but have tended to gain biomass density. Tree recruitment has outpaced mortality (Phillips et al., 2004) and total tree above-ground biomass has increased over recent decades (Phillips et al., 1998; Lewis et al., 2009; Phillips et al., 2009). It has been estimated that, on average, trees in tropical forests add 0.49 Mg C ha^{-1} in above ground mass each year, implying a carbon sink of 0.9 Pg C yr^{-1} (Lewis et al., 2009). This process, however, is susceptible to drought, and for Amazonia the 2005 drought reduced the long-term above-ground carbon sequestration (Phillips et al., 2009).

Our biomass downscaling in pantropical forest plots implies that the calculated net carbon sink or the magnitude of any reversal or reduction in the sink due to drought may also be reduced for some regions as a direct result of *H* parameterisations using current pantropical biomass models. This assumes that the proportional sink remains unchanged. Our results indicate that *H* integration provides a tool to reduce uncertainty in estimating the magnitude of carbon stocks or sinks. Such *H* parameterisations might include LiDAR methods (e.g. Asner et al., 2010; Drake et al., 2003) and plot-specific ground-based tree *H* measurement.

Furthermore, biomass estimates for individual trees are frequently used to estimate nutrient stocks such as nitrogen and phosphorus in trees and stands (Feldpausch et al., 2010; Feldpausch et al., 2004; Buschbacher et al., 1988) based on component tissue concentrations (Martinelli et al., 2000). Downscaling biomass estimates due to *H* will therefore reduce the total estimated above ground nutrient stocks and flux due to land-use change (e.g., selective logging, deforestation, forest regrowth and fire).

4.4 Comparison with global emissions

The biomass and carbon downscaling due to *H* also affects estimates of carbon emissions. The most recent IPCC estimate of global emissions contribution of tropical deforestation estimates a net annual emission from this source of 1.6 PgC (range 1.0-2.2 PgC) (Denman et al., 2007) based on the mean of estimates by DeFries et al. (2002) and Houghton et al. (2003) from the 1980s and 1990s. The most recent “unofficial” estimate with the same methodology is 1.47 PgC yr^{-1} for the 2000-2005 period (Houghton, 2008). Our new results incorporating *H* into these estimates imply that this is an overestimate of ~0.1 Pg C yr^{-1}, this being based on the more recent number for the values used in the estimate for emissions from below-ground biomass and uptake of secondary forest regeneration, the contribution of live aboveground biomass cut in tropical deforestation is 0.85 PgC yr^{-1}, and a 0.13 downward adjustment for tree *H* (Table 5). For comparison, the last national inventory of the UK under Climate Convention indicates a total emission in 2007 of 0.17 Pg yr^{-1} of CO_2-equivalent carbon (UK Department of Energy and Climate Change, 2009).

4.5 Repercussions for carbon estimation and REDD

Integration of *H* into biomass estimates reduces estimates of tropical carbon storage by 13%. This estimated decrease has potential economic implications based on the calculated high carbon storage of pantropical forests under Reducing Emissions from Deforestation and Degradation (REDD) carbon-payment schemes (Miles and Kapos, 2008). In monetary terms, our calculated decrease in carbon storage represents a reduction in value per unit area of tropical forests based on current carbon market prices (e.g. Chicago Climate Exchange, European Climate Exchange) as a result of previous exclusion of *H* in biomass estimates. We stress the obvious, i) the actual carbon storage of these forests has not changed, only the estimated amount; ii) the large-scale RAINFOR South American estimates of biomass and change (e.g. Malhi et al., 2006; Phillips et al., 2009) used the Baker et al. (2004b) regional biomass model; for Africa, Weibull asymptotic continental-scale *H* equations were used in the Chave et al. (2005) pantropical allometric equations (Lewis et al., 2009); hence, the effect of accounting for *H* in their estimates remains unexplored; iii) that our adjustments in plot-based estimates are sensitive to the current pantropical biomass equations as discussed above. Future improvement and inclusion of additional data (e.g. from Africa), and harvested trees of larger diameter will further reduce uncertainty in estimates over a heterogeneous landscape and at a variety of scales. New models may eventually show that such downscaling is unnecessary; iv) tree *H* integration can reduce uncertainty in biomass estimates (Figure 2b, Figure 4), which should benefit REDD. Furthermore, the default tier-I estimation method of forest carbon density issued in support of REDD by the

Intergovernmental Panel on Climate Change (IPCC) is based on average carbon values for biomes (IPCC, 2006), not plot-based estimates. The approached outlined in the present study, harnessed to better measurement of *H* (e.g., using LiDAR: Asner et al., 2010) can help generate accurate, verifiable biomass estimates which will ultimately increase confidence in large-scale carbon estimates, lead to increased carbon credit, and greater investment per unit of carbon (Asner et al., 2010).

5 Conclusions and future considerations

Based on these results, it is possible to make a number of recommendations:

1) A global initiative is needed to improve the pantropical destructive tree data to support global carbon modelling and policy: additional sampling is needed from under-represented regions, forest types, growth forms (e.g., palms), and tree diameter classes to represent the full diversity of tropical forests. We showed distinct differences in the biomass distribution of tropical forests in Africa as compared to elsewhere, and such important differences will only be fully accounted for in biomass estimates when we have improved understanding through destructive sampling.

2) Pantropical permanent forest plots, some monitored since the 1970s, are now a baseline standard by which scientists and policymakers understand forest dynamics and potential changes in net gain, and carbon valuation under REDD. There is known large variation in *H* among these plots. To account for this variation and make full use of permanent-plot data, we recommend a stratified random sample of *H* measurements. If possible, *H* measurements of every tree are desirable. Where local *H*-diameter relationships are not known, using those described in this paper is recommended.

Biomass estimates of tropical forests are prone to error because of the very small destructive dataset, biomass models, *H* models and also because of uncertainty in their area. For example, the area of tropical forest at the start of the 21st century is between 1572 to 1852 × 10^6 ha, depending on the estimation method (Mayaux et al., 2005). Our study has explored the uncertainty associated with current biomass estimates and shown the importance of accounting for tree-level variation in *H*:*D* relationships for scaling to more precise regional and global biomass estimates. By reducing uncertainty in pantropical estimates, we make a step forward in providing realistic, verifiable carbon estimates for models and policy instruments such as REDD.

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Table 1: Pantropical models to estimate biomass from, Eq. 1 diameter (D, cm) and wood specific gravity (ρ_W, g cm^{-3}), and Eq. 2 also including tree height (H, m) for trees in pantropical forests, including the residual standard error (RSE), Akaike information criterion (AIC) and number of trees (n) based on destructively sampled moist forest tree data from Africa, Asia, and South America.

Model	***a***	***b***	***c***	***d***	***e***	**RSE**	**R^2**	**AIC**	***n***
Eq. 1: $\ln(B)=a+b\ln(D)+c(\ln(D))^2+d(\ln(D))^3+e\ln(\rho_W)$									
	-1.8222	2.3370	0.1632	-0.0248	0.9792	0.3595	0.973	1444	1816
Eq. 2: $\ln(B)=a+b\ln(D^2\rho_W H)$									
	-2.9205	0.9894	--	--	--	0.3222	0.978	1044	1816

Table 2: Efficacy of bootstrapped biomass models including or excluding tree *H* to predict true (destructively) sampled biomass for trees ≥10 cm *D* for individual sites excluded from model formulation. Values represent mean relative error, or bias ($(B_{predicted} - B_{measured})/B_{measured}$) for a site, in dry biomass estimated from a biomass model excluding *H* (Eq. 1) and biomass including *H* (Eqn. 2) using various *H* models (Eqs. 3-5) based on region- and continent- specific *H* models. Values in bold indicate the model with the lowest mean relative error (bias) for a site (this excludes the power model, which although has the lowest overall bias and standard deviation, fails to reduce error in the small diameter classes).*

				3PE		**Weibull**		**Power**		**No Ht**	**Data source**
Dropped Site$^{\#}$	**Location**	**Region**	***n***	**Continent**	**Region**	**Continent**	**Region**	**Continent**	**Region**		
BraCot	Cotriguaçu, Pará, Brazil	Brazilian Shield	151	**0.01**	-0.02	**0.01**	-0.09	-0.04	-0.07	0.09	Nogueira et al. 2008
BraJuruena	Juruena, Mato Grosso, Brazil	Brazilian Shield	49	**-0.04**	-0.06	-0.05	-0.13	-0.08	-0.11	0.05	Nogueira et al. 2008
BraMan1	Manaus, Amazonas, Brazil	E.-central Amazonia	315	**0.01**	-0.07	-0.05	-0.14	-0.05	-0.13	-0.01	Chave et al. 2005
BraMan2	Manaus, Amazonas, Brazil	E.-central Amazonia	123	0.05	**-0.03**	0.04	-0.06	0.00	-0.09	0.13	Chave et al. 2005
BraNPro	Novo Progesso, Mato Grosso, Brazil	Brazilian Shield	64	-0.22	-0.23	-0.25	-0.30	-0.25	-0.28	**-0.20**	Nogueira et al. 2008
BraPara1	Tomé Açu, Pará, Brazil	Brazilian Shield	127	-0.04	-0.12	**-0.02**	-0.10	-0.08	-0.16	0.07	Araujo et al. 1999
BraPara3	Belem, Pará, Brazil	Brazilian Shield	21	-0.14	-0.21	-0.09	-0.16	-0.18	-0.25	**0.01**	Chave et al. 2005
BraRond	Rôndonia, Brazil	Brazilian Shield	8	-0.50	-0.53	-0.46	-0.53	-0.52	-0.54	**-0.39**	Brown et al. 1995
FrenchGu	Piste St Elie, French Guiana	Guyana Shield	360	0.48	0.77	**0.37**	0.53	0.40	0.73	0.47	Chave et al. 2005
Llanosec	Llanos secondary	Western Amazonia	24	0.47	0.79	**0.45**	0.66	0.40	0.73	0.61	Chave et al. 2005
Llanosol	Llanos old-growth	Western Amazonia	27	**0.10**	0.35	0.17	0.35	0.07	0.35	0.32	Chave et al. 2005

CamCampo-Ma'an	Campo-Ma'an, Cameroon	Central Africa	71	0.15	0.34	**-0.01**	0.22	0.03	0.24	0.13	Djomo et al. 2010
CamMbalmayo	Mbalmayo, Cameroon	Central Africa	4	**0.09**	0.11	0.15	0.29	0.04	0.05	0.33	Deans et al. 1996
DRCYangambi	Yangambi, Democratic Republic of Congo	Central Africa	12	-0.07	-0.04	**-0.01**	0.12	-0.13	-0.11	0.13	Ebuy et al. 2011
GhaBoiTano	Boi Tano, Ghana	Western Africa	41	-0.18	-0.14	-0.13	-0.13	-0.14	-0.10	**-0.01**	Henry et al. 2010
IndoMala		South-east Asia	119	0.55	0.55	**0.37**	**0.37**	0.45	0.45	0.53	
Kaliman1	Kalimantan, Balikpapan, Indonesia	South-east Asia	23	-0.04	-0.04	-0.02	-0.02	-0.07	-0.07	**0.01**	Chave et al. 2005
Kaliman2	Kalimantan, Sebulu, Indonesia	South-east Asia	69	**-0.11**	**-0.11**	-0.18	-0.18	-0.15	-0.15	-0.13	Yamakura et al. 1986
Kaliman3	PT Hutan Labanan Sanggam Lestari, Kalimantan, Indonesia	South-east Asia	40	-0.08	-0.08	-0.07	-0.07	-0.12	-0.12	**-0.03**	Samalca 2007
Pasoh-01	Pasoh, Malaysia	South-east Asia	139	**-0.07**	**-0.07**	-0.13	-0.13	-0.11	-0.11	-0.09	Chave et al. 2005
Sumatra	Sepunggur, Sumatra, Indonesia	South-east Asia	29	0.27	0.27	**0.26**	**0.26**	0.22	0.22	0.33	Ketterings et al. 2001
Relative mean error				0.03	0.05	**0.06**	0.06	-0.01	0.02	0.13	
Std. Dev.				0.25	0.33	**0.22**	0.29	0.23	0.32	0.25	

*Biomass estimated from models based on tree diameter, wood density (Eqn. 1) and where applicable, *H* (Eqn. 2). Height is estimated from models developed from the pantropical tree *H-D* database of Feldpausch *et al*. (2011).

[#] Efficacy of the biomass model to predict biomass was independently assessed for each “dropped site” which was exlcuded from the development of the biomass model.

Table 3: Coefficients for Weibull-H region-, continent-specific and pantropical models ($H = a*(1-\exp(-b*D^c))$) to estimate tree height (H, m) from diameter (D, cm) $\geq$ 10 cm in pantropical forests, including the residual standard error (RSE), Akaike information criterion (AIC), and number of trees (n).*

Continent	**Region**	***a***	***b***	***c***	**RSE**	**AIC**	***n***
Africa		50.096	0.03711	0.8291	5.739	75422	11910
	C. Africa	50.453	0.0471	0.8120	6.177	16671	2572
	E. Africa	43.974	0.0334	0.8546	5.466	10343	1658
	W. Africa	53.133	0.0331	0.8329	5.165	47020	7680
S. America		42.574	0.0482	0.8307	5.619	121167	19262
	Brazilian Shield	227.35[#]	0.0139	0.5550	4.683	20639	3482
	E.C. Amazonia	48.131	0.0375	0.8228	4.918	39688	6588
	Guyana Shield	42.845	0.0433	0.9372	5.285	32491	5267
	W. Amazonia	46.263	0.0876	0.6072	5.277	24201	3925
Asia	S.E. Asia	57.122	0.0332	0.8468	5.691	18623	2948
Australia	N. Australia	41.721	0.0529	0.7755	4.042	48073	8536
Pantropical		50.874	0.0420	0.784	5.479	266169	42656

*Models adapted from the pantropical tree H:D database of Feldpausch et al. (2011).

[#] Although a unrealistic asymptotic maximum H coefficient (a), a tree of 10 and 160 cm diameter would have an estimated H of 11.0 and 47.2 m, respectively, with this model.

Table 4: Pantropical live tree above ground dry biomass (*B*) estimates (all values Mg ha^{-1} ±St. dev.) when calculating as column a) biomass estimated as per most published studies excluding *H* using our recalculation of the Chave et al. (2005) model from with new published data; b) biomass estimated based on height (*H)* integration from a regional *H* model; c) shows the difference (b - a) in biomass due to *H* integration for 329 plots.

Continent	Region	*n* plots	a) no *H**	b) with *H**	c) **Δ** *B* due to *H*
Africa	C. Africa	16	392.9±145.7	379.4±137.5	-13.5±8.3
	E. Africa	20	470.3±161.3	362.5±126.5	-107.9±34.9
	W. Africa	26	374.4±69.9	330.2±62.7	-44.2±7.8
S. America	Brazilian Shield	36	250.3±65.6	194.5±55	-55.9±12.5
	E.C. Amazonia	44	410.7±91.6	344.1±77.2	-66.6±14.5
	Guyana Shield	45	441.1±125.8	434.4±116.3	-6.7±12.4
	W. Amazonia	100	299.6±71.8	251.7±55.2	-47.9±17.7
Asia	S.E. Asia	16	434.6±137.3	424.2±134.7	-10.5±3.5
Australia	N. Australia	26	571.8±200.1	455.3±156.3	-116.5±44.0
Grand mean			405.1±118.8	352.9±102.4	-52.2±17.3

* Biomass estimated from the moist forest pantropical model based on tree diameter and ρ_W or based on tree diameter, ρ_W and *H*, where *H* is estimated from Weibull region-specific tree *H* models based on the pantropical tree *H*:*D* database from Feldpausch *et al*. (2011).

Table 5: Stocks and change in estimated pantropical C in above ground live trees due to *H* integrated into biomass estimates based on region-specific estimates of tree *H*, compared to the pantropical forest biomass model that excludes *H*.*

			without height	**with height**	**ΔC due to height---**	
Continent	**Region**	**Area**	**Total C**	**Total C**	**Total C**	**Relative reduction**
		(10^6 ha)	**(Pg)**	**(Pg)**	**(Pg)**	
Africa	C. Africa	422.6	83.0	80.2	-2.9	-0.03
	E. Africa	123.1	29.0	22.3	-6.6	-0.23
	W. Africa	69.8	13.1	11.5	-1.5	-0.12
	Total	**615.6**	**125.0**	**114.0**	**-11.0**	**-0.13**
South-Central America	Brazilian Shield	220.9	27.7	21.5	-6.2	-0.22
	E.C. Amazonia	106.2	21.8	18.3	-3.5	-0.16
	Guyana Shield	148.3	32.7	32.2	-0.5	-0.02
	W. Amazonia	286.4	42.9	36.0	-6.9	-0.16
	Total	**761.9**	**125.1**	**108.0**	**-17.1**	**-0.14**
Asia	S.E. Asia	185.0	40.2	39.2	-1.0	-0.02
Australia	N. Australia	105.1	30.1	23.9	-6.1	-0.20
Total		**1667.5**	**320.4**	**285.2**	**-35.2**	**-0.13**

*Tree height estimated from region-specific Weibull-*H* models adapted from the pantropical tree *H*:*D* database of Feldpausch *et al*. (2011). Mean ΔC values (0.5 of biomass values) from each region in Table 4 were applied. Region geographic extent is shown in Figure 1. Tropical forest area was estimated for each region based on the broadleaf deciduous open and closed and evergreen tree cover classification from GLC2000 (Global Land Cover Map 2000) (Bartholomé and Belward 2005).

Figure Text

Figure 1: Location of the pantropical permanent plots and a) biomass stocks (● Mg ha^{-1}) b) Δ biomass (Mg ha^{-1}) due to inclusion of *H* in biomass (*B*) estimates (relative to exclusion of *H*) for forests ($B_{\text{H}} - B_{\text{No Ht.}}$) in Africa, Asia, Australia and South America. Symbols indicate an increase (blue ▲) or decrease (red ▼) in biomass estimates after including *H* in biomass estimates compared to our biomass model Eq. 1 that excludes *H*. See Supplemental Information Table S1 for plot details. Biomass estimated from the moist forest pantropical models (Table 1) based on tree diameter and wood density, and when *H* (where applicable), with *H* estimated from Weibull region-specific tree *H* models (Eq 5) based on the pantropical tree *H-D* database from Feldpausch et al. (2011). Coloured shading indicates forest cover and different regions used in Figures 3 and 4.

Figure 2: a) Distribution of destructively sampled above ground tree dry mass (bars) by diameter class (cm) and cumulative biomass (line) on the second axis. Numbers above the bars indicate the number of trees sampled. The dataset represents the pantropical destructive data to date used to form biomass allometric models, including additional data from Africa, Asia, and South America; and b) Relative error associated with estimating the true (destructively) sampled above ground tree dry mass (($B_{\text{estimated}} - B_{\text{measured}}$)/$B_{\text{measured}}$) for the same dataset estimated with and without estimated *H* in the biomass model by diameter class (cm). Height estimated by three model forms and either a continental or regional parameterisation. Positive values indicate the biomass model overestimates true destructively sampled mass.

Figure 3: a) Biomass (Mg ha^{-1}) distribution (bars) among diameter class (cm) by region with cumulative AGB (Mg ha^{-1}) on the second axis (lines) for trees in pantropical permanent plots. Tree-by-tree biomass was estimated by model (1) without *H* or model (2) with Weibull (Eq. 5) region-specific *H*. See Table 4 for differences in biomass estimates due to *H* integration.

Figure 4: Error in biomass estimates (Mg ha^{-1}) for trees in pantropical permanent plots due to biomass model inputs excluding or including *H* (relative error propagated from destructive data). Tree-by-tree biomass was estimated by model (1) without *H* or model (2) with Weibull (Eq. 5) region-specific *H*.

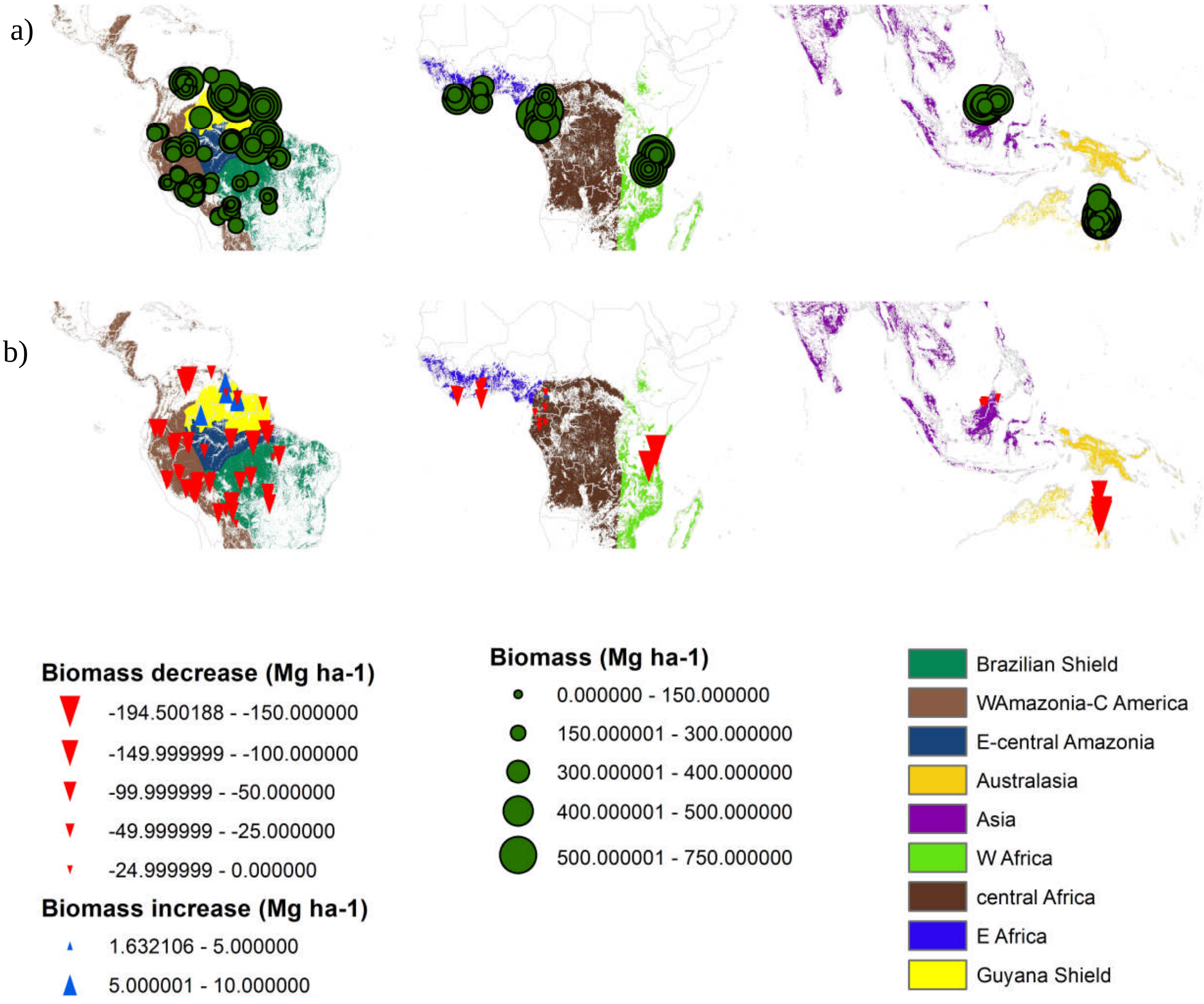

a)
b)
Biomass decrease (Mg ha-1)
-194.500188 - -150.000000
-149.999999 - -100.000000
-99.999999 - -50.000000
-49.999999 - -25.000000
-24.999999 - 0.000000
Biomass increase (Mg ha-1)
1.632106 - 5.000000
5.000001 - 10.000000
Biomass (Mg ha-1)
0.000000 - 150.000000
150.000001 - 300.000000
300.000001 - 400.000000
400.000001 - 500.000000
500.000001 - 750.000000
Brazilian Shield
WAmazonia-C America
E-central Amazonia
Australasia
Asia
W Africa
central Africa
E Africa
Guyana Shield

Figure 1

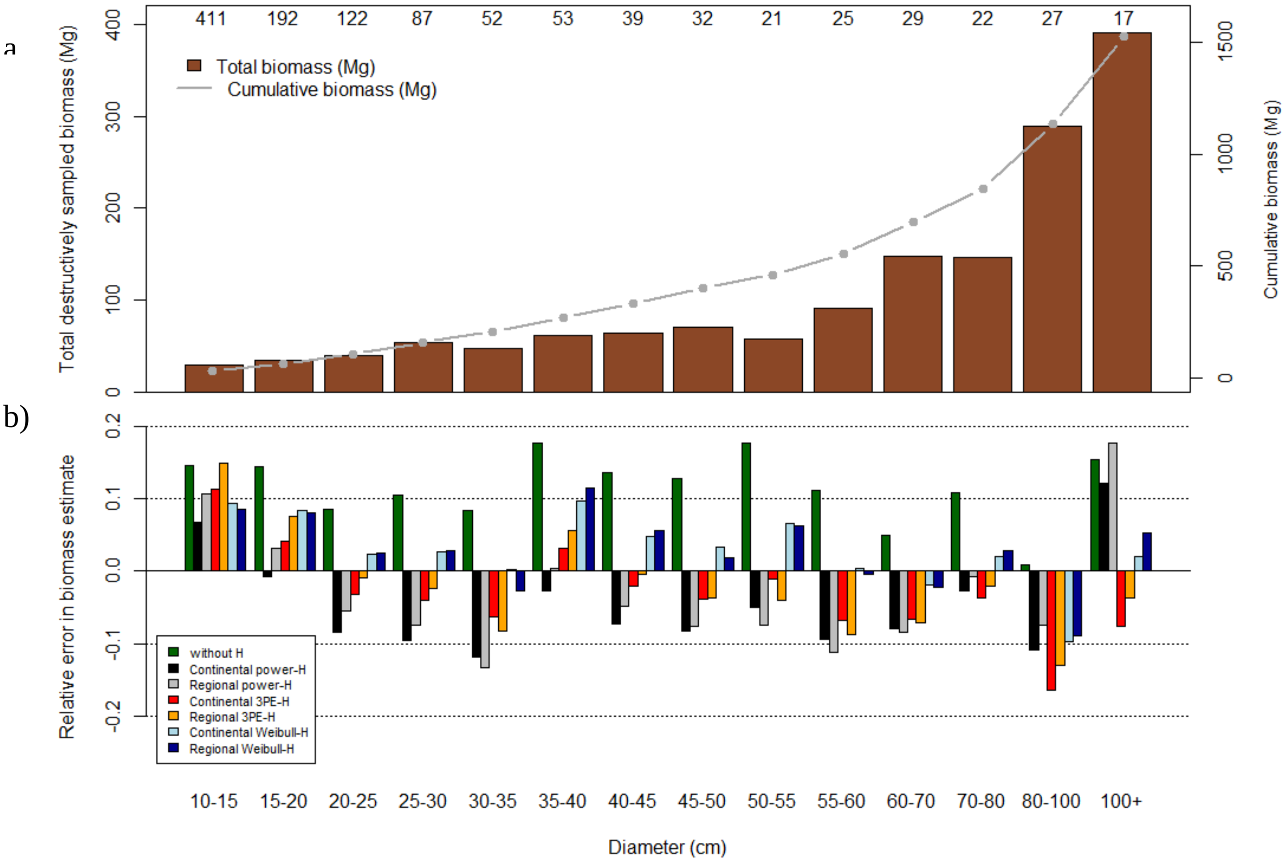
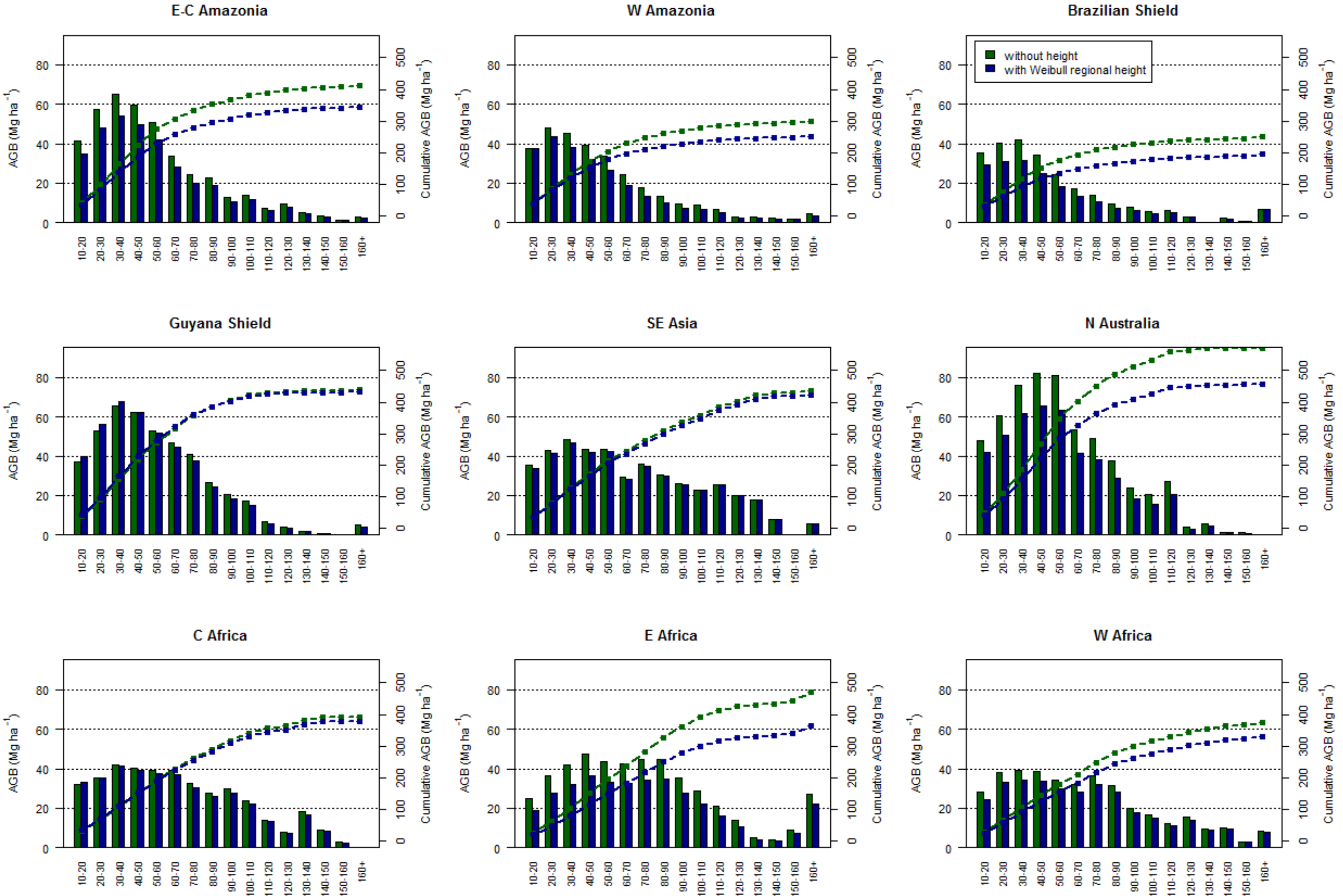

a
b)
411
192
122
87
52
53
39
32
21
25
29
22
27
17
Total biomass (Mg)
Cumulative biomass (Mg)
Total destructively sampled biomass (Mg)
0
100
200
300
400
Cumulative biomass (Mg)
0
500
1000
1500
Relative error in biomass estimate
-0.2
-0.1
0.0
0.1
0.2
without H
Continental power-H
Regional power-H
Continental 3PE-H
Regional 3PE-H
Continental Weibull-H
Regional Weibull-H
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
60-70
70-80
80-100
100+
Diameter (cm)

Figure 2



E-C Amazonia
W Amazonia
Brazilian Shield
Guyana Shield
SE Asia
N Australia
C Africa
E Africa
W Africa
without height
with Weibull regional height
AGB (Mg ha^{-1})
Cumulative AGB (Mg ha^{-1})
0
20
40
60
80
0
100
200
300
400
500
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
110-120
120-130
130-140
140-150
150-160
160+

Figure 3

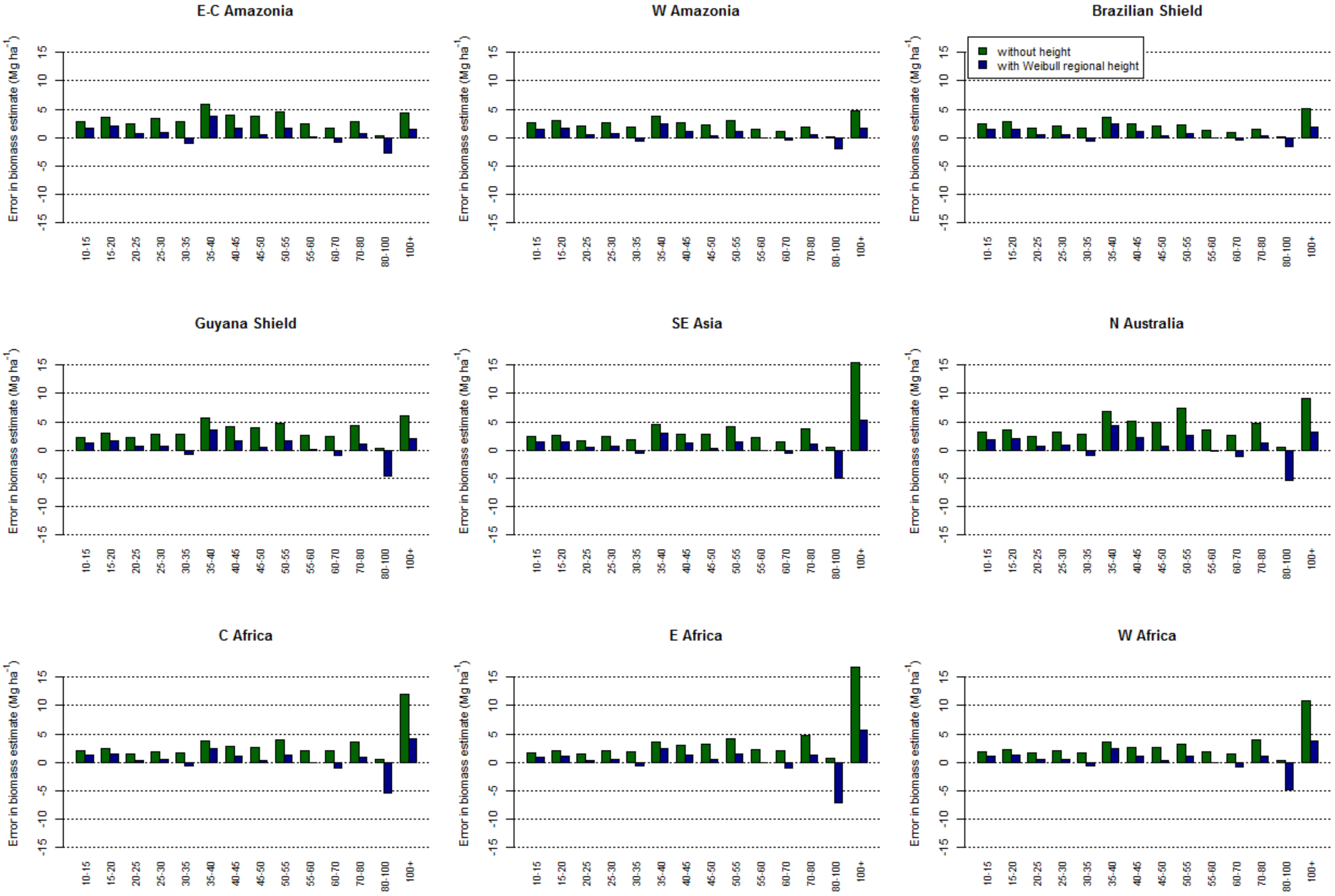

E-C Amazonia
W Amazonia
Brazilian Shield
Guyana Shield
SE Asia
N Australia
C Africa
E Africa
W Africa
without height
with Weibull regional height
Error in biomass estimate (Mg ha^{-1})
-15
-10
-5
0
5
10
15
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
60-70
70-80
80-100
100+

Figure 4