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Amazon palm biomass and allometry

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Abstract

Palms (family Arecaceae) are abundant in Amazonian forests, but the allometry of these monocotyledonous plants remains poorly quantified. Woody palm biomass is most commonly estimated with dicotyledonous tree models, which leaves substantial uncertainty as to their true biomass and productivity. We developed the first extensive dataset of directly-measured arborescent palm biomass: 136 individuals from nine species in *terra firme* and wetland forests —*Astrocaryum murumuru, Attalea phalerata, Bactris gasipaes, Euterpe precatoria, Iriartea deltoidea, Mauritia flexuosa, Mauritiella aculeata, Oenocarpus bataua,* and *Socratea exorrhiza*. We created single species (n = 8–21) and family-level (n = 97–106) allometric equations, using diameter, stem height, total height, and stem dry mass fraction, to estimate (i) total aboveground biomass for all species, (ii) belowground biomass for the two wetland species (*Mauritia* and *Mauritiella*), and (iii) leaf mass for all species. These new palm models were then applied to nine 1-ha plots in the southwestern Amazon (Tambopata) to calculate the impact on forest biomass estimates once palm mass is estimated with palm-specific models, rather than from models created for dicot trees. We found that stem height was the best predictor variable for arborescent palm biomass, but the relationship between stem height and biomass differed among species. Most species showed weak biomass–diameter relationships, but a significant relationship could be identified across all species. The new palm models were better estimators of palm mass than existing dicot models. Using our species-level models increased estimates of palm biomass at our study site by 14–27 %, compared to using recently published pantropical biomass models for trees. In other forests, the effect of using these palm equations on biomass estimates will depend on palm sizes, abundance, and species composition.

Key words: Arecaceae, equations, *Iriartea*, *Mauritia*, leaf mass, productivity, tropical forest

1 Introduction

Palms (family Arecaceae or Palmae) are an ancient part of tropical ecosystems (Bremer et al., 2004) and one of the most widespread and ecologically diverse plant families (Tomlinson, 2006; Eiserhardt et al., 2011). They play major roles in ecosystem processes (Peters et al., 2004; LaFrankie and Saw, 2005) and local livelihoods (May et al., 1985; Johnson, 1996; Runk, 1998). Arecaceae is one of the most heavily used plant families for non-timber forest products with multiple applications in indigenous and rural activities, mostly associated with food, fibres, animal fodder, and construction (Peters et al., 1989; Phillips and Gentry, 1993; Johnson, 1996; Zambrana et al., 2007).

Nearly 2,400 species of palms occur across the Neotropics, Africa, and Asia (Govaerts and Dransfield, 2005). Within the Neotropics, palms are most abundant in western Amazonia and Central America (Kahn et al., 1988; Terborgh and Andresen, 1998; Montufar and Pintaud, 2006; Eiserhardt et al., 2011). They are less prevalent in other regions but still occur, especially in forests with frequent inundation (Kahn et al., 1988; Terborgh and Andresen, 1998) and soils with poor physical properties, such as shallow rooting depth (Emilio et al., 2013). Arecaceae is the single most abundant arborescent plant family in western Amazonian forests, in both *terra firme* and flooded forests (Terborgh and Andresen, 1998). In some forests, palms have been found to represent over two-thirds of stems with diameter (D) ≥ 10 cm (Terborgh and Andresen, 1998) or nearly 100 % of stand biomass (Brown, 1997). Indeed, some species, such as *Mauritia flexuosa*, can establish nearly mono-dominant stands ('aguajales'; Kahn and Mejia, 1990) and are an integral part of many carbon-rich swamp ecosystems (Lahteenoja et al., 2009).

Despite their importance, there are no explicit studies of carbon stocks and dynamics of palms. While many models have been developed to estimate the biomass of dicotyledonous (dicot) trees (e.g., Brown et al., 1989; Baker et al., 2004; Chave et al., 2005; Basuki et al., 2009; Alvarez et al., 2012; Feldpausch et al., 2012), there are few available to estimate palm biomass. Thus, most stand-level and macro-ecological studies use dicot models to estimate palm mass (e.g., Malhi et al., 2004; Phillips et al., 2008; Baccini et al., 2012) or stem basal area to assess aboveground biomass (AGB) changes (e.g., Lewis et al., 2004; Malhi et al., 2004). The productivity of palms has also been poorly studied, and palms have even been described as a ‘missing term’ in coarse woody productivity assessments (Malhi et al., 2009). For example, palm leaves are often not included in litterfall assessments even though they may contribute substantially, and palm fruit productivity may be severely underestimated because they do not fit into standard leaf litter traps (Chave et al., 2010). Overall, these factors lead to substantial uncertainty in AGB stocks and productivity in areas where palms are prevalent.

Estimates of palm biomass and stem productivity made from dicot models are likely to be inaccurate, especially when using D and wood density (ρ), because the two groups of plants have very distinct growth patterns and internal properties. Palms are monocotyledons which grow in height but lack secondary (diameter) growth (Rich et al., 1986; Tomlinson, 2006). Thus, many species have weak or no relationship between height and diameter (Rich et al., 1986). The internal stem structure is also very different in palms (Parthasarathy and Klotz, 1976), with higher density and stiffness towards the peripheries and base of the stem (Rich, 1987b), and 'wood' density in Arecaceae is generally lower than in dicot families (Chave et al., 2009; Zanne et al., 2009). Furthermore, palms lack branches, which can contribute substantially to dicot biomass (Goodman et al., in press). This suggests that palm biomass may be overestimated by dicot equations, but this has yet to be tested on directly-measured palm biomass data.

The lack of palm biomass equations is puzzling: there are still no broadly accepted or applicable equations to estimate their mass. The few existing palm models are created for a single species and often do not cover a wide range of sizes. Most palm models appear in technical reports or other unpublished works (Hughes, 1997; Delaney et al., 1999; Brown et al., 2001; Freitas et al., 2006; Sierra et al., 2007; Kumar and Russell, unpublished, cited in Kumar, 2011). The only three peer-reviewed publications we could locate were each developed for a single species in a particular environment: *Prestoea montana* in sub-montane Puerto Rico (Frangi and Lugo, 1985), oil palm (*Elaeis guineensis*) under commercial cultivation (Thenkabail et al., 2004), and *Oenocarpus bataua* in a transition zone from lowland to premontane forests in Colombia (Sierra et al., 2007). One mixed-species model has been developed but only for very small individuals, $1 \leq \text{height} \leq 1.5$ m (Sierra et al., 2007). There is clearly a strong need to develop more widely applicable equations to estimate the biomass and productivity of this prevalent and important plant group.

Similarly, there has been no rigorous examination of the most appropriate form of palm allometric relationships. Most models are built with the simple form: biomass = $a + b$x (Frangi and Lugo, 1985; Thenkabail et al., 2004; Kumar and Russell, unpublished, cited in Kumar, 2011), but plant allometric relationships do not usually follow this simple linear relationship (e.g., West et al., 1997; Chave et al., 2005). Stem height is the most commonly used predictor variable (x) for palm mass (Frangi and Lugo, 1985; Delaney et al., 1999; Brown et al., 2001; Thenkabail et al., 2004; Sierra et al., 2007), but others have used total height (Frangi and Lugo, 1985), diameter (Hughes, 1997), or age (Kumar and Russell, unpublished, cited in Kumar, 2011) to estimate palm biomass. Brown (1997) suggested that palm biomass could be estimated using height and D as if palms were cylinders (i.e., D^2H), multiplied by wood density, and added to a term accounting for leaves, but this approach has yet to be applied. Estimating AGB with compound variable ρD^2H and a form factor to account for stem taper is common for dicots (Chave et al., 2005; Feldpausch et al., 2012) but may be particularly appropriate for palm allometry because they lack branches. Non-linear relationships between biomass and the predictor variable(s) —such as with a power-law, as has been suggested on theoretical grounds (West et al., 1997)— have also not been comprehensively tested.

Because palms exhibit primary (height) growth nearly independently of diameter and stems taper little, we expect that that (i) height will be highly predictive of palm biomass, and (ii) palm mass should be approximately proportional to its volume calculated as a cylindrical form with D^2 and total or stem height. Furthermore, because palm 'wood' density can vary 10-fold between species and even within individuals (Rich, 1987b), we expect that a variable accounting for density or moisture content will be necessary to include in mixed-species models. Our specific objectives are to (i) create single species and family-level models for arborescent palms using a variety of simple and compound predictor variables and model forms and then (ii) examine the impact of applying new palm models on forest biomass estimates in a well-studied western Amazonian site where arborescent palms are common.

2 Materials and methods

2.1 Species selection and study area

Species or genera were selected to include the six most dominant arborescent palm species in the Amazon —*Iriartea deltoidea*, *Attalea butyracea*, *Oenocarpus bataua*, *Euterpe precatoria*, *Socratea exorrhiza*, and *Astrocaryum murumuru* (Emilio et al., 2013)— and two prominent species in wetland forests, *Mauritia flexuosa* and *Mauritiella* spp. (Kahn, 1991; Roucoux et al., 2013). We focus on arborescent palms because these are included in most forest inventories ($D \geq$ 10 cm).

Palms were harvested from mature forests in western Amazonia. In 2006, *Mauritia flexuosa* and *Mauritiella aculeata* were harvested and weighed in wetlands within the Pacaya–Samiria National Reserve in Loreto, Peru. In 2011, biomass data were collected from seven species in *terra firme*, moist tropical forests within a forestry concession in Madre de Dios, Peru (Table 1).

2.2 Data collection

In total, 136 arborescent palms from nine species were individually measured, harvested, and weighed in 2006 and 2011 (Table 1). Similar methods were used throughout. Sampling was designed to represent the entire range of stem heights exhibited by each species. In Madre de Dios, individuals from each species were selected within a 100-m radius of dicot trees harvested in a concurrent study (Goodman et al., in press), and the first individual encountered to fulfil the stem height criteria was selected so that there was no bias towards any certain form or structural integrity. Before harvesting, D was measured at 1.3 m or above the highest root and total height (H_{tot}) was measured from the ground to the highest point of the highest leaf. After felling, stem height (H_{stem}) was measured from ground level to the point where the first (lowest) leaf parted from the stem. All leaves were counted, and, in the Madre de Dios dataset, the length of three randomly-selected leaves was measured from the base of the rachis to the tip of the terminal leaflet.

Fresh mass of all plant parts was measured in the field immediately after felling. Aboveground parts were divided into aboveground roots, stem, leaves (petiole, rachis, and leaflets), and other parts (flowers, fruits, bracts, etc), and measured in the field with a 250 kg capacity scale with 0.1 kg precision. In Loreto, belowground roots were also sampled following Gallardo-Ordinola (2001). Fine roots were sampled from eight soil cores (10 cm diameter and 90 cm deep). Four cores were excavated from each of two directions extending 80 cm from the base of the stem at 90°. The entire main root was then extracted using a 3-ton hand winch and weighed (Freitas et al., 2006).

Stem samples were collected from 3–4 individuals per species (except *Bactris*, n = 2) to estimate moisture content. In Madre de Dios, samples were collected from individuals in the lower, middle, and upper height classes per species; and three samples were collected from each individual —at the base, middle, and top of each stem (Table A.1). In Loreto, three individuals were randomly selected, and one stem sample was collected from each individual. In Madre de

Dios, we collected a composite leaf sample consisting of one leaf sample from each species including the rachis and attached leaflets. In Loreto, leaves were sampled from three individuals per species. Fresh mass of each sample was measured immediately in the field. Samples were then air-dried and transported to a drying oven. In this study, we did not measure ρ directly because volume measurement errors would have been virtually unavoidable. Measuring volume by water displacement would have relied upon doing so immediately, which was not possible in the field, and estimating volume by calliper or ruler measurements would have been inaccurate due to uneven edges and thickness of the sample cut.

[Table 1]

2.3 Laboratory work and data preparation

Stem samples were dried at 101 °C and leaf samples at 65 °C (Williamson and Wiemann, 2010), and dry mass was recorded after three consecutive days of constant mass with a digital scale with 1 mg precision. Dry mass fraction (*dmf*) was calculated as the proportion of dry mass per unit fresh mass (dry mass/ fresh mass or 1 – moisture content). Individual mean *dmf* was calculated as the mean of three samples taken at different points along the stem (Table A.1), and species mean *dmf* was calculated as the average of individual means (Table 2). Carbon content was determined for *Mauritiella* and *Mauritia* by calorimetry (Segura-Madrigal, 1997) at Universidad Nacional Agraria La Molina, Lima, Peru. To test whether *dmf* is a better explanatory variable than wood density, we followed the established practice of assigning ρ values to each individual species to the finest taxonomy available according the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009).

Stem, root, and leaf dry mass of every individual in the database was calculated as fresh mass × *dmf*, where *dmf* is mean *dmf* for each tissue for each species (Table 2). Mean individual leaf mass was calculated by dividing total leaf mass by the number of leaves.

2.4 Model development and evaluation

All species were arborescent with a single stem and multiple leaves. Because of their simple growth form (no or very little diameter growth and no branches), models were created using H_{stem}, H_{tot}, and two compound variables based on the premise that palms are nearly cylindrical (D^2H_{tot} and D^2H_{stem}). Single-species models to estimate AGB were created for each species, except *Bactris gasipaes* ($n = 3$), and to estimate belowground biomass for *Mauritia* and

Mauritiella. Given the ubiquity of forest inventories measuring D only, we also attempted to create models to estimate AGB without any height variable.

To create family-level equations, data from all species were combined. A subset of data —the individuals from which stem *dmf* samples were taken (n = 27)— were excluded to test the developed models. We used the same five variables as the single-species equations, plus four additional compound variables, $dmfD^2H_{tot,}$ and $dmfD^2H_{stem}$, ρD^2H_{tot}, ρD^2H_{stem}, where *dmf* is the species mean *dmf* of the stem determined in this study and ρ is 'wood' density for species, genus, or family obtained from Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). Finally, we created a mixed-species regression model to estimate mean leaf mass from leaf length.

For each explanatory variable, we tested five model forms: simple linear, third-order polynomial, exponential, logarithmic, and power. In several instances, variables in the linear models had to be transformed to satisfy the assumption of equal variance and normality of the residuals. Non-significant terms were removed via backwards elimination. All models were built using the linear model function (lm) in R, version 2.15.1. For family-level models, we also performed a generalised linear model (glm) analysis using the final linear model and species to test whether the slope and intercept terms were significantly different between species (e.g., AGB~D+Species). However, because no *a priori* factor —such as habitat or phylogeny— could explain species differences, we included all species in the final equations to make them the most broadly-applicable possible. We evaluated models based on coefficient of determination (R^2), residual standard error (RSE), and Akaike information criterion (AIC), when comparable.

Next, all family-level models were evaluated against the test data (n = 27) to examine their suitability. For the test data, dry mass was calculated from the directly-measured *dmf* and fresh mass and of each individual (Table A.1). Finally, we used the full directly measured palm biomass dataset (n = 136) to both further evaluate the recommended models and to assist the interpretation of the forest plot analysis. A correction factor, $\exp(\mathrm{RSE}^2/2)$, was applied to biomass estimates from logarithmically transformed models (Baskerville, 1972). We examined the errors produced by the recommended species-level models, selected family models, and two dicot equations (Feldpausch et al., 2012). Errors (kg) were calculated on the original scale as $\mathrm{mass}_{\mathrm{predicted}} - \mathrm{mass}_{\mathrm{observed}}$, and relative errors (%) were calculated as $\mathrm{error}/\ \mathrm{mass}_{\mathrm{observed}} \times 100$ %. We compared the equations based on mean error, mean % error (mean error / mean AGB × 100

%), and mean and standard deviation of relative errors. Overall predictability was assessed by standard deviation of the relative errors (Chave et al., 2005), and R^2 was calculated on the original scale as 1 – (SS_{error} / SS_{total}).

2.5 Implications for forest biomass

To explore the implications of using new palm models on palm and forest biomass estimates in western Amazonia, we estimated stand level AGB density on nine, 1-ha permanent plots within the Tambopata National Reserve in Madre de Dios, Peru (12.8^0 S, 69.3^0W). Plots were established between 1979 and 2010 and have been recensused every 2–3 years by RAINFOR researchers (Malhi et al., 2002). All individuals with $D \geq 10$ cm are included in the inventories and have been botanically identified. In 2011, *D* of all individuals was remeasured, and data were obtained from the ForestPlots.net database on 2 August 2012 (Lopez-Gonzalez et al., 2011; Lopez-Gonzalez et al., 2012). For this study, total and stem heights were measured on all palms with a laser hypsometer (Nikon Forestry 550) during the same year.

We estimated AGB using two published dicot and four new palm models. First, we used two new pantropical biomass models (Feldpausch et al., 2012) using ρ and *D* only (Feld 1) and ρ, *D*, and estimated *H* (Feld 2) to estimate AGB of all trees and palms. Total height was estimated from *D* using the Weibull model for western Amazonia (Table 3 in Feldpausch et al., 2012). Next, we recalculated AGB of all palms using the recommended species-level models and three family-level models (Table 3). For species without a specific model (*Astrocaryum gratum, Attalea butyracea, A. cephalotes, A. maripa,* and *O. mapora*; 7.4 % of all palms), we used the model for the same genus. Each of the new palm estimates were compared to estimates made by the two dicot models at the stand level.

3 Results

3.1 Architecture and internal properties

For most species, height–diameter relationships were weak and height could not be predicted from *D* (Figure 1A). Some species had a broad range of heights across a broad range of diameters with very little relationship between the two (*Astrocaryum* and *Attalea*); the two wetland species had a broad range of heights over a very narrow range of diameters (*Mauritia* and *Mauritiella*); others were clustered with very narrow height and diameter ranges (*Oenocarpus* and *Socratea*); while height and diameter were clearly related for *Euterpe* and *Iriartea*.

Dry mass fraction varied between species (Table 2), among individuals of the same species, and along the stem of the same individual (Appendix, Table A.1). There appeared to be a slight negative relationship between *dmf* and height at which the sample was collected (i.e., *dmf* greatest at base) and a very slight positive relationship between mean stem *dmf* and the height of the individual (i.e., mean *dmf* greater in taller individuals). However, no significant relationships could be determined, so we calculated individual *dmf* as the mean of the three samples taken along each stem and species-level *dmf* as the simple mean of the three individuals per species. Mean *dmf* was consistently higher for leaf tissue than stem or root tissues (Table 2). Carbon fraction was usually slightly < 50 % of dry mass in *Mauritia* and *Mauritiella* and similar between the two species in stem and root tissues, but it was more variable and slightly higher and in leaf tissue.

Individual AGB varied across more than three orders of magnitude, from as little as 0.7 kg to as much as 1231 kg. AGB generally increases with stem diameter when all species are combined (Figure 1B), but within a species AGB is more strongly related to stem height (Figure 1C). Belowground root biomass contributed 13–780 kg in *Mauritia* and *Mauritiella*, representing 13–47 % of total plant dry mass. Mean leaf mass varied by over an order of magnitude between species, ranging from 0.2 kg leaf^{-1} in *Bactris* to 14.2 kg leaf^{-1} in *Oenocarpus* (Table 2).

[Table 2]

3.2 Species-level models

Single-species models performed well, with $R^2 > 0.90$ for most species (Table 3, Figure 2). Height was the key variable to estimate AGB, and including D added little to or even worsened model performance. Models with H_{stem} alone were better than those with the compound variable D^2H_{stem} for most of species, and models with H_{tot} alone were always better than those with D^2H_{tot} (Table A.2). Models with only D were only significant for *Euterpe*, *Iriartea,* and *Socratea*. For all other species, AGB could not be estimated from D alone. The recommended models, one for each species, are listed in Table 3. Other models, with different predictor variables, are available in Table A.2.

[Table 3]

[Figure 2]

3.3 Family-level models

The transformed model with compound term $dmfD^2H_{stem}$ best estimated AGB of all species (Table 3). This model was selected as best from the metrics used to evaluate built models (R^2, RSE, AIC; Table A.3) and performed well against the test data (Table A.4). Separating these variables in a logarithmically-transformed additive model did not improve model performance. One individual with no stem ($H_{stem} = 0$ m) had to be removed as an outlier; thus, these models are only valid for individuals with $H_{stem} \geq 1$ m.

The best family-level model ($dmfD^2H_{stem}$) showed some differences between species, but the glm analysis revealed that slope and intercept were only significantly different for only one species each (*Astrocaryum* and *Mauritia*, respectively; $P < 0.05$). This model generally underestimated AGB for *Astrocaryum, Attalea, Mauritia,* and *Oenocarpus* and overestimated mass for *Bactris, Euterpe, Iriartea, Mauritiella,* and *Socratea* (Figure 3A).

To permit palm biomass estimation from inventories that have not measured H_{stem}, we explored the use of other predictor variables. Visible trends were observed between AGB and D, H_{tot}, and D^2H_{tot}, but the relationships were subject to outliers or anomalies (Figure A.1). Thus, we had to remove outliers, and the resulting equations are only valid within the given range (Table 3). Models with just D, or D and dmf, performed reasonably well but are only valid for individuals with diameters between 6 and 40 cm and stem heights > 3 m. Prediction errors from these models showed few differences between species, except that *Mauritia* was almost always underestimated and *Iriartea* with $D < 22$ cm was usually overestimated (Figure 3B,C). The compound variable D^2H_{tot} was especially prone to producing outliers when individuals have very short stems with tall leaves or short stems with large diameters: three *Attalea* and one *Oenocarpus* were identified as such, all of which had $H_{stem} \leq 3$ m and $H_{tot} < 5$ m. Models with H_{tot} had a tendency to overestimate AGB of shorter individuals and underestimate taller individuals (data not shown). For both pairs, the models with dmf (D+dmf and H_{tot}+dmf) were significantly better than the model with D or H_{tot} alone ($P < 0.05$). We also tested models with ρ instead of dmf, but ρ was never significant. Likewise, models with a compound predictor variable using ρ never performed as well as those with dmf (i.e., ρD^2H_{stem} vs. $dmfD^2H_{stem}$), so we do not report models with ρ.

Leaf mass can be estimated from leaf length (Table 3). We present a mixed species model, created from *Astrocaryum, Attalea, Bactris, Euterpe, Oenocarpus,* and *Socratea*. However, *Iriartea* leaves showed a very clear, and significantly different, relationship between leaf mass and length, so we have reported separate results for this species (Figure A.2).

[Figure 3]

3.4 Model evaluation

Comparing model predictions to the subset of test data, the recommended family model with the compound term $dmfD^2H_{stem}$ had the lowest bias (mean % error = 0.2 %), but another model using the log-transformed compound variable with total height ($dmfD^2H_{tot}$) performed best by all other criteria (Table A.4). All family-level models performed reasonably well, except the models with H_{tot} and $H_{tot}+dmf$ (Table A.4).

Testing model estimates against the full biomass dataset ($n = 136$), the species model estimates were always best, followed by the family-level $dmfD^2H_{stem}$ model (Table A.5). The two models without any height variable, D and $D+dmf$, and the two dicot models all overestimated AGB and performed very poorly when applied to the full biomass dataset ($-0.184 \leq R^2 \leq 0.145$). However, when the dataset was reduced to only the individuals for which all models were valid ($H_{stem} > 3$ m and $6 \leq D < 40$ cm; $n = 125$), results for the recommended species and family model estimates changed little, but estimates from the palm and dicot models without measured height improved substantially ($0.548 \leq R^2 \leq 0.615$; Table A.5). The species-level and Feld 1 models slightly overestimated AGB (mean % error = 3 and 6 %, respectively), the recommended family-level and Feld 2 models slightly underestimated AGB (mean % error = -5 and -7 %, respectively), while the D and $D+dmf$ model estimates were nearly neutral (mean % error = 0.6 and -0.03, respectively). By nearly all metrics, all palm models were better estimators of palm AGB than the dicot models.

The dicot models were poor estimators of individual palm AGB, with errors ranging from –844 to +1651 kg. Whether each one over- or underestimates palm mass was largely dependent upon species, diameter, and stem height. The magnitude of errors increased considerably with diameter, but the direction of errors was largely dependent on stem height (Figure 4). The dicot models typically overestimated AGB of palms with short stems but underestimated AGB of taller stemmed individuals. This crossover occurred at H_{stem} *c.* 14 and 15 m for the Feld 1 and 2 models, respectively. Prediction errors between species are consistent between the two dicot models, but the Feld 2 model estimates were usually lower. Both dicot models tended to overestimate AGB of *Astrocaryum*, *Oenocarpus*, and any palm with $D > 40$ cm and to underestimate AGB of *Mauritia*, *Socratea*, most palms with $H_{stem} > 15$ m, and all palms with $H_{stem} > 22$ m.

[Figure 4]

3.5 Implications for forest biomass

Across the nine plots in Tambopata, palms represented between 3 and 32 % of all stems ($D \geq 10$ cm) and, based on species-level equations, contributed from 5 to 43 Mg of above ground biomass per hectare. The two dicot models yielded different AGB estimates, for both trees and palms the Feld 2 (with estimated height) estimates were lower than the Feld 1 estimates (Table 4). Using estimates from the recommended species models (Table 3), palm AGB density in the nine plots was on average 29 or 40 % greater than would have been estimated with the Feld 1 and 2 dicot models, respectively. However, plot means may be artificially large due to large relative differences in two plots with very low palm presence (TAM05 and TAM07; Table 4). Thus, if palm biomass on all plots is combined as one unit, the overall difference in palm mass across all nine plots is 14 or 27 % greater than Feld 1 and 2 estimates, respectively. Total AGB density estimates of the whole stand (i.e., dicot trees and palms combined) were between 1 and 2 % greater than the Feld models (Table 4).

Stand-level palm AGB estimated from the other three palm models was usually lower than the species-level palm model estimates. Among the family-level equations, the model with D only yielded the most similar results to the species-level estimates, followed by the $dmfD^2H_{stem}$ model, but the D+dmf model produced much lower estimates. In some plots the family-level models gave lower AGB estimates than did the dicot models, but across all plots palm AGB is still higher than would have been estimating using dicot models (Table 4).

[Table 4]

4 Discussion

4.1 Architecture and intrinsic properties

Our data appear to have captured several different growth patterns of arborescent palms, as demonstrated by the differing relationships between diameter, height, and AGB among species (Figures 1 and A.1). These differing allometries have implications for the best single- and mixed-species biomass models. For example, *Iriartea* (Rich, 1987a), *Socratea* (Rich et al., 1986), and *Euterpe* (Avalos and Fernandez Otarola, 2010) can continue to increase in diameter via sustained cell expansion (Rich, 1987a; Renninger and Phillips, 2012), and as a result these are the same three genera for which we were able to estimate AGB from D alone. For other genera, such as *Mauritiella*, stem diameter is virtually the same at every height, so including D in allometric equations adds little or no explanatory value.

Variable moisture content between species, between individuals of the same species, and within a single stem make it difficult to determine the exact dry mass of palms. As with stem density (Rich, 1987b), dry mass fraction tends to be greatest at the base and decreases along the stem. Mean stem *dmf* may also increase with increasing stem height, as reported by Rich (1987b), perhaps because cell walls thicken with age (Rich, 1987a; Tomlinson, 2006). Nonetheless, our data show that using species mean *dmf* values works well. Using the test data, the differences in dry mass estimates, when calculated from fresh mass and either species mean *dmf* or *dmf* measured for each individual, are very small: the mean difference between the two calculations was only 2.5 kg or 1.9 %. Therefore, we consider the results reported here to be reliable and to represent an advance in improving palm biomass estimates. When utilising these models, values for *dmf* can be found in Table 2. For the genera included in this study, we recommend using mean stem *dmf* for the respective taxon and the overall mean (0.370) for all other genera.

4.2 New models

As hypothesised, height was always a very important parameter to consider in palm biomass equations. Total height was sometimes a better estimator than stem height. However, total height is likely to be a less reliable measurement than stem height, as it can be subjective and often difficult to measure if only one leaf is extending upwards. Thus, we recommended the second best model for each of these species, which includes H_{stem} in all cases. Estimating palm mass using compound variables (D^2H_{stem} or D^2H_{tot}) was often not necessary for single-species models but was best for family-level models because H–D relationships differed between species. As expected, accounting for dry mass fraction also improved mixed-species model estimates, and *dmf* was a better variable than ρ to account for internal species differences, perhaps because of the difficulty of measuring palm ρ accurately.

There proved to be a reasonable relationship between these two variables when all species were combined, and family-level models with D alone or D+*dmf* performed remarkably well given the weak relationship of diameter with biomass at the species-level. These models appeared to be unbiased when tested on the full biomass dataset and in plot estimates. However, these models should be applied with caution, as estimates made outside the diameter and height ranges used to build the models can be erroneous (Table A.5). We provide species- and family-level palm models with a variety of input data to accommodate existing inventories, and these models could be used to create new palm biomass estimates from existing forest inventory data (i.e., D and species). These estimates would be more accurate than estimates from dicot equations, but estimates from palm models including height would be far more accurate (Tables A.4, A.5). Likewise, because AGB could not usually be predicted from D within a single species, it is likely that the relationship between AGB and D within an individual is also unreliable and, therefore, that productivity of individual palm trees should preferably also be estimated from models that include stem height or total height.

4.3 Implications for forest biomass

Contrary to our expectations, palm biomass estimates were greater in each of the nine plots examined when applying our most reliable palm equations, compared to palm biomass estimated from standard dicot models. Although palms do not have branches or relatively dense stems, they often weigh more than dicot trees at small diameters because they can be much taller (Rich et al., 1986). As a result, AGB of many tall palms with small diameters can be underestimated by the dicot models (Figure 4). Evaluating model estimates on our directly-measured biomass dataset could not fully reflect this because the destructive dataset was designed to create reliable regression models across a broad range of sizes, and, thus, includes a higher proportion of short stemmed individuals than inventoried in mature forests in Tambopata ($D \geq 10$ cm). Mean H_{stem} of palms in the forest plots (15.3 m) was slightly greater than in the biomass dataset (12.7 m) and above the limit at which dicot models underestimate AGB of most palms (14–15 m). The effect of using new palm biomass models will also likely be determined by the species composition and the interaction between size and composition. In Tambopata, for example, *Iriartea deltoidea* makes up 54% of all registered palms with $D \geq 10$ cm, followed by *Euterpe precatoria* (14 %), *Socratea exorrhiza* (12 %), and *Mauritia flexuosa* (7 %). In the destructive biomass dataset, the dicot models estimated AGB of *Iriartea* moderately well but consistently underestimated AGB of *Socratea* and *Mauritia* (Figure 4). Thus, palm AGB estimates may be considerably higher than previously estimated in stands where these species, especially *Mauritia flexuosa*, are dominant. Conversely, new palm equations may slightly reduce AGB estimates, as compared to dicot model estimates, in forests where *Oenocarpus bataua* is the major palm component, such as in central Amazonia (Emilio et al., 2013), or in stands where the palm population is dominated by shorter individuals (Kahn and Mejia, 1990).

Our results show higher palm AGB density estimates in plots than would have been estimated from dicot equations, but the magnitude of this increase depends on the palm equation used to estimate AGB. When tested on the directly-measured biomass dataset, the species models slightly overestimated AGB but the recommended family-level model ($dmfD^2H_{stem}$; Table 3) underestimated AGB by a greater amount. Likewise, the Tambopata plot estimates were greater using the species-level models than this family model. Thus, the true 'increase' in palm AGB is likely to be in between these estimates but closer to the species model estimates. The overall differences (when all plots are combined) in palm AGB estimates between the two palm estimates discussed above are similar. Thus, despite some sensitivity to the palm model used, true palm AGB in Tambopata is greater than would have been estimated by dicot equations.

This dataset and new models do not, however, represent small palms, nor do they capture the reproductive parts of mature individuals. Though stemless and juvenile palms can be abundant in some ecosystems (Kahn and Mejia, 1990), they are not generally included in forest inventories and contribute little to forest biomass (Nascimento and Laurance, 2002). We also found that although palm leaves are large, they weigh little compared to the woody tissues. Because no individuals in the biomass dataset were fruiting at the time of harvest, these estimates do not accurately account for reproductive parts.

These new palm biomass equations should have multiple applications and facilitate more accurate estimates of carbon stocks and cycling in tropical forests. Though increases in whole forest estimates are locally small (0.9–1.8 % at Tambopata), this increase could be expected to impact total carbon stock estimates in tropical forests more broadly, particularly in forests with hydromorphic soils. These models may also finally assist accurate quantification of above- and belowground carbon stocks of the palm community in the extensive, carbon-rich peat ecosystems which cover *c.* 150,000 km^2 in Amazonia (Lahteenoja et al., 2009).

These new equations can also be used to improve palm productivity estimates. Palm stem productivity may also be greater than previously estimated by dicot models using diameter ―as commonly measured in permanent plot inventories― because palms grow in height with little or no corresponding increase in stem diameter (Rich et al., 1986). Estimating leaf mass by either the species mean or leaf length will allow researchers to account for litterfall from palms, which is usually ignored due to the technical difficulties of sampling palm leaf fall (Chave et al., 2010). Though other structures, such as inflorescences, bracts, and fruits, can contribute substantially to forest productivity (Phillips, 1993), they still remain poorly quantified or ignored in comprehensive studies (Chave et al., 2010; Malhi et al., in press). These ‘missing terms’ in forest productivity estimates (Malhi et al., 2009) need to be incorporated, particularly as they can be expected to vary substantially in space and time. For example, because palms are more abundant in the western Amazon (Kahn et al., 1988; Terborgh and Andresen, 1998; Eiserhardt et al., 2011), it is possible that the magnitude of increase in aboveground forest productivity from east to west across Amazonia may be even greater than previously considered (Malhi et al., 2004; Aragão et al., 2009; Quesada et al., 2012).

5 Conclusions and future directions

This study is the first to create a comprehensive dataset of arborescent palms and family-level allometric equations to estimate aboveground biomass. We report both single- and mixed-species models with a variety of input variables to accommodate different forest inventory methods. Single species models estimated palm biomass very well, as does the recommended family-level model with $dmfD^2H_{stem}$. The family-level models without a height variable provide unbiased estimates of palm AGB, but should be applied with caution. With these new models, we can finally estimate palm biomass and productivity more reliably. When equations were applied to forest plots at one location in western Amazonia, palm biomass density was on average 14 or 27 % greater than would have been estimated using two pantropical biomass models for dicot trees. In other forests, the effect of new palm equations on plot biomass estimates will depend on palm sizes, abundance, and species composition. The magnitude of palm productivity and carbon cycling fluxes will also likely be greater than previously estimated by dicot models, but the magnitude of this effect has yet to be formally explored. We recommend that palm stem height should be measured in future inventories to accurately estimate palm biomass and, especially, biomass changes in this important forest component.

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7 References

Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de las Salas, G., del Valle, I., Lema, A., Moreno, F., Orrego, S., Rodríguez, L., 2012. Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. For. Ecol. Manage. 267, 297-308.

Aragão, L.E.O.C., Malhi, Y., Metcalfe, D.B., Silva-Espejo, J.E., Jimenez, E., Navarrete, D., Almeida, S., Costa, A.C.L., Salinas, N., Phillips, O.L., Anderson, L.O., Alvarez, E., Baker, T.R., Goncalvez, P.H., Huaman-Ovalle, J., Mamani-Solorzano, M., Meir, P., Monteagudo, A., Patino, S., Penuela, M.C., Prieto, A., Quesada, C.A., Rozas-Davila, A., Rudas, A., Silva, J.A., Vasquez, R., 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences 6, 2759-2778.

Avalos, G., Fernandez Otarola, M., 2010. Allometry and stilt root structure of the neotropical palm *Euterpe precatoria* (Arecaceae) across sites and successional stages. Am. J. Bot. 97, 388-394.

Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S., Houghton, R.A., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat. Clim. Change 2, 182-185.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, J.N.M., Martinez, R.V., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol. 10, 545-562.

Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res./Rev. Can. Rech. For. 2, 49-53.

Basuki, T.M., van Laake, P.E., Skidmore, A.K., Hussin, Y.A., 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. For. Ecol. Manage. 257, 1684-1694.

Bremer, K., Friis, E.M., Bremer, B., 2004. Molecular phylogenetic dating of asterid flowering plants shows early Cretaceous diversification. Syst. Biol. 53, 496-505.

Brown, S., 1997. Estimating Biomass and Biomass Change of Tropical Forests: a Primer In. Food and Agriculture Organization of the United Nations, p. 55.

Brown, S., Delaney, M., Shoch, D., 2001. Carbon monitoring, analysis, and status report for the Rio Bravo Carbon Sequestration Pilot Project. In, Report to the Programme for Belize. Report to the Programme for Belize, Winrock International, Arlington, VA, USA.

Brown, S., Gillespie, A.J.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data For. Sci. 35, 881-902.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87-99.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351-366.

Chave, J., Navarrete, D., Almeida, S., Alvarez, E., Aragao, L.E.O.C., Bonal, D., Chatelet, P., Silva-Espejo, J.E., Goret, J.Y., von Hildebrand, P., Jimenez, E., Patino, S., Penuela, M.C., Phillips, O.L., Stevenson, P., Malhi, Y., 2010. Regional and seasonal patterns of litterfall in tropical South America. Biogeosciences 7, 43-55.

Delaney, M., Brown, S., Powell, M., 1999. Carbon-Offset Report for the Noel Kempff Climate Action Project, Bolivia. In. Report to The Nature Conservancy, Winrock International, Arlington, VA, USA.

Eiserhardt, W.L., Svenning, J.-C., Kissling, W.D., Balslev, H., 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. Ann. Bot. 108, 1391-1416.

Emilio, T., Quesada, C.A., Costa, F.R.C., Magnusson, W.E., Schietti, J., Feldpausch, T.R., Brienen, R.J.W., Baker, T.R., Chave, J., Álvarez, E., Araújo, A., Bánki, O., Castilho, C.V., Honorio C, E.N., Killeen, T.J., Malhi, Y., Oblitas Mendoza, E.M., Monteagudo, A., Neill, D., Alexander Parada, G., Peña-Cruz, A., Ramirez-Angulo, H., Schwarz, M., Silveira, M., ter Steege, H., Terborgh, J.W., Thomas, R., Torres-Lezama, A., Vilanova, E., Phillips, O.L., 2013. Soil physical conditions limit palm and tree basal area in Amazonian forests. Plant Ecol. Div., 1-15.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragao, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard, G.A., Baker, T.R., Banki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., Franca, M.B., Freitas, M.A., Higuchi, N., Honorio, E., Iida, Y., Jimenez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.H., Pena Cruz, A., Penuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramirez, F., Ramirez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomao, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonke, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vasquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H., Phillips, O.L., 2012. Tree height integrated into pantropical forest biomass estimates. Biogeosciences 9, 3381-3403.

Frangi, J.L., Lugo, A.E., 1985. Ecosystem dynamics of a sub-tropical floodplain forest. Ecol. Monogr. 55, 351-369.

Freitas, L., Otárola, E., del Castillo Torres, D., Linares, C., Martínez, C., Malca, G.A., 2006. Servicios Ambientales de Carbono y Secuestro de Carbono de Ecosistema Aguajal en la Reserva Nacional Pacaya Samiria, Loreto - Perú In. Instituto de Investigaciones de la Amazonía Peruana (IIAP), Iquitos, Perú.

Gallardo-Ordinola, J.L.E., Luizão, F.J., Fernandes, E.C., Wandelli, E., Afonso Meira, R., 2001. Root carbon and nutrient stocks in central Amazonian abandoned pastures and agroforestry systems. In. INPA-Ecology, Cornell University and EMBRAPA-CPAA.

Goodman, R.C., Phillips, O.L., Baker, T.R., in press. The importance of crown dimensions to improve tropical tree biomass estimates. Ecol. Appl.

Govaerts, R., Dransfield, J., 2005. World checklist of palms. Royal Botanic Gardens, Kew, Richmond, UK.

Hughes, R.F., 1997. Effects of deforestation and land use on biomass, carbon, and nutrient pools in the Los Tuxtlas Region, Mexico. In, Department of Forest Science. Oregon State University, Corvallis, Oregon, p. 105.

Johnson, D. (Ed.), 1996. Palms: Their Conservation And Sustained Utilization. IUCN, World Conservation Union, Gland, Switzerland.

Kahn, F., 1991. Palms as key swamp forest resources in Amazonia. For. Ecol. Manage. 38, 133-142.

Kahn, F., Mejia, K., 1990. Palm communities in wetland forest ecosystems of Peruvian Amazonia. For. Ecol. Manage. 33-4, 169-179.

Kahn, F., Mejia, K., Decastro, A., 1988. Species richness and density of palms in terra firme forests of Amazonia. Biotropica 20, 266-269.

Kumar, B.M., 2011. Species richness and aboveground carbon stocks in the homegardens of central Kerala, India. Agric. Ecosyst. Environ. 140, 430-440.

LaFrankie, J.V., Saw, L.G., 2005. The understorey palm Licuala (Arecaceae) suppresses tree regeneration in a lowland forest in Asia. J. Trop. Ecol. 21, 703-706.

Lahteenoja, O., Ruokolainen, K., Schulman, L., Oinonen, M., 2009. Amazonian peatlands: an ignored C sink and potential source. Global Change Biol. 15, 2311-2320.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Lezama, A.T., Vásquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P., Vinceti, B., 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 359, 421-436.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Baker, T.R., Phillips, O.L., 2012. www.forestplots.net. In. ForestPlots.net Database.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Phillips, O.L., 2011. ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. J. Veg. Sci. 22, 610-613.

Malhi, Y., Aragao, L., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., da Costa, A.C.L., Hutyra, L.R., Oliveira, P., Patino, S., Pyle, E.H., Robertson, A.L., Teixeira, L.M., 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Global Change Biol. 15, 1255-1274.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biol. 10, 563-591.

Malhi, Y., Farfán Amézquita, F., Doughty, C.E., Silva-Espejo, J.E., Girardin, C.A.J., Metcalfe, D.B., Aragão, L.E.O.C., Huaraca-Quispe, L.P., Alzamora-Taype, I., Eguiluz-Mora, L., Marthews, T.R., Halladay, K., Quesada, C.A., Robertson, A.L., Fisher, J.B., Zaragoza-Castells, J., Rojas-Villagra, C.M., Pelaez-Tapia, Y., Salinas, N., Meir, P., Phillips, O.L., in press. The productivity, metabolism and carbon cycle of two lowland tropical forest plots in SW Amazonia, Peru. Plant Ecol. Div.

Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W.F., Leano, C., Lewis, S., Meir, P., Monteagudo, A., Neill, D., Vargas, P.N., Panfil, S.N., Patino, S., Pitman, N., Quesada, C.A., Rudas-Ll, A., Salomao, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W.G., Valencia, R., Martinez, R.V., Vieira, I.C.G., Vinceti, B., 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). J. Veg. Sci. 13, 439-450.

May, P.H., Anderson, A.B., Balick, M.J., Frazao, J.M.F., 1985. Subsistence benefits from the Babassu palm (Orbignya martiana). Econ. Bot. 39, 113-129.

Montufar, R., Pintaud, J.-C., 2006. Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. Bot. J. Linn. Soc. 151, 127-140.

Nascimento, H.E.M., Laurance, W.F., 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. For. Ecol. Manage. 168, 311-321.

Parthasarathy, M.V., Klotz, L.H., 1976. Palm "wood" .1. Anatomical aspects. Wood Sci. Technol. 10, 215-229.

Peters, C.M., Balick, M.J., Kahn, F., Anderson, A.B., 1989. Oligarchic forests of economic plants in Amazonia - utilization and conservation of an important tropical resource. Conserv. Biol. 3, 341-349.

Peters, H.A., Pauw, A., Silman, M.R., Terborgh, J.W., 2004. Failing palm fronds structure Amazonian rainforest sapling communities. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 271, S367-S369.

Phillips, O., 1993. The potential for harvesting fruits in tropical rainforests: new data from Amazonian Peru. Biodivers. Conserv. 2, 18-38.

Phillips, O., Gentry, A., 1993. The useful plants of Tambopata, Peru: I. Statistical hypotheses tests with a new quantitative technique. Econ. Bot. 47, 15-32.

Phillips, O., Higuchi, N., Vieira, S., Baker, T.R., Chao, K.J., Lewis, S.L., 2008. Changes in Amazonian Forest Biomass, Dynamics, and Composition, 1980–2002. Geoph. Monog. Series 186, 373-387.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patino, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez Davila, E., Arneth, A., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, A.T., Lloyd, G., Lopez-Gonzalez, G., Luizao, F.J., Malhi, Y., Monteagudo, A., Neill, D.A., Nunez Vargas, P., Paiva, R., Peacock, J., Penuela, M.C., Pena Cruz, A., Pitman, N., Priante Filho, N., Prieto, A., Ramirez, H., Rudas, A., Salomao, R., Santos, A.J.B., Schmerler, J., Silva, N., Silveira, M., Vasquez, R., Vieira, I., Terborgh, J., Lloyd, J., 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9, 2203-2246.

Renninger, H.J., Phillips, N., 2012. "Secondary stem lengthening" in the palm Iriartea deltoidea (Arecaceae) provides an efficient and novel method for height growth in a tree form. Am. J. Bot. 99, 607-613.

Rich, P.M., 1987a. Developmental anatomy of the stem of *Welfia georgii*, *Iriartea gigantea*, and other arborescent palms - implications for mechanical support. Am. J. Bot. 74, 792-802.

Rich, P.M., 1987b. Mechanical structure of the stem of arborescent palms. Botanical Gazette 148, 42-50.

Rich, P.M., Helenurm, K., Kearns, D., Morse, S.R., Palmer, M.W., Short, L., 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. Bulletin of the Torrey Botanical Club 113, 241-246.

Roucoux, K.H., Lawson, I.T., Jones, T.D., Baker, T.R., Coronado, E.N.H., Gosling, W.D., Lähteenoja, O., 2013. Vegetation development in an Amazonian peatland. Palaeogeogr., Palaeoclimatol., Palaeoecol. 374, 242-255.

Runk, J.V., 1998. Productivity and sustainability of a vegetable ivory palm (Phytelephas aequatorialis, Arecaceae) under three management regimes in northwestern Ecuador. Econ. Bot. 52, 168-182.

Segura-Madrigal, M.A., 1997. Almacenamiento y fijación de carbono en *Quercus costaricensis*, en un bosque de altura en la Cordillera de Talamanca, Costa Rica. In, Escuela Ciencias Ambientales, Facultad de Ciencias de la Tierra y el Mar. Heredia, Universidad Nacional, CR, p. 147.

Sierra, C.A., del Valle, J.I., Orrego, S.A., Moreno, F.H., Harmon, M.E., Zapata, M., Colorado, G.J., Herrera, M.A., Lara, W., Restrepo, D.E., Berrouet, L.M., Loaiza, L.M., Benjumea, J.F., 2007. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. For. Ecol. Manage. 243, 299-309.

Terborgh, J., Andresen, E., 1998. The composition of Amazonian forests: patterns at local and regional scales. J. Trop. Ecol. 14, 645-664.

Thenkabail, P.S., Stucky, N., Griscom, B.W., Ashton, M.S., Diels, J., Van der Meer, B., Enclona, E., 2004. Biomass estimations and carbon stock calculations in the oil palm plantations of African derived savannas using IKONOS data. Int. J. Remote Sens. 25, 5447-5472.

Tomlinson, P.B., 2006. The uniqueness of palms. Bot. J. Linn. Soc. 151, 5-14.

West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. Science 276, 122-126.

Williamson, G.B., Wiemann, M.C., 2010. Measuring Wood Specific Gravity ... Correctly. Am. J. Bot. 97, 519-524.

Zambrana, N.Y.P., Byg, A., Svenning, J.-C., Moraes, M., Grandez, C., Balslev, H., 2007. Diversity of palm uses in the western Amazon. Biodivers. Conserv. 16, 2771-2787.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global wood density database. In. Dryad Digital Repository.

Tables

Table 1. Directly measured biomass data analysed in this study from Madre de Dios (MdD) and Loreto, Peru: number of individuals (*n*), diameter at 1.3 m or above roots (*D*), stem height (H_{stem}), and total height (H_{tot}).

Location	**Species**	***n***	**D** (cm)	$\mathbf{H_{stem}}$ (m)	$\mathbf{H_{tot}}$ (m)
MdD	*Astrocaryum murumuru*	19	15-29	1.5-9.0	7.1-14.7
MdD	*Attalea phalerata*	21	17-50	0-20.1	7.1-25.6
MdD	*Bactris gasipaes*	3	11-15	9.3-18.1	13.0-20.8
MdD	*Euterpe precatoria*	8	12-19	10.2-20.4	13.3-22.8
MdD	*Iriartea deltoidea*	21	6-33	3.3-21.8	5.6-25.1
Loreto	*Mauritia flexuosa*	16	19-36	5.1-30.5	9.1-38.4
Loreto	*Mauritiella aculeata*	18	8-15	3.5-20.6	5.3-26.1
MdD	*Oenocarpus bataua*	10	21-41	2.9-14.5	14.2-25.9
MdD	*Socratea exorrhiza*	20	4-24	2.0-21.9	3.2-23.9
Total	**9 species**	**136**	**4-50**	**0-30.5**	**3.2-28.4**

Table 2. Dry mass fraction (dry mass / fresh mass) and carbon fraction (dry mass$_{\text{carbon}}$ / dry mass$_{\text{total}}$) in stem, leaf, and root tissue, and mean and standard deviation of individual leaf dry mass of the nine species sampled.

Species	**Stem**	**Leaf**	**Root**	**Leaf dry mass (kg)**	
	Dry mass fraction			**mean**	**SD**
Astrocaryum murumuru	0.400			2.687	1.057
Attalea phalerata	0.357			2.649	0.938
Bactris gasipaes	0.619			0.471	0.132
Euterpe precatoria	0.398			0.620	0.269
Iriartea deltoidea	0.244			4.065	3.787
Oenocarpus bataua	0.338			9.315	1.683
Socratea exorrhiza	0.339			1.764	1.629
mixed species (above)		0.463			
Mauritia flexuosa	0.367	0.517	0.402	11.444	5.845
Mauritiella aculeata	0.269	0.320	0.297	0.951	0.447
mean	**0.370**	**0.433**	**0.350**	**3.774**	**1.754**
	Carbon fraction				
Mauritia flexuosa	0.481	0.494	0.491		
Mauritiella aculeata	0.480	0.529	0.485		
mean	**0.481**	**0.512**	**0.488**		

Table 3. Recommended models for each genus and mixed-species to estimate aboveground biomass (AGB; kg dry mass) or belowground root biomass (BGB; kg dry mass) from stem height (H_{stem}; m), diameter (D; cm), and dry mass fraction (dmf; g g^{-1}), and leaf dry mass (kg) from mean leaf length (m). All models follow the form $y = a + bx_1 + cx_2$. The family-level model with $dmfD^2H_{stem}$ is only valid for individuals with $H_{stem} \geq 1$ m; and the family-level models without a height term are only valid for individuals with $H_{stem} > 3$ m and $6 \leq D < 40$ cm.

Genus or group	**y**	**x_1**	**x_2**	***a***	***b***	***c***	***R^2***	***n***	**RSE**	**F**	**dfe**	***Pr* < F**	**AIC**
Aboveground biomass													
Astrocaryum	AGB	H_{stem}		.	21.302		0.957	18	26.1	379	17	<0.0001	171.4
Attalea	ln(AGB)	$\ln(H_{stem}+1)$		3.2579	1.1249		0.858	21	0.371	115	19	<0.0001	21.9
Euterpe	AGB	H_{stem}		-108.81	13.589		0.973	8	8.37	215	6	<0.0001	60.4
Iriartea	ln(AGB)	$\ln(D^2H_{stem})$		-3.483	0.94371		0.967	21	0.311	560	19	<0.0001	14.5
Mauritia	ln(AGB)	$\ln(H_{stem})$		2.4647	1.3777		0.897	16	0.273	121	14	<0.0001	7.7
Mauritiella	AGB	H_{stem}		.	2.8662		0.972	18	8.21	591	17	<0.0001	129.9
Oenocarpus	ln(AGB)	H_{stem}		4.5496	0.1387		0.784	10	0.237	29	8	0.000658	3.4
Socratea	ln(AGB)	$\ln(D^2H_{stem})$		-3.7965	1.0029		0.976	20	0.227	740	18	<0.0001	1.3
Family-level	$AGB^{0.25}$	$(dmf \times D^2H_{stem})^{0.25}$		.	0.55512		0.990	106	0.367	10410	105	<0.0001	91.5
	ln(AGB)	ln(D)		-3.3488	2.7483		0.802	97	0.588	384	95	<0.0001	176.1
	ln(AGB)	ln(D)	ln(dmf)	-2.0752	2.6401	0.8426	0.815	97	0.570	208	94	<0.0001	171.1
Belowground root biomass													
Mauritia	ln(BGB)	$\ln(H_{stem})$		-0.3688	2.0106		0.929	16	0.323	184	14	<0.0001	13.1
Mauritiella	ln(BGB)	H_{stem}		1.0945	0.11086		0.951	18	0.132	310	16	<0.0001	-18.0
Leaf dry mass													
Family-level	$mass^{0.3}$	length		0.66020	0.10896		0.732	76	0.171	202	74	<0.0001	-48.5
Iriartea	ln(mass)	length		-5.1751	1.4547		0.803	21	0.649	78	19	<0.0001	45.4

Table 4. Palm and dicot tree aboveground biomass density estimates for nine RAINFOR plots in Tambopata National Reserve, Peru. Estimates were made using two recent pantropical dicot models (Feldpausch et al., 2012) based on diameter and wood density (F 1) or diameter, wood density, and estimated height (F 2); three family-level palm equations (D, $D+dmf$, and $dmfD^2H_{stem}$; Table 3); and the recommended species-level model for each species or genera (Table 3). Percent differences are shown for each palm model compared to each dicot model. Results are summarised as mean of all plots, sum of all plots, and overall percent difference.

Plot	No. stems	% palm stems	Aboveground biomass estimate (Mg)						% Difference: (Palm - Dicot)/Dicot × 100 %							
			Dicot		Palm equation				D		D+dmf		dmfD^2H_{st}		Species	
			F 1	F 2	D	D+dmf	dmfD^2H_{st}	Species	F 1	F 2	F 1	F 2	F 1	F 2	F 1	F 2
TAM01	598	31.9	279	233					3.4	5.1	0.9	2.1	2.7	4.2	1.4	2.7
	191		27	25	36.5	29.3	34.4	30.9	35.4	48.6	8.9	19.5	27.6	40.1	14.9	26.1
TAM02	659	28.8	262	223					2.6	3.9	0.7	1.7	2.8	4.1	1.8	2.9
	190		24	22	31.1	26.0	31.5	28.8	28.4	39.3	7.3	16.4	29.9	40.9	18.9	29.0
TAM03	617	15.9	372	312					-0.2	1.6	0.4	2.3	-0.7	0.9	0.3	2.2
	98		42	36	41.1	43.3	39.0	42.9	-1.5	13.6	3.7	19.7	-6.6	7.7	2.8	18.6
TAM04	714	9.0	354	299					-0.3	0.1	-0.6	-0.3	-0.6	-0.3	1.1	1.7
	64		14	13	12.8	11.7	11.6	17.7	-7.7	1.6	-15.7	-7.2	-16.3	-7.9	27.3	40.1
TAM05	526	3.8	316	262					-0.1	0.0	-0.1	-0.1	0.1	0.2	0.6	0.8
	20		3	3	2.6	2.4	3.2	4.8	-8.0	-2.8	-14.6	-9.7	13.1	19.5	70.3	79.9
TAM06	660	31.8	359	297					2.7	4.4	0.8	2.2	1.7	3.2	0.4	1.7
	210		34	30	43.6	36.9	40.0	35.4	28.8	43.0	9.0	21.0	18.2	31.2	4.6	16.1
TAM07	507	3.4	267	224					-0.4	-0.4	-0.4	-0.4	-0.3	-0.4	0.8	1.0
	17		3	3	1.7	1.8	1.9	4.9	-39.2	-36.8	-35.2	-32.6	-33.2	-30.5	74.9	81.8
TAM08	513	12.3	266	222					0.6	1.0	-0.1	0.2	0.5	0.9	1.1	1.6
	63		9	9	10.9	9.1	10.6	12.3	15.6	25.0	-3.8	4.1	12.8	22.0	30.2	40.8
TAM09	552	15.2	271	228					1.5	2.3	0.4	0.9	1.0	1.7	0.6	1.3
	84		13	11	16.5	13.5	15.3	14.2	32.0	45.4	7.6	18.6	22.2	34.7	13.6	25.1
Mean of all plots	594		305	256					1.1	2.0	0.2	0.9	0.8	1.6	0.9	1.8
	104	16.9	19	17	21.9	19.3	20.8	21.3	9.3	19.7	-3.6	5.5	7.5	17.5	**28.6**	**39.7**
Sum or Overall % diff.	**Sum of all plots (Mg)**								**Overall % Difference (∑Diff /∑Estim × 100 %)**							
	4673		2745	2300					1.0	2.0	0.2	1.0	0.7	1.6	0.9	1.8
	938	20.1	168	152	197	174	187	192	17.0	29.8	3.4	14.8	11.4	23.7	**14.1**	**26.6**

Figure captions

Figure 1. Raw data showing the relationships between (A) stem height and diameter and (B) aboveground biomass and diameter, and (C) aboveground biomass and stem height for each species.

Figure 2. Aboveground biomass (AGB) data and recommended model (line) for each genus to estimate AGB (kg dry mass) from stem height (H_{stem}; m) and diameter at 1.3 m or above stilt roots (D; cm). Equations are given in Table 3.

Figure 3. Aboveground biomass (AGB) data for all species (points) and three family-level model estimates (lines) using (A) $dmfD^2H_{stem}$, (B) D, and (C) $D+dmf$. Equations are given in Table 3.

Figure 4. Errors ($\mathrm{AGB}_{\mathrm{estimated}}–\mathrm{AGB}_{\mathrm{observed}}$) for harvested palm aboveground biomass (AGB) when estimated by dicot models using and diameter and wood density (Feld 1) and diameter, wood density, and estimated height (Feld 2; Feldpausch et al., 2012) compared with diameter and stem height.

Figure 1 color

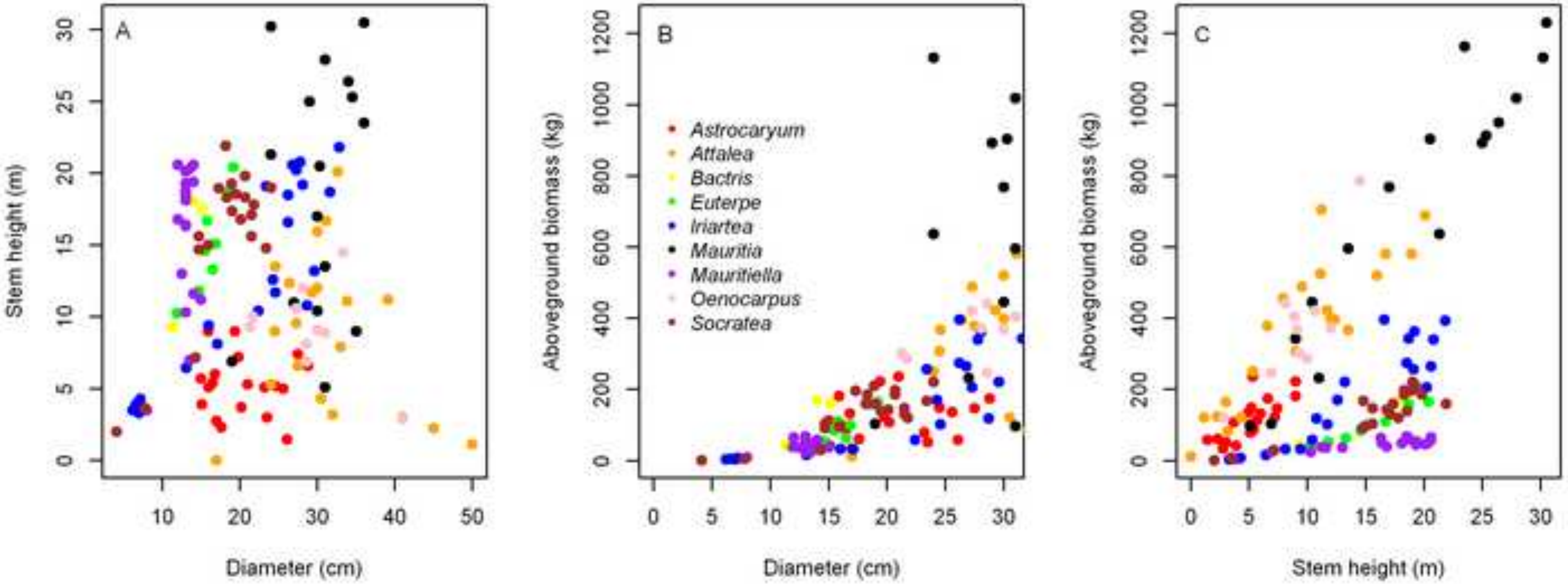
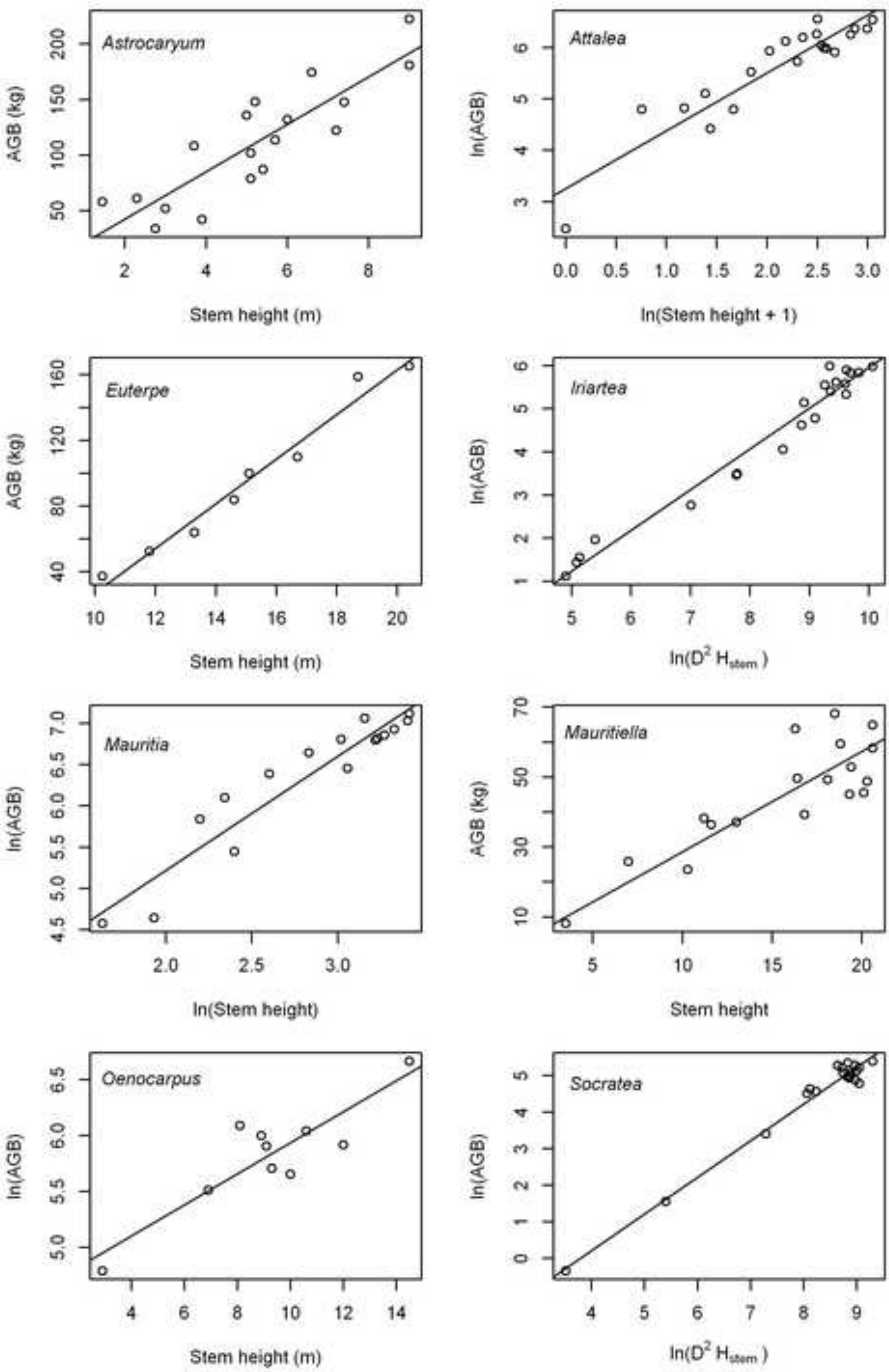


Figure 2


Astrocaryum
AGB (kg)
50
100
150
200
2
4
6
8
Stem height (m)
Attalea
ln(AGB)
3
4
5
6
0.0
0.5
1.0
1.5
2.0
2.5
3.0
ln(Stem height + 1)
Euterpe
AGB (kg)
40
80
120
160
10
12
14
16
18
20
Stem height (m)
Iriartea
ln(AGB)
1
2
3
4
5
6
5
6
7
8
9
10
ln(D² H_stem)
Mauritia
ln(AGB)
4.5
5.0
5.5
6.0
6.5
7.0
2.0
2.5
3.0
ln(Stem height)
Mauritiella
AGB (kg)
10
30
50
70
5
10
15
20
Stem height
Oenocarpus
ln(AGB)
5.0
5.5
6.0
6.5
4
6
8
10
12
14
Stem height (m)
Socratea
ln(AGB)
0
1
2
3
4
5
4
5
6
7
8
9
ln(D² H_stem)

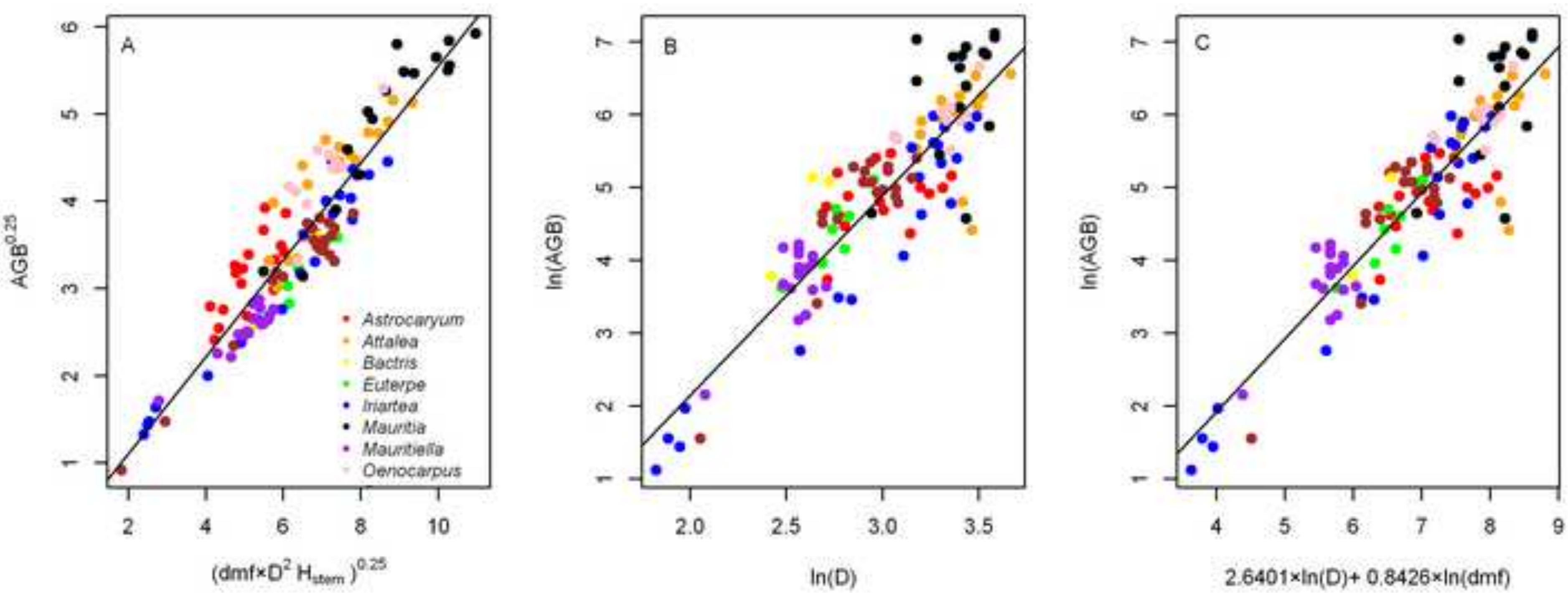

A
$AGB^{0.25}$
1
2
3
4
5
6
2
4
6
8
10
$(dmf \times D^2 H_{stem})^{0.25}$
● *Astrocaryum*
● *Attalea*
● *Bactris*
● *Euterpe*
● *Iriartea*
● *Mauritia*
● *Mauritiella*
● *Oenocarpus*
B
ln(AGB)
1
2
3
4
5
6
7
2.0
2.5
3.0
3.5
ln(D)
C
ln(AGB)
1
2
3
4
5
6
7
4
5
6
7
8
9
2.6401×ln(D)+ 0.8426×ln(dmf)

Figure 4 color

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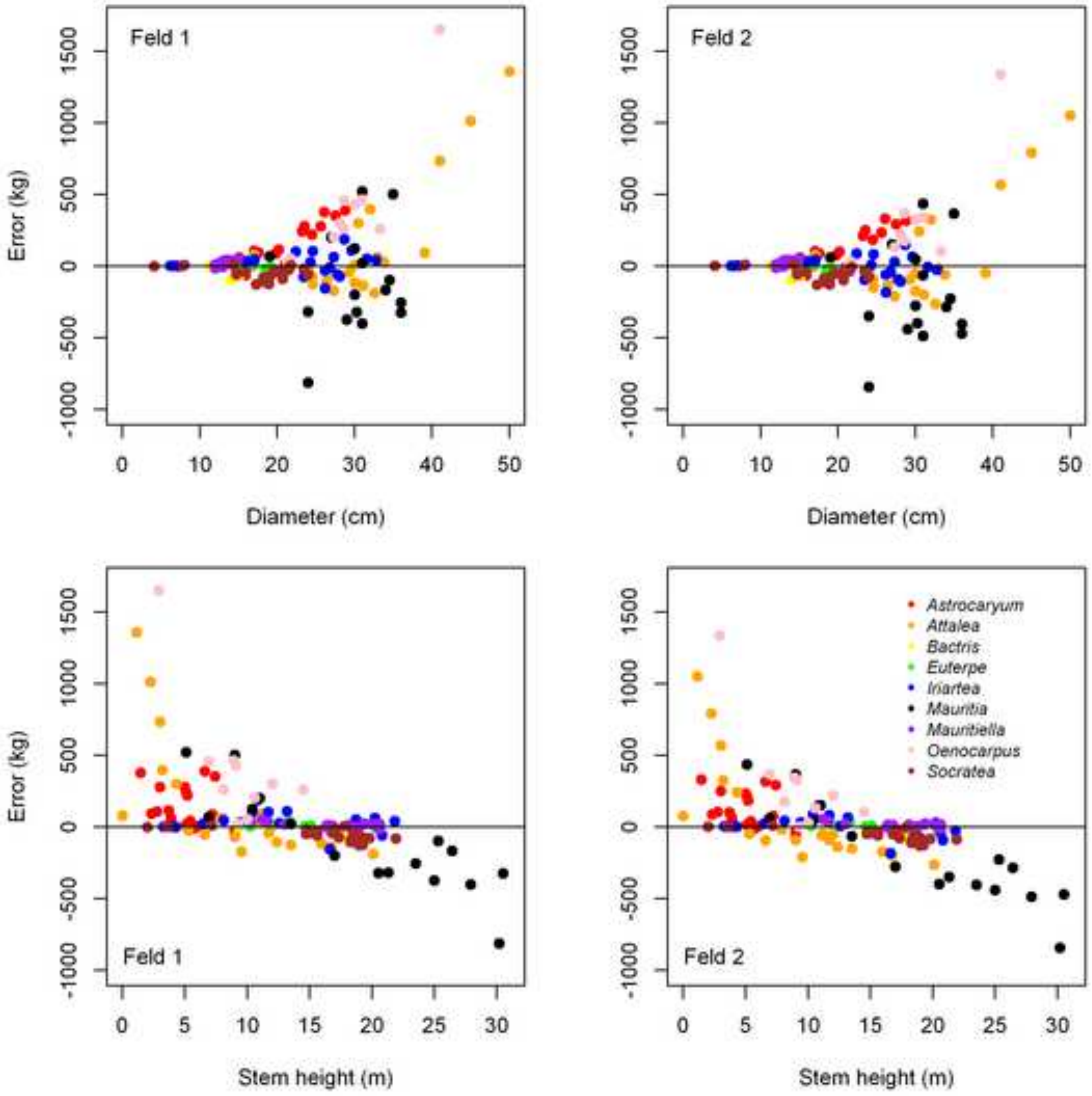
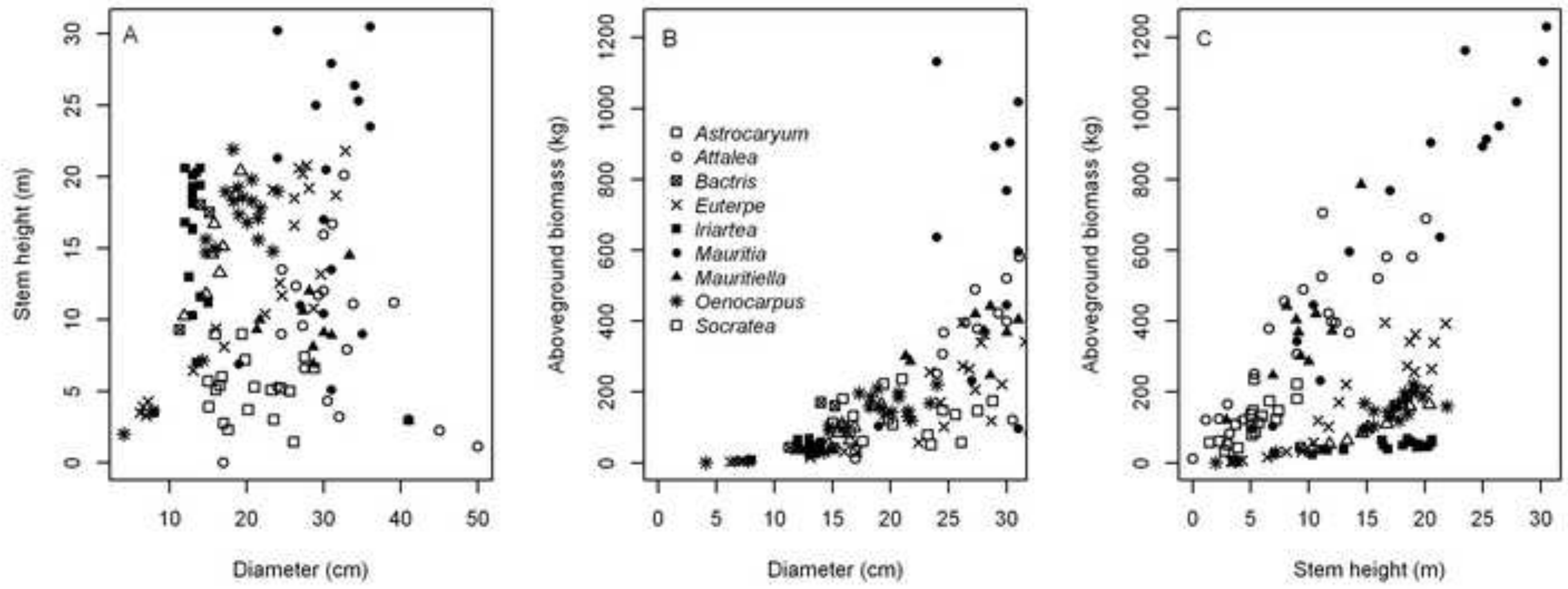


Figure 1 Black and white



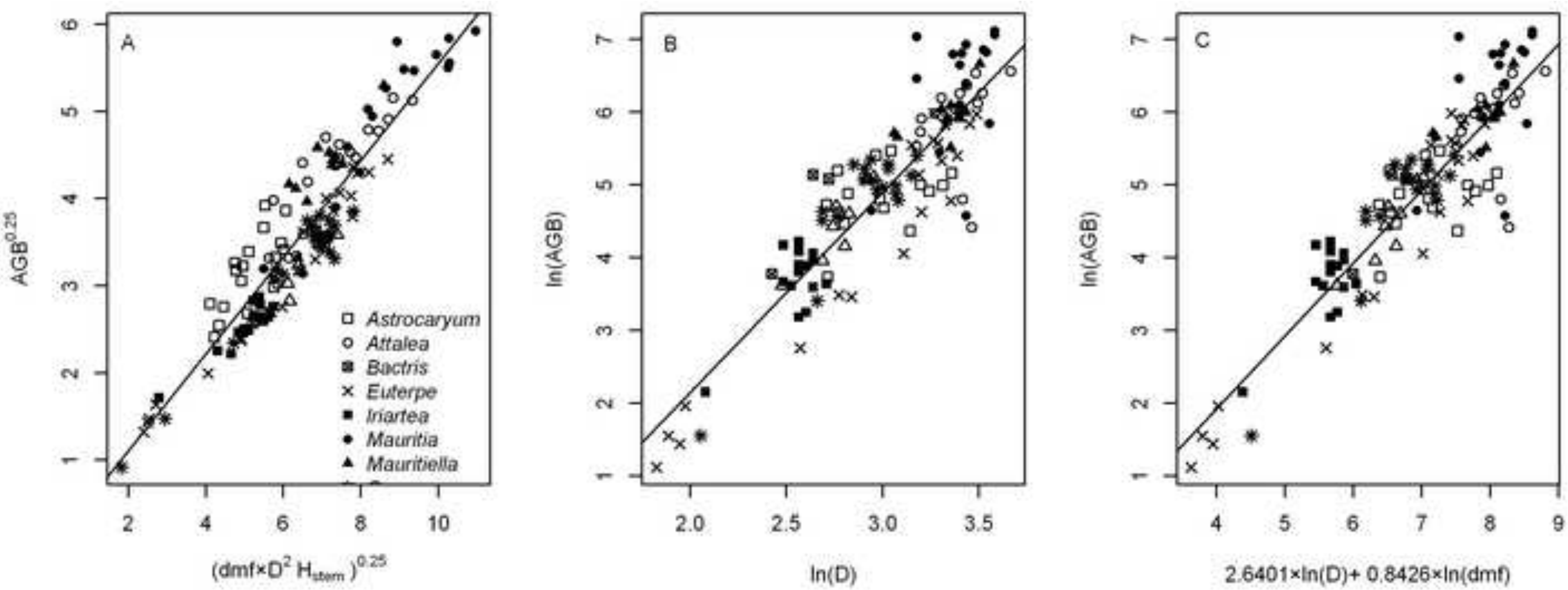

A
AGB$^{0.25}$
$(\text{dmf}\times D^2\ H_{\text{stem}})^{0.25}$
1
2
3
4
5
6
2
4
6
8
10
☐ *Astrocaryum*
○ *Attalea*
▨ *Bactris*
× *Euterpe*
■ *Iriartea*
● *Mauritia*
▲ *Mauritiella*
B
ln(AGB)
ln(D)
1
2
3
4
5
6
7
2.0
2.5
3.0
3.5
C
ln(AGB)
2.6401×ln(D)+ 0.8426×ln(dmf)
1
2
3
4
5
6
7
4
5
6
7
8
9

Figure 4 Black and white

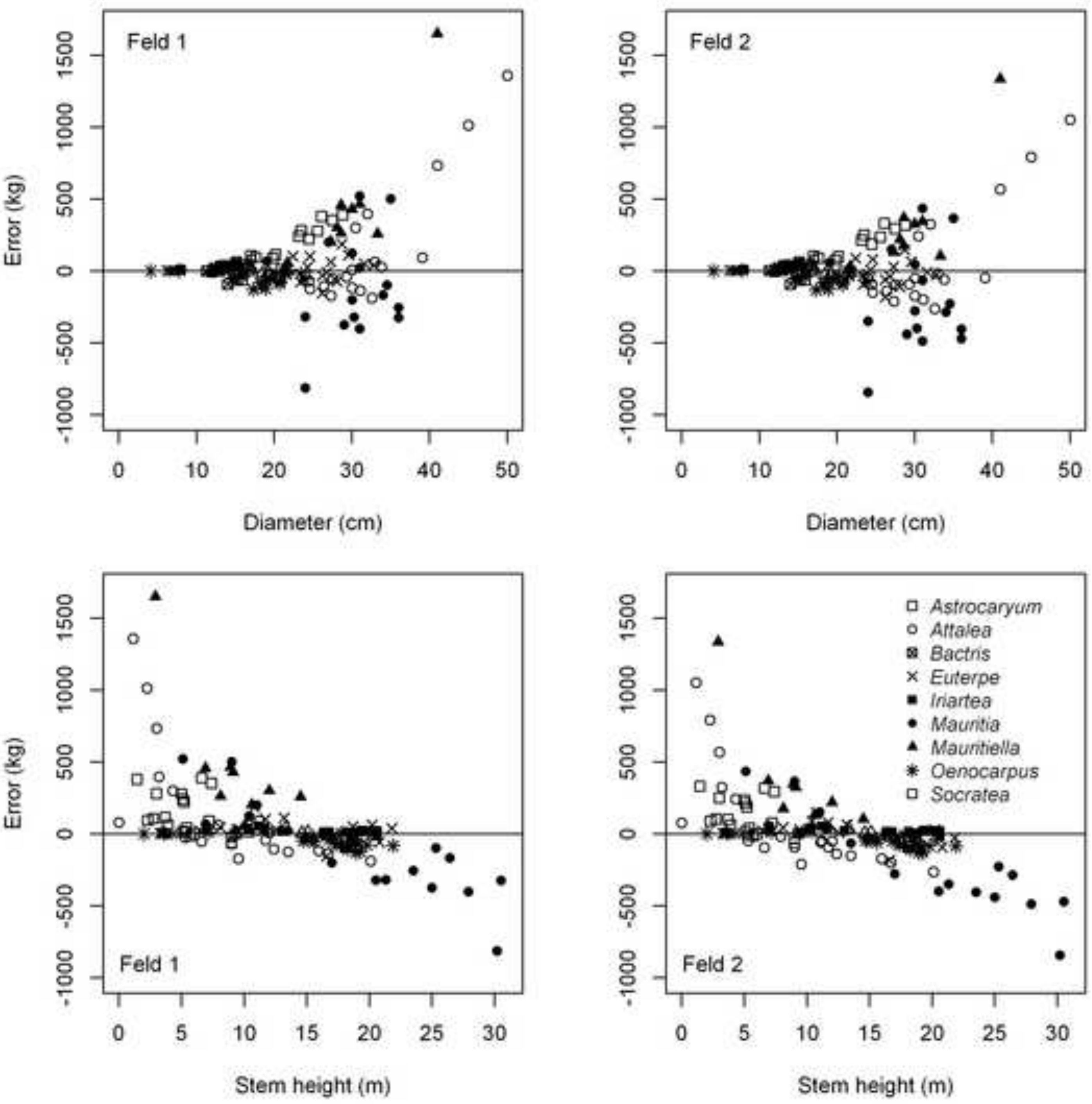


Figure A1

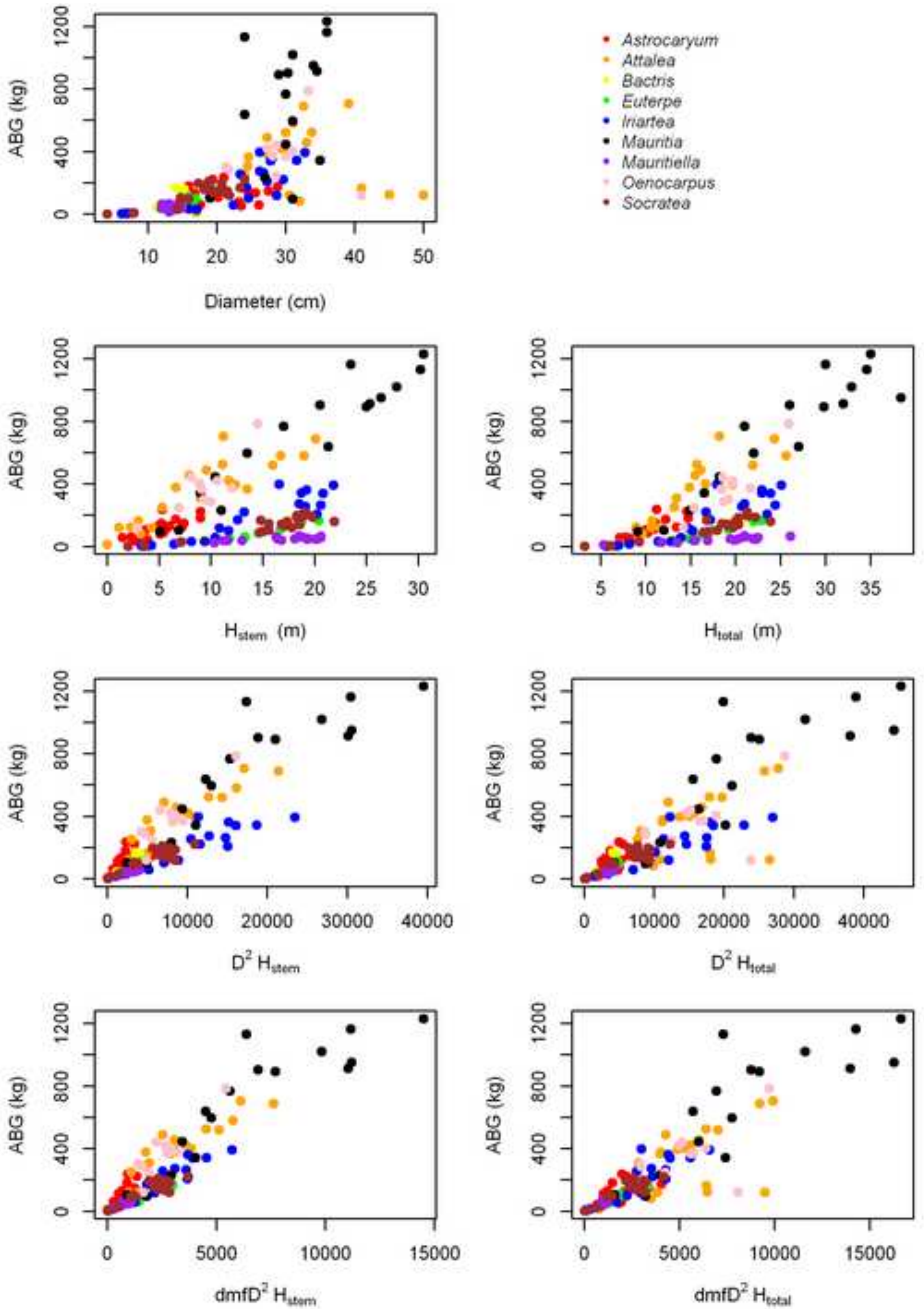

ABG (kg)
0
400
800
1200
10
20
30
40
50
Diameter (cm)
● *Astrocaryum*
● *Attalea*
● *Bactris*
● *Euterpe*
● *Iriartea*
● *Mauritia*
● *Mauritiella*
● *Oenocarpus*
● *Socratea*
0
5
10
15
20
25
30
H_{stem} (m)
5
10
15
20
25
30
35
H_{total} (m)
0
10000
20000
30000
40000
$D^2 H_{stem}$
$D^2 H_{total}$
0
5000
10000
15000
$dmfD^2 H_{stem}$
$dmfD^2 H_{total}$

Figure A2

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