Tropical tree and palm allometry and implications for forest carbon dynamics in southwestern Amazonia

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others. Details on jointly-authored publications are listed below:

Chapter 2: two associated publications

Reference 1: Goodman, R. C., O. L. Phillips, and T. R. Baker. 2012. Tropical forests: Tightening up on tree carbon estimates. Nature 491:527-527.

Reference 2: Goodman, R. C., O. L. Phillips, and T. R. Baker. in press. The importance of crown dimensions to improve tropical tree biomass estimates. Ecological Applications.

R. Goodman led all fieldwork associated with the data collected for these papers and conducted all data analysis with some feedback from T. Baker and O. Phillips. She wrote both articles, which incorportated corrections and suggestions from my supervisors.

The structure of the first article was modified by journalists at Nature. The second paper also incorporated comments from Dr. Simon Lewis (University of Leeds), two anonymous peer-reviewers, and the subject matter editor of the journal. R. Goodman was corresponding author during the review process.

Chapter 3: one associated publication

Reference 3: Goodman, R. C., O. L. Phillips, D. del Castillo Torres, L. Freitas, A. Monteagudo, and T. R. Baker. 2013. Amazon palm biomass and allometry. Forest Ecology and Management 310:994-1004.

R. Goodman collected all data from Madre de Dios, and additional data were obtained from D. del Castillo Torres, L. Freitas, and A. Monteagudo. The distinction is made clear in the article and thesis chapter. Again, I conducted all data analysis, wrote the article (incorporating corrections and suggestions from T. Baker and O. Phillips), and am corresponding author during the review process.

Chapter 4 : one associated publication

The final publication will focus on the results reported in Chapter 4. R. Goodman led a partial forest inventory of Tambopata plots, but the majority of plot data were made available through the ForestPlots.net database and derives from work by O.

Phillips, T. Baker and other RAINFOR (Amazon Forest Inventory Network) researchers at Tambopata and elsewhere in southwestern Amazonia, and mostly funded through grants led by O. Phillips. As per database policy, Principal Researchers responsible for leading fieldwork were contacted and invited for co-authorship. Some authors have accepted this invitation, and others have asked to be included in the Acknowledgements only. In the thesis, all Principal Researchers have been included in the Acknowledgements of Chapter 4. R. Goodman has conducted the analysis and written both chapters with assistance from T. Baker and O. Phillips. She will also write the associated journal article, with the comments and suggestions from her supervisors and other co-authors, and serve as corresponding author during the review process.

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Abstract

Tropical forests play a vital role in the global carbon cycle and international policy, such as the United Nations Collaborative Programme on Reducing Emissions from Deforestation or Degradation (REDD+), but the amount of carbon they contain and its spatial distribution remain uncertain. Allometric equations used to estimate tree mass are a key source of this uncertainty, because large-scale variation in tree allometry and fundamental differences between functional groups are not accurately represented in pantropical biomass equations. This research tests the effects of accounting for sources of variation not currently explained in tree models (i.e., crown size and structure) and recognising important distinctions between functional groups (monocots vs. dicots) at both the level of individuals and across the landscape.

Southwestern Amazonian forests are politically and ecologically important, but biomass estimates may be particularly uncertain in this region. Specifically, tree biomass estimates vary greatly among published models, but these models do not account for crown structure nor have their predictions been tested against directly-measured data in the southwestern Amazon. Palms are also abundant in western Amazonia but their mass has been widely misrepresented: using models developed for dicotyledonous trees is likely inaccurate because these two groups have very different structures.

To test these ideas, 51 trees and 136 arborescent palms were harvested and weighed in Peru, including the heaviest tropical tree on record. Existing pantropical equations that included height underestimated tree biomass by 11–14 % because large crowns partially compensate for lower stature. Including crown parameters in new allometric models greatly improved performance and reduced error, especially for the largest trees. Palm biomass was often underestimated by dicot models because they can be much taller at small diameters, and stem height was the most important variable in new equations.

These results were confirmed on a larger scale. Based on a network of 53 forest plots, biomass carbon in trees and palms in the southwestern Amazon is 9 % greater than estimated by the recommended pantropical biomass equation. Original total aboveground carbon stocks over the entire 746,653 km^2 ecoregion is estimated at 11.5 Pg C. Nearly one third of forests in this region are at imminent risk of deforestation and forest degradation, which would result in emissions up to 4.4 Pg C. These results significantly advance allometric modelling and reduce uncertainty in forest biomass estimates, especially in southwestern Amazonia, which should help to underpin effective forest management and provide better forest biomass estimates for REDD+ and other carbon-based conservation projects.

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CHAPTER 1 Introduction and background

1.1 The context of tropical forests in global carbon cycling

1.1.1 Role of tropical forests in the carbon cycle and international policy

Tropical forests store more than 70 % of living biomass in forests worldwide (Pan et al. 2011), and are home to over half of the world's known species (Terborgh 1992). However, deforestation, forest degradation, and other land uses threaten these ecosystems. Deforestation is regarded as the second highest source of anthropogenic carbon emissions (e.g., van der Werf et al. 2009), and the majority of deforestation occurs in tropical regions (Pan et al. 2011). Tropical forests also supply non-timber forest products and provide other locally and globally significant ecosystem services. These factors make tropical forest conservation a particularly attractive possibility for reducing carbon dioxide emissions and slowing global climate change, while potentially providing biological, environmental, and even social benefits (Phelps et al. 2012).

The use of international carbon trading to avoid tropical forest deforestation was originally proposed under the Clean Development Mechanism of the Kyoto Protocol in 1997 (Fearnside 1999) and has enjoyed renewed support since 2005 (Laurance 2007), especially as part of the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Degradation (REDD+) (Ebeling and Yasue 2008). However, due in part to the large uncertainties in carbon stock estimates, estimates of emissions from tropical deforestation vary widely. Recent studies have estimated that gross emissions from tropical deforestation and degradation are between 1.1 and 2.9 Pg C/year (Malhi 2010, Pan et al. 2011, Baccini et al. 2012), but both the spatial distribution and total emissions are subject to large uncertainties (Houghton et al. 2000, Baccini et al. 2012). Thus, how forest conservation may reduce the rate of climate change, where to concentrate conservation efforts, and the value of each hectare in terms of carbon are also uncertain. It is, therefore, important both locally and globally to improve estimates of biomass density in tropical trees and tropical forests, by actually measuring them. One of the primary aims of this thesis is therefore to acquire and analyse new directly-measured data from the ground in southwestern Amazon forests, where to date there has not been a single study that has weighed trees directly.

1.1.2 Tropical forest biomass

Tropical forests store large, but still remarkably uncertain, quantities of carbon (C) in plant biomass, with recent estimates ranging widely from 175 to 340 Pg C (Houghton et al. 2009, FAO 2010, Pan et al. 2011, Saatchi et al. 2011, Baccini et al. 2012, Feldpausch et al. 2012). The largest remaining intact tropical forests are found in South America (Potapov et al. 2008), which contains nearly half of all tropical forest biomass (Pan et al. 2011, Saatchi et al. 2011).

Tropical forest biomass is estimated through a number of steps, each of which is subject to uncertainty and can vary between studies. Usually, plot inventories are conducted and the biomass of measured trees is estimated using allometric equations. AGB density is estimated by adding the biomass of all individuals included in the inventory, and 'other components', such as necromass, small trees, lianas, and roots are often added as mean estimates for the region or as a percentage of tree biomass. Finally, biomass density of measured plots must be extrapolated across the landscape or used to calibrate remote sensing data to estimate biomass of the entire region.

Aboveground biomass (AGB) density varies across the tropics (Silk et al. 2013). Estimates have ranged from 95 to 669 Mg/ha (summarized by Dixon et al. 1994, Houghton et al. 2000, Chave et al. 2001), probably due to both natural variation and methodological differences. Within the Amazon, AGB density estimates ranges from 200 to 350 Mg/ha (Malhi et al. 2006) or 138 to 458 Mg/ha (Quesada et al. 2009). Biomass density is greatest in central and northeastern Amazonia and lowest on the western, southern, and eastern margins of the basin (Figure 1.1). By combining plot-level data over a large scale, an estimated 120 Pg C is stored in biomass in lowland Amazonian forests (Malhi et al. 2006; Figure 1.1). The majority of this is stored in AGB of trees (76 %), followed by belowground biomass (16 %), and necromass (8 %), but both belowground biomass and necromass are poorly sampled (Malhi et al. 2006).

Estimates vary for a number of reasons related to how forest carbon density is estimated and how those densities are extrapolated across the landscape. In large scale studies, forest biomass density is the largest single source of uncertainty in carbon emissions estimates (Houghton et al. 2000, Baccini et al. 2012), and the largest source of uncertainty in carbon density is usually related to the allometric model used to estimate biomass from forest inventories (Chave et al. 2004). This thesis, therefore, focuses on improving tropical allometric models. More details on allometric models and sources of uncertainty are discussed in the following sections.

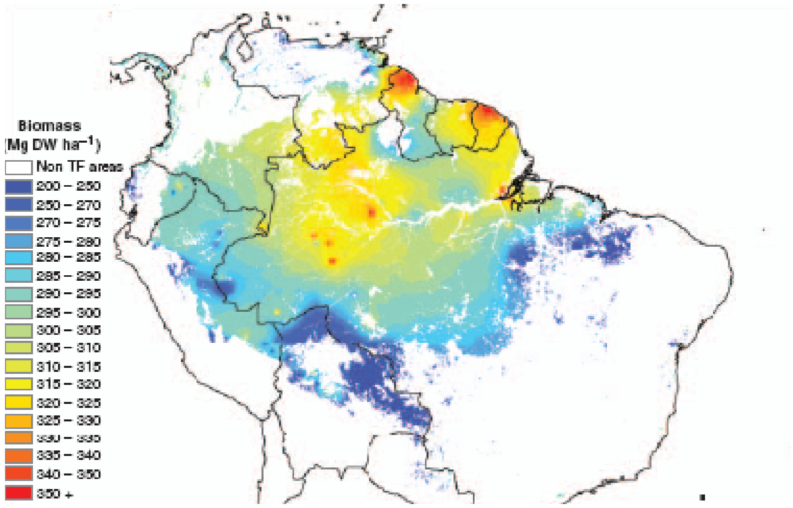

Figure 1.1. Biomass in lowland tropical forests of South America estimated by overlaying basal area estimates with maps of the forest structure and wood density (Malhi et al. 2006).

1.2 Allometric theory and mathematical reasoning

1.2.1 Physics and physiology behind tree allometric relationships

All trees photosynthesize and must subsequently allocate these photosynthates to both structural (i.e., biomass) and biochemical components. Biomass allocation is important, as each part of a tree (e.g., stem, roots, leaves, flowers, and fruits) performs a different function and together determine a tree's performance and survival in its current and future environments. A tree is an organism within which all parts are related, connected, and functioning together, so it is not surprising that several allometric relationships exist between the many structural parameters of a tree. Identifying relationships between these variables may improve our understanding of plant life strategies and, more practically, allows us to estimate additional parameters from measurements of more easily-measured parameters.

The term 'allometry' can be defined as "the study of correlations between the dimensions of different traits of an organism" (Brouat et al. 1998, p. 459) or used "to designate the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration" (Gould 1966, p. 587). The first definition logically implies that all plant structural traits are related in some way, and the second definition adds a level of complexity: proportions change with size.

These ideas have a long history. In the fifteenth century, Leonardo da Vinci wrote that "all the branches of trees at every stage of their height, united together, are equal to the thickness of their trunk below them", which he related to the course of water within the branches and main stem of the tree (Richter 1970, p. 393). In basic terms, Corner's rules postulated that there was a relationship between stem diameter and leaf area (Corner 1949). This was elaborated upon with the pipe model, which related leaf area to the width of the 'pipe' (e.g., stem or branch) serving as both vascular tissues and mechanical support (Shinozaki et al. 1964) and further clarified to relate total leaf area to cross-sectional area of the sapwood (Waring et al. 1982).

The pipe model was later improved upon with the metabolic scaling theory (Enquist et al. 1998, West et al. 1999, Enquist and Niklas 2001). Allometric scaling laws relate a biological variable (Y) to body mass (M) in the following general formula, $Y = Y_0M^b$, where Y_0 is a constant pertaining to a given type of organism and b is a scaling exponent (West et al. 1997). This model is based on an idealised version of principles based on how branches fill space (Mandelbrot 1982), how vessels taper width (Schmidt-Nielsen 1984), and the energy required to transport and deliver resources is minimised (Thompson 1942).

Metabolic scaling theory was later expanded upon to connect size, structure, and allometry to constraining physiological processes like water use and transport, photosynthesis, and growth, with an emphasis on convergence among species (West et al. 1999, Niklas and Enquist 2001, Meinzer 2003, Meinzer et al. 2003, Niklas and Spatz 2004). In specific reference to vascular plants, West et al. (1999) combined models of hydrodynamics, biomechanics, and branching geometry and predicted fractal-like tree architecture where allometric exponents were multiples of ¼ that were constant within and between individuals. These theoretical predictions are applicable to tapering of conducting vessels, maximum tree height, and height/diameter-ratios and were expanded to examine several other mechanical and physiological relationships in trees (West et al. 1999). As examples, mass should be proportional to 8/3-power of stem diameter: $mass \propto diameter^{8/3}$ (Enquist and Niklas 2001) and basal area (a function of D^2) scales as to the 3/4-power: $basal\ area \propto mass^{3/4}$ (West et al. 1997).

However, the theoretical equation related tree biomass to its diameter proposed by West et al. (1997) and Enquist (personal communication, published in Chambers et al. 2001), $\ln(mass) = -2.30 + 2.67\ln(diameter)$, consistently overestimates measured tree biomass based on diameter (Figure 1.2). This indicates that other factors limit actual biomass accumulation, as should be expected for plants growing with environmental limitations and competition. Indeed, the 8/3 scaling exponent was violated by large trees in four Amazonian sites (Nogueira et al. 2008b).

One reason for variation from perfect allometry may be that branches have long been ignored in allometric scaling theory, despite early findings that the proportion of crown mass affects AGB in trees worldwide (Cannell 1984). Most importantly to allometric theory, crown ratio affects AGB even after considering D and H (Cannell 1984). Nearly a decade after allometric scaling laws were introduced as such (West et al. 1997), the effect of branch losses on crown ratios, heartwood accumulation, and tapering was introduced into this framework (Mäkelä and Valentine 2006). All of these factors affected the relationship between stem diameter and tree mass, but the model developed focused on the relationship between leaf mass and crown ratio rather than improving biomass estimates (Mäkelä and Valentine 2006). Though the Mäkelä and Valentine (2006) work does not directly improve models pertaining to tropical angiosperm trees, it does introduce the idea that branches must also be considered in allometric theory. Some years later, allometric relationships between height, diameter, and crown diameter were studied over a range of environmental conditions and compared to predictions made by metabolic scaling theory (Lines et al. 2012). The study concluded that, unlike metabolic scaling theory predictions, the relationships between these variables do vary with environmental conditions and competition (Lines et al. 2012). These findings have important implications for estimating tree mass, but the role of branches has yet to be directly incorporated into allometric theory.

1.2.2 Mathematical reasoning behind allometric equations

Allometric relationships often have a clear basis in biological and/or physical principles. These relationships must, then, be integrated into widely applicable allometric equations with convincing mathematical theory. This section reviews the mathematical reasoning behind allometric equations with a focus on how the number of variables in these equations is reduced.

In the development of pantropical biomass equations, the typical basic reasoning is that AGB should be proportional to the volume of the trunk multiplied by wood density (ρ) (Brown 1997, Chave et al. 2005). For example, in Brown (1997) a 'biomass expansion factor' was used to estimate aboveground biomass from the mass of the inventoried bole, and Chave et al. (2005) argued that the volume of a cylindrical trunk would be calculated by the basal area ($\pi[D/2]^2$, where D is diameter of the main stem at breast height or just above buttresses) multiplied by total tree height (H). Tree trunks are not perfectly cylindrical, so a form factor (F) was introduced to account for taper (as a constant), and derived the following theoretical equation:

Equation 1: $$\boldsymbol{AGB = F \times \rho \times \left(\frac{\pi D^2}{4}\right) \times H}\,.$$

However, calculations performed on available data suggest that the following formula, which allows for further deviation from the assumption that tree volume can be estimated as a cylinder, provides a more accurate estimates of tree AGB (Brown et al. 1989, Chave et al. 2005):

Equation 2: $$\boldsymbol{AGB = F \times \left(\rho \times \left(\frac{\pi D^2}{4}\right) \times H\right)^{\beta}},$$

where $\beta < 1$.

To remove height from the equation, height can be estimated from diameter based on an additional underlying allometric relationship. In this case, Chave et al. (2005) assumed a power-law relationship between height and diameter —$H \propto D^B$ (McMahon and Kronauer 1976)— so Equation 1 became the following:

Equation 3: $$\boldsymbol{AGB = c\rho D^{B+2}},$$

where c is the taper of an average tree.

In an analysis of a large dataset of directly-measured tree biomass, Chave et al. (2005) used three variations of Equation 2 based on the assumptions about the parameters. The authors began with a basic, logarithmically transformed model that was first introduced by Schumacher and Hall (1933):

Equation 4: $\boldsymbol{\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho)}$.

If β_1, β_2, and β_3 are assumed to be 2, 1, and 1, respectively, then the equation becomes the following:

Equation 5: $\boldsymbol{\ln(AGB) = \alpha + 2\ln(D) + \ln(H) + \ln(\rho)}$,

which is equivalent to the following expression:

Equation 6: $\boldsymbol{AGB = e^{\alpha} \times D^2 H\rho}$.

The above assumptions about β_1, β_2, and β_3 return to the assumption that tree volume can be estimated as a cylinder based on D and total H, as in Equation 1. However, if at least one value of β is not assumed to be known, as in Equation 2, the equation becomes the following:

Equation 7: $\boldsymbol{\ln(AGB) = \alpha + \beta \ln\left(D^2 H\rho\right)}$.

The resulting equations (6 and 7) use only the compound variable, $D^2H\rho$, to predict biomass.

A second approach was to assume a polynomial relationship between ln(H) and ln(D) to remove tree height from the equation, yielding the following model:

Equation 8 $\boldsymbol{\ln(AGB) = a + b\ln(D) + c[\ln(D)]^2 + d[\ln(D)]^3 + \beta_3 \ln(\rho)}$.

When $c = d = 0$, the model expresses the power-law relationship:

Equation 9: $\boldsymbol{\ln(AGB) = e^{a} \times D^{b} \times \rho^{\beta_3}}$,

which is similar to Equation 3.

1.2.3 Critique of mathematical reasoning

The mathematical forms in the models above have been developed based on natural allometric relationships and the Chave et al. (2005) allometric equations, in particular, have become the most widely-used global equations for aboveground biomass estimates of tropical trees. However, these predictions were later found to be inaccurate in many cases, especially for large trees. This section will review the assumptions made to create these models that may not be accurate in natural systems.

Errors with the mathematical reasoning explained above may begin first with the assumption that tree volume can be estimated as a cylinder using D and H. Stems not only taper, but they also support branches. This problem could be resolved with an appropriate 'form' or 'biomass expansion factor', but these equations typically assume a constant form among all individuals, which is not an accurate assumption (Mäkelä and Valentine 2006). Rather, tropical trees have different branching patterns (Hallé et al. 1978) and proportions of their biomass in branches (da Silva 2007, Basuki et al. 2009). The compound variable, $D^2H\rho$, also assumes a constant relationship between biomass and these three variables (D, H, and ρ), all of which may differ independently from one another along environmental gradients and among regions, functional groups, or forest age.

Chave et al. (2005) accounted for potential ecological variation by dividing forests into successional status ('successional' or 'old-growth') and three forest types ('wet', 'moist', or 'dry'). Though correlation coefficients were always greater for separate forest types than for all types combined, adding the qualitative parameters (successional status and forest type) did not significantly improve the regression models. Equations also did not differ significantly by continent, even though species tended to be unique to each continent (Chave et al. 2005). However, allometric relationships do vary at this scale: asymptotic maximum height and H–D relationships are significantly different among continents, even after accounting for environmental differences, such as temperature, precipitation seasonality, and solar radiation (Banin et al. 2012).

Secondly, errors may be introduced when height is removed from the model. For example, the assumed power-law relationship between height and diameter (Equation 2 to 3) may not be accurate in all forest types (Aiba and Kohyama 1996, Thomas 1996, Feldpausch et al. 2011, Banin et al. 2012). Moreover, the polynomial model (Equation 8) has little biological justification, as polynomial relationships between H and D are not common (Banin et al. 2012), nor are the resulting polynomial terms for D well explained.

In the first widely-used pantropical biomass models (Chave et al. 2005), error was always greater in models that did not include height, suggesting that including more quantitative variables (e.g., height) may be able to account for regional variations in allometry. This idea was taken forward in the most recent pantropical biomass models (Feldpausch et al. 2012), which used two of the model forms developed above (Equations 7 and 8) but included height values estimated from regionally developed H–D models. However, it may not be correct to assume that the model with the most variables is entirely accurate. For example, models with H may have higher correlation coefficients than equations without this variable, even when H is poorly measured (Chave et al. 2001).

Finally, the importance of wood density may have been substantially diminished in the regression models above. First, species- or genus-level mean values were often used for wood density in the Chave et al. (2005) dataset, rather than directly-measured from each individual. As a result, the variation within a species would not have been recorded, making the true influence of ρ on individual tree AGB less detectable. Additionally, the coefficients associated with wood density were dropped (i.e., assumed to be 1) in some models, even when coefficients for D and H remained in the regression analysis (II.5 and II.6 in the original manuscript; Chave et al. 2005). Together, there is room to improve allometric equations to estimate tropical tree biomass by re-evaluating the role height and wood density in these models and especially by including crown dimensions and other aspects of tree structure.

1.3 Variation in allometry and its significance for biomass

1.3.1 Tree architecture

Tree architecture emerges as an outcome of growth and may influence the relationships between tree mass and predictor variables, such as diameter and height. Hallé et al. (1978) defines four major architectural types based on their apical meristems and construction. These ideas are used to identify variables that affect allometric relationships and may, therefore, improve biomass estimates if included in allometric equations. For example, trunk formation (monopodial or sympodial) likely has a large influence on stem volume; the presence or absence of branches affects crown biomass; branch orientation may affect crown (branch and/or foliage) biomass; and the occurrence of secondary growth will affect height/diameter-ratios.

1. *Trees built by one meristem:* These trees have only one apical meristem and produce a single, unbranched stem. This includes both monocotyledons (e.g., palm trees) and dicotyledonous trees. These trees are considered 'mono-axial'.

All other trees are 'poly-axial':

2. *Trees with modular construction:* In these trees, all meristems are equal and branching is sympodial (i.e., the shoot apex divides), thus producing a repeating or 'modular' construction.
3. *Trees with trunk-branch differentiation:* have a clear morphological and functional distinction between the main trunk and the branches. The trunk "determines the overall stature of the tree, is the central system of communication between roots and crown, and it maintains the mechanical stability of the whole organism" (p. 5), and branches are designed for photosynthesis and reproduction. Most trees fall within this category, including many tropical fruit and timber species. There is a wide variety of structures in this category. Trunks may be monopodial (i.e., one main stem) or sympodial; differentiation between trunk and branches can vary; and branch orientation may be vertical or horizontal.
4. *Trees with changes in orientation:* In these trees, the same meristem produces both stems and branches. Both vertical and horizontal shoots may become reoriented, and the final tree construction depends on this series of indefinite growth. In the tropics, most leguminous trees fall into this category.

Though trees may have an inherent architectural structure, there will always be deviations from this form. Trees rarely grow in optimal conditions and must, therefore, adapt to the environmental conditions or recover from some type of damage (Jiménez-Rojas et al. 2002). The term 'reiteration' refers to any modification of the tree's inherent architecture in response to such suboptimal conditions and is accomplished by activating a previously resting apical meristem that would not otherwise be involved in this role or by altering the orientation of a shoot (Hallé et al. 1978, Jiménez-Rojas et al. 2002).

1.3.2 Allometry of functional groups

Tree construction has obvious ecological implications, as tree height, branching pattern, and leaf size determine a tree's access to light and photosynthetic capacity, and it is likely to vary among species. For example, single-species models are better predictors of biomass than mixed species models (Nelson et al. 1999, Kohyama et al. 2003). This is an unsurprising reiteration that variation in wood density, height/diameter-ratios, crown architecture, and many other factors largely under genetic control influence allometric relationships and total tree biomass. However, given the abundant biodiversity found in the tropics, it is very impractical, even impossible, to study the allometry of individual species. Species are, therefore, often described or categorised into 'functional groups' based on regeneration requirements, early strategies for growth and survival, adult stature, and phenology. Many of these strategies can be viewed in terms of a tree's adaptation to the vertical, horizontal, and temporal variation in the light environment. These ideas may be used to guide the development of allometric equations and thereby improve biomass estimates.

1.3.2.1 Palms

As stated above, the monocot family Arecaceae (palms) have a completely different growth structure than all dicot trees. They grow vertically with little or no increase in secondary (diameter) growth (Rich et al. 1986, Tomlinson 2006). They lack branches and have relatively few, but very large, leaves. The internal stem structure is also very different in palms (Parthasarathy and Klotz 1976). 'Wood' density in family Arecaceae is generally lower than in dicot families (Chave et al. 2009, Zanne et al. 2009), and density and stiffness are higher towards the peripheries and base of the stem (Rich 1987b). These differences have implications for palm mass and the allometric equations used to estimate it.

1.3.2.2 Regeneration requirements and early growth strategies

In dicot tree seedlings, tree architecture —especially height and crown structure— are affected by their inherent regeneration requirements and ecological strategy, as well as the current light environment. Early successional species and species that are 'optimistic' about early gap formation often have monopodial stems, as they are better suited for vertical growth necessary to reach the canopy, while late-successional or ‘pessimistic’ species tend to exhibit sympodial branching, which is more conducive to the lateral spread necessary to capture light in a shaded environment (Boojh and Ramakrishnan 1982, Kohyama 1987, Sakai 1990). These allometric differences affect the structure of models used to estimate tree biomass. For example, the allometric equations to estimate AGB from *D* and *H* were significantly different between saplings with different ecological strategies (Kohyama 1987), perhaps because of the differences in branch mass between ‘optimists’ or ‘pessimists’ with the same diameter and height. However, these differences in biomass gain and allocation between these functional groups may be important in young trees but diminish as trees mature and reach the canopy (Keeling et al. 2008).

1.3.2.3 Tree height and adult stature: canopy, sub-canopy, understory

Tree height largely determines light capture, stem respiration (Chambers et al. 2004), and susceptibility to stem breakage, all of which increase with height (Thomas 1996). Maximum tree height is theoretically restricted to approximately 100 m due to water flow resistance through ever branching and taper vessels (West et al. 1999). However, aside from physical constraints, species have different maximum heights set genetically in accordance with their life strategy or ‘adult stature’. Some species reach the canopy, while others remain in the sub-canopy or understory. These ecological strategies are achieved by varying tree growth patterns and tree architecture and, therefore, have implications for estimating biomass.

Height-diameter relationships tend to vary between canopy, sub-canopy, and understory species. Saplings of understory and sub-canopy species generally have lower height/diameter-ratios than canopy species (King 1990, Thomas 1996, Kohyama et al. 2003, Bohlman and O'Brien 2006), though, the opposite relationship can be found in some species (Sterck and Bongers 1998). Interestingly, the relative height/diameter relationship (understory vs. canopy species) seems to change with size, age, and site. Studies have found that differences between the two groups disappear (Bohlman and O'Brien 2006) or reverse (Thomas 1996) as trees mature, or that differences do not become evident until trees nearly reach the canopy (Aiba and Kohyama 1996).

Canopy dimensions and several other characteristics may also differ between species of different adult statures. Adults of understory species generally have larger crowns than saplings of canopy trees with of similar heights (King 1996). In other words, understory trees have higher crown width/height-ratios than canopy species (Sterck and Bongers 1998). Canopy depth also increases steadily with total tree height, but canopy width increases sharply after trees reach their maximum height (Thomas 1996).

1.3.3 Wood density

Wood density obviously affects carbon storage via volume-mass relationships, but wood density may also be related to several functional traits, such as growth rates, regeneration requirements, and adult stature, which also affect biomass. Wood density varies among genera (Baker et al. 2004b), within a species (Wiemann and Williamson 2002), and within individuals (Higuchi et al. 1998, da Silva 2007, Henry et al. 2010). Fast growing, light demanding species tend to have lower wood densities than slow growing, shade tolerant species (Putz et al. 1983, Zimmerman et al. 1994, Thomas 1996, Muller-Landau 2004, Keeling et al. 2008). There is also a generally inverse relationship between wood density and mechanical damage (e.g., wind damage increases with decreasing wood density; Putz et al. 1983, Zimmerman et al. 1994), pathogen damage (Turner 2001), and the ability to recover from damage (Zimmerman et al. 1994). It also has physiological significance. For example, saturated water content, maximum leaf specific hydraulic conductivity, photosynthetic rate, and minimum leaf water potential were all significantly, negatively correlated with wood density across 20 species in Panama (Santiago et al. 2004).

1.3.4 Changes in allometry with size and age

In general, tree structure varies throughout its ontogeny (Bohlman and O'Brien 2006). These changes may be a result of biophysical limitations, such as maximum height, as well as environmental conditions and biological interactions that also change as individuals grow. As discussed in the previous sections, height/diameter-ratios tend to decrease with size as tree height approaches its upper limit asymptotically (Aiba and Kohyama 1996, Thomas 1996). The relationships between crown, height, and the light environment will also change with size. For example, seedlings growing in high light environments allocate more biomass to height growth, while seedlings growing in low light environments allocated more biomass to foliage (King 1994). However, when trees emerge from the canopy, vertical height growth slows while horizontal branch growth increases (Sterck and Bongers 2001). Larger trees therefore also have much higher proportions of crown to trunk biomass than smaller trees (Araújo et al. 1999). Stem taper has also been found to increase slightly with tree diameter (Nogueira et al. 2008a), but unlike most other parameters, wood density does not appear to change with tree size (Nogueira et al. 2005). Because allometric relationships and biomass vary with both size and age, it is important to examine trees of all sizes when developing models to estimate biomass.

1.3.5 Variation in allometry over geographic space and along environmental gradients

A number of important factors that may affect allometric relationships vary across the tropics. Thus, the relationships between structural variables and total AGB of individual trees will also vary geographically and along environmental gradients. *H–D* relationships are affected by variation in rainfall, length of dry season, temperature, wood density, and stand basal area, but still differ between continents even after accounting for environmental and structural variation (Feldpausch et al. 2011, Banin et al. 2012). At the same diameter, maximum height and *H–D* ratios were highest in Asia, followed by Africa, South America, and Australia (Banin et al. 2012). Within the Amazon, trees in northeastern and central forests are taller than those in western and southern forests (Nogueira et al. 2008b, Feldpausch et al. 2011). Average stem taper may also vary between regions (Nogueira et al. 2008a).

Functional traits, such as maximum heights and wood density, also vary deterministically across Amazonia, with lower wood densities and tree stature in the west (Baker et al. 2009). This variation in wood density across Amazonia is owed to biological composition, with more low density taxa occurring in western forests (Baker et al. 2004b). Another wood property, moisture content, also varies across Amazonia. Wood moisture content is inversely related to wood density and is higher in trees of southern Amazonian open forests than closed forests of central Amazonia (Nogueira et al. 2008a).

Tree crown biomass can vary across wide geographical areas, but data are sparse. Mean crown mass, as a proportion of the whole tree AGB, is greater in trees of the open forests of southern Amazonia (39 %) than in the dense forests of central Amazonia (31 %; da Silva 2007, Nogueira et al. 2008a) or in lowland *Dipterocarp* forests of Indonesia (33 %; Basuki et al. 2009). Satellite imagery also suggests that crown size is larger in southern, compared to northern, moist Amazonian forests (Barbier et al. 2010), but the variation in crown allometry, and how it affects tree biomass, has yet to be rigorously explored in the tropics.

1.3.6 Biological and compositional effects on tree allometry

Species composition changes by geographic region and along soil gradients (Bohlman et al. 2008), and differences in species composition and forest type may affect individual tree allometry in unexpected ways. For example, the presence of lianas and bamboo are associated with an increase in tree crown damage and lower tree heights (Putz et al. 1983, Nogueira et al. 2008b). For example, trees in bamboo-dominated forests of the southwestern Amazon were shorter than those in dense forests in the same area (Nogueira et al. 2008b). In contrast, maximum height and H–D relationships may be driven, in part, by species composition, whereby very tall taxa (e.g., Dipterocarpaceae) may drive all individuals to grow tall in order to compete and survive (Banin et al. 2012). The effect of these differences on tree biomass and allometric relationships has not been directly studied in many parts of the tropics, but is likely to vary by forest type and stand structure.

1.3.7 Summary

Many aspects of tree structure vary genetically (e.g., regeneration strategy, wood density, adult stature, and architectural type), but they are also affected by the light environment and the surrounding vegetation and forest structure. These relationships also vary systematically with size and across geographic and environmental space. Two themes emerge from this review: (i) crown dimensions are probably highly affected by each of these factors and highly variable, but have been ignored in allometric theory and equations, and (ii) palms are very different from dicot trees but have also been entirely ignored from allometric theory.

1.4 Existing allometric equations and findings

1.4.1 Summary of published equations for dicot trees

Many allometric equations have been published over the last several decades (Table 1.1, Figure 1.2; Brown et al. 1989, Higuchi and Carvalho 1994, Overman et al. 1994, Deans et al. 1996, Brown 1997, Higuchi et al. 1998, Araújo et al. 1999, Nelson et al. 1999, Chambers et al. 2001, Chave et al. 2001, Keller et al. 2001, Chave et al. 2005, Nogueira et al. 2006, da Silva 2007, Basuki et al. 2009, Djomo et al. 2010, Henry et al. 2010, Alvarez et al. 2012, Feldpausch et al. 2012). Diameter (D at 1.3 m or above buttresses) is always used as a predictor variable; and wood density, total height, and sometimes height of the commercial bole are also included. One study even included crown diameter (Henry et al. 2010), but the reported equations are not usable and, therefore, not included. Most models are for mixed species and predict AGB of trees with $D \geq 5$ or 10 cm only.

For mixed-species models, D, H, and ρ are important predictors of tree biomass, but single species models may use just one of these terms. For example, in single-species equations for four commercial species occurring in lowland *Dipterocarp* forests in Indonesia, only D was needed as a predictor variable; commercial bole height and wood density improved estimates very little (Basuki et al. 2009). However, single-species models are not practical in Amazonia. Thus, more variables will likely be needed to reduce the error inherent to mixed-species models. Many models are created from data transformed to the natural logarithm, but linear and non-linear equations have also been attempted (Table 1.1).

Table 1.1. Summary table of published allometric equations: sample size, range and distribution of diameter (D; in cm) of trees sampled, data source, area of study, species included, selected models, model selection criteria, and author(s). AGB is aboveground biomass (kg dry mass) and FM is fresh mass (kg). Equations in blue are represented in Figure 1.2. Where data source is listed 'others', see list of citations below.

Sample size	D range (cm)	Distribution of sizes	Data source	Area	Species	Model		Author
AMAZONIA								
54	8-100	fairly evenly # in ea. 10cm DBH size class	original	superhumid, terra firme; Araracuara, Colombia	mixed, randomly selected	$\ln(AGB) = 0.465(D^{2.202})$ $\ln(AGB) = -1.12(D^{2})$ $\ln(AGB) = -1.966 + 1.242(D^{2})$ **$\ln(AGB) = -2.904+ 0.993\ln(D^{2}H\rho)$**	$\ln(AGB) = -0.906 + 1.177\ln(D^{2}\rho)$ $\ln(AGB) = -3.843 + 1.035\ln(D^{2}H)$ $\ln(AGB) = -1.02+1.185\ln(D^{2})+1.071\ln(\rho)$	Overman et al 1994
1261	5 - 79	5-10cm (584 tr), ... >60 (6)	original	central Amazonia (Manaus)	mixed	$FM = \exp[3.323+2.546\ln(D)]$	----	Carvalho et al. 1998
315	5-130	49% trees <10cm; 77% trees <20cm; 2 trees > 90cm; 1 tree > 120cm	original	Central Amazonia; Manaus, Brazil; terra firme	mixed	>5cm DBH: $\ln(FM)=-1.497+2.548\ln(D)$ $\ln(FM)=-2.694+2.038\ln(D)+0.902\ln(H)$ $FM= 0.077+0.492D^{2}H$ $FM= 0.001*D^{1.579}*H^{2.621}$	>20cm DBH: $\ln(FM)= -0.151+2.17\ln(D)$ $\ln(FM)= -2.088+1.837\ln(D)+0.939\ln(H)$ $FM= 0.393+0.473D^{2}H$ $FM= 0.0009*D^{1.585}*H^{2.651}$	Higuchi et al. 1998
516	5-138	9 trees ≥ 80cm 2 trees ≥ 100 cm	others & original	Manaus & Tomé Açu, Brazil; Colombia,	mixed	$FM = 0.0268(D^{1.529})*(H^{1.47})$ $FM=0.465*(D^{2.202})/(1-M)$		Araújo et al. 1999
132	1.2-28.6	13 tr ≥ 20cm; 4 tr ≥ 25cm	original	central Amazonia (secondary forest)	7 spp; excluding *Cecropia* & damaged trees	$\ln(AGB)=-1.9968+2.4128*\ln(D)$ $\ln(AGB)=-2.5202+2.14*\ln(D)+0.4644*\ln(H)$ $\ln(AGB)=-1.4278+2.3836*\ln(D)+0.7655*\ln(\rho)$ $\ln(AGB)=-1.8985+2.1569*\ln(D)+0.3888*\ln(H)+0.7218*\ln(\rho)$ $\ln(AGB)=-1.4702+2.4449*\ln(D)+0.9028*\ln(\rho_{mean})$		Nelson et al. 1999
303	5-110	20 tr ≥ 50cm; 6 tr ≥ 70cm; 1 tr > 100 cm	original	central Amazonia (Manaus)	mixed	$\text{dry mass} = 0.899(D^{2}H\rho)$		Nogueira et al. 2006
AG: 494 BG: 131	AG: 5-120 DBH, 5.6-41.4 m ht BG: 5-85 DBH, 5.9-34.5 m ht		Carvalho et al. 1995 +original (1980-2001)	primary forests, central Amazonia	mixed	Total C (AG + course roots) $\text{Total } C = 2.7179(D)^{1.8774}*0.584*0.485$ $\text{Total } C = 0.5521(D)^{1.6629}*H^{0.7224}*0.584*0.485$		da Silva 2007
300	5-124		others	southern Amazonia	mixed; 155 spp	$\ln(AGB)= -1.716+2.413*\ln(D)$		Nogueira et al. 2008 (FEM 256)
315 (≥ 5 cm)	5 - ca. 110	8 trees ≥ 60cm 2 trees ≥ 75 cm	others	central Amazonia	mixed	$\ln(AGB)= -0.37 + 0.33\ln(D) + 0.933(\ln[D])^{2} -0.122(\ln[D])^{3}$		Chambers et al. 2001
140	0.5-198.9		original	Colombia	mixed	$\ln(AGB) = -2.286 + 2.471*\ln(D)$		Sierra et al. 2007
631	10.0-198.9		original + others	Colombia	mixed	$\ln(AGB) = -1.218 + 2.404*\ln(D) + \ln(\rho)$		Alvarez et al. 2012

Sample size	Range DBH (cm)		Data source	Area	Species	Model		Author
AFRICA, ASIA, CENTRAL AMERICA								
14	0.001-57.5	fairly evenly distributed	original	Cameroon; plantations or previously-logged secondary forest	2^{o} regen. spp; 5 spp; 6 *Terminalia*	$AGB=-3.37+0.02483(D^2H)$		Deans et al. 1996
191	3-30.		Brown et al. 1989; Martinez-Yrizar et al. 1992	dry forests; India & Mexico		AGB=10^[-0.535+$\log_{10}$(Basal area)]		Brown 1997
122	6-200 cm DBH: 6-20 cm (29 tr), 20-40 (36), 40-60 (28), 60-80 (12), 80-100 (9), 100-200 (9)		original (comcl spp) + Samalca 2007	lowland, Indonesia	4 comcl spp (19-24 ea); 39 non- c trees	$\ln(AGB) = -1.201 + 2.196\ln(D)$ $\ln(AGB) = -1.935 + 1.981\ln(D) + 0.541\ln(H_{com})$ $\ln(AGB) = -0.744 + 2.188\ln(D) + 0.832\ln(\rho)$		Basuki et al. 2009
42	2.6-170		original	Ghana	16 spp	$AGB = 0.30(D)^{2.31}$		Henry et al., 2010
PAN-TROPICAL								
5300	5-39 (dry) 5-130 (moist) 4-110 (wet)		others	43 plots; dry, moist, & wet in Asia, Oceania, Brazil	mixed	moist: $AGB=38.4908-11.7883+1.1926(D^2)$ $AGB=\exp(-3.1141+0.9719\ln(D^2H))$ **$AGB=\exp(-2.4090+0.9522\ln(D^2H\rho))$**	wet: $TAGB=13.2579-4.8945(D)+0.6713(D^2)$ $TAGB=\exp\{-3.3012+0.9439\ln(D^2H)\}$ $H = \exp\{1.2017+0.5627\ln(D)\}$	Brown et al. 1989
169	4-112		Brown & Iverson 1992	wet	mixed	$AGB=21.297-6.953(D)+0.74(D^2)$		Brown 1997
170	5-148		Gillespie et al, pers. com; Brown et al. 1989	moist	mixed	$AGB=42.69-12.8(D)+1.242(D^2)$ **$AGB=\exp(-2.134+2.53\ln(D))$**		Brown 1997
2163	996 trees < 5cm, 378 tr ≥ 10; 135 ≥ 30, 32 trees ≥ 70cm		others	Asia, NE & C Amazonia, Colombia, Cent. Am.	mixed	$\ln(AGB)= -2.00 + 2.42\ln(D)$	----	Chave et al. 2001
2410 (≥ 5 cm)	5-156; 8 tr > 100	29 tr > 60; 8 tr > 100	others	27 sites: central America, Carribean, Amazon, Asia, Oceania	mixed; included Cecropia	Moist: $AGB=0.0509(\rho D^2H)$ $AGB=\rho*\exp[-1.499 + 2.1481\ln(D) + 0.207(\ln D)^2 - 0.0281(\ln D)^3]$	Wet: $AGB=0.0776*(\rho D^2H)^{0.94}$ $AGB=\rho*\exp[-1.239 + 1.98\ln(D) + 0.207(\ln D)^2 - 0.0281(\ln D)^3]$	Chave et al. 2005
443	1-148		71 original + 372 others	moist tropical forests	mixed	$\ln(AGB) = -2.1801 + 2.5624*\ln(D)$		Djomo et al., 2010
1816	0.12-180	719<10; 95>60; 44>80	others	Cent. & S.America, Africa, Asia, Australia	mixed	$\ln AGB=-2.9205+0.9894(\rho D^2H)$ $\ln AGB= -1.8222+2.3371(\ln(D)) + 0.1632(\ln(D))^2 - 0.0248(\ln(D))^3 + 0.9792(\ln(\rho))$		Feldpausch et al.2012
GLOBAL								
1211	0.3 - 80.4		30 datasets	Global (temperate & tropical)	angiosperm & conifers	$AGB = 0.1424(D)^{2.3670}$		Zianis 2008
THEORETICAL								
						$\ln[AGB]=-2.3+2.67\ln[D]$		West et al. 1997; Enquist

Table 1.1 continued

Study	Data used
Brown et al. 1989	Dry: Bandhu 1970; Mann & Saxena 1982; Vyas et al. 1972. Moist: Hoxumi et al. 1969; Jordan & Uhl; Russell 1983; Yamakura et al. 1986. Wet: Edwards & Grubb 1977; Ovington & Olson 1970
Brown 1997 (wet)	Gillespie, pers. comm; revised from Brown et al. 1989
Higuchi et al. 1998	Higuchi et al. 1994; Higuchi and Carvalho Jr 1994; Araujo 1995; Santos 1996
Araujo et al. 1999	Overman et al. 1994; Higuchi & Cavalho 1994; Araújo 1995
Chambers et al. 2001	Carvalho et al. 1995; Santos 1996; Higuchi et al. 1998
Chave et al. 2001	Lescure et al. 1983; Overman et al. 1994, Higuchi et al. 1998; Araujo et al. 1999; Ovington & Olson 1970; Edwards & Grubb 1977; Brown et al. 1997 (published and unpublished data sets)
Chave et al. 2005	Mackensen et al. 2000; Hozumi et al. 1969; Overman et al. 1994; Lescure et al. 1983; Bandhu 1973; Tanner 1980; Ruhiyat 1989; Yamakura et al. 1986; Rai & Proctor 1986; Hase & Folster 1982;
Nogueira et al. 2008	Feldpausch et al. 2005; Pereira et al. 2005; Nogueria et al. 2007
Djomo et al. 2008	original; Brown 1997; Araujo et al. 1999; Nelson et al. 1999; Ketterings et al. 2001
Alvarez et al. 2012	Saldarriaga et al. 1988; Overman et al. 1994; Brandeis et al. 2006; Sierra et al. 2007

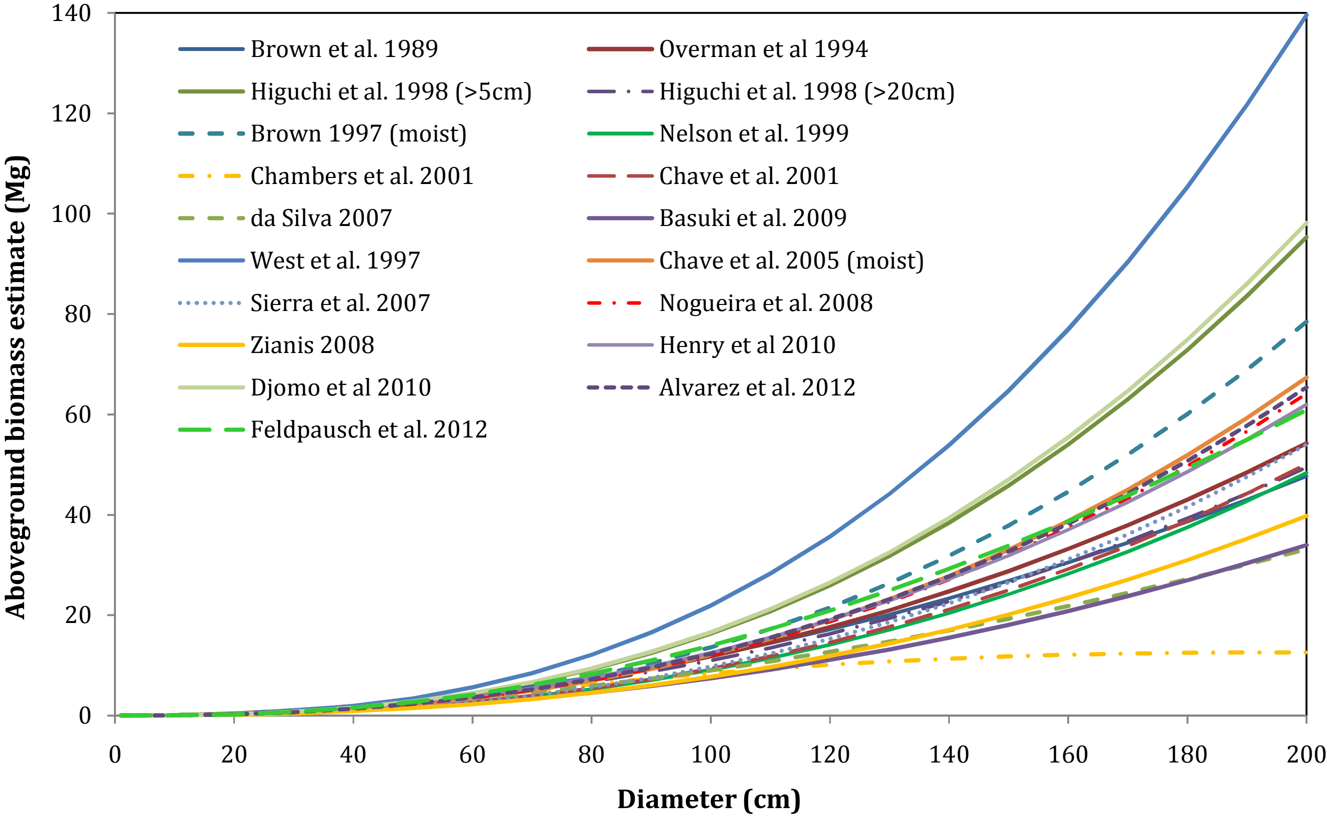

Figure 1.2. Biomass estimates from several published equations —using diameter only, or diameter and wood density— for theoretical trees with diameter ranging from 0 to 200 cm. Equations displayed are shown in blue in Table 1.1. Mean wood density values used as explanatory variables, are listed in Brown (1997).

1.4.2 Published equations for arborescent palms

Compared to the plethora of allometric equations published to estimate dicot tree biomass, there are very few models to estimate palm mass. The few existing palm models have been created for a single species and often do not cover a wide range of sizes. Most palm models appear in 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), and 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). There are still no broadly accepted or applicable equations to estimate their mass.

Furthermore, there has been no rigorous examination of the most appropriate form of palm equations. Most models are built with the simple form biomass = $a + bx$ (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 (section 1.2). The most common predictor variable is stem height (Frangi and Lugo 1985, Delaney et al. 1999, Brown et al. 2001, Thenkabail et al. 2004, Sierra et al. 2007), but some models have used total height (Frangi and Lugo 1985), diameter (Hughes 1997), or age (Kumar and Russell, unpublished, cited in Kumar 2011). In a comprehensive report, Brown (1997) suggested that palm biomass could be estimated using height and diameter 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. This approach mirrors that used for trees (section 1.2.2), but seems far more appropriate for palms. Non-linear relationships between biomass and the predictor variable(s), such as the power-law, have also not been tested extensively.

1.5 Problems with existing equations

1.5.1 Differences found when calculating tree biomass from different equations

Biomass estimates from the many existing allometric equations can have very different values from each other (Figure 1.2) and from directly-measured biomass values, thus illustrating the imperfection of existing equations. This error and variation between equations is especially evident for large trees. For example, the measured mass of a tree with 200 cm *D* was 35 Mg, but published equation estimated the mass of this tree from 20 to 75 Mg (Basuki et al. 2009).

There can also be systematic deviations among equations related to tree size. For example, Keeling et al. (2008) compared estimates from Chambers et al. (2001) and Chave et al. (2005) equations and found that one model estimated higher biomass for trees with $D < 60$ cm and the other equation estimated higher biomass for trees with $D > 60$ cm. For trees characteristic of secondary forests (excluding *Cecropia* spp.), Nelson et al. (1999) found that most equations (Saldarriaga et al. 1988, Uhl et al. 1988, Brown et al. 1989) overestimated biomass at the smallest trees ($D \geq 5$ cm) but underestimated biomass for trees between 10 and 25 cm *D*, though this relationship was affected by the variables included (Brown et al. 1989). For trees of southern Amazonia (Nogueira et al. 2008a), the Higuchi et al. (1998) and Chambers et al. (2001) equations both underestimated trees $D < 10$ and $D > 70$ cm and overestimated trees from 10–70 cm *D*, where as the da Silva (2007) equations vastly overestimated smaller trees and began to underestimate trees greater than *c.* 50 cm *D* (Figure 1.3).

Differences in predictions also occur at the stand-level or over a larger scale. Baker et al. (2004b) reported that the Chambers et al. (2001) estimates for stand AGB density were 50–100 Mg/ha greater than Chave et al. (2001) estimates across Amazonia. Similarly, the power-law equation proposed by Lescure et al. (1983) overestimated total stand biomass by 36 %, and the quadratic equation proposed by Brown (1997) underestimated total biomass by 23 %, compared to estimates using Chave et al.'s (2001) model. Applying biomass equations created from trees in central Amazonia consistently overestimated trees in the southern and southwestern parts of Amazonia; accounting for lighter wood density and shorter trees reduced stand biomass estimates by 45 to 76 Mg/ha (16 to 39 %; Nogueira et al. 2008b).

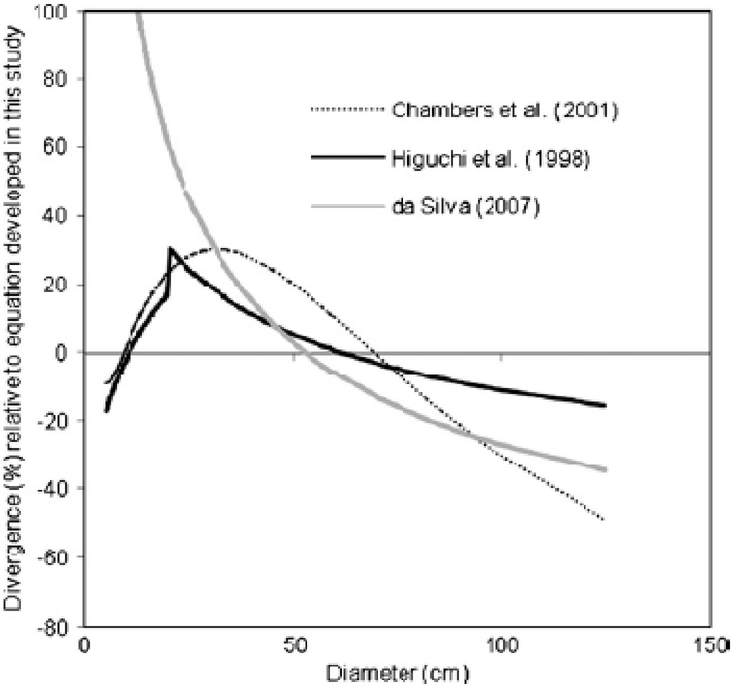

Figure 1.3. Relative difference in biomass estimations from three previously-published equations —the log-transformed linear equations by Higuchi et al. (1998) and da Silva (2007) and the cubic equation by Chambers et al. (2001)—compared to equations produced by Nogueira et al. (2008a). Figure from Nogueira et al. (2008a).

1.5.2 Errors associated with using dicot models to estimate palm biomass

As there are no broadly applicable or accepted allometric equations for palms, 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), but these estimates are likely to be inaccurate. Because there are no appropriate methods to estimate palm biomass, they have been called a 'missing term' in coarse woody productivity assessments (Malhi et al. 2009). Estimates may be especially poor when the equations include only D and ρ because dicots and monocots have very distinct growth patterns and internal properties. Palms grow in height but exhibit little or no corresponding increase in diameter (Rich et al. 1986, Tomlinson 2006). Palms also lack branches, which can contribute substantially to dicot biomass.

1.6 Sources of error in biomass estimates

1.6.1 Identified sources of error

Forest biomass estimates require several steps, each of which is subject to error. Four sources of error have been identified when estimating AGB across the landscape: (i) tree measurement, (ii) choice of an allometric equation, (iii) plot sampling , and (iv) representativeness of small plots across the entire landscape (Chave et al. 2004). As errors associated with the allometric model are the greatest (Chave et al. 2004), I will focus on the second source of error and look further into the development and application of the allometric models.

As shown above, comparisons between several published equations all yield immensely different biomass estimates, especially for large trees. Again, several possibilities may explain the differences in allometric equations, including that *H*–*D* relationships differ among sites, variation in the extent and frequency of structural damage, wood density, and methodological differences (Chambers et al. 2001). These explanations imply that published allometric equations are correct, and the differences between them are real. On the other hand, these equations may not be correct. Biomass predictions can have error because the biomass of an individual deviates from mean biomass of a tree with the same diameter, the allometric model chosen may not be the correct one, and the parameter estimates used in the allometric equation were derived from a small sample and may not be applicable to other sites (Ketterings et al. 2001). This section will elaborate upon both of these concepts: that actual variation in allometry exists between studies and individual trees and that real error exists in each of the published models.

1.6.2 Size distribution of the dataset

As previously illustrated, existing allometric equations show particularly great differences when estimating the biomass of large trees (Figure 1.2). One problem is the low number of directly-measured large trees included in each analysis (Table 1.1). Another problem is that deviation from model predictions seems to increase with increasing *D* regardless of the model used (Nelson et al. 1999). This would be consistent with the natural world and allometric theory: true variation exists between the relationship between biomass and *D*, and this variation increases with size (Brown et al. 1989).

With so few samples of large trees, the relationship between D and total biomass at the upper size limits can be described by very different mathematical equations depending on the biomasses of one or a few trees in the biomass dataset. For example, one particularly heavy tree ($D = 170$ cm) seemed to have altered the allometric equation created from 122 trees in lowland *Dipterocarp* forests in southeast Asia, causing biomass for nearly all trees < 150 cm D to be overestimated (Basuki et al. 2009). In central Amazonia, Chambers et al. (2001) developed an equation with a cubic fit, which was later found to severely underestimate the biomass of the large trees. These equations were created from 315 trees, including only 8 trees with $D \geq 60$ cm and only 2 trees with $D \geq 75$ cm. When the larger trees ($D \geq 60$ cm) were removed from the regression analysis, the resulting equation predicted even lower masses of the large trees than the equation developed from all trees (Chambers et al. 2001), indicating that large trees were needed in this dataset.

This size-distribution problem can also be viewed from the perspective of small trees. The sheer number of small trees may disproportionately influence regression equations and, consequently, reduce the influence of large trees. For example, biomass equations created from all trees > 5 cm D vastly overestimated biomass with increasing D, but when all trees < 20 cm D were removed, the resulting equations were consistent with other published equations (Table 1.1, Figure 1.2; Higuchi et al. 1998).

Alternatively, equations developed from a more even distribution of tree sizes are less influenced by the presence or absence of a single tree. For example, Overman et al. (1994) developed equations from 54 trees with a fairly even distribution among the D size classes , and when the 11 trees with $D \geq 45$ cm were removed, the regression coefficients were not significantly altered. However, this approach has been criticised because equations created from equal size classes may lead to biased estimates, because an even distribution does not represent actual forest structure (Nelson et al. 1999). Even when sample sizes are roughly representative of stand size distributions, equations can be highly influenced by the few large trees and cause overestimations of the smaller of trees, which represent the vast majority in terms of frequency (Aiba and Kohyama 1996). Keller et al. (2001) argued that despite the massive contributions of large trees to total stand biomass when present, they are rare enough not to cause substantially erroneous estimates of whole stands. Specifically, assuming that the biomass of very large trees ($D \geq$ 125 cm) was uncertain by a factor of 2, whole forest AGB estimates would vary by less than 3 %. However, allometric equations used to predict tree biomass of this size can vary by much more than a factor of two, and the effect on total stand biomass would depend on the stand structure.

It is broadly acknowledged that large trees contribute disproportionately to forest biomass density estimates and uncertainty (Brown et al. 1995, Clark and Clark 2000, Baker et al. 2004b, Chave et al. 2004). In one study, a single large tree (138 cm D) accounted for 18 % of the total fresh weight, and trees with $D \geq 60$ cm represented 4 % the number of tree stems but held 43 % of total tree biomass (Araújo et al. 1999). In Rondonia, Brazil, 15 trees with $D \geq 55$ cm represented 3 % tree stems and over 50 % of total stand biomass (Brown et al. 1995). In French Guiana, 12-13 trees with $D \geq 70$ cm represented 3 % tree stems and over one third of biomass in all trees with $D \geq 10$ cm (Chave et al. 2001).

1.6.3 Species and functional groups

As previously discussed, single species models more accurate predict biomass than mixed species models (Nelson et al. 1999, Kohyama et al. 2003), which strongly suggests that different species have different allometries. Differences in allometric relationships (i.e., mass vs. D) between species have been owed to differences in wood density and tree architecture (Basuki et al. 2009). Though it may be viable to create separate equations for a few important and abundance commercial species of trees and palms, it is generally considered impractical to develop single species models for tropical trees. One strategy is to remove obviously different species or groups. For example, Nelson et al. (1999) excluded *Cecropia* spp. from their analysis due to their highly irregular characteristics (very light wood and hollow branches). However, Chave et al. (2005) included this genus, while other studies do not specify. It is, therefore, important to be aware of the definition of 'mixed species' when applying the resulting equations to another population.

1.6.4 Irregularities and structural damage

A substantial amount of the variation in allometry, especially as tree size increases, may be attributable to irregularities and damage in the main stem and tree crown. The severity and frequency of irregularities (e.g., buttresses and fluted trunks), damage (e.g, branch breakage), and hollow trunks increase with tree size (Zimmerman et al. 1994, Fearnside 1997, Clark and Clark 2000, Chambers et al. 2001, Nogueira et al. 2006).

Irregularly shaped stems can cause very large errors in both biomass estimates from allometric equations and in the development of these equations, even when measured above buttresses (Clark and Clark 2000, Clark 2002, Nogueira et al. 2006). Some biomass studies deliberately omit damaged trees (Nelson et al. 1999) while many others may have inadvertently omitted them, which would cause an overestimate of biomass in natural forests. In central Amazonia, not accounting for irregularly shaped (i.e., non-circular) or hollow boles caused an 11 % overestimate of actual basal area, resulting in an 11 % overestimate of bole volume (Nogueira et al. 2006). Individually, stem cross-sectional area of irregularly shaped trees could overestimate diameter by up to 400 % (Nogueira et al. 2006).

Loss of biomass due to structural damage, branch shedding, and senescence should also be accounted for in biomass estimates. In central Amazonia, the majority of biomass lost was due to partial stem loss (57 %), followed by crown loss (37 %) and partial crown loss (6 %; Chambers et al., 2001). Crown damage should be accounted for if samples are selected randomly, but this may not always be the case.

1.6.5 Wood density, moisture content, and carbon fraction

Variation in wood density, moisture content, and carbon fraction can affect the quality of the raw or 'directly-measured' biomass data from which allometric equations are developed. For example, variation in ρ within an individual can be problematic when biomass measurements are not directly weighed but estimated from volume measurements. Especially in the case of large trees, mass is sometimes estimated from a series of diameter measurements along the main stem and a subsample of wood disks (e.g., Araújo et al. 1999, Henry et al. 2010).

Similarly, moisture contents vary between tree parts (Higuchi et al. 1998, da Silva 2007, Nogueira et al. 2008a). Thus, using a single wood sample at breast height to measure moisture content could overestimate moisture contents in some species and underestimate it in others (Nelson et al. 1999). This can introduce errors in the raw data (dry mass estimates). However, variation in moisture content is especially problematic when models are developed to estimate fresh mass and the end user is left to estimate dry mass from a mean value because moisture content varies more widely among species (Carvalho et al. 1998, Higuchi et al. 1998, da Silva 2007).

Carbon content is another important intrinsic property that affects how carbon stocks are estimated from biomass. Many studies assume that 50 % of the dry mass is carbon, as was recommended by the Intergovernmental Panel on Climate Change (IPCC 2003). However, actual carbon content may be slightly lower than this and vary among species and sites and within a tree. In primary forests of central Amazonia, carbon concentration was 48.5, 47.0, and 45.7 % in the trunk, coarse roots, and fine roots, respectively, for a weighted average of 48.5 % (da Silva 2007). In secondary forests, carbon contents were lower, 44.8 % in all three tree parts (da Silva 2007). Given that forests of western Amazonia tend to have lighter wood (Baker et al. 2004b), the carbon concentration in trees of western Amazonia may also be lower than that of primary forests of central Amazonia. On the contrary, carbon fraction may be underestimated by studies that do not include volatile carbon fraction, which raises the average carbon fraction by nearly 2.5 % (Martin and Thomas 2011).

1.6.6 Sampling methods

As the form and the coefficients of allometric models determined in regression analysis are determined by the trees used to develop the models, it is important that sampling methods are unbiased. However, this is often difficult to achieve given the practical, legal, and ethical constraints of harvesting and weighing trees. If trees with ‘perfect’ form are selected, the resulting biomass models will overestimate true biomass of a stand (Clark and Kellner 2012). Because biomass fieldwork is often carried out in associated with logging companies (e.g., Basuki et al. 2009, Henry et al. 2010), this bias towards well-formed individuals is sometimes inevitable.

Sampling approaches also vary between studies. Some studies harvest all trees in a randomly selected area (Carvalho et al. 1995, Araújo et al. 1999). Another strategy is to mimic the frequency of diameter sizes found in forest inventories and randomly select sample trees within predefined quotas for each given size classes

(Nogueira et al. 2006, Nogueira et al. 2007, Basuki et al. 2009). A different approach is to aim for a more even number of samples in each size class (Overman et al. 1994). A comprehensive FAO report recommended that each diameter size class should be represented, though no specifics were given (Brown 1997).

Largely because biomass data are so difficult to obtain, datasets are often recycled (e.g., Higuchi et al. 1998, Chambers et al. 2001, da Silva 2007) or combined for pantropical analyses (Chave et al. 2005, Feldpausch et al. 2012). Sampling methods are often poorly defined in the literature or not stated at all, so sampling biases are often unknown. Even when potential biases and sampling methods are stated in the original reports, all available data may be added to pantropical datasets, regardless of biases or methodological quality. Some datasets may also be missing key variables, such as height, wood density, or species identification. Furthermore, the influence of different investigators is unknown. Though no study has examined the effect of different researchers in biomass sampling, significant differences were found in height measurements taken by just two investigators using slightly different measurement methods in the same location over just two years (Bohlman and O'Brien 2006). Thus, the measurement errors and biases inherent to each investigator, and their associated instruments and methodologies, who have contributed to the pantropical biomass dataset over several decades and continents, are unknown but potentially significant.

1.6.7 Geographic representation of biomass data

Another source of error in tropical biomass estimates is the poor sampling across geographic and environmental space in the database used to create both regional and pantropical allometric equations (Houghton et al. 2009). The database used to develop the first widely-adopted pantropical biomass equations (Chave et al. 2005) comprises many trees from southeast Asia, central America, and eastern and central Amazonia, but none from Africa or southwestern Amazonia. In a recent compilation of pantropical biomass data (Feldpausch et al. 2012), new data have been added from Africa, southern Brazil, and Indonesia, but large portions of Africa and South America are still missing.

As discussed in previous sections, this is problematic because tree allometry varies geographically. Equations created using data from a specific geographic region or group of regions incorporate a particular relationship between whichever explanatory variables are included in the model and AGB. Thus, it may be inappropriate to use them elsewhere (Nelson et al. 1999, Clark and Clark 2000, Ketterings et al. 2001, Nogueira et al. 2008a).

1.6.8 Data analysis

Transforming data to the natural logarithm is widely used to satisfy the assumption of linear regression analysis but can introduce problems both in the regression analysis and when back-transforming to the normal scale. In addition to disproportionally few samples of large trees, logarithmic transformations further reduce the influence of large trees. Small trees can influence a regression slope just as much as large tree due to minimising error on a logarithmically transformed scale, rather than on the original scale (Nelson et al. 1999). Furthermore, estimations outside the range of observations used to create the model often yield serious errors (Nelson et al. 1999), and even small errors on a log scale translate to very large errors on the original scale.

Estimates must also be back-transformed to the original scale. Uncorrected log-transformations theoretically underestimate actual values because large, transformed numbers lose their relative influence (Beauchamp and Olson 1973), and back-transforming yields the median value of a prediction rather than the mean (Baskerville 1972). Back-transformed values are therefore multiplied by a correction factor (Baskerville 1972), but this may lead to overestimates (Chave et al. 2005).

The problems associated with log-transformations have spurred questions as to whether the traditional method of developing allometric equations (linear regression on data transformed to the natural logarithm) is legitimate, or whether building non-linear models developed from untransformed data is better. The most appropriate modelling approach appears to depend on the structure of the error term (Mascaro et al. 2011, Xiao et al. 2011). In the case of additive errors, variation is homogeneous across the spectrum of explanatory variables; but in the case of multiplicative errors, variation increases as the explanatory variable increases (Figure 1.4), which is typically the case for plant biomass data.

Two recent studies have conducted meta-analyses comparing log-transformed linear models, nonlinear models with additive error, and nonlinear models with multiplicative error. Because most nonlinear models assume additive error (i.e., nlm in R), these models violate allometric theory and perform worse than log-transformed models (Figure 1.4) (Figure 1.4; Mascaro et al. 2011, Xiao et al. 2011). Nonlinear models with multiplicative error may be marginally better in some cases, but log-transformed models are best in other cases (Mascaro et al. 2011, Xiao et al. 2011). Thus, despite their problems, it is concluded that log-transformed linear models are legitimate for allometric equations, because tree biomass data typically have multiplicative errors.

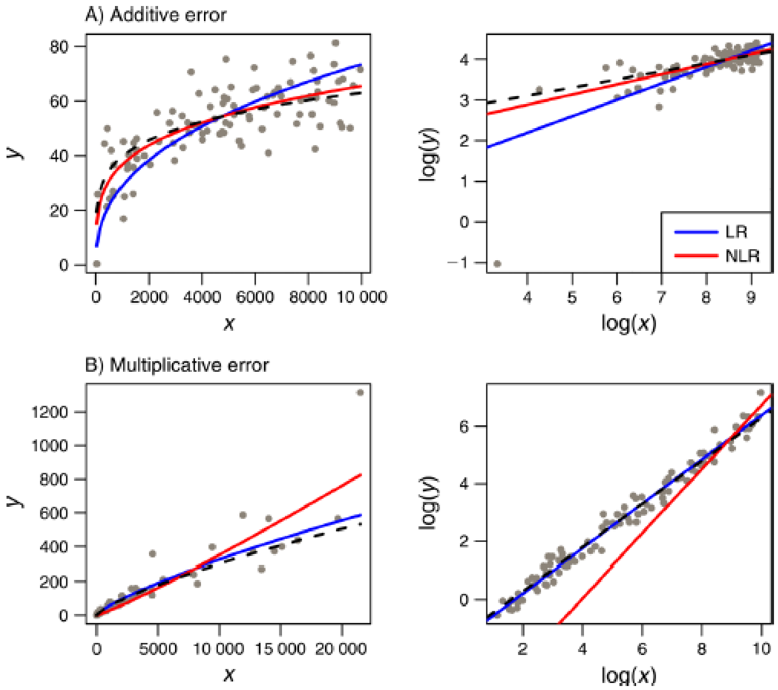

Figure 1.4. Figure from Xiao et al. (2011) showing data with additive (A) and multiplicative (B) error structures plotted on the original and logarithmic scales. The data have also been fit using both log-transformed linear (LR; blue) and nonlinear (NLR; red) regression. The log-transformed linear regression shows a better fit to the data with multiplicative error than nonlinear regression.

1.7 Belowground and stand-level biomass

1.7.1 Belowground biomass

Average root/shoot-ratios, or the relationship between aboveground and belowground biomass, in tropical forest trees has been estimated at 0.25, but this varies greatly between forest types: 0.12 for lowland rain forests to 0.60 for tropical forests on Spodosols (reported in Brown 1997). The IPCC default root/shoot-ratio is 0.24 in primary tropical moist forests and 0.42 in secondary tropical forests (Table 3A.1.8; IPCC 2003). In central Amazonia, this ratio was 0.37 (N. Higuchi 2000-2006, unpublished data reported in Phillips et al. 2008). In Cameroon, there was a nearly linear relationship between tree size (D^2H) and aboveground, belowground, and total biomass of directly-harvested trees, and root/shoot-ratios could be calculated by the following formula:

$$\frac{root}{shoot} = 0.223 + 0.199(D^2H)$$

($r^2 = 0.60$; $P < 0.05$) (Deans et al. 1996). However, this formula was constructed from only 14 trees from five species growing in moist tropical forests of Cameroon with a maximum tree diameter of 60 cm. Multiple equations were also developed to estimate root biomass from stand basal area in Colombia and Venezuela (Saldarriaga et al. 1988). A recent study used the following equation to estimate belowground biomass from AGB at the stand-level based on a compilation of reliable data (Saatchi et al. 2011):

$$BGB = 0.489 \times AGB^{0.89}.$$

The most reliable and appropriate model or ratio will need to be chosen to estimate belowground root biomass from the aboveground biomass estimates, but these models are still associated with a high level of uncertainty.

1.7.2 Other forest components

Typical forest inventories measure only trees, and sometimes palms, above a certain size limit (i.e., $D \geq 5$ or 10 cm). In addition to these trees, forest carbon is also held in other aboveground living vegetation, necromass, belowground biomass, and soil organic matter. Complete aboveground inventories may include small trees (< 5 or 10 cm D), palms, lianas, bamboo, herbaceous vegetation, epiphytes, coarse woody debris, and leaf litter. Necromass can include standing snag trees, coarse woody debris, fine woody debris, and litterfall. Belowground biomass includes both coarse and fine roots. Soil carbon can contribute substantially to total forest carbon stocks (Pan et al. 2011), but is not included in biomass estimates.

Additionally, carbon cycles through forests via volatile organic compounds, dissolved organic carbon deposition and leakage, and respiration (Malhi et al. 2009). All of these components are important for ecosystem functioning and even carbon cycling. Unfortunately, measuring each of these would be very labour intensive and expensive. Scaling-up factors are, therefore, sometimes useful to predict total forest carbon storage from an inventory of other components.

Scaling up from forest inventory data (e.g., trees with $D \geq 10$ cm) to stand-level biomass estimates can be accomplished by creating equations or ratios between large tree biomass and other components (Nascimento and Laurance 2002, Nogueira et al. 2008a). For example, an intensive study in Central Amazonia estimated that inventoried trees made up 82 % of total forest biomass and therefore used a 22 % ‘biomass correction factor’ to estimate total forest AGB from tree AGB.

However, scaling up from large tree biomass in this way assumes a positive relationship between all variables and inventoried tree biomass, which may not always be accurate. Some components may have a negative, constant, or non-linear relationship with tree AGB. For example, bamboo-dominated forests have lower biomass than forests without bamboo (Salimon et al. 2011), so a model adding bamboo biomass as a proportion of tree biomass across a wide range of forest types would be inaccurate. The same might be the case for a regenerating patch of forest, which has high biomass in small trees and little biomass in inventoried trees (i.e., $D \geq 10$ cm). Indeed, Salimon et al. (2011) found that tree AGB was not significantly correlated with any other forest biomass component or all other components combined, making it unclear how a constant correction factor will reliably predict total forest biomass. Thus, estimating the contribution of other forest components as a proportion of tree biomass may not be appropriate, and there is much room for improvement in estimating the contribution of other forest components, especially in the western Amazon.

1.8 Applications for forest management and policy

1.8.1 Forest management

Over 400 million ha of tropical moist forests are designated for production (Blaser et al. 2011), most of which is harvested for timber (Putz et al. 2008b). In Amazonia, the area of forests degraded by selective logging is near to or perhaps even greater than the area deforested each year (Asner et al. 2005). Thus, improvements in forest management and timber harvest practices could greatly reduce global carbon emissions from forest degradation (Putz et al. 2008b). One of the key additions to REDD+, over REDD, is the inclusion of sustainable forest management, which may allow projects to claim credits for reduced emissions from reduced impact over conventional logging practices (Sasaki et al. 2012).

Conventional logging practices can release up 100 Mg C per ha logged (Pinard and Putz 1996, Putz et al. 2008b). Reduced impact logging may reduce carbon emissions over conventional logging practices, but still damages surrounding forests (Pinard and Putz 1996, Feldpausch et al. 2005, Putz et al. 2008b). Carbon is released from the woody debris left from branches, buttresses, and stump of the harvested tree as well as many other trees damaged or killed during the harvest (tree fall gaps) and extraction from the forest (roads, log decks, skid trails) (Pinard and Putz 1996, Feldpausch et al. 2005, Sist and Ferreira 2007, Blanc et al. 2009).

Many of the ideas addressed in this thesis are relevant for quantifying the biomass removed during and remaining after timber harvests. For example, large trees will again be of great importance, as these are the trees removed in selective harvests. The focus on crown dimensions and mass will also be important, as crown size affects the amount of damage caused during felling operations, necromass left in branches, and the proportion of carbon damaged vs. exported as a result of the harvest (Feldpausch et al. 2005). Furthermore, a better understanding of forest dynamics may help to predict forest recovery after logging operations or respond to management interventions.

1.8.2 Remote sensing

Remote sensing may help gain large-scale forest AGB estimates, especially of inaccessible areas like the Amazon River basin. Different technologies can be used to detect changes in land use (Potapov et al. 2008, Perz et al. 2013), the intensity and extent of selective logging (Asner et al. 2005, Chambers et al. 2007), and the effects of changes in species composition and environmental gradients on carbon storage over a large scale (Chambers et al. 2007, Asner et al. 2009a, Asner et al. 2009b, Huang et al. 2009). Several techniques exist, each with its own advantages and disadvantages, such as IKONOS, Landsat, Light Detection and Ranging (LiDAR), Moderate Resolution Imaging Spectroradiometer (MODIS), and QuickBird.

To estimate forest biomass, remote sensing data should be coupled or calibrated with field studies (Chambers et al. 2007). LiDAR, specifically, creates vertical profiles of laser returns, which must be calibrated with field biomass estimates. This has been well-calibrated for Hawaiian rain forests (Asner et al. 2009a, Asner et al. 2009b) and received recent attention in the Amazon (Asner et al. 2010, Saatchi et al. 2011). The largest source of uncertainty has been identified as the poor correlation between field and LiDAR biomass estimates (Asner et al. 2009a). It is also vitally important that ground-based biomass estimates, upon which remote sensing metrics are calibrated, are also accurate, but the uncertainty in these ground-based forest biomass density estimates is sometimes ignored (e.g., Saatchi et al. 2011). Collaborations between forest inventories, direct biomass measurements, and remote sensing should be beneficial for each. As remotely sensed images primarily assess canopy characteristics of the forest, calibration with forest biomass could be improved through a better understanding of the role of forest structure and dominant trees in determining forest stand biomass.

1.9 Site selection and project rationale

1.9.1 Biomass estimates in the southwestern Amazon

As Amazonia accounts for over half of the world's tropical moist forests, it is a major focus of research, conservation, and management efforts. While allometric equations to estimate biomass and dry mass have been developed for many parts of Amazonia —central (Higuchi and Carvalho 1994, Chambers et al. 2001, Nogueira et al. 2008a), eastern (Araújo et al. 1999), northwestern (Overman et al. 1994, Alvarez et al. 2012), and southern (Nogueira et al. 2008a)— no such data exist for the western Amazonian forests. Thus, this large region is also missing from the pantropical database used to develop pantropical models (Chave et al. 2005, Feldpausch et al. 2012).

Applying previously published allometric equations to trees in western Amazonia may lead to severe inaccuracies in biomass estimates, as can 'correcting' for allometric differences between this area and areas for which biomass equations are developed. The western and southwestern Amazonian forests have been the subject of recent controversy in this regard. As discussed in earlier studies, several aspects of tree allometry vary across the Amazon. Thus, two recent studies have begun to address this variation by accounting for tree height in equations and biomass estimates (Nogueira et al. 2008b, Feldpausch et al. 2012). Both studies first created new allometric equations from biomass data collected from other areas. Then, they developed regional models to estimate height from diameter. Finally, they used these estimated heights, in addition to measured D and ρ, to estimate tree biomass in another region or at broader scales.

With these methods, new forest AGB estimates were substantially lower than previously estimated, and the southwestern Amazon was especially affected. AGB estimates in southwestern Amazonia were reduced by 6 to 11 % (Nogueira et al. 2008b) and 16 % in the western Amazon (Feldpausch et al. 2012) compared to estimates made without explicitly accounting for tree height. Including adjustments for lower wood density further reduced estimates, calling for 22–39 % downgrades in the southwestern Amazon (Nogueira et al. 2007, Nogueira et al. 2008b). However, these models were based on assumptions about allometric relationships that may not be accurate. Namely, they do not account for regional variation in crown mass. The first study assumed that the proportion tree biomass in the crown did not change with tree height (Nogueira et al. 2008b), and the second study did not make any explicit assumptions about crown mass but assumed that difference between estimates from models with and without height was due to overestimates made by models not including height. The results of these assumptions have large implications, but tree-level estimates were not compared to directly measured biomass data in the southwestern Amazon.

The need to test both pre-existing equations and corrections to them on directly-measured data is exemplified in the Nogueira papers themselves. Nogueira et al (2007, 2008b) compared biomass estimates calculated from previously published equations from other parts of the Amazon (Overman et al. 1994, Higuchi et al. 1998, Araújo et al. 1999, Chambers et al. 2001) to directly-measured biomass data collected from the previously unrepresented southern Brazilian Amazon and found that these equations produced poor estimates of carbon stocks. More importantly, however, it was also determined that corrections (for differences in form, crown mass, height, and wood density) to existing models did not accurately estimate biomass for trees in southern Amazonia, and it was necessary to create new allometric equations (Nogueira et al. 2008a). Thus, directly measured biomass data from the southwestern Amazon would clarify the true biomass of trees in this region.

1.9.2 Political and ecological significance

The southwestern Amazon also has large ecological and political importance. This region is both biologically rich (Myers et al. 2000) and contains large expanses of intact forest cover, making it an important area for conservation (Brooks et al. 2006). Conversely, it is also an area of rapid development and resource extraction, especially in the MAP region (Madre de Dios, Peru – Acre, Brazil – Pando, Bolivia). With the recent completion of the Interoceanic highway, which runs from ports on the Atlantic coast through Brazil and Peru to the Pacific coast, pressures on forests are expected to accelerate (Almeyda Zambrano et al. 2010, Asner et al. 2010, Southworth et al. 2011, Perz et al. 2013). Forests are cleared for agriculture, cattle ranching, gold mining, infrastructure building, and urbanisation (Almeyda Zambrano et al. 2010, Asner et al. 2010, Southworth et al. 2011), and forests are primarily degraded via selective logging (Asner et al. 2010).

In response to imminent threats of deforestation and forest degradation, the MAP region is also home to many upcoming projects under the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation (REDD/REDD+) and other carbon based projects (Asner et al. 2010, Rendón Thompson et al. 2013). This region also hosts a number of protected areas, Forest Stewardship Council (FSC) certified forestry concessions, and Brazil nut concessions, which may play an important role in conservation, sustainable management, and reducing carbon emissions. Improving biomass estimates in this area will reduce uncertainty and should, therefore, improve confidence and credibility of these efforts.

1.10 Research aims and objectives

Thesis aims: This thesis will focus on accounting for allometric variation not currently considered in tropical biomass models and test the relevance of new estimates in a previously unrepresented region via (1) testing the importance of including of crown parameters to improve tree biomass estimates, (2) developing new biomass models for trees and palms in this region, and (3) investigating the effect of new models on forest carbon stock estimates in the southwestern Amazon.

Thesis objectives:

Objective 1: Test the importance of including of crown parameters to improve tree biomass estimates

1.1 Collect the first directly-measured tree biomass dataset in this region, across the full size-class range
1.2 Test whether accounting for crown parameters can improve biomass estimates
1.3 Examine how well published models estimate biomass of trees in a previously unrepresented area
1.4 Develop allometric equations using diameter, height, wood density, crown radius, and variables for architectural type

Objective 2: Develop appropriate biomass models for arborescent palms in the western Amazon

2.1 Collect and compile directly-measured biomass from the most common arborescent palm species in Amazonia
2.2 Create species- and family-level allometric equations to predict palm biomass using a variety of explanatory variables
2.3 Explore the implications of estimating palm biomass with new palm models, as opposed to than models developed for dicotyledonous trees

Objective 3: Test the effect of new tree and palm models on a large scale

3.1 Estimate AGB and carbon density in plots in southwestern Amazonia
3.2 Estimate total biomass and carbon stocks across the southwestern Amazon ecoregion
3.3 Estimate landscape-level uncertainty associated with these estimates
3.4 Compare estimates to those produced using the most recent pantropical biomass models

CHAPTER 2 The importance of crown dimensions to improve tropical tree biomass estimates

Abstract

Tropical forests play a vital role in the global carbon cycle, but the amount of carbon they contain and its spatial distribution remain uncertain. Recent studies suggest that once tree height is accounted for in biomass calculations, in addition to diameter and wood density, carbon stock estimates are reduced in many areas. However, it is possible that larger crown sizes might offset the reduction in biomass estimates in some forests where tree heights are lower because even comparatively short trees develop large, well-lit crowns in or above the forest canopy. While current allometric models and theory focus on diameter, wood density, and height, the influence of crown size and structure has not been well studied.

To test the extent to which accounting for crown parameters can improve biomass estimates, we harvested and weighed 51 trees (11–169 cm diameter) in southwestern Amazonia where no direct biomass measurements have been made. The trees in our study had nearly half of total aboveground biomass in the branches (44 ± 2 %), demonstrating the importance of accounting for tree crowns. Consistent with our predictions, key pantropical equations that include height, but do not account for crown dimensions, underestimated the sum total biomass of all 51 trees by 11 to 14 %, primarily due to severe underestimates of many of the largest trees.

In our models, including crown radius greatly improves performance and reduces error, especially for the largest trees. In addition, over the full dataset, crown radius marginally explained more variation in aboveground biomass (10.5 %) than height (6.0 %). Crown form is also important: trees with a monopodial architectural type are estimated to have 21–44 % less mass than trees with other growth patterns. Our analysis suggests that accounting for crown allometry would substantially improve the accuracy of tropical estimates of tree biomass and its distribution in primary and degraded forests.

2.1 Introduction

Accurately quantifying the aboveground carbon stocks of tropical forests is essential to understand the role of these ecosystems in the global carbon cycle and to successfully implement payments for ecosystem services, such as those proposed in the United Nations Collaborative Programme on Reducing Emissions from Deforestation or Degradation (REDD/REDD+) (Ebeling and Yasue 2008). Tropical forests store large, but still remarkably uncertain, quantities of carbon (C) in living biomass, with recent estimates ranging from 175 to 340 Pg C (Houghton et al. 2009, FAO 2010, Pan et al. 2011, Saatchi et al. 2011, Baccini et al. 2012, Feldpausch et al. 2012). Furthermore, uncertainty may increase at smaller scales (Saatchi et al. 2011), which are often the focus of carbon-based projects and where degradation caused by the removal of some of the largest trees is particularly important (Asner et al. 2005). Due to these large uncertainties in tree and forest C estimates, it is unclear exactly how much tropical deforestation, degradation, and sequestration affect global carbon cycling, how forest conservation may slow the rate of climate change, and how much each hectare is valued in the carbon market.

The choice of allometric model used to calculate aboveground biomass (AGB) from forest inventory data is one of the key sources of uncertainty (Chave et al. 2004). Though there are a multitude of published equations, estimates can vary greatly, especially as tree size increases (Baker et al. 2004b, Chave et al. 2004). One reason for this is that most models have been developed with very few or even no data from large trees. With few samples in the upper size classes, the relationship between diameter (*D*) and total AGB can be described by very different mathematical shapes based upon on a single or very few individuals (Houghton et al. 2001, Basuki et al. 2009). These different shapes may be related to variation in height-diameter (*H*-*D*) ratios (Aiba and Kohyama 1996, Thomas 1996), the proportion of AGB in the tree crown (Araújo et al. 1999), or structural damage (Chambers et al. 2001), which may all vary systematically with tree size, region, or phylogeny or less predictably among individuals according to local conditions. Overall, these different shapes lead to substantial variation in AGB estimates.

Another key issue causing uncertainty in tropical biomass estimates is the poor sampling across geographic and environmental space in the database used to create both regional and pantropical allometric equations (Houghton et al. 2009).

For example, one widely-used pantropical database (Chave et al. 2005) comprises many trees from southeast Asia, central America, and eastern and central Amazonia, but none from Africa nor the southwestern third of Amazonia. Together, these lacunae represent nearly half of the tropical forest biome. A new pantropical biomass dataset (Feldpausch et al. 2012) has added some data from Africa, southern Brazil, and Indonesia, but still omits much of Africa and South America. This is problematic because a number of important factors —such as species composition and wood density (ρ) (Baker et al. 2004b), stem turnover (Quesada et al. 2012), forest structure (Banin et al. 2012), maximum height (Banin et al. 2012), H–D relationships (Nogueira et al. 2008b, Feldpausch et al. 2011, Alvarez et al. 2012, Banin et al. 2012), and crown size (Barbier et al. 2010)— vary across the tropics, implying that allometric relationships between measurable variables and total AGB of individual trees may also differ by region. For example, trees in southeast Asia are much taller than trees of the same D in South America, and trees in northeastern Amazonia are taller than those in northwestern and southern Amazon forests (Feldpausch et al. 2011). However, crown size across Amazonia shows a different pattern: satellite imagery suggests that crown size is larger in southern compared to northern moist Amazonian forests (Barbier et al. 2010). When equations are created using data from a specific geographic region or group of regions, they incorporate a particular relationship between whichever explanatory variables are included in the model and AGB. As a result, applying these equations to predict the biomass of trees in other regions may be inappropriate (Nelson et al. 1999, Clark and Clark 2000, Ketterings et al. 2001, Nogueira et al. 2008a).

Thus, a key requirement for developing more accurate allometric equations is to incorporate all of the appropriate structural variables that affect AGB, including those that vary geographically, such as ρ, H, and crown width. Two recent studies have begun to address this by accounting for tree height variation across Amazonia (Nogueira et al. 2008b) and the tropics (Feldpausch et al. 2012). Both studies first created new allometric equations from directly measured biomass data. Then, they developed regional H-D relationships from several areas across Amazonia or the tropics and used these estimated heights, in addition to measured D and ρ, to estimate tree biomass at broader scales. The resulting estimates of AGB density were substantially lower in many forest types than had previously been estimated.

For example, these studies calculated that using estimated heights resulted in a 6–11 % reduction forest AGB estimates in southwestern Amazonia (Nogueira et al. 2008b), a 16 % reduction in the western Amazon (Feldpausch et al. 2012), and a 14 % reduction across Amazonia (Feldpausch et al. 2012) compared to estimates made without explicitly accounting for H. However, the tree-level estimates were not compared to directly measured biomass data in most of the highly affected areas and do not account for variation in crown mass, which may contribute substantially to tree AGB.

The role of tree crowns has also been largely overlooked in theoretical biomass work. Allometric scaling theory was initially based on the relationship between AGB and D alone. For example, in the "WBE" theoretical model (West et al. 1997), tree mass = aD^b, where b is a universal scaling exponent with a value of 8/3 based on an idealised vascular architecture (West et al. 1999). Later, a was proposed to be related to ρ (Enquist et al. 1999, Pilli et al. 2006), and the relationship between AGB and D was suggested to be dependent on H–D relationships (Ketterings et al. 2001, Zianis 2008). However, crown characteristics have only recently begun to be incorporated into this framework (Mäkelä and Valentine 2006, Lines et al. 2012), despite early findings that the proportion of crown mass affects AGB worldwide even after considering D and H (Cannell 1984). Variation in crown mass has yet to be tested in empirical tropical studies or applied to practical models to estimate biomass. In a benchmark biomass study (Chave et al. 2005), allometric models including H were based on the theory of tree shape being intermediate between a cylinder and cone, where the mass can be predicted by multiplying tree basal area, ρ, H, and a form factor based on stem taper. Again, these models do not account for any variation in the contribution of crown mass, though the size and quantity of branches should influence tree mass beyond that explained by D and H. Furthermore, the contribution of crown mass may change as the tree develops and in relation to the surrounding vegetation. For example, when trees emerge from the canopy, vertical height growth slows while horizontal branch growth increases (Sterck and Bongers 2001), but generic allometric models may struggle to capture this behaviour because canopy height and light availability varies among different forest types. It follows that we expect that trees growing in lower canopy forests to have proportionally greater crown mass than trees of the same D in taller forests. Accordingly, we might expect that the lack of consideration of crown mass variation and large spatial gaps in directly-measured biomass data may together contribute considerable uncertainty to AGB estimates across unsampled areas and forest types.

Incorporating both crown size and tree height, particularly of large trees, may improve estimates from remote sensing data for both standing carbon stocks and carbon stock changes due to deforestation, selective logging, and other forest degradation. This may be especially applicable to methods based on small footprint light detection and ranging (LiDAR). LiDAR is an emerging technology with potential to achieve relatively low-cost estimates of tropical forest carbon stocks (Lefsky et al. 2002, Asner et al. 2009a, Asner et al. 2010), which could be used to support emerging REDD/REDD+ projects (Asner 2011, Saatchi et al. 2011). Most research has focused on forest canopy height to estimate AGB (Drake et al. 2003, Asner 2009, Asner et al. 2010), but small footprint LiDAR data can also detect both crown area and height of individual trees (Morsdorf et al. 2004, Bortolot and Wynne 2005, Kato et al. 2009, Thomas et al. 2013). Other techniques have also shown promise at detecting individual (IKONOS; Clark et al. 2004) or mean tree crown size (Google Earth®; Barbier et al. 2010) over larger areas. Thus, estimating AGB of emergent trees directly from these two parameters, crown area and H, may avoid error associated with first estimating D from H or crown diameter (e.g., Zhou et al. 2010).

To test the possible importance of crown size and architecture on AGB estimates, we harvested and weighed trees in a previously unsampled region: southwestern Amazonia, which spans nearly 75 million ha ("Southwest Amazon Moist Forests" terrestrial ecoregion; Olson et al. 2001). Specifically, we worked in Madre de Dios, Peru, which is currently experiencing rapid immigration and development, largely due to the completion of the Interoceanic highway (Oliveira et al. 2007, Asner et al. 2010), and is the site of many upcoming REDD/REDD+ projects (Rendón Thompson et al. 2013). We hypothesise that although trees are relatively short in southwestern Amazonia (Nogueira et al. 2008b, Feldpausch et al. 2011), larger crowns (Barbier et al. 2010) will at least partially compensate for their lower stature, and accounting for tree height but ignoring crown dimensions will systematically underestimate AGB. Specifically, we (i) test the importance and influence of crown dimensions and architecture on AGB, (ii) examine the suitability of applying published allometric equations, using different explanatory variables, to estimate AGB of trees in a previously unrepresented region, and (iii) create the first allometric equations for this area, with a focus on models that account for crown size and which are of practical application for estimating AGB from both ground and remotely sensed data.

2.2 Materials and methods

2.2.1 Study site

This study was carried out in the Maderacre forestry concession near Iñapari, Madre de Dios, Peru, which lies in southwestern Amazonia (Figure 1). The forest is broadly classified as lowland moist forest (Achard et al. 2002) or *terra firme,* moist, semi-evergreen rain forest (Whitmore 1998). In our study area, bamboo is sometimes present but does not dominate the understory, and the vertical canopy structure is uneven but closed. The forest within the concession has never been intensively harvested. Mean annual temperature is 24.5 ^{0}C, and mean annual precipitation is 1811 mm, distributed seasonally (Hijmans et al. 2005). The dry season usually extends from May to September (3-4 months), and mean precipitation is 113 mm during the driest quarter and 724 mm in the wettest quarter (Hijmans et al. 2005). Land type is classified by FAO (1998) as medium gradient hills with elevation range from approximately 250 to 375 m above sea level.

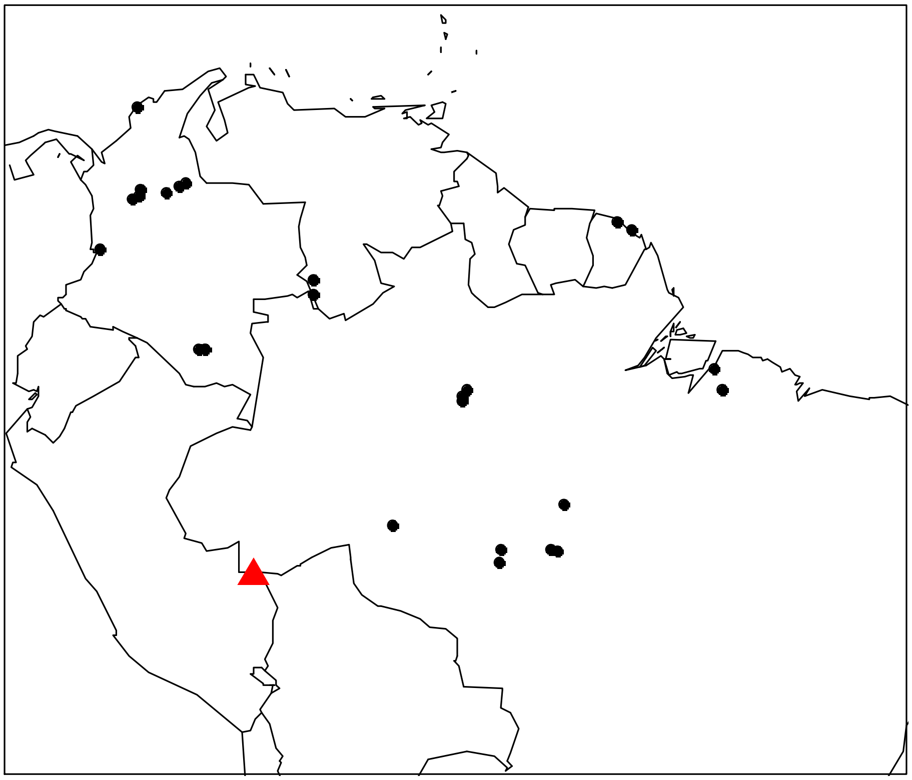

Figure 2.1. Location of all biomass datasets collected within tropical South America including our site (red triangle). Coordinates from published data (black circles) were obtained directly from tables in Chave et al. (2005) and Alvarez et al. (2012) and ascertained from Nogueira et al. (2008a) and associated publications (Nogueira et al. 2006, Nogueira et al. 2007).

2.2.2 Sample selection

An exploratory survey of the concession was used as a guide to sample both the species and functional composition of the forest with equal numbers of individuals from different diameter classes. In 2005, the company established 66 transects on an unstratified grid (2 × 2.5 km) throughout the entire 50,000-ha concession: trees with $D \geq 30$ cm were measured in 500 × 10 m transects, and trees with $D \geq 10$ cm were measured in the central 100 × 10 m section of the transect. All individuals fitting the diameter size criteria above were included in this survey, regardless of commercial value, trunk or crown form, hollowness, structural damage, or any other irregularities. For the current study, scientific names were matched with the common names reported in the exploratory survey using available resources (Maderacre 2009) and local expertise. Wood density values were then assigned to each species or genus according to the Global Wood Density Database (Chave et al. 2009, Zanne et al. 2009). Next, we used these data to calculate the most common species and average ρ, excluding palms, in each 20-cm diameter size class ($10 \leq D < 30$, $30 \leq D < 50$… $D \geq 110$ cm).

We selected an equal number of trees in each 20-cm D size class for the destructive biomass sampling within the area of annual harvest, but independently of the company surveys and commercial operations. Within each size class, we identified species according to their natural abundance and ρ so that mean ρ of the sample was approximately equal to that of the forest. We avoided bias towards selecting trees with 'perfect' form by including the first individual that met our criteria (D and species). In total, 51 trees were harvested and weighed during 2010 and 2011. Of the trees harvested, four had some amount of crown damage and five had rotten or hollow sections in the stem or branches. Timber quality was not specifically assessed, but seven trees had branch scars on the bole, bent stems, very fluted trunks, or substantial portions of rotten wood or hollowness in the bole.

2.2.3 Pre-harvest measurements

D was measured at 1.3 m above the ground or directly above buttresses. Point of measurement (POM) was marked on each tree and recorded. Crown radius was measured as the distance from the midpoint of the trunk to the projected edge of the crown in four cardinal directions (Kitajima et al. 2005, Poorter and Bongers 2006). Canopy quality was recorded as good (symmetrical and vigorous), average (some defects with respect to the symmetry and density of the foliage), or poor (not vigorous, substantial portions of the limbs without foliage or branching, markedly asymmetrical) (Jiménez-Rojas et al. 2002). Crown illumination index was assessed on a scale from 1 to 5 (Dawkins and Field 1978, Keeling and Phillips 2007). Crown architecture (branching patterns) was classified as monopodial (i.e., one main stem), dividing, or changing in orientation, based on Hallé et al. (1978). Prominent branch orientation was recorded as vertical, horizontal, or a combination of these. Notes were taken of any damage (e.g., hollow stem, broken branches) or irregularity (e.g., fluted or swollen stem, buttresses).

2.2.4 Biomass data collection

Selected trees were felled, re-measured, and weighed in the field. D was measured at the same *POM* as pre-felling. Total height (*H*) and height of the first major branch (> 5 cm diameter at base or first branch of any size on small trees without branches > 5 cm diameter; H_{FMB}) were measured with metric tape on fallen trees. For all measurements, the base (i.e., 0 m) was considered to be mineral soil level on the high side of the trunk. Crown was defined as everything above the first major branch.

Biomass data collection began immediately after trees were cut. The tree was separated into small branches (< 10 cm diameter) with attached leaves and fruit, large branches (≥ 10 cm diameter), bole, and stump. The stump was cut at ground level. Fresh mass of branches, leaves, non-commercial bole, and the stump were measured in the field with a 250 kg capacity scale with 0.1 kg precision. Fresh mass of commercial boles and some of the very large branches were measured with a 6000 kg capacity scale (5 kg precision) attached to a fork lift. The mass of 10 stems was estimated from volume measurements based on length and diameter measurements every 1 m on each log section. Buttresses and any irregular parts were cut and weighed directly so that volume was estimated from only cylindrical sections.

To estimate moisture content and ρ, wood samples of each tree part (top and bottom of commercial bole, large branches, and small branches) were taken from freshly-cut wood. When the stem was cut into more than two sections, a sample was collected from the bottom or top of every section (with the top of one section corresponding to the bottom of the next). Wood samples were cut as disks of constant thickness in small branches and as wedges of constant thickness, extending from the centre to the bark, in large branches and stems (minimum 100 g). Fresh mass was measured immediately with a hanging scale with 1 g precision.

All individuals were identified to species with botanical vouchers collected from each tree, except when no leaves were present at the time of felling. Botanical samples were dried, stored, and identified at the Universidad Nacional de San Antonio Abad del Cusco (CUZ) in 2010 and Universidad Nacional Amazónica de Madre de Dios (GHMDD) in 2011.

2.2.5 Laboratory work and data preparation

Wood samples were transported to the laboratory for further analysis. Wood density was only assessed for stem wood, and green volume was measured by water displacement on a digital scale with 5 g precision. For moisture content and ρ, all wood samples were dried at 101 °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. Wood density was calculated as the ratio of dry mass to fresh volume (dry mass / fresh volume)c. Moisture content was calculated as the difference between fresh and dry mass per unit fresh mass ([fresh mass – dry mass] / fresh mass). Dry mass for each tree part was calculated as fresh mass times the proportion of wood dry mass (fresh mass × [1 – moisture content]) or as volume multiplied by ρ. Dry mass of the each stem section was calculated as the mean of the two applicable moisture content or ρ values (e.g., top and bottom of the section).

Crown depth was calculated as the distance from the first major branch to the top of the canopy ($CDepth = H - H_{FMB}$). Average crown radius (CR) was the mean of the four crown radius measurements. Crown ellipse area (CEA) was calculated as $\pi \times (CR_{NS}) \times (CR_{EW})$, where CR_{NS} and CR_{EW} are the average crown radii for the N-S and E-W directions respectively. 'Crown mass' was the sum of large branches, small branches, and attached leaves and fruit.

2.2.6 Evaluating existing models

We estimated AGB of our trees using 38 published equations. Models were obtained from four pantropical studies (Brown et al. 1989, Chave et al. 2005, Djomo et al. 2010, Feldpausch et al. 2012), four original Amazonian studies —central Amazonia (Higuchi et al. 1998, Chambers et al. 2001), southern Brazil (Nogueira et al. 2008a), and Colombia (Alvarez et al. 2012)—, two adjusted Amazonian equations (Baker et al. 2004b, Nogueira et al. 2008b), a global model (Zianis 2008), and a theoretical model (West et al. 1997). When applicable, we examined the equations for both 'moist' and 'all' forest types. Two models are reported by Chambers et al. (2001): one in which all trees with $D \geq 5$ cm (Cham≥5) were included and another restricted to trees $D > 10$ cm (Cham>10).

For the Higuchi estimates, dry mass was calculated by multiplying fresh mass estimates (as given by the published model) by 0.6028 (1 – mean moisture content). AGB corrections for H (Nogueira et al. 2008b) were made by multiplying the Higuchi estimates by $[0.66(H_{SW}/H_C) + 0.34]$, where H_{SW} and H_C were estimated heights for trees in the southwestern dense forests and central Amazonian forests, respectively, using the ln-transformed H–D equations. A correction factor (CF = $\exp[\mathrm{RSE}^2/2]$) was applied to back-transformed predicted values to remove the bias from predictions made on log-transformed data (Baskerville 1972, Chave et al. 2005), except for the Higuchi model because there was no mention of whether a correction factor was included in the methods used to develop the modified models described by Nogueira et al. (2008b).

We compared values predicted by each model to observed values measured in this study. Errors (Mg) were calculated on the original scale as $\mathrm{AGB}_{\mathrm{predicted}} - \mathrm{AGB}_{\mathrm{observed}}$, and relative error (%) was calculated as $(\mathrm{AGB}_{\mathrm{predicted}} - \mathrm{AGB}_{\mathrm{observed}})/\ \mathrm{AGB}_{\mathrm{observed}} \times 100\ \%$, so that negative values indicate underestimates and positive values indicate overestimates. Overall predictability was assessed by standard deviation of the relative errors ($\mathrm{SD}_{\mathrm{RE}}$) (Chave et al. 2005). We also compared the equations based on true error criteria: mean error ($\mathrm{mean}_{\mathrm{E}}$), standard deviation of the errors (SD_{E}), sum of errors, and R^2 (1 – SSE/SST). Results are also discussed as mean percent error ($\mathrm{mean}_{\%\mathrm{E}} = \mathrm{mean}_{\mathrm{E}}$ / mean AGB × 100 %).

2.2.7 Testing the importance of crown dimensions and architecture in new allometric models

Linear models were used to test the importance of different structural variables (D, POM, H, H_{FMB}, ρ, $CDepth$, and CR) for predicting total tree AGB. For all variables except CR and CEA, post-harvest measurements were used for the data analysis. CR and CEA were too highly correlated with one another ($r > 0.95$) to include in the same model, but no other explanatory variables presented problems with multicollinearity. Therefore, we used the crown variable that would be directly assessed: CEA for remote sensing models and CR for all others.

To determine the most robust models using different explanatory variables and to test the significance of crown dimensions and other structural parameters, we built new models via three different methods: (i) based on the six model forms developed by Chave et al. (2005) using D, ρ, and H, (ii) adding continuous and categorical variables to these six base models to account for crown dimensions, architecture, quality, and illumination index; structural damage; and stem irregularities, and (iii) starting with all seven continuous variables (above) and using backwards elimination until a minimum adequate model was reached. We also constructed models to estimate biomass directly from *H* and crown area, which can be obtained from remote sensing data, and from *D* and *H* to estimate mass from simple forest inventories. For backward elimination, we used the 'dropterm' function and F-test in the MASS package in R until all variables were significant ($P < 0.05$).

All data were transformed to the natural logarithm for analysis to follow allometric theory, based on power-law relationships, and the error structure of the data. As per the nature of most biomass data, variation increases with increasing *D.* Thus, the error term should be multiplicative, as modelled by log-transformed linear regression, rather than additive, as assumed in most nonlinear models (Mascaro et al. 2011, Xiao et al. 2011). Homogeneous variance and linearity were evaluated by plotting residuals against fitted values. Normality of the residuals was tested using normal Q-Q plots (standardised residuals vs. theoretical quantiles) and the Anderson-Darling test of normality. In the case of non-normal distribution, we performed the Box-Cox procedure to determine an appropriate transformation. If the 95 % confidence interval for λ included 1, indicating that no transformation was necessary, we considered that the log-linear models were adequate.

Models were compared using R^2, Akaike's information criterion (AIC), and the residual standard error (RSE). We also manually calculated errors on the original, rather than logarithmic, scale and compared predictions by the same methods used to compare published models. The proportion of variation marginally explained by each variable was assessed by dividing Type III sum of squares for each variable by the total sum of squares. Type III sum of squares was calculated using the 'Anova' function in the 'car' package. All statistical analysis was performed using the R statistical package, version 2.15.2.

2.3 Results

2.3.1 Biomass and allometric relationships

Fifty-one trees were weighed, representing 41 species, 38 genera, and 17 families. Diameters ranged from 10.6 to 169.0 cm, including 12 trees with $D > 100$ cm. Single tree AGB varied between 0.042 Mg to the most massive tropical tree ever weighed, 76 Mg (Goodman et al. 2012c; Figure 2). The fraction of total AGB in the crown ranged from 14 to 71 % with a mean (± SE) of 44 ± 2 %. Wood density and moisture content of samples varied greatly both between and within individuals (Table A2.1). Overall, ρ in the destructively sampled trees was close to that of the whole stand, and especially so for the largest size class (Table 2.1).

H-*D* relationships were explored to identify the relationship between these two variables and to test model predictions from estimated, rather than directly measured, heights. The following power-law relationship best fit our data:

$$H = 4.871 \times D^{0.4407},$$

where H is total height (m), D is diameter at 1.3 m or above buttresses (cm), and the correction factor for back-transforming estimates has been incorporated (R^2= 0.737 in log-transformed models; $P < 0.001$)

Table 2.1. Wood density statistics (mean, lower (LCL) and upper (UCL) 95 % confidence limits) and sample size (n) in each diameter size class. Wood density values (g/cm3) for trees in the forest inventory were deduced from matching scientific names to common names and applying values from a Global Wood Density Database (Chave et al. 2009, Zanne et al. 2009); wood density of destructive biomass samples was obtained from tree stems measured in this study.

Diameter class	Forest inventory				Biomass samples			
	n	mean	LCL	UCL	*n*	mean	LCL	UCL
$10 \le D < 30$	1117	0.561	0.552	0.569	8	0.598	0.517	0.679
$30 \le D < 50$	949	0.545	0.534	0.556	10	0.473	0.348	0.598
$50 \le D < 70$	373	0.562	0.543	0.581	7	0.586	0.44	0.733
$70 \le D < 90$	115	0.548	0.517	0.578	8	0.619	0.508	0.731
$90 \le D < 110$	50	0.63	0.572	0.688	10	0.657	0.535	0.78
$D \ge 110$	41	0.551	0.474	0.627	8	0.55	0.411	0.69

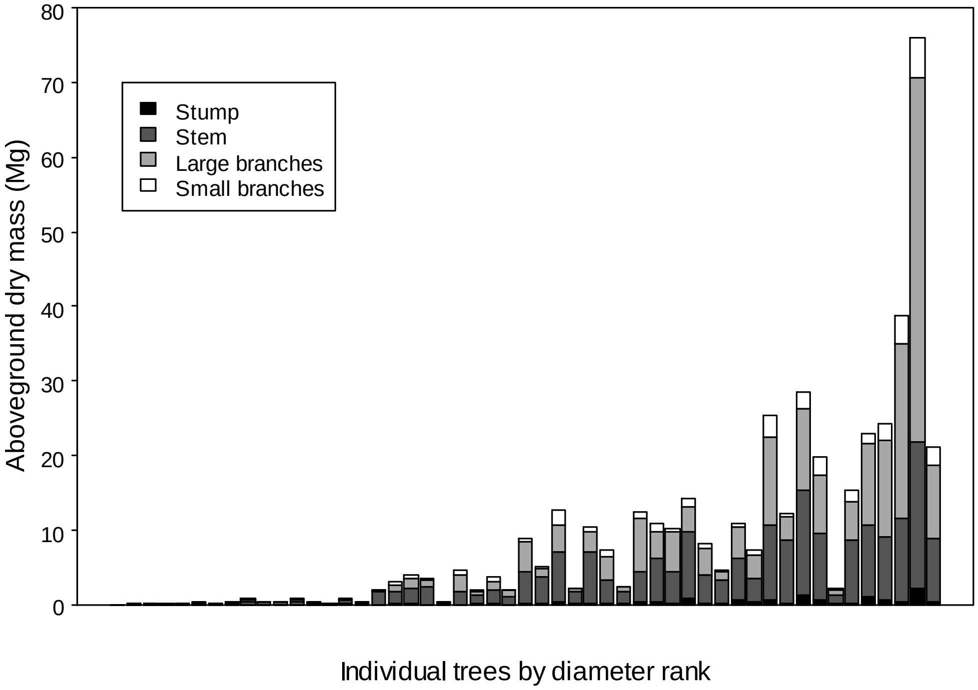

Figure 2.2. Aboveground dry mass in each part (small branches and leaves, large branches, stem, and stump) of the 51 trees harvested and weighed in this study.

2.3.2 Evaluating existing models

Most equations were poor predictors of AGB for our southwestern Amazonian trees, primarily due to poor estimates of the largest trees. On the original scale (Mg), R^2 ranged from 0.019 to 0.884 (Table 2.2). Choice of the 'best' equation depends on the evaluation criteria used —R^2, mean and SD of true errors (mean$_{\mathrm{E}}$ and SD$_{\mathrm{E}}$), and mean and SD of relative errors (mean$_{\mathrm{RE}}$ and SD$_{\mathrm{RE}}$). Often, conflicting conclusions could be drawn from true and relative errors because of differences amongst diameter size classes, with the largest trees having a dominant influence on true errors. Furthermore, many models created from the same datasets, but using different model forms and explanatory variables, showed very different results (e.g., Alv, Ch, and Feld).

All models with D as the only explanatory variable performed poorly across all size classes. Models with the polynomial D form (e.g., Cham) severely underestimated AGB of the largest trees, leading to large overall underestimates for our 51 trees. Including ρ greatly improved both precision and accuracy of estimates. In fact, the Ch II.6 equation appeared to best predict AGB amongst all the equations evaluated. Again, all models with a polynomial D form underestimated AGB of the largest size class, with the exception of Feld 1; and, on average, the models without polynomial terms for *D* performed better (Table 2.2).

Models including *H* did not consistently improvement estimates. Published models with *H* regularly underestimated AGB and had lower overall predictability (i.e., greater SD_{RE}) compared to models which only used *D* and ρ (Table 2.2). The effect of *H* on AGB estimates can be more clearly identified by comparing specific pairs of models from the same study that include and exclude *H*. Models without *H* often overestimated AGB, but models with *H* always resulted in large underestimates, primarily due to severe underestimates of the largest trees (Figure 3). In the two studies that downgraded AGB of the southwestern Amazon based on tree height (Nogueira et al. 2008b, Feldpausch et al. 2012), we found that including *H* improved estimates by some measures (lowered $mean_{RE}$ and SD_{RE}) but decreased the accuracy by other measures (increased $|mean_{E}|$ and SD_{E} and lowered R^2). The Higuchi model from central Amazonia underestimated AGB of our trees (Higuchi in Table 2.2), so applying the subsequent *H* and ρ 'corrections' introduced by Nogueira et al. (2008b) only exacerbated these underestimates (Nog H and Nog H-ρ in Table 2.2; Figure 3). Among the Feld models, AGB was overestimated without *H* ($mean_{E}$ = +0.50 Mg/ tree in Feld 1), but it was underestimated by over twice this amount when *H* was included ($mean_{E}$ = –1.19 Mg/ tree in Feld 2). The same pattern was also observed in the two models recommended by Chave et al. (2005) for moist forests: on average, Ch II.3 (without *H*) overestimated AGB by +0.36 Mg/ tree, but Ch I.5 (with *H*) underestimated AGB by nearly three times this amount (–1.00 Mg/ tree). Mean estimates by size class show that all three models without *H* overestimated AGB of small and medium-sized trees ($D < 90$ cm), but the models that included *H* underestimated AGB of medium and large trees ($D \geq 50$ cm), with severe underestimates of the largest size class ($D \geq 90$ cm; Figure 3).

Table 2.2. Summary of errors (sum, mean, standard deviation (SD), and coefficient of correlation (R^2)) and relative error (Rel. Err.; mean and SD) for each published equation examined in this study. In Location, ST refers to subtropical; in model forms, '1' refers to the parameter coefficient being constrained to 1; and *n* is the sample size used to create each model. Models are arranged from highest to lowest R^2 among all equations with the same explanatory variables. Numbers in bold indicate the 'best' (highest R^2 or lowest absolute value of all other criteria) within each group of equations, and the corresponding model information is also in bold. See footnote for model references.

Model*	Forest type	Location	*n*	Form	Error (Mg)				Rel. Err. (%)	
					Sum	Mean	SD	*R^2*	Mean	SD
Nog	**Open**	**S. Amazon**	**262**	**D**	**-29**	**-0.57**	**7.9**	**0.64**	70	179
Higuchi	Moist	C. Amazon	315	D	-58	-1.14	8.2	0.60	81	194
Djo P2	Moist	Tropical	443	D	136	2.67	8.3	0.56	117	291
Cham >10	Moist	Central	161	$D+D^2+D^3$	-54	-1.07	8.9	0.53	111	243
Zianis	**All**	**Global**	**1211**	**D**	-179	-3.50	9.1	0.44	**12**	**118**
Cham ≥5	Moist	Central	315	$D+D^2+D^3$	-168	-3.29	10.6	0.28	74	210
WBE	All	Theoretical	n/a	D	329	6.46	11.2	0.02	173	230
Mean for all models with only D					**-3**	**-0.06**	**9.2**	**0.44**	**91**	**209**
Ch II.6	**All**	**Trop/(ST)**	**2410**	**$D+1\rho$**	**2**	**0.03**	**5.1**	**0.85**	24	65
Ch II.1	Moist	Trop/(ST)	1504	$D+D^2+D^3+\rho$	23	0.45	5.1	0.85	38	74
Ch II.3	Moist	Trop/(ST)	1504	$D+D^2+D^3+1\rho$	18	0.36	5.2	0.84	38	76
Feld 1	All	Tropical	1816	$D+D^2+D^3+\rho$	25	0.50	5.2	0.84	41	79
Alv II.6	All	Colombia	631	$D+\rho$	-16	-0.31	5.3	0.84	27	67
Alv II.5	Moist	Colombia	631	$D+\rho$	-29	-0.57	5.4	0.82	27	67
Ch II.4	**All**	**Trop/(ST)**	**2410**	**$D+D^2+D^3+1\rho$**	-75	-1.48	6.2	0.76	15	**63**
Ch II.2	All	Trop/(ST)	2410	$D+D^2+D^3+\rho$	-56	-1.09	6.3	0.76	28	80
Ch II.5	Moist	Trop/(ST)	1504	$D+1\rho$	132	2.60	5.9	0.76	52	81
Alv II.2	All	Colombia	631	$D+D^2+D^3+\rho$	-75	-1.48	7.1	0.69	30	84
Alv II.4	All	Colombia	631	$D+D^2+D^3+1\rho$	-91	-1.79	7.1	0.69	20	69
Alv II.3	Moist	Colombia	370	$D+D^2+D^3+1\rho$	-133	-2.60	8.0	0.59	16	69
Alv II.1	Moist	Colombia	370	$D+D^2+D^3+\rho$	-141	-2.77	8.9	0.49	34	115
Baker	**Moist**	**Amazon**	**315**	**$D+D^2+D^3+\rho$**	-213	-4.19	10.1	0.30	**5**	73
Mean for all models with D and ρ					**-45**	**-0.88**	**6.5**	**0.72**	**28**	**76**
(not including those with D^2 and D^3)					**22**	**0.44**	**5.4**	**0.82**	**33**	**70**
Alv I.6	**All**	**Colombia**	**631**	**$1\rho D^2H$**	51	1.01	**4.3**	**0.88**	38	66
Ch I.3	Moist	Trop/(ST)	1348	ρD^2H	-37	-0.73	4.9	0.86	12	53
Ch I.6	All	Trop/(ST)	2410	$1\rho D^2H$	-36	-0.72	4.9	0.85	14	54
Ch I.1	Moist	Trop/(ST)	1348	$D+\rho+H$	-8	-0.15	5.0	0.85	25	69
Ch I.5	**Moist**	**Trop/(ST)**	**1348**	**$1\rho D^2H$**	-51	-1.00	5.1	0.84	10	**52**
Ch I.2	All	Trop/(ST)	2410	$D+\rho+H$	-32	-0.63	5.3	0.83	21	67
Alv I.5	Moist	Colombia	370	$1\rho D^2H$	133	2.61	4.6	0.83	61	77
Ch I.4	All	Trop/(ST)	2410	ρD^2H	-58	-1.14	5.3	0.83	10	53
Feld 2	**All**	**Tropical**	**1816**	**$D^2H\rho$**	-60	-1.19	5.3	0.83	**9**	53
Alv I.3	Moist	Colombia	370	ρD^2H	-55	-1.09	5.6	0.81	21	62
Brown	Moist	Tropical	94	ρD^2H	-63	-1.24	5.6	0.81	16	58
Alv I.4	All	Colombia	631	ρD^2H	-62	-1.22	5.7	0.80	20	62
Alv I.1	**Moist**	**Colombia**	**631**	**$D+\rho+H$**	**4**	**0.08**	6.0	0.79	50	113
Alv I.2	All	Colombia	631	$D+\rho+H$	-78	-1.53	6.2	0.76	19	72
Djo P5	Moist	Tropical	274	$D^2+D^3+D^2H+\rho$	-17	-0.33	6.9	0.72	66	143
Nog H	Moist	SW Amazon	n/a	$D\times H_{corr}$	-80	-1.56	8.4	0.57	69	182
Nog H-ρ	Moist	SW Amazon	n/a	$D\times H_{corr}\times\rho_{corr}$	-137	-2.69	8.9	0.50	43	154
Mean for all models with D, ρ, and H					**-35**	**-0.68**	**5.8**	**0.79**	**30**	**82**

* Alv (Alvarez et al. 2012), Baker (Baker et al. 2004b), Brown (Brown et al. 1989), Ch (Chave et al. 2005), Cham (Chambers et al. 2001), Djo (Djomo et al. 2010), Feld (Feldpausch et al. 2012), Nog (Nogueira et al. 2008a), Nog H and H-ρ (Nogueira et al. 2008b), WBE (West et al. 1997), Zianis (Zianis 2008)

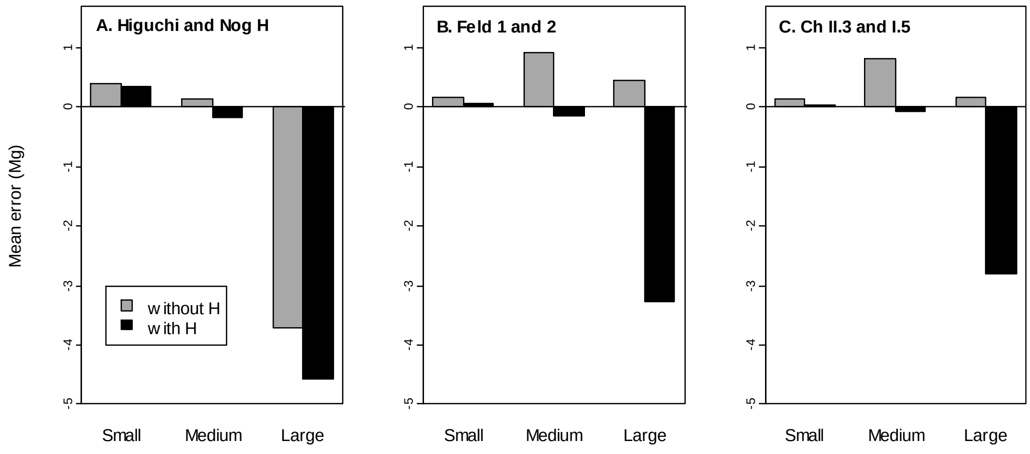

Figure 2.3. Mean error in estimates ($\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{observed}}$) by diameter (*D*) size class —small ($10 \leq D < 50$ cm; $n = 17$), medium ($50 \leq D < 90$ cm; $n = 16$), and large trees ($D \geq 90$ cm; $n = 18$)— for three key model pairs. Models are (A) Higuchi et al. (1998) and Nogueira et al. (2008b) with height correction, (B) Feldpausch et al. (2012) 1 and 2, and (C) Chave et al. (2005) II.3 and I.5 for moist forests, listed without and with height, respectively.

2.3.3 New models using diameter, wood density, and height

Before we could test the importance of crown dimensions for AGB estimates, we first created new models using the three standard variables, *D*, *ρ*, and *H*. Within our dataset, all models with *H* performed better than all those without *H*, and models with unconstrained variable coefficients performed better than those with constrained coefficients. By all criteria, model I.1 (with *D*, *ρ*, and *H*) performed best (Table 2.3). Of the models without *H*, model II.1 was best, and R^2 values for models without *H* rivalled that of models I.1–I.5 (with *H*). Unlike models in many other studies, not all terms for *D* were significant in the polynomial models. For all models created using *D*, *ρ*, and *H*, we found that the residuals were not distributed normally, due to a slight negative skew, but the 95 % confidence interval for λ always included 1. In this case, we consider these equations to be reasonably reliable, but they are further evaluated in section 3.6.

Table 2.3. All models including diameter (D; cm), wood density (ρ; g/cm³), and total height (H; m) to estimate aboveground biomass (AGB; kg dry mass) created from 51 trees with diameter range 11–169 cm.

Code	Form	a	b	c	d	R^2	RSE	AIC	F	dfe	$Pr < F$
I.1	$\ln(AGB) = a + b\ln(D) + c\ln(H) + d\ln(\rho)$	-2.6512	2.0212	0.9302	1.3257	0.971	0.317	33.4	531	47	< 0.001
I.3	$\ln(AGB) = a + b\ln(D^2H\rho)$	-3.2458	1.0221	-	-	0.967	0.332	36.1	1450	49	< 0.001
I.5	$\ln(AGB) = a + \ln(D^2H\rho)$	-3.0046	-	-	-	-	0.331	34.8	-	50	< 0.001
II.1	$\ln(AGB) = a + b\ln(D) + d\ln(\rho)$	-1.0165	2.4186	-	1.5241	0.965	0.347	41.6	661	48	< 0.001
II.3	$\ln(AGB) = a + b(\ln(D))^2 + \ln(\rho)$	3.1128	0.3165	-	-	0.951	0.399	54.9	943	49	< 0.001
II.5	$\ln(AGB) = a + b\ln(D) + \ln(\rho)$	-1.4823	2.4519	-	-	0.950	0.400	55.2	933	49	< 0.001

2.3.4 New models accounting for crown dimensions and architecture

Beginning with the six base models (Table 2.3), we then added terms to account for crown size and architecture (Table 2.4). The effect of the variable for crown size (crown radius; *CR*) was highly significant ($P < 0.001$) in every model tested. Adding *CR* greatly improved estimates, increasing R^2 and reducing RSE and AIC, and models were significantly better than the equivalent equation without *CR* (Table 2.4). Furthermore, including *CR* normalised residuals in most models. Model I.1 *CR*, with all four variables, was best in terms of having the lowest RSE and AIC and was the minimum adequate model determined by backwards elimination of all seven continuous variables, but model II.1 CR (with *ρ, D, CR*) had the greatest coefficient of correlation ($R^2 = 0.999$). Including *CR* in models was always better than crown ellipse area (*CEA*), so equations with *CEA* are not reported.

Several analyses show that *CR* is even more effective than *H* at explaining variation in AGB. First, the model with *D*, *ρ*, *CR* (II.1 CR) performed better than the equivalent model with *H* instead of *CR* (I.1). Second, when we calculated the proportion of variation in AGB explained marginally by each variable (Type III SS) in the model with all four variables (I.1 CR), *CR* (10.5 %) was more informative than *H* (6.0 %; Figure 4A). Furthermore, in single variable models, *CR* explained the most variation in AGB (86.6 %), more than *D* (85.9 %) or *H* (82.8 %; Figure 4B).

Monopodial (*M*) was the only significant architectural variable in the models tested (Table 2.4). On the logarithmic scale, models with *M* had higher R^2 values, lower RSE and AIC, and were significantly better than the equivalent models without this variable. However, improvements were much smaller than those seen for *CR*, and residuals were only normalised in two of six models. The coefficients for *M* were always negative, indicating a strong downwards adjustment for monopodial trees. When back-transformed, the model prediction for monopodial trees is multiplied by $\exp(f \times M)$, which translates to a 21–44 % reduction in the models listed (when $M=0$ then $\exp(f \times M) = 1$, indicating no adjustment for trees that are not monopodial). When *M* was added to models already including *CR*, *M* was no longer significant, except in two instances (Table 2.4). In these models, the coefficient for *M* was lower than the equivalent model not including *CR*, indicating a less severe adjustment for monopodial trees when *CR* was already considered. None of the other categorical classifications —such as stem irregularity, structural damage, crown quality, or crown illumination index— had a significant effect in any of the models explored.

Table 2.4. All models that include crown dimensions (average crown radius (CR; m)), tree architecture (M=1 if monopodial, M=0 if not), diameter (D; cm), wood density (ρ; g/cm3), and total height (H; m) to estimate aboveground biomass (AGB; kg dry mass) created from 51 trees with diameter range 11–169 cm. RSE is residual standard error. ~N indicates whether residuals were distributed normally using the Anderson-Darling normality test (P ≥ 0.05).

Code	Form	a	b	c	d	f	R^2	RSE	AIC	F	dfe	*Pr* < F	~N	*Pr* < F*
I.1 CR	$\ln(AGB) = a + b\ln(D) + c\ln(H) + d\ln(\rho) + f\ln(CR)$	-1.8733	1.4378	0.9379	1.0678	0.7624	0.983	0.250	10.0	649	46	< 0.001	yes	< 0.001
I.3 CR	$\ln(AGB) = a + b\ln(D^2H\rho) + f\ln(CR)$	-2.1788	0.8025	-	-	0.7147	0.978	0.277	18.7	1050	48	< 0.001	no	< 0.001
I.5 CR	$\ln(AGB) = a + \ln(D^2H\rho) + f\ln(CR)$	-3.3639	-	-	-	0.1926	0.973	0.313	30.2	1748	49	< 0.001	no	0.013
II.1 CR	$\ln(AGB) = b\ln(D) + d\ln(\rho) + f\ln(CR)$	-	1.7586	-	1.2708	0.8202	0.999	0.288	18.7	13540	48	< 0.001	yes	< 0.001
II.3/5 CR	$\ln(AGB) = b\ln(D) + \ln(\rho) + f\ln(CR)$	-	1.6382	-		0.9931	0.999	0.300	25.9	18670	49	< 0.001	yes	< 0.001
I.1 M	$\ln(AGB) = b\ln(D) + c\ln(H) + d\ln(\rho) + fM$	-2.4821	1.9611	0.9513	1.2297	-0.2520	0.974	0.306	30.8	428	46	< 0.001	no	0.042
I.3 M	$\ln(AGB) = a + b\ln(D^2H\rho) + fM$	-2.8205	0.9894	-	-	-0.3145	0.972	0.313	31.1	818	48	< 0.001	no	0.011
I.5 M	$\ln(AGB) = a + \ln(D^2H\rho) + fM$	-2.9410	-	-	-	-0.2949	0.972	0.310	29.3	1693	49	< 0.001	no	0.007
II.3 M	$\ln(AGB) = a + b\,(\ln(D))^2 + \ln(\rho) + fM$	3.4227	0.3040	-	-	-0.4411	0.961	0.363	46.2	584	48	< 0.001	yes	0.002
II.5 M	$\ln(AGB) = a + b\ln(D) + \ln(\rho) + fM$	-1.0299	2.3622	-		-0.3966	0.958	0.372	48.9	550	48	< 0.001	yes	0.005
I.3 CR.M	$\ln(AGB) = a + b\ln(D^2H\rho) + d\ln(CR) + fM$	-1.9421	0.7954	-	0.6571	-0.2387	0.980	0.265	15.1	767	47	< 0.001	no	0.023
II.3 CR.M	$\ln(AGB) = a + b\ln(D) + \ln(\rho) + d\ln(CR) + fM$	3.2284	0.2350	-	0.7207	-0.2708	0.971	0.315	32.6	532	47	< 0.001	yes	0.031

* From ANOVA comparing this model and an equivalent model with and without the last variable listed (CR or M).

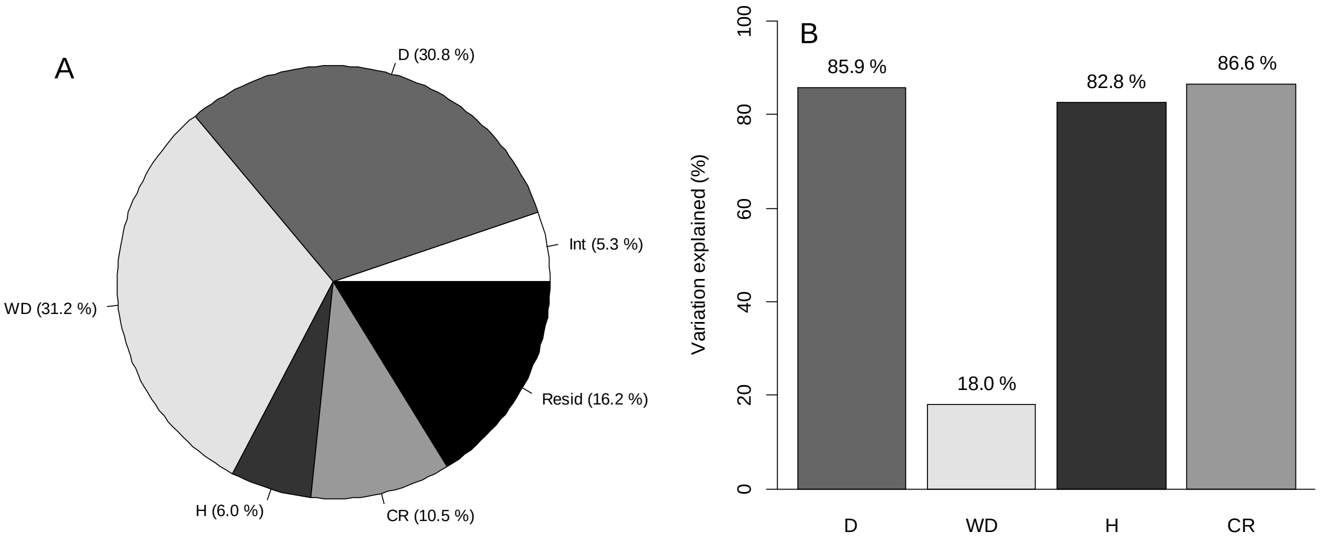

Figure 2.4. (A) Variation in AGB explained marginally by each component in the log-transformed model including all four continuous variables: ln(AGB) = a + $b$ln(D) + $c$ln(WD) + $d$ln(H) + $f$ln(CR) + ε. Percentage variation was determined as (Type III sum squares)$_i$/(total sum squares) × 100 %, where i = a (int), diameter (D), wood density (WD), total height (H), average crown radius (CR), and ε (Resid). (B) Variation in AGB explained by each component (R^2) in four separate log-transformed simple linear models.

2.3.5 Practical models for remotely-sensed and forestry data

Five models were created to estimate AGB directly from variables potentially obtainable from remote sensing data (H and CEA) or simple forest inventories (D and H; Table 2.5). The model including only CEA performed better than the model with H as the only predictor variable, but the model with both variables was best. This model, P.H-CEA, performed reasonably well but not as well as models with D and ρ (see Table 2.3). Of the simple inventory models, the model with H (P.D-H) performed better than the model with only D (P.D), but neither performed as well as the model with H and CEA.

Table 2.5. All models including total height (H; m), crown ellipse area (CEA; m^2), and/or diameter (D; cm) to predict aboveground biomass (AGB; kg dry mass) created from 51 trees diameter range 11–169 cm. RSE is residual standard error. ~N indicates whether residuals are distributed normally using the Anderson-Darling normality test ($P \geq 0.05$).

Code	Form	*a*	*b*	*c*	R^2	RSE	AIC	F	dfe	*Pr* < F	~N
P.H	ln(AGB) = a + b ln(H)	-8.2985	4.8114	-	0.828	0.760	120.7	237	49	< 0.001	yes
P.CEA	ln(AGB) = a + c ln(CEA)	1.0933	-	1.4064	0.866	0.672	108.2	316	49	< 0.001	yes
P.H-CEA	ln(AGB) = a + b ln(H) + c ln(CEA	-4.3316	2.4118	0.8490	0.938	0.462	70.9	362	48	< 0.001	yes
P.D	ln(AGB) = a + b ln(D)	-2.3713	2.5154	-	0.859	0.688	110.6	299	49	< 0.001	no
P.D-H	ln(AGB) = a + b ln(D) + c ln(H)	-5.9754	1.5022	2.2988	0.909	0.559	90.4	240	48	< 0.001	no

2.3.6 Evaluation of all new models

Finally, we evaluated how well the 27 new equations developed in this study estimated AGB on the original scale (Mg; Table 2.6). Results were similar to model evaluation on the log-transformed scale, and new models generally estimated AGB of our trees better than published models with the same variables even when *CR* was not included (Tables 2 and 6). Furthermore, estimates were much more stable than the range of estimates derived from published models. Using *H* in models tended to increase model precision but consistently lowered estimates, and *H* did not explain variation in AGB as well as *CR*. Including *CR* greatly improved estimates, especially of the largest trees, but the monopodial variable was less successful.

Overall, models I.1 CR and II.1 CR performed best. Numerically, *CR* improved estimates because it reduced the absolute value of errors, compared to equivalent models without *CR* (Figure 5). This was true for trees of all sizes, but the magnitude of improvements were especially important in the largest trees.

The three models designed to estimate AGB from tree measurements obtainable from remote sensing data (*H* and *CEA*) performed moderately well (Table 2.6). The model with both variables (P.H-CEA) was best, but models with only *H* and *CEA* substantially overestimated AGB, especially the model with only *CEA*. Including *CEA* in models had a similar effect to that of *CR*: errors were brought closer to zero compared to the model with only *H*. For most individuals, *CEA* was more effective than *D* at reducing errors. However, in all these models, errors were still substantial, especially for the largest trees.

Recommended equations are listed below, according to the inventory or remotely-sensed data available. AGB is measured in kg dry mass, *D* in cm, *H* and *CR* in m, *CEA* in m^2, and ρ in g/cm^3, and correction factors have been incorporated.

When *CR* is available, model I.1 CR:

$$\begin{aligned} AGB = \exp\,(&-1.8421 + 1.4378\ln(D) + 0.9379\ln(H) \\ &+ 1.0678\ln(\rho) + 0.7624\ln(CR)) \end{aligned}$$

When *H* is available, model I.1:

$$AGB = \exp\,(-2.6009 + 2.0212\ln(D) + 0.9302\ln(H) + 1.3257\ln(\rho))$$

When H is not available, model II.1:

$$AGB = \exp\left(-0.9563 + 2.4186\ln(D) + 1.5241\ln(\rho)\right)$$

When H and CEA are available, model P.H-CEA:

$$AGB = \exp\left(-4.2248 + 2.4118\ln(H) + 0.8490\ln(CEA)\right)$$

Table 2.6. Summary of errors (sum, mean, standard deviation (SD), and coefficient of correlation (R2)) and relative error (Rel. Err.; mean and SD) for each new equation created in this study. In model form, numbers refer to the coefficient being constrained to that value (1 or 8/3). Models are arranged from highest to lowest R2 among all equations with the same explanatory variables. Numbers in bold indicate the 'best' (highest R2 or lowest absolute value of all other criteria) within each group of equations; and the corresponding model information is also in bold.

		Error (Mg)				**Rel. err. (%)**	
Name	**Form**	**Sum**	**Mean**	**SD**	R^2	**Mean**	**SD**
P.D	**D**	**-3**	**-0.06**	**7.8**	**0.65**	**70**	**179**
II.1	**D+ρ**	**-5**	**-0.09**	**4.5**	**0.88**	13	**46**
II.5	D+1ρ	-33	-0.64	5.4	0.83	19	62
II.3	D^2+1ρ	-32	-0.62	5.4	0.83	**10**	54
Mean of all models with D & ρ		**-23**	**-0.45**	**5.1**	**0.85**	**14**	**54**
P.D-H	D+H	-28	-0.55	6.9	0.72	43	145
I.1	**D+ρ+H**	**-17**	**-0.34**	**4.3**	**0.89**	**11**	**43**
I.3	ρD^2H	-25	-0.48	4.7	0.87	13	53
I.5	1ρD^2H	-40	-0.78	5.0	0.85	13	54
Mean of all models with D, ρ, & H		**-27**	**-0.54**	**4.6**	**0.87**	**12**	**50**
II.1 CR	**D+ρ+CR**	**-3**	**-0.05**	**3.1**	**0.94**	9	32
I.1 CR	**D+ρ+H+CR**	-8	-0.16	3.2	0.94	**6**	**28**
II.3/5 CR	D+1ρ+CR	-12	-0.24	3.3	0.93	10	34
I.3 CR	ρD^2H + CR	-14	-0.27	3.8	0.92	8	36
I.5 CR	1ρD^2H + CR	4	0.08	4.0	0.91	11	46
Mean of all models with CR		**-7**	**-0.13**	**3.5**	**0.93**	**9**	**35**
I.1 M	**D+ρ+H+M**	-22	-0.43	**4.5**	**0.88**	**10**	39
I.5 M	1ρD^2H + M	-23	-0.44	4.7	0.87	11	44
I.3 M	ρD^2H + M	-28	-0.55	4.9	0.86	11	44
II.5 M	D+1ρ+M	-30	-0.59	5.4	0.83	18	53
II.3 M	**D^2+1ρ+M**	**9**	**0.18**	5.5	0.82	14	47
Mean of all models with M		**-19**	**-0.37**	**5.0**	**0.85**	**13**	**45**
I.3 CR.M	ρD^2H + CR + M	-17	-0.34	4.0	0.91	7	32
II.3 CR.M	D+1ρ+CR+M	-438	-8.58	13.0	-0.42	-91	14
Mean of all models with CR & M		**-228**	**-4.46**	**8.5**	**0.24**	**-42**	**23**
P.H-CEA	**H+CEA**	**17**	**0.34**	**6.1**	**0.78**	**23**	**55**
P.CEA	CEA	68	1.33	6.6	0.73	55	113
P.H	H	21	0.42	10.2	0.39	86	238
Mean of all models with H & CEA		**35**	**0.69**	**7.6**	**0.63**	**55**	**135**

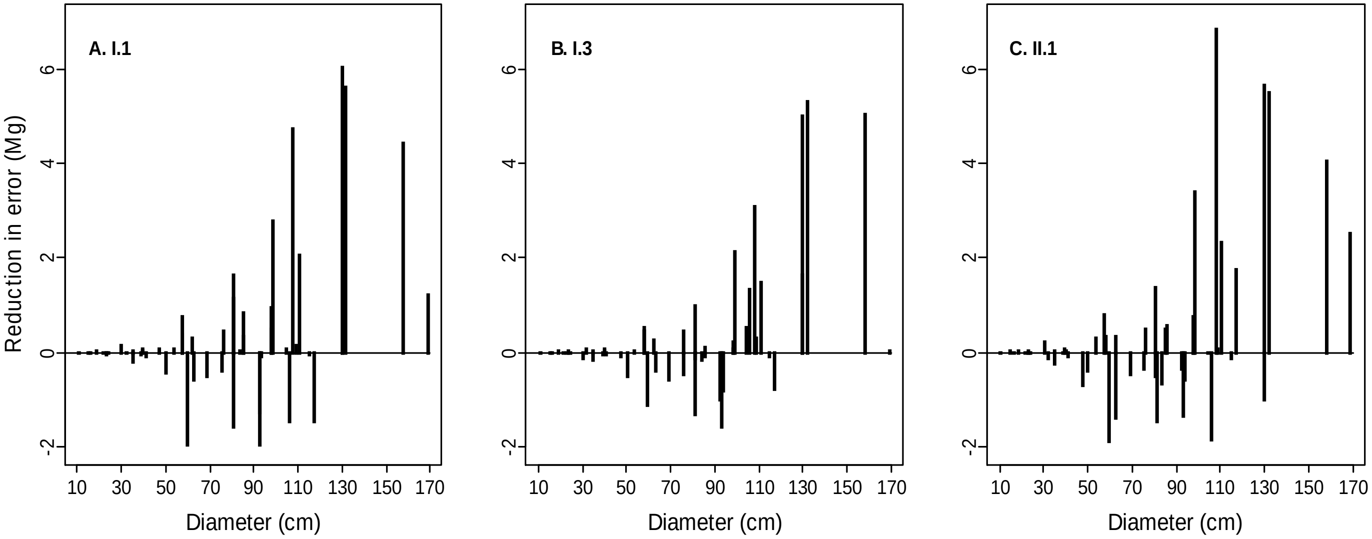

Figure 2.5. Improvements in aboveground biomass estimates in comparable models with and without crown radius (*CR*): reduction in error is calculated as |error without *CR*| – |error with *CR*| for each tree in our dataset. Negative values indicate that the model *CR* did not improve the estimate. Models are (A) I.1 and I.1 CR, (B) I.3 and I.3 CR, and (C) II.1 and II.1 CR, listed without and with *CR*, respectively. Models with constrained coefficients are not shown.

2.4 Discussion

2.4.1 Biomass and allometric relationships

Destructive biomass harvest datasets from tropical forests are relatively rare and not distributed evenly across tropical forest regions (Clark and Kellner 2012). This new dataset consists of AGB of 51 trees from a previously unrepresented geographic region (southwestern Amazonia) and country (Peru), each of which represent large and important areas for forest management and carbon storage. It contains trees across a broad range of diameters (11–169 cm) including 12 individuals with $D > 100$ cm, nearly doubling the number of very large tree data available in the entire tropical database (14 trees in Chave et al. 2005 and 17 in Feldpausch et al. 2012). This presents a unique opportunity to test how well pantropical and regional equations estimate AGB of trees from a distant locale and across a broad range of size classes. Our data often show different results than obtained from other studies, which may be predominately influenced by our sampling scheme that most notably includes many very large trees.

The enormous sum of errors (Table 2.2) exemplifies the need to improve AGB estimates, especially for large trees. The sum of errors in just 51 trees ranged from –438 to +329 Mg from both published and new equations, with the most extreme values exceeding total per-hectare AGB density estimates in this area (Cummings et al. 2002, Baker et al. 2004b, Salimon et al. 2011). Although our dataset does not a represent an actual forest stand, the importance of just one large tree in this environment is clear. AGB density of neighbouring forests in Acre, Brazil has recently been estimated at 224 ± 50 Mg/ha (Salimon et al. 2011), in which case the most massive tree in our dataset (76 Mg) would represent over one-third of this. Several other studies have also found that large trees contribute substantially to AGB density estimates and uncertainty (Brown et al. 1995, Clark and Clark 2000, Baker et al. 2004b, Chave et al. 2004). Clearly, more accurate determination of large tree biomass is required for better mapping and, especially, monitoring of tropical forest biomass and carbon stocks.

Additionally, the importance of representing new geographic regions and forest structures should not be understated. Uncertainty in C emission estimates is high in the ‘arc of deforestation’ —which spans southern Brazil and northern Bolivia and may extend into southern Peru— largely because of the lack of data in these forest types (Fearnside et al. 2009). A better understanding of this area will also have important implications for national C budgets (Fearnside et al. 2009), and our results suggest that these forests hold more biomass than reported in recent studies (Nogueira et al. 2008a, Nogueira et al. 2008b, Feldpausch et al. 2012) especially because large trees, which are prevalent here, may be more massive than previously estimated.

This dataset may also be the first to sample trees with approximately equal numbers across all diameter size classes with mean wood density in each size class constrained to be approximately equal to that of the forest. The trees sampled in our dataset had mean ρ very close to the stand-level mean (Table 2.1), though it should be noted that the values deduced from the inventory were only first-order estimates to serve as a guide and cannot be considered entirely reliable. Fortunately, mean ρ of our largest size class ($D \geq 110$ cm) was nearly identical to that of the forest. Therefore, our findings that published equations consistently underestimate AGB of the largest trees should not be due to sampling bias toward atypically dense trees.

As hypothesised, our trees had a greater proportion of crown mass (44 ± 2 %) than other Amazonian trees, reported as 31 % (da Silva 2007) and 34 % (Higuchi et al. 1998) in the dense forests of central Amazonia and 39 % in trees of the open forests of southern Amazonia (da Silva 2007, Nogueira et al. 2008a). Thus, accurately accounting for variation in the relative contribution of crown mass may be important for understanding how total AGB relates to tree height and how this relationship differs geographically. For example, Chambers et al. (2001) contended that although crown proportions varied between central and southern Amazonia, total crown mass was invariant and that trees in the south weigh less due to shorter stems; and Nogueira et al. (2008b) assumed that the proportion of crown mass did not change with tree height. However, comparing our data to published data shows that both the proportion of crown mass and total mass did vary between these regions. To further explore this issue, we estimated crown mass from D of our trees using crown-specific equations reported for both central (Chambers et al. 2001) and southern (Nogueira et al. 2008a) Amazonia and found that these equations substantially underestimated crown mass at our southwestern site. In both cases, underestimates in crown mass explained most (Chambers et al. 2001) or all (Nogueira et al. 2008a) of the whole tree biomass underestimates produced by these equations (Table 2.2). Thus, correctly estimating crown mass may be an essential component of achieving accurate estimates of total AGB.

2.4.2 Evaluating existing models

We estimated AGB of our trees from 38 published pantropical and Amazonian equations to test how well these models predict biomass in a previously unrepresented region. As hypothesised, many models generated from other areas produced large errors when estimating AGB of our trees. Estimates were particularly poor for very large trees, and models including H often produced substantial underestimates. We examined outcomes from models using different input variables (D, D and ρ, and D, ρ, and H; Table 2.2) with special attention paid to studies that have lowered AGB estimates for the southwestern Amazonian forests due to lower tree heights. Because accuracy, or total AGB, is required for global carbon budget estimates (Clark and Kellner 2012), we put more emphasis on true, rather than relative, errors.

Our data suggest that AGB estimates from published models that include H are too low because proportionally greater crown mass at least partially compensates for shorter tree stature in our study area. Several models without H overestimated AGB, but nearly all models that include H underestimated AGB substantially (Table 2.2). However, the recent reductions in AGB estimates due to lower tree heights appear to be too extreme compared to our data, especially for large trees (Figure 3). In the first instance, the downward adjustments in total AGB estimates by Nogueira et al. (2008b) due to H was less than reported: 5.5 % reduction using our measured D and estimated H ($\text{mean}_{\%E}$ = –5.5 % if the Higuchi estimates were considered accurate) vs. 6 or 11 % reduction reported in Nogueira et al. (2008b). The Feld 1 model (D and ρ) resulted in an overall 6 % overestimate of AGB, but the Feld 2 model ($\rho D^2 H$) underestimated AGB by 14 %. The same pattern was also seen in the two models recommended by Chave et al. (2005) for moist tropical forests: Ch II.3 (D and ρ) overestimated total AGB by 4 % in all 51 trees, but model Ch I.5 ($\rho D^2 H$) underestimated AGB by 11 %. The difference in these two pairs (19 or 15 %) is comparable to the reduction in AGB recently reported for the western Amazon (16 %; Feldpausch et al. 2012), but our data show that it is not accurate to conclude that this difference is due to overestimates caused by not including H.

Rather, a majority of the difference was due to underestimates from models that did include *H*.

To further test the effect of using estimated *H* as an explanatory variable, we calculated AGB from three of our models with estimated *H* values obtained from the *H*–*D* equation developed in this study (section 3.1). We found that this method did not work well with our data. Predictions made from our models I.1, I.3, and I.5 using *D*, ρ, and estimated *H* were generally not as good as those from the best equation that did not include *H* at all (II.1), even though *H* was estimated from a *H*-*D* relationship developed from the same 51 trees. Several other authors have also warned against including tree height in regression equations (Lescure et al. 1983, Overman et al. 1994, Chave et al. 2001, Leuschner et al. 2007). For example, it may systematically increase correlation coefficients, over equations using *D* only, even when *H* is poorly measured (Chave et al. 2001).

We attribute poor estimates from published models, especially the underestimates in models including *H*, to the architectural differences between the trees in our area vs. other regions represented in Amazonian and pantropical datasets. It has recently been shown that maximum height and *H*–*D* relationships are lower in South America than in Asia and Africa (Feldpausch et al. 2011, Banin et al. 2012), and within Amazonia, trees in the south are shorter than those in the northeast (Nogueira et al. 2008b, Feldpausch et al. 2011). We propose that this is likely to be a result from the trade-off between vertical height growth and horizontal crown growth to maximize light capture (King 1996, Aiba and Kohyama 1997, Sterck and Bongers 1998, Bohlman et al. 2008). This, in turn, suggests that models with only *D* and ρ may be more universal than models with *D*, ρ, and *H*. Indeed, many studies across the tropics have found that trees with greater adult stature and more slender stem allometry are also associated with narrower crowns (Poorter et al. 2003, Bohlman and O'Brien 2006, King et al. 2006, Poorter et al. 2006, Aiba and Nakashizuka 2009, Iida et al. 2012). This concurs with our hypothesis that although our trees are shorter (Nogueira et al. 2008b, Feldpausch et al. 2011), they tend to have larger crowns relative to trees in other areas, especially compared to regions that have been well-represented in the pantropical biomass dataset (i.e., southeast Asia and central and eastern Amazonia). Vegetation height itself may be influenced by forest structure, whereby the presence of tall, dominant trees, especially in Asia, may drive other canopy trees to grow tall (Banin et al. 2012). In contrast, the large crowns in our forest may be related to the slightly fragmented canopy, which provides no incentive for height growth after becoming emergent but does allow branches to expand horizontally.

Crown variation may also explain why neither of the equations from the geographically closest studies, southern Amazonia (Nogueira et al. 2008a) and northwestern Amazonia (Alvarez et al. 2012), consistently estimated AGB of our trees well. Although Colombia, Ecuador, and Peru are often grouped together as the western Amazon, it has been suggested that there is a north–south gradient in crown size, from Colombia to Peru, paralleling a gradient of increasing moisture seasonality (Barbier et al. 2010). Likewise, there may be greater variation in crown sizes in the forests of the southern Amazon than in the southwest (Barbier et al. 2010). More directly-measured data on crown dimensions are needed to confirm these patterns.

Several studies have proposed that equations that lack *H* will tend to overestimate AGB of trees with *D* outside of the range used to create these models (Chambers et al. 2001, Zianis and Mencuccini 2004, Chave et al. 2005, Vieilledent et al. 2012). One of the reasons stated, which is also the rationale for the polynomial–*D* model form, is that crown and stem structural damage increase with tree size (Chambers et al. 2001), especially in the southern and southwestern Amazonian forests (Nogueira et al. 2008b). The severity and frequency of irregularities and hollow trunks have also been reported to increase as tree size increases (Zimmerman et al. 1994, Fearnside 1997, Clark and Clark 2000, Chambers et al. 2001, Nogueira et al. 2006). However, the current dataset includes several very large trees with diameters outside the range of nearly all the published equations evaluated. We found that empirical published equations both over- and underestimated AGB of individual large trees, but, on average, they underestimated AGB of the largest trees (Table 2.2, Figure 3). Furthermore, we observed very little crown or structural damage in our forest type due to bamboo, lianas, or any other natural influence. In fact, structural damage in the crown was only observed in 4 of 51 trees, with > 10 % estimated loss only seen in one tree. In a regression analysis, neither crown nor stem structural damage was related to tree size, nor did they significantly reduced biomass in our models. The rarity of substantial structural damage may be one of the reasons why all published models with the negative cubic term for *D* severely underestimated AGB of our trees and why no more than one term for *D* was ever significant in our models.

In addition to the natural variation found in large trees, the poor estimates for large tree biomass may be a result of sampling schemes, data analysis, and model selection, all of which have allowed considerable errors for large trees to remain. First, all data sets examined have sampled a great proportion of small trees, often for good reasons, and then data are log-transformed for analysis. Both these factors reduce the influence of large trees in regression analysis, and the resulting models can have very different shapes and regression coefficients depending on the few large tree data included (Higuchi et al. 1998, Nelson et al. 1999). Second, basing model selection on relative error criteria will tend to weight improvements for small tree biomass fits equally to improvements in the fits of large trees. However, our results show that very different conclusions about 'best' models can be derived from criteria based on true and relative errors. In both pantropical and Amazonian model AGB predictions, mean_{RE} was almost always positive, but mean_{E} was more often negative because AGB for most of our trees with $D < 70$ cm ($n = 25$) was overestimated while AGB of many large trees was severely underestimated. Thus, evaluating only relative error can lead to different conclusions about model performance than evaluating true error on models created from equal samples sizes in each *D* size class.

2.4.3 New models using diameter, wood density, height, and crown dimensions

To our knowledge, this is the first study to have explicitly examined the effect of crown size and architectural type on measured tropical tree biomass. As hypothesised, the new models presented here show that incorporating crown size or structure into allometric equations can capture variation in tree biomass not explained statistically by *D, ρ,* or *H* (Figure 4A), because it helps account for the contribution of crown mass to total tree AGB. *CR* explains more variation in AGB than any other single variable (Figure 4B) and marginally explains more variation than *H* in the full model with all four variables (Figure 4A). In models with multiple variables, including *CR* reduced estimate errors in trees of all sizes, but the magnitude of its effect was most notable in the largest trees (Figure 5), whose biomass has been notoriously difficult to predict. For example, in a large pantropical dataset, errors for small trees could be reduced by including *H* in models, but errors for large trees remained (Feldpausch et al. 2012). In our analysis, we found the same effects of *H* as above, whereas *CR* was effective at reducing error for all tree sizes. Thus, we suggest that this parameter should be included in allometric equations when higher accuracy of AGB estimates is desired.

Using local data, including *CR* greatly improved model estimates, even more so than *H*, and it may not be necessary to include *H* when *CR* is already included. This is apparently in contrast to expectations that both *H* and *CR* would be needed to account for trade-offs between vertical height and horizontal branch growth (King et al. 2006, Poorter et al. 2006, Iida et al. 2012). However, including both *H* and *CR* may be necessary to account for architectural variation and accurately assess AGB if comparing different geographical regions or attempting to create widely applicable allometric equations. For example, AGB of trees in northwestern Amazonia were overestimated by Chave et al. (2005) models without *H* (Alvarez et al. 2012), where trees may have smaller crowns than in southwestern Amazonia (Barbier et al. 2010). The relationship between maximum height, *H*-*D* ratios, and crown size may also change with tree development and geography. In a Liberian forest, crown width and depth were negatively correlated with adult stature in trees throughout their ontogeny (Poorter et al. 2003). However, in Bolivia, the same negative relationship was observed in young trees only, and the relationship became positive in adult trees (Poorter et al. 2006). This reinforces the view that accounting for *CR* may always be important in both local and pantropical models and suggests that, like *H*, the relationship between *CR* and AGB may not be consistent across all forest types or tree sizes. Tropical forest biomass estimates could be improved by more research on crown dimensions and allometry.

Of all models not including crown factors, those developed in this study better estimated AGB of trees than published models with the same variables. Predictions from new equations (Table 2.6) are also far more stable than those from published studies, in which models created from the same dataset have yielded very different results when estimating AGB of our trees (Table 2.2). This may be a result of our sampling scheme, which has a fairly even *D* distribution and includes several large trees, as was also observed in another dataset with a similar design (Overman et al. 1994).

Another key difference between the new and published models is the importance and influence of wood density. In published equations, the coefficient for ρ is always < 1 and sometimes very low (< 0.5). However, in our new models, this coefficient is always > 1, and equations without the coefficient constrained to 1 always performed better. Thus, our data suggests that ρ plays a more important role in allometry and total AGB than merely converting volume to mass. It may be correlated to other, unmeasured variables related to ecological strategy, tree architecture, and mechanics (King et al. 2006, Anten and Schieving 2010, Iida et al. 2012). Specifically, ρ has been positively correlated with crown width (Sterck et al. 2006, Anten and Schieving 2010, Iida et al. 2012) and related to variation between height and crown width with diameter (King et al. 2006). In this dataset, we also found that ρ was significantly and positively related to CR. In our regression analysis, this idea is further supported by the reduction in the coefficient for ρ when CR or M was included. Our sampling design, with a wide range of AGB and ρ in every D size class, may have allowed the influence of this variable to be expressed statistically. The importance of ρ is also clear in the ANOVA, in which ρ explained more variation in tree biomass than any other variable, when all other variables and interactions are already included in the model (31.2 %; Figure 4A), even though, as a lone variable, ρ explains the least variation in total AGB (18 %; Figure 4B). This is likely an effect of multicollinearity between the other three variables —D, H, and CR— while the effect of ρ is more independent and explains additional variation in AGB after structural effects are considered. For example, AGB of two large trees of comparable size, one species with low ρ and one with high ρ, can vary by over an order of magnitude (Goodman et al. 2012c). Though we did not explicitly study species effects, our results are consistent with recent findings that allometric relationships are highly affected by species (Lines et al. 2012). Thus, wood density, an intrinsic property, appears to largely explain variation among species after accounting for superficially-measured size variables.

Including CR also helps resolve many of the statistical problems associated with current allometric equations, as it reduced error for all tree sizes and normalised distribution of the error. Conversely, non-normal error distributions call into question the validity of equations not including CR. However, our models without CR were generally better estimators of AGB than published models, demonstrating that the accuracy of our models has not been undermined. In our analysis, non-normal distributions were usually caused by a slight negative tail, often caused by the largest D tree in our dataset (169 cm), confirming that irregularly-shaped boles can cause very large errors in biomass estimates (Clark and Clark 2000, Clark

2002, Nogueira et al. 2006). For this tree, *D* was measured over a highly fluted stem, as specified by standard protocols when the entire stem is fluted —e.g., RAINFOR (Phillips et al. 2009a) and Winrock International (Pearson et al. 2005). Thus, actual basal area was lower than indicated by measured *D*. Nonetheless, we chose to keep this tree in the dataset because it was selected via our unbiased methodology and, thus, represents true variability in the relationship found between *D* and AGB. As recently highlighted, it is important not to bias allometric equations by excluding 'imperfect' trees in biomass data (Clark and Kellner 2012).

Although including *CR* in allometric equations greatly improves AGB estimates, collecting crown dimension data can be an expensive and time-consuming task. Thus, we realise that it will most likely not become part of extensive forest inventories. Nonetheless, the problem posed by errors in large trees makes it important to determine the value of *D* at which the gains in accuracy merit measuring *CR*. Examining improvements in our dataset, it appears that *CR* should be measured and used to estimate AGB of all trees $D \geq 95$ cm, as it consistently and greatly improves estimates of these trees (Figure 5).

The monopodial variable (*M*) was not as effective as *CR*, but the significance of this variable shows that a simple architectural classification system has the potential to improve AGB estimates without labour-intensive data collection. The lower biomass of monopodial trees also demonstrates that crown form, or how branches fill space, may be important as well as the peripheral dimensions. Equations with both *CR* and *M* performed very poorly, suggesting these two parameters covary, and theoretical work has also noted that total branch length is lesser in monopodial trees than trees with other growth patterns (Mäkelä and Valentine 2006). In the current dataset, only 11 trees were classified as having monopodial architecture. Hence, a larger sample size may help improve the performance of this architectural variable in future models.

The lack of significant influence of crown position (illumination index) was somewhat surprising, even when separated into binomial variables: emergent/ not emergent or suppressed/ not suppressed. We expected that crowns of emergent trees would be much larger (c.f., King 1996, Thomas 1996, Poorter et al. 2006) and thus change the relationship between *D*, ρ, and *H* and AGB. Again, the lack of significant effects may be due to the small sample size in this dataset, and more samples could help improve our understanding of the relationship between forest structure, individual tree allometry, and biomass. We suggest that new biomass studies should attempt to include these factors, as well as crown architectural classification (even applied retrospectively) and, most importantly, crown dimensions.

2.4.4 Practical models for remotely-sensed and forestry data

Models designed to allow AGB to be inferred from LiDAR or other remote sensing data, using only H and CEA, were relatively successful considering that they exclude the two variables usually regarded as the most important, D and ρ (e.g., Baker et al. 2004b). Including crown area (CEA) in models greatly improved estimates over models with only H. The model including both H and CEA actually performs better than the equation with H and D, probably because CEA is both related to D and acts as a weak proxy to ρ. Indeed, ρ was significantly, linearly related to CEA ($R^2 = 0.068$; $P = 0.036$) but not significantly related to D ($R^2 = 0.034$; $P = 0.193$). This further demonstrates the importance of crown dimensions and the potential to improve AGB estimates from remote sensing. Estimating CEA from LiDAR data may be restricted practically to emergent trees, but, as illustrated earlier, more accurately estimating AGB of the largest trees will improve AGB density estimates greatly. Furthermore, given that the largest trees are most likely to be removed by selective logging or increased mortality (Lindenmayer et al. 2012), applying these methods could help improve estimates of carbon stock changes in degraded and managed forests.

2.5 Conclusions

Current maps and models of the magnitude, distribution, and sensitivity of tropical forest carbon stocks and fluxes are in part limited by the great challenge of developing robust allometric models to estimate tree biomass. This study shows that including crown dimensions in allometric equations to predict tropical tree biomass can greatly improve estimates, especially for trees with $D > 95$ cm (Table 2.6, Figure 5), which have long been the cause of much uncertainty in forest biomass estimates and are the focus of widespread degradation via selective logging across the tropics. Tree crowns have been largely ignored both in allometric theory and in practical attempts to improve biomass estimates for the vast regions where little or no directly measured biomass data exist.

By testing published model estimates on new biomass data from a previously unrepresented region (southwestern Amazonia), we show that the majority of published equations were poor predictors of our 51 trees, predominately due to severe underestimates of most of the largest trees. For both the most widely adopted (Chave et al. 2005) and recently proposed new pantropical biomass equations (Feldpausch et al. 2012), models without height slightly overestimated AGB of our trees, but models with height always underestimated AGB by a greater amount (Table 2.2, Figure 3). Therefore, adjusting biomass equations for height alone may be insufficient to account for allometric variation between regions and forest types because crown mass must also be considered. In southwestern Amazonia, crowns are relatively large (Figure 2), which substantially compensate for their lower height. These results also show that the difference in predictions from models with and without height cannot be attributed simply to overestimates of models without height. More generally, 'best estimates', even from models with all possible variables, should not be considered as entirely accurate or baselines to which all other estimates are compared.

In new models, crown radius accounts for variation in AGB not explained by diameter, wood density, or height. In fact, crown radius explained more variation and improved model estimates more than height (Figure 4). Given the apparent geographic variation of crown size across both broad geographical regions and within local scales (Barbier et al. 2010), the inclusion of crown dimensions in allometric equations is likely to be widely important for improving the performance of both pantropical and regional models. Models developed from this dataset, which contains several very large trees and includes and crown radius as a parameter, show promise for improving tropical AGB estimates and carbon stock changes via both traditional field inventories and emerging remote sensing technologies.

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CHAPTER 3 Amazon palm biomass and allometry

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 and family-level 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.

3.1 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. 2004b, 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 ≤ height ≤ 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 = $a + bx$ (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.

3.2 Materials and methods

3.2.1 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 3.1).

3.2.2 Data collection

In total, 136 arborescent palms from nine species were individually measured, harvested, and weighed in 2006 and 2011 (Table 3.1). 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 A3.1). 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 3.1. 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)	H_{stem} (m)	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**

3.2.3 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 A3.1), and species mean *dmf* was calculated as the average of individual means (Table 3.2). 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 3.2). Mean individual leaf mass was calculated by dividing total leaf mass by the number of leaves.

3.2.4 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 A3.1). 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 $1 - (\mathrm{SS}_{\mathrm{error}} / \mathrm{SS}_{\mathrm{total}})$.

3.2.5 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 3.3). 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.

3.3 Results

3.3.1 Architecture and internal properties

For most species, height–diameter relationships were weak and height could not be predicted from *D* (Figure 3.1A). 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 3.2), among individuals of the same species, and along the stem of the same individual (Table A3.1). 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 3.2). 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 3.1B), but within a species AGB is more strongly related to stem height (Figure 3.1C). 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 3.2).

Table 3.2. 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**		

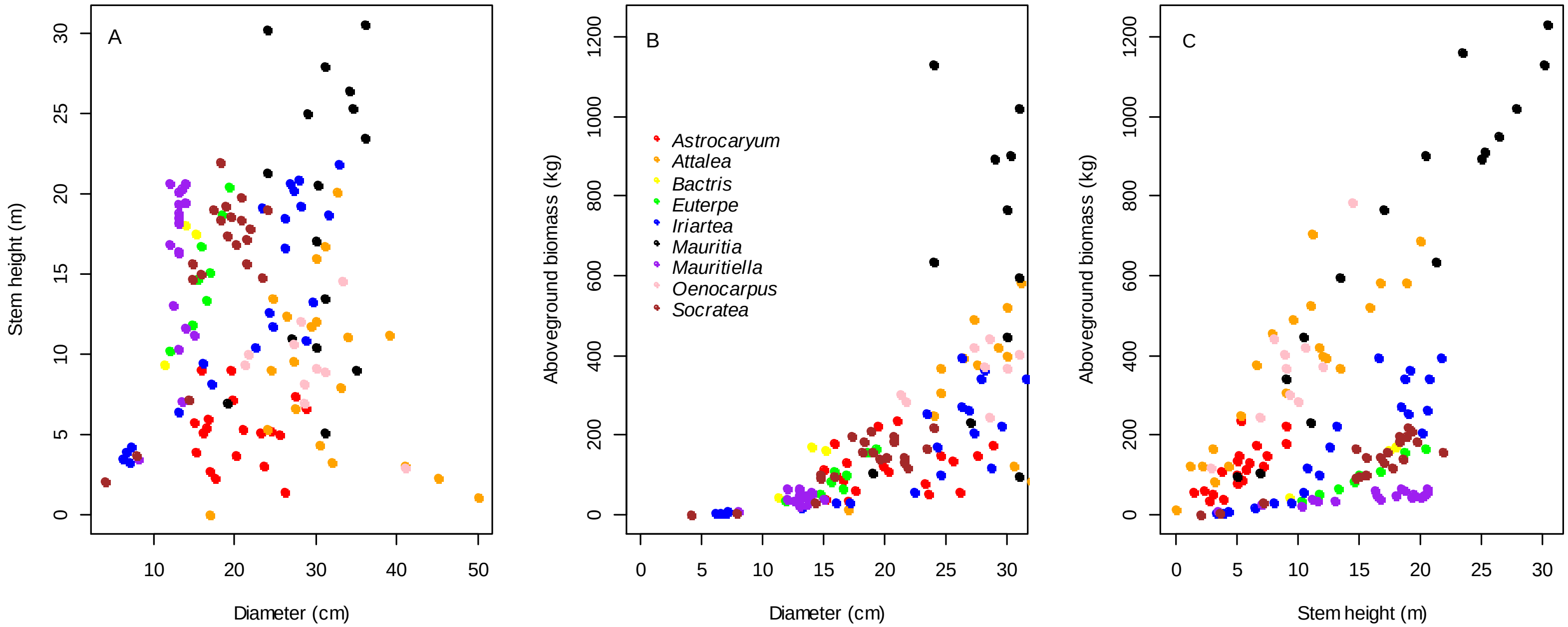

Figure 3.1. Raw data showing the relationships between (A) stem height and diameter and (B) aboveground biomass and diameter, and (C) aboveground biomass and stem height for each species.

3.3.2 Species-level models

Single-species models performed well, with $R^2 > 0.90$ for most species (Table 3.3, Figure 3.2). 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 A3.2). 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 3.3. Other models, with different predictor variables, are available in Table A3.2.

Table 3.3. 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	RSE	F	dfe	Pr < F	AIC
Aboveground biomass												
Astrocaryum	AGB	H_{stem}		.	21.302		0.957	26.1	379	17	<0.0001	171.4
Attalea	ln(AGB)	$\ln(H_{stem}+1)$		3.2579	1.1249		0.858	0.371	115	19	<0.0001	21.9
Euterpe	AGB	H_{stem}		-108.81	13.589		0.973	8.37	215	6	<0.0001	60.4
Iriartea	ln(AGB)	$\ln(D^2H_{stem})$		-3.483	0.94371		0.967	0.311	560	19	<0.0001	14.5
Mauritia	ln(AGB)	$\ln(H_{stem})$		2.4647	1.3777		0.897	0.273	121	14	<0.0001	7.7
Mauritiella	AGB	H_{stem}		.	2.8662		0.972	8.21	591	17	<0.0001	129.9
Oenocarpus	ln(AGB)	H_{stem}		4.5496	0.1387		0.784	0.237	29	8	0.00066	3.4
Socratea	ln(AGB)	$\ln(D^2H_{stem})$		-3.7965	1.0029		0.976	0.227	740	18	<0.0001	1.3
Family-level	$AGB^{0.25}$	$(dmf \times D^2H_{stem})^{0.25}$		.	0.5551		0.990	0.367	10410	105	<0.0001	91.5
	ln(AGB)	ln(D)		-3.3488	2.7483		0.802	0.588	384	95	<0.0001	176.1
	ln(AGB)	ln(D)	ln(dmf)	-2.0752	2.6401	0.843	0.815	0.570	208	94	<0.0001	171.1
Belowground root biomass												
Mauritia	ln(BGB)	$\ln(H_{stem})$		-0.3688	2.0106		0.929	0.323	184	14	<0.0001	13.1
Mauritiella	ln(BGB)	H_{stem}		1.0945	0.11086		0.951	0.132	310	16	<0.0001	-18.0
Leaf dry mass												
Family-level	$mass^{0.3}$	length		0.66020	0.10896		0.732	0.171	202	74	<0.0001	-48.5
Iriartea	ln(mass)	length		-5.1751	1.4547		0.803	0.649	78	19	<0.0001	45.4

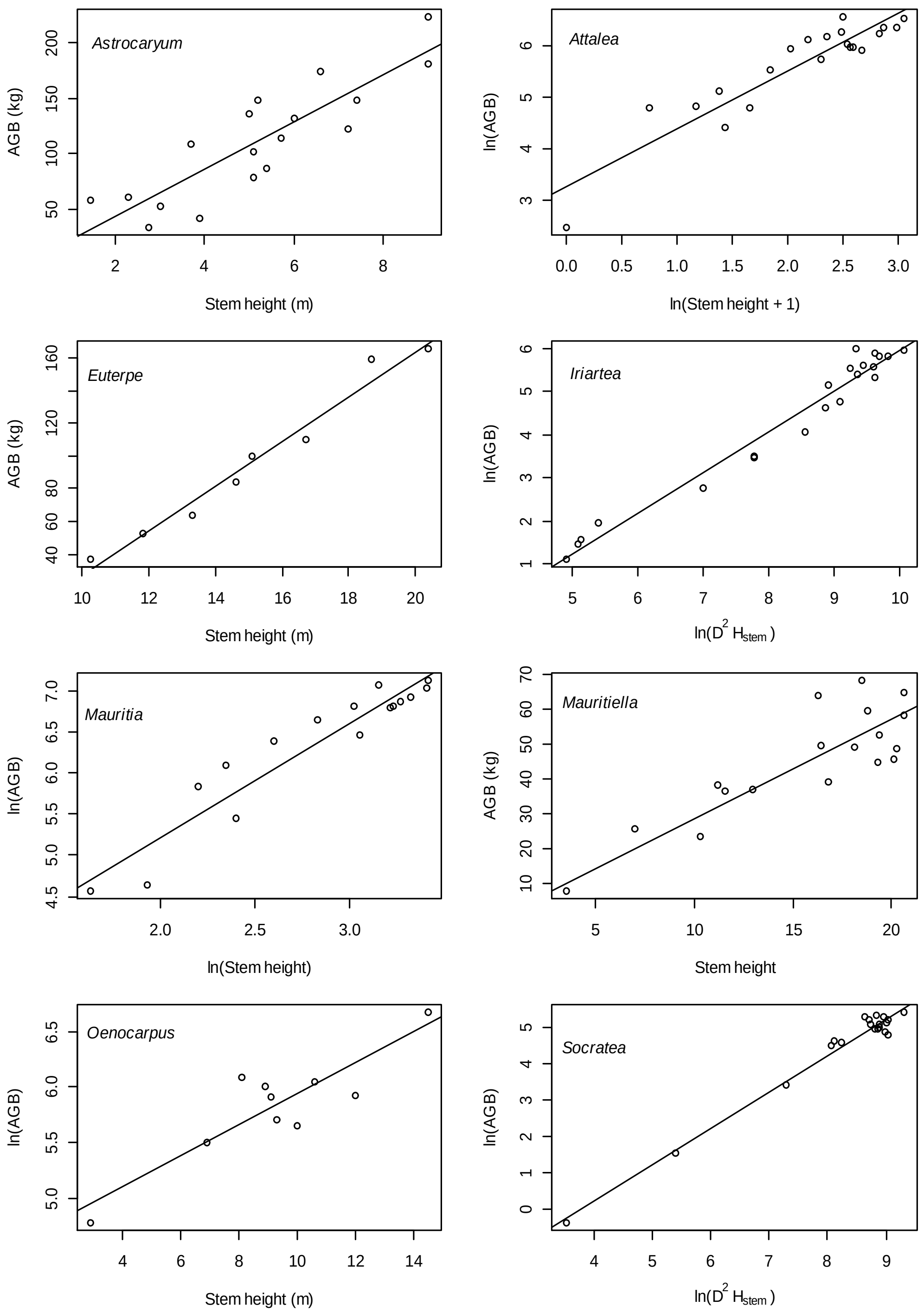

Figure 3.2. Aboveground biomass (AGB) data and recommended model (line) for each genus to estimate AGB (kg dry mass) from stem height (H_{stem}; m) and diameter at 1.3 m or above stilt roots (D; cm). Equations are given in Table 3.3.

3.3.3 Family-level models

The transformed model with compound term $dmfD^2H_{stem}$ best estimated AGB of all species (Table 3.3). This model was selected as best from the metrics used to evaluate built models (R^2, RSE, AIC; Table A3.3) and performed well against the test data (Table A3.4). 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 3.3A).

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 A3.1). Thus, we had to remove outliers, and the resulting equations are only valid within the given range (Table 3.3). 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 3.3B,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 3.3). 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 3.4).

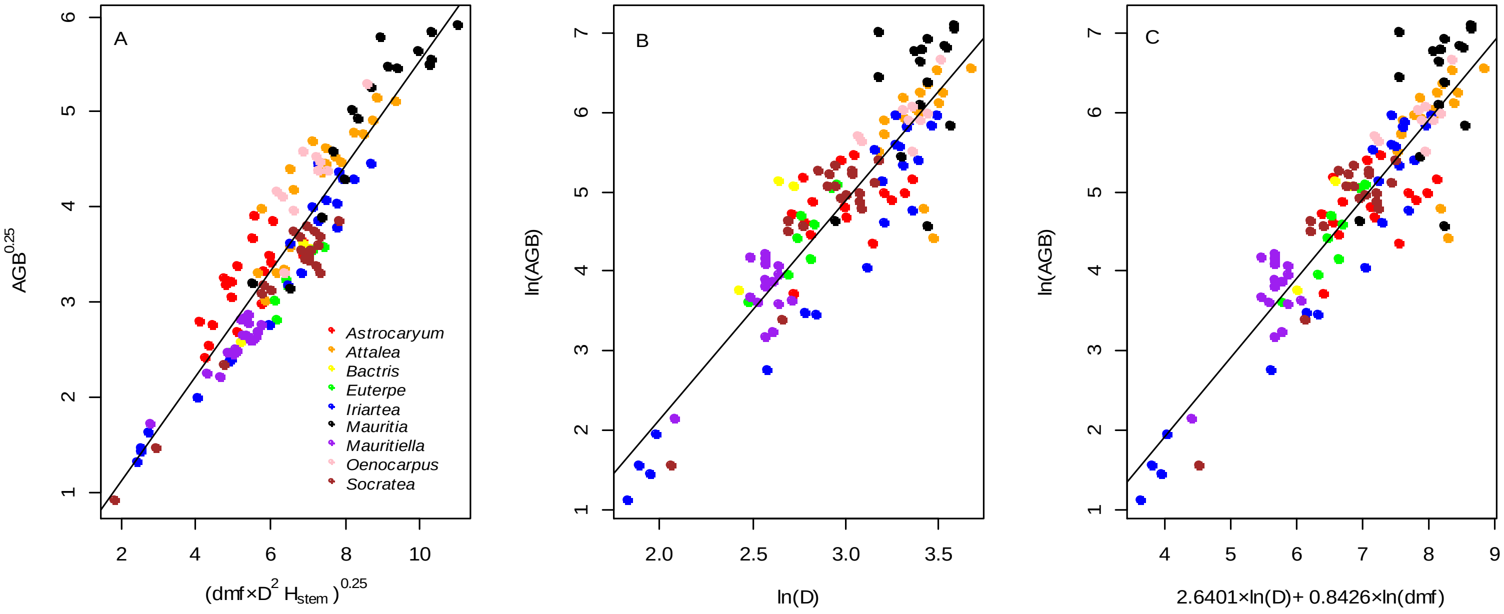

Figure 3.3. Aboveground biomass (AGB) data for all species (points) and three family-level model estimates (lines) using (A) $dmfD^2H_{stem}$, (B) *D*, and (C) *D+dmf*. Equations are given in Table 3.3.

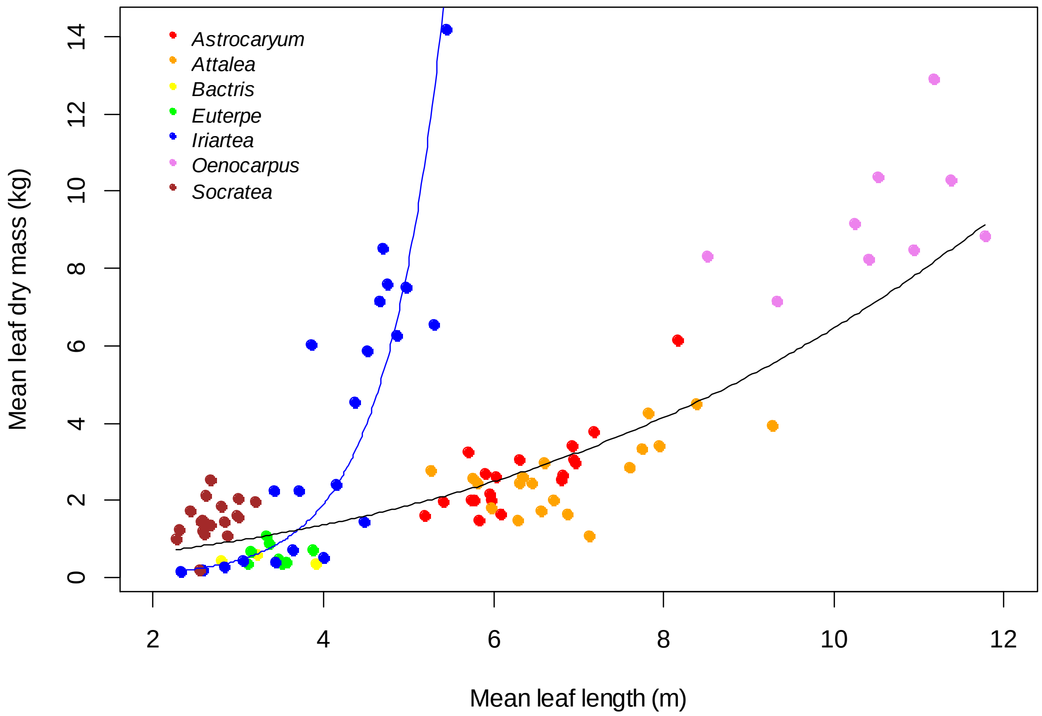

Figure 3.4. Mean leaf mass and mean length of leaves for individuals in each species. Lines are regression models for *Iriartea* (blue) and all other species (black) as listed in Table 3.

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 A3.4). All family-level models performed reasonably well, except the models with H_{tot} and $H_{tot}+dmf$ (Table A3.4).

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 3.4). 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 3.4). 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 3.5). 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.

Table 3.4. Evaluation of palm and dicot model estimates. Recommended species-level models are given in Table 3, family-level palm models are shown in Table A.3, and dicot models are from Feldpausch et al. (2012).

	Model	**Sum (Mg)**	**error (kg)**	**Mean %error**	**Mean RE**	**SD RE**	R^2
All biomass data (n = 136)							
Palm models	Species	0.8	5.6	2	8	31	0.919
	$(\text{dmf}\times D^2 H_{\text{stem}})^{0.2}$	-1.8	-13.1	-5	13	45	0.852
	ln(D)+ln(dmf)	5.8	42.9	18	77	211	-0.110
	ln(D)	6.0	44.4	18	77	211	-0.184
Dicot models	Feld 1	7.5	55.3	23	81	207	-0.124
	Feld 2	2.5	18.3	8	66	175	0.145
All data within range of validity for all models (H_{stem} > 3 m, 6 ≤ D < 40 cm; n = 125)							
Palm models	Species	0.8	6.6	3	7	28	0.917
	$(\text{dmf}\times D^2 H_{\text{stem}})^{0.2}$	-1.8	-14.1	-5	15	45	0.847
	ln(D)+ln(dmf)	0.0	-0.1	-0.03	32	93	0.615
	ln(D)	0.2	1.5	0.6	35	96	0.576
Dicot models	Feld 1	1.8	14.1	6	38	97	0.548
	Feld 2	-2.1	-17.0	-7	30	87	0.564

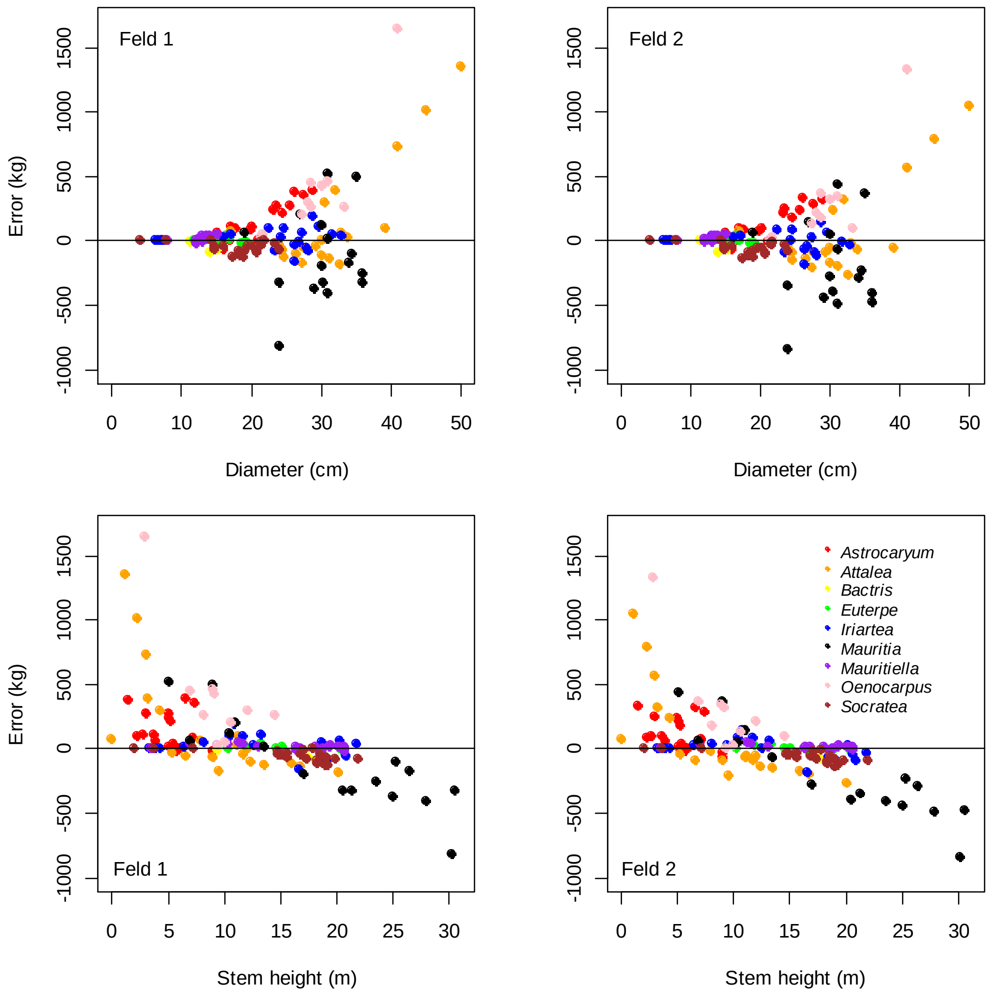

Figure 3.5. Errors ($AGB_{estimated}$–$AGB_{observed}$) for harvested palm aboveground biomass (AGB) when estimated by dicot models using and diameter and wood density (Feld 1) and diameter, wood density, and estimated height (Feld 2; Feldpausch et al. 2012) compared with diameter and stem height.

3.3.5 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 3.5). Using estimates from the recommended species models (Table 3.3), 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 3.5). 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 3.5).

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 3.5).

Table 3.5. 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 3.3); and the recommended species-level model for each species or genera (Table 3.3). 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**

3.4 Discussion

3.4.1 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 3.2. 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.

3.4.2 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 3.4). 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.

3.4.3 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 3.5). 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 3.5). 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 3.3) 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).

3.5 Conclusions

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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CHAPTER 4 Extending the arc of deforestation: forest carbon stocks and uncertainty in southwestern Amazonia

Abstract

The forests of southwestern Amazonia are increasingly contested due to pressures from multiple development, extractive, and conservation land uses. Accurate inventory of the forest resource base is therefore a priority for land use planning. Current forest biomass estimates in this area are uncertain, in large part because of geographic variation in tree allometry that is not accurately represented in pantropical biomass models. To test the effect of applying the first regionally-appropriate allometric equations for trees in the southwestern Amazon and the first family-level biomass models for Amazon palms, I derive aboveground biomass densities for 53 permanent plots in the southwestern Amazon and estimate regional carbon stores. Mean tree and palm aboveground biomass was 218 and 272 Mg/ha in forests with and without bamboo, respectively. Accounting for non-inventoried aboveground forest components, including necromass, contributed an additional 52–72 Mg/ha. Thus, total average forest AGB stocks were 277 and 335 Mg/ha, in forests with and without bamboo, respectively. Original aboveground carbon stocks over the entire 746,653 km^2 ‘southwest Amazon moist forest ecoregion’ are estimated at 11.5 Pg C with 8 % uncertainty. This value is 0.8 Pg (800 million tonnes) of carbon greater than an estimate made with the widely used pantropical model that explicitly includes tree height, but 0.9 Pg C lower than indicated by the current pantropical model that excludes height. Including belowground biomass carbon brings this regional estimate to 13.9 Pg C with 11 % uncertainty. Nearly one third of this region has been deforested or significantly impacted by humans. Thus, 4.4 Pg C have been or are immediate risk of being released via continued forest degradation and deforestation.

4.1 Introduction

The southwestern Amazon is an important region for conservation or development and resource extraction. Forests are still mostly intact in this region, which spans nearly 75 million ha over northern Bolivia, southwestern Brazil, and eastern Peru (Olson et al. 2001). However, with the recent completion of the Interoceanic highway, deforestation and forest degradation are expected to accelerate (Asner et al. 2010, Southworth et al. 2011, Perz et al. 2013) and perhaps push Brazil's 'arc of deforestation' westward. In response to this threat, the southwestern Amazon, and especially the MAP region (Madre de Dios, Peru – Acre, Brazil – Pando, Bolivia), is also a focus for many carbon-based conservation projects (Asner et al. 2010, Rendón Thompson et al. 2013) linked to the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation (REDD/REDD+). Individual REDD projects in this region include a range of land tenure types and management schemes, such as national and state reserves and parks, conservation concessions, Brazil nut concessions (Nunes et al. 2012), and sustainable forest management in forestry concessions and indigenous land (Rendón Thompson et al. 2013).

Accurately quantifying the biomass and carbon stocks of in this region is a crucial component to the success of these carbon-based projects (Houghton et al. 2009, Baker et al. 2010). Only with reasonably constrained values of carbon stocks can the climate threat, and climate-change mitigation potential, embodied in these forests and changes be set in wider context. Forest carbon stock density estimates are the largest single source of uncertainty in tropical carbon emissions from deforestation and land use change (Houghton et al. 2000, Baccini et al. 2012, Dutra Aguiar et al. 2012) and will therefore need to improved to accurately assess any reduction in emissions. Without accurate measurement, REDD projects may suffer from high uncertainty and lack the credibility needed to garner sufficient finance and policy traction to have significant impact.

Yet, aboveground biomass (AGB) estimates in this region are highly variable from one publication to another in the southwestern Amazon, with mean estimates ranging two-fold, from 177 to >350 Mg/ha (Baker et al. 2004a, Saatchi et al. 2007, Nogueira et al. 2008b, Asner et al. 2010, Saatchi et al. 2011, Salimon et al. 2011, Feldpausch et al. 2012). Two key sources of uncertainty are the choice of allometric equation (Chave et al. 2004) and the poor sampling across geographic and environmental space in the pantropical database used to develop these equations (Houghton et al. 2009). For example, AGB estimates can vary substantially depending on the equation used to estimate biomass from forest inventory data (Baker et al. 2004b, Chave et al. 2004), and pantropical tree models (Chave et al. 2005, Feldpausch et al. 2012) lack data from the southwestern portion of Amazonia. This is problematic because a number of important factors affecting individual and forest biomass vary across the tropics and Amazonia. Compared to other Amazonian forests, trees in the southwest are generally shorter (Nogueira et al. 2008b, Feldpausch et al. 2011), crowns are larger (Barbier et al. 2010), mean wood density is lower (Baker et al. 2004b, Nogueira et al. 2007), and palm abundance is greater (Kahn et al. 1988, Terborgh and Andresen 1998, Emilio et al. 2013). Allometric equations developed to estimate biomass from any number of explanatory variables intrinsically incorporate the relationships between these variables in the data used to create them. Thus, this allometric variation introduces a source of error when equations from other areas are used to estimate biomass in the southwestern Amazon, as has been found in other areas (Nelson et al. 1999, Clark and Clark 2000, Ketterings et al. 2001, Nogueira et al. 2008a).

Researchers have begun to address the errors in AGB estimates from allometric variation by accounting for tree heights, and as a result substantially reduced estimates of tree AGB in the southwestern Amazon (Nogueira et al. 2008b, Feldpausch et al. 2012). For example, Feldpausch et al. (2012) developed height–diameter (H–D) equations for regions across the tropics. Then, heights estimated from these equations were used —in addition to measured D and sometimes wood density (ρ)— to estimate AGB with a pantropical model. Because trees are on average shorter in the southwestern Amazon than elsewhere, new AGB estimates were 16 % lower in western Amazonia, compared to estimates made from models that do not explicitly account for H (Feldpausch et al. 2012). However, these estimates were not tested against directly-measured biomass data, because none existed, nor was the error associated with choice of allometric model evaluated.

Addressing these issues could improve biomass estimates and reduce uncertainty in the southwestern Amazon. Using the first directly-measured biomass dataset from the southwestern Amazon, I show that although trees are shorter in this region, as compared to other tropical regions, the branch mass in larger crowns partially compensate for their shorter stature (Chapter 2). Furthermore, the difference between AGB estimates based on models with and without H is not entirely due to overestimates made by the model with only D and ρ (Chapter 2). Rather, the pantropical models without H overestimated AGB and the models including H, but not crown width, underestimated AGB of harvested trees (Chapter 2).

Current methods for estimating arborescent palm biomass further contribute to uncertainty in AGB estimates of southwestern Amazonian forests. For convenience in large-area and multi-site studies, palm biomass is often estimated with the same equations as applied to dicot trees (e.g., Malhi et al. 2004, Phillips et al. 2008, Baccini et al. 2012), but these models can underestimate arborescent palm biomass (Chapter 3). Because arborescent palms are abundant in western Amazonia (Kahn et al. 1988, Terborgh and Andresen 1998, Emilio et al. 2013), estimating their biomass using palm-specific models could impact forest biomass estimates in this region.

Beyond uncertainties in stand-level AGB estimates, the variation of AGB density across the landscape is another important source of uncertainty in forest carbon stock estimates (Chave et al. 2004). One problem is that many different forest types exist within the southwestern region of the Amazon, but there is no consistent forest type classification or spatially explicit map delineating them across national borders. 'Bamboo-dominated' forests are unique to this region (Nelson 1994) and have lower AGB than forests without bamboo (Nogueira et al. 2008b, Salimon et al. 2011), but the spatial extent of this forest type has only begun to be mapped across international borders (Carvalho et al. 2013).

In this study, I therefore applied the first regionally-developed models to estimate AGB of dicot trees (Chapter 2) and the first family-level models to estimate AGB of arborescent palms (Chapter 3) in southwestern Amazonia. Specifically, I address the following questions: (i) how do new tree and palm models affect forest biomass estimates in this region?, (ii) how much carbon is held in intact forests, and how much is likely to be lost in the coming decades?, and (iii) what is the uncertainty associated with new estimates?

4.2 Methods

4.2.1 Biomass density estimates in southwestern Amazonia

For this study, the southwestern Amazon was defined as the 'southwest Amazon moist forest' terrestrial (SWA) ecoregion (Olson et al. 2001, WWF 2004). As there is no consistent forest type classification across Bolivia, Brazil, and Peru, I used the ecoregion classification system because it broadly defines moist forests based on their biota regardless of national boundaries (Olson et al. 2001).

Forest inventory data were obtained for 53 lowland (< 500 masl) permanent plots distributed within the SWA ecoregion (Olson et al. 2001, WWF 2004) (Figure 4.1), each of which have been developed according to careful and consistent, internationally standardised protocols of tree measurement, identification, and data quality control (Phillips et al. 2009a). Plot data were downloaded from the ForestPlots.net database on 1 May 2013 (Lopez-Gonzalez et al. 2011, Lopez-Gonzalez et al. 2012). Plots ranged from 0.42 to 2.25-ha in area and census dates from 1991 to 2009. The forest plots analysed encompassed many forest types. Plots were categorised by RAINFOR researchers according to composition (mixed forest, bamboo-dominated, or palm-dominated) and hydrological conditions (*terra firme*, former floodplain, rarely flooded, or swamp). The majority of plots were considered to be mixed, *terra firme* forest (n = 35), and all were 'old growth' (i.e., 'apparently undisturbed'; Malhi et al. 2006). As forests with bamboo are common in this region (Carvalho et al. 2013) and have lower AGB than forests without bamboo (Nogueira et al. 2008b, Salimon et al. 2011), I separated plots with this classification (n = 3). All other forest types were grouped (n = 50), as there were no significant differences in AGB between any other forest type classifications ($P >$ 0.05).

Tree AGB was calculated using the Good II.1 model (D and ρ; Chapter 2) and compared to estimates by two pantropical models —using D and ρ only (Feld 1) and D, ρ, and H (Feld 2; Feldpausch et al. 2012). Palm AGB was calculated using the two pantropical dicot models and the D+dmf palm model (Chapter 3). Inventoried stand AGB density estimates were the sum of Good II.1 model estimates for dicots and D+dmf model estimates for palms.

Total aboveground forest biomass estimates were made by adding inventoried estimates (trees and palms with $D \geq 10$ cm) to estimates of all other forest components. The biomass contribution of non-inventoried forest components were obtained from the literature for the most geographically appropriate studies available and separated by forest type and edaphic conditions when data were available (Table 4.1). As no liana AGB or necromass density values could be obtained specifically for forest with bamboo, I used liana data available for 'non-dense' forests in the southwestern Amazon (Nogueira et al. 2008a) and the same necromass values for forest without bamboo. In total, 52.39–71.72 Mg/ha were added to AGB estimates of inventoried trees and palms in each of the 53 plots according to their forest type and edaphic classifications.

Belowground biomass (BGB) was estimated at the stand-level using a pantropical model relating BGB to AGB: $BGB = 0.489 \times AGB^{0.89}$ based on a compilation of available aboveground and root biomass data (Saatchi et al. 2011). In this case, AGB is AGB estimated from the inventoried trees and palms ($D \geq 10$ cm) only. Carbon stocks were estimated as 47.35 % of total biomass, as found for tropical angiosperm trees in Panama (Martin and Thomas 2011).

Table 4.1. Mean values from the literature for forest components not included in the plot inventories.

	Density (Mg/ha)						
Forest component	**Mean**	**SD**	**SE**	***n***	**Location**	**Forest type***	**Source****
Bamboo	7.51	0.17	0.12	2	MdD: bamboo	B	a
Fine litter	6.00	0.40	0.07	33	Colombia	B,N	b
Herbaceous vegetation	0.60	0.10	0.02	33	Colombia	B,N	b
Lianas	5.95	6.25	3.13	4	Rondonia & Amazonas	B	c
Lianas	15.00	10.60	4.33	6	MdD: no bamboo	N	d
Necromass	29.30	6.47	2.64	6	MdD: *terra firme*	B,N	e
Necromass	19.42	1.89	0.85	5	MdD: lowland	B,N	e
Small trees (5-10 cm)	11.75	10.49	1.38	58	MdD: bamboo	B	a
Small trees (5-10 cm)	13.71	12.00	0.66	332	MdD: no bamboo	N	a
Small trees (D <5 cm)	1.16	0.29	0.17	3	MdD	B,N	a
TOTALS							
***terra firme*, bamboo**	**62.27**						
lowland, bamboo	**52.39**						
***terra firme*, all others**	**71.72**						
lowland, all others	**61.84**						

*** Forest type: forest with bamboo (B) or non-bamboo forests (N)**

****Sources: [a](Goodman et al. 2012b), [b](Sierra et al. 2007), [c](Revilla Cardenas 1987, Graca et al. 1999, Cummings et al. 2002); mean and standard error are calculated from four study means reported in Nogueira et al. (2008a) for non-dense forests in Rondônia and Amazonas, Brazil, [d](DeWalt and Chave 2004), [e](Araujo-Murakami et al. 2011) using Chao et al. (2009) estimates for wood density.**

4.2.2 Carbon stock and potential emissions estimates in the southwestern Amazon

Areas of each forest type and classification in the southwestern Amazon were obtained from freely available downloadable files, and all spatial analyses were performed using ArcMap® version 9.3.1 (Environmental Systems Resource Institute, Redlands, California). Spatially explicit Terrestrial Ecoregions of the World data files (Olson et al. 2001, WWF 2004) were used for spatial analysis and area calculation (Figure 4.1). Intact forest landscape (IFL) —"defined as an unbroken expanse of natural ecosystems within areas of current forest extent, without signs of significant human activity, and having an area of at least 500 km^2" (Potapov et al. 2008)— was downloaded to serve as an indicator of stable forest cover and potential deforestation. Original carbon stocks were estimated for both bamboo and non-bamboo forests as the product of total aboveground carbon stock density and total area within the southwestern Amazon ecoregion. Stable carbon stocks and potential emissions were estimated using the areas categorised as intact (stocks) and no longer intact (emissions) assuming that 100 % of aboveground forest carbon has been, or will be, released in areas outside of the IFL.

The area covered by 'bamboo-dominated' forests within the southwestern Amazon was estimated from Carvalho et al. (2013). 132,966 km^2 of the SWA ecoregion was classified as bamboo forest (18 % of the total ecoregion) using the following calculations and assumptions: (i) the intersection between the southwestern Amazon ecoregion the Carvalho study area was 391,076 km^2 (Figure 4.1) and (ii) the proportion of bamboo forests occurring in the original Carvalho study area (34 %) is the same the proportion of bamboo forests occurring in the 391,076 km^2 intersection.

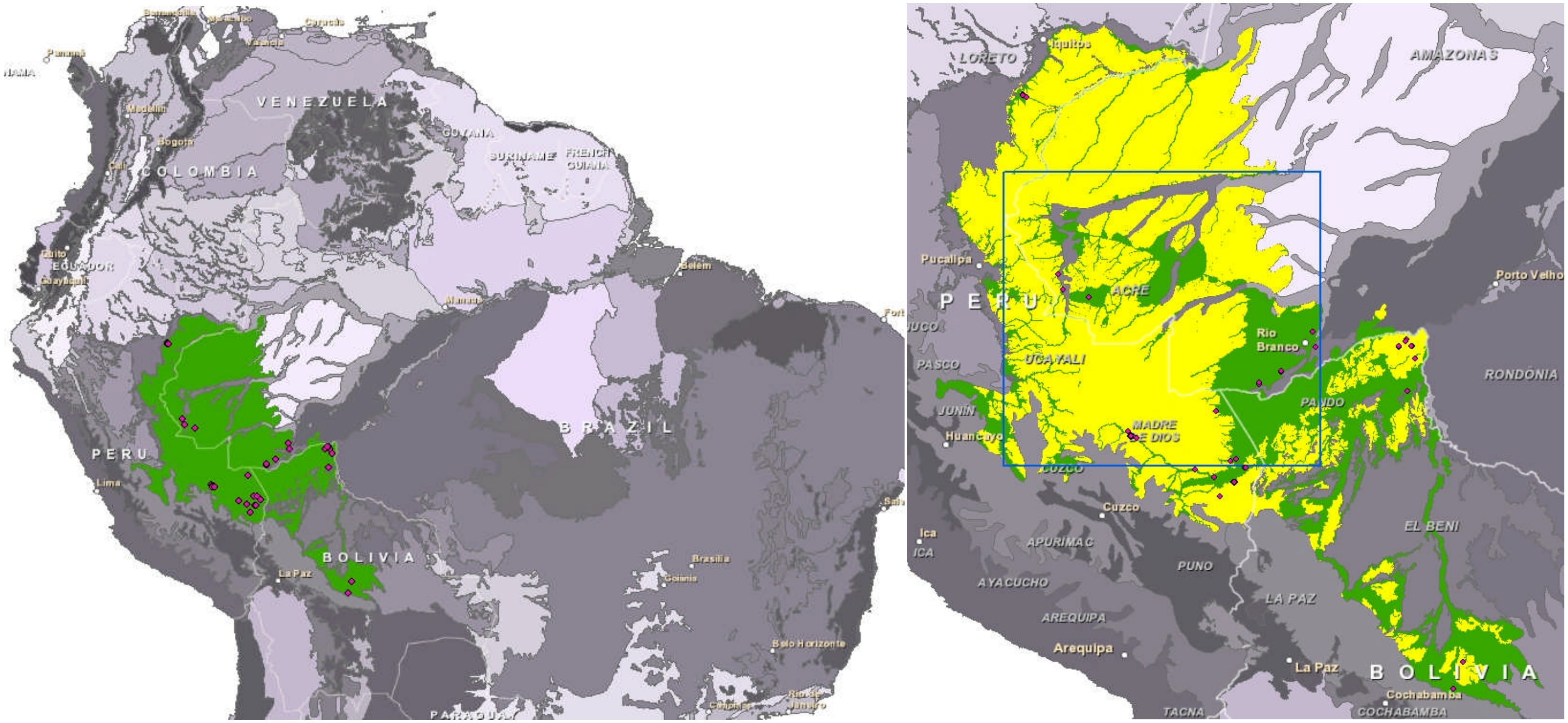

Figure 4.1. Map of ecoregions (Olson et al. 2001, WWF 2004), with the southwest Amazon moist forest (SWA) ecoregion in green, and the 53 lowland forest plots analysed (dots) within South America (left panel). In the right panel, the SWA ecoregion is shown in detail and overlain by the intact forest landscape (yellow; Potapov et al. 2008) and spatial extent of bamboo study (blue rectangle; Carvalho et al. 2013).

4.2.3 Uncertainty analysis

Uncertainty was estimated by propagating errors at each level of the analysis for above- and belowground biomass and carbon stocks. For AGB, errors were estimated for the allometric differences between sites, choice of allometric model and other forest components, variability in AGB across the landscape, and forest type classification. Errors associated with single trees —i.e., tree measurement error and error from the allometric equation itself— were not included because these errors have been found to average out at the stand-level (Chave et al. 2004). Furthermore, there should be few errors associated with D and ρ because of strict protocols for D measurements, species identification, and database management. Plot sizes were assumed to be sufficiently large (0.42–2.25 ha) to not introduce errors associated with the scale of sampling (Nascimento and Laurance 2002, Chave et al. 2004). Errors (ε) were estimated as standard error (SE) as a percentage of the mean estimate, $\varepsilon = \frac{SE}{mean} \times 100\ \%$. Details are given below.

Allometry error ($\varepsilon_{Allometry}$*)*: To determine the uncertainty associated with differing tree allometry across the region, allometric relationships were compared between two datasets from southeast Peru —Tahuamanu province, where biomass models were developed (Chapter 2), and Tambopata province, where an intensive forest inventory was conducted (Appendix 4.1). I tested for differences in allometric relationships between the two sites (H–D, CR–D, and CR–H) in generalised linear models (glm) with the dependent variable, site, and site × dependent variable interaction. For this analysis, subsets of the Tambopata data were randomly selected from each 20-cm D size class so that the sample size in each size class was equal to that of the Tahuamanu dataset. Ten glm analyses were performed, using different randomly selected subsets of data, to determine which relationships were significant. All analyses were performed using the R statistical platform, version 3.0.0 (R Core Team 2013).

Model selection error ($\varepsilon_{Model\ selection}$*)*: To explore the effects of using different equations to estimate AGB in this region, AGB density of trees was estimated in five *terra firme* forest plots in Tambopata, using four models developed in southwestern Amazonia (Chapter 2) — models I.1, II.1, I.1CR, and II.1CR, using D, ρ, and sometimes H and/or CR (Appendix 4.5). Mean and SE of the four estimates were used to determine % error of tree AGB. For palms, mean, SE, and % error were determined from the four palm equations used to estimate plot-level palm AGB in Tambopata (Chapter 3). Next, the estimated % error of trees and palms (i.e., $\varepsilon_{model\ selection\_trees}$) from the Tambopata plots were used to estimate SE of tree and palm estimates in the 53 plots across the SWA ecoregion (i.e., $SE_i = AGB_{trees} \times \varepsilon_{model\ selection\_trees} / 100\ \%$; Table 4.3). SE for all other components were taken from the literature (Table 4.1).

In each forest type, $\varepsilon_{Model\ selection}$ for trees, palms, and all other forest components was calculated by summing SE of each component and dividing by the mean of total forest AGB density:

$$\varepsilon_{Model\ selection_j} = \frac{\Sigma SE_{ij}}{AGB_j} \times 100\ \%$$

where *i* is forest component, *j* is forest type, and AGB_j is mean forest AGB estimated in each forest type (Table 4.2). Finally, $\varepsilon_{Model\ selection}$ of the entire ecoregion was estimated as the sum of SE in each forest type divided by total AGB estimate in both forest types, which is nearly identical to the area-weighted average of each forest:

$$\varepsilon_{Model\ selection} = \frac{\Sigma(\varepsilon_{model\ selection_j} \times Density_j \times Area_j)}{\Sigma(Density_j \times Area_j)}$$

$$= \frac{(SE_{bamboo} + SE_{no\ bamboo})}{Total\ AGB\ estimate}$$

where *j* is forest type, *Density* is AGB density (Mg/ha), and *Area* is area (ha). For both steps used to estimate $\varepsilon_{Model\ selection}$ (by forest type and overall), standard errors were summed directly, rather than in quadrature, because these two estimates were not independent (Keller et al. 2001). Many values for SE_i were the same for both forest types (Table 4.1, 4.3).

Landscape variability error ($\varepsilon_{Landscape}$): This error was assessed using the mean and SE of plot AGB densities (Sierra et al. 2007) in each forest type ($\varepsilon_{Landscape\_j}$). The error was assessed over the entire ecoregion as per the equation above for $\varepsilon_{Model\ selection}$ (Table 4.4). In this case, standard errors were also summed directly as a conservative estimate of error because plots were not distributed randomly across the landscape (Taylor 1997).

Forest type classification error ($\varepsilon_{Forest\ classification}$): This error was estimated by calculating AGB over the total ecoregion using two estimates for area of bamboo forests —i.e., the area estimated in this chapter and that reported in the original study (Carvalho et al. 2013). Mean and SE of total AGB in the region were estimated using both estimates of land areas in each forest type.

Total AGB error (ε_{AGB}): Total uncertainty in AGB estimates was calculated with the following formula, assuming that errors are independent and random (Taylor 1997, Saatchi et al. 2011):

$$\varepsilon_{AGB} = \left(\varepsilon^2_{Allometry} + \varepsilon^2_{Model\ selection} + \varepsilon^2_{Landscape\ variation} + \varepsilon^2_{Forest\ classification}\right)^{0.5}$$

Total BGB error (ε_{BGB}): BGB uncertainty was estimated from total ε_{AGB} and the model relating BGB to AGB using the following formula:

$$\varepsilon_{BGB} = [23.2^2 + (0.89\varepsilon_{AGB})^2]^{0.5},$$

where 23.2 % is the error of the model to estimate BGB and 0.89 is the exponent for AGB in the model (section 4.2.1; Saatchi et al. 2011).

Total carbon error: Finally, the error associated with converting AGB to carbon was estimating using the mean wood carbon fraction, standard deviation, and sample size reported in Martin and Thomas (2011). Above- and belowground carbon stock estimates were separately assuming that the errors were independent and random:

$$\varepsilon_{Carbon} = \left(\varepsilon^2_{Biomass} + \varepsilon^2_{Carbon\ fraction}\right)^{0.5}$$

Total uncertainty and confidence intervals: The combined standard error (CSE) was estimated as the product of error (%) and the mean estimates. As BGB was estimated from AGB, their errors could not be assumed independent. Thus, the CSE of both total biomass and carbon were estimated as the sum of above- and belowground uncertainties:

$$CSE_i = \left(\varepsilon_{AG_i} \times mean_{AG_i}\right) + \left(\varepsilon_{BG_i} \times mean_{BG_i}\right),$$

where *i* is biomass or biomass carbon. Finally, the 95 % confidence limits were determined as mean estimate ± 1.96(CSE).

4.3 Results

4.3.1 Biomass density estimates in southwestern Amazonia

Area weighed mean of tree AGB is 247.6 Mg/ha using the Good II.1 model, which is 9.7 % less than the Feld 1 estimate and 9.1 % greater than the Feld 2 estimate. In both forest types, palm AGB estimates were greater using the palm-specific model than either pantropical dicot model. Thus, the area-weighted average of AGB density of inventoried trees and palms is 8.9 % lower and 9.4 % higher than the Feld 1 and 2 estimates, respectively. Tree and palm biomass in forests classified as 'bamboo-dominated' is 54.6 Mg/ha or 20 % lower than in forests without bamboo (Table 4.2). Including all other aboveground biomass components brought total AGB estimates to 277 and 355 Mg/ha in forests with and without bamboo, respectively. BGB estimates were 59 and 72Mg/ha in forests with and without bamboo, respectively. Thus total forest biomass (above- and belowground) estimates are 335 and 407 Mg/ha in forests with and without bamboo, respectively, with a weighted average of 394 Mg/ha. At 47.35 % carbon fraction, total carbon density estimates are 159 and 193 Mg/ha in forests with and without bamboo, respectively, with an area-weighted average of 189 Mg/ha.

Table 4.2. Summary of aboveground (AG) and belowground (BG) biomass (B) and carbon (C) estimates in the southwestern Amazon for forests with and without bamboo. Allometric equations for trees and palms are described in Chapters 2 and 3, respectively. Values for other forest components are listed in Table 4.1 and carbon is estimated as 47.35 % of biomass.

	Forests with bamboo		Forests without bamboo		
	mean	SE	mean	SE	Overall mean
Tree AGB (D≥10cm)					
Good II.1	209.1	42.0	255.9	6.8	247.6
Feld 1	231.7	39.8	282.7	7.1	273.6
Feld 2	191.6	32.6	234.4	5.6	226.8
Palm AGB (D≥10cm)					
D+dmf	8.5	6.1	16.3	1.8	14.9
Feld 1	7.8	5.5	15.8	1.7	14.4
Feld 2	7.3	5.1	14.3	1.5	13.1
Tree and palm AGB (D≥10cm)					
Good II.1 + *D+dmf*	217.6	41.8	272.2	6.4	262.5
Feld 1	239.5	39.8	298.5	6.8	288.0
Feld 2	198.9	33.0	248.7	5.3	239.8
Other forest components					
AGB	59.0	3.3	62.8	0.6	62.1
Total forest biomass (Goodman estimates)					
AGB	276.6	42.5	335.0	6.3	324.6
BGB	58.7	10.0	71.7	1.5	69.4
AGB+BGB	335.2	52.5	406.7	7.8	394.0
Total forest carbon (Goodman estimates)					
AGC	131.0	20.1	158.6	3.0	153.7
BGB	27.8	4.8	34.0	0.7	32.9
AGC+BGC	158.7	24.9	192.6	3.7	186.6

4.3.2 Total aboveground biomass and carbon stock estimates in southwestern Amazonia

Original aboveground biomass and carbon stock estimates in the ecoregion are 24.24 Pg AGB and 11.48 Pg C, 85 % of which is held in forest without bamboo. Over the same area, these estimates are 0.90 Pg C lower than estimates made with the Feld 1 model and 0.80 Pg C greater than Feld 2 estimates calculated in this study. Including BGB adds 5.2 Pg biomass and 2.5 Pg carbon (Table 4.5).

Over a total area of 746,653 km^2 in the southwestern Amazon ecoregion, only 68.4 % remains as intact forest. Aboveground carbon stock estimates in the remaining 510,454 km^2 of intact forest are 7.85 Pg C, and including BGB brings 'stable' carbon stock estimates to 9.52 Pg. If all aboveground biomass has been or will be lost in the non-intact forest, emissions will amount to an estimated 3.63 Pg C. If all the carbon from decaying roots has been or will be released as well, total carbon emissions would total 4.41 Pg C.

4.3.3 Uncertainty analysis

Allometry error ($\varepsilon_{Allometry}$): Allometric relationships were similar between the two sites studied: neither $CR–D$ nor $CR–H$ relationships were significantly different between sites, but trees in Tambopata are taller at the same D (Appendix 4.4). Because only the site variable, not the interaction between site and D, was significantly different for $H–D$ relationships, allometry error was assessed by comparing the mean values for intercept in each site based on 20 glm analyses (H~D+Site) using different subsamples of trees in Tambopata. Mean intercepts from the glm analyses were -17.89 and -16.16 in Tahuamanu and Tambopata, respectively. Comparing these two values, SE = 1.22 and $\varepsilon_{Allometry}$ = 5.07 %.

Model selection error ($\varepsilon_{Model\ selection}$): Mean and SE of each forest component was compiled to calculate errors as a percentage of total AGB density per forest type (Table 4.3). Model selection error in Tambopata was estimated as 1.65 % for trees and 2.19 % for palms (Appendix 4.5). Using mean estimates and SE of other forest components (Table 4.1) and mean forest AGB density in each forest type (Table 4.2), $\varepsilon_{Model\ selection}$ was estimated at 4.03 and 3.72 % in forests with and without bamboo, respectively (Table 4.3), which equates to 3.77 % error across the region.

Table 4.3. Mean estimate, standard error (SE), and error (ε) for each component in each forest type.

Component	mean	SE_i	% error
Forest with bamboo			
Trees	209.1	3.45	1.65
Palms	8.5	0.19	2.19
Bamboo	7.5	0.12	
Fine litter	6.0	0.07	
Herbaceous vegetation	0.6	0.02	
Lianas	6.0	3.13	
Necromass	29.3	2.64	
Small trees (5-10 cm)	11.7	1.38	
Small trees (D <5 cm)	1.2	0.17	
	AGB_j	ΣSE_{ij}	$\Sigma SE_{ij}/AGB_j$
	276.6	11.16	**4.03**
Forest without bamboo			
Trees	255.9	4.22	1.65
Palms	16.3	0.36	2.19
Fine litter	6.0	0.07	
Herbaceous vegetation	0.6	0.02	
Lianas	15.0	4.33	
Necromass	29.3	2.64	
Small trees (5-10 cm)	13.7	0.66	
Small trees (D <5 cm)	1.2	0.17	
	AGB_j	ΣSE_{ij}	$\Sigma SE_{ij}/AGB_j$
	335.0	12.46	**3.72**

Landscape variability error ($\varepsilon_{Landscape}$): Errors were calculated using the mean and SE of AGB density in each forest type to estimate total AGB stocks and SE, and area weighted error totalled 4.85 % (Table 4.4).

Table 4.4. Errors associated with variability across the landscape: mean, standard error (SE), error, and area for each forest type and combined error due to landscape variability ($\varepsilon_{Landscape\_j}$).

Forest type	Mean	SE	error	Area	Estimate	SE
	(Mg/ha)		(%)	(km^2)	(Pg)	
bamboo	276.6	26.6	9.6	132,966	3.68	0.35
no bamboo	335.0	13.4	4.0	613,687	20.56	0.82
Sum				746,653	24.24	1.18
					$\varepsilon_{Landscape}$ (%) =	**4.85**

Forest type classification error ($\varepsilon_{Forest\ classification}$): This error was assessed using total AGB stock estimates using the two estimates for the spatial extent of bamboo forests in this region. Using my estimate of 132,966 km^2 of bamboo forests, total AGB was estimated at 24.24 Pg. Using 161,500 km^2 of bamboo forests and 585,153 km^2 of forest without bamboo, total AGB estimates would be 24.07 Pg. Comparing these two estimates, SE = 0.08, and ε = 0.35%.

Total AGB error (ε_{AGB}): Total uncertainty in AGB estimates was estimated as 24.26 % using the errors estimated above in the following formula:

$$\varepsilon_{AGB} = \left(5.07^2 + 3.77^2 + 4.85^2 \ + 0.35^2\ \right)^{0.5} = 7.97\ \%$$

Total BGB error (ε_{BGB}): Uncertainty in BGB was estimated using ε_{AGB} in the following formula:

$$\varepsilon_{BGB} = [23.2^2 + \ (0.89 \times 7.97)^2]^{0.5} \ = 24.26\ \%.$$

Total carbon error: Finally, the error associated with converting AGB to carbon was estimating with mean = 47.35 %, standard deviation = 2.51, and *n* = 190 (Martin and Thomas 2011). Thus, the additional error introduced by this conversion is 0.385 %. Adding this error to ε_{AGB} and ε_{BGB} brings total uncertainty of carbon stock estimates to 7.98 and 24.26 % for above- and belowground stocks, respectively:

$$\varepsilon_{AGC} = \left(7.97^2 + 0.385^2\ \right)^{0.5} = 7.98\ \%$$

$$\varepsilon_{BGC} = \left(24.26^2 + 0.385^2\ \right)^{0.5} = 24.26\ \%$$

Total estimates and uncertainty: Combined SE of AGB and BGB were 1.8 and 1.2 Pg, respectively, for a total of 3.0 Pg (Table 4.5). Thus, the 95 % confidence interval for AGB and total biomass stock estimates are [20.4, 28.0] and [23.2, 35.7] Pg, respectively. Combined standard uncertainty of above- and belowground carbon stock estimates were 0.9 and 0.6 Pg, respectively, for a total of 1.5 Pg. Thus, the 95 % confidence interval for aboveground and total carbon stock estimates are [9.7, 13.3] and [11.0, 16.9] Pg, respectively.

Table 4.5. Summary of aboveground (AG) and belowground (BG) biomass (B) and biomass carbon (C) stock estimates in the southwestern Amazon ecoregion.

	Biomass and carbon stock estimates (Pg)					
	AGB	**BGB**	**Tot B**	**AGC**	**BGC**	**Tot C**
Estimate	24.24	5.18	29.42	11.48	2.45	13.93
Combined standard uncertainty	1.93	1.26	3.19	0.92	0.60	1.51
Lower confidence limit (95 %)	20.4	2.72	23.17	9.68	1.29	10.97
Upper confidence limit (95 %)	28.0	7.65	35.67	13.27	3.62	16.89

4.4 Discussion

4.4.1 Biomass density in southwestern Amazonia

Because of the ecological and political interests in forests in the southwestern Amazon, it is important to establish reliable models to estimate forest biomass and carbon stocks here, which will also improve estimates of carbon emissions from deforestation. AGB of trees estimated by regionally-appropriate models were intermediate between estimates made by the two pantropical models, and palm AGB is greater when estimated by a family-level model than by either dicot model. These stand-level results are consistent with the directly measured biomass data for trees (Chapter 2) and palms (Chapter 3). In this study, the difference between the two Feldpausch model density estimates was 48.1 Mg/ha or 16.7 % of the Feld 1 values, which is nearly identical to the reduction in forest biomass estimates called for in Feldpausch et al. (2012). However, using new biomass data and allometric equations, I estimate that the biomass of trees and palms is this region is, on average, only 8.8 % lower than the Feld 1 estimate (3.1–18.8 % lower in individual plots). These results emphasise the importance of improving the spatial coverage of directly-measured biomass data, as just one dataset drastically changed forest biomass estimates in this region.

These new biomass estimates and focus on this geographic region provide clarity to the vast array of estimates reported in the literature, which are highly variable and dependent on the equation used to estimate tree and palm biomass from forest inventories. Using several of the same forest plots as this study mean AGB density of trees and palms in forests without bamboo (272 Mg/ha; Table 4.2) and overall, area-weighted mean (262 Mg/ha) are within the ranges of values reported in prior studies for the western Amazon: 225–326 Mg/ha (Baker et al. 2004a) and 252–300

Mg/ha (Feldpausch et al. 2012), which further confirms that previously published models have both over- and underestimated tree biomass in this region (Chapters 2 and 4). As expected from the biomass study (Chapter 2), the regional estimates in this study are much higher than those reported for both forest types in the southwestern Brazilian Amazon (Nogueira et al. 2008b): using my models, tree and palm biomass estimates were 84 % higher in bamboo-dominated open forests and 17 % higher in bamboo-free dense forests, perhaps because the adjustments for lower tree height and wood density (Nogueira et al. 2008b) underestimated tree biomass (Chapter 2). Interestingly, the area-weighted mean AGB density estimated in this study for trees is only 1 % higher than mean AGB density reported for Acre, Brazil (Salimon et al. 2011), even though biomass was estimated with an outdated model using diameter only (Brown 1997) and Acre has a high concentration of bamboo-dominated forests (Carvalho et al. 2013). As found in other studies, AGB density is lower in forest more open forests with bamboo than in dense forests without bamboo (Nogueira et al. 2008b, Asner et al. 2010, Salimon et al. 2011). Palm biomass is also lower in forests with bamboo (Foody and Hill 1996, Carvalho et al. 2013).

Because many remote sensing metrics are based on forest height and pantropical models that include height underestimate AGB of trees in this region (Chapter 2), it is no surprise that some remote sensing studies have estimated forest biomass density much lower than this study. In the southern Peruvian Amazon, a study using high-resolution light detection and ranging (LiDAR) estimated that median total forest carbon densities were 85–125 Mg C/ha in lowland forests (Asner et al. 2010), which is 19–45 % lower than my estimates. Likewise, in comparison to a large-scale remote sensing analysis, mean forest aboveground living biomass density found in this study was higher than those estimated in the first earth observation based analysis (150–250 Mg/ha; Saatchi et al. 2007). Oddly, a subsequent analysis including forest canopy height raised AGB estimates in the southwestern Amazon to 250–400 Mg/ha (Saatchi et al. 2011), which better corresponds to our density estimates but does not match with the effect of including tree height in biomass estimates in every other example.

The biomass of other forest components was estimated by adding mean values reported in the literature, rather than estimating their contribution as a proportion of inventoried tree AGB (e.g., Nogueira et al. 2008a), because the latter method assumes a positive linear relationship between inventoried and non-inventoried components. There was not enough data available to explore relationships rigorously, but the liana (DeWalt and Chave 2004) and necromass (Araujo-Murakami et al. 2011) data used suggested that these two components were not related to AGB of trees in the same stand. This concurs with an intensive field study in the Brazilian Amazon, in which inventoried tree biomass ($D \geq 10$ cm) was not significantly related to any other living or dead component or all other components combined (Nascimento and Laurance 2002). Furthermore, the proportion or relationship between AGB of inventoried trees and other biomass components will be dependent upon the tree AGB estimate used in the study, which may not have been accurate in past studies in the southwestern Amazon.

4.4.2 Total aboveground biomass and carbon stock estimates in southwestern Amazonia

The importance of improving biomass density estimates is demonstrated when extrapolated over a large scale. In this case, a difference of 48 Mg/ha, as found between the two pantropical models, results in a discrepancy of 3.6 billion tonnes in pre human-impact biomass carbon stock estimates when scaled over the entire 746,653 km^2 area. Forest AGB was estimated at 24.2 Pg, or 1.7 billion tons more than the recommended pantropical model (Feld 2), but could still be improved.

Firstly, more appropriate forest type classifications would improve the accuracy biomass estimates. Though detailed studies have both defined different forest types and found distinct AGB densities between them (Nogueira et al. 2008a, Fearnside et al. 2009, Asner et al. 2010, Salimon et al. 2011), there is no consistent forest type classification or spatially explicit map delineating them across national borders. I used the southwestern ecoregion because it delineated moist tropical forests based on natural assemblages (Olson et al. 2001), but it was created considering both plant and animal largely communities and was largely designed as a tool for biodiversity conservation (Olson et al. 2001). Consequently, it may not be the most appropriate for biomass estimation, and forest carbon estimates across the landscape could be improved by a more detailed classification of forest type. Once forest types are defined, better representation of less common forest types, such as palm- and bamboo-dominated forests, would further improve forest biomass estimates in this region (Salimon et al. 2011). However, forest type classification should not be too narrowly defined. For example, the Regional Government of Madre de Dios defined 23 vegetation types —based on the adaptations, ecology, and distribution of plants— in Madre de Dios alone (Encarnación Cajañaupa et al. 2009), which were far more than necessary to estimate forest biomass (Goodman et al. 2012a). Large-scale remote sensing studies may side-step the problem of defining forest types, but basing biomass estimates purely on canopy height criteria is an oversimplification.

Estimates of current carbon stocks and emissions to date could also be improved upon with better estimates of forest cover, degradation, and secondary regrowth. Like many forest type classifications, forest status classifications have also been developed for biodiversity conservation purposes (McCloskey and Spalding 1989, Bryant et al. 1997, Sanderson et al. 2002, Kareiva et al. 2007) and may not best represent what is most important for determining forest biomass. 'Intact' is generally based on ecological integrity (Potapov et al. 2008) and being 'beyond significant human influence' (Bucki et al. 2012), but degraded forests can still maintain substantial carbon stocks and biodiversity (Ansell et al. 2011, Putz et al. 2012) and even regrow (Houghton et al. 2000, Naughton-Treves 2004, Asner et al. 2010). Thus, IFL was used to estimate 'stable' forest, rather than current forest cover, but even 'stable' forest may be underestimated by IFL (Southworth et al. 2011, Figure 4.1). This binary measure of intact forests also does not account for less extreme changes in land use or carbon fluxes, such as secondary growth and degradation, which can influence net carbon emissions significantly (Naughton-Treves 2004, Asner et al. 2010).

Although ILF underestimates current forest cover, it offers a warning for future scenarios in which areas with higher accessibility are at high risk of being cleared, fragmented, or degraded (Southworth et al. 2011, Bucki et al. 2012, Perz et al. 2013), much like Brazil's 'arc of deforestation'. Though uncertainty cannot be estimated, 9.52 Pg is likely to be the minimum estimate of remaining carbon stocks and 4.41 Pg is likely a maximum estimate of carbon emissions. This emissions estimate rivals that of the southern portion of the arc of deforestation: in Mato Grosso and Rondônia, over 343,000 km^2 of forest and cerrado were cleared, resulting in 4.14 Pg C lost by 2007 (Fearnside et al. 2009). Both IFL and deforestation models (Soares-Filho et al. 2006) show that the MAP region is especially vulnerable to human pressures. In fact, the arc of deforestation already extends into Acre, Brazil. In contrast, large expanses of stable forest exist in much of the rest of the southwestern Amazon. As both deforestation and forest regrowth are heavily influenced by political and economic incentives or restrictions (Naughton-Treves 2004), the fate of these forests, and their respective carbon stocks, have yet to be determined. They have the potential to be a great store of biomass, biodiversity, and sustainable forest management or a large source of carbon emissions.

4.4.3 Uncertainty in biomass and carbon estimates

Uncertainty in forest biomass accounts for over half of total uncertainty in forest carbon flux estimates (Houghton et al. 2000), but using regionally-appropriate allometric equations and high-quality inventory measurements reduces much of this uncertainty (Chave et al. 2004). At the stand-level, there was little variation between tree AGB estimates made by the four regional models tested. Thus, error from choice of allometric model ($\varepsilon_{Model\ selection}$ of trees) was much lower in this study (1.65 %) than reported for models developed from only 50 trees in Panama (10 %; Chave et al. 2004).

In this study, I determined that using the Goodman model II.1 was appropriate to use in another area, but did not ignore slight allometric differences. Variation in allometry was, in fact, the largest single source of uncertainty in AGB estimates. However, standard error was large because allometry was studied at only two sites. If error were assessed using standard deviation, as a measure of true variability, then variation across the landscape would be the largest source of error, as determined in Chave et al. (2004).

Forests with bamboo are often poorly represented (Salimon et al. 2011), and this study is unfortunately no exception. The error associated with landscape variability was more than double (9.6 %) that of forests without bamboo (4.0 %), primarily due to the small sample size in these forests. AGB density in forests with bamboo may also be poor, and even underestimated, because of the disconnect between ground measurements and remote sensing analysis determining the spatial extent of bamboo-dominated forests. For example, perhaps only plots with a high bamboo component are classified as ‘bamboo-dominated’ in ground-based forest inventories, but the spatial mapping of ‘bamboo-dominated’ forests may cover a broad spectrum of bamboo presence and even included areas that have been populated by bamboo at any time over four decades (Carvalho et al. 2013). Despite the substantial differences in AGB density of forests with and without bamboo, forest type classification between forests with and without bamboo contributed very little to overall uncertainty of regional forest biomass and carbon stocks. However, this study has not considered all forest type classifications or the different human pressures on each forest type. Spatially explicit forest type classification or biomass estimates will also improve estimates of losses from deforestation and degradation (Dutra Aguiar et al. 2012).

Unlike other studies (Keller et al. 2001, Sierra et al. 2007), uncertainty in AGB estimates was not dominated by the tree component. Rather, very limited data about lianas and necromass led to high levels of error from these components, even though their contributions to forest AGB are an order of magnitude less than inventoried trees. Though the errors were not estimated with the same methods for trees as compared to other forest components, this may reflect reality. Inventoried trees and palms are, by definition, actually measured, whereas mean values for necromass and lianas have been estimated from only a few sites and often do not span environmental gradients or large geographic space. In fact, no data were available from forests with bamboo. Furthermore, error associated with the model —calculated from residual standard error (RSE; Chave et al. 2004)— used to estimate any of aboveground the components was not included. Though model RSE were not reported for the liana (Putz 1983, DeWalt and Chave 2004) or necromass (Araujo-Murakami et al. 2011) studies used in this report (Table 4.1), the errors associated with these models may be greater than those for trees. Coefficients of determination (R^2) are much lower for liana biomass equations (0.694; Schnitzer et al. 2006) than for tree models (0.965 for model II.1; Chapter 2); and necromass is estimated by a series of steps —including estimating volume, adjustments for hollow sections, wood density, and level of decay (Chao et al. 2009, Araujo-Murakami et al. 2011)— each of which may introduce error. Because the relative error is so high for necromass (up to 9 %; Table 4.1) and especially lianas (up to 52 %) forest biomass estimates could potentially be improved fairly easily by conducting more studies of the biomass contribution of these components.

Though it is very difficult, forest biomass estimates could be improved and uncertainty reduced enormously by improving belowground biomass estimates. Compared to aboveground biomass data, belowground data far less common and often unreliable (Cairns et al. 1997, Mokany et al. 2006). In this study, BGB contributed less than 18 % to total above- and belowground biomass estimates across the region but nearly 40 % to total uncertainty. Error associated the BGB estimates was much higher than ε_{AGB}, which was almost entirely from the error associated with the equation used to estimate BGB from AGB, rather than from ε_{AGB}. Even if there was no uncertainty from AGB estimates, ε_{BGB} would be only marginally lower (23 %) than the current estimate (24 %).

The uncertainty introduced when converting carbon to biomass was nearly negligible, despite the range of mean values reported for carbon fraction and its significance in terms of the final mean carbon estimate. For example, using the IPCC (2003) default of 50 % would have resulted in 0.6 Pg C or 6 % more than estimated with a carbon fraction of 47.35 %. It appears that the new IPCC (2006) default of 47 % is more appropriate though perhaps conservative. Error due to carbon conversion was low because the standard error of the mean was very small in the chosen study (Martin and Thomas 2011). Though Martin and Thomas (2011) appears to be appropriate —angiosperm tropical trees— it is not known how well the species sampled in Panama represent the species and individuals in the southwestern Amazon.

4.5 Conclusions and future directions

The stand-level analysis confirmed the results found from the directly measured biomass data for trees and palms (Chapters 2 and 3): tree biomass density is intermediate between estimates made by the two pantropical models, and arborescent palm AGB is greater when estimated by a family-level model than by either dicot model. New biomass and carbon density estimates are greater than or within the range of forest biomass density estimates previously reported for the southwestern Amazon, and the importance of improving biomass density estimates is demonstrated when extrapolated over a large area. In this study, new carbon stock estimates in the southwestern Amazon were 800 million tonnes greater than an estimate made with the recommended pantropical tree model.

More accurate forest biomass density estimates will also improve estimates of carbon emissions and emissions reductions, which may increase in this area as the arc of deforestation expands to the west. ‘Intact forest’ underestimated the current forest cover but the fact that nearly one third of the region may no longer support intact forests highlights the imminent threat of deforestation and forest degradation expanding outwards from human settlements and transportation routes.

Forest biomass estimates would be improved by developing a forest type classification system relevant to biomass storage and dynamics, increasing the number of inventories in lesser known forest types and of lianas and necromass, and improving estimates of root biomass. Nonetheless, applying regionally-appropriate and palm-specific allometric equations reduces much of the uncertainty in forest biomass estimates in this region, which should aid in the success of carbon-based projects and a comprehensive effort to make REDD+ a reality.

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CHAPTER 5 Conclusions

5.1 Synthesis of research

This research focuses on improving allometric models and forest biomass estimates by accounting for sources of variation not currently explained in tree models and fundamental differences between functional groups. The primary research objectives were to (1) test the importance and influence of crown dimensions and architecture on biomass of trees, (2) determine important allometric differences between trees and palms and develop models to estimate the biomass of arborescent palms accurately, and (3) examine the effect of new models on a large scale by estimating forest carbon stocks in the southwestern Amazon. To achieve these objectives, I collected the first set of directly-measured tree biomass data in this region (Chapter 2), collected and compiled the first comprehensive palm biomass dataset in the tropics (Chapter 3), and developed new allometric equations to estimate biomass using a variety of explanatory variables (Chapters 2 and 3). New tree and palm models were then applied to forest inventory plots in the southwestern Amazon to estimate total forest biomass and carbon stocks and compare to estimates made from pantropical biomass models (Chapter 4).

These results significantly advance allometric modelling and regional biomass estimates in the southwestern Amazon. The inclusion of crown dimensions, which has been ignored in both theoretical and empirical work, significantly improves biomass estimates for trees. Additionally, I found that accounting for one aspect of allometric variation between regions (i.e., height) leads to underestimates of AGB in the southwestern Amazon because larger crowns partially compensate for their shorter stature. Secondly, I found that the relationships between biomass, height, and diameter are very different between palms and dicotyledonous trees. Palm biomass in forests is generally greater when estimated by tree models because they weigh more than dicots at small diameters. Finally, I estimate that total forest carbon stocks are 11.5 Pg over an area of nearly 750,000 km^2, which is 0.8 Pg or 7.5 % greater than would have been estimated by the current pantropical model including height (model 2; Feldpausch et al. 2012).

Together, these results show that attention to allometric differences between trees in different geographic regions or forest types and between major taxonomic and functional groups (i.e., dicotyledonous trees vs. monocotyledonous palms) can substantially improve biomass estimates on both local and broad geographic scales.

Objective 1, Chapter 2: Including crown dimensions improves tropical tree biomass estimates

By including crown radius in allometric models, in addition to the three traditional variables (diameter, wood density, and height), I show that accounting for crown dimensions significantly improves biomass estimates, especially for large trees. Crown radius explained more variation and improved model estimates more than height. Of all four variables, crown radius was the best single predictor of tree AGB. Crown structure is also important, even after accounting for crown size, and trees with monopodial architecture had less biomass than other architectural types. By testing published model estimates on new biomass data from this previously unrepresented region (southwestern Amazonia), I found that the majority of published equations were poor predictors of the 51 trees weighed in this study, predominately due to severe underestimates of most of the largest trees. In recent years, two studies have included estimated height in models to account for allometric differences across the tropics (Nogueira et al. 2008b, Feldpausch et al. 2012), which have substantially downgraded AGB estimates in the southwestern Amazon. However, I show that although trees are shorter in this area, the branch mass in proportionally larger crowns partially compensates for their lower heights in terms of whole tree biomass. Thus, true biomass was generally intermediate between pantropical model estimates with and without height.

Objective 2, Chapter 3: Palm allometry differs from dicot trees and their biomass should be estimated separately

Palm biomass is typically estimated with the same equations as applied to dicot trees, but I show that this method is not accurate. Even though palms lack branches and are generally light ‘wooded’, they can be taller at small diameters (Rich et al. 1986) and subsequently weigh more. When palm mass is estimated with dicot models, the magnitude of error increases with stem diameter, but the direction of error depends on height of the stem. Palms with stem height less than 14–15 m tend to be overestimated by dicot models, but taller palms are underestimated. Because most palms in mature forests exceed 15 m, their biomass is consistently greater than would have been estimated by dicot models. In the nine plots studied, best estimates were 14 or 27 % greater than pantropical dicot model estimates, resulting in 1–2 % higher estimates for forest AGB density (palms and trees), compared to pantropical model estimates. In other forests, the effect of new palm equations on plot biomass estimates will likely depend on palm sizes, abundance, and species composition. I report both single- and mixed-species allometric equations with a variety of input variables to accommodate different forest inventory methods. However, I recommend stem height (i.e., excluding leaves) as the most reliable estimator of palm biomass, especially to estimate woody productivity.

Objective 3, Chapter 4: New forest carbon stock estimates in the southwestern Amazon

The effects of new tree and palm models were confirmed on a larger scale: tree mass estimates are between pantropical model estimates made with and without height, and palm mass is greater than estimated by either dicot model. In 53 RAINFOR plots in lowland, moist forests in the southwestern Amazon, mean tree and palm AGB was estimated at 218 and 272 Mg/ha in forests with and without bamboo, respectively. Accounting for non-inventoried aboveground forest components (bamboo, herbaceous vegetation, lianas, small trees, and necromass contributed an additional 52–72 Mg/ha. Thus, mean total forest AGB stocks were estimated at 277 and 335 Mg/ha, in forests with and without bamboo, respectively. Over the total area of 746,653 km^2 in the southwestern Amazon ecoregion (Olson et al. 2001, WWF 2004), original aboveground biomass and carbon stock estimates were 24.2 Pg AGB and 11.5 Pg C, both with 8 % uncertainty. Including carbon in belowground biomass brings this estimate to 13.9 Pg C with 11 % uncertainty. Using appropriate tree and palm models reduced uncertainty from model selection dramatically, but uncertainty could be further reduced by improving estimates of lianas, necromass, and especially belowground roots. Stable aboveground carbon stock estimates in this region are 7.8 Pg in remaining intact forests, but 32 % of this region has been deforested or significantly impacted by humans. Thus, 3.6 Pg C have been or are in immediate risk of being released via continued forest degradation and deforestation.

5.2 Implications of research

5.2.1 Allometric theory and fundamental drivers of tropical tree allometry

On a more fundamental level, this work changes how we must think about allometric models and theory. I demonstrate that ‘best estimates’, even from models with many variables, should not be regarded as true biomass or baselines to which all other estimates are compared. Rather, they are still estimates, and only direct measurements can reveal true biomass.

This work also shows that adjusting allometric equations for height alone is insufficient to account for the allometric variation between regions or forest types because crown mass must also be considered. Crown size (Barbier et al. 2010) and its relative mass (da Silva 2007, Nogueira et al. 2008a, Basuki et al. 2009) also vary across the landscape and according to the light environment (King 1994), perhaps inversely with height because these two growth patterns are competing uses of photosynthates (King 1996, Aiba and Kohyama 1997, Sterck and Bongers 1998, Bohlman et al. 2008). For example, small trees will either maximise height growth to reach the canopy or put resources into horizontal branches to maximize light capture in the understory. However, when trees emerge from the canopy, vertical height growth slows while horizontal branch growth increases (Sterck and Bongers 2001). These processes will occur in both individual trees (i.e., ecological strategy and position in the canopy) and over a large scale, where forest structure drives the overall light environment and allometric relationships (Banin et al. 2012).

Both crown dimensions and form should therefore be considered in allometric theory and empirical models, rather than relating tree mass to diameter alone (e.g., West et al. 1997) or modelling trees as cylinders or cones based on diameter and height (e.g., Chave et al. 2005). If height and crown radius were perfectly anti-correlated, then just diameter and wood density would predict tree mass, but this has been disproven many times, including this thesis (Chapters 2 and 4). Though branches could theoretically be collapsed into a conical shape along with the main stem, the number and length of branches, as well as how they fill space, will determine how they ‘collapse’ into a solid form.

Furthermore, this research suggests that wood density may play a more important role in allometry and total AGB than merely converting volume to mass. This supports other research findings that wood density may be correlated to other, unmeasured variables related to ecological strategy, tree architecture, and mechanics (King et al. 2006, Sterck et al. 2006, Anten and Schieving 2010, Iida et al.

2012). For example, crown width increases with increasing wood density (Sterck et al. 2006, Anten and Schieving 2010, Iida et al. 2012), which I also confirmed in Chapter 2.

5.2.2 Biomass and carbon stock estimates

These results dramatically affect biomass estimates in this important area for conservation (Brooks et al. 2006). This region comprises large expanses of intact forest cover (Potapov et al. 2008) and is rich in biodiversity (Myers et al. 2000), but these forests are under imminent threat of deforestation and degradation following the completion of the Interoceanic highway (Southworth et al. 2011, Perz et al. 2013). This area has therefore been the focus of many carbon based projects and large-scale efforts to reduce emissions from deforestation and degradation (UN-REDD Programme) (Asner et al. 2010, Rendón Thompson et al. 2013), but carbon stocks estimates here have been highly variable and uncertain.

Weighted mean AGB density of trees and palms estimated with the new model II.1 (262.5) Mg/ha) are 9.7 % lower and 8.6 % higher than the pantropical Feldpausch et al. (2012) models without and with height, respectively. Over the entire southwestern Amazon ecoregion (Olson et al. 2001, WWF 2004), pantropical model estimates would have estimated original tree and palm aboveground carbon stocks at 8.5 or 10.2 Pg, depending on the model used, resulting in a discrepancy of 1.7 Pg C. If the model with height (Feld 2) were assumed to be correct, this would result in a 17 % 'downgrade' in forest carbon estimates in this region. This figure is nearly identical to the 16 % downgrade reported in Feldpausch et al. (2012) for the western Amazon. However, using my regionally developed model, I estimated tree and palm ($D \geq 10$ cm) carbon stocks at 9.3 Pg, which is between the two values calculated using the pantropical models. This shows that that although the pantropical model without height overestimates AGB here, the pantropical model accounting for lower heights —but ignoring other allometric differences, such as greater branch mass— underestimates AGB of trees in this region.

5.2.3 Large tree biomass

This work also improves our understanding of large tree biomass, which is well known to be a large source of uncertainty in forest biomass estimates (Brown et al. 1995, Clark and Clark 2000, Baker et al. 2004b, Chave et al. 2004). The tree biomass dataset developed here includes 12 individuals with $D > 100$ cm, which nearly doubles the quantity of very large tree data available for the entire tropical forest biome (*cf.* 14 trees in Chave et al. 2005 and 17 in Feldpausch et al. 2012). I found that previously published model estimates were very poor for very large trees and varied greatly between one another. In my new models, crown radius was again vitally important for accounting for variation not explained by diameter, wood density, or height, especially among very large trees.

5.2.4 Palm biomass and productivity

New palm models presented in Chapter 3 allow palm biomass and productivity to be estimated much more accurately. The single species models with stem height or stem height and diameter estimate AGB very well. The first family-level models for palms, that do not need height measurements, provide unbiased estimates of palm AGB, which can be applied to forest inventory databases that often only include diameter measurements and species identification. In both the detailed plot analysis (Chapter 3) and large scale analysis (Chapter 4), I found that palm biomass was greater than would have been estimated using dicot tree models. This will increase forest biomass estimates, especially in the western Amazonia and central America, where palms are most abundant (Kahn et al. 1988, Terborgh and Andresen 1998, Eiserhardt et al. 2011). These models will also allow more accurate quantification of above- and belowground carbon stocks of the palm community in the 150,000 km^2 of carbon-rich peat ecosystems in Amazonia (Lahteenoja et al. 2009).

5.2.5 Carbon accounting and REDD+

Regionally or nationally-developed allometric models for dicot trees and palms will help countries in the southwestern Amazon, especially Peru, achieve Tier 3 methodologies according to the Intergovernmental Panel on Climate Change (IPCC) Guidelines for National Greenhouse Gas Inventories (IPCC 2006) for REDD+ (Figure 5.1). Tier 3 calculations are the most complex level of carbon accounting, using process-based estimates of forest carbon stocks and changes, such as directly-measured forest inventory data and country-specific allometric equations (IPCC 2006). Uncertainty is reduced with each tier, and higher tiered methods (Tiers 2 and 3) will be required for important carbon pools (Srivastava 2008). Although these methods incur additional costs and efforts (Angelsen et al. 2009, Angelsen et al. 2012), the conservative approach to carbon accounting, as has been taken by REDD+, should 'provide a clear incentive for increasing the quality of the reporting' (Mollicone et al. 2007). It has been suggested that more complete and accurate reporting will increase emissions reductions estimates and, therefore, allow a country or project to claim more credits (Mollicone et al. 2007) and that greater confidence in the estimates may inspire a higher payments per unit carbon as performance-based benefits are introduced (Asner et al. 2010, MFW 2012).

Recent studies have shown that Tier 3 baseline biomass estimates may be lower than Tier 1 estimates (Asner et al. 2010, Jubanski et al. 2013). In Peru, a high-resolution analysis of carbon stocks estimated total carbon stocks 33% lower than IPCC Tier 1 default values (Asner et al. 2010). The large discrepancies between values may result from the greater ability of the high-resolution analysis to account for forest degradation, different land uses, and variation within forests. However, this finding is likely to be predominately driven by the very low forest carbon density estimates in intact forests determined in Asner et al. (2010; 85–125 Mg C/ha), which are much lower than carbon density estimates determined in this thesis (Chapter 4).

In my analysis, mean aboveground living biomass stocks (i.e., excluding necromass), weighted by area in each forest type, would be estimated at 297.2 Mg /ha, which is 0.9 % less than the IPCC default value (Tier 1) for 'wet' tropical forests (300 Mg/ha) and 35 % higher than the default value for 'moist' tropical forests[1] (220 Mg/ha) (IPCC 2006). When converting biomass to carbon, the default carbon fraction given by the IPCC (2006) is slightly lower (47 %) than has been recently determined for tropical angiosperm trees (47.35 %; Martin and Thomas 2011). Thus, carbon density determined in this study is 0.2 % less and 36 % greater than the IPCC default for wet forests and moist forests, respectively (Table 5.1).

It is difficult to compare my Tier 3 estimates with Tier 1 default values across the landscape because maps defining forest moisture regimes are not consistent or

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[1] Wet forests are defined as having ≤ 3 dry months/year, and moist forests have 3–5 dry months/year.

spatially explicit. In the IPCC reports (2003, 2006), most of the 'southwest Amazon moist forest ecoregion' is categorised as 'wet' forest, but a more recent and spatially explicit analysis of rainfall patterns across South America show that most of the ecoregion is 'moist' forest by the same definition[1] (Butt et al. 2008), and all of the plots examined in Chapter 4 have also been classified as moist forests. The large difference between Tier 1 values for the two forest types, 2.8 Pg, highlights the enormous uncertainty associated with these generic values. If forests in this region are classified as 'wet', then carbon estimates are nearly identical to values estimated in this study, but my analysis shows that Tier 1 values for moist forests substantially underestimate forest carbon stocks in this region.

Table 5.1. Aboveground living biomass (AGLB) by IPCC definition (no necromass), carbon fraction, and carbon density estimated in this study and obtained from the IPCC default values (Tier 1) for 'wet' and 'moist' tropical forests (IPCC 2006).

Forest type	**ALGB density**	**Carbon fraction**	**Carbon density**	**Total AGLB**	**Total carbon**
	(Mg/ha)	(%)	(Mg/ha)	(Pg)	(Pg)
This study	297.2	47.35	140.7	22.2	10.5
'wet'	300	47	141.0	22.4	10.5
'moist'	220	47	103.4	16.4	7.7

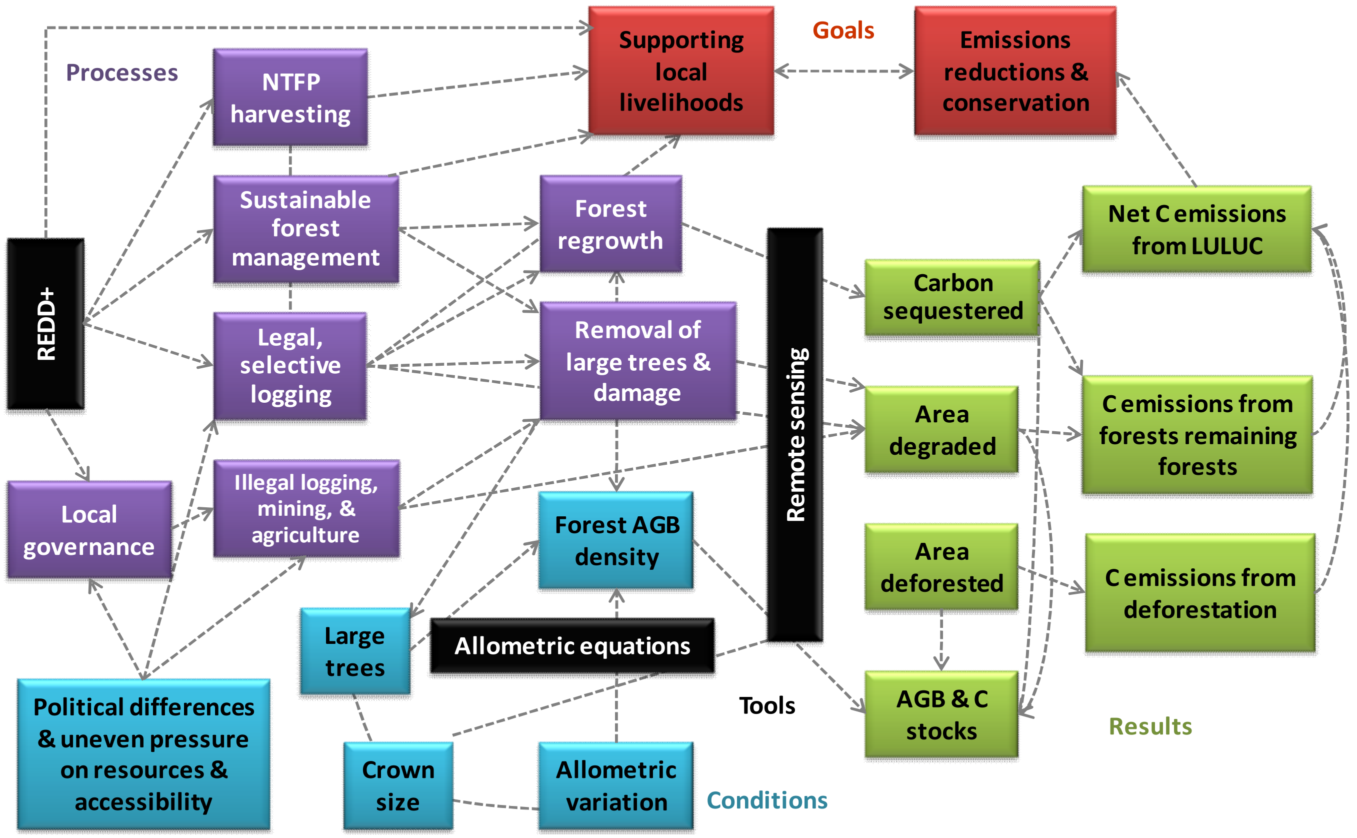

Figure 5.1. Conceptual diagram of conditions of the forest and pressures on forest resources, processes that influence carbon dynamics, tools to influence and estimate these processes, results of land use and land uses changes, and overarching goals for forest and land management in Madre de Dios.

5.3 Future directions

5.3.1 Pantropical models incorporating crown dimensions and architecture

Ideas presented in this thesis, especially in Chapter 2, lead to a number of questions about the broader application of including crown dimensions and architectural type in pantropical models. If crown radius were measured as part of future biomass data collection, new models could be developed with all four parameters (D, ρ, H, and CR) from data spanning geographic space and environmental gradients. It would be interesting to test whether the inclusion of both height and crown radius can appropriately account for allometric differences between regions or whether variation still remains. As biomass data collection is a laborious and slow process, an alternative approach would be to explore the influence of architectural type on a larger dataset: the simple classification proposed in Chapter 2 —monopodial or not— could be applied retrospectively to the existing database.

5.3.2 Forest productivity, carbon dynamics, and ecological function

Improved tree and palm models also give researchers more precise methods of estimating forest dynamics and carbon cycling. The results of the first two chapters both suggest that tropical forests may be more productive than previous models could detect. Because branch length increases non-linearly with diameter (Figure A4.3), the crowns of mature trees may continue to grow, even as diameter growth slows. Thus measuring crown dimensions may show that large, old trees are accumulating more biomass than can be detected via diameter increments and allometric equations to estimate biomass changes that do not include crown radius. This might add to the body of evidence suggesting that forest biomass in mature tropical forests is increasing over time (Phillips et al. 1998, Phillips et al. 2008, Lewis et al. 2009, Malhi 2010), which is detected via changes in mortality, recruitment, and diameter or basal area growth. In contrast, and additionally, equations that include crown radius may also be able to account for progressive biomass losses due to crown damage, for example in senescent trees. However, to do so accurately, this would require more biomass data collection from trees with a range of crown damage.

This work also suggests that palm productivity may also be greater than previously estimated by dicot models, especially when height is not included, because palms grow in height with little or no corresponding increase in stem diameter (Rich et al. 1986). Given that palms are also most abundant in western Amazonia (Kahn et al. 1988, Terborgh and Andresen 1998, Eiserhardt et al. 2011), the magnitude of increases in 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). A study with repeated stem height measurements of palms could test this idea by quantifying palm stem productivity. New equations for leaf mass will also help researchers estimate the non-woody productivity of palms. Together, what have been referred to as a 'missing term' (Malhi et al. 2009), palms, may finally be incorporated into forest productivity estimates.

A better understanding of the growth and carbon dynamics of palms may also help clarify the relationships between forest biodiversity and ecological function. It is often concluded that diversity increases ecosystem function because greater functional diversity allows different plants to access and use more resources (Cadotte et al. 2009). In grasslands, phylogenetic diversity explained ecosystem productivity better than species richness, functional group richness, or individual traits (Cadotte et al. 2009), which suggests that there may be fundamental differences between arborescent monocots and dicots in tropical forest ecosystems, as well. However, this distinction has been ignored in both global analyses (Loreau et al. 2001, Cardinale et al. 2012) and even tropical studies (Balvanera et al. 2005, Vance-Chalcraft et al. 2010). This suggests that the different roles of trees and palms, especially relating to how they store and process carbon, would become easier to distinguish if palm biomass and biomass changes were estimated with appropriate models. This work now makes it possible to test these ideas in tropical ecosystems.

An extension of this debate examines the magnitude of ecosystem functions and functional structure, which again emphasises the importance of large trees. Slow growing large trees contribute substantially to forest carbon stocks despite their low abundance in the ecosystem and are the most sensitive to management (Balvanera et al. 2005). Namely, they are the first to be removed from selective logging, which has large ramifications for remaining forest biomass density, residual damage to the ecosystem, and net carbon emissions from forest degradation (Figure 5.1). Large trees may also be the most sensitive to droughts, which are projected to increase with a changing climate, and many important trees may be lost from the ecosystem (Nepstad et al. 2007, Phillips et al. 2009b, Phillips et al. 2010, Silk et al. 2013). A number of human related, environmental, and ecological factors could slow or reverse the carbon sink of Amazonian forests, which would have a profound effect on global carbon cycling (Phillips et al. 1998, Wright 2005, Phillips et al. 2008), and large trees play a key role in the carbon cycle and total forest biomass (Stegen et al. 2011, Silk et al. 2013). Thus, new models that focusing on accurately estimating the biomass of large trees will help researchers quantify long-term changes to forest carbon fluxes.

5.3.3 Quantifying the effects of selective logging in the southwestern Amazon

A key application of this research is to aid in better land management, especially in relation to production forests (Figure 5.1). One of the implications of large tree crowns in this region is the potentially large impact on the forests from timber harvests. Not only is the biomass from branches, buttresses, and stump left as coarse woody debris, but many other trees are damaged or killed when these trees fall and are extracted from the forest (Pinard and Putz 1996, Feldpausch et al. 2005, Sist and Ferreira 2007, Blanc et al. 2009). As the damage caused by felling is positively correlated with crown depth (Feldpausch et al. 2005), I would expect that damage is also strongly related to crown width. Because tree heights are lower and crowns are larger, in terms of both size and relative mass, it follows that the proportion of forest AGB damaged during logging operations per unit timber extracted could be greater in the southwestern Amazon compared to other areas, where detailed studies of the effects of selective logging have been conducted —e.g., French Guiana (Blanc et al. 2009), central Brazil (Miller et al. 2011), and southern Brazil (Feldpausch et al. 2005). In the geographically closest study, an FSC certified operation using reduced impact logging techniques harvested 1.1–2.6 trees/ha, and all operations left only 4.9–8.8 Mg C/ha in coarse woody debris (Feldpausch et al. 2005). However, mean diameter of harvested trees in this study was only 75 cm, and crowns are much wider in larger trees (Figure A4.3.). As forest dynamics are also different in the western Amazon (Baker et al. 2004b, Malhi et al. 2004, Baker et al. 2009), the speed and extent to which forests can recover from a logging operation may also differ in this region compared to other areas. Higher growth rates in the western Amazon may help forests recover biomass more quickly. Conversely, forests with bamboo may recover at slower rates if bamboo inhibits tree regeneration (Griscom and Ashton 2006).

The biomass models developed in this thesis may also change estimates of the ratios of biomass damaged and exported during selective logging. Because the crowns are proportionally larger and total heights are relatively shorter than in other regions, it follows that the ratio of coarse woody debris left in the forests (branches) to bole volume removed will be larger here. Secondly, using the Chapter 2 model I.1 CR (*D, ρ, H*, and *CR*) yields the lowest biomass estimates for small trees and the highest estimate for the largest tree (Figure A4.6). Thus, the proportion of forest biomass held in very large trees may be higher than estimated in other studies elsewhere, making the conservation of large trees particularly important for maintaining forests with high carbon density.

5.3.4 Linking allometry, biomass, and remote sensing

The new ideas about allometry and models introduced in Chapters 2 and 3 can be used in many ways to improve forest AGB estimates from remote sensing (Figure 5.1). First, the new equations could be employed to estimate AGB in the forest plots used to calibrate remotely sensed metrics. With the ability to detect individual crowns of emergent trees (Morsdorf et al. 2004, Bortolot and Wynne 2005, Kato et al. 2009, Thomas et al. 2013) a combination of ground and remotely sensed variables could be used in the allometric equations —*viz.* diameter and species identification from ground inventories and crown area and height from LiDAR or other remote sensing techniques. Palm-dominated stands could be identified (Sánchez-Azofeifa et al. 2009) and calibrated with AGB separately. Though AGB of palm-dominated stands will likely be much lower than that of dicot-dominated or mixed forests, attention should also be paid to carbon-rich soils that are often associated with this forest type (Lahteenoja et al. 2009).

Secondly, large scale studies detecting or measuring individual (IKONOS; Clark et al. 2004) or mean tree crown size (Google Earth®; Barbier et al. 2010) and height (Feldpausch et al. 2011, Saatchi et al. 2011) could be used to ascertain the spatial extent to which allometric models developed in one or a few areas are applicable. This could be done by examining the relationships between height, crown area, and, diameter (if known), as well structure of the whole forest, which may also drive allometric relationships (Banin et al. 2012).

Individual tree AGB could be estimated directly from remotely sensed images to estimate standing AGB or changes over time. As small footprint LiDAR can detect both crown area and height of individual trees (Morsdorf et al. 2004, Bortolot and Wynne 2005, Kato et al. 2009), the new tree and palm models could be used to estimate tree AGB directly from crown area or height and crown area for trees and palm AGB from height only, thus avoiding error associated with first estimating diameter from height or crown diameter (e.g., Zhou et al. 2010). Although, estimating crown area from LiDAR or other remotely sensed imagery may be restricted practically to emergent trees (Thomas et al. 2013), more accurately estimating AGB of the largest trees will greatly improve forest AGB density estimates. Given that these trees are also the most likely to be removed by selective logging or increased mortality (Lindenmayer et al. 2012), applying these methods should help improve estimates of carbon stock changes in degraded and managed forests. This would allow more accurate estimates of carbon lost via selective logging or other forms of forest degradation by following high resolution images through time (Asner et al. 2005, Asner et al. 2010, Huang and Asner 2010).

The same ideas could be applied to improve remote sensing calibration with plot data. Plot biomass is often correlated with mean canopy height (Drake et al. 2003, Asner 2009, Asner et al. 2010), but this could be enhanced by a more detailed analysis of stand and canopy structure. Because large trees account for much of the variation in forest biomass (Brown et al. 1995, Clark and Clark 2000, Baker et al. 2004b, Chave et al. 2004, Stegen et al. 2011), calibration with ground plots could possibly be enhanced by adding biomass for very large emergent trees. In fact, total forest biomass may even be closely related to the mass of the largest individual tree (Stegen et al. 2011). The number of large, fully emergent trees or total crown area of these could be incorporated into the remotely sensed metrics used to calibrate with plot biomass. However, this would require an extensive dataset of forest plots to determine the effects of forest structure on stand-level AGB.

5.3.5 REDD+ and forest management in Madre de Dios

REDD+ could be a powerful tool to help improve forest and land use management in tropical countries (Nepstad et al. 2008), but many scientific, economic, and social issues still need to be resolved for REDD+ to be both implemented and successful at actually reducing emissions from deforestation and degradation

(Figure 5.1). The results of this thesis primarily contribute to the scientific aspect of carbon accounting, but could possibly be applied to economic issues as well. Economic concerns, especially the opportunity costs of improved forest management and implementing REDD+, will need to be addressed and evaluated practically (Putz et al. 2012). Better ground data and biomass estimates may help assess these costs, which vary greatly according to the land use (Engel et al. 2012). Unfortunately, it is very unlikely that the value of carbon will ever rival profits to be gained from mining, timber, grazing, or many other land uses. Even in the unlikely scenario of a very high price for carbon, low discount rate, and low timber value, the value of timber exceeds that of carbon by at least five-fold (Khatun 2010). Thus, there is a very real need to incorporate some extractive activities to improve co-benefits and economic viability of conservation and carbon-based programmes (Nunes et al. 2012, Putz et al. 2012).

In Madre de Dios, there is great potential to either degrade the forest landscape or pursue sustainable management. Nearly half of the land (40,442 km^2) is protected as natural protected areas, conservation concessions, or ecotourism concessions, and an additional 15 % (12,561 km^2) is set aside for indigenous and native communities. Over one quarter of the land is designated as productive forests: 9,481 km^2 in Brazil nut concessions (GOREMAD 2012), 12,355 km^2 in forestry concessions, and 533 km^2 in one native community (E. Condori[2], personal communication, 12 July 2013; Figure 5.2). In areas where logging operations take place, 4,759 km^2 of forestry concessions and the native community Belgica have been certified by the Forest Stewardship Council (FSC; E. Condori, personal communication, 12 July 2013; Figure 5.3).

One of the key additions to REDD+, over REDD, is the inclusion of improved or sustainable forest management (Sasaki et al. 2012). As forestry concessions cover 15 % of the land area in Madre de Dios and nearly 40 % of those have FSC certification, the opportunities for sustainable forest management are large. However, reduced impact logging, sustaining timber yields, and sustainable forest management should not be confused (Putz et al. 2008a). Thus, although reduced

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[2] Edith Condori, World Wildlife Fund – Peru

impact logging is part of FSC certified logging operations (Feldpausch et al. 2005, Sist and Ferreira 2007), it should not be assumed that FSC certified concessions are sustainable or carbon neutral. In reality, timber extraction competes with carbon stocks and other ecosystem services (Khatun 2010), and the ecological integrity of a logged forest can only be achieved by reduced impact logging operations, lowering yields, and lengthening rotation cycles (Huth et al. 2004, Putz et al. 2012, Sasaki et al. 2012), but more research is likely needed to understand the forests in this region. Again, the crown volume and mass of trees will be an important point of debate, as the branches are both left in the forest as necromass and damage the stand during felling (Feldpausch et al. 2005). Thus, large crowns will result in more carbon losses, which should be evaluated against the quantity and value of the commercial bole. A large-scale analysis in the Brazilian Amazon suggests that carbon emissions from selective logging continue for 2–3 decades following harvest, and forest biomass may not fully recover for 100 years (Huang and Asner 2010). Thus, although carbon emissions from degradation are much smaller than from clear cutting, the effects should not be ignored. Conversely, improved forest management has a much smaller risk of 'leakage' —i.e., increasing timber extraction and carbon emissions in other areas— than strict conservation (Putz et al. 2008a, Putz et al. 2012), giving this approach a very real chance of reducing global carbon emissions from the forestry sector.

Brazil nut concessions, which are extensive and economically important in the area, also offer a unique opportunity for sustainable forest management and emission reductions in Madre de Dios (Nunes et al. 2012). Though timber can be harvested legally in these concessions (Giudice et al. 2012), Brazil nut (*Bertholletia excelsa*) trees themselves are protected in Peru (INRENA 2002). This offers a good opportunity to receive multiple profits from these forests while still conserving very large trees. However, more careful management and oversight will be needed, as there are currently no regulations for timber harvest of other species in Brazil nut concessions (Giudice et al. 2012).

Unfortunately, 'protected areas' and other official land use designations do not always protect forests from deforestation or degradation in Madre de Dios (Vuohelainen et al. 2012). Mining and agriculture have affected over 14 % of the landscape (8,312 km^2 by mining and 3,800 km^2 by agriculture), much of which has invaded other land use designations (GOREMAD 2012). Mining primarily occurs along rivers in the southern part of department and affects forestry concessions, whereas agriculture occurs predominantly along the Interoceanic highway in the eastern part of the department. Deforestation and degradation also exist in native communities, from both internal use (Vuohelainen et al. 2012) and outside logging contracts (e.g., Belgica). Ecotourism and conservation concessions tend to be the most effective at preventing deforestation, due to surveillance, monitoring, and good relations with surrounding communities (Vuohelainen et al. 2012), but make up only 2.5 % of the landscape (GOREMAD 2012). Unfortunately, immigration, strong economic incentives, and weak local governance leave much of the 'protected areas' in Madre de Dios vulnerable to deforestation and degradation.

The Peruvian government aims to end net deforestation by 2021 (Painter 2008), though considerable efforts and commitment will be needed to be made this a reality. Several small scale REDD projects exist in Madre de Dios, but the country lacks a National REDD+ Plan and may not be considering the effects of degradation on forest biomass stocks. Nonetheless, there is a great deal of overlap in the social, political, and governance needed to make both sustainable forest management (Ros-Tonen et al. 2008) and a national REDD+ programme succeed. Thus, the implementation of REDD+ in Peru is a prime opportunity to explore truly sustainable forest management and large scale conservation efforts (Figure 5.1).

The results and ideas reported in this thesis should help Peru move towards these goals. The region should use the allometric models for trees and palms presented in this thesis to establish a more reliable (Tier 3) carbon baseline and explore changes in carbon stocks from selective logging and land use changes. In addition, detailed monitoring of land use and carbon stock changes will be necessary to move into Phase 3 of REDD+ implementation, where payments for emissions reductions are results-based (Simula 2010, Angelsen et al. 2012).

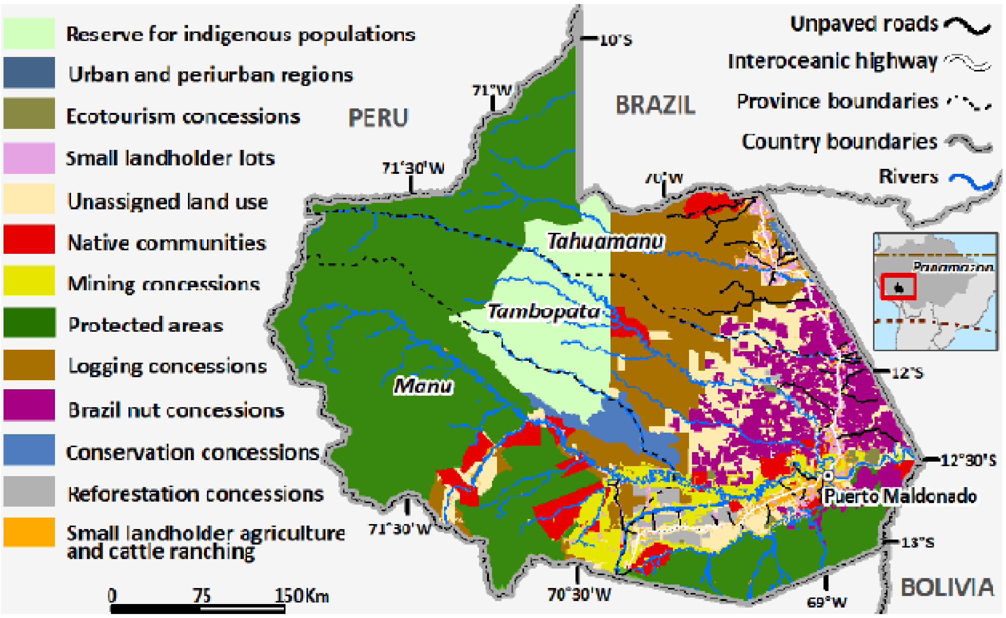

Figure 5.2. Current land use zoning in Madre de Dios, Peru. Image from Nunes et al. (2012).

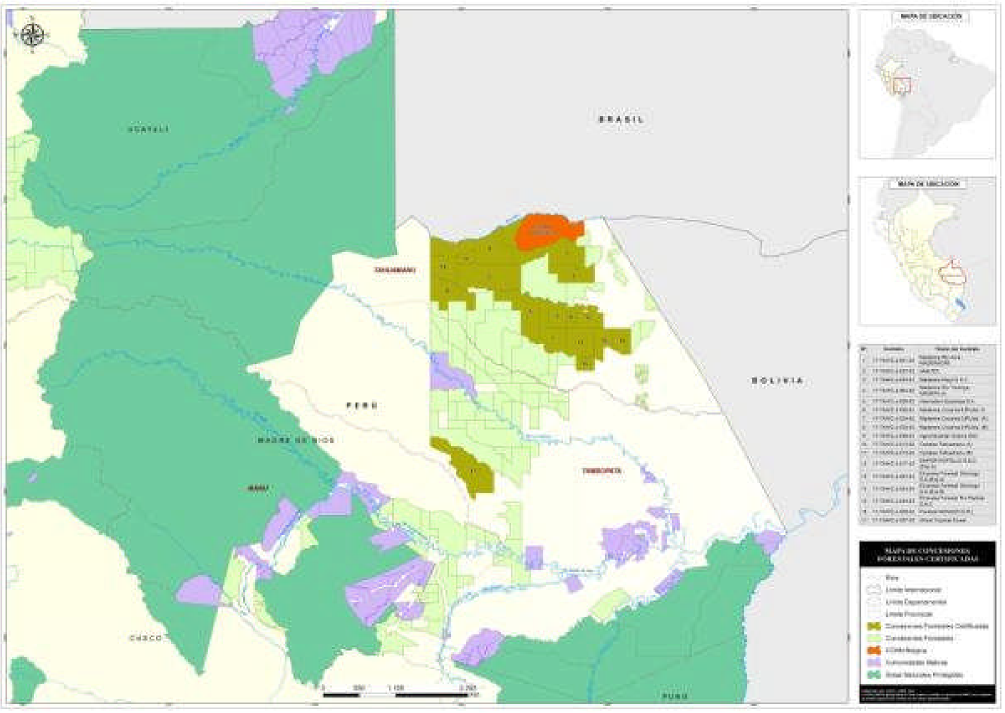

Figure 5.3. Forestry concessions in Madre de Dios with (olive green) and without (mint green) FSC certification. Image provided by Edith Condori, World Wildlife Fund, Lima, Peru (12 July 2013).

5.4 Summary

This thesis shows that allometric variation in trees across the tropics and distinctions between functional groups are important and should be accounted for in both tree and palm biomass models. Directly measured biomass data show that both trees and palms are poorly estimated by allometric equations developed in other regions, due to allometric differences. Namely, trees have proportionally larger crowns in this region as compared to other regions were biomass data have been collected, and palms can be much taller at a given diameter than dicotyledonous trees. In new allometric equations, including crown dimensions in tree models and creating separate models for palms greatly improved biomass estimates. Applying the new models to forest plots in the southwestern Amazon confirmed these results. Aboveground biomass density estimates of trees and palms is 262 Mg/ha, which is 9 % greater than estimates made by the currently available pantropical model including estimated height. Over the entire 746,653 km^2 ecoregion, original aboveground carbon stocks are estimated at 11.5 Pg with 8 % uncertainty. These results improve allometric modelling and reduce uncertainty in forest biomass estimates and should be applied to improve forest management and provide more confidence for REDD+ and other carbon-based conservation projects.

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Acronyms, abbreviations*, and units

*Variables are listed in italics and the units used in this thesis appear in brackets.

AGB	aboveground biomass (Mg dry mass)
AGC	aboveground carbon (Mg)
AIC	Akaike's information criterion
ANOVA	analysis of variance
BGB	belowground biomass (Mg dry mass)
BGC	belowgroun carbon (Mg)
C	carbon
CDepth	Crown depth ($H - H_{FMB}$) (m)
CEA	crown elipse area (m^2)
CF	correction factor
cm	centimetres (10^{-2} m)
CR	average crown radius (m)
D	diameter of the main stem at breast height (1.3 m) or just above buttresses (cm)
dicot	dicotyledonous
dmf	dry mass fraction (unitless)
FSC	Forest Stewardship Council
GLM	generalised linear model (glm in R statistical package)
H, H_{tot}	total tree height (m)
H_{FMB}	height of the first major branch (diameter ≥ 5 cm) (m)
H_{stem}	stem height (m)
ha	hectare (10^4 m^2)
IFL	Intact forest landscape
IPCC	Intergovernmental Panel on Climate Change
km	kilometre (10^3 m)
km^2	square kilometre (10^6 m^2), equivalent to 100 hectares
LiDAR	light detection and ranging
ln	natural logarithm
m	metres
MAP	Madre de Dios, Peru – Acre, Brazil – Pando, Bolivia
masl	metres above sea level

mean_E	mean error (kg)
$\text{mean}_{\%E}$	mean percent error (mean_E / mean AGB × 100 %) (%)
M	Monopodial
MdD	Madre de Dios
Mg	Megagram (10^6 g or 10^3 kg), equivalent to 1 metric tonne (t)
monocot	monocotyledonous
Pg	Petagram (10^{15} g or 10^{12} kg), equivalent to 10^9 metric tonnes or 1 Gigatonne (Gt)
POM	point of measurement (m)
R^2	coefficient of determination
RAINFOR	Amazon forest inventory network
RE	relative error (%)
REDD+	United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries
RSE	residual standard error
SD	standard deviation
SE	standard error
SWA	southwest Amazon moist forest
ε	error (%)
ρ	wood density (g/cm^3)

APPENDIX

Appendix 2 Supplementary material for Chapter 2

Table A2.1. Moisture content by tree part —stump, stem, large branches (diameter ≥ 10 cm) and small branches (diameter < 10 cm) with attached leaves and fruit— and average stem wood density of the 51 trees destructively sampled in this study. Values are species means, and n refers to the number of individuals sampled in each species.

			Moisture content (proportion)				Wood
Name	**Family**	***n***	**Stump**	**Stem**	**Large branches**	**Small branches**	**density (g/cm^3)**
Acacia loretensis	Fabaceae	1		0.249		0.306	0.6007
Acacia polyphylla	Fabaceae	1	0.264	0.338	0.354	0.356	0.7225
Amburana cearensis	Fabaceae	2	0.424	0.475	0.478	0.552	0.5858
Apeiba tibourbou	Tiliaceae	1	0.610	0.563	0.481	0.447	0.2603
Apuleia leiocarpa	Fabaceae	1	0.295	0.292	0.369	0.421	0.8554
Aspidosperma vargasii	Apocynaceae	1	0.327	0.479	0.490	0.600	0.6097
Brosimum alicastrum	Moraceae	1	0.362	0.379	0.411	0.442	0.6498
Calycophyllum spruceanum	Rubiaceae	1	0.314	0.318	0.384	0.234	0.7810
Cariniana decandra	Lecythidaceae	1	0.433	0.446	0.412	0.438	0.5727
Castilla ulei	Moraceae	1	0.514	0.517	0.487	0.525	0.4952
Cavanillesia umbellata	Malvaceae	2	0.748	0.799	0.622	0.632	0.1954
Ceiba samauma	Malvaceae	2	0.572	0.551	0.523	0.502	0.5069
Ceiba lupuna	Malvaceae	2	0.693	0.624	0.617	0.609	0.3937
Celtis schippii	Ulmaceae	1	0.375	0.425	0.470	0.464	0.6546
Clarisia racemosa	Moraceae	1	0.419	0.394	0.400	0.499	0.6591
Copaifera reticulata	Fabaceae	1	0.365	0.409	0.392	0.420	0.5900
Crepidospermum goudotianum	Burseraceae	1	0.354	0.313	0.373	0.446	0.7000
Dipteryx micrantha	Fabaceae	4	0.309	0.334	0.349	0.419	0.8713
Drypetes amazonica	Euphorbiaceae	1		0.474	0.442		0.7103
Erythrina ulei	Fabaceae	1	0.607	0.598	0.637	0.583	0.3618
Ficus insipida	Moraceae	1	0.597	0.554	0.530	0.584	0.4510
Gallesia integrifolia	Phytolacaceae	1	0.579	0.525	0.549	0.572	0.5302
Hymenaea courbaril	Fabaceae	1	0.333		0.402	0.430	0.7800
Inga striata	Fabaceae	1		0.363	0.325		0.6065
Jacaratia digitata	Caricaceae	1		0.854	0.825	0.915	
Luehea cymulosa	Tiliaceae	1	0.414	0.444	0.448	0.547	0.5425
Mezilaurus itauba	Lauraceae	1	0.470	0.456	0.398	0.556	0.6149
Myroxylon balsamum	Fabaceae	1	0.318	0.407	0.352	0.421	0.7750
Ocotea javitensis	Lauraceae	1		0.559		0.664	0.5117
Phyllocarpus riedelii	Fabaceae	1		0.351	0.383	0.346	0.5323
Pourouma cecropiifolia	Cecropiaceae	1		0.599	0.555	0.555	
Pseudobombax septenatum	Bombacaceae	1		0.667	0.480	0.480	0.3595
Pseudolmedia laevis	Moraceae	2	0.464	0.471	0.429	0.447	0.6235
Pterygota amazonica	Sterculiaceae	1	0.415	0.421	0.503	0.522	0.7051
Qualea tessmannii	Vochysiaceae	1	0.431	0.448	0.513	0.423	0.5890
Spondias mombin	Anacardiaceae	3	0.623	0.666	0.602	0.580	0.3275
Sterculia apetala	Sterculiaceae	1	0.485	0.522	0.438	0.539	0.4411
Swartzia jorori	Fabaceae	1	0.375	0.375	0.377		0.8376
Swietenia macrophylla	Meliaceae	1	0.326		0.369	0.441	0.6300
Theobroma cacao	Sterculiaceae	1		0.401		0.223	0.4741
Trichilia adolfi	Meliaceae	1		0.434	0.546		0.6856

Appendix 3 Supplementary material for Chapter 3

Table A3.1. Dry mass fraction (dry mass/fresh mass) for each stem sample, taken at three locations along stem (base, centre, and top), and the mean for each individual.

	H_{stem}	H_{total}	D	Dry mass fraction			
Species	**(m)**	**(m)**	**(cm)**	**Base**	**Centre**	**Top**	**Mean**
Astrocaryum murumuru	5.3	11.2	21.0	0.4697	0.3859	0.4600	0.4385
	9.0	14.6	19.4	0.4691	0.3195	0.2724	0.3537
	5.1	10.0	16.0	0.4183	0.4538	0.3472	0.4064
Attalea phalerata	11.1	15.7	33.8	0.3606	0.2509	0.3024	0.3046
	16.7 .		31.1	0.3955	0.3091	0.3046	0.3364
	13.5	18.4	24.6	0.4781	0.4515	0.3589	0.4295
	20.1	24.3	32.6	0.4747	0.3063	0.2924	0.3578
Bactris gasipaes	17.5	19.7	15.2	0.7307	0.6771	0.4295	0.6124
	18.1	20.8	14.0	0.7321	0.5943	0.5525	0.6263
Euterpe precatoria	16.7	19.2	15.8	0.4574	0.4582	0.4576	0.4577
	20.4	22.8	19.2	0.4282	0.4845	0.3993	0.4373
	11.8	14.8	14.7	0.3424	0.2803	0.2775	0.3001
Iriartea deltoidea	19.1	20.7	23.4	0.3586	0.2105	0.1836	0.2509
	12.6	17.2	24.3	0.2748	0.1529	0.1229	0.1835
	20.2	23.5	27.3	0.3918	0.2920	0.2084	0.2974
Oenocarpus bataua	12.0	21.6	28.1	0.4339	0.3636	0.3462	0.3813
	10.0	18.7	21.7	0.4250	0.4298	0.2608	0.3719
	6.9	15.4	28.6	0.3034	0.2705	0.2095	0.2612
Socratea exorrhiza	17.1	19.2	21.5	0.3262	0.2630	0.1695	0.2529
	19.8	22.2	20.7	0.5813	0.4540	0.3018	0.4457
	15.0	16.9	15.9	0.4433	0.4214	0.3335	0.3994
	15.6	18.5	21.5	0.3066	0.2963	0.1742	0.2591

Table A3.2. Best species model with each predictor variable, y = *a* + *b*(x_1) + *c*(x_2), to estimate aboveground biomass (AGB; kg dry mass) or belowground root biomass (BGB; kg dry mass) from stem height (H_{stem}; m), total height (H_{tot}; m), diameter (D; cm), and dry mass fraction (dmf). RSE is residual standard error.

Genus	y	x_1	x_2	a (int)	b	c	R^2	RSE	F	dfe	*Pr* < F	AIC
Astrocaryum	AGB	H_{stem}		.	21.302		0.957	26.05	379	17	<0.0001	171.4
	AGB	H_{tot}		-108.1	20.975		0.827	22.45	76	16	<0.0001	167.0
Attalea	ln(AGB)	ln(H_{stem}+1)		3.2579	1.1249		0.858	0.3712	115	19	<0.0001	21.9
	AGB	ln(H_{tot})		-1083	535		0.810	90.92	77	18	<0.0001	241.0
Euterpe	AGB	D^3		.	0.02228		0.971	19.18	237	7	<0.0001	72.9
	AGB	H_{stem}		-108.8	13.5885		0.973	8.368	215	6	<0.0001	60.4
	AGB	H_{tot}		-151	13.921		0.987	5.821	448	6	<0.0001	54.6
Oenocarpus	ln(AGB)	ln(H_{stem})		3.7073	0.9856		0.791	0.2334	30	8	0.0006	3.0
	AGB	H_{tot}		-573.5	49.575		0.834	74.96	40	8	0.0002	118.5
	AGB	D^2H_{stem}		.	0.0485		0.969	75.64	284	9	<0.0001	117.8
Iriartea	ln(AGB)	ln(D)		-4.107	2.8675		0.933	0.4449	264	19	<0.0001	29.5
	ln(AGB)	ln(H_{stem})		-1.824	2.5702		0.962	0.3362	477	19	<0.0001	17.7
	ln(AGB)	ln(H_{tot})		-4.256	3.2247		0.955	0.3642	404	19	<0.0001	21.1
	ln(AGB)	ln(D^2H_{stem})		-3.483	0.94371		0.967	0.3112	560	19	<0.0001	14.5
	ln(AGB)	ln(D^2H_{tot})		-4.352	1.01575		0.962	0.3358	478	19	<0.0001	17.7
Socratea	ln(AGB)	ln(D)		-4.885	3.3269		0.922	0.4129	211	18	<0.0001	25.3
	ln(AGB)	ln(H_{stem})		-1.59	2.31472		0.971	0.2513	601	18	<0.0001	5.4
	ln(AGB)	ln(H_{tot})		-3.428	2.8371		0.972	0.2474	621	18	<0.0001	4.8
	ln(AGB)	ln(D)	ln(H_{stem})	-2.904	1.1287	1.604	0.986	0.1827	577	17	<0.0001	-6.5
	ln(AGB)	ln(D)	ln(H_{tot})	-4.156	1.1017	1.986	0.985	0.1834	573	17	<0.0001	-6.3
Mauritiella	AGB	H_{stem}		.	2.8662		0.972	8.212	591	17	<0.0001	129.9
	ln(AGB)	ln(H_{tot})		.	1.2912		0.999	0.1457	11940	17	<0.0001	-15.3
Mauritia	ln(AGB)	ln(H_{stem})		2.4647	1.3777		0.897	0.2727	121	14	<0.0001	7.7
	AGB	H_{tot}		-261.1	39.068		0.867	141.6	92	14	<0.0001	4.5
Mauritiella	ln(BGB)	H_{tot}		0.6399	0.11657		1.000	0.0024	1E+06	16	<0.0001	-15.5
	ln(BGB)	H_{stem}		1.0945	0.11086		0.951	0.1319	310	16	<0.0001	-18.0
Mauritia	BGB	H_{tot}		-3.2373	2.7136		0.950	0.2732	263	14	<0.0001	7.7
	ln(BGB)	ln(H_{stem})		-0.3688	2.0106		0.929	0.3234	184	14	<0.0001	13.1

Table A3.3. All family-level models developed in this study. Models have the form y = *a* + *b*(x_1) + *c*(x_2) + *d*(x_3), to estimate aboveground biomass (AGB; kg dry mass) from stem height (H_{stem}; m), total height (H_{tot}; m), diameter (D; cm), and dry mass fraction (dmf).

y	x_1	x_2	x_3	a (int)	b	c	d	R^2	RSE	F	dfe	*Pr* < F	AIC	Spp	Spp×x
ln(AGB)	$\ln(D^2H_{stem})$			-3.62189	1.0133			0.8591	0.5154	634.3	104	<0.0001	164.3	3	3
ln(AGB)	ln(D)	$\ln(H_{stem})$		-4.02054	2.3456	0.7673		0.8847	0.4686	395	103	<0.0001	142.1	6	.
AGB0$^{.25}$	$(D^2H_{stem})^{0.25}$			.	0.42			0.9855	0.4423	7144	105	<0.0001	130.9	1	1
ln(AGB)	$\ln(dmf \times D^2H_{stem})$			-2.51208	1.0162			0.904	0.4254	979.8	104	<0.0001	123.6	4	3
AGB0$^{.25}$	$(dmf \times D^2H_{stem})^{0.25}$			.	0.5551			0.9903	0.3673	10410	105	<0.0001	91.5	1	1
ln(AGB)	ln(dmf)	ln(D)	$\ln(H_{stem})$	-2.08111	1.4611	2.1687	0.8648	0.9191	0.3943	386.5	102	<0.0001	109.4		
ln(AGB)	ln(D)			-3.3488	2.7483			0.802	0.5876	384	95	<0.0001	176.1	3	2
ln(AGB)	ln(D)	ln(dmf)		-2.0752	2.6401	0.8426		0.815	0.5699	208	94	<0.0001	171.1	3	.
ln(AGB)	$\ln(H_{tot})$			-1.1268	2.1751			0.545	0.8870	126	105	<0.0001	279.6	3	1
ln(AGB)	$\ln(H_{tot})$	ln(dmf)		1.4882	2.2432	2.5152		0.676	0.7436	108	104	<0.0001	245.2	7	.
ln(AGB)	$\ln(D^2H_{tot})$			-4.5660	1.0684			0.862	0.4824	648	104	<0.0001	150.3	0	0
ln(AGB)	$\ln(dmf \times D^2H_{tot})$			-3.0883	1.0311			0.878	0.4529	749	104	<0.0001	136.9	0	0

Table A3.4. Family-level model evaluation on subset of data (n = 27) with metrics calculated from error and relative error (RE).

Model	**Mean error (kg)**	**Mean % error**	**Mean RE (%)**	**Standard deviation RE**	R^2
$\ln(D^2H_{stem})$	10.5	4.1	27.1	68.7	0.947
$\ln(D)+\ln(H_{stem})$	-7.7	-3.0	12.4	54.5	0.958
$(D^2H_{stem})^{0.25}$	-15.0	-5.9	15.4	62.4	0.950
$\ln(\mathrm{dmf}\times D^2H_{stem})$	18.8	7.4	22.2	49.7	0.955
$(\mathrm{dmf}\times D^2H_{stem})^{0.25}$	0.5	0.2	15.1	47.0	0.962
$\ln(\mathrm{dmf})+\ln(D)+\ln(H_{stem}$	14.2	5.6	15.9	41.9	0.963
$\ln(D)$	-17.4	-6.9	7.8	51.4	0.946
$\ln(D)+\ln(\mathrm{dmf})$	-15.3	-6.0	5.6	32.7	0.970
$\ln(H_{tot})$	50.5	19.9	108.6	206.6	0.857
$\ln(H_{tot})+\ln(\mathrm{dmf})$	162.0	63.7	134.7	240.1	0.230
$\ln(D^2H_{tot})$	-27.7	-10.9	4.0	46.8	0.958
$\ln(\mathrm{dmf}\times D^2H_{tot})$	-22.0	-8.6	1.9	29.1	0.972

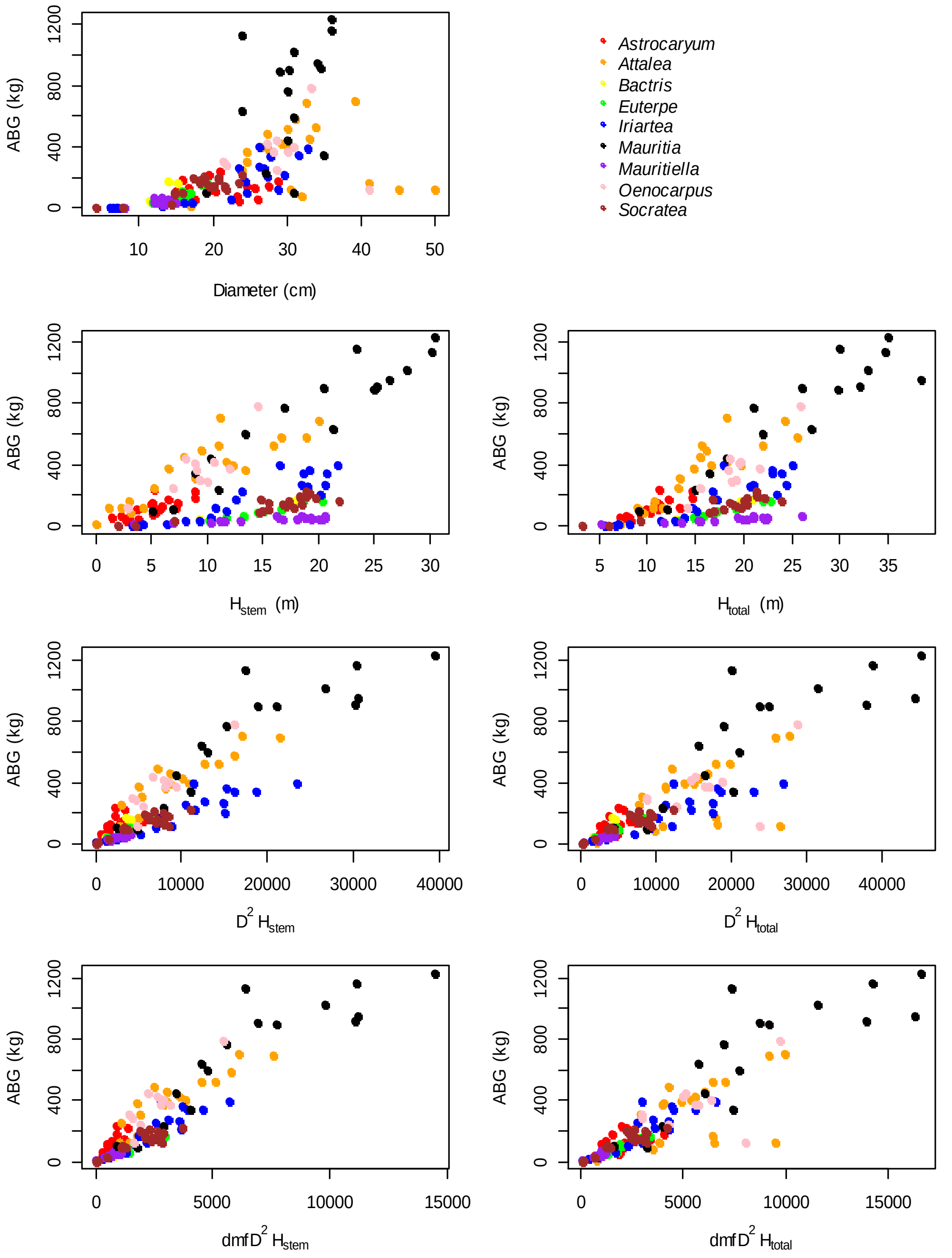

Figure A.1. Relationships between aboveground biomass (AGB; kg dry mass) and diameter, stem height (H_{stem}), total height (H_{tot}), and dry mass fraction (dmf) for every individual in the biomass dataset.

Appendix 4 Supplementary material for Chapter 4

A4.1 Forest inventory in Tambopata

Detailed inventories were conducted in five *terra firme* forests plots within Tambopata National Reserve in Madre de Dios, Peru (12.8^0 S, 69.3^{0}W). These plots were established by RAINFOR researchers in 1979–1983 (Gentry 1988), and all trees and palms with $D \geq 10$ cm are included in the inventories (Malhi et al. 2002). The inventories include D measurements and botanical identification, and plots are recensused every 2–3 years. Data for the 2011 census were downloaded from the ForestPlots.net database on 2 August 2012 (Lopez-Gonzalez et al. 2011, Lopez-Gonzalez et al. 2012). For this study, total height (H) and crown radius (CR) were measured on all trees with $D \geq 30$ cm and on all trees with $10 \geq D > 30$ cm within four 0.04-ha subplots per 1-ha plot. All height measurements were taken with a laser hypsometer and corrected for measurement error (A 4.2). CR was measured with a metric tape in four cardinal directions, and the average of these four measurements was used in the analysis.

A4.2 Height corrections

I found that laser hypsometer readings on standing trees often underestimated true H measurements taken post-harvest, similar to a recent assessment of tree H measurement techniques (Larjavaara and Muller-Landau 2013). Some measurements were quite accurate, but the majority of tree heights were underestimated and some were severely underestimated (Figure A4.1). Thus, I developed a height correction model to adjust measured heights in Tambopata (below) and used corrected total heights in Tambopata for the remainder of the analysis.

$$H_{corrected} = \exp\left(0.41098 + 0.91091 \times ln(H_{measured})\right)$$

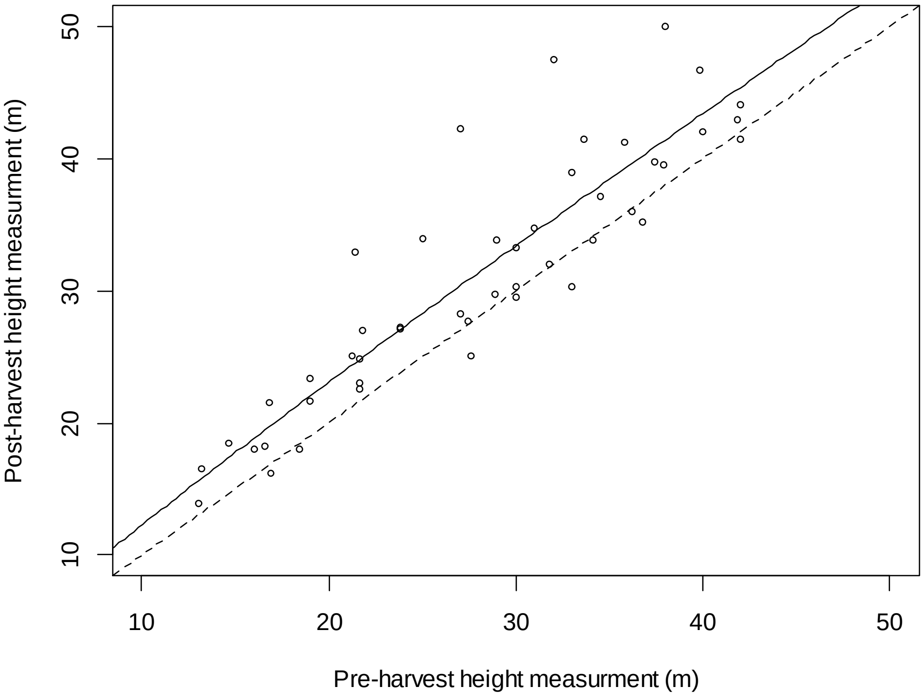

Figure A4.1. Height measurements taken pre-harvest with a laser hypsometer on standing trees and post-harvest with metric tape on fallen trees. Dotted line shows a 1:1 relationship, and solid lines shows the statistically fit corrected height model: y = exp(0.40329+0.91091×ln(x))×CF, where the correction factor (CF) is exp(RSE²/2) (R^2=0.8559, RSE = 0.124, $F_{1,45}$ = 267.3, *p* < 0.001).

A4.3 Estimating crown radius and height from diameter

Models were developed to estimate H and CR from D for small trees (D < 30 cm; Figure 2). Models are below, where average crown radius in m, height in m, and D in cm; and R^2 values correspond to the transformed data in which models were built. The correction factor has been incorporated in the H–D model.

D < 30 cm: $$CR = \left(1.141 + 0.0231(D)\right)^2$$

$R^2 = 0.326$, $P < 0.001$, RSE = 0.2064

D < 30 cm: $$H = -11.110 + 10.337 \times \ln(D)$$

$R^2 = 0.5436$, $P < 0.001$, RSE = 3.218

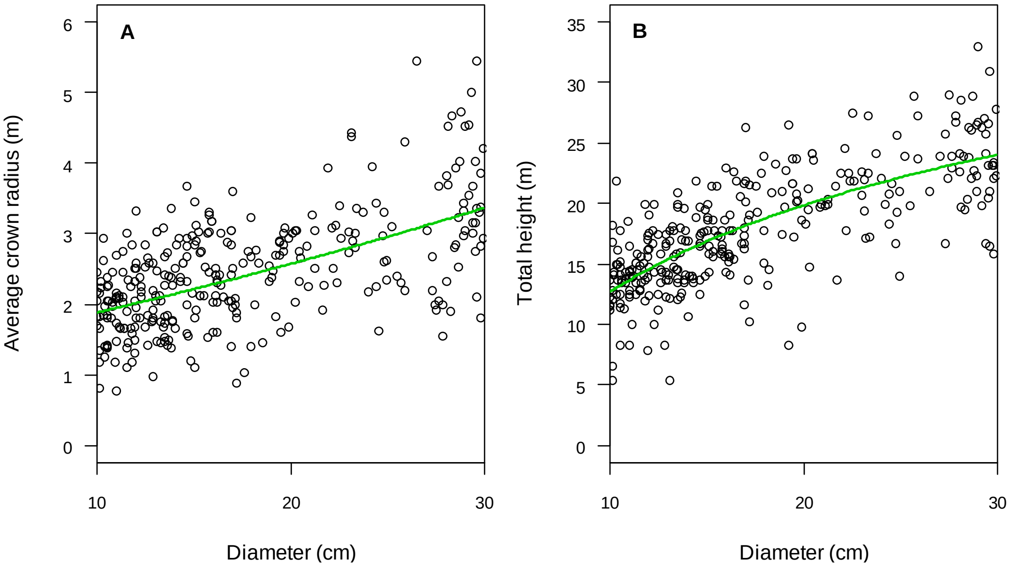

Figure A4.2. Average crown radius–diameter (A) and height–diameter (B) regressions determined for trees in *terra firme* forests with diameter < 30 cm.

For the interest of the broader scientific community, models were developed for trees of all sizes to estimate crown radius from diameter (Figure A4.3). To satisfy the assumptions of linear regression, data had to be divided for trees with diameter below and above 50 cm:

$D < 50$ cm: $$Crown\ radius = \left(1.1308 + 0.02315(Diameter)\right)^2$$

$R^2 = 0.517$, $P < 0.001$, RSE = 0.254

$D \geq 50$ cm: $$Crown\ radius = \left(1.5295\ + 0.01582(Diameter)\right)^2$$

$R^2 = 0.6275$, $P < 0.001$, RSE = 0.350

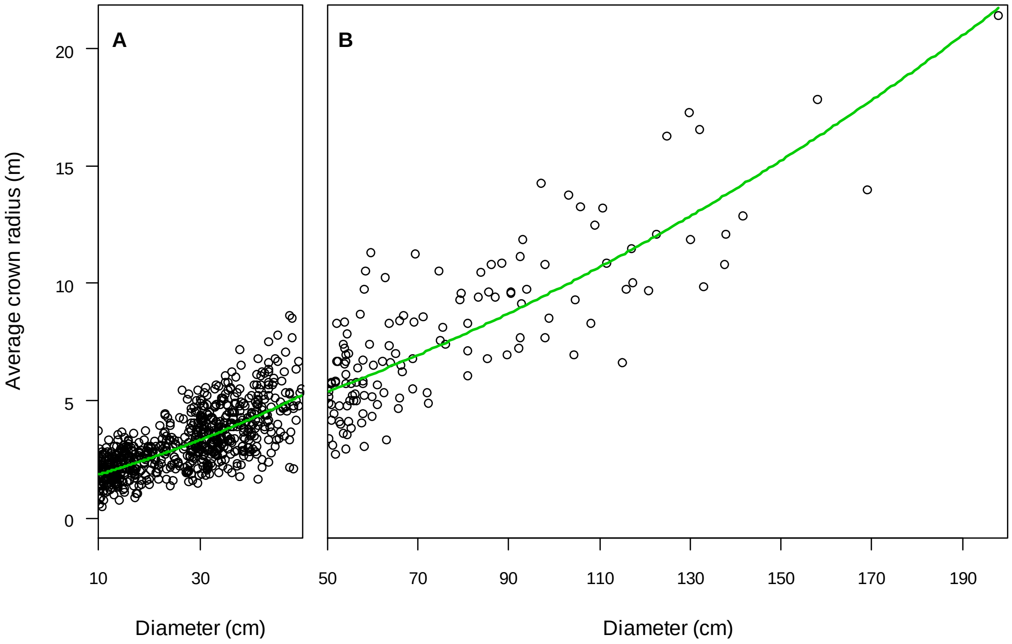

Figure A4.3. Average crown radius–diameter regression (line) determined for trees in five *terra firme* forest plots and one swamp plot with (A) diameter < 50 cm and (B) diameter ≥ 50 cm.

A4.4 Quantifying allometric uncertainty

I tested for differences in allometric relationships between the two sites (*H*–*D, CR*–*D*, and *CR*–*H*) in generalised linear models (glm) with the dependent variable, site, and site × dependent variable interaction. For this analysis, only individuals with directly-measured variables (diameter, height, and crown radius) were included, and subsets of the Tambopata data were randomly selected from each 20-cm *D* size class so that the sample size in each size class was equal to that of the Tahuamanu dataset. Ten glm analyses were performed, using different randomly selected subsets of data, to determine which relationships were significant. For significant relationships, twenty glm analyses were performed, and the coefficient means for each site were compared. All analyses were performed using the R statistical platform, version 3.0.0 (R Core Team 2013).

Allometric relationships are similar between the two sites studied, but trees in Tambopata are taller at the same *D* and may have slightly smaller crowns at the same *H* (Figure A4.4). Using random subsets of Tambopata data, neither site nor site nor site × dependent variable interaction were ever significant. If the interaction term was removed, the effect of site was consistently significant for *H*–

D relationships (10 of 10 comparisons), but it was seldom significant for *CR*–*H* relationships (2 of 10 comparisons). Allometry differed by site such that trees in Tambopata were taller at a given diameter and had slightly smaller *CR* at a given *H*, as compared to Tahuamanu. Comparing *CR*–*D* allometry, neither site nor the interaction term was significant. This suggests that allometric relationships between the two sites may be very slightly, but not strongly, different.

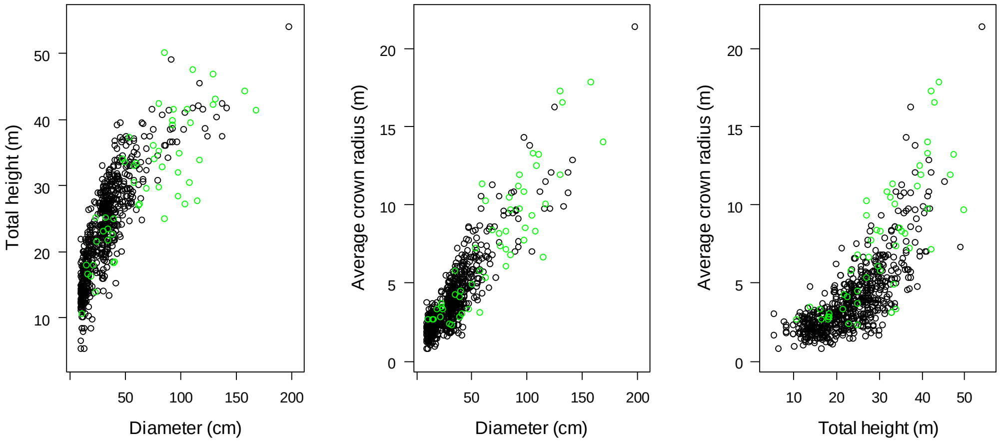

Figure A4.4. Allometric relationships between all trees directly measured in Tambopata (black) and those from the biomass study (green).

A4.5 Quantifying model selection error

To explore the effects of using different equations to estimate AGB in this region, AGB density of trees was estimated in five *terra firme* forest plots in Tambopata, using four models developed in southwestern Amazonia (Chapter 2) —with *D* and *ρ* (Good II.1); *D*, *ρ*, and *H* (Good I.1); *D*, *ρ*, and *CR* (Good II.1CR); and *D*, *ρ*, *H*, and *CR* (Good I.1CR). To estimate AGB density using all four models proposed in Chapter 2, I used the equations developed to estimate *H* and *CR* for small trees ($D < 30$ cm) that were not directly measured in the field inventory (A 4.3).

Mean density estimates from the models developed in Chapters 2 ranged from 258.1 to 277.3 Mg/ha for trees in five forest plots (Figure A4.5). Examining mean and SE of the four model estimates, model selection error in Tambopata was estimated as 1.65 % (mean = 267.1, SE = 4.41) for trees and 2.19 % (mean = 21.5, SE = 0.47) for palms (Chapter 2).

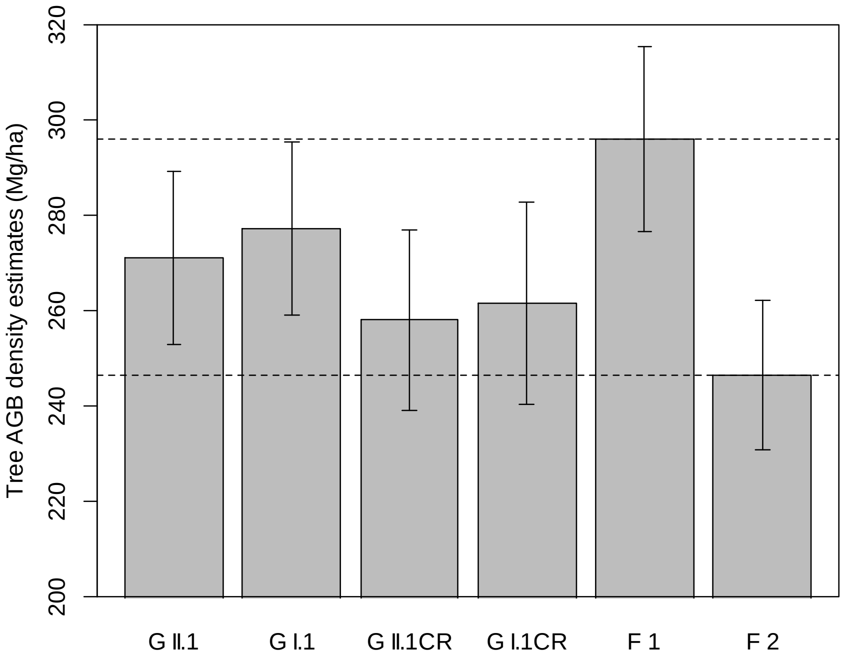

Figure A4.5. AGB density estimates of trees in five *terra firme* plots (TAM 02, 04, 05, 06, and 07) using four models developed for the southwestern Amazon (G; Goodman —Chapter 2) and two pantropical models (F; Feldpausch et al. 2012). Values are mean (bars) ± 1 standard error (arrows).

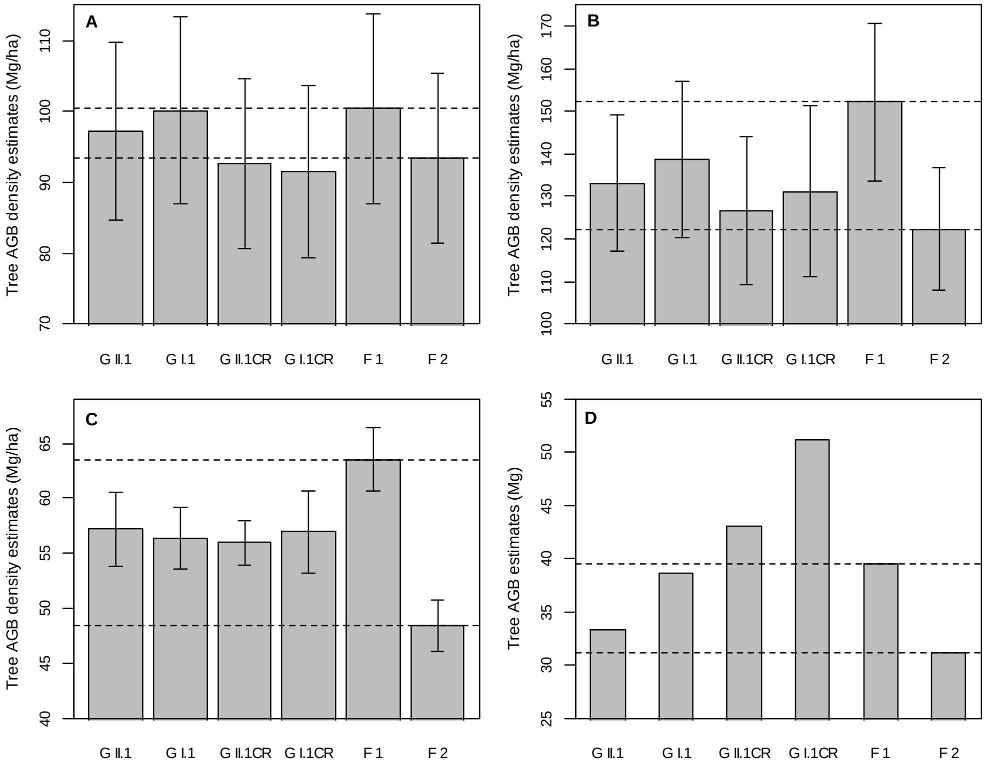

Figure A4.6. Six aboveground biomass (AGB) density estimates for trees with (A) *D* < 30 cm where height and crown radius were directly measured, (B) 30 ≤ *D* < 95 cm, and (C) *D* ≥ 95 cm and AGB estimates for (*D*) the single largest diameter (198 cm) tree measured in Tambopata. Values are mean ± 1 standard error.