Improving estimates of biomass change in buttressed trees using tree taper models

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Summary

1. Repeat censuses of tree plots are key tools for investigating forest carbon fluxes. Current measurement procedures for trees with buttresses or trunk irregularities – trees that account for a large fraction of tropical forest biomass –introduce substantial systematic error in plot-level estimates of biomass change. The diameters of buttressed trees are measured above the standard height of 1·3 m, and the measurement heights on individual trees are often moved upwards as buttresses grow. Because tree trunks taper (diameter decreases with height), biomass growth in buttressed individuals tends to be underestimated. Methods have been introduced to correct biomass growth estimates in individual trees for increases in measurement height; however, these methods change the distribution of effective measurement heights over time, introducing biases in plot-level estimates of biomass change.

2. In this study, we developed and applied new methods to measure and model trunk taper, and to use taper models to correct estimates of AGB change for changing measurement heights. We measured trunk taper above buttresses in 190 stems on Barro Colorado Island, Panama (BCI), a site where more than half of forest biomass is in trees measured above standard height. We compared proposed taper models to see which best described our measured taper data, then used the best taper model to correct for changing measurement heights in the historical plot data. Specifically, for all diameter measurements taken above 1·3 m, we calculated equivalent diameters at 1·3 m and substituted these into allometric equations to examine biomass change over time.

3. We found that measured taper was best fit by an exponential model with a rate parameter that varied with measured diameter (tree size), height of measurement (buttress height) and species. Whereas uncorrected data show a decrease in biomass of 0·21% year^{-1} between 1985 and 2010 on BCI, taper-corrected data show an increase of 0·18% year^{-1}.

4. The novel correction method presented here converts all measured diameters to one standard effective measurement height. This corrects for biases at the plot level and provides a stronger foundation for measuring biomass change in tropical forests.

Key-words: above-ground biomass, Barro Colorado Island, forest dynamics, permanent sample plot, tropical forest

Introduction

Understanding the dynamics of tropical forests is essential for quantifying global carbon budgets. Intact tropical forests are estimated to be carbon sinks of 1·5 Pg year^{-1} and regrowing tropical forests sinks of an additional 1·4 Pg year^{-1} (Pan *et al.* 2011). However, there is still much uncertainty regarding tropical forest carbon fluxes and their responses to global change (Clark 2004; Malhi 2010; Wright 2013). The data used to estimate these carbon fluxes come largely from permanent sample plots (PSPs), in which all trees in an area are repeatedly measured over time. PSP diameter measurements are used together with allometric equations to estimate above-ground biomass (AGB) (Chave *et al.* 2005) and thereby determine whether forests are acting as a carbon source or sink (Chave *et al.* 2003; Baker *et al.* 2004; Pan *et al.* 2011). Unfortunately, many

sources of uncertainty exist for measurements and estimations from PSPs, and some of these have the potential to substantially bias estimates of forest biomass and/or forest biomass change (Sheil 1995; Muller-Landau *et al.* 2014).

Buttressed trees pose a special challenge – many tropical trees have buttresses that extend well above the standard measurement height of 1·3 m. Tree trunks that are not cylindrical at 1·3 m are instead measured above the height of buttresses, and the height of measurement often changes in time as buttresses grow upwards (Condit 1998). Widely used allometric equations relating AGB to diameter were developed based on diameter measurements 'at 130 cm above-ground or above buttresses' in destructively harvested trees (Chave *et al.* 2005). Because tree trunks taper, or decrease in diameter with height, a tree measured above 1·3 m will have a smaller diameter measurement compared to the same tree measured at 1·3 m. Consequently, a tree measured above 1·3 m will have a smaller diameter for a given biomass, and thus, diameter-AGB

allometries are dependent on the distribution of measurement heights in the harvested trees (Muller-Landau *et al.* 2014). If a PSP has a different distribution of measurement heights than the destructive sample used to fit an allometric equation, then that equation will systematically over- or underestimate AGB in the plot. Further, changes in measurement height distributions within a PSP over time will affect the magnitude and potentially the direction of this error, introducing systematic error in estimates of biomass change.

In the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama, the proportion of trees measured at non-standard height has increased over time, and these trees constitute over 50% of estimated biomass in recent censuses (Fig. 1). Increasing measurement height distributions create downward biases in estimates of biomass change, and the
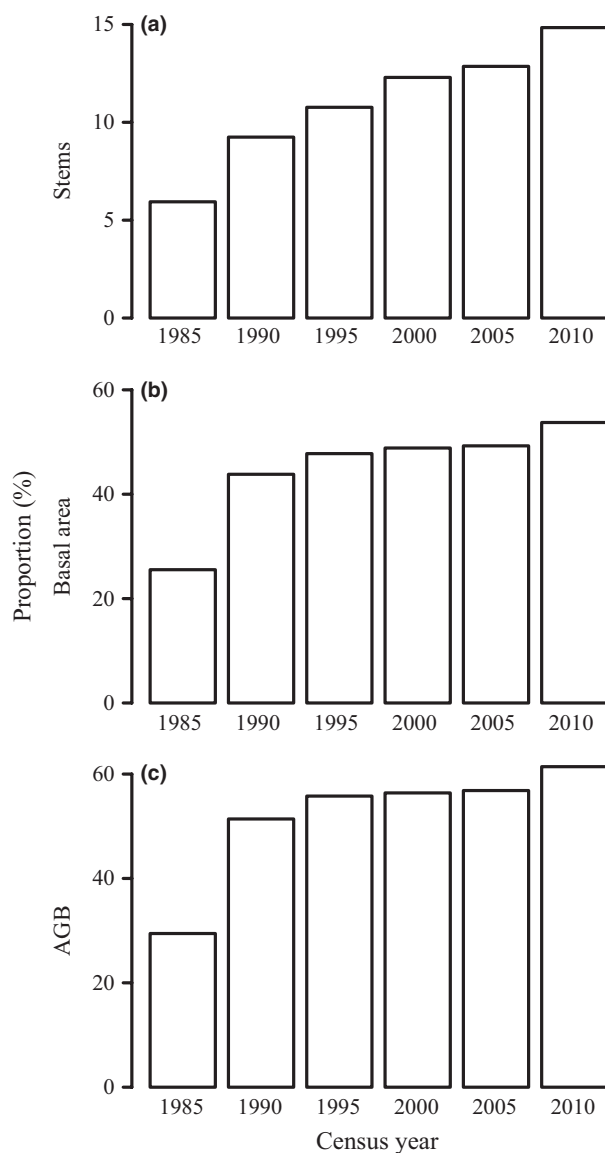
quantity of buttressed trees in this site means such bias could be substantial. Various approaches have been used to correct for changing measurement heights on individual trees, but different correction methods yield different values for biomass change (Lewis *et al.* 2009), and little attention has been given to the potential for correction methods themselves to introduce systematic error at the plot level (Muller-Landau *et al.* 2014).

The objective of this study was to develop an unbiased correction procedure for changing heights of measurement and to apply this method to improve estimates of temporal biomass trends in the BCI plot. We accomplish this by measuring tree taper above buttresses, fitting alternative models to taper measurements, and applying the best taper model to historical records of tree diameter and diameter measurement heights. For measurements taken above standard height, we estimate the equivalent diameter at 1·3 m and use these diameters to provide consistent estimates of AGB and thus unbiased estimates of relative AGB change over time. We compare these AGB change estimates with those obtained using other previously applied procedures.

Materials and methods

STUDY SITE

The research took place on Barro Colorado Island (BCI), Panama. BCI is a forested 1500-ha island that was separated from the mainland during the construction of the Panama Canal (Leigh 1999). The lowland tropical forest of BCI receives an annual average rainfall of 2600 mm, with a dry season lasting from approximately December to April. About half of the island has been essentially undisturbed by humans for 500 years. Elsewhere, farming occurred as recently as the 1920s.

Data were collected within the 50-ha BCI Forest Dynamics Plot, of which 48 hectares are in older forest. In this plot, all free-standing woody stems at least 1 cm diameter were mapped, identified to species, tagged and measured in stem diameter in 1982 (Hubbell, Condit & Foster 2005). Recensuses occurred every 5 years beginning in 1985. In the initial census, diameter was always measured at 1·3 m height, around any buttress or stem irregularity present at this height (Condit 1998). In 1985, diameters were measured 'just below' local irregularities and 'just above' the height of buttresses, if present. Since 1990, the protocol for measuring trees with buttresses or irregularities at 1·3 m has been to choose measurement heights 20 mm below local swellings or constrictions, or 50 cm above the top of buttresses. Condit (1998) estimates that buttresses grow upwards at rates less than 3 cm year^{-1}, so measurement heights 50 cm above buttresses should still be above buttresses after 5 years. A new height of measurement is selected if a buttress has grown within 30 cm of the previous height of measurement. In these cases, diameters are measured at both the old and new height of measurement. Non-standard measurement heights are recorded and marked with paint. At least in part because of these changes in methods, the proportion of trees measured above standard height on BCI has increased markedly over time (Fig. 1).

Fig. 1. Percentage of stems (a), basal area (b) and AGB (c) measured above standard height on BCI. Here, basal area and total AGB are estimated without correcting for taper. Percentages and all subsequent analyses are for stems ≥ 10 cm diameter and exclude strangler figs (17 individual strangler figs were excluded).

FIELD TAPER MEASUREMENTS

We selected 100 trees in the BCI plot that were measured above 1·5 m in the 2010 census for taper measurement. These trees were selected as

a biomass-weighted random sample, using published biomass values from the 2010 census. We selected 92 additional individuals of the 10 species with the most biomass in trees measured above 1·5 m, seeking to obtain sample sizes of 15 individuals per species. For two species (*A. excelsum* and *C. platanifolia*), fewer than 15 individuals had measurement points above 1·5. In other cases, the actual number of stems measured differs from the number of trees selected because trees died since the 2010 census (Table 2). In all, the sample constituted 25·2% of the total biomass of trees measured above 1·5 m in the 2010 census, with the random sample alone constituting 10·4%. For analyses by species, the categorical species variable differed for every focal species, while all other species were combined into a single group (51 individuals) for a total of 11 groups, henceforth referred to as species groups.

Trunk taper was measured in the 3–6 m above the top of the buttresses. Specifically, diameter was measured every 0·3 m height beginning above the height of buttress and continuing until 8 m from the ground or 3 m from the top of buttresses, whichever was higher. For individuals whose trunk forked below 8 m, we measured diameter until the fork. Diameters were measured with a precision of approximately 1 cm using a Criterion RD 1000 optical dendrometer (Laser Technology Inc, Centennial, CO, USA). We chose to use an optical dendrometer because it enabled relatively rapid measurements by a single person from the ground, and increased the ease of measuring trees with lianas or spines. We also measured the total height of each tree by directly measuring vertical distance to the topmost visible leaf using a Nikon Forestry 550 laser rangefinder (the sine measurement method, Larjavaara & Muller-Landau 2013).

To evaluate the performance of the optical dendrometer relative to more traditional methods, we measured 23 individuals with both an optical dendrometer and diameter tape. Twelve of those trees were also measured with large calipers parallel and perpendicular to the direction from which optical dendrometer measurements were taken. There was considerable variation in the taper model parameters depending on the measurement method, as would be expected given that trunks were not perfectly cylindrical (Fig. S1). However, there was no pattern of systematic difference in taper parameter values, so we concluded that the optical dendrometer was sufficiently precise and comparable to diameter tape for use in this study.

TAPER MODEL SELECTION

We compared five taper models proposed in the literature (Table 1) (Kozak, Munro & Smith 1969; Ormerod 1973; Forslund 1991; Riemer, Gadow & Sloboda 1995; Rojo *et al.* 2005; Metcalf, Clark & Clark 2008).These models were selected from a larger set of candidate models by choosing those that had three or fewer parameters and fit preliminary taper measurements well. For every stem, we fit each taper model to diameter data using maximum likelihood, assuming normally distributed errors. We compared the goodness-of-fits using the Akaike Information Criterion corrected for finite sample sizes (AICc). We

determined the overall best taper model by counting the number of times that each model provided a best fit for an individual stem.

For the random sample, and for each species group, we fit log-normal distributions to the individual tree parameter values of the best-fit model using maximum likelihood. The resulting distributions were tested for significant differences from a log-normal distribution using the Shapiro–Wilk test on log-transformed data. Normal distributions were subsequently fit to species samples that were significantly different from a log-normal distribution.

For the best taper model, we used multiple linear regression models to examine the relationship of taper parameter values with the following potential predictor variables: species group, 2010 diameter (an indicator of tree size), height of measurement (an indicator of buttress height) and wood density (a species level trait). We omitted the few individuals that had negative parameter values. (Negative parameter values indicate diameter that tends to increase with height over the measurement interval due to irregular trunk swellings. Such irregularities are avoided when the point of diameter measurement is chosen for field censuses.) Models were fit for each possible combination of these predictor variables, and we used AIC comparison to select the model that best described the variation in taper parameters among individuals.

TAPER MODEL APPLICATION

We applied the fitted taper model to diameter measurements from the BCI plot for each census from 1985 to 2010. (The first census was not included because measurements were taken at 1·3 m regardless of buttresses.) A taper parameter was assigned to every tree based on the best multiple linear regression model. For every diameter measurement not taken at 1·3 m, we used the taper model to calculate an equivalent diameter at 1·3 m. We estimated total tree height from both the original diameter measurement and the taper-corrected diameters, using the Weibull model from Feldpausch *et al.* (2012) fit to data from the BCI plot (Fig. S3). We used the Chave *et al.* (2005) pantropical moist forest allometric equation to estimate 'uncorrected' AGB from the original diameter measurements above 1·3 m, heights estimated from this diameter and species-specific wood specific gravity values. We used the same equation to estimate 'corrected' AGB from the estimated equivalent diameters at 1·3 m, the corresponding tree height estimates and species-specific wood densities.

We estimated 95% confidence intervals by resampling taper model parameter values using the uncertainty and covariance of the linear regression model (1000 resamples). We evaluated the robustness of our results by repeating the analysis using the Chave *et al.* (2005) allometry without total tree height. Additionally, we conducted a sensitivity analysis examining how biomass patterns changed with the taper parameter if all stems were assigned the same taper. Finally, we repeated our analysis using alternate correction methods for stems whose height of measurement changes in a census interval: assuming zero AGB change, assuming a size-dependent average AGB change

Table 1. Trunk taper models compared in this study

Model 1	$d = D \cdot e^{-b_1(h-1\cdot3)}$	Metcalf, Clark & Clark 2008
Model 2	$\left(\frac{d}{D}\right)^2 = b_1\left(1 - 2\left(\frac{h}{H}\right) + \left(\frac{h}{H}\right)^2\right)$	Kozak, Munro & Smith 1969
Model 3	$\frac{d}{D} = \left(\frac{H-h}{H-1\cdot3}\right)^{b_1}$	Ormerod 1973
Model 4	$\frac{d}{D} = \left(1 - \left(\frac{h}{H}\right)^{b_1}\right)^{\frac{1}{b_2}}$	Forslund 1991
Model 5	$d = \frac{b_1 \cdot D}{1-e^{b_3(1\cdot3-H)}} + \left(\frac{D}{2} - b_1 \cdot D\right)\left(1 - \frac{1}{1-e^{b_2(1\cdot3-H)}}\right) + e^{-b_2\cdot h}\left(\frac{e^{1\cdot3b_2\left(\frac{D}{2}-b_1\cdot D\right)}}{1-e^{b_2(1\cdot3-H)}}\right) - e^{b_3\cdot h}\left(\frac{b_1\cdot D\cdot e^{-b_3\cdot H}}{1-e^{b_3(1\cdot3-H)}}\right)$	Riemer, Gadow & Sloboda 1995

d– diameter at height *h* (cm), *D*– diameter at 1·3 m height (cm), *h*– height of diameter measurement (m), *H*– total tree height (m), b_i– *i*th parameter.

and assuming a size-dependent average diameter change (Chave *et al.* 2003; Lewis *et al.* 2009). Average AGB and diameter change rates (absolute growth per year) were fit to initial AGB and diameter, respectively, using a third-order polynomial, as in Muller-Landau *et al.* (2014) (Table S1). Percentage change per year was calculated assuming yearly compounding. For alternate correction methods, we only calculated absolute biomass change per census interval. Calculating percentage change per year for these alternatives is problematic because there is not a straightforward way to calculate absolute biomass after the second census: different trends are observed if absolute biomass considered the uncorrected 1985 AGB plus all subsequent corrected AGB changes versus the uncorrected AGB from the census immediately prior plus the correct AGB change.

All analyses were conducted in the R statistical environment (R Development Core Team 2013).

Results

TAPER MODEL SELECTION

Model 1 provided the best fit to taper data for the most individuals, with Model 3 performing second best (Table 2). Both models have only one fitted parameter, but Model 3 includes total tree height as a variable. Thus, based on its fit and its simplicity, we selected Model 1 for subsequent analyses. Model 1 was clearly outperformed in only a single species sample (*C. pentandra*) where Model 3 was more often the best fit. There was variation in how well Model 1 fit data for individual trees, but this model appropriately described trunk shape in the region in which diameter measurements are taken (Figs 2, S2).

There was considerable inter- and intraspecific variation in the taper parameter for Model 1 (Figs 3, S4). The taper param-

eter values were log-normally distributed in the random sample, with a geometric mean of 0·029 and an arithmetic mean of 0·039 (Fig. S4). Taper parameter values were also log-normally distributed within most individual species and within the non-focal species group (Fig. S4). The exceptions were three species – *H. crepitans*, *A. blackiana* and *T. arborea* – with normally distributed parameter values.

Overall variation in taper parameters among all measured individuals was best explained by a model that included species group, diameter and height of measurement (Fig. 3, Tables 3, S2). We chose to use the model with the lowest AIC value, though models with one fewer and one more parameter were not significantly worse (Tables S3 and S4). Taper parameter values decreased with 2010 diameter (i.e. tree size) and increased with 2010 height of measurement (i.e. buttress height).

TAPER MODEL APPLICATION

Correcting for tree taper in stems not measured at standard height affected the direction of apparent biomass change over the last 25 years in the BCI plot (Fig. 4). Uncorrected measurements show a slight decrease in plot biomass over the entire interval, whereas taper-corrected data suggest that biomass has in fact *increased* during this period. This is due mostly to disagreement in 1985–1990, an interval over which the proportion of stems measured above 1·5 m increased from 5·9% to 9·2% with a corresponding increase from 29% to 51% of estimated AGB in trees measured above standard height (Fig. 1). In this interval, the uncorrected data show a decrease of almost 5% of the initial value, while the taper-corrected data show an *increase* of about 5%. After 1995, the uncorrected

Table 2. Sample size and taper model fit comparisons for each sample group. More than one model provided a best fit to an individual if the difference in AICc was less than 2. Percentage of total stems and AGB includes only trees greater than 10 cm diameter measured > 1·5 m in the 2010 census
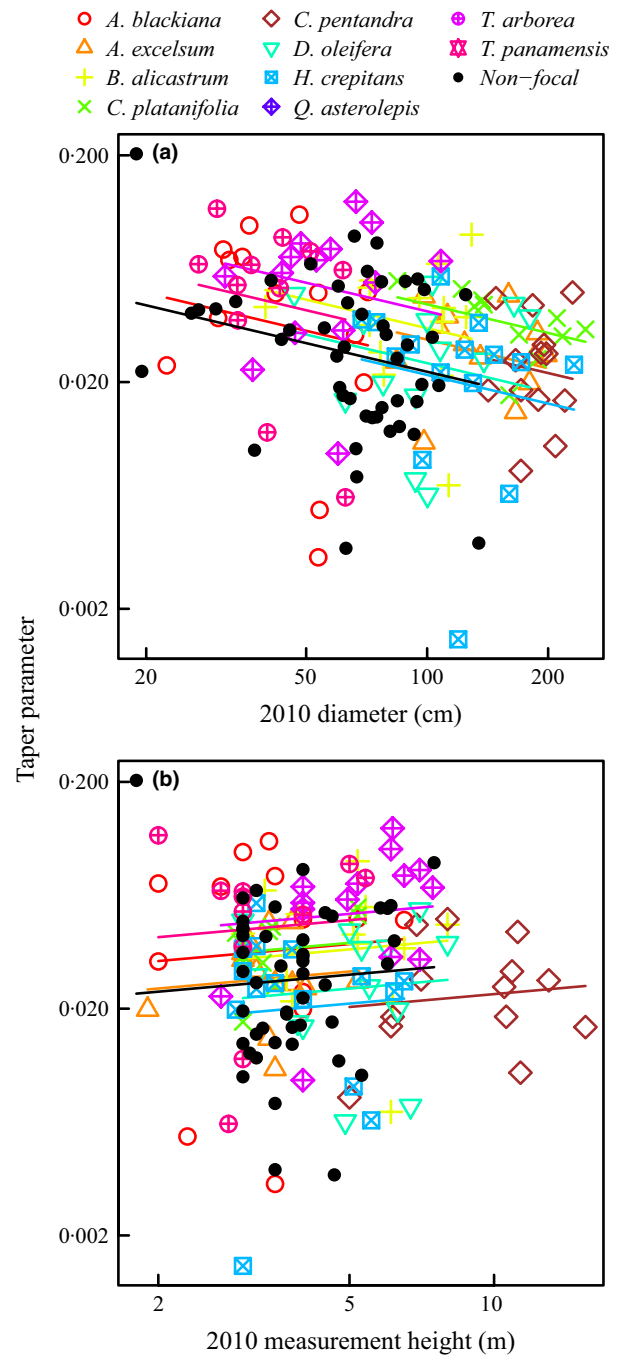
	Stems measured (No.)	Stems measured (% of plot)	AGB measured (Mg C)	AGB measured (% of plot)	Individuals for which model was best				
					Model 1	Model 2	Model 3	Model 4	Model 5
Total sample	190	5·8	2178	25·2	130	9	86	64	40
Non-focal species	51	2·4	331	7·6	36	0	0	2	33
Quararibea asterolepis	14	3·7	46	5·7	9	1	5	7	1
Ceiba pentandra	14	50·0	353	62·3	7	3	12	2	0
Hura crepitans	15	36·6	224	41·7	10	0	7	7	1
Dipteryx oleifera	15	50·0	380	74·1	9	1	11	4	2
Alseis blackiana	14	4·2	32	6·4	10	0	6	7	1
Brosimum alicastrum	14	30·4	181	48·9	12	0	11	8	0
Cavanillesia platanifolia	11	100	284	100	6	1	6	5	0
Anacardium excelsum	13	100	267	100	9	3	10	7	0
Tetragastris panamensis	16	21·1	57	24·3	11	0	11	9	1
Tabernaemontana arborea	13	9·1	23	10·2	11	0	7	6	1
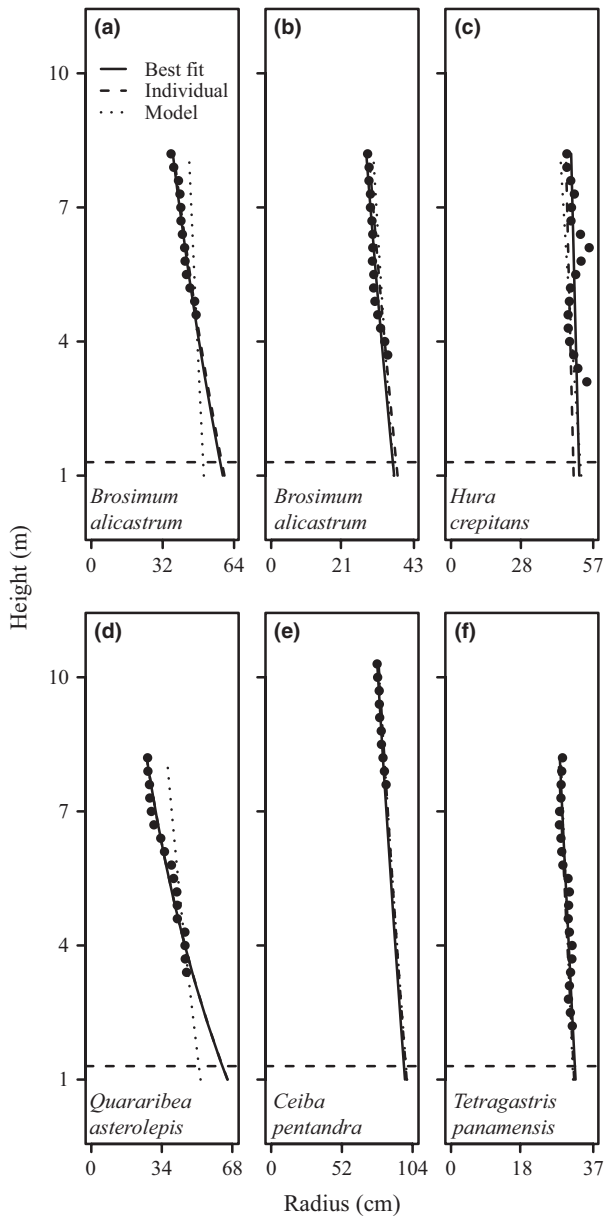
Fig. 2. Measured taper data (points) and fitted taper models (lines) for individual trees. Solid lines show the best-fit curves to the measured data for each stem (solid), dashed lines show the taper curves obtained by extrapolating from the 2010 diameter measurement for each tree using the best-fit taper value for the stem, and dotted lines show the extrapolation from the 2010 diameter using the general model applied to that stem. The horizontal dashed line is at 1·3 m, the height at which diameter estimates are used to estimate AGB in this analysis. Trees were randomly selected from the entire sample (a-b) or from focal species groups (c–f).

Fig. 3. Relationship of taper parameter values with 2010 diameter (an indicator of tree size) (a), and 2010 height of diameter measurement (an indicator of buttress height) (b). Every measured stem is included; each species group is shown with a different symbol and line.

and corrected data show similar trends in biomass. Nevertheless, AGB change in corrected data is somewhat more positive as the proportion of trees measured above 1·5 m has continued to increase modestly.

The overall pattern of relative biomass change is robust to variation in the details of the taper-correction implementation. Using the Chave *et al.* (2005) equation without total tree height increased the absolute estimate of biomass in the plot,

but had almost no effect on the percentage of AGB change over time (Fig. S5). Estimates of biomass change were highly sensitive to the taper parameter (Fig. 5). AGB increased for the entire interval from 1985 to 2010 when all stems were assigned any parameter value > 0·01. The species group with the least measured taper still had an average taper parameter > 0·01, so even a very conservative forest-level estimate of taper indicates increasing AGB.

Table 3. Fitted parameter values for the best model for among-tree variation in taper parameter values (b_1 of taper Model 1). This model is of the form $\log(b_1) \sim \log(\text{diameter}) + \log(\text{height of measurement}) + \text{species group}$. Species group coefficients reflect deviations from the base class (non-focal species). The residual standard error was 0·685. Asterisks indicate coefficients significantly different from zero, with ** indicating $P < 0.01$, * indicating $P < 0.05$ and (*) indicating $0.05 < P < 0.10$

	Coefficient	
Taper parameter covariate	Value	Std. Error
Intercept	−2·0205	0·6695**
Diameter	−0·5053	0·1652**
Height of measurement	0·3748	0·2093(*)
Species group		
Quararibea asterolepis	0·4865	0·2285*
Ceiba pentandra	0·0495	0·3061
Hura crepitans	0·0086	0·2325
Dipteryx oleifera	0·0150	0·2353
Alseis blackiana	0·1440	0·2245
Brosimum alicastrum	0·3874	0·2247(*)
Cavanillesia platanifolia	0·7982	0·2846**
Anacardium excelsum	0·4371	0·2600(*)
Tetragastris panamensis	−0·5141	0·2083*
Tabernaemontana arborea	0·3576	0·2485

Estimates of AGB change depend strongly on the correction method used (Fig. 4). Assuming zero AGB change for stems that have a change in measurement height during a census interval yields a smaller increase in AGB change compared to our taper-correction method (Table S5). Alternative methods assigning mean AGB growth or mean diameter growth rates to stems that have a change in measurement height show greater AGB increase than taper correction.

Discussion

### COMPARISONS WITH CORRECTION METHODS IN OTHER STUDIES

The problem posed by buttressed trees in estimates of biomass change has long been recognized (Sheil 1995; Metcalf, Clark & Clark 2008), and a number of procedures have been used to attempt to correct associated errors. The focus has generally been on individuals whose point of measurement moves upwards during a given census interval. Because tree trunks taper, diameter and biomass growth in these individuals is underestimated if calculated from the initial lower diameter and the final higher diameter. However, even though uncorrected diameter measurements are problematic at the individual level, they will produce *unbiased* estimates of relative biomass change at the plot level, *provided* that the distribution of measurement heights is the same across censuses. As long as measurement procedures and the distributions of measurement heights are the same, the frequency of biomass underestimation (and overestimation) is expected to be the same in both censuses, and thus, biomass change estimates are expected to be unbiased. *Not* changing diameter measurement heights over time will tend to upwardly bias
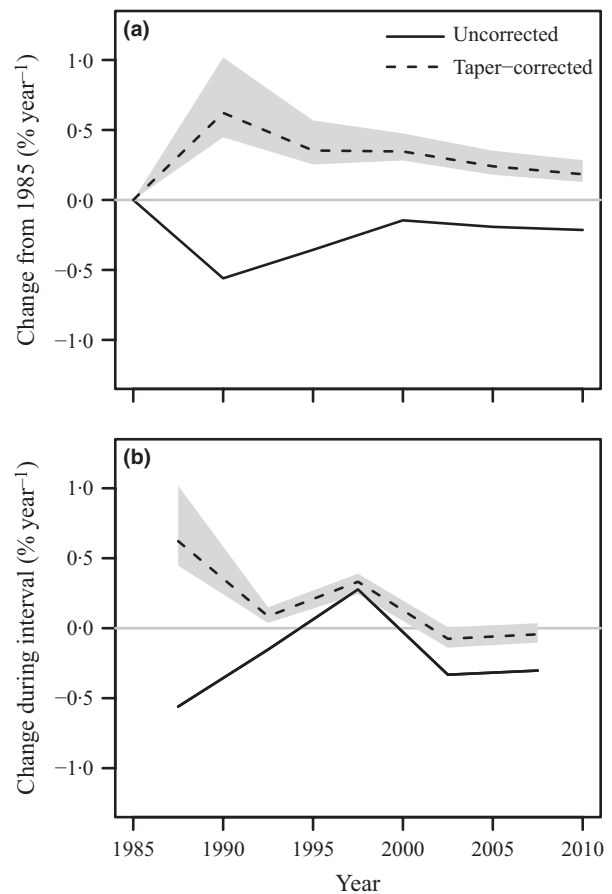
Fig. 4. Estimates of biomass change on BCI obtained from uncorrected and taper-corrected data. Percentage changes in AGB are based on the AGB value in 1985 (a) and at the beginning of each census interval (b). The shaded band shows 95% confidence intervals around taper model estimates (based on 1000 resamples of parameter sets from the fitted parameters given their estimated variances and covariances).

AGB trends, as trees measured at higher heights die over time and new recruits are measured at lower heights on average. (As buttresses grow up, the distance between the buttress and the height of measurement decreases, resulting in a decrease in AGB underestimation and a positive bias on AGB change.)

In contrast, standard well-intentioned correction methods for addressing changes in points of measurement induce biases in plot-level estimates of biomass change, even though they improve individual-level estimates. One common correction method replaces observed diameter differences in stems whose height of measurement changes during a given census interval with an average growth rate calculated on similarly sized stems that did not change measurement point (Chave *et al.* 2003, 2008; Lewis *et al.* 2009). This procedure no doubt improves estimates of growth for individual affected stems. However, it will upwardly bias biomass change at the plot level, because it decreases the effective distribution of diameter measurement heights. This is because in the initial census, diameters on trees with buttresses are all from actual measurements above buttresses, while in the final census, diameters on trees with buttresses that have grown upwards are in effect estimated as
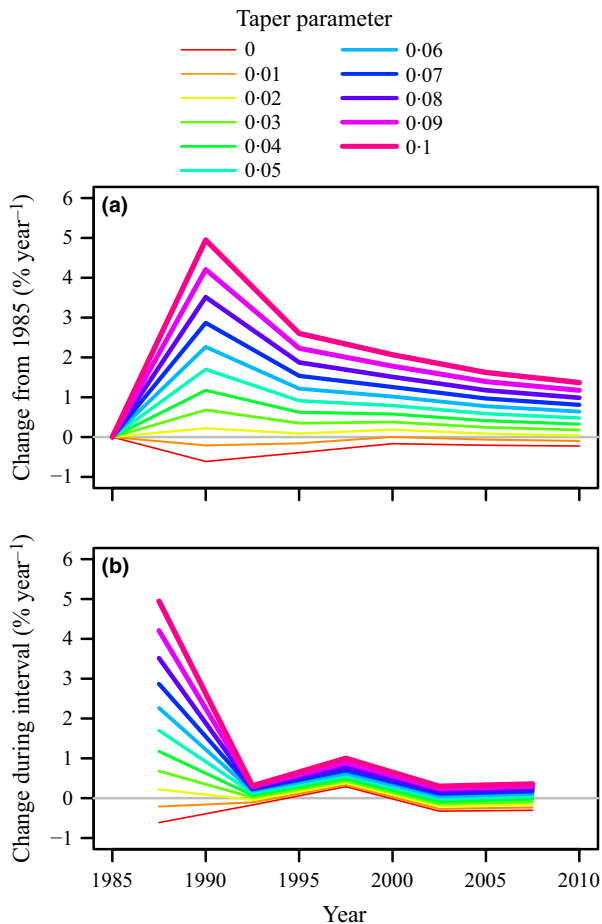
Fig. 5. Sensitivity of biomass change estimates to the taper parameter value. In this analysis, all stems were assigned the same taper parameter value. Percentage changes in AGB are based on the AGB value in 1985 (a) and at the beginning of each census interval (b).

equivalent diameters at lower heights of measurement. Another method assumes a growth rate of zero for all stems whose height of measurement changes (Chave *et al.* 2003; Feeley *et al.* 2007). This clearly underestimates biomass growth in the affected individuals. (Though when the new measured diameter is smaller than the original one, this underestimation is less than in uncorrected data.) Its effect on plot-level estimates of biomass change is unpredictable, depending on how the assumption of no change in diameter translates into a distribution of effective measurement heights in the final census. (That is, for stems where points of measurement changes, assign effective measurement heights in the final census based on the heights at which diameters are equivalent to those measured at the lower height in the first census; if this results in lower measurement heights than the first census, then biomass change estimates will be upwardly biased, whereas if it results in higher measurement heights, they will be downwardly biased.)

This study presents a new and improved method for correcting biomass change estimates for changing measurement heights on individual trees and changing measurement height distributions within plots. Whereas previous correction methods focused only on individual trees with changes in heights of measurement, and thus did not mitigate (or even worsened) biases resulting from changes in measurement height distributions, our correction method applies to all stems with non-standard points of measurement, inherently adjusting for measurement height distributions. Our taper-correction method improves estimates of biomass change at the plot level, unlike previous correction methods in which improvements in estimates of biomass change in individual trees came at the cost of upward bias in plot-level estimates.

Our method has one important shortcoming – a bias in standing AGB estimates when biomass is calculated from allometric equations that include measurements of diameter above 1·3 m, such as those of Chave *et al.* (2005). Fortunately, this bias is consistent over time and thus leads to no bias in estimates of relative AGB change, which is why this metric is our focus in this study (absolute AGB estimates are given in Table S7). This bias results from our use of equivalent diameters at 1·3 m in allometries derived from a mix of data on diameters at this height and above buttresses. The magnitude of this bias depends on the height distribution in the calibration data set, which is not currently known (Chave *et al.* 2005). This bias would disappear if our method were applied together with biomass equations developed exclusively from measured or equivalent diameters at 1·3 m on harvested trees. We recommend that future destructive harvest studies report measurement heights on all trees. Indeed if height of measurement was included directly in biomass allometry equations, then this would enable a more direct correction for shifting heights of measurement when applied to PSP data, provided that the PSP data also include heights of measurement.

BIOMASS CHANGE ON BCI

Our study presents a significantly different trend in AGB over time compared to two previous analyses of BCI plot data (Chave *et al.* 2003, 2008). Chave *et al.*'s initial study (2003) found a nearly significant decrease in AGB of −0·14 (−0·38, 0·01)% year^{-1} during 1985–2000. A subsequent study found AGB change of −0·08 (−0·39, 0·21)% year^{-1} during 1985–2005, again not significantly different from zero (Chave *et al.* 2008). These previous analyses trend less negative but are not significantly different from our uncorrected values of −0·26 and −0·27% year^{-1} during the intervals of 1985–2000 and 1985–2005, respectively. In contrast, our correction method yields significant increases of 0·35 (0·28, 0·48)% year^{-1} during 1985–2000 and 0·24 (0·18, 0·35)% year^{-1} during 1985–2005. Over the entire interval of 1985–2010, corrected AGB change for BCI was 0·18 (0·13, 0·28)% year^{-1}, a substantial increase over the uncorrected AGB change estimate of −0·21% year^{-1}.

Discrepancy between uncorrected and taper-corrected AGB estimates is driven largely by the single census interval 1985–1990 (Fig. 4). A corresponding large increase in the amount of trees measured above standard height from 1985 to 1990 explains this divergence (Fig. 1). The corrected AGB increase from 1985 to 1990 is large compared to both uncorrected and corrected estimates in any other interval. On BCI, a strong El

Niño event in 1983 caused a longer and more severe dry season than average (Leigh 1999). This drought disturbance caused high tree mortality relative to later census intervals, and larger trees were most strongly affected (Condit, Foster & Hubbell 1995). Thus, forest recovery after the 1983 drought disturbance can explain the AGB increase in 1985–1990 in the taper-corrected analysis (Yang, Luo & Finzi 2011). The AGB decrease in uncorrected estimates is unrealistic in this context; it is driven by apparent AGB decreases in stems whose heights of measurement increase in this interval. When AGB change is set to zero for all such stems, there is a slight increase in AGB (Fig. 4). Furthermore, trees with larger changes in measurement height had larger apparent decreases in AGB (Table S6).

Our correction method brings estimated AGB change for BCI somewhat closer to values reported for tropical forests in other parts of the world. Baker *et al.* (2004) found that Amazonian plots showed an average increase of 0·50 (0·33, 0·67)% year^{-1} for 1979–2003, and Lewis *et al.* (2009) found that African plots showed average AGB change of 0·29 (0·05, 0·50)% year^{-1} over an average period of 1987–1996. In general, biomass dynamics vary considerably among forest types and locations, so we do not expect all sites to have identical AGB change. However, it is notable that a substantial proportion of the differences in biomass trends previously reported for BCI relative to other sites appear to be an artefact of varying measurement and analysis procedures, rather than true underlying variation in forest dynamics. Of course, the Amazonian and African studies applied different methods to address changing measurement heights, and application of the taper-correction procedure developed here to those data sets could increase or decrease differences from BCI, or have no effect, depending on whether distributions of effective measurement heights have increased, decreased or remained unchanged over time, respectively.

RECOMMENDATIONS

Buttressed trees are common in many tropical forests, and the percentage of trees with buttresses on BCI (15%) is not unusually high. Buttressed trees constitute 12–28%, 21% and 32% of trees greater than 10 cm diameter in plots in South America, Africa and China, respectively (Mori *et al.* 1983; Thompson *et al.* 1992; Chapman, Kaufman & Chapman 1998; Milliken 1998; Zhiyuan *et al.* 2013). As on BCI, buttressed trees are likely to account for an even larger proportion of estimated AGB, because buttresses are more common among trees in larger size classes (Chapman, Kaufman & Chapman 1998; Zhiyuan *et al.* 2013) This suggests a widespread potential for substantially biased estimates of AGB change due to shifting distributions of effective measurement heights in PSPs, especially in forests of low latitude and altitude where the proportion of buttressed trees is highest (Smith 1972).

Current procedures for estimating biomass change in plots with buttressed trees introduce variable errors in AGB change estimates and thereby confound temporal and spatial patterns in AGB change. Differences in measurement protocol among sites and changes in protocols over time clearly bias comparisons of AGB change, but buttressed trees are a problem even when consistent methods are observed. As stands age and trees grow, the proportion of trees measured above standard height can change even when measurement techniques do not. Change in the distribution of measurement heights will bias trends in AGB change in either case. An accurate estimate of the overall average biomass change in tropical forests is crucial for closing the global carbon budget (Pan *et al.* 2011). Further, knowledge of geographical and temporal variation in biomass change is important for correctly attributing causes of biomass change and for the development of useful models to predict future tropical forest carbon fluxes. All current estimates of biomass change in tropical forest depend on methods for estimating biomass and biomass change in buttressed trees, either directly (PSPs) or indirectly (remote sensing calibrated to PSPs). Thus, it is imperative to develop and implement improved methods for developing unbiased estimates of biomass change in plots with buttressed trees, methods such as the taper-correction procedure introduced here.

We strongly recommend recording diameter measurement height in all PSP censuses, to enable detection and correction of potential associated biases. Ideally the height of buttresses would also be recorded. When biomass change is estimated using allometric equations that do not include measurement height (e.g. Chave *et al.* 2005), we further recommend correcting diameter measurement of trees measured above standard height to a constant height using trunk taper. The tree taper model fitted here to BCI data can provide first estimates of taper parameters; collection of additional taper data at other sites should establish the generality of this model and inform the development of improved general models and/or additional site-specific models, as appropriate (models without species effects are included in Tables S8–S10). Collection and analyses of biomass harvest data that include data on the height of diameter measurements can provide a direct method for testing whether this method better predicts AGB in trees measured above standard height, and also provide a basis for improved biomass allometries that explicitly incorporate height of measurement.

Acknowledgements and contributions

Data accessibility

Measured taper data (taper.data.csv), fitted taper parameters for all measured trees (taper.parameters.csv), information about measured trees (tree.info.csv), and wood specific gravity values for trees in the BCI plot (wsg.data.csv) are uploaded as online supporting information.

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Supporting Information

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

Appendix A. R-code for fitting taper functions to measured height and diameter data and comparing fits for different functions (fit.taper.models.R).

Appendix B. R-code for applying the results of taper models to the BCI Forest Dynamics Plot data to estimated AGB change over time and correct for changing diameter measurement heights (apply.taper.correction.R).

Figure S1. Comparison of taper parameter values from measurements of the same trees using diameter tape (a,b,c) versus an optical dendrometer (a,d,e) versus calipers (b-f).

Figure S2. Measured taper data (points) for individual trees and the estimated taper obtained by extrapolating from the 2010 measurement point for each tree using individual (solid line) and general model (dashed line) taper parameter values.

Figure S3. Allometric relationship between diameter and total tree height in the BCI 50-ha plot.

Figure S4. Taper model parameter values for trees in the random sample (a) and in the species groups (b-l) in the BCI plot, with their best-fit log-normal distributions (solid line).

Figure S5. Comparison of biomass change estimated from Chave *et al.* (2005) allometric equations including (black) and not including (red) total tree height.

Table S1. Model coefficients describing size-dependent average growth rates for each census interval.

Table S2. AICc values for alternative models for among-tree variation in taper parameters.

Table S3. Fitted parameter values for the second-best model of among-tree variation in taper parameter, a model that differed in AICc from the best model by only 1.4.

Table S4. Fitted parameter values for third-best model of among-tree variation in taper parameters, a model that differed in AICc from the best model by only 1.8.

Table S5. Estimated AGB change (Mg C ha^{-1} yr^{-1}) in each census interval based on uncorrected diameter measurements, compared with those based on taper-corrected diameter measurements and on the following alternative correction methods for stems whose height of measurement changes in a census interval: assuming zero AGB change, assuming a size-dependent mean AGB change, and assuming a size-dependent mean diameter change.

Table S6. Number of stems, total biomass change, and average biomass change for classes of measurement height change between 1985 and 1990.

Table S7. Estimated absolute AGB (Mg C ha^{-1}) based on using uncorrected or taper-corrected diameter measurements in the Chave *et al.* (2006) moist forest equation with height estimated from the corresponding allometry (Fig. S3).

Table S8. Fitted parameter values for the best model of among-tree variation in taper parameters not including species group effects.

Table S9. Fitted parameter values for the second-best model of among-tree variation in taper parameters not including species group effects.

Table S10. Fitted parameter values for the third-best model of among-tree variation in taper parameters not including species group effects. This model is of the form $\log(b_1) \sim \log(\text{diameter})$.