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Measuring and modelling above-ground carbon and tree allometry along a tropical elevation gradient

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ABSTRACT

Emerging international policy aimed at reducing carbon emissions from deforestation and forest degradation (REDD+) in developing countries, has resulted in numerous studies on above-ground live carbon (AGC) in tropical forests. However, few studies have addressed the relative importance of disturbance, topography, climate, soil and methods for stem measurement, on the estimation of AGC, or the costs of improving AGC estimates by altering sample regimes. We established 18 one hectare plots containing 7201 stems, stratified along forested elevation gradients in Tanzania. We recorded a broad set of physical, climatic and edaphic predictors of AGC and tree stature. AGC estimates using stem diameter, height and wood density, gave a mean value of 174.5 t ha^{-1}, compared with 229.6 t ha^{-1} when height was excluded. Regression models revealed that stems were tallest for a given diameter at mid-elevation (1000–1250 m), on south-facing slopes, and without past logging. High AGC was strongly associated with shallow slopes, followed by intermediate elevation, elephant absence, low potential evapotranspiration and low soil pH. Further regression models to investigate the structural habitat features associated with AGC, revealed significant positive influence of basal area, stem density, and height:diameter ratio, rather than the mean wood density of species present. Large stems ($\geqslant$70 cm dbh; 4.6% of stems) contained 52% of AGC in all plots, declining to 36% in lowland plots. We discuss the cost:benefit of different measurements and recommend a tiered approach to AGC monitoring, depending on available resources. AGC assessments in African forests could exclude small stems, but should aim to record disturbance, topography and species. Stem height is vital for AGC estimation and valuation; when excluding height our 55 t ha^{-1} over-estimation of AGC would have over-valued the carbon resource by 24% (US$3300 ha^{-1}).

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1. Introduction

Tropical forests contain approximately 17–25% of the carbon in the terrestrial biosphere (Bonan, 2008; IPCC, 2001) on only ~10% of the land surface (Lewis, 2006). The biome is in flux, on the one hand tropical deforestation is estimated at 476,000 ± 49,000 km^2 yr^{-1} (0.5%; Hansen et al., 2010), releasing 2.9 ± 0.5 Pg C yr^{-1} into the atmosphere – more than one third of global carbon emissions (Pan et al., 2011). On the other, forest regeneration in tropical areas is removing 1.6 ± 0.5 Pg C from the atmosphere, in part offsetting the emissions from deforestation (Pan et al., 2011).

Carbon has become a major consideration for the conservation of tropical forests, with carbon payment schemes aiming to mitigate climate change through reduced deforestation (Ebeling and Yasue, 2008; Kindermann et al., 2008). Since most of the world's biodiversity hotspots lie within tropical forest regions (Myers et al., 2000), payments could not only secure carbon storage, but also reduce conversion of biodiverse regions, and potentially assist economic and social development (CCBA, 2008; Nelson et al., 2009; Gardner et al., this issue). Reliable and practical methods for monitoring, reporting and verifying carbon stocks are therefore a necessary component of a functioning international policy to

"Reduce Emissions from Deforestation and Degradation" in developing countries (REDD+; Goetz et al., 2010).

Carbon stock estimation requires a combination of ground-based and remote-sensing methods (Gibbs et al., 2007; Saatchi et al., 2011). While remote methods provide broad geographic coverage, they are reliant on good quality ground-truthing data for calibration and verification (Mitchard et al., 2011) and may not always be available to developing nations. As such, development of good practice for both methods is necessary to assist prioritising efforts towards metrics that are accurate, precise and cost-effective (Herold et al., 2006).

Most studies on tropical forest carbon have been conducted in South America and south-east Asia, with far fewer in Africa (but see Lewis et al. (2009) for ground-based approaches, and Mitchard et al. (2009a,b) for remote-sensing approaches). Africa contains over one-third of all tropical forests (using the FAO forest definition: Lewis et al., 2009) and 25% of the tropical forest carbon stock (Saatchi et al., 2011). The rate of deforestation is estimated at 3.4 Mha yr^{-1} (FAO, 2010). Human activities have further degraded 37.2% of African humid tropical forests such that canopy cover is below 50% (Asner et al., 2009b). The resulting carbon emissions in Africa through deforestation and degradation was 0.59 Pg yr^{-1} (2000–2007; Pan et al., 2011).

Knowledge of the environmental predictors of carbon and tree stature will help to prioritise data collection for future assessments and for extrapolation to larger areas. There is little consensus on the relative impact of climate, soil or forest structure on spatial patterns in above-ground live carbon (AGC) in tropical forests (Baraloto et al., 2011). Studies across broad elevation ranges are particularly valuable because they show high variation in environmental

conditions. Above-ground biomass typically decreases with elevation (and hence also temperature; Girardin et al., 2010), but water stress and precipitation have the biggest influence on the presence/absence of tropical forests (Zelazowski et al., 2011). The relationship between soil and biomass is less consistent, and has shown high variation between studies and regions (Slik et al., 2010; Baraloto et al., 2011).

The stature or "architecture" of tropical trees may follow many models or forms (Hallé et al., 1978; Philip, 1994). Individual tree height does not correlate with diameter in a simple manner (Nagendra, 2012) but instead the ratio is related to species, precipitation, temperature and region (Feldpausch et al., 2011; Banin et al., 2012), and typically decreases with elevation (Bruijnzeel and Veneklaas, 1998; Aiba and Kitayama, 1999). Yet measures of tree height are not always included in estimates of biomass and carbon. This is primarily due to a lack of height data and reported similarity between biomass estimates with and without the inclusion of height (Brown, 2002; Lewis et al., 2009). The precision of biomass estimates has however been shown to improve when using height data (Chave et al., 2005), and in disturbed areas of South America, the inclusion of height estimates reduced biomass estimates by 3.6–11.0% (Nogueira et al., 2008b).

Increased frequency and severity of disturbance (e.g. logging, storms, fire) has been observed to decrease AGC (Smithwick et al., 2007). Vegetation structure and species composition are also impacted by elephants across sub-Saharan Africa (Guildemond and van Aarde, 2007) but this has not been studied previously in moist forests. Moreover, disturbance does not always occur independently from environmental gradients, e.g. some elevations may be more accessible than others (Waide et al., 1998; Lovett, 2006).
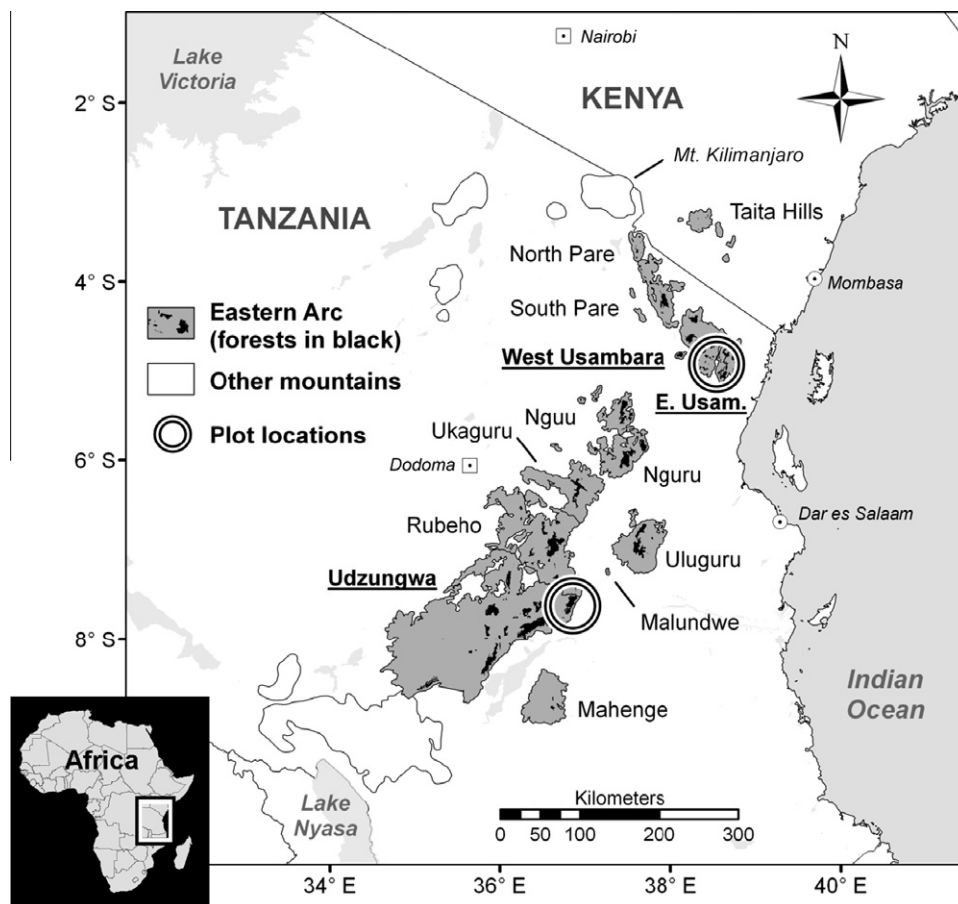

Fig. 1. Location of 18 one hectare plots for assessing above-ground carbon in Tanzania (Udzungwa, n = 11; East and West Usambara, n = 7). Adapted from Platts et al. (2011).

The present study was conducted in the Eastern Arc Mountains of Tanzania (Fig. 1), a region of global importance for biodiversity (Myers et al., 2000) with a large elevation range and varied climate (121–2636 m; rainfall 158–3814 mm yr^{-1}; Platts et al., 2010, 2011). Anthropogenic disturbance and clearance for agriculture have impacted the forest extent of the region, particularly at low elevations (Hall et al., 2009). AGC estimates range between 74 and 517 t ha^{-1} (Munishi and Shear, 2004; Zahabu, 2006). Reducing the high level of uncertainty in AGC estimates is becoming increasingly important in Tanzania, which is piloting methods for implementing REDD + policy (Burgess et al., 2010) and where projections for AGC loss due to land use change are between 4 and 25% (2000–2025; Swetnam et al., 2011).

Here we aim to determine the most important environmental and structural measurements for estimating and monitoring AGC in tropical forest via (1) the first estimate of AGC by internationally recognised methods for the Eastern Arc Mountains, (2) development of plot-specific allometric equations, (3) calculation of the effect of stem height data on the estimation of AGC, (4) empirical modelling of stem stature and AGC to compare the influence of physical, climatic and edaphic variables, (5) further modelling to identify the structural traits most associated with AGC stocks, (6) calculation of AGC per stem size class (and hence an estimate of monitoring efficiency).

2. Methods

2.1. Vegetation plots

One hectare permanent sample plots were positioned in the Udzungwa Mountains (n = 11; Mwanihana, Gologolo and Magombera forests) and Usambara Mountains (n = 7; Amani-Zigi, Mazumbai-Baga and Ambangulu forests) between March 2007 and March 2008. Positioning of plots near the latitudinal extremes of the region maximised geographical coverage and captured a range of environmental conditions (Fig. 1). Plots were placed using randomised co-ordinates stratified by elevation (271–2021 m) in predominantly closed-canopy forest. Plot selections were rejected if within 1 km of another plot, had discontinuous canopy, or occurred in dangerous locations. The plot network encompassed several forest types (White, 1983; Lovett et al., 1988; Table A.1): Zanzibar-inhumbane lowland forest (n = 5; <750 m), transitional/submontane forest (n = 5; 750–1200 m), and afromontane forest (n = 8; >1200 m).

Plot methods followed internationally accepted protocol for collection of AGC data (Kuebler, 2003). The diameters of stems ⩾10 cm diameter at breast height (dbh; 1.3 m) were measured within 25 sub-plots (20 × 20 m). Smaller stems were not sampled as they we are expected to hold ∼5% of AGC in mature African tropical forests (Chave et al., 2008; Lewis et al., 2009). Stem heights were measured from the tree base to the highest point from the ground (parallel to the main trunk), across the full range of size classes (10–19, 20–29, 30–39, 40–49 and ⩾50 cm dbh), using a laser rangefinder (Bushnell Yardage Pro 700; accuracy ±1 m). We aimed to measure at least 10 stems per size class, with the number reduced in some instances by time, a lack of stems or the density of vegetation (mean 10.6 [95% confidence 9.9–11.3]) – a common problem in tropical forests (Jørgen and Karsten, 1994). Height estimates for 20 stems were verified by correlation with more time-consuming trigonometric measurements (Pearson r^2 = 0.977; height 8–36 m). The rangefinder could not measure distances below 8 m, for which we instead used a pole of known length.

Trees were identified following taxonomy of the Africa Plant Phylogeny Group (Bremer et al., 2003). Where there was doubt in field identification, voucher specimens were collected for verification at the Royal Botanic Gardens (Kew, London).

2.2. Above-ground carbon estimation

AGC was estimated for each stem with a commonly used moist forest biomass equation, and assuming 50% of biomass is carbon (moist forest equation in Chave et al., 2005). We calculated biomass (B; metric tonnes, t) both including and excluding stem height estimates. The first equation using dbh (cm) and taxon-specific values of wood specific gravity (WSG; g cm^{-3}):

$$B_d = WSG \times \exp\{-1.499 + [2.148 \times dbh] + [0.207 \times dbh^2] - [0.0281 \times (\log_n dbh)^3]\},$$

the second equation incorporating the height (m) of each stem in order to discern its influence on biomass (and AGC) estimates:

$$B_h = \exp[-2.977 + \log_n(WSG \times dbh^2 \times height)].$$

WSG was estimated as the mean value for each species from a database of 2961 records from 844 species (Zanne et al., 2009). Where WSG data were not available for a species, we took the mean value for all records of the nearest taxonomic unit (genus, family), or where these were unavailable, the mean of all remaining taxa in the same plot. WSG data were available to at least genus level for 66.9% of stems (44.1% to species level), and to at least family level for 96.4% of stems.

Statistical analyses were carried out using R (version 2.12.1; http://cran.r-project.org). Two alternative height–diameter allometric equations were used to estimate height for those stems not measured: (1) a log-linear ordinary least squares regression of height versus $\log_n$(dbh) for each plot, and (2) an exponential model, selected because of low bias and high precision compared to 30 other models ($H_{est} = H_{min} + \{[H_{max} - H_{min}] \times [1 - \exp(-c \times \{dbh - 10\})]\}$; Fang and Bailey, 1998), where H_{min} and H_{max} were the minimum and maximum measured heights per plot, and c was the rate of change in height versus dbh for each plot.

The most effective of the two height–diameter allometric equations was selected according to the minimum residual sum of squares (RSS). For this model we also investigated the effect of reducing the number of stem heights measured, through bootstrapped selection of samples from 10 down to 1 stem per dbh class (50 iterations, 999 bootstraps), each time calculating the root mean square error (RMSE = square root[RSS/n]). We did not explore separate equations for species-specific, functional or structural groups due to small sample sizes.

The differences between the two estimates of AGC (derived from B_d and B_h) were also correlated against the height–diameter relationship (height:$\log_n$[dbh], square transformed to remove skew; hereafter "height–diameter slope"), to determine how any disparity could have arisen. All summary data are presented as mean ±95% confidence interval (CI; 999 bootstrapped samples).

2.3. Environmental influence on AGC and stature

2.3.1. Data collation and refinement

In order to model variation in the total AGC per plot and the height–diameter slope, we selected a broad set of "environmental" predictor variables describing physical, climatic and edaphic factors.

The subset of physical variables included slope and aspect, measured using a clinometer and compass in each sub-plot, and averaged for each plot. The aspect of each sub-plot was first cosine transformed to remove circularity (i.e. 0° = 360°), giving a measure of "northness" (Roberts and Cooper, 1989). Presence/absence of topographic features representing the microhabitat of each plot were noted, including presence of a ridge, presence of running water within 50 m, and presence of rocks >1 m diameter in at least two sub-plots. Presence/absence of disturbance was also recorded, including evidence of past logging of timber within 100 m, and

signs of cut stumps or elephants inside each plot (e.g. dung, foot-prints, damage).

Climatic variables were selected based on empirical associations with plant species distributions in East Africa (Platts et al., 2010; Marshall et al., 2012). Mean, minimum and range in annual temperature (tmean, tmin, trange) were obtained from WorldClim and annual surface-received orographic precipitation (ppt) was derived from the Tropical Radar Measuring Mission (for methods and sources see Platts et al. (2010) and Marshall et al. (2012)). Potential evapotranspiration (PET), an estimate of the amount of evaporation expected given sufficient water (closely related to temperature), was calculated following Thornthwaite (1948). An annual moisture index (AMI) was calculated by dividing mean annual precipitation by PET, and a maximum water deficit was calculated as the highest cumulative deficit in mean monthly precipitation (deficit defined as <100 mm month^{-1}).

Soil samples for edaphic variables were collected using a 30 cm depth corer from the four corners and centre of each plot, and then air dried for around 6 weeks. The H_2O and 0.1 M KCl methods of Rowell (1994) were used to measure pH, from which we used the former because it had the most even distribution. Bray's phosphorus (P) was derived following Weaver et al. (1994). Exchangeable aluminium (Al) and exchangeable cations, namely calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K), were derived following Allen et al. (1974). Percentage nitrogen (%N) and carbon (%C) were derived following Quesada et al. (2010), using a Eurovector EA elemental analyser, calibrated using IRMM443-4 (Eurosoil 4), containing 1.45%C and 0.16%N and checked using B2152 Low Organic Content Soil Standard OAS.

2.3.2. Statistical modelling

Before modelling, variables with strong skew were transformed as follows: ppt, Mg, K, Al, %C, %N, basal area ⩾90 cm (square root); P (fourth root); AMI, PET (seventh root); trange (power 10).

Because of the large set of predictor variables, and to reduce intercorrelation, we then used Pearson correlation and Variance Inflation Factors (VIF) to assess covariation between all predictor variables (Zuur et al., 2010), first within the three subsets (physical, climatic, edaphic), and then between subsets. In the event of high covariation between predictor variables (Pearson $r \geqslant 0.7$ and/or VIF $\leqslant 5.0$), the variable with the strongest univariate relationship with the response variable was retained.

Generalised linear models (GLM) with a Gaussian error function were used to investigate the influence of predictor variables on AGC, and on height–diameter slope. Models were first run on the three subsets separately (physical, climatic, edaphic), before combining the reduced subsets into "holistic" GLM models. Elevation was excluded from at least one holistic model for each response variable, due to intercorrelation with both climatic and edaphic variables.

Minimum adequate models were obtained using backward–forward stepwise selection based on the Akaike Information Criterion (Murtaugh, 2009). Where trends deviated from linear relationships, quadratic terms were introduced. Final models were validated through observation of residual spread. Analyses of deviance (likelihood ratio tests) were used to test the probability that the amount of deviance explained was not reduced from full (unreduced) models ($p[D]$; Crawley, 2005; Zuur et al., 2010). For all minimum adequate models we determined the probability that the slope estimate (b) of each variable (i) was significantly different from zero, based on a t distribution (where $t_i = b_i/SE(b_i)$; Quinn and Keough, 2002). For these slope estimates we employed the False Discovery Rate (FDR; Benjamini and Hochberg, 1995) correction of alpha values for repetitive testing, resulting in a 95% significance alpha cut-off value of 0.0225 for models of height–diameter slope versus environmental variables, and 0.020 for models of AGC versus environmental variables.

2.4. Structural determinants of AGC

A set of non-intercorrelated "structural" predictor variables was selected for identifying the structural attributes of forests associated with variation in AGC, and hence to determine the features important for future monitoring. Given the parameters used to estimate biomass (dbh, height and WSG), changes in AGC could feasibly result from changes in stem shape, size, number and/or species (the latter through WSG variation between species). Structural variables therefore included the number of stems, height–diameter slope (to indicate stem shape/stature), two variables indicating the size of stems (mean dbh, basal area of large stems [⩾90 cm dbh]), and two variables indicating the influence of species composition on wood density (mean WSG per species, mean WSG per species ⩾90 cm dbh [power 6 transformed to remove skew]). Using the same procedure as for environmental variables, a Gaussian GLM was used to determine the relationship between structural variables and total AGC, with an FDR adjusted alpha of 0.050.

AGC estimates were also calculated per plot and per dbh size class. To assess the consistency of carbon distribution across stem size classes, and hence determine variation in work effort in different habitats, we employed chi-squared goodness-of-fit tests of AGC per size class between forest types and presence/absence of past logging.

3. Results

3.1. AGC estimation

The 18 plots contained 7201 stems (mean 400 stems ha^{-1} [95% CI 358–445]) from 308 species (mean 37.2 species ha^{-1} [33.0–41.3]), with mean basal area 33.3 m^2 ha^{-1} [28.9–37.9], mean dbh 25.8 cm ha^{-1} [24.2–27.4], and mean stem WSG per plot 0.62 g cm^{-3} ha^{-1} [0.60–0.64]. A total of 967 stem heights were measured (13.4% of stems), ranging from 3 m to 55 m. Of the two allometric equations, the log-linear model produced the better fit (mean RSS 1177.3, versus 1276.8; Fig. A.1), explaining 67% [62–73] of the variance in height. Using the logarithmic equation for each plot, height was estimated for all unmeasured stems, giving a mean stem height of 15.2 m [13.7–16.5] per plot (maximum 55 m). Bootstrapped reduction in sample size for modelling heights revealed that the mean RMSE of height estimates changed little beyond 4–6 stems per dbh size class (RMSE 3.3–1.7% below 10 stems), but mean precision (95% CI) continued to improve with increasing sample size (e.g. 4 stems 42.8%, 8 stems 8.3%; Fig. A.2).

Mean AGC per plot was estimated at 174.6 t ha^{-1} [144.8–205.5], including height estimates (AGC$_h$). The estimate of AGC was 55.0 t ha^{-1} [41.1–70.6] or 37.5% [27.5–48.5] higher when estimated without height (AGC$_d$; 229.6 t ha^{-1} [196.1–268.7]). The overestimate in AGC when excluding height varied significantly amongst plots (Table A.1), and was positively related to plot height–diameter slope ($r = 0.740$, $p = 0.00044$). AGC$_h$ was greater in Usambara (214.5 t ha^{-1} [170.9–246.4]; $n = 7$) than in Udzungwa (149.3 t ha^{-1} [113.1–193.8]; $n = 11$). AGC$_h$ was higher in transitional mid-elevation forest (205.2 t ha^{-1} [130.7–268.9]; $n = 5$), compared with lowland forest (127.0 t ha^{-1} [106.9–153.2]; $n = 5$) and montane forest (185.3 t ha^{-1} [138.6–225.9]; $n = 8$; Table A.1) but the differences were not significant (Kruskal–Wallis $\chi^2 = 3.4$, $p = 0.18$).

3.2. Environmental and structural influences on AGC and stature

Total AGC$_h$ per plot was best modelled by physical variables slope, elevation and the presence/absence of elephants, by climate variable PET, and by soil pH (Table 1). Physical variables were the strongest predictors, with slope and elevation explaining 63.7% of the variation in AGC$_h$. However, holistic models resulted in

Table 1
Generalised linear models of total above-ground live carbon (AGC_h) versus physical, climatic and edaphic predictor variables. Statistics include the probability of deviation from a slope of zero ($p[t]$), direction of the trend (positive +, negative −), percent deviance explained (%D) and probability of decreased deviance explained from the full model ($p[D]$). Bold type indicates significant variables following FDR correction (alpha = 0.0175). See methods for abbreviations and transformations.

| Model name (and variables tested)	Minimum adequate model
Physical (elevation, slope, aspect, elephants, rocks, water, ridge, cutting, logging)	**Slope (simple, −): $p[t]$ = 0.0036** **Elevation (quadratic, −): $p[t]$ = 0.0098** (AIC = 194.5, %D = 63.7, $p[D]$ = 0.81)
Edaphic (pH, P, K, %C)	pH (simple, −): $p[t]$ = 0.048 (AIC = 204.3, %D = 22.2, $p[D]$ = 0.87)
Climatic (ppt, PET)	PET (simple, −): $p[t]$ = 0.059 (AIC = 204.7, %D = 20.5, $p[D]$ = 0.29)
Holistic 1 (slope, aspect, elephants, rocks, logging, ppt, pH, K, %C)	**Elephants (simple, −): $p[t]$ = 0.0041** **pH (simple, −): $p[t]$ = 0.0090** Slope (simple, −): $p[t]$ = 0.039 K (simple, +): $p[t]$ = 0.078 (AIC = 193.16, %D = 70.0, $p[D]$ = 0.77)
Holistic 2 (slope, aspect, elephants, rocks, ppt, PET, Mg, K)	**Slope (simple, −): $p[t]$ = 0.0063** **PET (simple, −): $p[t]$ = 0.0071** Elephants (simple, −): $p[t]$ = 0.036 (AIC = 191.46, %D = 69.5, $p[D]$ = 0.65)
Holistic 3 (carbon, elevation, slope, aspect, elephants, rocks, AMI, MWD, pH)	**Slope (simple, −): $p[t]$ = 0.0036** **Elevation (quadratic, −): $p[t]$ = 0.0098** (AIC = 194.5, %D = 63.7, $p[D]$ = 0.53)
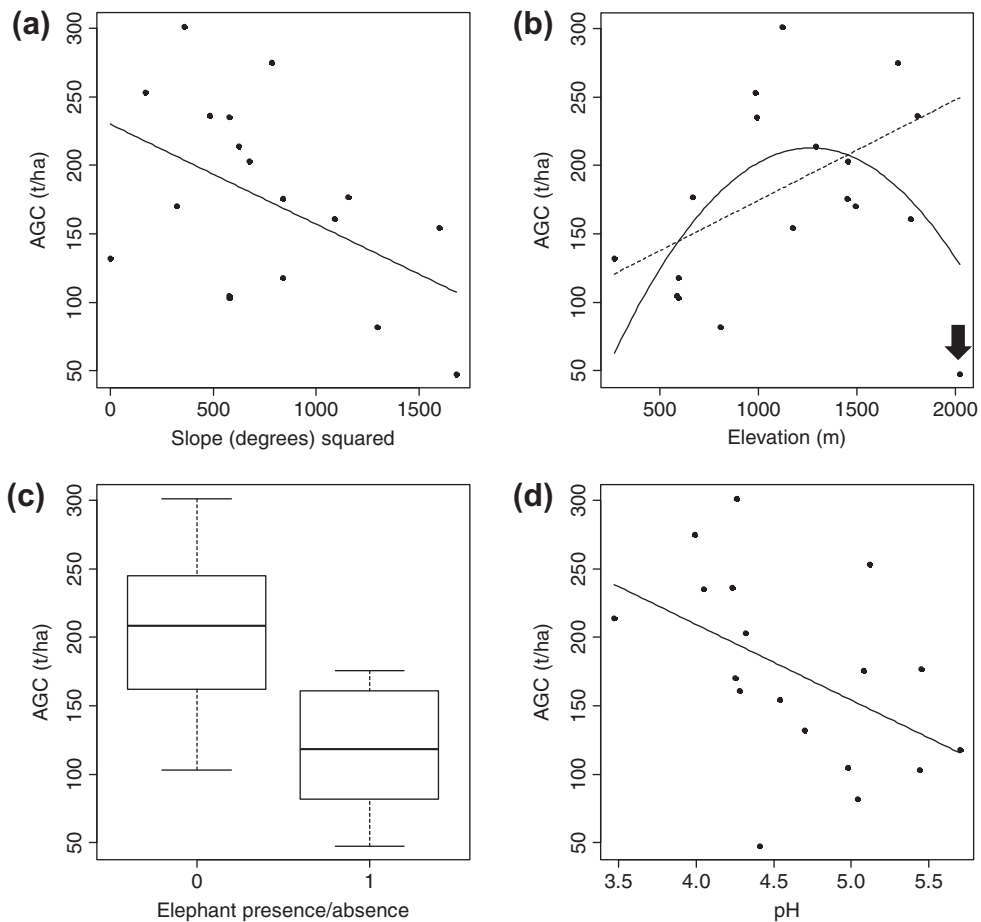
Fig. 2. Plots showing the four strongest predictor variables, (a) slope^2, (b) elevation, (c) elephant presence, and (d) pH, for total above-ground live carbon (AGC_h). Trendlines are univariate Gaussian generalised linear models (including a quadratic term where curved). Dashed line represents an alternative univariate model excluding the potential outlier indicated (Cook's distance < 0.1).

minimum adequate models with a combination of either physical and climate variables, or physical and edaphic variables explaining the highest variation in AGC_h (physical + climate 70.0%, physical + soil 69.5%). Relationships were mostly linear, with the exception of elevation, for which AGC_h peaked at 1200–1600 m (Fig. 2). A potential outlier in high elevation elfin forest did not
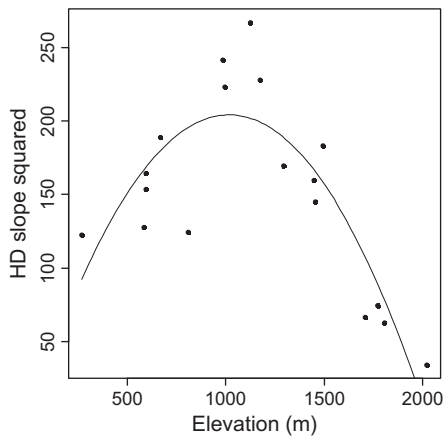
Fig. 3. Relationship between elevation and the stem height–diameter slope (height:log$_n$[dbh]^2). The trendline is from a univariate Gaussian generalised linear model with a quadratic term (AIC = 184.8, %D = 73.2, p = 0.000064).

have high leverage in the multiple GLMs (Cook's $D \ll 1.0$). A univariate GLM of AGC$_h$ versus elevation without the potential outlier produced a less significant, positive, linear relationship (Percentage deviance explained, %D = 29.1, p = 0.0254; Fig. 3b). Our results are compared to the published literature in Table A.2, indicating inter-correlations between predictors that were used to reduce subsets of variables for modelling (Tables 1 and 2).

Tree stature (height–diameter slope) was best modelled by physical variables elevation, aspect and logging, and by climate variable tmin, but soil variables could not produce a stable model (Table 2). When variables were combined into two holistic models, physical variables were the strongest predictors (93.6% variance explained; Table 2). Relationships were mostly linear, with the exception of elevation and the correlated variable tmin, for which the height–diameter slope peaked at 1000–1250 m and 12–15 °C (Fig. 3).

In our "structural" analysis, we found that AGC$_h$ did not have a strong univariate relationship with the height–diameter slope (Gaussian GLM: AIC = 205.5, %D = 16.6, p = 0.094; Fig. A.3a). However, a multivariate GLM showed that 93.1% of variation in AGC$_h$ was explained by the height–diameter slope in conjunction with

stem size and number (minimum adequate model AIC = 166.7, %D = 93.1, p[D] = 0.24: basal area of stems >90 cm dbh p = 0.000052, mean dbh p = 0.00024, number of stems p = 0.00070, height:log(dbh) slope p = 0.00081). Species-related variables were not retained in the reduced models. When modelled alone, the strongest predictor, i.e. basal area of stems > 90 cm dbh, was found to explain 64.5% of variation in AGC$_h$ (AIC = 190.2, %D = 64.5, p = 0.000059; Fig. A.3), but explained significantly less than the minimum adequate model (analysis of deviance: p[D] = 1.2 × 10^{-11}).

3.3. AGC per size class

The majority of AGC was attributed to the largest stems. Stems $\geqslant$90 cm dbh comprised 34.3% of total AGC$_h$ in only 2.1% of stems measured (n = 151; Table A.3), while stems 10–19.9 cm dbh comprised only 4.4% of total AGC$_h$ in 56.3% of stems (n = 4052; Table A.3). Furthermore, stems $\geqslant$70 cm dbh comprised more than half of total AGC$_h$ (52.0%) in only 4.7% of stems (n = 338). The number of species observed was also greatly reduced for stems $\geqslant$70 cm dbh (57 versus 308 species identified overall [18.5%]).

The distribution of AGC$_h$ among stem size classes did not vary between transition and afromontane forest (chi-squared goodness-of-fit χ^2 = 2.04, p = 0.98), but differed in lowland forest, where the proportion of AGC$_h$ in stems $\geqslant$90 cm was lower (15.9% versus 37.7% [transition χ^2 = 32.1, p = 0.00050] and 34.5% [afromontane χ^2 = 33.1, p = 0.00050]; Table A.4). The class distribution of AGC$_h$ did not differ between plots with or without signs of past logging (χ^2 = 1.65, p = 0.99; Table A.5).

4. Discussion

The results indicate a number of considerations for the measuring and monitoring of AGC, particularly the importance of (1) disturbance, topographic and climatic influences on AGC, (2) stem height for accurate measurement of AGC, and (3) large stems as the dominant pool of AGC. The consistently small size of 95% confidence limits (e.g. Tables A.3–A.5) suggests that sample size has not seriously hindered the conclusions, however 18 plots is a modest number with which to draw firm conclusions. We use our findings and previous work to propose a system for prioritising field data collection for assessing AGC depending on available resources

Table 2
Generalised linear models of the slope of the stem height–diameter slope (height:log$_n$[dbh]^2) versus physical, climatic and edaphic variables. Statistics include the probability of deviation from a slope of zero (p[t]), direction of the trend (positive +, negative −), percent deviance explained (%D) and probability of decreased deviance from the full model (p[D]). Bold type indicates significant variables following FDR correction (alpha = 0.0225). See methods for abbreviations and transformations.

Model name (and variables tested)	Minimum adequate model
Physical (elevation, slope, aspect, elephants, rocks, water, ridge, cutting, logging)	**Elevation (quadratic, −): p[t] = 0.0000012** **Logging (simple, −): p[t] = 0.00036** **Aspect (simple, −): p[t] = 0.0018** (AIC = 163.0, %D = 93.6, p[D] = 0.90)
Edaphic (P, Na, K, Al)	None found
Climatic (AMI, tmin, MWD)	**Tmin (quadratic, −): p[t] = 0.00031** AMI (simple, +): p[t] = 0.078 (AIC = 189.5, %D = 68.8, p[D] = 0.65)
Holistic 1 (slope, aspect, elephants, rocks, ridge, logging, AMI, tmin, Na, K)	**Tmin (quadratic, −): p[t] = 0.00036** **Elephants (simple, −): p[t] = 0.0041** Logging (simple, −): p[t] = 0.063 Aspect (simple, −): p[t] = 0.098 (AIC = 175.9, %D = 88.2, p[D] = 0.97)
Holistic 2 (elevation, slope, aspect, elephants, rocks, ridge, logging, AMI, Na, K)	**Elevation (quadratic, −): p[t] = 0.0000012** **Logging (simple, −): p[t] = 0.00036** **Aspect (simple, −): p[t] = 0.0018** (AIC = 163.0, %D = 93.6, p[D] = 0.60)

(Fig. 4) using three tiers for consistency in line with existing guidelines on the monitoring of greenhouse gasses and biodiversity (IPCC, 2006; Gardner et al., this issue).

Our estimate of 174.6 t ha^{-1} [144.8–205.5] AGC in live trees is comparable to a quality-controlled set of plots from more pristine forest across Africa (202 t ha^{-1} [174–244]; $n = 79$; Lewis et al., 2009). Some of our plots were impacted by anthropogenic and natural (elephant-related) disturbance, but were located predominantly in closed-canopy forest, and thus the mean AGC for the Eastern Arc Mountains is likely to be lower than our estimates. Conversely, our estimate is towards the lower end of previously published estimates for the same region (74–517 t ha^{-1}; Munishi and Shear, 2004; Zahabu, 2006). However, it is unclear if all trees were correctly measured above buttresses in these studies, and consequently the upper estimate appears unlikely given the quality-controlled range across Africa (65.5–397.8 t ha^{-1}; Lewis et al., 2009).

4.1. Environmental influences

4.1.1. Environmental influences on AGC

AGC$_h$ was greatest at mid-elevation, on shallow slopes, where PET and pH were low, and where elephants were absent. Elevation, disturbance and slope are also consistently the strongest predictors in the biomass literature (Table A.2). Steep slopes may reduce AGC due to high soil erosion and leaching of nutrients (Pimentel et al., 1995). The mid-elevation peak in AGC may have resulted from a more complex combination of respiration, photosynthesis and disturbance.

At higher elevations, growth can be limited by water shortage, exposure, reduced temperature, reduced transpiration rates, and poor soil quality (Bruijnzeel and Veneklaas, 1998; Way and Oren, 2010; Moser et al., 2011). Respiration costs increase with temperature (Lloyd and Farquhar, 2008), and hence may reduce growth at low elevation. Mid-elevations may therefore occupy a "Goldilocks" environment, where respiration costs are lower, yet photosynthesis is not yet inhibited by low air temperatures. Disturbance of all types can also be greatest at both low and high elevation, result-

ing in a mid-elevation peak in biomass (Waide et al., 1998) and can mask the effects of temperature (Sierra et al., 2007). However, human disturbance can be hard to quantify, because signs of cutting can quickly decay (95% of dead tropical forest wood can decay within 22 years; Yang et al., 2010). In the study area, tree stumps were cut mostly between 15 and 30 years prior to our surveys and were rarely evident.

The suspected mid-elevation peak in AGC is supported by an early study of basal area in the region (Lovett et al., 2006), yet is inconsistent with studies from other tropical forests, where biomass declines with elevation (Girardin et al., 2010). Our single plot from elfin cloud forest suggests that the high elevation decline in AGC is quite rapid, although more data are required given that the mid-elevation peak was non-significant with removal of this plot (Fig. 3b). Similarly more data are required to explore the microhabitat influence on AGC at a finer scale (e.g. rocks, water, ridge), which did not show any relationship with AGC at our one hectare scale.

While elephants have positive impacts on habitats, for example as seed dispersers (Helm et al., 2011), a large volume of literature indicates that the net impact of savanna elephants on the abundance of woody vegetation is negative (Guildemond and van Aarde, 2007). In the Udzungwa Mountain moist forests, savanna elephant populations have increased, posing a difficult tropical forest management scenario that must balance biodiversity conservation with animal and human welfare (Marshall, 2007). Elephant impact upon habitat structure in nearby areas has led to a call for their temporary exclusion (Bonnington et al., 2009). However, the negative impact of elephants is disputed in some areas due to the collective influence of other large browsers (White and Goodman, 2009), which were mostly absent from our study area.

As recently seen for biomass in South America (Baraloto et al., 2011), soil properties were not found to be the strongest predictors of AGC. Spatial and temporal variabity in tropical forest soils can be high, and hence difficult to measure (Quesada et al., 2009). Accordingly, results from studies correlating soil properties to tropical forest biomass have produced highly variable results (Table A.2). However, our study took place in mostly evergreen forest habitats

		TIER 1	TIER 2	TIER 3
Resources	Time	Short	Medium	Long
	Funding	Low	Intermediate	High
	Technical	Basic ecological knowledge/equipment	Basic ecological/statistical; local herbarium	Advanced ecological/statistical; international herbarium; laboratory
Measurements	**CARBON**			
	Stems	Large stems only (e.g. ≥50cm dbh)	Stems ≥10cm dbh	Stems >10cm plus lianas (consider smaller stems if abundant)
	Species ID	Field identification	Field identification with some collection	Identification across seasons with full herbarium support
	Allometry	Height predicted from dbh using general allometric equations	Local equations or height measured and extrapolated (10 stems/class, min 4-6)	Height measured for all stems
	Biomass	General equation using predicted heights; WSG from database	Regional equation using predicted heights; WSG from database	Regional equation (actual heights); wood collections to improve WSG
	ENVIRONMENT			
	Physical	Disturbance (human and large mammal)	Disturbance; elevation; slope; position (ridge/hillside/valley/etc)	As tier 2; aspect; microclimate
	Climatic	No measurement	Temperature; precipitation	As tier 2; PET; moisture; water deficit
	Edaphic	No measurement	Texture; type	Collection for laboratory analysis

INCREASING PRECISION OF CARBON ESTIMATES

Fig. 4. Proposed tiers for field assessment of above-ground live carbon (AGC). Tier 1 indicates minimal resources that permit only basic estimation of AGC, but ensuring that information is collected on physical threats. Tier 2 indicates improved resources such that priority can be placed upon ensuring precise measurement of stems and the most consistent environmental predictors (see Table A.2). Tier 3 indicates maximum resources enabling full consideration of biomass and environmental measurement.

on sandy-loams overlaying crystalline bedrock, and hence may not have represented a sufficient range of soils for the identification of significant soil-AGC relationships.

4.1.2. Environmental influences on tree stature

Stems were tallest for a given diameter at mid-elevation, on south-facing slopes and where evidence of logging was low. The observed strong quadratic relationship between elevation and height–diameter slope (%D 73.2) suggests that stems show taller stature at mid-elevation. This deviation from the near pantropical trend in decreasing stature with elevation adds to a few previous anomalies in the literature (Lovett et al., 2006; Sahu et al., 2008). Precipitation, dry season length, stem density and mean annual temperature are all key drivers of variation in height:diameter relationships at pantropical and regional scales (Feldpausch et al., 2011; Banin et al., 2012). Secondary forest trees are also often taller for a given diameter (Montgomery and Chazdon, 2001). Therefore tall stature at mid-elevation has most likely resulted from a balance of disturbance, slope and climate as discussed for AGC.

4.1.3. Cost:benefit analysis for prioritising environmental measurements

While some of our environmental variables are likely to be proximate rather than ultimate causes of AGC, the consistent retention of more than one variable in minimum adequate models also emphasises the value of measuring multiple predictors, including physical, edaphic and climatic variables. We cannot be certain which variables had the ultimate influence on AGC, because most were intercorrelated, including various climatic and edaphic intercorrelations with elevation and PET. Typically slope also influences soil nutrients, exposure and erosion, aspect is related to solar radiation and exposure, while elephants may be attracted by secondary vegetation associated with human disturbance. Only logging has an unambiguous direct impact on carbon.

Inclusion of cost-effective environmental predictors in monitoring programmes will facilitate improved understanding of AGC distribution, and hence input to national and international policy. A cost:benefit assessment of the various predictors is therefore shown in Table A.2. Climatic and physical variables include the strongest predictors and are easily gathered during the routine process of planning and establishing AGC plots (respectively 6.5 and 1.5 days plus US$415 and $1000 equipment costs for 18 plots). Basic disturbance data are vital for assessing the success of conservation measures and can be gathered without extensive technical expertise (Tier 1; Fig. 4), while elevation and climatic variables require technical input (Tier 2–3). However the cost for equipment purchase besides that required for establishing plots was only US$15 (Table A.2). The computational methods for measuring climatic variables were largely independent of sample size, but would increase if measured on the ground.

Edaphic variables were the least cost-effective (approximately US$270 per sample), as they required laboratory fees, permits and specialised equipment beyond that required for establishing plots. Costs required for edaphic variables would also increase with sample size, particularly for the transportation of material. Together with their inconsistent effectiveness for the prediction of carbon, edaphic variables may therefore not be a priority for carbon monitoring projects unless soil expertise/analysis is readily available (Tier 2–3; Fig. 4). However, the influence of edaphic variables on AGC has been under-researched and warrants further consideration following improved data. Notable successes in explaining AGC variation using multiple alternative edaphic variables (Quesada et al., 2009; Slik et al., 2010), suggests that soil has not been adequately addressed by the literature. Furthermore, a lack of data has precluded an estimation of soil carbon stocks, which are likely to be substantial.

4.2. Measuring and monitoring AGC

4.2.1. Importance of height for estimating AGC

The observed variation in tree stature has further implications for the estimation of biomass. Our observation of a 55 t ha^{-1} (24%) overestimate of carbon when not incorporating height was consistent across all plots (95% CI: 27.5–48.5% overestimate). Therefore previously observed accuracy of biomass models based on diameter alone (Brown, 2002; Lewis et al., 2009) does not hold for all locations. We assume that biomass equations incorporating height are the most likely to be accurate, as they incorporate more information on the size of stems than equations based on diameter alone. A pantropical analysis of allometry in destructively sampled trees lends further support to this assumption (Chave et al., 2005).

4.2.2. Importance of structure for estimating AGC

Our observation that structural variables explain greater variation in AGC than environmental variables (93.1% versus 70.0%) is consistent with previous studies (Baraloto et al., 2011), and is expected given that structural measurements are components of the biomass equations. Strong correlation between the height–diameter slope and the difference in AGC$_h$ and AGC$_d$ emphasises that in the absence of height, AGC was most considerably over-estimated at mid-elevation, where the slope was steepest. Although AGC was related to the height–diameter slope, our structural model emphasises that high AGC is not necessarily found where stems are tallest for a given diameter. Instead the basal area of large stems, the number of stems, and mean dbh, all influence the amount of AGC. This observation is consistent with trends in AGC being accounted for by the number of large stems (Clark and Clark, 1996; Chave et al., 2003; Alves et al., 2010) and may have implications for the design of rapid (Tier 1; Fig. 4) assessments of carbon stocks.

The majority of AGC of carbon was stored in stems ⩾70 cm dbh and was measured in just over one tenth of the time taken to measure all stems. Similarly, the reduced number of species ⩾70 cm required only 18% of botanical collection/identification time. Allowing for travel, plot establishment, and other logistical constraints, for surveys of tropical forest AGC we estimate that measurement and herbarium time could be reduced by half when measuring only stems ⩾70 cm dbh. The choice to employ this form of survey does however assume there is sufficient prior information on the composition of size classes to extrapolate AGC estimates, and reduces their value for biodiversity monitoring (see below).

For lowland forest, the proportion of AGC in large stems was reduced, and stems ⩾50 cm dbh would be required to measure the majority of carbon (64% AGC in 11% of stems; Table A.4). Our habitat types defined by elevation should be treated with caution as forests in the region have shown a consistent elevation continuum in species composition, rather than distinct species zones (Lovett, 1996; Lovett et al., 2006). However, the narrow width of confidence limits for AGC per size class in lowland forest suggests that the relative contribution was consistent between plots. A reduction in the contribution of large stems would also be expected for habitats that are younger, drier, or more heavily logged (Chave et al., 2003; Faria et al., 2009; Glélé Kakaï and Sinsin, 2009; Baraloto et al., 2011) and thus Tier 2–3 surveys should aim to incorporate all size classes (Fig. 4).

4.2.3. Further implications of stem measurement for monitoring

The observed AGC deficit of 55 t ha^{-1} when comparing calculations including and excluding height measurements has potential economic implications. The European Union Emission Trading Scheme trades CO_2 at €10.40 t^{-1} (US$13.89; www.pointcarbon.com [accessed 7th October 2011]), and hence a carbon trade value of US$ 50.93 (CO_2 × 3.667). Therefore the biomass equation excluding height (B_d) over-valued AGC by US$2801 ha^{-1} (24%). The more widely accepted "social cost" of carbon (the estimated

cost of the physical impact of climate change associated with carbon loss) could range from US$49–71 t^{-1} (mean of peer-reviewed estimates; Tol, 2008), giving an over-valuation of US$2695–3905 ha^{-1} (mean $3300).

A growing body of evidence suggests that biological, social and economic measures should all be central to conservation planning (Rapport et al., 1998; Wiegand et al., 2010), and hence REDD+ will require a relatively holistic approach to monitoring. While social, cultural and economic assessments require methods beyond the scope of this study, methods for monitoring biodiversity are compatible with methods for measuring AGC (Gardner et al., this issue). Species composition has influenced variability in biomass across a broad range of habitats and is also predicted for tropical forests (Bunker et al., 2005). However, without species-specific biomass equations, and where height and diameter are measured directly, the only influence of species on AGC estimation is through species variation in WSG.

Following destructive sampling of 2410 neotropical trees, it was shown that WSG is the second most important measurement for the estimation of biomass after diameter (Chave et al., 2005). However our observation that WSG per species was not retained in models of AGC concurs with previous work in Borneo (Slik et al., 2010), suggesting that identification may be less important than stem stature, size and number. Use of a community average WSG may therefore be sufficient in some cases (Brown, 1997; Fearnside, 1997; but see also Chave et al., 2006), potentially including the current study where the observed variation in WSG was low (0.62 [0.60–0.64], range 0.21–0.98). Where variation in WSG is high (e.g. Fearnside (1997): range 0.14–1.21), species identification remains important for the estimation of AGC, even for Tier 1 surveys (Fig. 4).

Given that species identification is also vital for monitoring biodiversity and ecosystem function, we do not advocate carbon monitoring schemes that do not incorporate this. Biodiversity is an assumed co-benefit of REDD+ and is a requirement of all voluntary standards (Waldon et al., 2011). However, large tree species richness may not be representative of overall biodiversity (Gentry and Dodson, 1987; Platts et al., 2010). Hence, our suggestion for rapid AGC surveys based on large stems alone would have seriously reduced value for biodiversity assessment (e.g. only 18.5% of species had stems ⩾70 cm dbh) and should only be considered an option under Tier 1 surveys where minimal resources are available (Fig. 4).

5. Conclusion

Future measurement of AGC would benefit from the inclusion of height and the development of locally-specific height–diameter equations. In Africa, fieldwork that focuses on the largest stems may improve efficiency of AGC estimates where resources are limited. However, in using the largest stems, periodic checks would be required to support assumptions regarding forest structure and biodiversity, particularly for younger, drier, or more disturbed habitats. Species identification is considered important, for which expert taxonomic input should be sought. Climatic, edaphic, topographic and disturbance data can all be used to explain the distribution of AGC and hence extrapolate to broader areas for making management plans. Among these data, climatic and topographic variables are more consistent predictors of AGC with reduced cost over edaphic variables, and more easily measured than both edaphic and disturbance variables. While more work is needed to improve both accuracy and precision, and to understand carbon stocks beyond AGC in tree stems, we see AGC estimation based on ground surveys as vital for forest management.

Appendix A
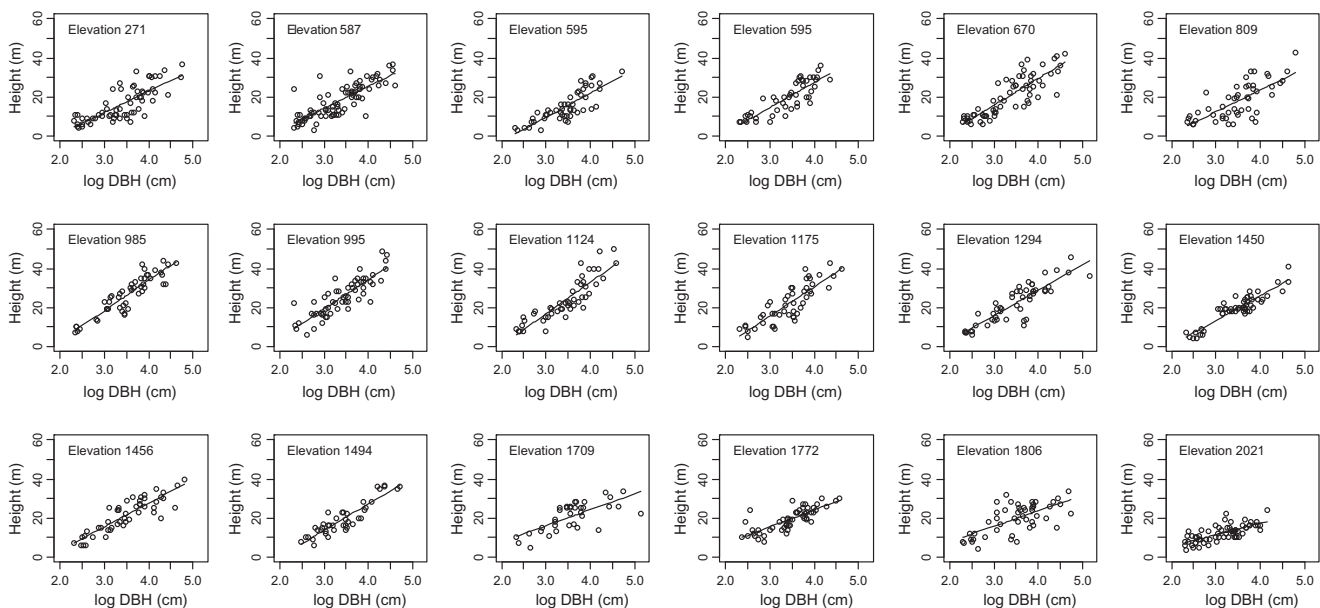
See Figs. A.1–A.3 and Tables A.1–A.5.

Fig. A.1. Height versus log$_n$ diameter (DBH) relationships for tree stems in 1 ha plots, ordered by elevation, showing ordinary least squares regression lines, RSS = mean 1177.3 [95% CI 951–1415], r^2 = 0.67 [0.62–0.73].
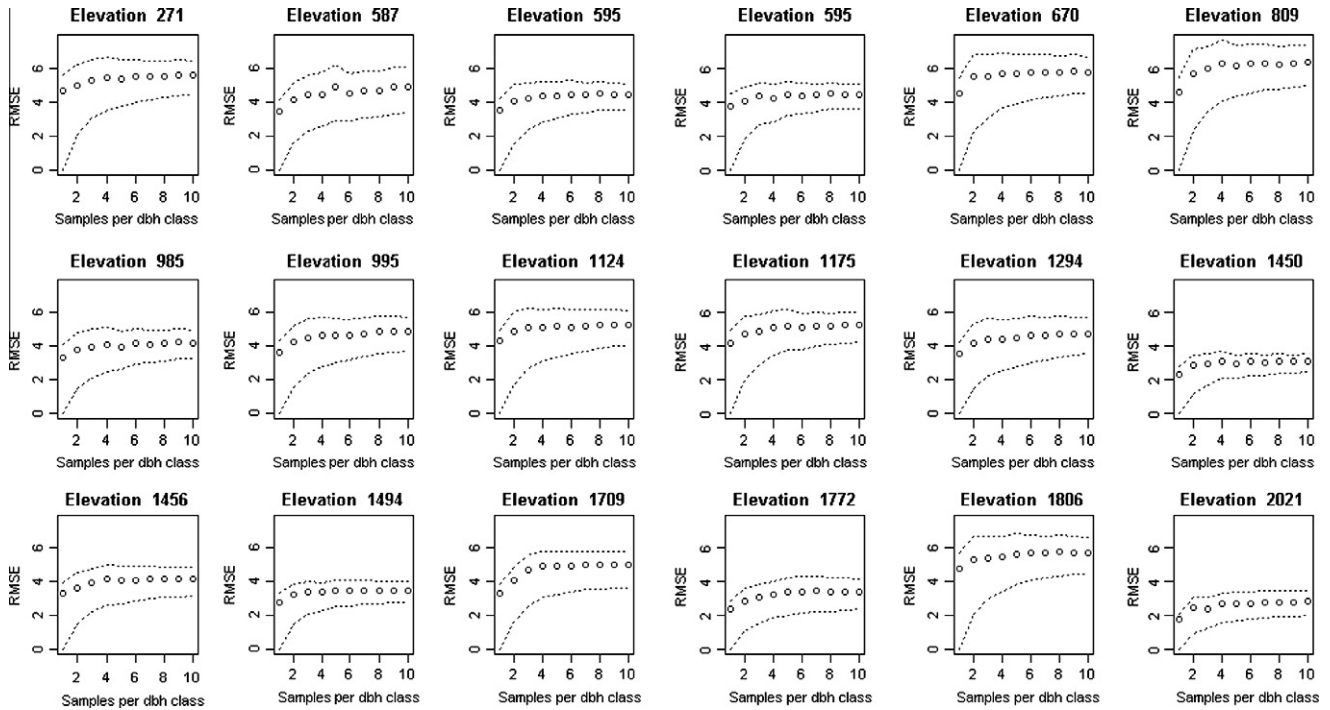
Fig. A.2. Effect of sample size per diameter (dbh) class on model fit (mean standardised residuals; RMSE ± 1000 bootstrapped confidence intervals) for the estimation of height using $\log_n$(dbh).
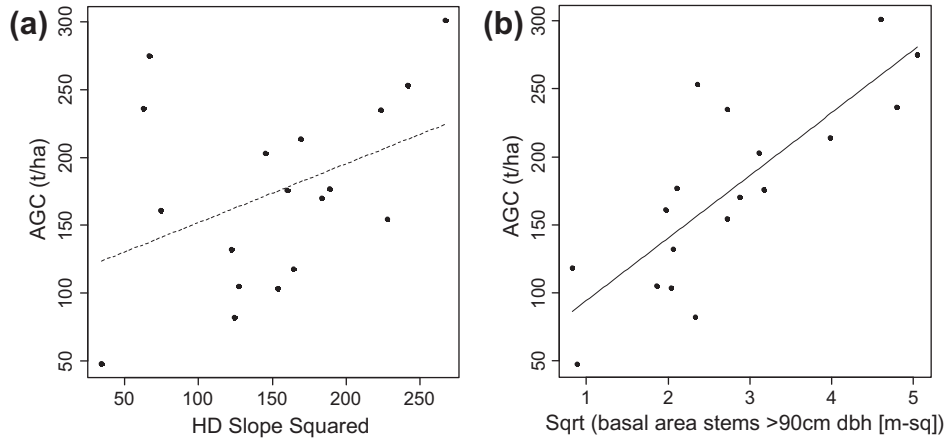

Fig. A.3. Predictors of above-ground live carbon (AGC$_h$) from Gaussian GLMs, (a) height–diameter (HD) slope (height:$\log_n$(dbh)^2; %D = 16.6, p = 0.094; line dashed as slope not significant), and (b) basal area of trees greater than 90 cm dbh (%D = 64.5, p = 0.000059).

Table A.1
Above-ground live carbon (AGC) estimates for 18 one hectare vegetation plots in the Eastern Arc Mountains.

Elevation	Range	Forest type	AGC$_h$	AGC$_{dbh}$	Difference
271	Udzungwa	Zanzibar-inhumbane lowland	132.1	203.5	+71.3
587	Udzungwa	Zanzibar-inhumbane lowland	104.9	148.2	+43.3
670	Udzungwa	Zanzibar-inhumbane lowland	176.7	217.0	+40.3
595	Udzungwa	Zanzibar-inhumbane lowland	103.3	179.6	+76.3
809	Udzungwa	Lowland-montane transition	82.0	122.4	+40.4
1450	Udzungwa	Afromontane	175.8	242.9	+67.1
1456	Udzungwa	Afromontane	203.1	267.5	+64.4
1175	Udzungwa	Lowland-montane transition	154.3	184.3	+30.0
1124	Udzungwa	Lowland-montane transition	301.3	307.7	+6.4
1772	Udzungwa	Afromontane	160.9	236.3	+75.5
2021	Udzungwa	Afromontane (elfin)	47.6	92.4	+44.9
995	Usambara	Lowland-montane transition	235.1	245.6	+10.5
985	Usambara	Lowland-montane transition	253.3	267.4	+14.1
595	Usambara	Zanzibar-inhumbane lowland	118.0	158.7	+40.7
1494	Usambara	Afromontane	170.0	223.9	+53.9
1709	Usambara	Afromontane	275.0	412.8	+137.8
1806	Usambara	Afromontane	236.3	361.9	+125.7
1294	Usambara	Afromontane	214.0	261.0	+47.0

Table A.2
Cost:benefit assessment of the predictor variables used to model the distribution of above-ground live carbon(AGC$_h$) for 18 one hectare plots in the Eastern Arc Mountains. Costs include staff time (rather than salary, as this varies hugely between regions and individuals) and financial expenses (equipment purchase and fees), with parentheses denoting costs that were already in place under the routine planning and establishment of plots. The benefits are the relative contributions of each variable to the prediction of AGC or biomass in this study and the peer-reviewed literature (high = strongest predictor in at least one study, moderate = significant predictor, low = very weakly significant or inconsistent predictor, none = no statistical evidence).

Predictor variable	Costs[**]		Benefits[*]
	Time (days)	Expense (US$)	
Physical variables			
Elevation[e]	(0.25)	(370)	(Low–)high
Slope	1.25	15	Moderate–high
Aspect	1.0	(15)	(None)
Ridge	0.5	0	Low–high
Water	1.0	(30)	(None)
Rocks	0.5	0	(None)
Logging/deforestation	1.0	0	High
Elephant damage	1.0	0	(None–)moderate–high
Climatic variables			
Mean temperature[b]			None–high[***]
Temperature range[b]			Low
Minimum temperature[b,e] (or dry season length)	1.0		Low–high
Precipitation (ppt)[a]		(1000)	None–high
Evapotranspiration (PET)[b]			(High)
Moisture index (AMI)[a]	+0.5		(None)
Water deficit (MWD)[a]			
(or AWC[****])	+0.5		None–moderate
Edaphic variables			
pH[c]			Low–high
Phosphorus			(None–)high
Aluminium[c,d,e]			Low
Calcium[c]			Low–moderate
Magnesium[c]	2.5	2435	Low–moderate
Sodium[d]			None–moderate
Potassium			Low–high
Carbon[d]			None–moderate
Nitrogen[d]			None–high

[a–e] Variables sharing the same letters were intercorrelated in the present study. Among the physical variables, there were no strong intercorrelations (Pearson correlation: $0.000 \leq |r| \leq 0.621$). Among the climate variables, ppt was correlated with AMI and MWD ($r = -0.863, -0.713$) and tmean correlated strongly with trange, tmin and PET ($r = -0.740, 0.986, 0.987$). Among the edaphic variables, pH correlated strongly with Ca, Mg and Al ($r = 0.904, 0.891, -0.761$), and Na and Al both correlated strongly with %N and %C ($r[Na] = 0.773, 0.808, r[Al] = 0.791, 0.798$). Between these three subsets, elevation, tmin and Al were strongly intercorrelated ($0.874 \leq |r| \leq 0.952$).

[*] Pimentel et al. (1995), Laurance et al. (1999), Lovett et al. (2006), Mahli et al. (2006), Guildemond and van Aarde (2007), Sierra et al. (2007), Nogueira et al. (2008a,b), Paoli et al. (2008), Asner et al. (2009a), Quesada et al. (2009), Alves et al. (2010), Girardin et al. (2010), Slik et al. (2010), Baraloto et al. (2011), Pan et al. (2011), Marshall et al. (this study). Parentheses show results from only one study, or a small minority of studies.

[**] The cost for equipment to measure physical/climate variables was only $15 for a clinometer, because other equipment (computer, GPS, compass, tape measure) were already available for the establishment of plots. Time costs were equivalent for most climate variables as they were mostly available for free download (except for AMI and MWD). Edaphic costs included collecting/drying samples, equipment purchase (corer, collection bags), and lab fee $112 per sample (required only once for all soil variables). Transport/export permit acquisition for soil samples incurred no extra cost beyond that already required for plant specimens collected for identification, but would be expected to increase with larger sample sizes.

[***] In most published studies on the influence of temperature on biomass, it is not explicit, rather implied from observed strong relationships with elevation.

[****] Available water content = time in which less than 20% water was attained.

Table A.3
Mean (and 95% bootstrapped confidence interval) above-ground live carbon (AGC$_h$) and stem/species number, per one hectare plot ($n = 18$), for each stem diameter size class in the Eastern Arc Mountains. Mean percentage of total per one hectare plot for each measure are given in italics.

Size (cm)	AGC$_h$ (t)	Stem number	Species richness
10–19.9	7.7 (6.2–9.4)	225 (193–257)	28.9 (25.5–32.7)
	4.4 (3.6–5.4)	*56.3 (48.3–64.2)*	*77.8 (68.5–87.8)*
20–29.9	12.7 (9.9–15.5)	76.8 (63.8–90.4)	16.7 (14.3–19.0)
	7.3 (5.7–8.9)	*19.2 (16.0–22.6)*	*44.9 (38.5–51.1)*
30–39.9	14.8 (12.2–17.4)	37.0 (31.7–42.1)	12.2 (10.3–13.9)
	8.5 (7.0–9.9)	*9.2 (7.9–10.5)*	*32.8 (27.8–37.5)*
40–49.9	17.0 (13.8–20.2)	21.9 (18.4–25.6)	9.2 (7.6–10.8)
	9.7 (7.9–11.6)	*5.5 (4.6–6.4)*	*24.8 (20.3–29.1)*
50–59.9	16.4 (12.8–19.6)	12.5 (10.4–14.6)	5.9 (4.8–7.0)
	9.4 (7.4–11.2)	*3.1 (2.6–3.6)*	*15.8 (13.0–18.8)*
60–69.9	15.2 (12.4–17.9)	8.0 (6.6–9.5)	4.6 (3.7–5.6)
	8.7 (7.1–10.2)	*2.0 (1.6–2.4)*	*12.4 (10.0–14.9)*
70–79.9	17.8 (12.9–22.7)	6.7 (4.9–8.5)	3.4 (2.7–4.2)
	10.2 (7.4–13.0)	*1.7 (1.2–2.1)*	*9.3 (7.2–11.3)*
80–89.9	13.0 (9.0–17.5)	3.7 (2.6–4.9)	2.2 (1.7–2.7)
	7.4 (5.1–10.0)	*0.9 (0.5–1.2)*	*6.0 (4.5–7.2)*
≥ 90	60.0 (38.5–85.2)	8.4 (6.1–11.1)	3.6 (2.7–4.6)
	34.3 (22.0–48.8)	*2.1 (1.5–2.8)*	*9.7 (7.3–12.4)*

Table A.4
Mean (and 95% bootstrapped confidence interval) stem density and above-ground carbon (AGC_h) per stem diameter size class per one hectare plot, for different forest types. Percentage contributions are given in italics.

Size class (cm)	Lowland (n = 5)		Transition (n = 5)		Afromontane (n = 8)	
	Stems	AGC_h (t)	Stems	AGC_h (t)	Stems	AGC_h (t)
10–19.9	196 (133–262)	5.9 (3.3–8.4)	254 (221–288)	8.7 (7.1–10.2)	225 (178–298)	8.2 (6.4–10.9)
	53.0 (47.8–58.3)	*4.6 (3.0–6.7)*	*60.5 (49.8–70.6)*	*4.9 (3.3–6.4)*	*54.3 (48.1–59.9)*	*5.9 (3.1–9.7)*
20–29.9	71.6 (51.4–96.0)	10.6 (7.0–15.0)	74.2 (43.0–106.6)	14.1 (7.2–20.9)	81.6 (63.0–96.5)	13.2 (10.0–16.3)
	19.9 (17.4–21.8)	*8.4 (6.1–12.0)*	*16.7 (10.7–22.8)*	*7.1 (4.0–10.4)*	*19.9 (16.0–23.3)*	*9.2 (5.4–15.0)*
30–39.9	36.8 (27.2–47.2)	13.5 (8.6–18.6)	35.4 (22.4–47.8)	16.0 (8.9–21.4)	38.1 (31.1–44.9)	14.8 (11.9–17.7)
	10.3 (9.6–10.9)	*10.8 (7.2–15.4)*	*8.1 (5.5–10.4)*	*7.5 (5.5–9.6)*	*9.7 (7.8–11.7)*	*9.8 (6.3–14.7)*
40–49.9	21.4 (17.0–25.8)	15.6 (12.9–18.5)	22.2 (16.4–28.4)	18.9 (12.6–25.2)	22.0 (16.1–28.8)	16.6 (11.4–21.9)
	6.2 (5.0–7.6)	*12.4 (11.1–14.4)*	*5.2 (3.9–6.5)*	*9.3 (7.9–10.8)*	*5.4 (4.0–6.9)*	*9.6 (6.6–12.4)*
50–59.9	14.0 (11.2–16.4)	19.1 (16.4–22.2)	12.0 (8.0–17.0)	16.1 (9.5–22.8)	11.9 (8.6–15.5)	15.0 (10.1–19.9)
	4.3 (3.0–5.5)	*16.0 (11.3–18.9)*	*2.8 (1.9–3.7)*	*7.4 (5.7–9.2)*	*3.0 (2.2–3.8)*	*8.6 (5.9–11.5)*
60–69.9	8.0 (6.0–9.8)	15.1 (10.6–19.2)	7.0 (4.6–9.4)	14.6 (9.7–19.3)	8.6 (6.1–11.3)	15.7 (10.7–19.8)
	2.5 (1.5–3.3)	*11.9 (8.8–14.7)*	*1.7 (1.1–2.2)*	*7.8 (4.9–10.6)*	*2.1 (1.6–2.7)*	*8.4 (6.4–10.8)*
70–79.9	5.2 (3.2–7.0)	14.7 (8.7–20.6)	8.2 (4.4–12.6)	21.2 (11.5–31.5)	6.6 (3.5–9.4)	17.7 (9.4–25.9)
	1.6 (0.9–2.5)	*11.1 (8.1–14.4)*	*1.9 (1.0–2.9)*	*10.2 (7.0–14.2)*	*1.8 (0.8–2.6)*	*8.6 (4.8–13.5)*
80–89.9	3.4 (1.8–5.2)	12.0 (5.7–19.0)	4.6 (1.8–7.4)	17.2 (6.2–28.3)	3.4 (1.9–5.0)	11.0 (6.8–15.3)
	1.0 (0.6–1.5)	*9.1 (4.9–13.2)*	*1.1 (0.5–1.8)*	*8.1 (4.0–12.4)*	*0.9 (0.5–1.3)*	*5.4 (3.3–7.5)*
⩾ 90	3.8 (2.2–5.4)	20.5 (11.1–29.1)	9.0 (6.4–12.2)	78.4 (45.3–135.2)	10.9 (7.0–14.6)	73.1 (40.5–107.4)
	1.2 (0.6–1.9)	*15.9 (8.1–21.2)*	*2.1 (1.5–3.0)*	*37.7 (25.4–51.3)*	*2.9 (1.7–4.1)*	*34.5 (22.7–45.9)*

Table A.5
Mean (and 95% bootstrapped confidence interval) stem density and above-ground live carbon (AGC_h) per stem diameter size class per one hectare plot, for plots with and without signs of past logging within 100 m. Percentage contributions are given in italics.

Size (cm)	Logging (n = 8)		No logging (n = 10)	
	Stems	AGC_h (t)	Stems	AGC_h (t)
10–19.9	196 (148–242)	5.7 (4.2–7.4)	249 (215–291)	9.3 (7.7–11.1)
	55.3 (46.4–63.9)	*4.3 (2.9–5.9)*	*56.0 (52.0–60.2)*	*6.0 (4.0–8.9)*
20–29.9	63.5 (44.8–84.8)	9.4 (6.3–13.0)	87.4 (72.3–101.0)	15.4 (12.3–18.6)
	18.0 (13.7–21.9)	*6.7 (4.3–9.6)*	*19.9 (16.5–22.5)*	*9.8 (6.6–14.1)*
30–39.9	34.6 (25.0–44.5)	12.8 (8.6–17.2)	38.9 (33.8–44.3)	16.4 (13.5–19.4)
	9.9 (7.8–11.9)	*8.8 (6.0–12.0)*	*9.0 (7.7–10.1)*	*9.9 (7.2–13.5)*
40–49.9	20.3 (15.5–25.3)	14.4 (11.6–17.4)	23.2 (18.4–28.4)	19.0 (14.3–23.9)
	5.9 (4.6–7.4)	*10.4 (8.2–12.7)*	*5.3 (4.2–6.5)*	*10.2 (7.9–12.3)*
50–59.9	11.4 (8.4–14.3)	15.1 (10.5–19.3)	13.4 (10.6–16.2)	17.6 (12.9–21.8)
	3.5 (2.3–4.7)	*11.7 (7.5–16.2)*	*3.1 (2.4–3.8)*	*9.2 (7.3–11.3)*
60–69.9	7.8 (6.3–9.3)	14.6 (11.5–17.5)	8.2 (5.9–10.5)	15.7 (11.3–19.8)
	2.4 (1.8–3.1)	*10.7 (8.1–13.2)*	*1.9 (1.4–2.3)*	*8.0 (6.3–9.8)*
70–79.9	6.0 (4.1–8.0)	16.3 (10.1–21.8)	7.2 (4.2–10.3)	19.1 (11.7–27.1)
	1.8 (1.2–2.5)	*10.5 (8.5–12.9)*	*1.7 (1.0–2.4)*	*9.1 (5.6–13.9)*
80–89.9	3.3 (1.9–4.8)	11.4 (6.4–16.8)	4.1 (2.3–6.1)	14.3 (8.0–20.7)
	1.0 (0.6–1.3)	*7.5 (4.8–10.7)*	*1.0 (0.5–1.4)*	*6.9 (4.2–9.8)*
⩾90	7.0 (3.6–10.8)	51.1 (20.7–86.8)	9.5 (6.7–12.8)	67.1 (41.4–103.0)
	2.2 (1.2–3.4)	*29.4 (16.6–42.4)*	*2.3 (1.5–3.2)*	*30.8 (21.5–41.2)*

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