

Above- and Belowground Carbon Stocks in a Miombo Woodland Landscape of Mozambique

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ABSTRACT

Quantifying ecosystem carbon stocks is vital for understanding the relationship between changes in land use and carbon dioxide emissions. Here, we estimate carbon stocks in an area of miombo woodland in Mozambique, by identifying the major carbon stocks and their variability. Data on the biomass of tree stems and roots, saplings, and soil carbon stocks are reported and compared with other savannas systems around the globe. A new allometric relationship between stem diameter and tree stem and root biomass is presented, based on the destructive harvest of 29 trees. These allometrics are combined with an inventory of 12,733 trees on 58 plots over an area of 27 ha. Ecosystem carbon stocks totaled 110 tC/ha, with 76 tC/ha in the soil carbon pool (to 50 cm depth), 21.2 tC/ha in tree stem biomass, 8.5 tC/ha in tree coarse root biomass, and 3.6 tC/ha in total sapling biomass. Plot-level tree root:stem (R:S) ratio varied from 0.27 to 0.58, with a mean of 0.42, slightly higher than the mean reported for 18 other savanna sites with comparable aboveground biomass (R:S = 0.35). Tree biomass (stem + root) ranged from 3.1 to 86.5 tC/ha, but the mean (32.1 tC/ha) was well constrained (95% CI 28–36.6). In contrast, soil carbon stocks were almost uniformly distributed and varied from 32 to 133 tC/ha. Soil carbon stocks are thus the major uncertainty in the carbon storage of these woodlands. Soil texture explained 53 percent of the variation in soil carbon content, but only 13 percent of the variation in woody carbon stocks. The history of disturbance (fire, elephants, logging/charcoal production, and shifting cultivation) is likely to decouple changes in woody carbon stocks from soil carbon stocks, mediated by tree–grass interactions.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: biomass; carbon stocks; miombo; Nhambita; root; soil; stem.

MIOMBO WOODLANDS ARE CHARACTERISTIC SAVANNA WOODLANDS IN SUBTROPICAL SOUTHERN AFRICA, dominated by species of the genera *Brachystegia*, *Julbernardia*, and *Isoberlinia*. They occupy 11 African countries: Angola, Burundi, Botswana, Democratic Republic of the Congo, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, and Zimbabwe. Miombo woodlands occur on nutrient poor soils and in areas with distinct wet and dry seasons (annual rainfall of 700–1400 mm). They are characterized by frequent fires in the dry season (Frost 1996, Ryan & Williams 2010). The range of biophysical ecosystem goods and services provided by these woodlands is extensive, ranging from the provision of food, fuel, medicine and construction materials to larger-scale carbon and water management services. More than 100 million people live in, or obtain resources from, miombo, and a high proportion (up to 50% in some areas) of rural income is dependant on the woodlands, particularly among the poorest (Campbell *et al.* 2007). These woodlands formerly covered 2.7 million km² (Frost 1996), but are currently being lost and degraded to meet agricultural and energy needs (Brouwer & Falcão 2004). Rural land use in the miombo region has for centuries been dominated by subsistence agriculture, in which woodland is cleared, by burning and felling, to grow staple crops such as maize and sorghum for a number of years before abandonment (Frost 1996, Williams *et al.* 2008).

Rapidly increasing atmospheric CO₂ concentrations have prompted increasing attention to the preservation of carbon stocks in tropical ecosystems. The development of a system of payments to

reduce emissions from deforestation and degradation (Angelsen *et al.* 2009), relies on knowledge of the magnitude of such carbon stocks. Indeed Houghton (2005) shows that knowledge of the carbon density (tC/ha) of tropical land cover is the major uncertainty in the estimation of carbon emissions from land use change. Here, we address the need for carbon density information, reporting ecosystem carbon stocks for a site in the relatively understudied, but widespread and unique, miombo savanna woodlands. There is a high degree of uncertainty in carbon density estimates for savannas, particularly in the belowground component of biomass, which in some savannas are reported to exceed the aboveground biomass (Grace *et al.* 2006). Furthermore, in savanna woodlands, soil carbon stocks typically exceed woody carbon stocks, and when the woodland is cleared, loss of soil carbon can be a significant flux (Walker & Desanker 2004). Thus there is a need for: (1) estimates of carbon densities in all the major carbon pools of miombo woodlands; (2) an assessment of the spatial variability of these stocks; and (3) a quantification of the correlation between the different carbon pools, which might allow for efficient sampling.

This paper seeks to address these needs by providing estimates of ecosystem carbon stocks in miombo woodlands for a part of Africa where such data have not been collected. The possible existence of a large belowground biomass pool is investigated and the root:stem biomass ratio is placed in the context of a global data set. We also examine the links between soil and woody carbon stocks and relate these to soil textural properties. The focus here is the woodlands of Sofala Province, in central Mozambique. This paper is novel in that it presents a stem diameter–root biomass allometric for the miombo ecosystem, and quantifies all the major ecosystem carbon stocks at a single miombo site.

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METHODS

SITE DESCRIPTION.—The Nhambita area (Figs. S1 and S2) is in the south of Gorongosa District in the province of Sofala in central Mozambique (18°58'44" S, 34°10'34" E). The area is partly inside the Gorongosa National Park, and occupies the western flank of the Rift valley, the Bárúè Midlands (Tinley 1977). Nhambita falls into the Köppen Aw climate classification (tropical savanna) with a hot wet summer and cooler dry winter. The nearest source of meteorological data is a weather station at Chitengo, 25 km to the east of Nhambita. Here, mean annual rainfall (October 1–September 30) for the years 1956–1969 and 1998–2007 was 850 ± 269 mm (mean \pm SD). The rainfall is highly seasonal, with 82 percent falling in the 5 mo between November and March. From May to September, average monthly rainfall is < 20 mm. Most of the study area is on free-draining sandy soils derived from metamorphic and migmatitic gneiss and granite (Tinley 1977). The soils in the southeast of Nhambita are more hydromorphic in nature. On the sandy soils, termite (*Macrotermes*) mounds provide 'islands' of loamy fertile soils and occur at a density of around one per hectare (Tinley 1977). The vegetation consists of open woodlands, mainly dominated by species of the Caesalpinioideae, which includes the miombo species. In the less well-drained areas, species from the genera *Acacia* and *Combretum* dominate. The trees form an open canopy surrounded by a continuous grass layer. The grass senesces in the dry season and provides fuel for the frequent wildfires.

CARBON STOCK ASSESSMENT.—The major carbon pools of the ecosystem were quantified (tree stem and root biomass; sapling stem and root biomass; and soil carbon from 0 to 50 cm depth). To estimate vegetation (tree and sapling) carbon stocks, we used the standard approach (Chave *et al.* 2004) of a tree inventory recording stem diameter (diameter at breast height [dbh]) and an allometric relationship to convert diameter to estimates of woody mass. Previous work has shown that the choice of allometric equation can strongly influence the calculation of tree biomass in miombo (Williams *et al.* 2008), a widespread problem (Chave *et al.* 2005). Thus, we developed a new site-specific allometric equation for both above- and belowground biomass.

TREE STEM AND ROOT BIOMASS.—Stem and root biomass are calculated based on the inventory of 58 plots (total area 27.2 ha) and a new allometric model that relates diameter to stem and root biomass. Our approach was to compile as much inventory data as possible, even if it was collected for different purposes. As such we used data from 58 plots recorded between 2004 and 2007: (i) 15 square permanent sample plots (PSPs) of 1 ha, randomly located with respect to the network of tracks and roads in the study area. We established the plots 250 m from, and perpendicular to, 15 randomly chosen points on the road and track network ('road markers'). (ii) Thirty square plots of 0.25 ha (Williams *et al.* 2008), also perpendicular to the 15 road markers (above), but at different distances from the road marker (randomly selected from 200, 450, 700 and 950 m). (iii) Eight triangular 0.28 ha plots subsequently

used in the fire experiment of Ryan and Williams (2010), near the center of the study area. (iv) Five circular plots of 0.5 ha sampled away from the road network on a randomly chosen path through the study area. Figures S1 and S2 show the plot locations. On each plot all live standing stems > 5 cm dbh (1.3 m) were inventoried.

DESTRUCTIVE HARVEST.—To estimate biomass from dbh, allometric models of stem, root and total (stem+root) biomass were parameterized from destructively sampled stems in the study area. The allometric models are of the form:

$$\log(B) = \alpha \cdot \log(\text{dbh}) + \beta,$$

where B is the biomass of the stem or root, and dbh is the stem diameter. α and β are parameters to be estimated with linear least squares (MATLAB[®], MathWorks, Natick, Massachusetts, U.S.A.) and log indicates the natural logarithm.

In October 2007, 29 trees were destructively harvested. Target trees were chosen from the dominant four species in the inventory. The dbh range of the target trees exceeded the inter-quartile range of each species in the inventory. At five randomly located points on the road network, we located trees that matched the dbh and species criteria as closely as possible. These trees were felled and weighed, separating trunk and branch biomass. Thereafter, multiple subsamples were taken from the felled trees from both the trunk (cubes $\sim 10 \times 10 \times 10$ cm) and branches (cylinders ~ 10 cm long). These subsamples were weighed and then dried in an oven ($\sim 80^\circ\text{C}$ until constant mass) to determine their dry mass fraction (DMF, defined as dry mass/wet mass). Three subsamples from 19 of the trees were returned to Edinburgh for %C analysis (Carbo-Erba/400 automated CN analyzer). Biomass (B_{dest} kg C) was calculated as the product of wet mass, DMF and %C.

Twenty-three of the destructively harvested trees were excavated to provide data on coarse root biomass. For each sampled stem, the area under the canopy was excavated to approximately 1 m depth using a mechanical digger. The excavated soil was sifted by hand and large root (> 2 cm diam) biomass was collected, weighed and then subsampled for moisture content and %C using the same method as for the aboveground parts (see above). Any large roots that extended deeper than 1 m were excavated individually, although it was often impossible to follow them to their very end; we excavated beyond 2 m in most cases, and until the remaining roots had a diam < 5 cm. Large primary roots (> 10 cm diam) were weighed and subsampled separately from smaller roots.

We parameterized separate allometric models for stem, root and total biomass, using the log-transformed variables to reduce heteroskedasticity. Values were back transformed directly without the application of correction factors (Sprugel 1983).

SAPLING STEM AND ROOT BIOMASS.—Saplings, defined as stems < 5 cm dbh but greater than 0.3 cm at 10 cm aboveground level (d10), were measured and recorded on the eight fire experiment plots in 2007. Allometric models of sapling stem, root and total biomass were parameterized with data from a destructive sample of 45 saplings. The harvested saplings were located in the areas that

had to be cleared to excavate the large trees (see above). Power fits did not give satisfactory results, so second-order polynomials were fitted to the data, to relate d10 to wet biomass. Because the saplings typically had three or four similar-sized stems growing from a single root stock, we calculate an 'effective' d10e of each organism, defined as

$$d10e = 2\sqrt{\frac{\sum_{i=1}^s \pi \left(\frac{D_{10}}{2}\right)^2}{\pi}} \quad (1)$$

where d10e is the effective diameter of a multiple stemmed sapling and d10 is the diameter at 10 cm above the ground of each of the of the s stems.

Ten of the saplings were dried ($\sim 80^\circ\text{C}$ for 24 h) and reweighed to determine DMF. We measured %C on subsamples of seven saplings using the same equipment as for the large trees (above).

SOIL PROPERTIES.—Soil was sampled on 13 of the PSPs. On each PSP, nine sampling points were established on a 20 m grid. At five of the sampling points small pits were dug, and soil sampled at depths of 0, 5, 15, 25 and 50 cm. At the remaining sampling points only surface soil was sampled.

For elemental analysis (%C and %N) all samples were dried, sieved (2 mm sieve) and ball milled to produce a fine flour. Percentage C and N was determined using the same equipment as the woody samples (above). For particle size analysis, samples at similar depths were blended to produce one sample per depth per plot. These blended samples were sieved (< 2 mm), and then air dried. To deflocculate the sample before particle size analysis, each sample was left overnight in a sonic bath, in a solution of 4 percent sodium hexametaphosphate. It was then analyzed for percent particle size by volume using a Beckman Coulter LS 230 laser diffraction system (Brea, California, U.S.A). We report the percentage (by volume) of clay ($d < 0.002$ mm), silt ($0.002 < d < 0.05$ mm) and sand ($0.05 < d < 2$ mm), where d is the particle diameter.

To estimate bulk density, three replicate samples were extracted using a sharpened steel cylinder of known volume (209 cm^3) from the depth profile at the center of each plot at 2.5 and 30 cm depth. Dry soil bulk density was calculated from dry weight (samples were placed in an oven at 40°C for 24 h). Total soil carbon stock was determined by stepwise integration of the profile data of soil carbon content from 0 to 50 cm.

STATISTICAL TESTS.—The distribution of plot-level carbon stocks was tested for goodness of fit to the normal and Weibull distributions, using the Jarque–Bera (J–B) and Anderson–Darling test, respectively. Having established an appropriate distribution, we report the estimated population mean and its 95% CI, estimated by maximum likelihood using MATLAB[®]. Unless otherwise stated, \pm indicates the standard error of the mean. For piecewise curve fitting we used the Shape Language Modeling (SLM) tool (D'Errico 2009). We also assessed the degree of spatial dependence of our sampled plots by plotting and inspecting an experimental semi-variogram. All curve fitting was done in MATLAB[®] using the

curve fitting toolbox (v2.1). We report the adjusted r^2 and the root mean-squared error (RMSE) of each fit.

TERMINOLOGY.—Throughout this paper we use B to denote tree biomass, SB for sapling biomass, R:S for the root:stem ratio. Subscript 's' for stem, 'r' for root, 't' for $s+r$. dbh indicates diameter at 1.3 m in cm, d10 diameter at 10 cm above the ground, in mm. All stocks are in tC/ha on a dry weight basis. We refer to the attributes of the destructively harvested stems with the subscript 'dest' and log indicates a natural log. All species names follow Coates Palgrave *et al.* (2002).

RESULTS

TREE STEM AND ROOT BIOMASS.—The 29 sampled trees ranged in dbh from 5 to 73 cm. As well as the 20 target trees of the four dominant species (*Brachystegia boehmii* Taub., *Brachystegia spiciformis* Benth., *Combretum adenogonium* Steud. ex A.Rich., *Diplorhynchus condylocarpon* (Muell.Arg.) Pichon), we included nine other trees including two further species (*Crossopteryx febrifuga* [Afzel. ex G.Don] Benth. and *Pericopsis angolensis* [Baker] Meeuwen) that were excavated to allow access to the target species. The sampled stems had wet mass from 8 to 10,309 kg (mean 1043 kg). The subsamples had DMF (fresh mass/dry mass) that averaged 0.65 ± 0.01 for the trunk and 0.59 ± 0.02 for the branches. Trunk subsample moisture content was significantly different from the branch subsamples (two-tailed t -test, $P < 0.0001$), so dry mass was calculated separately for branch and trunk mass, using stem-specific moisture content values. This calculation yielded dry mass estimates of 4–6954 kg dry matter (mean 674 kg). Percentage C values were not different (two-tailed t -test, $P = 0.366$) between trunk and branch subsamples, so the mean ($47 \pm 0.20\%$) was used for all conversions to carbon mass. Final values of stem biomass ranged from 2 to 3268 kg C (mean 320 kg C).

Root mass for the 23 excavated trees varied from 1760 kg C, with a mean of 123 kg C. dbh of the excavated trees ranged from 5 to 72 cm. Similar to stem values, root carbon content also averaged 47 ± 0.23 percent. DMF averaged 0.59 ± 0.01 .

We pooled all destructive data from all species to produce one allometric model for the site, after preliminary analysis showed no significant difference (no separation of 95% CIs) in the model parameters for a fit of dbh_{dest} and B_{dest} for the different species.

Natural log-transformed allometric models of diameter (cm) vs. stem, root and total woody biomass (kg C) fitted well (Fig. 1A; Table 1). The stem and root allometric models showed that root:stem decreases with stem size (Fig. 1B; Table 1).

INVENTORIES.—The allometric equations were applied to the inventory data to estimate stem, root and total woody biomass at a plot level. Plot total tree biomass (B_t) was not normally or log-normally distributed, but the Anderson–Darling test showed that our sample followed a Weibull distribution. B_t varied from 3.1 to 86.5 tC/ha, with a mean of 32.1 (95% CI 28.4, 36.6). B_s ranged from 1.9 to 60.9 tC/ha with a mean of 21.2 (18.7, 24.3). B_r ranged from 1.1 to

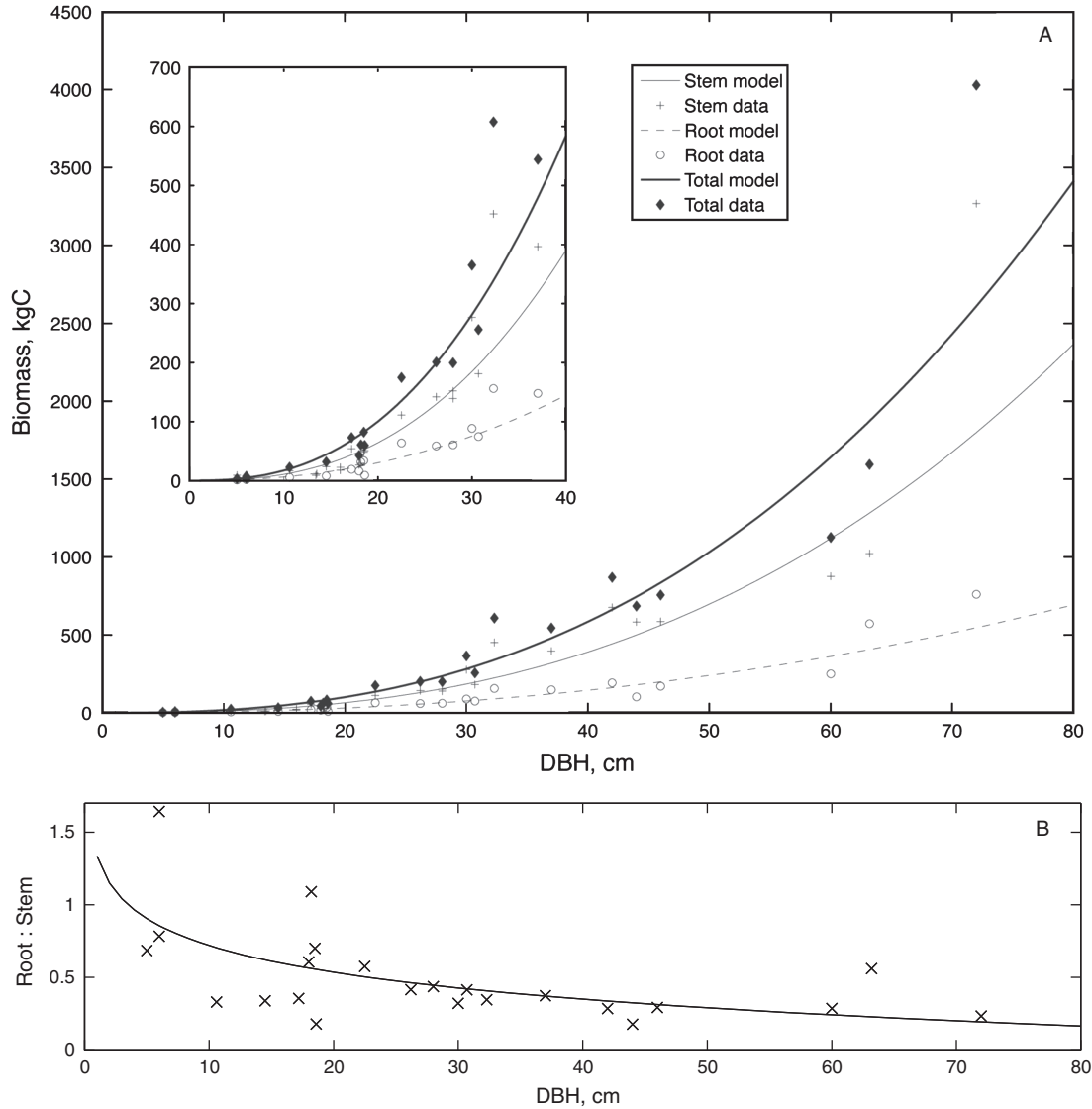


FIGURE 1. (A) The allometric models of stem, root and total biomass and the destructively harvested data. The models are fitted to the log of dbh and B_{dest} but are shown back transformed. (B) The allometry of the root:stem ratio of the destructively harvested stems.

17.0 with a mean of 8.5 (7.7–9.6). Plot-level R:S was normally distributed and varied from 0.27 to 0.58, mean 0.42 (0.41–0.44) and was weakly but significantly correlated with B_t ($R:S = -0.00238$

$B_t + 0.499$, $r^2 = 0.45$, $P < 0.0001$). B_r was well correlated with B_s ($B_r = 0.87 B_s^{0.76}$, $r^2 = 0.94$, RMSE = 0.87 tC/ha, $N = 58$).

Plot basal area was a good predictor of plot total woody carbon stock (Fig. S3):

$$B_t = 3.972 \cdot BA, \tag{2}$$

$r^2 = 0.76$, RMSE = 7.82 tC/ha, $N = 58$, where B_t is total (above- and belowground) tree carbon stock (tC/ha) and BA is tree basal area (m^2/ha).

TABLE 1. Tree biomass allometric equations. $B_{dest,s}$ is the destructively sampled tree stem biomass (s), tree coarse root biomass (t) and total tree biomass (t, i.e. stem+root), all in kg C. dbh_{dest} is diameter at breast height in cm. log is the natural log. $R:S_{dest}$ is the root stem ratio.

Equation	r^2	RMSE	N
$\log(B_{dest,s}) = 2.601 \log(dbh_{dest}) - 3.629$	0.93	0.52 log(kg C)	29
$\log(B_{dest,t}) = 2.262 \log(dbh_{dest}) - 3.370$	0.94	0.43 log(kg C)	23
$\log(B_{dest,t}) = 2.545 \log(dbh_{dest}) - 3.018$	0.98	0.30 log(kg C)	23
$(R:S_{dest}) = -0.2671 \log(dbh_{dest}) + 1.334$	0.36	0.27	23

SAPLING BIOMASS.—The allometric equations for sapling stem and root biomass were fitted with second-order polynomials and had r^2 from 0.65 to 0.75 (Table 2). DMF was 0.61 ± 0.05 , based on moisture measurements of the ten saplings that were dried. Percentage C was 44.6 ± 0.3 , based on seven subsamples.

TABLE 2. Sapling biomass allometric equations. SB_{dest} is wet sapling biomass in kg, $d10e$ is the effective diameter (mm) of the harvested saplings at 10 cm aboveground (see equation [1]).

Equation	r^2	RMSE (kg)	N
$SB_{dest,s} = 0.0007645 \cdot d10e^2 + 0.004645 \cdot d10e + 0.03876$	0.65	0.47	45
$SB_{dest,r} = 0.001784 \cdot d10e^2 + 0.0001413 \cdot d10e + 0.15839$	0.72	0.84	45
$SB_{dest,t} = 0.0025485 \cdot d10e^2 + 0.0047865 \cdot d10e + 0.19715$	0.75	1.1	45

Using these allometric equations, and the dry mass and %C data to calculate standing stock of sapling biomass, yielded the following plot-level data: SB_s , ranged from 0.7 to 5.1 tC/ha, with a mean of 2.5 tC/ha (95% CI 1.0–3.9). SB_r ranged from 0.3 to 2.4 tC/ha, with a mean of 1.1 tC/ha (0.49–1.8); SB_t ranged from 1.0 to 7.5 with a mean of 3.6 tC/ha (1.5–5.6). Plot-level sapling root:stem averaged 2.16 (2.13–2.19).

SOIL CARBON AND NITROGEN.—Across the 13 PSPs with soil data, soil carbon content was ~3 percent at the surface (Fig. S4), decreasing to ~1 percent at 15 cm depth, and remained around this value at greater depths. Nitrogen content followed a similar profile (Fig. S4) with the C:N ratio decreasing from 17.2 at the surface to 14.5 at a depth of 0.5 m.

Soil carbon stocks (Fig. 3) averaged 8.0 ± 0.4 tC/ha (± 1 SEM) from 0 to 2.5 cm, 17.7 ± 2.0 from 2.5 to 10 cm, 16.0 ± 2.4 from 10 to 20 cm and 34.5 ± 5.4 tC/ha from 20 to 50 cm. Summing the 0–50 cm profile, soil carbon stocks averaged 76.3 ± 9.9 tC/ha. However, the distribution of the 13 plot-level soil carbon stock values was almost uniform and ranged from 32 to 133 tC/ha (Fig. 2), so that estimating the population mean is prob-

lematic. The mean bulk density at the surface was 1.2 ± 0.03 t/m³, and 1.5 ± 0.04 t/m³ at 30 cm.

SOIL TEXTURE.—Soil texture at plot level varied from 3 to 9 percent clay, 20 to 48 percent silt and 46 to 76 percent sand, with a profile mean of 6, 33 and 60 percent, respectively. There was very little variation in soil texture with depth: mean silt content decreased down the profile from 34 to 28 percent and clay content increased from 5.6 to 6.7 percent (Fig. S4).

Soil texture was correlated with plot-level soil carbon stock (Fig. 4; Table 3). There was no correlation between plot-level tree biomass (B_t) and soil carbon stock (C_s) ($P = 0.5$, $r^2 = 0.05$, $N = 13$), and total tree biomass was only weakly negatively correlated with clay content ($P = 0.16$, $r^2 = 0.10$; see Table 3).

DISCUSSION

OVERVIEW AND COMPARISON WITH OTHER SITES.—At our site, ecosystem carbon stocks totaled 110 ± 13 tC/ha (Table 4). Soil carbon dominated the total, contributing 76.2 tC/ha (70%). Woody biomass totaled 33.3 tC/ha (30%), dominated by tree biomass

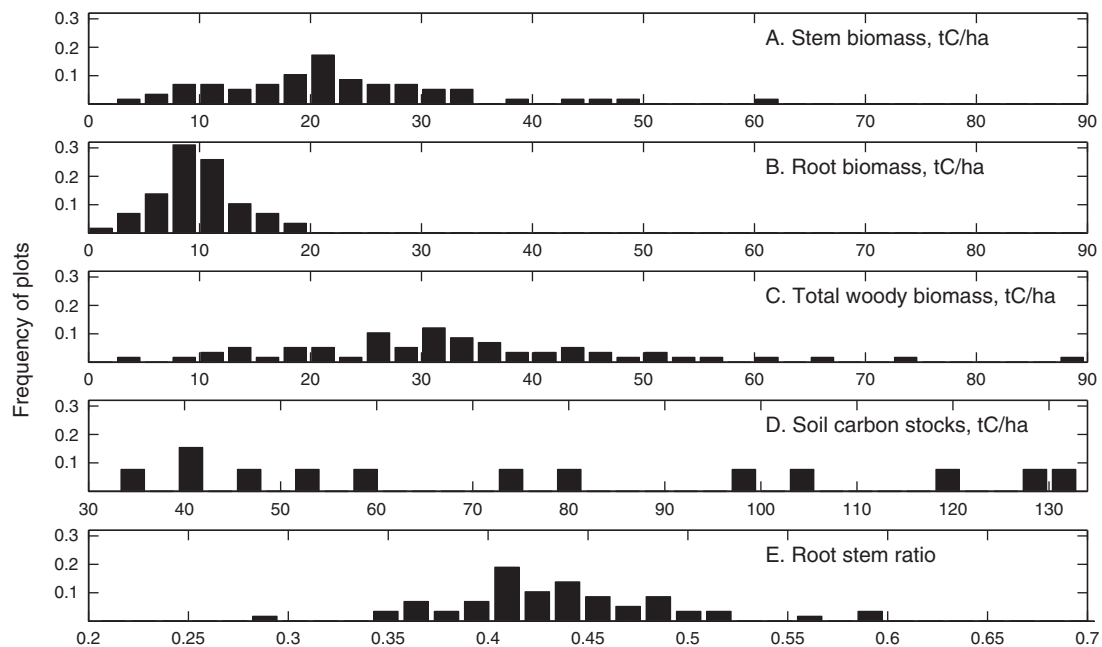


FIGURE 2. Histograms of plot-level stem, root and total woody biomass carbon stocks on the 58 plots, and soil carbon stocks (to 50 cm depth) on 13 plots, as well as plot-level root:stem on the 58 plots. Note change in X-axis values for soil carbon stocks.

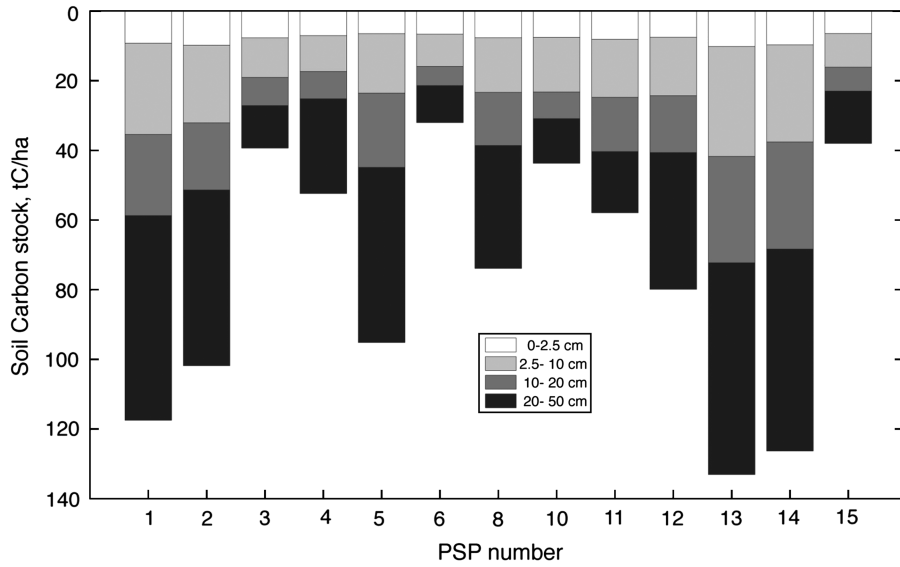


FIGURE 3. Soil carbon stocks at various depths on 13 of the 1 ha permanent sample plots.

(29.7 tC/ha). The division between soil carbon and total carbon stocks in Nhambita (70% in soil) is similar to the 60 percent reported in Walker and Desanker (2004) for Malawian miombo.

Aboveground woody biomass in Nhambita (21.2 tC/ha) can be compared with Frost’s (1996) ‘average for dry miombo’ in Zimbabwe and Zambia of 26 tC/ha (dry mass is converted to carbon mass assuming 47% C throughout this discussion). Comparing this study with that of Ribeiro *et al.* (2008a) in Niassa Reserve in miombo woodland in northern Mozambique (annual rainfall

900–1200 mm), our woodlands falls into their ‘medium density woodland’ class for which B_s was 19.5 tC/ha. Williams’ (2007) summary of the data in Post *et al.* (1982) and Gibbs (2006) found a ‘live biomass’ of 28.2 tC/ha (our data 29.7 tC/ha) at the latitude of Nhambita (interpolating their data points with a spline), and soil carbon stocks of 86.6 tC/ha (to 1 m depth; our data 76.2 tC/ha, to 50 cm).

Frost (1996) developed a relationship between annual rainfall and aboveground woody biomass in miombo: using a value for our

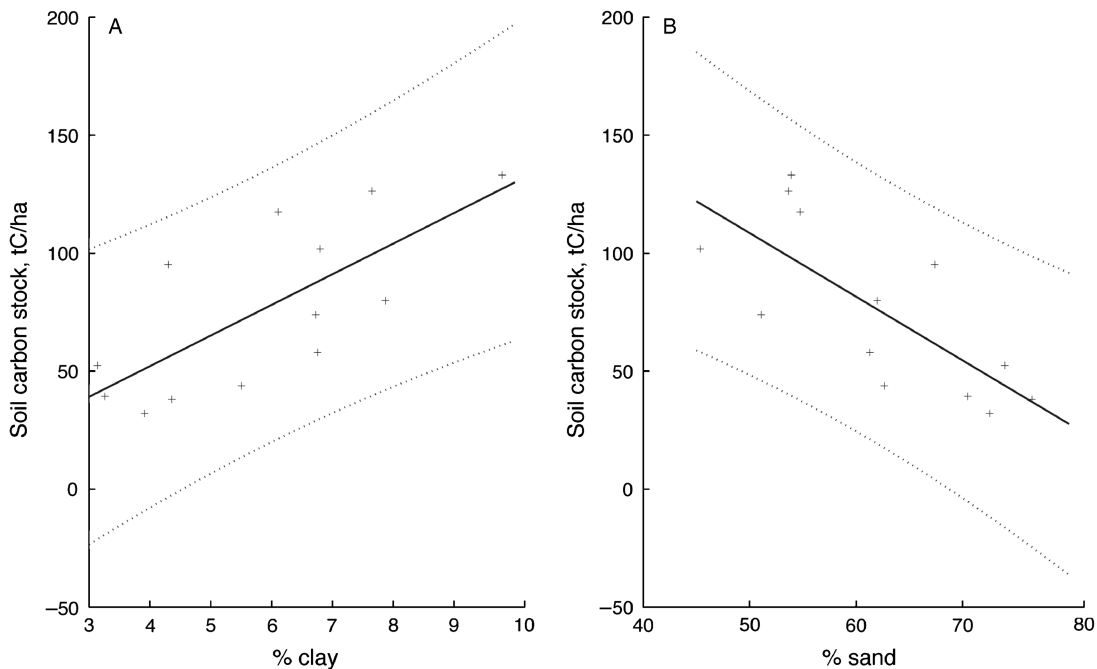


FIGURE 4. Soil texture regressed against soil carbon stock. All data are plot means ($N=13$) averaged down the profile (0–50 cm depth) in the case of texture, and summed down the profile in the case of carbon stock. Thick lines shows the line of best fit, and the dotted lines show the 95% prediction intervals.

TABLE 3. Relationships between soil texture and carbon stocks. C_s is soil carbon stock (0–50 cm) in tC/ha, B_s is tree carbon stock (above- and below-ground, tC/ha), K and Z are clay and sand contents in percent by volume.

Equation	r^2	RMSE (tC/ha)	P	N
$C_s = 12.98 \cdot K + 0.2$	0.53	25.5	0.004	13
$C_s = -2.70 \cdot Z + 243$	0.51	24.9	0.004	13
$B_s = -3.70 \cdot K + 54.3$	0.10	16.8	0.16	13
$B_s = 0.81 \cdot Z - 17.2$	0.13	16.6	0.13	13

site of 850 mm/yr, and Frost's equation ($Y = 0.14X - 56.21$; Y is Mg/ha of dry matter; X is rainfall in mm), our biomass data (21.2 tC/ha) are lower than the equation's prediction (29.5 tC/ha).

Plot-level root:stem ratios in this study varied from 0.28 to 0.58, with a mean of 0.42. Root biomass estimates in miombo are rare, but the average of root:stem in this study (0.42) can be compared with Chidumayo's (1997) values of 0.53 and 0.47 for two wet miombo plots in Zambia (calculated in Frost 1996). Outside of the miombo region, we found comparable data on B_s and R:S for 18 sites in 11 countries in Latin America and Africa (Sarmiento & Vera 1979, Murphy & Lugo 1986, Castellanos *et al.* 1991, Wooller 1993, Malimbwi *et al.* 1994, Frost 1996, De Castro & Kauffman 1998, Tiessen *et al.* 1998, Lilienfein *et al.* 2001, Jaramillo *et al.* 2003). This summary shows that R:S falls rapidly as B_s increases, but is very variable, up to values of B_s of around 10 tC/ha (Fig. 5), thereafter R:S levels off at between 0.3 and 0.5. It can be modeled with a piecewise linear equation, fitted with SLM (Fig. 5):

$$\begin{aligned} \text{where } B_s < 11 : \quad R:S &= -0.30 B_s + 3.62, \\ \text{where } B_s \geq 11 : \quad R:S &= 0.35, \end{aligned} \quad (3)$$

TABLE 4. Summary of ecosystem carbon stocks in the Nhambita area. All values in tC/ha. \pm indicates the standard error of the mean.

Carbon pool	Carbon stock (tC/ha)
Saplings	
Stem	1.1 \pm 0.3
Roots	2.5 \pm 0.6
Sapling total	3.6 \pm 0.9
Trees	
Stem	21.2 \pm 1.4
Roots	8.5 \pm 0.5
Tree total	29.7 \pm 2.1
Soil	
0–2.5 cm	8.0 \pm 0.4
2.5–10 cm	17.7 \pm 2.0
10–20 cm	16.0 \pm 2.4
20–50 cm	34.5 \pm 5.4
Soil total	76.3 \pm 9.9
Grand total	110 \pm 13

where R:S is the root:stem ratio, B_s is aboveground biomass (tC/ha).

For the data from this study, a simple linear model can be fitted:

$$R:S = -0.0046 \cdot B_s + 0.498, \quad (4)$$

$N = 60$, $r^2 = 0.46$, RMSE = 0.041.

The mean R:S found in this study (0.42) was slightly higher than that found at sites with comparable aboveground biomass (R:S = 0.35), according to our review of the literature (Fig. 5). Also, our plot-level R:S data showed a different relationship with aboveground biomass: the Nhambita plots with low B_s had much lower R:S than comparable sites in the literature (Fig. 5). This suggests a difference, probably in stem-size distributions, between low biomass miombo plots, and other savannas with low biomass. Some of our low B_s plots are dominated by a few, large trees, and thus have a lower R:S than if they were composed of many small trees which tend to have a high individual R:S.

The B_s vs. R:S relationship can be compared with the IPCC LULCF Good Practice Guidelines (Penman *et al.* 2003) default figure for 'woodland/savanna' of 0.48 ± 0.19 SD, which is based on Australian and Indian data. This default figure appears to underestimate root biomass for low biomass savannas in the Neotropics and West Africa, but is similar to values from this study, and for savannas with $B_s > 11$ tC/ha.

THE RELATIONSHIP BETWEEN CARBON STOCKS IN MIOMBO WOODLAND.—This study has shown that soil and woody carbon stocks are the dominant carbon pools in miombo woodland, but that the size of each carbon pool was not correlated. Soil carbon is highly variable (32–133 tC/ha; Fig. 2), and soil texture explained around half of this variation (Fig. 4; Table 3) as is common in tropical soils (Feller & Beare 1997). Woody biomass was less variable (3.1–86.5 tC/ha), but only weakly correlated with soil texture. This decoupling of the soil and woody carbon stocks is expected, because although the dynamics of wood and soil carbon are clearly linked, there are many other controls on pool size. We summarize the key processes below.

Woody biomass in miombo shows both regional trends with rainfall (see above, Frost 1996) and smaller scale trends with topography (Chidumayo 1997). The topographic trends relate to the catenal patterns, with low woody biomass in dambos (bottom lands with impeded drainage, von der Heyden 2004) and higher biomass on interfluves (Chidumayo 1997). This catenal pattern may account for the weak negative correlation between clay content and woody biomass found in this study. However, this simple dambo-interfluve pattern is far from universal, and we have frequently observed higher levels of woody biomass along river lines, compared with interfluves, primarily on deeper, more fertile alluvial soil.

The spatial pattern of woody biomass described above is subject to frequent and widespread disturbances (Frost 1996) that reduce biomass: primarily clearance for agriculture (Williams *et al.* 2008), charcoal production (Brouwer & Falcão 2004, Falcão 2008) and fire (Ryan & Williams 2010). Elephant activity can also reduce tree populations significantly (Guy 1989, Ribeiro *et al.* 2008b), as

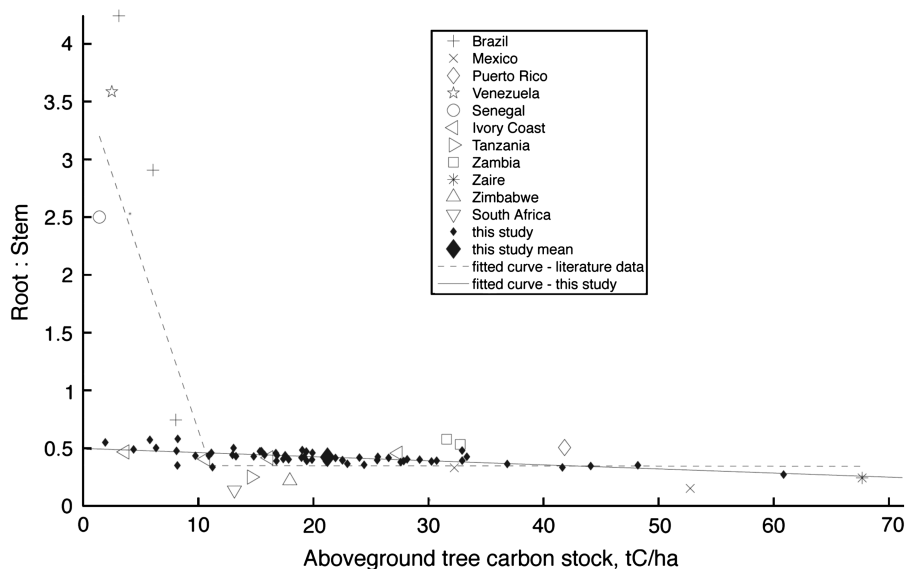


FIGURE 5. Root:stem ratios as a function of aboveground biomass, across the seasonally dry tropics. Definitions of stem and root biomass vary according to the source, but are 'coarse' roots (often > 2 cm diam) and trees (mainly > 5 cm dbh).

can rare frosts (Tafangenyasha 1997), and the interactions of all these effects. Clearance for agriculture is the start of a cycle whereby woody biomass is reduced nearly to zero for the duration of the agricultural activity, but then recovers to pre-disturbance levels within around 30 yr of abandonment (Williams *et al.* 2008) creating a mosaic of land cover. The regular fires in the miombo region can, if too frequent or intense, cause mortality of large and small trees and prevent regeneration (Ryan & Williams 2010), thus leading to a gradual degradation of the woodlands until no woody tree biomass is present (Furley *et al.* 2008).

Soil carbon is also generally reduced after clearance for agriculture (Walker & Desanker 2004). Indeed Walker and Desanker (2004) report that upon conversion to agricultural land, miombo woodland loses around 47 percent of its soil carbon (to 1.5 m depth). Using the same proportion, conversion to agriculture at our site would thus result in a loss of 36 tC/ha from the soil, slightly larger than that if all the tree biomass were to be lost (29.7 tC/ha). Soil carbon is also lower on plots subjected to frequent fires, but the effect of different fire regimes is similar in magnitude to the influence of soil texture (Bird *et al.* 2000).

It is important to note that there is no a priori reason to think that low woody cover leads to lower inputs to the soil carbon pool. Grass productivity in miombo is comparable with tree productivity and because low woody biomass tends to encourage high grass biomass (Frost 1996), the input to the soil could be similar under high and low woody cover. Evidence from Bird *et al.* (2000) suggests that soil carbon stocks are higher beneath trees than in adjacent open areas of woodland, which argues for the importance of carbon inputs from trees (or animals that defecate beneath them). The lack of a correlation between woody and soil carbon stocks in this study, however, indicates that many other factors influence this relationship at larger scales.

The correlation between soil texture and soil carbon stocks shown here (Fig. 4) offers the most promising route to mapping soil carbon stocks and dealing with their variability on a range of spatial scales. In contrast, tree belowground biomass is very well correlated with aboveground biomass, and B_r can easily be estimated using the R:S reported here (where only plot-level data are available) or our allometric equations (if stem-level data are available).

LIMITATIONS.—In summarizing ecosystem carbon stocks, several caveats must be mentioned. Firstly our plots are located on a transition from miombo woodland to the plains of the Rift valley, where a change in soil type produces a more diverse and complex woodland formation. Secondly, our plots are not evenly or randomly distributed across the landscape, but instead follow the network of small tracks and roads that provide access, and are clumped together. To address this, we examined a variogram of B_r (Fig. S5). The variogram showed no relationship between separation distance and the variance. This suggests that the variance between closely located plots (< 2 km apart) is no different from more widely spaced plots (> 10 km) and supports the use of the closely spaced plots as independent data. Furthermore, if we use the mean of each set of plots perpendicular to the same road marker as a single value, then our result for aboveground woody biomass is 21.0 (95% CI 18.1–23.8; $N=28$), very similar to the mean of the 58 plots: 21.2 (18.7–24.3).

A further caveat is that the use of allometric models, even site specific ones, can introduce significant biases depending on their form, and how the heteroskedasticity of the destructive data is dealt with (Brown *et al.* 1989, Parresol 1999). Our estimates are bound to be subject to such biases, a subject we will address in a further paper. We also note that soils were only sampled at 13 of the plots rather than at all 58. Finally, we did not measure the more transient carbon pools such as fine root, tree leaves and grass biomass, which

contribute to the total ecosystem carbon stocks. The major missing pool is likely to be grass biomass.

CONCLUSIONS

At a site in the miombo woodlands of Mozambique, carbon stocks are dominated by soil carbon: 76 tC/ha of the total 110 tC/ha are in the surface 50 cm of soil. However, soil carbon is very variable across the landscape, and has a broad and almost uniform distribution, rather than converging around a mean. This requires further investigation at various spatial scales if estimates of carbon stocks in this ecosystem are to be better constrained. Soil texture is a reasonable predictor of soil carbon stocks, but soil carbon was not obviously correlated to woody carbon stocks.

Woody tree carbon averaged 21.3 ± 1.4 tC/ha aboveground and 8.6 ± 0.5 tC/ha belowground, based on allometric relationships. Sapling total biomass averages 3.6 ± 0.9 tC/ha. Coarse root biomass is a major carbon pool in these ecosystems and is proportionally more important at low values of aboveground biomass because of shifts in the root:stem ratio of trees as they grow.

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SUPPORTING INFORMATION

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

FIGURE S1. Study area location.

FIGURE S2. Plot locations.

FIGURE S3. Plot-level woody carbon stocks regressed against plot basal area. The dashed line shows the 95% prediction interval for a new observation.

FIGURE S4. Mean depth profiles of soil texture and elemental concentrations for the 13 plots. The black line shows the mean and the gray area the full range of the observations.

FIGURE S5. Variogram of the aboveground biomass of the sample plots.

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