Gabon’s Overlooked Carbon
A tropical forest study of coarse woody debris

by

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Abstract

Large dead trees and other large forest detritus (collectively known as coarse woody debris, or CWD) play an important role in the global carbon cycle. In tropical systems, CWD stocks (necromass) have been found to constitute 5% to 33% of total biomass. Despite harboring the second largest rain forest on earth, in Central Africa there have been virtually no studies of coarse woody debris. In this study 15 plots were established in 5 forest zones in Gabon, Africa to measure CWD stocks and potential environmental and land-use determinants of CWD. Necromass of CWD was found to be positively correlated with precipitation and was higher in logged forests than in primary forests. Extrapolated to the entire country, Gabon is estimated to contain carbon CWD content of between 0.34 Pg C to 0.72 Pg C (14 Mg C ha\(^{-1}\) to 30.1 Mg C ha\(^{-1}\)). The results of this study will help improve tropical forest carbon flux estimates.
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Introduction

Coarse woody debris (CWD), defined as any dead vegetative mass > 10cm in diameter, plays an important role in the forest carbon cycle (Harmon 1986, Clark 2002). Global estimates of the carbon contained in CWD biomass (necromass) are highly variable due to the paucity of data, and range from 25 to 230 Pg C (Harmon 1993). Most large-scale studies of tropical forest carbon focus on live biomass or deforestation, which can be detected using remote sensing technologies (Saatchi 2011). However, these studies potentially underestimate the total amount of carbon in the system, as coarse woody debris produced by both natural tree death and forest degradation is difficult to measure using remotely sensed data (Asner 2005). In tropical forests, local estimates of necromass can range from 2.5 to 86.6 Mg/ha (Chao 2009) and can make up 5% to 33% of total biomass (Chao 2009, Clark 2002). The residence time of CWD in tropical forests is estimated to be between 4.7 and 9 years (Chambers et al. 2000, Baker et al. 2007, Clark et al. 2002). This large CWD carbon pool and fast decomposition rate results in a large and understudied carbon flux in tropical forest systems. With growing concern over increasing concentrations of atmospheric carbon, understanding the size and determinants of the tropical CWD pool is critically important to understanding the carbon cycle.

Tropical Forest Carbon

The Intergovernmental Panel on Climate Change defines five carbon pools: above ground live biomass, below ground live biomass, coarse woody debris, fine woody debris, and soil carbon (IPCC 2003). Carbon is sequestered in above ground biomass in woody stems and branches, and below ground in roots. In the absence of disturbance, carbon also tends to accumulate in soils. Litter, which includes leaves and fine woody debris (stems and branches < 10cm in diameter), has a short residence time (<1
yr) in the tropics (Gautam and Pietsch 2012). Dead wood has a longer, but still relatively short residence time of 4.7 to 9 years.

Up to 80% of the world's above ground carbon is stored in forests, and tropical forests contain 59% of global forest carbon (Dixon 1994). Saatchi et al. (2011) estimate that in the early 2000s the tropics stored 193 Pg C in above ground biomass and 54 Pg C in below ground biomass, however this estimate does not account for CWD. Estimates of the total carbon stored globally in the tropical CWD pool are not available. In tropical ecosystems, most CWD studies are site-specific and have occurred in the Neotropics. In the only meta-analysis of CWD to date, Chao (2009) extrapolated data from 20 field studies across the Amazon, and estimated that the CWD pool of the Amazon rainforest stores 8.6 to 10.6 Pg C, approximately 9.1% to 12.3% of the carbon found in live biomass.

**The Coarse Woody Debris Carbon Pool**

The flux of the CWD carbon pool is a function of the input to the pool (the size and number of trees that die) and the residence time in the pool (the rate of decay of the necromass) (Olsen 1963). The size of trees in a tropical forest is likely dependent on factors such as precipitation, nutrient availability, and life history. Tree mortality can occur for many reasons, including climatic factors (prolonged drought), senescence, disease, pests, or natural and anthropogenic disturbance (Phillips & Gentry 1994).

Disturbance has been shown to play a major role in the input to the of CWD pool (Espírito-Santo 2011). The Amazon experiences large-scale blow downs (Nelson 1994, Espírito-Santo 2010) which contribute to the CWD pool. High disturbance rates can cause a forest to convert from a net sink to a net source of carbon. Rice (2004) estimated CWD stocks of 44 Mg C/ha in Tapajos national forest in Brazil, much higher than many areas of the tropics and higher even than nearby forests. High mortality and
subsequent heterotrophic respiration led to a net carbon release from the forest, even when accounting for increased recruitment. Rice (2004) hypothesized that a major disturbance, possibly drought conditions from a recent ENSO event, caused the high CWD pool. Harmon (1995) working in the tropical dry forest of the Yucatan compared undisturbed sites to disturbed sites and found significantly higher stocks in sites that had been recently disturbed by either hurricane or fires.

Logging is an important source of anthropogenic disturbance in the tropics. Logging often takes the largest trees out of the forest, but has been shown to increase adjacent tree mortality and therefore increase the input to the necromass pool. Trees destroyed due to logging in Gabon contributed 25.6 Mg ha$^{-1}$ to the necromass pool (Medjibe 2011). In estimates of CWD pools in Brazil, studies show that logged sites have higher CWD than unlogged sites (Keller 2004, Palace 2007).

Many factors affect the residence time in the CWD pool. Globally the most important factor is temperature as increased temperature is associated with increased rates of decay and reduced time in the pool (Chambers 2000). In the tropics where temperature is regionally constant, other factors play a larger role, including the size of the CWD, the density, and substrate quality of the wood (Hérault 2009, Chambers 2000). Although precipitation has not been shown to be a globally important control over residence time (Chambers 2000), it may play a role at the regional level.

CWD is highly variable at local scales, but has been shown to follow physical gradients at regional scales (Chao 2009). In the Amazon, major east to west gradients include increasing mortality rates of trees, decreasing forest biomass, and decreasing average wood density (Phillips et al. 2004, Baker et al. 2004, Malhi et al 2006, cited in Chao 2009). In addition to these gradients Chao (2009) found that necromass stocks decrease from east to west.
Central African Coarse Woody Debris

The Central African tropical forest is the second largest contiguous moist tropical forest on the planet (Mayaux et al. 1999), and stores an estimated 48 to 62 Pg of carbon (Saatchi 2011). African forests are understudied compared to Neotropical forests, and few studies of CWD have been performed in Central Africa.

Bartholomew (1953), working in the Yangambi region (Democratic Republic of Congo), quantified CWD in fallow fields as part of a nutrient mobilization study of slash-and-burn agriculture. The published data included estimates of necromass for early successional forests and is representative of only a specific type of forest. More recently, Djomo et al. (2011) examined all five IPCC defined carbon pools in three forest types: national park (primary), indigenous, multi-use (secondary), and managed (logged) forests. Their study area in Cameroon occurred across a strong precipitation gradient, ranging from 2950 mm yr\(^{-1}\) on the coast to 1670 mm yr\(^{-1}\) inland. The study reported average carbon per forest type, ranging from 2.5 Mg C ha\(^{-1}\) in national parks, to 7.2 Mg C ha\(^{-1}\) in managed forests. Although the study area has a strong rain gradient, the effects of precipitation on the CWD pool were not considered. Gautam and Pietsch (2012) estimated CWD in Monts Birougou National Park, Gabon, finding that CWD carbon ranged from 3.7 Mg C ha\(^{-1}\) to 29.7 Mg C ha\(^{-1}\) with a mean of 13.9 Mg C.

Unfortunately, results from both Gautam and Pietsch (2012) and Djomo et al. (2011) are difficult to compare to other CWD studies because they used different methods to estimate necromass than most other studies of CWD. Both studies used live tree density to estimate necromass, rather than directly measuring CWD density. Chao (2008) did not find any relationship between live wood density and heavily decayed CWD. Density decreases as decay increases (Clark 2002, Baker 2007), so using live wood density to estimate necromass may inflate necromass values. Djomo et al. used a small plot size
(20m x 250m), while Gautam and Peitsch used a variable plot size and a point sampling inventory method (Bitterlich 1948, Avery & Burkhart 1983). For accurate and globally comparable estimates of CWD, large scale studies with a consistent methodology are needed.

The forests of Central Africa differ from those of the Neotropics in several important ways. Stem density and diversity in Central Africa tends to be lower, while trees are generally larger (Corlett and Primack 2011). This fact may affect the CWD pool, as both size of trees and number of trees affect the input to the CWD carbon pool. Since large trees have high necromass and longer residence time, a single large tree has greater impact on the CWD pool than many small trees (Chao 2009). Greater average tree size and longer average residence size could result in a larger CWD pool per ha in Central Africa than in other tropical systems.

**Spatial Estimates Using GIS**

Large-scale estimates of CWD are usually part of inventories of forest carbon, in which CWD is estimated coarsely (Houghton 2001, Saatchi 2007) or estimated by applying average plot-level values to a large spatial extent (Chao 2009). The size of the CWD pool is a function of the diameter and number of inputs, the density of the input material and the rate of decay (Chambers 2000, Chao 2009), factors that vary continuously and have been shown to be correlated with large environmental gradients such as precipitation, soils and disturbance history. Linking CWD to these physical and land use layers could improve regional estimates of the CWD pool by using GIS technologies to produce finer-grained, spatially explicit necromass estimates.
**Study Questions**

In this study, I ask two overarching questions:

1. What is the total carbon stored in the CWD pool in Gabon?
2. What are the major controls over the size of the CWD pool in Gabon?

I hypothesize that 1) CWD necromass will be greater in logged areas than in unlogged areas; 2) CWD necromass will vary by precipitation levels, with larger CWD necromass in areas with more precipitation; and, 3) CWD necromass will vary by forest zone, defined by seasonality, precipitation, topography, and geography.

**Methods**

**Study Site**

Gabon is located on the coast of equatorial Africa, at the western end of the Congo Basin rainforest. The country has a strong precipitation gradient, with a nearly three-fold change in total annual precipitation between the dryer interior (1300 mm yr\(^{-1}\)) and the wet coastal areas (3200 mm yr\(^{-1}\)) (Figure 11). Gabon is sparsely populated, with a population of 1.5 million people, 700,000 of which are concentrated in Libreville, the capital city. The country is prosperous and stable compared to many other Central African countries, and retains 85% of its original forest cover (Figure 12). The relative lack of deforestation can largely be attributed to its sparse population – the lowest in Central Africa – but the government also set aside 11% of its total area as national parks (ANPN 2011) (Figure 13). Saatchi (2011) estimates that Gabon stores 4 Pg C in above and below ground biomass, and has one of the highest carbon densities in the tropics (164 Mg C ha\(^{-1}\)), second only to Malaysia (179 Mg C ha\(^{-1}\)). A large percentage of Gabon’s forested area is committed to logging concessions (Figure 13), however logging operations are selective and large clear-cuts are rare.
Gabon has recently established a low-carbon development policy, and is undertaking a national effort to inventory its carbon stocks. The project is currently establishing 100 plots throughout the country. Each plot is randomly located inside a grid of 100 squares that span the country (Figure 10). This study of CWD is part of that effort.

**Forest Zones**

We classified Gabonese forests into eleven different forest zones by combining annual precipitation, seasonality, geology, and topography (Error! Reference source not found.). Precipitation values were taken from bioclim data (Hijmans et al. 2005). We used geology as a proxy for soil properties, and derived geology by processing the 2000 national geology map. Within these forest zones, I selected plots that were established for the national carbon inventory for CWD estimation. Plots were selected so that each forest zone had an even coverage of primary, secondary, and logged forest types.

![Forest zones](image)

*Figure 1. Forest zones as defined by precipitation patterns, geology, and topography. Plot placement is based on the national carbon inventory, and selection is based on logistical factors and an attempt to have each forest type in the major zones.*
Volume and Density Sampling

I sampled CWD using line intercept transects (Warren 1964, Van Wagner 1966), a method for estimating CWD volume from measurements of the diameter of CWD traversed by the transect. The line transect method assumes a random orientation and distribution of CWD, as well as a random orientation of the plot. Since CWD distribution may not be random, and since plot orientation in this study was not random, transects in a single direction may introduce estimate bias (Bell 1996). To compensate for possible orientation error, I located transects perpendicular to each other in a “pin-wheel” design: each approximately 200 m transect extended from a corner of the plot (Figure 2). I established CWD transects outside of the plot to avoid disturbing the permanent plots through destructive density sampling (Baker et al. 2007, Chao et al. 2008).

I sampled Fallen CWD along the transects by measuring the diameter of branches and logs with a field tape. In cases where the CWD was partially buried, I estimated the diameter by taking the geometric mean of the horizontal diameter and vertical diameter. I then used the diameters of all CWD on a transect and the transect length estimate volume per unit area (m³ ha⁻¹) using equation 1 as specified by Van Wagner (1966).

\[ \frac{\pi^2 \sum d_i^2}{8L} \]  

(Equation 1)

All standing CWD >10m from the line transect was measured for volume. If the standing CWD was shorter than 1.37m then the height, I measured top diameter and bottom diameter. If the standing
CWD was taller than 1.37 m, I measured DBH using the field tape and measured height using a hypsometer. I estimated the top diameter using a taper function (Chambers 2000, Equation 2).

\[ d_h = 1.59DBH(h^{-0.091}) \]  

(Equation 2)

I calculated volume using Smalian’s Formula (Harmon 1986, Equation 3). To find volume per ha (m³ ha⁻¹) I summed all standing volumes per transect and then divided by the area of the transect (transect length * 20m).

\[ V = L \left[ \frac{\pi(D_1/2)^2 + \pi(D_2/2)^2}{2} \right] \]  

(Equation 3)

I recorded the decay state of both downed and standing CWD by assigning a decay class, with decay class 1 representing newly fallen wood and 5 representing rotten wood (Table 1).

Table 1. Decay Classes of CWD range from 1 least decayed to 5 most decayed.

<table>
<thead>
<tr>
<th>Decay Classes</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Solid wood, recently fallen, with intact bark and fine branches still attached.</td>
</tr>
<tr>
<td>2</td>
<td>Solid wood, but with no fine branches, and bark starting to fall off. Also applies to “hard hearts” - hard, weathered hearts that have no bark but for which the wood is still sound.</td>
</tr>
<tr>
<td>3</td>
<td>Non-solid wood, in poorer condition. The tip of a nail may go into the wood but the nail can't be pushed any further. Bark may be rotten or sloughing off.</td>
</tr>
<tr>
<td>4</td>
<td>Soft, rotten wood, a nail may be pushed into the wood past the tip, but may stop before entering completely. Easily broken when kicked. Outer bark may be case hardened. Bark may be mostly sloughed off.</td>
</tr>
<tr>
<td>5</td>
<td>Soft, rotten wood, which collapses easily when stepped on. A nail may be easily pushed into the log. Material is easily pulled apart by hand. Logs are elliptical in cross section.</td>
</tr>
</tbody>
</table>

Using a chainsaw, I cut round disks out of all fallen CWD. On the disk, I chose a random radial direction A-H in one of eight possible directions (Figure 3), and cut out 2cm samples using a machete (Keller 2004). I measured the samples for height, width and depth in the field. If a sample did not have a
sufficiently rectangular shape, then I measured volume using the displacement method (Chave 2006). For pieces that were extremely friable, I filled a container of known size with the material. I oven dried all samples at 65°C until subsequent daily weight measurements did not differ by more than 0.5%. I calculated density (g cm\(^3\)) as dry weight divided by volume.

**Necromass Calculation**

I calculated CWD necromass per ha (Mg ha\(^{-1}\)) as volume per ha (m\(^3\) ha\(^{-1}\)) multiplied by density (g cm\(^3\)). For each transect, I calculated total volume per decay class, and then multiplied by average density for that decay class. I did not measure density for standing CWD because it was not feasible to fell snags in the field. For necromass for which I did not have a measured decay class at the site, I substituted mean average density from the other transects from the same plot and for that decay class. In rarer cases, a density estimate for a given decay class did not exist for that plot. In this case, I used the average density for that decay class for the plot’s forest zone.

**Statistical Analysis**

I employed a combination of ANOVA and ANCOVA to analyze the data. I used ANOVAs to examine differences in volume, density, and necromass when considering forest zone and forest type. I used ANCOVAs to analyze relationships between volume, density and necromass and total annual rainfall and forest type. When necessary I log transformed data in order to satisfy the assumptions of normality and homoscedasticity.
Gabon does not experience large-scale blow downs and thus most CWD is due to individual tree deaths. Since all transects were separated by more than 100m, a distance greater than the height of the tallest trees, I considered each transect an independent event. Unless otherwise stated, analyses use individual transects as an independent observations.

**Spatial Model**

I created a spatially explicit estimate of CWD necromass using ESRI 10.1 software, several geospatial data layers, and a regression model of necromass on precipitation and forest type, at a pixel resolution of 300m. Annual precipitation was found for each pixel using Bioclim data. There is not a forest type data set for Gabon based on remote sensing data, so I created this layer using an “expert” approach. I used Globcover 2009 data (ESA 20010) to delineate all forested areas, removing water bodies, savannah, and developed areas. I also removed roads and villages, based on the WRI Gabon Atlas (WRI 2009). Any forested areas that were in a logging concession were considered “logged”. I defined secondary forest as any forest within 5 km of a village, or forest designated as “light” forest in Globcover. I classified any forested area remaining that was not logged or secondary as primary (Figure 14). This coarse determination of forest type does not account for forests such as swamps or seasonally flooded forest that might have different necromass characteristics.

All spatial analyses were performed using the GTM coordinate system.

**Results**

Necromass was estimated at a total of 15 sites in 5 forest zones throughout Gabon. Ten of these sites were measured for both volume and density, whereas five sites were measured for volume only. A total of five plots were in primary forest, four were in secondary forest, and six were in logged forest (Table
5). We measured CWD along 10,390 meters of transects, with a minimum of 400 and a maximum of 2396 meters for forest zone/forest type combination (Table 6).

**Density**

We extracted 531 wood samples from 184 pieces of CWD. Mean and median density (g cm\(^{-3}\)) decreased in more decayed material (higher decay class) as expected (Figure 4, Table 2). All decay classes had highly variable density, with standard deviation increasing as decay class increased. Decay class 1 showed the least variability, probably because of the small number of samples for this class (n=10 from 3 pieces of CWD).

![Figure 4. Box plots of CWD density by decay class (as defined in Table 1). As decay class increased (i.e. wood is more decayed) mean density decreased.](image)

**Table 2. Summary statistics for each decay class. Mean and median density decreased as material was more decayed, while standard deviation increased.**

<table>
<thead>
<tr>
<th>Class</th>
<th>Mean Density ((g \text{ cm}^{-3}))</th>
<th>Median Density ((g \text{ cm}^{-3}))</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.56</td>
<td>0.56</td>
<td>0.07</td>
</tr>
<tr>
<td>2</td>
<td>0.44</td>
<td>0.43</td>
<td>0.17</td>
</tr>
<tr>
<td>3</td>
<td>0.41</td>
<td>0.39</td>
<td>0.16</td>
</tr>
<tr>
<td>4</td>
<td>0.36</td>
<td>0.34</td>
<td>0.17</td>
</tr>
<tr>
<td>5</td>
<td>0.34</td>
<td>0.29</td>
<td>0.21</td>
</tr>
</tbody>
</table>
not significantly different from one another, although densities of non-adjacent decay classes differed significantly (ANOVA, $F=8.0$, $df=4,526$, $p<0.001$). Mean density of CWD by decay class was significantly lower in Continental-Mixed forest and Mixed-Tropical forest than in Hyperhumid-Sedimentary Basin (Table 3, ANOVA, $F=8.78$, $df=3,507$, $p<0.001$), and did not differ among other forest zones.

Mean density was significantly different between primary forest and secondary forest (ANOVA, $F=8.68$, $df=2,528$, $p<0.001$) but was not different between primary and logged, or between secondary and logged forest.

Density varied significantly with precipitation by decay class and forest type ($R^2=0.11$, $F=9.53$ $df = 7,523$, $p < 0.001$). Density varied significantly with decay classes 2, 3, and 4, with density decreasing by -0.006 (g cm$^{-3}$), -0.0099 (g cm$^{-3}$), and -0.0097 (g cm$^{-3}$) respectively for each 100mm increase in annual precipitation (Table 4). Decay class 2 and 3 have the strongest relationship to precipitation ($p = 0.003$ and $p < 0.001$), while decay class 4 has a slightly less significant relationship ($p = 0.005$). Decay class 5 has only a moderate relationship with precipitation ($p = 0.06$). Decay class 1 was found for only three pieces of CWD, so no regression with precipitation was run.

Density (g cm$^{-3}$) had significant relationships with diameter and distance from diameter after controlling for decay class. Density increased by

<table>
<thead>
<tr>
<th>Decay Class</th>
<th>Change Precip (100mm yr$^{-1}$)</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>2</td>
<td>-0.0061</td>
<td>0.0026</td>
</tr>
<tr>
<td>3</td>
<td>-0.0099</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>4</td>
<td>-0.0097</td>
<td>0.0054</td>
</tr>
<tr>
<td>5</td>
<td>0.0083</td>
<td>0.0609</td>
</tr>
</tbody>
</table>

Table 3. The relationship between CWD density (g cm$^{-3}$) and precipitation, by decay class. Density decreased with increasing precipitation, and significance decreased with increasing decay class.

Table 4. CWD density was significantly affected by decay class, forest zone, forest type and the interaction between decay class and forest type. Note that the interaction between decay class and forest type was marginally significant, with a relative low effect size.
0.002 (g cm\(^{-3}\)) for each additional cm in diameter, and decreased by 0.003 (g cm\(^{-3}\)) for each additional cm from the center. Density did not have a relationship with radial direction in general, however samples in direction F or D did have a significant relationship, with density increasing by 0.08 (g cm\(^{-3}\)) above samples from direction A.

**Volume and Necromass**

We measured a total of 468 snags and 521 downed pieces of CWD. Plot level volume of CWD ranged from 20.17 m\(^3\) ha\(^{-1}\) in dryer secondary forest, to 265.18 m\(^3\) ha\(^{-1}\) in wetter, logged forest, while mean plot necromass ranged from 11.49 Mg ha\(^{-1}\) to 111.91 Mg ha\(^{-1}\) (Table 5). Standing volume ranged from 0.47 percent to 45.28 percent of total (standing plus downed) plot level volume of CWD. Standing necromass ranged from 0.42 to 46.64 percent of total plot level necromass.

Mean plot volume by forest zone and forest type ranged from 20.17 m\(^3\) ha\(^{-1}\) in secondary forest in the Continental-Mixed forest zone to 214.74 in logged forest in the Tropical-Mixed/Mountain forest zone. Mean necromass by forest zone and forest type ranged from 11.50 Mg ha\(^{-1}\) to 91.38 Mg ha\(^{-1}\) (Table 6).

When considering only forest zone, mean plot volume was lowest in the Continental-Mixed forest zone, which had 89.84 m\(^3\) ha\(^{-1}\), and highest in Hyperhumid-Sedimentary Basin forest zone, which had a mean of 202.68 Mg ha\(^{-1}\). Mean necromass varied in a similar fashion with a minimum of 43.73 Mg ha\(^{-1}\) and a maximum of 76.90 Mg ha\(^{-1}\).
Table 5. Mean CWD volume, CWD necromass, and CWD C per ha for each of the 15 plots in this study.

<table>
<thead>
<tr>
<th>Plot Number</th>
<th>Forest Type</th>
<th>Annual Precipitation (mm yr(^{-1}))</th>
<th>Total Transect Length (m)</th>
<th>CWD Volume (m(^3) ha(^{-1}))</th>
<th>CWD Necromass (Mg ha(^{-1}))</th>
<th>CWD C (Mg ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Down Standing Total</td>
<td>Down Standing Total</td>
<td>Down Standing Total</td>
</tr>
<tr>
<td>Continental-Mixed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>111 Primary</td>
<td>62.9</td>
<td>1.6</td>
<td>800</td>
<td>128.7</td>
<td>103.5</td>
<td>4.9</td>
</tr>
<tr>
<td>112 Primary</td>
<td>159.6</td>
<td>212.7</td>
<td>9.9</td>
<td>222.6</td>
<td>103.5</td>
<td>4.9</td>
</tr>
<tr>
<td>113 Primary</td>
<td>161.8</td>
<td>31.4</td>
<td>18.3</td>
<td>49.6</td>
<td>15.2</td>
<td>9.5</td>
</tr>
<tr>
<td>131 Secondary</td>
<td>176.4</td>
<td>400</td>
<td>15.8</td>
<td>20.2</td>
<td>9.3</td>
<td>2.2</td>
</tr>
<tr>
<td>Austral-Mixed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 Primary</td>
<td>1661</td>
<td>800</td>
<td>122.0</td>
<td>130.3</td>
<td>46.4</td>
<td>3.4</td>
</tr>
<tr>
<td>Tropical-Mixed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36 Logged</td>
<td>1897</td>
<td>800</td>
<td>173.8</td>
<td>182.1</td>
<td>74.5</td>
<td>3.3</td>
</tr>
<tr>
<td>37 Primary</td>
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</tr>
<tr>
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<tr>
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Table 6. Mean CWD Volume, CWD Necromass and CWD Carbon per ha by Forest Zone and Forest Type

<table>
<thead>
<tr>
<th>Forest Type</th>
<th>Annual Precipitation (mm yr(^{-1}))</th>
<th>Total Transect Length (m)</th>
<th>CWD Volume (m(^3) ha(^{-1}))</th>
<th>CWD Necromass (Mg ha(^{-1}))</th>
<th>CWD C (Mg ha(^{-1}))</th>
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<td>Down Standing Total</td>
<td>Down Standing Total</td>
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<td></td>
</tr>
<tr>
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</tr>
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<td></td>
</tr>
<tr>
<td>Primary</td>
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<tr>
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<td>1155</td>
<td>128.7</td>
<td>13.7</td>
<td>142.4</td>
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</table>
Table 7. Mean CWD Volume, CWD Necromass and CWD Carbon per ha by Forest Zone.

<table>
<thead>
<tr>
<th>Forest Zone</th>
<th>Annual Precipitation (mm yr(^{-1}))</th>
<th>Total Transect Length (m)</th>
<th>CWD Volume (m(^3) ha(^{-1}))</th>
<th>CWD Necromass (Mg ha(^{-1}))</th>
<th>CWD C (Mg ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>Down Standing Total</td>
<td>Down Standing Total</td>
<td>Down Standing Total</td>
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<tr>
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<tr>
<td>Austral-Mixed</td>
<td>1661</td>
<td>800</td>
<td>122.0 8.3 130.3</td>
<td>46.4 3.4 49.8</td>
<td>1.6 21.8 23.4</td>
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<td>2350</td>
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<tr>
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<td>2000</td>
<td>184.7 18.3 203.0</td>
<td>69.9 7.0 76.9</td>
<td>3.3 32.9 36.1</td>
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</tbody>
</table>

Min 1646 800 81.4 4.0 89.8 39.4 1.5 43.7 0.7 18.5 20.7
Max 3020 2841 184.7 32.0 203.0 69.9 14.0 83.5 6.6 32.9 39.2
Mean 2021 2078 140.5 14.2 154.7 57.4 6.1 63.5 2.8 27.0 29.8

Logging & Precipitation

Mean volume varied significantly between for Continental-Mixed and Hyperhumid-Sedimentary Basin forest zones (ANOVA, \(F=2.851, df=4,51, p = 0.03\)) and for interaction for Continental-Mixed secondary forest and Hyperhumid-Sedimentary Basin secondary forest (ANOVA, \(F=4.096, df=2,51, p=0.02\)). There was no significant difference for forest type; however mean volume was significantly different for forest zone and forest type interaction for secondary forests in Continental-Mixed and Hyperhumid-Sedimentary Basin forest zones (ANOVA, \(F=4.096, df=2,51, p=0.02\)). Mean necromass was only moderately different for Continental-Mixed and Hyperhumid-Sedimentary Basin forest zones (ANOVA, \(F=2.237, df=4,51, p=0.08\)), and forest zone and forest type interaction is only moderately significant for secondary forests in Continental-Mixed and Hyperhumid-Sedimentary Basin forest zones (ANOVA, \(F=3.0804, df=2,51, p=0.08\)).

Volume had a significant relationship with precipitation \(R^2 = 0.13, F=2.678, df=3,56, p=0.03\), increasing by 0.09 Mg ha\(^{-1}\) per 100mm of rainfall, but did not have a significant relationship with forest type.

Necromass was only moderately related to annual precipitation \(R^2 = 0.10, F=1.98, df=3,56, p = 0.07\) and was not related to forest type. Adding geology as a factor to either model causes only geology to be
significant, while including interaction terms to either model causes the coefficients and variable significance to change considerably.

Only one forest zone (Tropical-Mixed) in this study had both logged and primary sites. Due to a low sample size ($n_{\text{logged}} = 13$, $n_{\text{primary}} = 4$), and unequal variances, a bootstrap permutation test was performed (Ho: Primary < Logged). The permutation test supported the hypothesis ($p=0.041$) that logged sites have higher necromass than unlogged sites, within the Tropical-Mixed forest zone.

**Spatial Estimate of Necromass**

To estimate necromass at the national level, we extrapolated our results to unsampled areas using precipitation and forest type. Average necromass for the study, multiplied by the forested area of Gabon yields an estimate of 0.72 Pg C stored in CWD. Doing the same procedure with minimum and maximum estimates of plot-level CWD provides upper and lower estimates of 1.25 Pg C and 0.34 Pg C for Gabon. The spatial estimate based on the best fitting regression model of precipitation and forest type predicted about half of the average value, 0.34 Pg C.

**Discussion**

CWD necromass has high local variation, in one case ranging from $14.7 \text{ Mg ha}^{-1}$ to $247.6 \text{ Mg ha}^{-1}$ within the space of a several hundred meters. Over wider extent CWD density and volume show correlations with precipitation. CWD density and volume are also broadly affected by forest type; secondary forests have different density than primary and logged forest, and logged forest has higher volume than unlogged forest. These relationships can be used to predict the spatial distribution of CWD necromass over a broad geographic area.
Density

Wood decay is a continuous process and is often modeled as an exponential decay function (Olson 1963). The division of CWD into decay classes is standard CWD density estimation methodology (Harmon 1986, Ståhl 2001, Clark 2002, Keller 2004, Chao 2008) but is somewhat arbitrary. It is not a surprise that most studies, including this one, find that adjacent decay classes do not have significantly different densities, while non-adjacent decay class densities are significantly different.

Large scale east to west density gradients exist in the Amazon (Baker et al. 2004). My results provide evidence for a CWD density gradient in Gabon, with increasing CWD density from west to east, following the principal precipitation gradient. Barajas-Morales (1987) and Chave (2006) found that areas of low rainfall had higher average tree density, whereas areas of high rainfall had lower average density. This may also be the case across Gabon’s rain gradient. My results show that necromass that is less decayed has a stronger relationship with annual precipitation than necromass that is more decayed, with the density of the original input material likely reflecting the live tree density. This relationship is then disrupted in more decayed wood by the stochastic decay process in which the presence of decomposers, soil moisture, and structural properties override any relationship with initial live tree density (Harmon 1986).

Mean density per decay class was significantly different between primary and secondary forest types. Secondary forests contain pioneer species that have lower wood density than species characteristic of primary forests. This density difference is likely reflected in CWD density as well. Chao (2008) found that CWD density was significantly related to basal area weighted live tree density. My results show that primary and logged forests do not have significantly different CWD pool densities. Selective logging removes targeted species from the forest, but does not bias its collateral damage towards any particular
species. It follows that primary and logged forests would not have significantly different CWD density, assuming the logging activity had taken place in a primary forest. My results support this. Surprisingly, however, logged forest density was not significantly different from secondary forest density.

My results show that the density of individual CWD samples is related to both the diameter of the CWD and the distance of the sample to the center of the CWD. Respiration is a major cause of log decay (Chambers et al. 2001), and logs with a low surface to volume ratio show slower decay (Hérault et al. 2010) as the interiors of these logs are less accessible to decomposers, water, and gas exchange. In addition, many tropical species have extremely dense heartwood and softer sapwood. Logs have been shown to decay more quickly when they are in contact with the ground, as detritivores have easier access to the material, which leads to the hypothesis that the underside of a log is most likely more decayed than the top of the log. Keller (2004) found that density was related to radial direction. However, similar to our findings for Gabon, Palace (2007) found that wood density was not related to radial direction of logs.

Volume and Necromass

All other factors being equal, higher precipitation areas are generally more productive than lower precipitation areas. My results show that the CWD volume also exhibits this trend, with the lowest volumes found in low precipitation forest and the highest volumes found in high precipitation forest.

Necromass (Mg ha\(^{-1}\)) was highly variable even between transects of the same plot (Figure 5). The plot with the most intertransect variability, for example, had necromass of 14.7 Mg ha\(^{-1}\) on one transect, and 247.6 Mg ha\(^{-1}\) on another transect several hundred meters away. Gabon does not experience large scale blow downs or clear-cuts, so most CWD is the result of individual tree death or selectively felled trees.
The stochastic nature of these events is reflected in the high variability of transect level necromass – fallen large trees will contribute disproportionately to the level of necromass of a transect. When forest type is considered, average standard deviation is higher at the transect level for logged sites than for unlogged sites.

All primary forest plots in this study were concentrated in low precipitation areas (ranging from 1596 to 1908 mm yr\(^{-1}\)), limiting my ability to compare high rain and low rain primary forest. Plots in logged sites were more spread across the gradient (ranging from 1644 to 3122 mm yr\(^{-1}\)), and these plots do show an increasing volume with increasing rainfall (Figure 6). However, the relationship between logging and precipitation is confounded by the time since the site was logged, and how intensely the site was logged, as the different logging practices can have variable impact on the CWD pool (Keller 2004).

Forest zones are large scale divisions of the country comprised of precipitation, geology, and terrain characteristics. These divisions are somewhat arbitrary, as the forests at this scale are continuous without strong ecotones. It is not surprising that volume for adjacent forest zones were not significantly different from each other, but volume for the two zones at opposite ends of the gradient were significantly different from each other.

Interestingly, volume was more strongly related to precipitation than necromass. Volume and density are the two components of necromass, and both of these components showed significant relationships with precipitation. As precipitation increased, density decreased while precipitation increased. So, these two relationships worked against each other, resulting in necromass that was only moderately related to precipitation.
Logging

When plotted against precipitation, a separation of necromass between logged sites and primary sites is detectable (Figure 6), with the clearest separation occurring between plots 36 and 37, both of which are in the Tropical-Mixed forest zone and are only 12 kilometers from each other. Indeed, a bootstrap t-test of necromass in this forest zone revealed that logged sites have significantly higher necromass than unlogged sites ($p = 0.04$).

Figure 5. Necromass was highly variable among transects, even in the same plot. Necromass appears to be more variable in logged forest than in other forest types.
Figure 6. Mean plot necromass plotted against annual precipitation. A separation between necromass in primary sites and necromass in logged sites is detectable.

Comparison to Other Studies

The two African CWD studies, Djomo et al. (2011) and Gautam & Pietsch (2012), and most Amazonian studies of CWD have been conducted in primary forest (Chao et al. 2009). A comparison of mean primary forest plots by forest zone from this study to those studies reveals that necromass tends to be on the higher side, even though most primary plots are located in low precipitation areas (Figure 7). The largest reported CWD pool in the Amazon was hypothesized to be recovering from a drought (Rice et al. 2004). In this study, if secondary forests are included, the necromass pool in the Hyperhumid zone is nearly as high as the one reported by Rice et al. African tropical forests have fewer stems on average but the trees are generally larger. Chao (2009), using 53 plots from all published Amazon CWD studies, found that the most important factor to the size of the CWD pool was the size of the piece of CWD (i.e.
“mortality mass input”). The larger size of African trees may be contributing to a larger CWD pool than comparable Amazonian sites.

![Primary Forest Necromass](image)

Figure 7. Comparison of primary forest necromass among Amazon studies, other African studies, and this study. Primary forests in this study had high necromass but were in low rainfall areas in Gabon. Hyperhumid-Sedimentary Basin forest is secondary, but has CWD nearly as high as the area studied by Rice (2004).

There are few estimates of CWD in logged sites in tropical systems. In Cameroon, Djomo compared measured logged plots in “managed forest” and found average necromass for logged sites to be higher than average necromass for primary sites. In sites impacted by RIL logging in Amazonia, Keller et al. (2004) and Palace et al. (2007) found significantly higher necromass than in comparable undisturbed sites and necromass value similar to this study (Figure 8).
Spatial Estimate of Necromass

A simple estimate of total carbon stored in CWD, based on the multiplying the average of all plot-level necromass and the total forested area of Gabon is 0.72 Pg C. This average method is somewhat similar to the approach taken by Chao et al. (2009). To my knowledge, only Chao et al. (2009) provide a regional estimate of the carbon in CWD through a meta-analysis of field studies. In the study Chao et al. averaged plot level necromass by amazon region (NE, E, NW, SW and S), and then multiplied by the total “tropical forest” area of the region as defined by the FAO 2000 report, resulting in a total of 9.6 Pg C over an area of $5.83 \times 10^6$ km$^2$. Relativized by area, this is 16.5 Mg C ha$^{-1}$. This result is about half of the per ha estimate for Gabonese CWD carbon using the averaging approach (30.1 Mg C ha$^{-1}$), but is comparable to the spatial modeled estimate at 14.2 Mg C ha$^{-1}$ (Figure 9).
Limitations

An important limitation to this study is in the distribution of plots. Since my study was part of a larger carbon inventory study, I was not able to pick the placement of the plots and did not have a strong
influence on the order that plots were established and CWD measured. Thus, the plots are unevenly distributed over the country, and this may have important impacts on my results. All forest zones are not evenly weighted with plots of each forest type. Plots in primary forest tend to be in low rainfall areas, which plots in logged forest are in higher rainfall areas. Since I have shown that necromass is higher in logged areas, this may make the relationship with precipitation stronger than it appears.

There are also uncertainties associated with both the averaging approach and the model approach to necromass estimation. The averaging approach ignores areas such as swamp forest, mangrove, or floodplain that might have an impact on the estimates, and may weigh the effects of logging incorrectly, depending on the ratio of logged to unlogged area. The model result also has uncertainties. Possibly due to uneven distribution of plots over the country, the relationship between necromass and precipitation and forest type is not a strong one. Due to the fact that regional data on forest degradation is difficult to collect (Asner et al. 2005) and is not available for Gabon, the forest type layer had to be made based on the location of logging concessions and villages. For example, all logging concessions are considered to have a logged forest type, although location in a concession does not necessarily mean that an area has been logged. As more data is added to this study, the relationships between necromass and precipitation and forest type are likely to strengthen, and the model is likely to produce more robust results.

**Conclusion**

Linking CWD pool size to physical gradients and land-use types is an important step in scaling-up studies of forest carbon (Chao 2009). Here, I present relationships with two such factors: precipitation and forest type, which is comprised of primary, secondary, and logged forest. These relationships allow for estimation of CWD that is both fine grained (300m) and of broad extent.
Central African forests tend to have higher CWD pools than Central African forests. The forests in Central African are known to have larger trees than comparable Neotropical forests, and large tree inputs are known to increase the size of the CWD pool (Chao 2009). This larger input into the CWD pool may be a leading cause of a larger Central African CWD pool size.

**Acknowledgements**

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References


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Figure 10. Plot configuration for the Gabonese National Carbon Inventory. Each plot is randomly located inside of a grid square.
Figure 11. Gabon has a strong east to west precipitation gradient.
Figure 12. Gabon is densely forested, retaining 85% of its original forest cover.
Figure 13. Gabon has 11% of its country protected as forested area, and a large percentage of its area committed to logging concessions.
Figure 14. Forest type was derived based on Globcover, land use, and administrative data. All non-forested areas (savanna, developed area, roads, villages, and water bodies) were removed. All area in logging concessions was assumed to be logged. Areas 5km from village and area classified as “light” forest is secondary. Anything not logged or secondary was considered primary.