BIOMASS ESTIMATION AND CARBON STORAGE IN MANGROVE FORESTS OF TANZANIA

BY

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY OF SOKOINE UNIVERSITY OF AGRICULTURE, MOROGORO, TANZANIA

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EXTENDED ABSTRACT

This study aimed to develop tools for biomass estimation and quantify carbon stored in mangrove forests of Tanzania mainland. The study was carried out in four sites along the Tanzanian coastline; Pangani, Bagamoyo, Rufiji and Lindi-Mtwara. A total of 120 plots were measured along transects running perpendicular to sea/rivers. From each plot, one tree was destructively sampled for aboveground biomass. Thirty among 120 trees were sampled for belowground biomass. Data analysis was carried out in R software. Procedures for quantification of belowground biomass for *Avicennia marina* (Forssk.) Vierh, *Sonneratia alba* J. Smith and *Rhizophora mucronata* Lam. were documented in detail. Root sampling is recommended for *A. marina* and *S. alba* while for *R. mucronata*, total root excavation method may be applied. The methods are more comprehensive than previously reported methods, therefore they should be applied in quantification of BGB. The study found an overall mean tree aboveground basic density of 0.60±0.00 (SE) g cm$^{-3}$, 0.54 ± 0.01 (SE) g cm$^{-3}$ and 0.69 ± 0.01 (SE) g cm$^{-3}$ for *A. marina*, *S. alba* and *R. mucronata*, respectively. Similarly, the overall mean tree belowground basic density was 0.57 ± 0.02 (SE) g cm$^{-3}$, 0.32 ± 0.01 (SE) g cm$^{-3}$ and 0.53 ± 0.02 (SE) g cm$^{-3}$ for *A. marina*, *S. alba* and *R. mucronata*, respectively. The study also showed that basic density varied between species, tree sizes and tree components. Accordingly, if properly determined and applied, basic density may be useful as a conversion factor and yield accurate biomass estimates. Otherwise they are likely to be a source of uncertainties in biomass estimation. Common (multi-species) and species-specific above- and belowground biomass models for the three mangrove species were developed.
Species-specific models had better fit than common models. Evaluation of existing biomass models on data from this study generally showed large and significant prediction errors. Possibly this may be due to application of the models beyond data size ranges, geographical locations, and differences in forest structure and tree architecture. Species-specific models from this study are therefore recommended. The use models to unrepresented species is not recommended, where necessary however a conservativeness principle (i.e. when accuracy of estimates cannot be achieved, the risk of over- or under-estimation should be minimised) need to be applied. Using biomass models from this study and forest inventory data collected by National Forest Resources Monitoring and Assessment (NAFORMA) of Tanzania, the study quantified aboveground carbon (AGC), belowground carbon (BGC) and total carbon (TC) stored in mangrove forests of Tanzania mainland. Results showed that, AGC, BGC and TC were 33.5 ± 5.8 Mg C ha⁻¹ (53% of TC), 30.0 ± 4.5 Mg C ha⁻¹ (47% of TC) and 63.5 ± 8.4 Mg C ha⁻¹ respectively. Given that, mangroves of Tanzania mainland cover approximately 158, 100 ha, a total of 10.0 millions Mg C (i.e. 37.2 millions Mg CO₂e) is stored in mangrove forests of Tanzania. Results from this study are essential for REDD+ initiatives and provides useful input in management of mangrove forests in the country.
THESIS ORGANIZATION

This thesis begins with an extended abstract followed by declaration statement, copyrights statement, acknowledgements, and dedication. The extended abstract summarises briefly the study objectives, approaches to sampling, main findings conclusions and recommendations. The thesis also consists of three chapters. The first chapter cover introduction which include, background information, problem statement and study objectives. Conceptual and theoretical framework of the study are also included in Chapter one. Besides chapter one includes methods sub-section which provide descriptions of the study area, sampling, and data analysis. Chapter two presents in summary the major findings, conclusion and recommendations. Chapter three contains a series of original published papers (Paper 1 and Paper 3) and publishable manuscripts (Papers 2 and Paper 4).
DECLARATION

I, MARCO ANDREW NJANA, do hereby declare to the Senate of Sokoine University of Agriculture that, this thesis is my own original work, done within the period of registration and that it has neither been submitted nor being currently submitted in any other institution.

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Prof. T. Eid                             Date
(Supervisor)
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DEDICATION

This work is dedicated to God almighty; my dear wife, Grace; daughter, Precious; son, Savio and to the memories of my late brother, Raphael.
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<tr>
<td>AGB</td>
<td>Aboveground Biomass</td>
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<td>AGC</td>
<td>Aboveground Carbon</td>
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<tr>
<td>ANCOVA</td>
<td>Analysis of Covariance</td>
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<td>BD</td>
<td>Basic Density</td>
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<tr>
<td>BGB</td>
<td>Belowground Biomass</td>
</tr>
<tr>
<td>BGC</td>
<td>Belowground Carbon</td>
</tr>
<tr>
<td>C</td>
<td>Carbon</td>
</tr>
<tr>
<td>CO₂</td>
<td>Carbon dioxide</td>
</tr>
<tr>
<td>DF-ratio</td>
<td>Dry to fresh weight ratio</td>
</tr>
<tr>
<td>FAO</td>
<td>Food and Agriculture Organisation of the United Nations</td>
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<tr>
<td>GHGs</td>
<td>Green House Gases</td>
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<tr>
<td>GLM</td>
<td>General Linear Model</td>
</tr>
<tr>
<td>GWD</td>
<td>Global Wood Density database</td>
</tr>
<tr>
<td>ha</td>
<td>Hectare</td>
</tr>
<tr>
<td>IPCC</td>
<td>Intergovernmental Panel on Climate Change</td>
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<tr>
<td>LMM</td>
<td>Linear Mixed-Effects Model</td>
</tr>
<tr>
<td>Mg</td>
<td>Mega gram</td>
</tr>
<tr>
<td>MNRT</td>
<td>Ministry of Natural Resources and Tourism</td>
</tr>
<tr>
<td>MPE</td>
<td>Mean Prediction Error</td>
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<tr>
<td>MRV</td>
<td>Monitoring, Reporting and Verification</td>
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<tr>
<td>NAFORMA</td>
<td>National Forest Resources Monitoring and Assessment</td>
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<tr>
<td>NLME</td>
<td>Nonlinear Mixed-Effects Model</td>
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<td>Acronym</td>
<td>Description</td>
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<tr>
<td>REDD+</td>
<td>Reduce Emissions from Deforestation and forest Degradation</td>
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<tr>
<td>RMSE</td>
<td>Root Mean Squared Error</td>
</tr>
<tr>
<td>SE</td>
<td>Standard Error of a mean</td>
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<tr>
<td>STD</td>
<td>Standard Deviation</td>
</tr>
<tr>
<td>SUA</td>
<td>Sokoine University of Agriculture</td>
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<tr>
<td>TB</td>
<td>Total Biomass</td>
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<tr>
<td>TC</td>
<td>Total Carbon</td>
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<tr>
<td>UNFCCC</td>
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DECLARATION OF THE PAPERS

I, Marco Andrew Njana, do hereby declare to the Senate of Sokoine University of Agriculture that the above listed papers comprising this thesis, summarise my independent efforts and they constitute my own original work and they will not be part of another thesis in any other University.
CHAPTER ONE

1.0 INTRODUCTION

1.1 Background information

Mangroves are forests found in the tropical and sub-tropical coastlines between 30° South and North of Equator (FAO, 2007; Spalding et al., 2010). In Africa, mangroves grow naturally both at the western and eastern coasts. At the eastern coast of Africa, 14 mangrove species are growing naturally, and 10 among these are found in Tanzania. *Avicennia marina* (Forssk.) Vierh, *Sonneratia alba* J. Smith and *Rhizophora mucronata* Lam. are the three most dominant mangrove species in Tanzania (MNRT, 1991; Luoga et al., 2004; Nshare et al., 2007).

Mangroves are an important and productive ecosystem. Among other functions, mangroves store carbon and sequester CO$_2$ (e.g. Donato et al., 2011; Kauffman et al., 2011) hence plays an important role in regulating global climate (UNEP, 2014). Mangroves are also important for biological (e.g. wildlife habitat, Nagelkerken et al., 2012), ecological (e.g. nutrient cycling, Kristensen et al., 2008), economic (e.g. timber provision, Spalding et al., 2010) and protection (e.g. protection against tsunamis, Zhang et al., 2012) reasons.

Despite their importance, mangroves are threatened by deforestation and forest degradation, which led to a loss of 35% of the World’s mangrove cover between 1980 and 2000 (Valiela et al., 2001; Langner et al., 2007). In Tanzania, mangrove declined from 109,593 ha in 1990 to 108,138 ha in 2000 (Wang et al., 2003) which is
equivalent to deforestation rate of 145.5 ha per year. The annual deforestation rate is likely to be higher than that due to uncertainties of Landsat imageries applied by Wang et al. (2003). Anthropogenic factors are the main causes for decline of mangrove covers in Tanzania (Bryceson, 1981; Semesi, 1992; Wang et al., 2003; Mangora, 2011) and in different parts of the world (FAO, 2007).

Deforestation and forest degradation result into emissions of CO$_2$ which contribute to climate change, loss of carbon sequestration capacity and loss of other ecosystem goods and services. Jointly, deforestation and forest degradation account for about 12% of total annual anthropogenic emissions of CO$_2$ (van der Werf et al., 2009).

Initiatives to manage mangroves sustainably exist. For example, in Tanzania mangroves are legally declared as forest reserves (MNRT, 1991; URT, 2002). National Forest Policy also clearly states that, foster management of forest resources including mangroves aims to improve both forest conditions and livelihoods (URT, 1998). Management planning of mangrove forests is an important step towards achieving their sustainable management. Information on quantity and quality of mangrove forest resources is an essential input in the planning process. In Tanzania management plans for mangrove forests have been developed (MNRT, 1991; Semesi, 1992), such plans however are out-dated. Updating or development of new management plans is therefore argent.

Similarly, there are global initiatives aiming at mitigation and adaptation on impacts of climate change. Such initiatives include REDD+ (Reduce emissions from
deforestation and forest degradation). REDD+, a system of financing mechanisms and incentives aiming at mitigating climate change by reducing deforestation and forest degradation through sustainable management of forests, conservation and enhancement of carbon stocks (Angelsen and Hofstad, 2008; UNFCCC, 2011).

REDD+ therefore offer an opportunity for conservation and management of forests including mangroves. Successful implementation of REDD+ relies on robust capabilities of participating countries, including Tanzania, to routinely and reliably monitor changes of forest area, carbon stocks and associated greenhouse gas emissions through establishment of a Monitoring, Reporting and Verification (MRV) system (Hewson et al., 2013). In line with this, Tanzania has, under the National Forest Resources Monitoring and Assessment (NAFORMA) program, established permanent sample plots which will be monitored over time (URT, 2010).

Effective MRV system requires that carbon stocks and change be done in a consistent, complete and transparent manner. This should consider five carbon pools, i.e. aboveground biomass (AGB), belowground biomass (BGB), dead wood, litter and soil organic matter (IPCC, 2003). Biomass can be quantified in different ways, but most commonly by applying a biomass model to forest inventory data leading to single tree or stand level estimates. Biomass models, based on allometric theory, relating easily measurable tree variables such as diameter at breast height (dbh) and total tree height (ht) to biomass, are considered to be the most efficient tools for tree level biomass prediction (Brown, 1997; Chave et al., 2014). Development of biomass models requires destructive sampling of trees, where above- and belowground
biomass are determined from harvested trees. Fresh weights of the sample trees are measured in field, and subsequently dry weights are determined using the dry to fresh weight ratio (DF-ratio) derived from oven dried sub-samples. Aboveground biomass usually refers to stem, branch and foliage while belowground biomass refers to all live roots down to 2 mm in diameter (IPCC, 2006).

Data for the MRV system of carbon stocks are organised into three hierarchical tiers; tier 1 where estimates are based on IPCC default values, tier 2 where estimates are based on regional or country specific values and tier 3 where estimates are based on country- and forest specific values (IPCC, 2003). Estimation of mangrove carbon stocks at tier 2 or 3 will help Tanzania to benefits more from the global carbon mitigation strategies such as REDD+ and hopefully contribute to conservation and sustainable management of mangroves in the country. Such estimates are useful for proper management decisions and actions on mangrove forests since our ability to prioritise conservation and restoration efforts relies on accurate information on carbon stocks (Keith et al., 2009).

1.2 Problem statement

Information on carbon stocks is important in order to support management of mangrove forests in Tanzania through REDD+ initiatives. Within the REDD+ framework, it is emphasised that, all sources of uncertainties in carbon estimates should be minimised as much as possible (IPCC, 2006).

Quantification of carbon stocks by means of biomass models may be considered efficient and accurate because they relate biomass and easily measurable tree
parameters (e.g. diameter at breast height, measured through forest inventories) based on allometric theory (Small, 1996; Niklas, 2006).

AGB and BGB models for mangrove forests have been reported in literature. A review by Komiyama et al. (2008) identified 13 species-specific and two common (i.e. multi-species) AGB models for mangroves, while nine species-specific models and one common model were identified for BGB. Additional studies on mangroves that developed models for prediction of biomass not present in this review also exist (e.g. Kairo et al., 2009; Kauffman and Donato, 2012; Sitoe et al., 2014). With the exception of the models developed by Kairo et al. (2009) in Kenya and Sitoe et al. (2014) in Mozambique, most of the models have been developed for mangroves in Asia.

The relatively few studies on BGB of mangroves are obviously due to the diverse and complex nature root systems for mangrove species coupled by the difficult and tedious working conditions. In attempts to quantify BGB, a number of different excavation methods have been applied.

Methods where the link between BGB and tree variable is possible include trench method (e.g. Komiyama et al., 1987), root ball method (e.g. Comley and McGuinness, 2005), pull up method (e.g. Tamai et al., 1986) and total excavation (Ong et al., 2004). However, for all these methods not all BGB is sampled. For example, for the root ball method, only roots within 2 m radius around a sample tree is sampled.
Similarly, review of studies on BGB of mangroves revealed that both excavation procedures and procedures for determining dry weight quite often are imprecisely or insufficiently documented. Many studies for example failed to mention whether the DF-ratios are based on average of the sub-samples, from the whole tree, from all belowground parts only or from different root components (e.g. root crown, roots, above- and belowground stilt roots) (e.g. Komiyama et al., 1987). It is obvious that if conversion of fresh to dry weight is not done appropriately, the final estimates of belowground biomass are subject to uncertainty.

Based on previous studies, uncertainties are likely to occur at each of the following stages of biomass quantification: (i) sampling design, (ii) field measurements, (iii) tree level estimates, (iv) selection of biomass model and (v) selection of basic density values when used as a biomass predictor variable (Ketterings et al., 2001; Chave et al., 2004; Henry et al., 2010; Clark and Kellner, 2012; Roxburgh et al., 2015).

Similarly, uncertainties may occur in the use of basic density as a volume to biomass conversion factor (IPCC, 2006). For example, guidelines for destructive sampling of trees suggest that, for large trees, dry weight may be derived by determining volume in the field and subsequently multiply with basic density (BD) (i.e. indirect method) (Brown, 1997; Picard et al., 2012). However, the accuracy of determining tree AGB using indirect method is unknown. Extraction of sub-samples from sample trees for determination of basic density without knowledge on how basic density varies between species, among individuals of the same species and between sites is likely to introduce uncertainties when such values are applied for volume to biomass
conversion factor or predictor variable. Literature on basic density and its variation
for mangrove species is scarce and the sources of variation are hardly documented.
Adedeji et al. (2013) however, reported BD variations from pith to bark and along
stem for Rhizophora racemosa GFW Meyer in Nigeria.

Since no biomass models for mangroves of Tanzania, models reported in literature
may be applied. However if models developed elsewhere are applied to quantify AGB
and BGB of mangroves in Tanzania, they would be used beyond their spatial validity
hence uncertainty to relevant estimates. It is important that models are used within
valid ranges in terms of geographical location, species and tree size. Models
calibrated on data from other regions are therefore more likely to violate these
requirements and subsequently hamper tier 2 and 3 biomass estimation.

It could be worthy applying the mangrove AGB models from neighbouring countries
of Kenya (Kairo et al., 2009) and Mozambique (Sitoe et al., 2014). However both are
based on data from a single site, limited sample size (e.g. n = 5, Kairo et al., 2009, n
= 31 for six species, Sitoe et al., 2014) and limited tree size ranges (dbh up to 42 cm,
Sitoe et al., 2014). Therefore the standard procedure of testing the applicability of
such models using local data is essential.

Due to lack of biomass models for mangroves in Tanzania, generic and indirect
procedures have been applied by NAFORMA to quantify biomass and carbon stocks
for mangroves in the country (MNRT, 2015). NAFORMA results showed that,
mangrove forests of Tanzania stored about 11.5 Mg C ha\(^{-1}\) and 3.2 Mg C ha\(^{-1}\) as
aboveground carbon (AGC) and belowground carbon (BGC) stocks respectively. AGB was estimated by initially estimating volume using generic models followed by conversion of volume to dry weight using BD (MNRT, 2015). Similarly, BGB was estimated using root to shoot ratio (RS-ratio). Generic and indirect procedures as applied by NAFORMA are likely to yield uncertain estimates hence inaccurate decisions pertaining management of mangroves.

In order to support management of mangrove forests through REDD+ initiatives, this study aimed to develop tools for biomass estimation and determine the amount of carbon stored by mangrove forests in Tanzania. Such tools included AGB and BGB models for quantification of carbon stocks using forest inventory data (Paper 3). The biomass models facilitate non-destructive measuring and reporting of carbon stocks for REDD+. Besides comprehensive procedures for quantification of BGB were documented in detail (Paper 1). BD and uncertainties in biomass estimation were also determined (Paper 3). The study also estimated carbon stock using models developed in this study (Paper 4). The use of these biomass models reported recently to quantify carbon stocks provided relatively more accurate information necessary for REDD+ and support conservation and sustainable management of mangroves in the country.
1.3 Study objectives

1.3.1 Main objective
The main objective of this study was to develop tools for biomass estimation and subsequently quantify carbon stored in mangrove forests of Tanzania mainland.

1.3.2 Specific objectives
To achieve the main objective, four specific objectives were addressed. Each specific objective comprised a full length paper. Objectives (i), (ii) and (iii) focused on the three dominant species in Tanzania.

(i) To document procedures for quantification of belowground biomass of three mangrove tree species (Paper 1).

(ii) To determine tree basic density and uncertainties in biomass estimation (Paper 2).

(iii) To develop above- and belowground tree biomass models (Paper 3).

(iv) To quantify carbon storage in mangrove forests of Tanzania (Paper 4).

1.4 Conceptual and theoretical framework of the study
Despite their importance, mangroves are threatened by deforestation and forest degradation, which led to a loss of 35% of the World’s mangrove cover between 1980 and 2000 (Valiela et al., 2001; Langner et al., 2007). Loss of mangroves implies loss of goods and services offered by the ecosystem (Figure 1). Therefore informed planning and management of mangrove forests is imperative. REDD+ offer an opportunity to support management of forests including mangroves. Among other
things, REDD+ aims to reduce the trend of deforestation and forest degradation, conserve and enhance carbon stock, and support sustainable forest management.

REDD+ is one among the global climate change mitigation measures (URT, 2012; FAO, 2013). Climate change is driven by global warming caused by human activities (such as deforestation and forest degradation) that results into emissions of heat-trapping gases known as greenhouse gases (GHGs) (FAO, 2013). Carbon dioxide (CO₂) is a key GHG (ibid).

In order to engage in REDD+, countries like Tanzania need to have necessary and reliable forest monitoring systems for carbon stocks and their changes. However, information on forest carbon stocks and their changes has been hampered by poor quality of data or unreliable statistics. For example due to lack of biomass models for mangroves in Tanzania, biomass have been estimated using generic models (MNRT, 2015).

This study therefore was undertaken in order to support management of mangrove forests through REDD+ initiatives. The central focus of the study was to develop biomass models and applying such models to quantify carbon stored by mangrove forests. The models are applicable to forest inventory data to measuring and reporting of carbon stocks for REDD+.
Figure 1: Conceptual and theoretical framework of the study.

The study assumed that reliable information on carbon stored by mangrove forests will influence positive decisions and actions and contribute to improved conditions of mangrove forest and improved livelihoods of coastal communities. In the context of climate change, improved conditions of mangrove forests will serve as carbon sink as opposed to being sources. Forests absorb CO₂ through photosynthesis, store it as carbon and release it through decomposition and combustion. The carbon sink
function of a forest increases with the forest’s rate of growth and the permanence with which it retains carbon (ibid). This can be achieved through effective and informed forest management planning. Through deforestation and forest degradation, which is a consequence of ineffective forest management, poverty and population growth, forests emit large quantities of CO₂ but also result into loss of valuable ecosystem goods and services offered by mangrove forests.

1.5 Methods

1.5.1 Study area

In Tanzania, mangrove forests cover about 158,100 hectares (MNRT, 2015). The present study was carried out at four sites along the coastline of Tanzania. The sites included Pangani (5° 38' S, 38° 54'E to 5° 40' S, 38° 53'E), Bagamoyo (6° 20' S, 38° 50'E to 6° 33' S, 39° 06'E), Rufiji (7° 38' S, 39° 16'E to 7° 55' S, 39° 24'E) and Lindi (10° 02' S, 39° 39'E)-Mtwara (10° 23' S, 40° 23'E) (Figure 2). The sites are located in the largest continuous naturally growing mangrove forests along the coastline and are characterised by three dominant species namely A. marina, S. alba and R. mucronata (MNRT, 1991; Luoga et al., 2004; Nshare et al., 2007). Climate in the study area is influenced by north-east monsoon winds blowing from October to March and south-east monsoon winds blowing from April to October. Average annual rainfall varies from 879 mm (Rufiji) to 1240 mm (Pangani) while average annual temperatures range from 25.7 °C (Lindi) to 27.0 °C (Rufiji).
Figure 2: A map of Tanzania showing the study sites.
1.5.2 Sampling and measurements

Sampling aimed to generate data for determination of aboveground biomass, belowground biomass, basic density and carbon stock. Two data sets therefore were collected, plot and tree data. The tree data were used to address objective (i), (ii) and (iii) while objective (iv) which constitute the fourth paper was addressed using NAFORMA data.

Data from this study were collected from temporarily established sample plots laid along transect lines. Generally, site conditions in mangroves vary transversely with reference to the sea/river (e.g. Dahdouh-Guebas et al., 2004; Lovelock et al., 2005). Therefore transects were established perpendicular to the sea/rivers. A total of 120 plots were established: 15 in Pangani, 45 in Bagamoyo, 45 in Rufiji and 15 in Lindi–Mtwarra. Nested plot design with 2 and 10 m radius concentric plots were applied. On each plot diameter at breast height (dbh) (1.3 m above soil surface for all species except for *R. mucronata* dbh was measured at 0.3 m above the highest stilt root) were measured for all trees with dbh $\geq 1$ and $\geq 5$ cm within the 2 and 10 m radius plots, respectively. All trees were identified for species.

From each plot, one tree was selected for destructive sampling. Therefore, a total of 120 trees were measured for AGB and 30 among them were excavated for determination of BGB. In addition to allocation of equal number of trees to each of the three tree species (40 each species for AGB and 10 each species for BGB), the selection of trees was based on strata defined by five dbh classes; 1–10, 10.1–20, 20.1–30, 30.1–40 and $> 40$ cm. The strata were established based on previous studies.
on mangrove structure in the country (Mattia, 1997; Luoga et al., 2004; Nshare et al., 2007).

In addition to dbh, selected trees for destructive sampling were also measured for basal diameter (bd, diameter at 15 cm above ground level for A. marina and S. alba or immediate above the highest stilt root for R. mucronata) using a diameter tape. Total height (ht), crown diameter (crd) and bole height (bht, height from ground level to first branch) were also measured. Total and bole tree height was measured using a Suunto hypsometer. Crown length (crl) was determined from the difference between ht and bole height.

Using a chainsaw, trees were cut 15 cm above ground level for A. marina and S. alba, while for R. mucronata trees were cut immediately above the highest stilt root. After felling, the aboveground part of a tree was cross cut into billets and weighed for their fresh weight.

A. marina and S. alba trees are structurally similar yet however both are different from R. mucronata. Given the complex nature of root system, for A. marina and S. alba trees (Figure 3), BGB was determined using root sampling method. For R. mucronata, stilt roots are highly entangled (Figure 4), therefore total root excavation was applied to quantify BGB. Determination of BGB for A. marina and S. alba trees involved excavation of root crown followed by selection and full excavation of one to two main cable roots originating from the root crown (Figure 3). In addition, one
to two side cable roots from each of the excavated main cable roots were selected and excavated.

Sample roots were excavated to their terminal ends. Both large and small roots were selected aiming at covering a wide range of root sizes. Fresh weights as well as root basal diameter of all excavated roots were recorded. In addition, basal diameter for unexcavated roots was recorded. Cable root data (i.e. basal diameter and dry weights) were later used to develop side and main cable root regression models, which were applied to predict biomass of the roots not excavated. For *R. mucronata*, fresh weights included all aboveground stilt roots and fully excavated belowground stilt roots (Figure 4).

**Figure 3: Tree root system for Avicennia marina (Forssk.) Vierh and Sonneratia alba J. Smith** (modified from Purnobasuki (2013)), the dashed lines indicate cut-off point between root crown and main cable roots and between main cable roots and side cable roots.
Sub-samples were extracted from each sample tree’s component and their fresh weight determined using a digital balance immediately. This was followed by labelling and packing of samples for dry weight determination in the laboratory.

The NAFORMA plot data were obtained through standard forest inventory procedures whereby sample plots were established along transects. The forest inventory data were generated using double sampling for stratification. The sampling involved two consecutive phases; the first phase involved overlaying a dense grid of clusters on the map of Tanzania mainland at distances of 5 km x 5 km between clusters (URT, 2010; Tomppo et al., 2014; MNRT, 2015). Based on predicted growing stock, accessibility and slope, the country was divided into 18 strata (Tomppo et al., 2014).

During the second phase, samples were systematically selected from first phase sample with different sampling intensities in each of the 18 strata. Higher sampling intensity was applied to strata with high variation and predicted growing stock while low sampling intensity was applied to strata with low variation and/low predicted growing stock. The second phase sample was the one actually measured in the field. Based on the sampling design, a total of 3,420 clusters with 32,660 plots were adopted. The distance between clusters varied from 5 km to 45 km (Tomppo et al., 2014). For each cluster plots spaced 250 m apart varied from 6 to 10 depending on estimated difficulty to access the plot.
Figure 4: Root system for *Rhizophora mucronata* Lam. tree (the dashed lines indicate cut-off point between root crown and stilt roots). The dashed lines indicate cut-off point between root crown and stilt roots.

Based on the described sampling strategy, a total of 24 clusters which is equivalent to 88 sample plots were inventoried within mangrove forests. Individual plots were regarded as sampling units (URT, 2010).

Individual plots were regarded as sampling units (URT, 2010). Plot clustering aimed to increase efficiency the forest inventory. Circular fixed area nested plot designs were applied. The nested plots included 1, 5, 10 and 15 m radius concentric plots. The minimum dbh of trees measured within each nested concentric circle are specified in Figure 5. For all sample plots, slope was recorded. Radius were corrected for slope when slope exceeded 5%.
1.5.3 Laboratory procedures and tree parameter determination

In the laboratory, sub-samples were soaked in distilled water and fresh volume determined by water displacement (Brown, 1997). Subsequently, sub-samples were oven-dried to constant weight at 105 °C and their dry weight determined by a digital balance (Picard et al., 2012).

Basic density was determined as sub-sample oven-dry weight (g) per fresh volume (cm³) while DF-ratio was determined as the ratio of dry to fresh weights. Dry weight was then obtained by multiplying tree- and component specific DF-ratio with component fresh weight. Total tree dry weight was finally obtained by summation. The volume of individual billets were computed using Huber’s formula (e.g. West, 2009) then summed to get total volume for each component (stem and branch). Tree aboveground dry weights were then indirectly determined by multiplying tree
component volume with tree- and component specific BD. Total tree aboveground dry weight included the sum of stem, branch, twig and leaf dry weights.

Tree belowground dry weight determination for *A. marina* and *S. alba* involved conversion of fresh weight of excavated root components using species-, tree- and component specific DF-ratios. From excavated sample root dry weight data, regression models for prediction of dry weight of unexcavated roots were developed and dry weights of unexcavated roots were predicted using basal diameter as a predictor variable. Therefore, total root dry weights comprised excavated and unexcavated (i.e. predicted) root dry weights. Total tree belowground dry weight, i.e. belowground biomass, was derived as the sum of root and root crown dry weights. For *R. mucronata*, the root materials were not partitioned into their respective components, therefore tree-specific DF-ratio (average) was applied as a total tree fresh weight (root crown, above- and belowground stilt roots) to total tree dry weight conversion factor.

1.5.4 Data Analysis

All statistical analyses were carried out in R software version 2.8.0 (R Core Team, 2013).

*Paper I*: Prior to tree dry weight determination, DF-ratios based on sub-samples were subjected to analysis of covariance (ANCOVA) to determine their variations between species, between individual trees within the same species and between root components within trees following general linear model (GLM) procedures.
Diameter at breast height (dbh) served as a covariate in the analyses and significance levels of 0.1, 1 and 5 % were applied.

During explorative data analysis, it was found that the relationships between main and side cable root dry weights and basal diameter were nonlinear. Therefore, several options were initially tested to describe the nonlinear relationships (e.g. second order polynomial functions and exponential functions) where the power function was found to be the best:

\[ B = \beta_0 \cdot x^\beta + \varepsilon, \]

where \( B \) = root dry weight of main/side cable roots (kg root\(^{-1}\)), \( x \) = main/side cable root basal diameter (cm), \( \beta_0 \) and \( \beta_1 \) are model parameters and \( \varepsilon \) is an additive error term.

The model fitting was done using \textit{nls2} function in R software. Both ordinary and weighted nonlinear least squares methods were employed in estimation of model parameters. Root mean squared error (MRSE) and mean prediction error (MPE (%)) served as indicators of goodness of fit.

\[
RMSE = \sqrt{\frac{\sum e^2}{n}}
\]

where \( e \) = residuals, i.e. differences between predicted and observed dry weights (kg) and \( n \) = number of observations, and
\[ MPE(\%) = \left( \frac{\sum (e)_i}{MB_{obs}} \right) \times 100 \]

where \( MB_{obs} \) = mean observed dry weight (kg).

Using BGB data from this study, selected existing belowground biomass models (Tamai et al., 1986; Comley and McGuinness, 2005; Komiyama et al., 2005; Kairo et al., 2009) were tested and their predictive accuracy determined using \( MPE(\%) \).

**Paper 2:** Variation in basic density between tree species and within species (between trees and tree components) was determined using linear mixed-effect model (LMM) procedures (Galecki and Burzykowski, 2013). The use of LMM was motivated by the hierarchical structure of data used in this study. Model fitting was done using \( lme \) function in \textit{nlme} package in R software.

Tree AGB estimation using basic density as a conversion factor was analysed by comparing estimated (indirect method) and observed (direct method) tree biomass. Total observed tree AGB was calculated as sum of the product of tree- and component-specific fresh weight and DF-ratio:

\[
AGB_{h,hi} = \sum_{i=1}^{n} (FW_{hi} \times DF_{hi}) + \sum_{i=1}^{n} (FW_{hi} \times DF_{hi}) + \sum_{i=1}^{n} (FW_{hi} \times DF_{hi}) + \sum_{i=1}^{n} (FW_{hi} \times DF_{hi})
\]

where \( n \) = total number of billets/twig bundles/leaf weights for a given aboveground tree component, \( s \) = stem, \( b \) = branch, \( t \) = twig, \( l \) = leaf, \( h = h^{th} \) tree, \( i = i^{th} \) sub-section, \( AGB_{h,hi} \) = observed total tree aboveground dry weight (kg), \( FW_{hi} \), \( FW_{hi} \), \( FW_{hi} \) and \( FW_{hi} \) are stem, branch, twig and leaf fresh weights (kg), respectively, and \( DF_{hi} \), \( DF_{hi} \) and \( DF_{hi} \) are stem, branch, twig and leaf DF-ratios, respectively. Tree
AGB determined through weighing was considered as observed values and assumed to have been determined without error.

The volume of individual billets was computed using Huber’s formula (e.g. West, 2009). Merchantable volume was calculated as the sum of the volumes of all billets for each tree component (stem, branch). Tree- and component specific BD values were applied to convert merchantable volume to biomass. Tree-specific and species-specific mean BD values were also tested. In addition, species-specific BD values from the GWD database were applied. The estimated tree AGB was calculated as follows:

$$\text{AGB}_{hw} = \sum_{i=1}^{n_s} (\text{FV}_{h_i} \times \text{BD}_{h_i}) + \sum_{i=1}^{n_b} (\text{FV}_{b_i} \times \text{BD}_{b_i}) + \sum_{i=1}^{n_t} (\text{FW}_{h_i} \times \text{DF}_{h_i}) + \sum_{i=1}^{n_l} (\text{FW}_{b_i} \times \text{DF}_{b_i})$$

where $n = \text{total number of billets/twig bundles/leaf weights for a given aboveground tree component}, s = \text{stem}, b = \text{branch}, t = \text{twig}, l = \text{leaf}, h = \text{h}^{\text{th}} \text{ tree}, i = \text{i}^{\text{th}} \text{ sub-section}, AGB_{hw} = \text{estimated total tree aboveground dry weight (kg)}, \text{ FV}_{h_i} \text{ and } \text{ FV}_{b_i}, \text{ are stem and branch fresh volume (m}^3\text{), respectively, and BD}_{h_i} \text{ and } \text{ BD}_{b_i} \text{ are stem and branch DF-ratios, respectively. Other abbreviations are as defined previously.}$

Measures of precision; standard deviation (STD) and 95% confidence interval were calculated separately for observed and estimated tree AGB. MPE (%) were also computed as a measure of accuracy. Tree AGB estimated using BD were considered precise when they showed lower STD, CI and lower value of RP than their corresponding values for observed tree AGB. Positive MPE (%) values and significantly different from zero signified over-estimation of tree AGB bias.
Similarly, negative MPE (%) values and significantly different from zero indicated under-estimation of tree AGB bias. Conversely, non-significant MPE (%) values implied unbiased estimations hence accurate (Walther and Moore, 2005; IPCC, 2003).

*Paper 3:* Various functional forms were initially we tested on data from this study, where power functional form was the best. Therefore, two variants of power functions with an additive error term ($\varepsilon$) were considered in the analysis. Power functions have been widely used to model biomass of mangrove trees (e.g. Tamai *et al.*, 1986; Komiyama *et al.*, 2005; Kairo *et al.*, 2009).

Three important assumptions for regression modelling are normality, homoscedasticity (if residual variance increases as a function of dbh) and independency of residuals. Results and conclusions based on regression analysis are only reliable if these assumptions are met (Ritz and Streibig, 2008; Zuur *et al.*, 2009). For biological data, however, such assumptions may be difficult to meet.

Nonlinear mixed-effects (NLME) modelling is one way of confronting challenges encountered in conventional regression approaches since it relaxes regression assumptions and take into account the complex nature of biological data (Pinheiro and Bates, 2000; Zuur *et al.*, 2009). Within the mixed-effects model framework, parameters may also be allowed to vary by grouping variables(s) (i.e. random variables(s)) (Ritz and Streibig, 2008).
Our data originated from four different sites and comprised three different species, where one tree was destructively sampled from each sample plot spatially distributed along transects. Since our data structure is hierarchical and the biomassdbh relationship is nonlinear, tree biomass was modelled using the NLME modelling approach. The use of NLME also ensured that, the original scale of data is preserved.

Model fitting was carried out using the NLME function in the NLME package in R software (Pinheiro et al., 2015). Random-effects variables included species and site. Three sets of tree biomass models were developed, (i) AGB, (ii) BGB and (iii) aboveground tree component (leaf, twig, branch, and stem) biomass models. In all cases the power model form was applied. For aboveground biomass models, predictor variables included dbh and ht while for the rest only dbh was used since they had limited number of observations (Harrell, 2001). RMSE (%) and MPE (%) were considered as indicators of goodness of fit. Based on a literature review, four common existing AGB models and eight species-specific models were selected and tested on data from this study in order to determine their predictive accuracy. RMSE (%) and MPE (%).

*Paper 4:* Species composition of mangrove forests was determined based on recorded species during the forest inventory. Tree AGB and BGB were computed using models reported in *Paper 3* for mangroves of Tanzania. Tree estimates were summed and subsequently up-scaled into per hectare. AGC (Mg C ha\(^{-1}\)) and BGC (Mg C ha\(^{-1}\)) stocks were determined from AGB and BGB by a carbon fraction of 0.47 for AGB and 0.39 for BGB (Kauffman and Donato, 2012; Abino *et al.*, 2014). TC (Mg C ha\(^{-1}\))
1 stock was finally obtained by summation of AGC and BGC. Uncertainty in both AGC and BGC estimates were reported using the 95% confidence intervals. Total quantity of carbon stored by mangroves of Tanzania was obtained by multiplying per hectare estimates with total area covered by mangroves. Test on variations of carbon stocks between and within stand types was done using lme function in nlme package where species name/species composition was treated as random-effects.
2.0 MAJOR FINDINGS, CONCLUSIONS AND RECOMMENDATIONS

2.1 Major findings

This study aimed to support management of mangrove forests in Tanzania and beyond through REDD+ initiatives. Carbon stock is a central variable within the REDD+ framework which can efficiently be quantified using biomass models. Methodological challenges in quantification of BGB is largely due to diversity and complexity of mangrove species. AGB models exist yet they are mostly based on data from other regions, limited sample sizes and data ranges thus uncertainties due to application of such models is unknown. Focusing on three mangrove species in the country, this study documented procedures for quantification of BGB (Paper 1), determined BD and uncertainties in tree AGB determination (Paper 2) and based on comprehensive sampling procedures both AGB and BGB models were developed (Paper 3). Using NAFORMA data and models developed in this study, AGC, BGC and TC were quantified (Paper 4). Major findings are detailed in sub-sections 2.1.1 to 2.1.4.

2.1.1 Procedures for quantification of belowground biomass of three mangrove tree species (Paper 1)

*A. marina, S. alba* and *R. mucronata* are the three studied mangrove species. Understanding root system is an important aspect in designing sampling for quantification of BGB. Root system for all the three species consist of root crown and
roots. Root system for *A. marina* and *S. alba* is detailed in Figure 3 while Figure 4 provide details on root system for *R. mucronata*. Since the three tree species are structurally distinct, quantification of their belowground biomass need to be approached differently. Root sampling (i.e. not all roots for a given tree were excavated) was applied for *A. marina* and *S. alba* while for *R. mucronata* total root excavation was employed. The stilt roots of *R. mucronata* trees are numerously stocked within a limited area (Figure 4) and are densely entangled, which made it impossible to trace individual roots. Instead a total excavation of all roots was performed.

Results showed that, DF-ratios varied between tree species and root components (Table 1). The DF-ratios also varied with dbh.

**Table 1: Descriptive statistics on distribution of DF-ratios**

<table>
<thead>
<tr>
<th>Species</th>
<th>Belowground component</th>
<th>n</th>
<th>Mean ± STD</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. marina</em></td>
<td>- Root crown</td>
<td>10</td>
<td>0.536 ± 0.040</td>
<td>0.442</td>
<td>0.580</td>
</tr>
<tr>
<td></td>
<td>- Root</td>
<td>10</td>
<td>0.444 ± 0.051</td>
<td>0.336</td>
<td>0.515</td>
</tr>
<tr>
<td></td>
<td>All components</td>
<td>10</td>
<td>0.490 ± 0.041</td>
<td>0.389</td>
<td>0.540</td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>- Root crown</td>
<td>10</td>
<td>0.424 ± 0.065</td>
<td>0.334</td>
<td>0.544</td>
</tr>
<tr>
<td></td>
<td>- Root</td>
<td>10</td>
<td>0.350 ± 0.073</td>
<td>0.262</td>
<td>0.537</td>
</tr>
<tr>
<td></td>
<td>All components</td>
<td>10</td>
<td>0.387 ± 0.027</td>
<td>0.339</td>
<td>0.437</td>
</tr>
<tr>
<td><em>R. mucronata</em></td>
<td>- Root crown</td>
<td>7</td>
<td>0.607 ± 0.048</td>
<td>0.551</td>
<td>0.680</td>
</tr>
<tr>
<td></td>
<td>- Aboveground stilt root</td>
<td>9</td>
<td>0.535 ± 0.045</td>
<td>0.466</td>
<td>0.621</td>
</tr>
<tr>
<td></td>
<td>- Belowground stilt root</td>
<td>10</td>
<td>0.363 ± 0.135</td>
<td>0.243</td>
<td>0.613</td>
</tr>
<tr>
<td></td>
<td>All components</td>
<td>10</td>
<td>0.470 ± 0.040</td>
<td>0.424</td>
<td>0.560</td>
</tr>
</tbody>
</table>

The developed side and main cable root dry weight models for *A. marina* and *S. alba* generally showed strong relationships between basal diameter and dry weight. Generally, the *A. marina* models showed better fit (lower RMSE values and higher R² values) than *S. alba* models (Table 2).
Table 2: Models for side and main cable root dry weight prediction

<table>
<thead>
<tr>
<th>Species</th>
<th>Component</th>
<th>$n$</th>
<th>Parameters</th>
<th>RMSE</th>
<th>$R^2$</th>
<th>MPE%</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. marina</td>
<td>Side cable root</td>
<td>20</td>
<td>$0.10123^{***}$</td>
<td>2.60603$^{***}$</td>
<td>0.085</td>
<td>0.76</td>
</tr>
<tr>
<td>A. marina</td>
<td>Main cable root</td>
<td>22</td>
<td>$0.20390^{**}$</td>
<td>1.60410$^{***}$</td>
<td>0.321</td>
<td>0.73</td>
</tr>
<tr>
<td>S. alba</td>
<td>Side cable root</td>
<td>13</td>
<td>$0.46310^{**}$</td>
<td>1.60600$^{***}$</td>
<td>0.519</td>
<td>0.45</td>
</tr>
<tr>
<td>S. alba</td>
<td>Main cable root</td>
<td>20</td>
<td>$0.01817^{*}$</td>
<td>3.48190$^{***}$</td>
<td>2.814</td>
<td>0.63</td>
</tr>
</tbody>
</table>

Note: Model form; $B = \beta_0 + \beta_1 x + \epsilon$ where $B = \text{root dry weight (kg root}^{-1}), x = \text{side/main cable root basal diameter (cm)}, \beta_0$ and $\beta_1$ are model parameters and $\epsilon$ is an additive error term. * = Significant at 5%, ** = Significant at 1% and *** = Significant at 0.1%

All models revealed non-significant ($p > 0.05$) MPE (%) values. For all models, the distributions of residuals were approximately normally distributed although the residuals slightly increased with increasing basal diameter of the roots.

Broadly procedures for quantification of BGB for the three mangrove species falls into three categories namely (a) field procedures, (b) laboratory procedures and (c) data analysis. For A. marina and S. alba BGB may be quantified using root sampling method:

a) Field procedures

(i) Root crown is fully excavated, one sub-sample extracted and fresh weight (root crown and sub-samples) determined,

(ii) Basal diameter of roots around the root crown is recorded,

(iii) For each sample tree, at least two main cable roots are selected, excavated to their terminal ends and fresh weight determined immediately,

(iv) At least two side cable roots are selected, excavated to their terminal ends and fresh weight determined immediately,
(v) Basal diameter for both excavated and unexcavated side cable roots is recorded,

(vi) At least two sub-samples are extracted from each sample root and their fresh weight determined immediately,

(vii) Sub-samples are labelled and packed for laboratory analysis.

b) Laboratory procedures

In laboratory sub-samples are dried to constant weight at 105 °C and their dry weight determined.

c) Data analysis

(i) For each fully excavated root and root crown, dry weight is determined as a product of fresh weight and tree- and component specific DF-ratio,

(ii) Based on side cable root dry weights, regression models relating dry weight (response variable) and basal diameter (predictor variable) are developed,

(iii) For each excavated main cable root, dry weights of unexcavated side cable roots is determined using models in (ii), therefore dry weight of main root include sum of excavated main cable root, excavated and unexcavated side root dry weights,

(iv) Based on main cable root dry weights in (iii), regression models relating dry weight (response variable) and basal diameter (predictor variable) are developed,

(v) For each sample tree, dry weights of unexcavated main cable roots is determined using models in (iv),
(viii) Total tree dry weight (i.e. tree BGB) comprises of the sum of root
crown dry weight plus excavated and unexcavated side root dry
weights,

(ix) Sub-samples are labelled and packed for laboratory analysis.

For *R. mucronata* BGB may be quantified using total root excavation method:

a) Field procedures

(i) For each sample tree root crown and aboveground stilt roots are
harvested and fresh weights of each component determined,

(ii) One sub-sample is extracted from root crown and at least two sub-
samples are extracted from above-ground stilt roots and their fresh
weights recorded,

(iii) Belowground stilt roots are fully excavated and their fresh weight
recorded,

(iv) At least two sub-samples are extracted from belowground stilt roots
and their fresh weight determined,

b) Laboratory procedures (same as for *A. marina* and *S. alba*)

c) Data analysis

(i) Dry weights of root crown, above- and belowground stilt roots are
determined using tree- and component specific DF-ratio,

(ii) Total tree dry weight comprises of the sum of root crown and above-
and belowground stilt root dry weights.
Results showed that, mean total tree BGB for *A. marina* (*n*=10), *S. alba* (*n*=10) and *R. mucronata* (*n*=14) were 100.5 ± 93.7 (STD) kg, 273.2 ± 346.7 (STD) kg and 166.0 ± 160.9 (STD) kg, respectively. On average for *A. marina*, the root crown contributed 34% (34.0 ± 35.5 (STD) kg) of the total BGB while 66% (66.5 ± 61.0 (STD) kg) came from the roots. The corresponding proportions were 90% (246.0 ± 329.6 (STD) kg) and 10% (27.6 ± 38.1 (STD) kg) for *S. alba*. This paper however, provides no information on biomass for the root components of *R. mucronata*. Tested on data from this study, existing BGB models generally under-estimated BGB. MPE ranged from -56.1 ± 62.5 (STD) kg tree\(^{-1}\) (-33.8%) to -186.6 ± 290.4 (STD) kg tree\(^{-1}\) (-68.3%).

2.1.2 Tree basic density, biomass estimation and associated uncertainties (*Paper 2*)

The study found overall mean tree aboveground basic density of 0.60 ± 0.00 (SE) g cm\(^{-3}\), 0.54 ± 0.01 (SE) g cm\(^{-3}\) and 0.69 ± 0.01 (SE) g cm\(^{-3}\) for *A. marina*, *S. alba* and *R. mucronata*, respectively. Similarly, the overall mean tree belowground basic densities were 0.57 ± 0.02 (SE) g cm\(^{-3}\), 0.32 ± 0.01 (SE) g cm\(^{-3}\) and 0.53 ± 0.02 (SE) g cm\(^{-3}\) for *A. marina*, *S. alba* and *R. mucronata*, respectively. The basic density varied significantly between species.

Among all factors considered as determinants for variation in basic density; number of trees per hectare was a significant source of variation in tree aboveground basic density and their monotonic relationship was negative (*A. marina*). For *S. alba* and *R. mucronata*, basal area (m\(^2\) ha\(^{-1}\)) significantly influenced aboveground basic density
and their relationship was strong and positive. Similarly, the relationship between tree aboveground basic density and dbh class was strong and positive and basic density varied significantly between site for *S. alba* and *R. mucronata*. Basic density also varied between and within tree components.

Testing of the accuracy and precision of biomass estimation using basic density as a conversion factor revealed that, the use of tree- and component-specific basic density resulted in unbiased tree AGB estimates for the three species. Generally uncertainties in tree AGB estimation increased from the use of tree- and component-specific basic density where estimates were quite accurate (low MPE) compared to the use of tree average basic density from the GWD database, where estimates were less accurate, i.e. higher MPE for all the three species.

### 2.1.3 Above- and belowground tree biomass models for three mangrove species in Tanzania (*Paper 3*)

For the three species, about 55% of total AGB was stored in stem while the rest stored in branch, twig and leaf. On average about 41% of the total tree biomass was stored in the root system. The root to shoot ratios for *A. marina*, *S. alba* and *R. mucronata* were 0.38, 1.29 and 0.62 respectively.

In this study, AGB and BGB models were developed (Table 3). Data from the three dominant mangrove species in Tanzania, *A. marina*, *S. alba* and *R. mucronata* were employed in model development. Site and species as random-effects variables improved model fit and species resulted into significant random-effects parameters.
Therefore species-specific models were reported. Generally species-specific models fitted better to data than common models. For the AGB common models (FE1 and FE2), inclusion of ht as a predictor variable resulted into decline of RMSE 42.6% to 38.4%, which is equivalent to a decline of about 10%. Similarly, for species-specific models, AGB models, inclusion of ht resulted into lower RMSE (%) and MPE (%) values for A. marina (models RE1 and RE4) and S. alba (RE2 and RE5). Mixed-results however were observed for R. mucronata.

Table 3: Above- and belowground biomass models

<table>
<thead>
<tr>
<th>Model type</th>
<th>n</th>
<th>Model</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>Model ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common</td>
<td>119</td>
<td>( AGB = 0.25128 \times dbh^{2.24034} )</td>
<td>42.6</td>
<td>-0.6</td>
<td>FE1</td>
</tr>
<tr>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. marina</td>
<td>40</td>
<td>( AGB = 0.25128 \times dbh^{2.24351} )</td>
<td>41.3</td>
<td>2.8</td>
<td>RE1</td>
</tr>
<tr>
<td>S. alba</td>
<td>39</td>
<td>( AGB = 0.25128 \times dbh^{2.21727} )</td>
<td>34.2</td>
<td>2.8</td>
<td>RE2</td>
</tr>
<tr>
<td>R. mucronata</td>
<td>40</td>
<td>( AGB = 0.25128 \times dbh^{2.26026} )</td>
<td>40.5</td>
<td>-6.6</td>
<td>RE3</td>
</tr>
<tr>
<td>Common</td>
<td>119</td>
<td>( AGB = 0.19633 \times dbh^{2.07919} \times ht^{0.29654} )</td>
<td>38.4</td>
<td>-1.0</td>
<td>FE2</td>
</tr>
<tr>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. marina</td>
<td>40</td>
<td>( AGB = 0.19633 \times dbh^{2.08791} \times ht^{0.29654} )</td>
<td>31.4</td>
<td>1.6</td>
<td>RE4</td>
</tr>
<tr>
<td>S. alba</td>
<td>39</td>
<td>( AGB = 0.19633 \times dbh^{2.04113} \times ht^{0.29654} )</td>
<td>23.1</td>
<td>2.0</td>
<td>RE5</td>
</tr>
<tr>
<td>R. mucronata</td>
<td>40</td>
<td>( AGB = 0.19633 \times dbh^{2.10853} \times ht^{0.29654} )</td>
<td>42.5</td>
<td>-4.6</td>
<td>RE6</td>
</tr>
<tr>
<td>Common</td>
<td>30</td>
<td>( BGB = 1.42040 \times dbh^{1.59666} )</td>
<td>89.6</td>
<td>-18.2</td>
<td>FE3</td>
</tr>
<tr>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. marina</td>
<td>10</td>
<td>( BGB = 1.42040 \times dbh^{1.44260} )</td>
<td>16.8</td>
<td>1.5</td>
<td>RE7</td>
</tr>
<tr>
<td>S. alba</td>
<td>10</td>
<td>( BGB = 1.42040 \times dbh^{1.65760} )</td>
<td>95.1</td>
<td>-32.1</td>
<td>RE8</td>
</tr>
<tr>
<td>R. mucronata</td>
<td>10</td>
<td>( BGB = 1.42040 \times dbh^{1.68979} )</td>
<td>38.7</td>
<td>1.6</td>
<td>RE9</td>
</tr>
</tbody>
</table>

Note: AGB = total aboveground biomass (kg tree\(^{-1}\)), BGB = total belowground biomass (kg tree\(^{-1}\))

Predictive accuracy of the existing aboveground biomass models was evaluated by testing them on our data. Where existing models over-estimated AGB, MPE ranged from 1.6% (Chave et al., 2005; \( p > 0.05; \) RMSE = 47%) to 37% (Komiyama et al., 2005; \( p < 0.001; \) RMSE = 105%) for A. marina data. Similarly, cases where existing models under-estimated AGB, MPE ranged from 18% (Chave et al., 2005; \( p > 0.05; \)
RMSE = 72% for *R. mucronata* data) to 99% (Kairo *et al.*, 2009; *p* < 0.05; RMSE = 162% for *S. alba* data).

### 2.1.4 Carbon storage in mangrove forests of Tanzania (*Paper 4*)

Based on NAFORMA data (88 plots), a total of 1942 trees (dbh ≥ 1 cm) were measured, whereby nine mangrove species were recorded. This included *Avicennia marina* (Forssk.) Vierh (Acanthaceae), *Bruguiera gymnorrhiza* (L.) Lam. (Rhizophoraceae), *Ceriops tagal* (Perr.) C. B. Rob. (Rhizophoraceae), *Heritiera littoralis* Dryand. (Malvaceae), *Lumnitzera racemosa* Willd. (Combretaceae), *Rhizophora mucronata* Lam. (Rhizophoraceae), *Sonneratia alba* J. Smith (Lythraceae), *Xylocarpus granatum* Koen. (Meliaceae) and *Xylocarpus moluccensis* (Lamk.) Roem. (Meliaceae). Weighed by basal area, *A. marina* (32%), *R. mucronata* (31%) and *C. tagal* (20%) were the dominant species.

Tree biomass and carbon storage estimates are summarised in Table 4. Given that mangrove forests cover about 158,100 ha, a total of 10.0 millions Mg C (i.e. 37.2 millions Mg CO$_2$e) is stored by mangroves of Tanzania. AGC contributed about 53% of total carbon stock while the rest was stored belowground (47%). The percentage of AGC increased with dbh class while BGC declined with dbh class.

Results showed that, pure stands (AGC = 29.6 Mg C ha$^{-1}$; BGC = 26.0 Mg C ha$^{-1}$; TC = 55.7 Mg C ha$^{-1}$) had slightly lower carbon stock compared to mixed-species stands (AGC = 37.2 Mg C ha$^{-1}$; BGC = 33.8 Mg C ha$^{-1}$; TC = 71.0 Mg C ha$^{-1}$) although they were not significantly different (*p* > 0.05).
Table 4: National biomass and carbon stock estimates for mangroves

<table>
<thead>
<tr>
<th>Parameter</th>
<th>n</th>
<th>95% CI</th>
<th>STD</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGB (Mg ha(^{-1}))</td>
<td>88</td>
<td>71.3 ± 12.4</td>
<td>59.1</td>
<td>0.4</td>
<td>282.7</td>
</tr>
<tr>
<td>BGB (Mg ha(^{-1}))</td>
<td>88</td>
<td>77.0 ± 11.6</td>
<td>55.6</td>
<td>2.1</td>
<td>254.1</td>
</tr>
<tr>
<td>TB (Mg ha(^{-1}))</td>
<td>88</td>
<td>148.3 ± 17.0</td>
<td>81.1</td>
<td>2.9</td>
<td>441.1</td>
</tr>
<tr>
<td>AGC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>33.5 ± 5.8</td>
<td>27.8</td>
<td>0.2</td>
<td>132.9</td>
</tr>
<tr>
<td>BGC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>30.0 ± 4.5</td>
<td>21.7</td>
<td>0.8</td>
<td>99.1</td>
</tr>
<tr>
<td>TC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>63.5 ± 7.3</td>
<td>35.3</td>
<td>1.2</td>
<td>192.5</td>
</tr>
<tr>
<td>AG-CO(_2)e (Mg CO(_2)e ha(^{-1}))</td>
<td>88</td>
<td>123.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BG-CO(_2)e (Mg CO(_2)e ha(^{-1}))</td>
<td>88</td>
<td>111.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T-CO(_2)e (Mg CO(_2)e ha(^{-1}))</td>
<td>88</td>
<td>235.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

2.2 Discussions

Generally this study aimed to develop biomass models as a means to support accurate estimation of biomass and carbon stocks for mangroves. Biomass modelling is preceded by destructive sampling of trees. Literature revealed that, there are methodological challenges in destructive sampling of BGB hence few models for BGB (Komiyama et al., 2008).

Due to the diverse and complex nature of root systems for mangrove species a number of methods for quantification of BGB have been tested. For example Tamooh et al. (2008) estimated BGB of *A. marina*, *S. alba* and *R. mucronata* using core sampling method while Comley and McGuinness (2005) applied root ball method (i.e. excavation of 2 m around sample tree) to quantify BGB of *A. marina*. So methods varied even for the same species, this has a number of consequences including limiting result comparability. This study propose a root sampling method for quantification of BGB of *A. marina* and *S. alba*. Similarly the study propose total excavation method for quantification of BGB of *R. mucronata*. 
The study attempted to address limitations for previously reported methods for quantification of BGB. Unlike previous studies, this study (i) documented in detail procedures for quantification of BGB, (ii) assessed variations of DF-ratio, and (iii) for A. marina and S. alba roots were traced to their terminal ends. Based on the nature of DF-ratio variations, the study recommend the use of species-, tree- and root component-specific DF-ratios in determining dry weight so as to minimise uncertainty in biomass estimation.

Evaluation of species-specific models (Comley and McGuinness, 2005; Tamai et al., 1986; Kairo et al., 2009) using BGB data from this study showed that, all of them significantly under-estimated tree BGB. The most likely the explanation for such under-estimations is loss of biomass due to the excavation methods applied when these models were developed. For example, for the root ball method, BGB includes roots within 2 m around the sample tree only (Comley and McGuinness, 2005). Therefore methods proposed in this study may be regarded to be comprehensive than previously reported methods and should be applied in quantification of BGB.

Despite attempts to minimise sources of uncertainties, in this study the root materials for R. mucronata were mixed up and average tree-specific DF-ratio as a fresh to dry weight conversion factor was applied. This may contribute to uncertainties in dry weight estimates, therefore future studies should consider separation of sample materials into their respective components. For the root models, residuals varied slightly with root size (basal diameter) a phenomena known as heteroscedasticity. This implies large prediction errors for large root sizes. Heteroscedasticity may be
caused by presence of outliers (Ritz and Streibig, 2008; Zuur et al., 2009). In this study large root sizes were few, therefore future studies should ensure adequate representation of large root sizes.

During quantification of BGB the study also encountered practical challenges. Mangroves grow in intertidal zones, the interval between consecutive high tides is about 12 hours on average (WIOMSA, 2008). Accordingly, destructive sampling for biomass is only possible between low and high tide which is about six hours. This allows a limited amount of working hours. Therefore careful planning based on tide tables is recommended. According to IPCC (2006), AGB comprises of stump, stem, branch, twig and leaf while BGB include all live roots. In order to include stump into AGB, trees have to be cut at soil level, this was not practical instead trees were consistently cut at 15 cm above soil level (A. marina and S. alba). Therefore stump was counted as BGB. Due to siltation particularly for riverine mangroves, portion of stems are silted thereby posing challenges on cut-off point between AGB and BGB. Since this is a typical environment for mangroves, in this study soil levels served as a cut-off point between AGB and BGB although pneumatophores aboveground were counted as BGB (A. marina and S. alba).

During destructive sampling of trees, AGB may be determined directly by actual weighing of aboveground fresh weights. Alternatively, AGB may be determined indirectly by first measuring volume and subsequently convert volume to dry weight using BD (Picard et al., 2012). At an application level, AGB may be quantified directly using biomass models but may also be quantified indirectly using volume
models and subsequently convert volume to dry weight using BD (Somogyi et al., 2007). For AGB and BGB models, BD may be applied as one of the predictor variable (e.g. Chave et al., 2005; Komiyama et al., 2005). Therefore, BD is important in biomass estimation.

This study reports tree AG- and BGBD values for three mangrove species in Tanzania. To our knowledge this is the first study to report BGBD for the three mangrove species. Generally, BD varied between species, trees of different sizes and tree components. BD values were comparable with previously reported values (e.g. R. mucronata; Komiyama et al., 2005), yet however differences were observed. The tree BD values reported in this study were different from those reported in the GWD database (Chave et al., 2009; Zanne et al., 2009). Among other factors, the variation of BD noted between different studies may be due to differences in site conditions, BD determination methods, sampling, sample size and the purpose for which the studies were undertaken. Variations in BD may be source of uncertainties in biomass estimates when such values are applied either as volume to dry weight conversion factor or predictor variables. Therefore, such uncertainties should be minimised by implementing an appropriate sampling strategy.

Accuracy and precision of indirect AGB determination (i.e. determine volume and convert volume to dry weight using BD as a volume to biomass conversion factor) was also tested. The results showed that, both methods yield consistent and unbiased estimates of tree AGB when applying tree- and component-specific AGBD values.
The relatively large and significant MPEs leading to biased estimates obtained when applying species-specific AGBD from the GWD database suggests that, BD sourced from the GWD database may lead into biased local biomass estimates. This calls for inclusion of all sources of variation in determination of BD as a volume to dry weight conversion factor and that, BD from the GWD database need to be used with caution.

Based on the “conservativeness principle” (i.e. the risk of over- and under-estimation should be minimised) (Grass et al., 2008), during destructive sampling the study recommend the use of direct method in biomass estimation. When it is not practical to apply the direct method, an indirect method of biomass estimation may be applied as an alternative. The following considerations are essential in order to minimise uncertainties in biomass estimation; when applying the direct method, sampling must take into account the variation of DF-ratios. On the other hand, tree- and component-specific BD values should be applied for an indirect method of biomass estimation. Moreover, for an indirect method we recommend working with a number of observations as large as 30, in order to obtain normally distributed residuals and unbiased estimates.

AGB and BGB models for three dominant mangrove species in Tanzania, i.e. A. marina, S. alba and R. mucronata were developed in this study. No similar models have previously been developed in the country and only a few models have been developed in Africa or are based on data from Africa. The existing biomass models from Africa (Kairo et al., 2009; Sitoe et al., 2014) are based on limited sample sizes and data from only one site. In addition, our belowground biomass models are based
on data generated using comprehensive procedures for quantifying tree BGB
involving root sampling (\textit{A. marina} and \textit{S. alba}) and complete root excavation (\textit{R. mucronata}).

Models reported in this study are based on a nonlinear mixed-modelling approach. Ordinary nonlinear regression is commonly used to develop biomass models (e.g. Chave \textit{et al.}, 2005; Komiyama \textit{et al.}, 2005). Models based on such a modelling approach are likely to violate regression assumptions of homoscedasticity and independence of residuals, which are difficult to meet for biological data (Zuur \textit{et al.}, 2009). The mixed effects modelling comprising both fixed and random effects applied in this study relax regression assumptions of homoscedasticity and independence of residuals (Ritz and Streibig, 2008; Zuur \textit{et al.}, 2009).

Inclusion of \textit{ht} as an additional predictor variable improved model goodness of fit (Table 3). This demonstrate the importance of appropriate model specification in model development. The use of species as a random-effects variable improved model fit by allowing some parameters to vary by species resulting into species-specific models. Assuming that BD serves as a species-distinguishing factor in common models, BD was not included as a predictor variable. However, previously reported studies argued that, inclusion of BD in common models improved goodness of fit (e.g. Chave \textit{et al.}, 2005). Therefore omission of BD in modelling biomass may introduce uncertainties biomass estimates. This could not be empirically verified in this study and need to be considered in future studies.
The tests of existing models on AGB data from this study generally showed large and significant prediction errors. Plausible explanations for the observed prediction errors could be application of the models beyond data size ranges, geographical locations, and differences in forest structure and tree architecture. Therefore the study recommend species-specific models to common models.

Despite models including ht being better, due to many reasons such as costs, trees are not frequently measured for ht in forest inventories. In such cases, users are obliged either to use models including dbh as the only predictor variable or initially estimate ht using relevant models and subsequently apply biomass models based on both dbh and ht as predictor variables. However, ht prediction models for mangroves are lacking in Tanzania and the rest of Africa. Therefore, the study recommend models based on dbh as the only predictor variable.

The biomass models reported in this study may be applied by to forest inventory data such as NAFORMA so as to generate tier 2 or tier 3 carbon stock estimates for REDD+ programmes. The use of the models beyond species considered in this study is not recommended. However in a scenario where models for species not represented in this study are lacking, a “conservativeness principle” (i.e. the risk of over- and under-estimation should be minimised) (Grassi et al., 2008) may be applied. Therefore assuming the three species represented in the models reported in this study represent average population characteristics of mangrove species, the common models may be applied to unrepresented species.
The study report tier 2 AGC, BGC and TC. Since carbon stocks were estimated using biomass models for *A. marina*, *S. alba* and *R. mucronata* (from this study), partly uncertainties to the carbon stock estimates may be due to application of biomass models to unrepresented species. Although reported biomass and carbon estimates vary considerably, our estimates fall within the range of estimates reported elsewhere (e.g. Ray et al., 2011; Patil et al., 2014). Despite that, biomass and carbon estimates from this study are different from some previously reported estimates (e.g. Abino et al., 2014; Ajonina et al., 2014; MNRT, 2015). This may be explained by a number of reasons including differences in species composition, average tree size, geographical locations, soils and climatic conditions. For example, carbon stock estimates in this study were higher than those reported by NAFORMA (MNRT, 2015) for mangroves of Tanzania, although both are based on the same data set. Most likely this is a consequence of differences in biomass estimation procedures applied between the two studies.

Findings from this study showed that, mangroves of Tanzania and elsewhere around the world (Abino et al., 2014; Liu et al., 2014) store large quantities of carbon. These results therefore should stimulate dialogues and influence decisions geared towards sustainable management of mangrove forests for instance through REDD+ initiatives. Carbon stock estimates reported in this study are more accurate than stocks reported previously by NAFORMA. Therefore they may serve as national estimates for REDD+ programmes.
2.3 Conclusions and Recommendations

Methods for quantification of BGB proposed in this study are more comprehensive than previously reported methods and contribute to improved accuracy of BGB estimates. Therefore, they should be applied in quantification of BGB for similar species. Tree BD varied between species and within species. Therefore sampling for BD should take into account all sources of variations. If properly determined and applied, BD may be useful as a conversion factor and yield accurate biomass estimates. Otherwise they are likely to be a source of uncertainties in biomass estimation. The biomass models reported in this study may be applied to forest inventory data such as NAFORMA so as to generate tier 2 or tier 3 carbon stock estimates for REDD+ programmes and support planning and sustainable management of mangrove forests in the country. Findings from this study showed that, mangroves of Tanzania and elsewhere around the world store large quantities of carbon. These results therefore should stimulate dialogues and influence decisions geared towards sustainable management of mangrove forests through REDD+ initiatives. The carbon stock estimates reported in this study are more accurate than stocks reported previously by NAFORMA. Therefore they may serve as national estimates for REDD+ programmes.

Based on what has been accomplished in this study the following areas for further research were identified:

i. Since mangrove species are quite diverse in structure, there is a need to test the documented procedures for quantification of BGB to other species not covered in this study.
ii Tree volume estimation is also an important part of planning in forest management, however volume models for mangroves in Tanzania and the rest of Eastern Africa region are lacking. Future studies should therefore fill the existing gap.

iii Basic density is important not only for biomass determination (volume to dry weight conversion factor, predictor variable), it could also be useful for many other issues such as industrial utilization of mangrove biomass. Determination of basic density for mangrove species not covered in this study is therefore urgent.

iv Based on results from this study, biomass models including tree height were superior to those based on diameter only. It is therefore important that height prediction models are developed for all mangrove species in Tanzania.

v Growth studies for mangroves are few or lacking in Tanzania and the rest of East African Region. It is therefore high time such studies are undertaken as an input to our understanding on the role of mangrove in carbon sequestration. Partly to achieve that the NAFORMA permanent sample plots need to be monitored while at the same time new permanent sampled plots designed specifically for the aim of understanding dynamics of mangrove ecosystems need to be established.
vi This study covered only two carbon pools, tree above- and belowground biomass, among the five (AGB, BGB, dead wood, litter and organic soils) recognised by IPCC. Therefore future studies should consider the measuring dead wood and soil carbon pools. Dead wood and soil carbon pools are important under the REDD+ framework since they are likely to be affected by land use.

vii Biomass and carbon stock estimates for mangroves of Tanzania are based on national sampling strategies. Accurate planning and informed decisions relies on site specific information which can hardly be deduced from national sampling. Therefore future studies should aim at providing site specific details. Mangrove site specific estimates on carbon stocks are also important for tier 3 reporting under the REDD+ programme.
REFERENCES


APPENDICES

Appendix 1: Tree volume and biomass data form

<table>
<thead>
<tr>
<th>Site name</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest name</td>
<td>Plot coordinates</td>
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<tr>
<td>District name</td>
<td>Easting</td>
</tr>
<tr>
<td>Region name</td>
<td>Northing</td>
</tr>
<tr>
<td>Transect No.</td>
<td>Tree coordinates</td>
</tr>
<tr>
<td>Plot No.</td>
<td>Easting</td>
</tr>
<tr>
<td>Tree No.</td>
<td>Northing</td>
</tr>
<tr>
<td>Crown height (m)</td>
<td>Crown diameter (m)</td>
</tr>
<tr>
<td>Mean crown diameter (m):</td>
<td>East - West North - South</td>
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</table>

<table>
<thead>
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<th>Species name:</th>
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<tr>
<td>Tree diameter</td>
<td>Basal diameter (cm)</td>
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<tr>
<td>Tree height</td>
<td>Angle top (%)</td>
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Comments: 

<table>
<thead>
<tr>
<th>*Section No./Type</th>
<th>Tree section</th>
<th>Green weight (Kg)</th>
<th>Length (m)</th>
<th>Mid-Diameter (cm)</th>
<th>Volume (m$^3$)</th>
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<tbody>
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<td>Type: Trunk/branch</td>
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Sub-samples: Discs

<table>
<thead>
<tr>
<th>Tree No.</th>
<th>Spp. code</th>
<th>Disc No./ID</th>
<th>Green weight (g)</th>
<th>Lab. Green weight (g)</th>
<th>Oven-dry weight (g)</th>
</tr>
</thead>
</table>

Note:
1 = Avicenia marina, 2 = Bruguiera gymnorrhiza, 3 = Ceriops tagal, 4 = Heritiera littoralis, 5 = Lumnitzera racemosa, 6 = Rhizophora mucronata, 7 = Sonneratia alba, 8 = Xylocarpus granatum, 9 = Xylocarpus moluccensis
## Crown: twigs and leaves

<table>
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<th>Spp. code</th>
<th>Type</th>
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<th>Sub-sample ID</th>
<th>Sub-sample green wt. (g)</th>
<th>Sub-sample green wt. at lab. (g)</th>
<th>Sub-sample dry wt at lab. (g)</th>
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<tr>
<td></td>
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</tr>
</tbody>
</table>

## Below ground (root) biomass

<table>
<thead>
<tr>
<th>Tree No.</th>
<th>Root component (root crown, tap root, lateral root)</th>
<th>Basal diameter (cm)</th>
<th>Root component green weight (g)</th>
<th>Sub-sample green weight (g)</th>
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Appendix 2: Stand structure assessment form

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<tr>
<td>Forest name:</td>
<td>Plot coordinates</td>
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<tr>
<td>District name:</td>
<td>Easting</td>
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<tr>
<td>Region name:</td>
<td>Northing</td>
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<tr>
<td>Transect No.</td>
<td>Canopy height (m)</td>
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<td>Plot No.</td>
<td>Canopy closure (%)</td>
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<td>Altitude (m)</td>
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Sample trees (fattest, medium and smallest)

<table>
<thead>
<tr>
<th>Species code</th>
<th>bd (cm)</th>
<th>dbh (cm)</th>
<th>Angle top (%)</th>
<th>Angle foot (%)</th>
<th>Distance (m)</th>
<th>Total tree height (m)</th>
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Comments:

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<th>dbh (cm)</th>
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<th>Distance (m)</th>
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Trees

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<tr>
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<th>Spp. code</th>
<th>dbh (cm)</th>
<th>*Tree classification</th>
<th>Spp. code</th>
<th>No. of individuals</th>
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Seedlings and saplings

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<th>No. of individuals</th>
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</table>

Species code

1 = *Avicenia marina*, 2 = *Bruguiera gymnorrhiza*, 3 = *Ceriops tagal*,
4 = *Heritiera litoralis*, 5 = *Lumnitzera racemosa*, 6 = *Rhizophora mucronata*,
7 = *Sonneratia alba*, 8 = *Xylocarps granatum*, 9 = *Xylocarps moluccensis*

*SS = Single stem and MS = Multiple stem
CHAPTER THREE

PAPER ONE

Procedures for quantification of belowground biomass of three mangrove tree species

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Abstract A review of studies on belowground biomass (BGB) of mangroves revealed that procedures for excavation and determination of dry weight are insufficiently documented. The main objective of this study was therefore to describe procedures for quantification of tree BGB for Avicennia marina (Forssk.), Sonneratia alba J. Smith and Rhizophora mucronata Lam. The study covered four sites in Tanzania where 30 trees were sampled (10 for each species). A new root sampling procedure applied for A. marina and S. alba seemed to work adequately. Dry to fresh weight ratios (DF-ratios) varied between tree species, between tree sizes and between root components. Therefore, for each tree species, tree- and root component-specific DF-ratios were applied for dry weight determination. For A. marina and S. alba trees, a significant proportion of total tree BGB is stored in the root crown (34 and 10 % respectively). Future studies should therefore ensure inclusion of root crown when accounting for total tree BGB. Tests of previously developed models on our data revealed large prediction errors, partly due to differences in site conditions and partly due to incomprehensive excavation procedures applied when these models were developed. Local tree BGB models for mangroves should therefore be developed.

Keywords Avicenia—Rhizophora—Sonneratia · Root biomass · Root sampling · Tanzania

Introduction

Mangroves are an important and productive ecosystem. Among other functions, mangroves store large amounts of carbon per unit area (e.g. Murdiyarso et al. 2009; Donato et al. 2011; Kauffman et al. 2011). Large proportions of carbon in mangroves is also stored belowground, which are highly vulnerable to disturbances whose consequences include the release of greenhouse gasses (Hutchings and Saenger 1987; Komiyama et al. 2000; Kauffman and Donato 2012). In Tanzania mainland, mangroves cover about 108,000 ha (Wang et al. 2003). In total there are ten tree species, and among them Avicenia marina (Forssk.) Vierh, Sonneratia alba J. Smith and Rhizophora mucronata Lam. are dominant (Wang et al. 2003; Luoga et al. 2004; Nshare et al. 2007). Despite their importance, mangroves are threatened by deforestation and forest degradation in Tanzania (e.g. Wang...
Various methods may be employed to quantify forest carbon stock. The most common and accurate approach involve the use of models for prediction of tree dry weight, from which carbon stock may be derived (e.g. Brown 1997; Chave et al. 2005, 2014). Development of models requires destructive sampling of trees, where aboveground biomass (AGB) and belowground biomass (BGB) are first determined for fresh weight. Subsequently dry weight is determined by using oven-dry to fresh weight ratio (DF-ratio) derived from sub-samples. Finally, models predicting dry weight biomass based on tree parameters such as diameter breast height (dbh) and total tree height (ht) are developed.

The diversity of tree forms among mangrove species, especially their unusual root systems, along with the growing conditions and changing tides, salinity levels and muddy soils, pose many challenges in field surveys of mangrove forests. In spite of this, quantification of biomass in mangroves has attracted much attention. A review by Komiyama et al. (2008) identified 72 published articles related to biomass and tree allometry. Most of these studies focused on AGB and were largely carried out in Asia while only two were carried out in Africa (Steinke et al. 1995; Slim et al. 1996). Besides, additional studies on biomass and allometry of mangroves by Kirui et al. (2006), Tamooh et al. (2008), Kairo et al. (2008, 2009), Cohen et al. (2013), Lang’at et al. (2013) and Sitoe et al. (2014) carried out in Africa exist. Studies on BGB particularly on allometry are however fewer in number compared to AGB for mangroves. Among the studies from Africa, Steinke et al. (1995), Tamooh et al. (2008), Kairo et al. (2008) and Lang’at et al. (2013) dealt with BGB issues while Kirui et al. (2006) and Kairo et al. (2009) dealt with allometry of BGB for R. mucronata. However, the latter two studies sampled the aboveground part of stilt roots only while the belowground part of stilt roots was not considered.

The relatively few studies on BGB of mangroves are obviously due to difficult and tedious excavation conditions. A number of different excavation methods have been applied, however. Some studies have applied full excavation of all roots on small sample plots (e.g. Steinke et al. 1995) or used soil core samples distributed randomly on plots (e.g. Lang’at et al. 2013). With these methods, however, it is not possible to link BGB to a particular tree. Thus, the development of models predicting BGB based on tree variables such as dbh and ht is not possible.

Based on previous literature, we identified four BGB sampling methods where the link between BGB and tree variables exists. The methods include (i) “trench method” (e.g. Komiyama et al. 1987, 2000), (ii) “root ball method” (e.g. Comley and McGuinness 2005), (iii) “pull up method” (e.g. Tamai et al. 1986) and (iv) “total excavation method” (e.g. Ong et al. 2004). The “trench method” is based on the establishment of a trench of a certain size in length, width and depth starting at the base of the subject tree while for the “root ball method” all roots surrounding the subject tree within a limited radius are excavated. For none of these two methods, however, roots are traced to their terminal end. The “pull up method” involves pulling up the roots of individual trees physically. In soft soils and for small trees, loss of root biomass with this method is probably relatively small. However, for large trees, where machinery is required, most likely larger roots will snap and remain unmeasured. The “total excavation method” assumes that all roots belonging to the subject tree are excavated. Although total excavation generally should give the most accurate BGB, probably some parts of the medium sized and fine roots in the deeper zones are lost even with this method.

In addition to the loss of biomass, the main challenge related to all the described methods is the amount of work involved. As a compromise between these two partly conflicting factors, i.e. work load and loss of biomass, one could consider, at least for some of the mangrove species, a “root sampling method” as an alternative. For this method, a few sample roots of different sizes for each tree are traced to their terminal end and weighed for fresh weight. Based on sampled roots from many trees, regression models predicting biomass from the basal diameter of the roots are developed. Finally, these models are used to predict biomass of all roots not excavated based on measurement of basal diameter of the root originating from the root crown. To our knowledge this method has never been applied for mangroves, but has proved successful for tropical dry forests (e.g. Mugasha et al. 2013).

The review of studies on BGB of mangroves also revealed that both excavation procedures and procedures for determining dry weight quite often are imprecisely or insufficiently documented. One...
example of insufficient documentation is related to the procedures applied for conversion of fresh weight to dry weight by means of dry to fresh weight ratios (DF-ratios) from sub-samples. The studies however failed to mention whether the DF-ratios are based on the average of the sub-samples from the whole tree, from all belowground parts only or from different root components (e.g. root crown, roots, above- and belowground stilt roots) (e.g. Komiyama et al. 1987). It is obvious that if conversion of fresh to dry weight is not done appropriately, the final estimates of BGB are subject to uncertainty.

The present study focused on the three dominant mangrove species in Tanzania; *A. marina*, *S. alba* and *R. mucronata*. The aims were to (i) describe procedures for excavation of tree BGB, (ii) document procedures for determination of tree BGB, (iii) provide basic information on tree BGB quantities and (iv) test relevant previously developed models for predicting tree BGB.

**Materials and methods**

Site and tree species descriptions

The study was conducted in four sites distributed along the Tanzanian coastline from north (border with Kenya) to south (border with Mozambique). Study sites included (i) Pangani, (ii) Bagamoyo, (iii) Rufiji and (iv) Lindi–Mtwara (Fig. 1). The study sites represent different soil types and climatic conditions (Table 1). The spring tidal range along the Tanzanian coastline vary from 2 to 4 m (Richmond 1997). The elevations from sea to inland were from 1 to 16 m and from river to inland 2–18 m.

The sites are located in the largest continuous naturally growing mangrove forests along the coastline and are characterised by the dominating three mangrove species in Tanzania, i.e. *A. marina*, *S. alba* and *R. mucronata* (MNRT 1991; Luoga et al. 2004; Nshare et al. 2007). The tree species are structurally distinct and adapted to different environments. For example, while *A. marina* tolerate salinity levels ranging from 12 to 31 ‰, *S. alba* and *R. mucronata* grow best at around 2 and 30 ‰, respectively (Ball and Pidsley 1995; Joshi and Ghose 2003). All three species are ever-green and may exist as single or multi-stemmed trees.

**Sampling and excavation procedures**

**Sample plots**

In general, site conditions in mangroves vary transversely with reference to the sea/river (e.g. Dahdouh-Guebas et al. 2004; Lovelock et al. 2005). To cover as much variation as possible, a total of 37 transects were established perpendicular to the sea/rivers. Within these transects, a total of 120 plots were established. The first plot was located close to the edge of the sea/river and the remaining plots were located at fixed distances of 150–250 m depending on the total extension of the forest along transects. For some transects it was not possible to establish all plots because of impenetrable mangrove stand or inaccessibility due to rivers/streams. Therefore the number of plots sampled within transects varied from one to four. Among the 120 plots, 15, 45, 45 and 15 were measured in Pangani, Bagamoyo, Rufiji and Lindi–Mtwara, respectively. Initially the study targeted Bagamoyo only since mangroves in the site represent a large range of functional types of mangrove stands (Spalding et al. 2010). Later we decided to cover more variation by adding sites, and the largest number of plots was allocated to Rufiji since the site represents the largest single block of mangroves in the country.

We established a nested plot design with 2 and 10 m radius concentric plots. On each plot we measured diameter at breast height (dbh) (1.3 m above soil surface for *A. marina* and *S. alba* and 0.3 m above the highest stilt root for *R. mucronata*) for all trees with dbh larger than 1 and 5 cm within the 2 and 10 m radius plots, respectively. All trees were identified for species.

**Tree selection**

For each plot, one tree was selected for destructive sampling. A total of 120 trees were measured for AGB (not reported on in this study) and 30 out of these were excavated and measured for BGB. In addition to allocation of equal number of trees to each of the three tree species (40), the selection of trees was based on strata defined by five dbh classes; 1–10, 10.1–20, 20.1–30, 30.1–40 and >40 cm. The strata were established based on previous studies on mangrove structure in the country (Mattia 1997; Luoga et al. 2004; Nshare et al. 2007). In the selection of trees for excavation we also checked the conditions on each
plot in order to avoid root system interference and cross-over. Finally, this resulted in the excavation of 3, 15, 9 and 3 trees, respectively, for Pangani, Bagamoyo, Rufiji and Lindi–Mtwar.

For all sample trees belong to *A. marina* and *S. alba* we measured dbh, basal diameter (bd, diameter 15 cm above soil surface), total tree height (ht, distance from soil surface to highest point of the tree), bole height
Table 1 Site, location, dominant soil type, temperature and precipitation for the study sites

<table>
<thead>
<tr>
<th>Site and location</th>
<th>Dominant soil type</th>
<th>Mean annual min. temperature (°C) Mean ± STD</th>
<th>Mean annual max. temperature (°C) Mean ± STD</th>
<th>Annual rainfall (mm) Mean ± STD</th>
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</thead>
<tbody>
<tr>
<td>Pangani (5°24’S, 38°59’E)</td>
<td>Alluvial, clay and sandy soils</td>
<td>22.4 ± 0.7</td>
<td>30.8 ± 0.3</td>
<td>1240 ± 333</td>
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<tr>
<td>Bagamoyo (6°26’S, 38°54’E)</td>
<td>Alluvial and sandy soils</td>
<td>21.0 ± 1.5</td>
<td>30.7 ± 0.8</td>
<td>940 ± 239</td>
</tr>
<tr>
<td>Rufiji (7°49’S, 39°15’E)</td>
<td>Alluvial, silt and clay soils</td>
<td>23.7 ± 0.5</td>
<td>30.3 ± 0.3</td>
<td>879 ± 200</td>
</tr>
<tr>
<td>Lindi (10°2’S, 39°39’E)–Mtwara (10°15’S, 40°10’E)</td>
<td>Alluvial and sandy soils</td>
<td>21.1 ± 0.5</td>
<td>30.2 ± 0.4</td>
<td>1072 ± 249</td>
</tr>
</tbody>
</table>


(bht, distance from soil surface to first living branch) and crown diameter (crd, average of the longest crown diameter and diameter perpendicular to the longest crown diameter). Crown length (crl) was determined as the difference between total tree height and bole height. For *R. mucronata* we measured the same parameters, but bd was defined to be at the same level as the highest stilt root, while dbh was measured 30 cm above this level. Bole height and ht were measured from the level of the highest stilt root. Diameter at breast height and bd were measured using a diameter tape while crd was determined using a distance tape. Total tree height was measured using a distance tape for small trees and a Suunto hypsometer for larger trees. Three sample trees (*R. mucronata*) were multi-stemmed, i.e. two trees with two stems and one tree with three stems. For these trees, dbh, bd and ht were determined for each stem while crd, bht and crl were recorded for the main stem only (i.e. the stem with the largest dbh). The sample trees covered large variations regarding plot level conditions, i.e. number of trees (N) (trees ha⁻¹) and basal area (G) (m² ha⁻¹) for trees with dbh larger than 5 cm, and tree parameters (Table 2).

**Excavation procedures**

In addition to the root crown, the root systems of *A. marina* and *S. alba* trees may be divided into four parts; cable roots (lateral growth), pneumatophores (vertical upward growth), feeder roots and anchor roots (Fig. 2). For *A. marina*, the pneumatophores are pencil-like, on average about 8 mm thick and peak to about 20 cm above ground level while for *S. alba* are conical-like, about 50 mm thick and peak to about 30 cm above ground level. The root system of *R. mucronata* (Fig. 3) comprises of root crown and above- and belowground stilt roots. Since the three tree species are structurally distinct, procedures for BGB destructive sampling are described separately. To quantify tree BGB we applied root sampling (i.e. not all roots for a given tree were excavated (e.g. Mugasha et al. 2013)) for *A. marina* and *S. alba*. For *R. mucronata* we applied total root excavation (e.g. Ong et al. 2004).

1) **Destructive sampling of BGB for *A. marina***

Trees were cut at 15 cm above ground level using a chain saw (Fig. 2). The cut-off point was guided by National Forest Resources Monitoring and Assessment (NAFORMA) of Tanzania definition of a stump (URT 2010). Then the root crown was excavated while at the same time the main cable roots originating from root crown were partially exposed up to about 0.5 m away from the stump. Finally, the main cable roots were cut from the crown at the point where root begin to swell abruptly. The approach of cutting and immediate felling, followed by excavation of the root crown, however, appeared to be laborious. We therefore employed a new strategy, where the tree was left un-cut while we excavated the root crown and exposed the main cable roots around the base of the tree. This approach proved to be efficient since the weight of the tree, with the help of pushing or wind, aided significantly in unearthing the root crown.

After felling, the root crown was fully excavated. We used a combination of pickaxes, hand hoes, machetes and spades. Subsequently, for each tree, one or two main cable roots including feeder and anchor roots were selected and traced to their terminal end. The root selection for each tree considered inclusion of small and large roots in order to cover a wide cable
root size ranges. Basal diameter of both excavated and unexcavated main and side cable roots (Fig. 2) were measured. Finally, the root crown and all selected cable roots were carefully washed and their fresh weights determined by means of a spring balance (0.1 kg accuracy). In total 20 main cable roots and 22 side cable roots were selected for *A. marina*. Basal diameter of excavated side cable roots ranged from 0.52 to 1.98 cm with a mean of 1.19 cm (the unexcavated roots had a mean basal diameter of 1.23 cm) while for main cable roots basal diameter ranged from 1.02 to 13.53 cm with a mean of 4.33 cm (the unexcavated roots had a mean basal diameter of 2.57 cm).

Excavation pits for exposing roots ranged from 0.2 to 1.4 m in depth while length of traced cable roots

### Table 2

<table>
<thead>
<tr>
<th></th>
<th><em>A. marina</em> (<em>n</em> = 10)</th>
<th><em>S. alba</em> (<em>n</em> = 10)</th>
<th><em>R. mucronata</em> (<em>n</em> = 10)<em>a</em></th>
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</thead>
<tbody>
<tr>
<td><strong>Plot variables</strong></td>
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<tr>
<td>N (trees ha$^{-1}$)</td>
<td>420 ± 290 0 892</td>
<td>602 ± 532 96 1719</td>
<td>343 ± 319 0 1083</td>
</tr>
<tr>
<td>G (m$^2$ ha$^{-1}$)</td>
<td>10.3 ± 11.0 0 35.6</td>
<td>8.8 ± 6.1 0.3 19.3</td>
<td>9.4 ± 7.1 0 24.2</td>
</tr>
<tr>
<td><strong>Tree parameters</strong></td>
<td></td>
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<tr>
<td>dbh (cm)</td>
<td>17.6 ± 13.2 3.0 38.6</td>
<td>17.1 ± 10.5 6.5 33.8</td>
<td>17.5 ± 10.7 1.4 32.6</td>
</tr>
<tr>
<td>bd (cm)</td>
<td>21.4 ± 14.3 4.1 45.4</td>
<td>24.7 ± 15.1 8.2 51.7</td>
<td>16.6 ± 12.2 1.9 39.1</td>
</tr>
<tr>
<td>ht (m)</td>
<td>9.6 ± 5.4 3.1 21.5</td>
<td>9.5 ± 4.7 4.0 20.9</td>
<td>7.4 ± 6.4 0.8 18.7</td>
</tr>
<tr>
<td>bht(m)</td>
<td>4.2 ± 3.4 0.8 11.0</td>
<td>2.9 ± 2.9 1.1 10.0</td>
<td>4.2 ± 4.9 0.2 12.5</td>
</tr>
<tr>
<td>crd (m)</td>
<td>5.2 ± 3.8 1.4 11.9</td>
<td>4.9 ± 3.3 0.7 10.1</td>
<td>4.3 ± 2.5 0.8 8.1</td>
</tr>
<tr>
<td>crl (m)</td>
<td>5.4 ± 3.2 1.2 10.2</td>
<td>6.6 ± 2.3 2.8 10.9</td>
<td>5.2 ± 3.1 0.6 9.7</td>
</tr>
</tbody>
</table>

*a* For *R. mucronata*, sample size (*n*) for all variables was 10 except for dbh, bd and ht where it was 14 because the stems for multi-stemmed trees were regarded as individual trees.

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Fig. 2 *Avicennia marina* and *S. alba* tree root system (modified from Purnobasuki 2013), the dashed lines indicate cut-off point between root crown and main cable roots and between main cable roots and side cable roots.
ranged from 1.4 to 16.1 m. Since *A. marina* constitute numerous pneumatophores, it was not possible to identify which ones belonging to which root for those located close to the stump. Pneumatophores located up to about 0.5 m from the stump were therefore excluded. However, beyond 0.5 m around the stump, adequate care was taken to identify and gather all pneumatophores from the main and side cable roots being traced.

Sub-samples from different parts of the root system were taken for laboratory analyses. One sub-sample was taken from each root crown by slicing them from the top down towards the tap root so as to secure an appropriate vertical representation. In addition, sub-samples were taken randomly along the lengths of the selected side or main cable roots. In total for all *A. marina* trees, 10 and 19 sub-samples were taken from root crowns and roots, respectively. All sub-samples were labelled and measured for fresh weight using a digital balance (0.01 g accuracy). On average, the sub-samples added up to about 450 g fresh weight per tree.

(2) Destructive sampling of BGB for *S. alba*

The same approach for excavation and destructive sampling as described for *A. marina* was applied for *S. alba*. In total, 20 main cable roots and 13 side cable roots were selected. Furthermore, 10 and 19 sub-samples were taken from root crown and roots, respectively. Excavated pits ranged from 0.2 to 1.8 m in depth and lengths of root tracing ranged from 1.3 to 14.5 m. The basal diameters ranged from 0.83 to 4.43 cm with a mean of 1.82 cm for the excavated side cable roots (the unexcavated roots had a mean basal diameter of 1.79 cm) and from 1.43 to 10.48 cm with a mean of 5.32 cm for the excavated main cable roots (the unexcavated roots had a mean basal diameter of 3.60 cm).

(3) Destructive sampling of BGB for *R. mucronata*

The excavated BGB for *R. mucronata* included root crown and stilt roots from both above and below the ground level (Fig. 3). This conform with IPCC (2006, 2013) guidelines stating that BGB should include all live roots. The same procedure was followed by Komiyama et al. (2005) for *R. mucronata*, Ong et al. (2004) for *Rhizophora apiculata* and Comley and McGuinness (2005) for *Rhizophora stylosa*. Although contrary to our approach, for example, Tamai et al. (1986) and Kairo et al. (2009) excluded the below-ground stilt roots when sampling BGB for *R. mucronata*.

The stilt roots of *R. mucronata* trees are numerously stocked within a limited area (Fig. 3) and are densely entangled, which made it impossible to trace.
individual roots. Instead we performed a total excavation of all roots. After taking tree measurements, the tree was cut just above the root crown (i.e. above the highest stilt root) and felled. Subsequently, the stilt roots were cut approximately at 0.3 m above ground level while the stilt root stumps were marked in order to avoid mixing roots of the subject tree with those of neighbouring trees. Then all belowground stilt roots were completely excavated. The excavation pits ranged from 0.3 to 1.0 m in depth and from 1.6 to 5.1 m in width.

For multi-stemmed *R. mucronata* trees, roots were partitioned based on the proportion of the individual stem basal areas, and each stem was assumed to be a stand-alone tree. For the 10 trees, we therefore have a total of 14 observations for BGB (see also Table 2). A similar procedure is detailed by Clough et al. (1997).

During field work, the different root components of *R. mucronata*, i.e. root crown, above- and belowground stilt roots, were mixed together because initially the study aimed at quantifying total BGB rather than individual component biomass. Despite this, sub-samples from root crown, and above- and belowground stilt roots were extracted separately, weighed for fresh weight, labelled and brought to laboratory for dry weight determination. A total of 7 (from 7 trees), 17 (from 9 trees) and 19 (from 10 trees) sub-samples were extracted from root crowns, and above- and belowground stilt roots, respectively.

Dry weight determination procedures

All sub-samples were taken to laboratory and oven-dried at 105 °C to constant weight. Dry weights of all sub-samples (kg) were determined by using a digital balance.

For *A. marina* and *S. alba*, dry weights of the belowground components, i.e. side and main cable roots and root crown, were determined by multiplying fresh weights and tree- and component-specific DF-ratios derived from the sub-samples. This resulted into individual cable root dry weight (kg root⁻¹) as well as root crown dry weight (kg tree⁻¹). The procedure for determination of total tree BGB (kg tree⁻¹) for *A. marina* and *S. alba* trees was as follows;

(1) From the dry weight of excavated side cable roots (B_{side, excav}) we developed regression models for prediction of dry weight of individual unexcavated side cable roots (B_{side, unexcav}) based on basal side root diameter as predictor variable.

(2) Total dry weight of side cable roots (B_{side}) belonging to an individual main cable root was then determined by adding all predicted dry weights of unexcavated side cable roots to dry weights of excavated side cable roots; $B_{side} = \sum B_{side, excav} + \sum B_{side, unexcav}$.

(3) Total dry weight of the individual sample main cable roots (B_{main}) was determined by adding dry weight of excavated main cable roots (B_{main, excav}) and dry weight from all side cable roots; $B_{main} = B_{main, excav} + B_{side}$.

(4) From the dry weight of individual sample main cable roots, we developed regression models for prediction of dry weight of unexcavated main cable roots (B_{main, unexcav}) based on basal main root diameter as predictor variable.

(5) Total tree root dry weight (B_{roots}) was determined by adding dry weights of excavated main cable roots (B_{main}) and dry weights of predicted main cable roots not excavated (B_{main, unexcav}); $B_{roots} = \sum B_{main} + \sum B_{main, unexcav}$.

(6) Total tree BGB was finally determined by adding total tree root dry weight (B_{roots}) and root crown dry weight (B_{rcrown}); $B_{GGB} = B_{roots} + B_{rcrown}$.

Since the *R. mucronata* trees were totally excavated and since we did not separate the root components (root crown, and above- and belowground stilt roots) when determining fresh weight in the field, dry weight determination procedure for this species was straightforward; we applied tree-specific DF-ratios without differentiating between the root components to convert fresh weight into total tree BGB.

Analyses

Statistical data analyses

All statistical analyses were carried out in R software version 2.8.0 (R Core Team 2013). Prior to dry weight determination, DF-ratios were subjected to analysis of covariance (ANCOVA) to determine differences between species, between individual trees within the same species and between root components within trees following general linear model (GLM) procedures. When analysing difference in DF-ratio between
species, the root component DF-ratios were summarised to tree level all components (i.e. root crown and root) average or simply tree average. When the differences were significant we applied Bonferroni post hoc tests. Diameter at breast height (dbh) served as a covariate in the analyses and significance levels of 0.1, 1 and 5 % were applied. Since DF-ratios varied between species, between individual trees within the same species and between root components, dry weights of *A. marina* and *S. alba* (as described above) were determined by multiplying fresh weight and tree- and component-specific DF-ratios derived from subsamples. ANCOVA was also applied when testing differences in total tree BGB between the tree species.

During explorative data analysis, we found that the relationships between main and side cable root dry weights and basal diameter were nonlinear. We therefore initially tested several options to describe the nonlinear relationships (e.g. second order polynomial functions and exponential functions) but found the power function as the best. The power function has also been widely used to describe biomass relationships (e.g. Niklas 2004; Komiyama et al. 2008). The model form was as follows:

\[ B = \beta_0 \times x^{\beta_1} + \varepsilon \]

where \( B \) = root dry weight of main/side cable roots (kg root\(^{-1}\)), \( x \) = main/side cable root basal diameter (cm), \( \beta_0 \) and \( \beta_1 \) are model parameters and \( \varepsilon \) is an additive error term.

The model fitting was done by using ‘nls2’ function in R software (R Core Team 2013). Both ordinary and weighted nonlinear least squares methods were employed in estimation of model parameters. Regression assumptions on homoscedasticity and normal distribution of residuals were examined by means of graphical plots (plots not displayed in results). Where heteroscedastic error distributions were observed, nonlinear weighted least squares were employed to compensate for violation of homoscedasticity and allocate less weight to extreme observations. Root mean square error (RMSE) and mean prediction error (MPE (%)) for the models were computed as follows:

\[ \text{MPE} (%) = \left( \frac{\sum (e)/n}{MB_{obs}} \right) \times 100 \]

where \( MB_{obs} \) = mean observed dry weight (kg). Two-tailed paired t-tests were employed to determine the significance of MPE (%).

Relationships between BGB and tree variables were determined using Spearman correlation tests. Significance levels of 0.1, 1 and 5 % were applied.

### Evaluation of existing models

Based on literature, we found four models for prediction of tree BGB relevant for testing on our data. The models included a common model developed by Komiyama et al. (2005) (model 1), a species-specific model for *A. marina* developed by Comley and McGuinness (2005) (model 2) and two species-specific models for *R. mucronata* developed by Tamai et al. (1986) (model 3) and Kairo et al. (2009) (model 4);

\[
BGB = 0.199 \times (0.899)^{\text{dbh}^{2.22}}, (R^2 = 0.95, SE = 1.81)
\]

(1)

\[
BGB = 1.28 \times (\text{dbh}^{1.71}), (R^2 = 0.80, \text{RMSE} = 0.268)
\]

(2)

\[
BGB = 0.00974(\text{dbh}^{2} \times \text{ht})^{1.0525}
\]

(3)

\[
\log_{10}(BGB) = -1.3010 + 2.4044 \times \log_{10}(\text{dbh}), (R^2 = 0.70, SE = 0.37)
\]

(4)

where BGB = total tree belowground dry weight (kg), \( \rho = \text{wood density (gcm}^{-3}\)), \( \text{dbh} = \text{diameter at breast height (cm)} \) and \( \text{ht} = \text{total tree height (m)} \). The model reported by Komiyama et al. (2005) requires wood density as a predictor variable. However, wood density values for mangrove species are lacking in Tanzania and Africa in general. We therefore used data from the global wood density (GWD) database (Zanne et al. 2009; Chave et al. 2009). Since we found more than one wood density value for *A. marina*, *S. alba* and *R. mucronata* in GWD database and the values were variable, we applied species-specific mean values, i.e. 0.648 for *A. marina*, 0.508 for *S. alba* and 0.814 for *R. mucronata*.

### Results

Dry to fresh weight ratios (DF-ratios) varied between the tree species and root components (Table 3). The
results based on the ANCOVA test showed that for all components DF-ratio varied significantly between tree species \((F_{(2, 26)} = 11.866, p < 0.001)\). The Bonferroni post hoc tests showed that all components DF-ratio for \(S. alba\) (0.387 ± 0.027 (STD)) was significantly lower than those of \(A. marina\) (0.490 ± 0.041 (STD)) and \(R. mucronata\) (0.470 ± 0.040 (STD)) \((p < 0.01)\). All components DF-ratios for \(A. marina\) and \(R. mucronata\) were not statistically different \((p > 0.05)\). For all the three species, DF-ratios also varied significantly between the belowground components: \(A. marina\) \((F_{(1, 17)} = 22.603, p < 0.001)\), \(S. alba\) \((F_{(1, 17)} = 5.562, p < 0.05)\) and \(R. mucronata\) \((F_{(2, 22)} = 15.163, p < 0.001)\). The Bonferroni post hoc tests showed that for \(A. marina\) and \(S. alba\), root crown DF-ratios were significantly larger than their corresponding root DF-ratios \((p < 0.05)\) while for \(R. mucronata\), root crown and aboveground stilt root DF-ratios were significantly larger than the belowground stilt root DF-ratio.

The tree level root component DF-ratios varied with tree size (dbh) (Fig. 4). The variation is explained by linear \((S. alba\) roots and \(R. mucronata)\) and second order polynomial functions \((A. marina\) and \(S. alba\) root crown\). With the exception of root crown DF-ratio for \(A. marina\) \((R^2 = 0.49, p > 0.05)\) and belowground stilt root DF-ratio for \(R. mucronata\) \((R^2 = 0.003, p > 0.05)\), the variations were significant \((p < 0.05)\).

Models for prediction of side and main cable roots dry weight were developed (Table 4; Fig. 5). Generally, the \(A. marina\) models showed better fit (lower RMSE values and higher \(R^2\) values) than \(S. alba\) models. All models revealed non-significant \((p > 0.05)\) MPE \((\%)\) values. For all models, the distributions of residuals were approximately normally distributed although the residuals slightly increased with increasing basal diameter of the roots.

Mean total tree BGB for \(A. marina\) \((n = 10)\), \(S. alba\) \((n = 10)\) and \(R. mucronata\) \((n = 14)\) were 100.5 ± 93.7 (STD) kg, 273.2 ± 346.7 (STD) kg and 166.0 ± 160.9 (STD) kg, respectively. Despite similarities in tree size (mean dbh of 17.6, 17.1 and 17.5 for \(A. marina\), \(S. alba\) and \(R. mucronata\), respectively, see Table 2) and root size (cable root diameters \((\sim\) up to 13 m) and root lengths \((\sim\) up to 16 m)), the ANCOVA test showed tree BGB was significantly different between species \((F_{(2, 30)} = 3.41, p < 0.05)\). Accordingly, Bonferroni post-hoc tests revealed that, tree BGB was significantly different between \(A. marina\) and \(S. alba\) while for the remaining pairs the differences were not statistically significant \((p > 0.05)\). On average for \(A. marina\), the root crown contributed 34 % (34.0 ± 35.5 (STD) kg) of the total tree BGB while 66 % (66.5 ± 61.0 (STD) kg) came from the roots. The corresponding proportions were 90 % (246.0 ± 329.6 (STD) kg) and 10 % (27.6 ± 38.1 (STD) kg) for \(S. alba\). This paper however, provides no information on biomass for the root components of \(R. mucronata\).

Spearman correlation coefficients described the relationships between total tree BGB and different tree variables (Table 5). All tree variables, except bole height (bht) for \(S. alba\), correlated positively with tree BGB. The correlations were generally strong (ranging from 0.85 to 0.99) and statistically significant \((p < 0.05)\), for dbh, basal diameter (bd) and crown diameter (crd). Total tree height (ht) and crown length (crl) correlated poorly with tree BGB for \(A. marina\) and \(S. alba\) and the relationships were statistically non-significant \((p > 0.05)\). However, the

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Descriptive statistics on distribution of DF-ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Belowground component</td>
</tr>
<tr>
<td>---------</td>
<td>-----------------------</td>
</tr>
<tr>
<td>(A. marina)</td>
<td>-Root crown</td>
</tr>
<tr>
<td></td>
<td>-Root</td>
</tr>
<tr>
<td></td>
<td>All components</td>
</tr>
<tr>
<td>(S. alba)</td>
<td>-Root crown</td>
</tr>
<tr>
<td></td>
<td>-Root</td>
</tr>
<tr>
<td></td>
<td>All components</td>
</tr>
<tr>
<td>(R. mucronata)</td>
<td>-Root crown</td>
</tr>
<tr>
<td></td>
<td>-Aboveground stilt root</td>
</tr>
<tr>
<td></td>
<td>-Belowground stilt root</td>
</tr>
<tr>
<td></td>
<td>All components</td>
</tr>
</tbody>
</table>

All components = root crown and root.
**Fig. 4** Tree level DF-ratios over species and dbh for root crown (upper panel) and roots (lower panel). Individual tree DF-ratio values (solid dots) and trend lines for individual tree values (solid line). Roots for *R. mucronata* (lower panel) are divided into aboveground stilt roots (solid dots, solid line) and belowground stilt roots (open dots, dotted line).

**Table 4** Models for side and main cable root dry weight prediction

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>n</th>
<th>Parameters</th>
<th>RMSE</th>
<th>R²</th>
<th>MPE %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>β₀</td>
<td>β₁</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. marina</em></td>
<td>Side cable root</td>
<td>20</td>
<td>0.10123***</td>
<td>2.60603***</td>
<td>0.085</td>
<td>0.76</td>
</tr>
<tr>
<td><em>A. marina</em></td>
<td>Main cable root</td>
<td>22</td>
<td>0.20390**</td>
<td>1.60410***</td>
<td>0.321</td>
<td>0.73</td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>Side cable root</td>
<td>13</td>
<td>0.46310**</td>
<td>1.60600***</td>
<td>0.519</td>
<td>0.45</td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>Main cable root</td>
<td>20</td>
<td>0.01817*</td>
<td>3.48190***</td>
<td>2.814</td>
<td>0.63</td>
</tr>
</tbody>
</table>

Model form: $B = \beta_0 \times x^{\beta_1} + \varepsilon$ where $B =$ root dry weight (kg root$^{-1}$), $x =$ side/main cable root basal diameter (cm), $\beta_0$ and $\beta_1$ are model parameters and $\varepsilon$ is an additive error term.

* Significant at 5 %, ** significant at 1 % and *** significant at 0.1 %
corresponding correlations were stronger for *R. mucronata*.

The prediction errors for the models selected from previous studies when tested on our data (Table 6). For all cases, except when the common model developed by Komiyama et al. (2005) was applied on *A. marina* data set, the models underestimated tree BGB (not significant for *S. alba*). Where tested models underestimated tree BGB, MPE values ranged from $-56.1 \pm 62.5$ (STD) kg ($-33.8 \%$) to $-186.6 \pm 290.4$ (STD) kg ($-68.3 \%$). When the common model developed by Komiyama et al. (2005) was applied on *A. marina* data set, the model over-estimated tree BGB by $26.2 \pm 69.8$ (STD) kg (26.1 %), although not statistically significant ($p > 0.05$).

**Discussion**

The basic task in any quantification of biomass dry weight is the determination of DF-ratio.

The DF-ratios varied significantly between the three species. Within species, DF-ratios also varied between root components and tree sizes. Based on our results we therefore suggest that future studies should avoid the use of mean DF-ratios across species, root components and trees. Instead, species-, tree- and root component-specific DF-ratios should be applied. Comparable results on DF-ratios for tree BGB of mangrove species are difficult to find in literature. Often DF-ratios are not reported (e.g. Tam et al. 1995; Komiyama et al. 2005; Comley and McGuinness 2005; Kairo et al. 2009). In addition, for the core sampling method (e.g. Tamooh et al. 2008) and the “trench method” (e.g. Komiyama et al. 1987), it is not clear how the root sub-samples for generation of DF-ratios were extracted, how the DF-ratios of roots from different species and tree sizes were distinguished and treated; and finally how they arrived at tree dry weight. Our study has clearly demonstrated that, unless the determination of DF-ratios is consciously and appropriately dealt with, the quantification of dry weight is subject to uncertainties.

The developed side and main cable root dry weight models for *A. marina* and *S. alba* generally showed strong relationships between basal diameter and dry weight.
weights. The mean prediction errors (MPE) for all models were statistically insignificant. It is, however, worth mentioning that main cable root residual variance increased with increasing root basal diameter. Although this pattern is normal for biomass regression models, this point at challenges concerning uncertainty when models are applied outside their data range, as is the case in the current study. For example, the largest basal diameter in the data used to develop the main cable root model for *A. marina* was 13.5 cm, while the largest basal diameter that we measured was 18.5 cm. Clearly when applying a root sampling procedure, like in the present study, extrapolation cannot be avoided. However, including as large data ranges as much as possible, when selecting sample roots, is vital to overcome such challenges. Selection of “one small and one big” root for each sample tree, as done in our study, was an attempt to include diverse root size covering a reasonable data range as a basis for the root dry weight models. Possibly the models would have improved if larger roots were included.

The mean total tree BGB for *A. marina* and *S. alba* were quite different. The larger pneumatophores of *S. alba* as compared to *A. marina* probably explains much of this difference. Larger side and main cable roots for *S. alba* could be another explanation for the observed differences in tree BGB between the two species. It is also worth mentioning that we found relatively large proportions of the total tree BGB for *A. marina* and *S. Alba* stored in root crowns. This suggest that sampling approaches such as root coring (e.g. Tamooh et al. 2008), where the sampling (coring) often is done around the subject tree without including root crown, leaves out an important part in accounting for total tree BGB. The total tree BGB for *R. mucronata* was determined, but unfortunately we do not have any information on the different components of the root system (root crown, above- and

Table 5  Correlation between total BGB dry weight and tree variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Total belowground dry weight (kg tree⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>A. marina</em> (<em>n</em> = 10)</td>
</tr>
<tr>
<td></td>
<td>( \text{dbh (cm)} )</td>
</tr>
<tr>
<td>( \text{dbh (cm)} )</td>
<td>+0.99**</td>
</tr>
<tr>
<td>( \text{bd (cm)} )</td>
<td>+0.98**</td>
</tr>
<tr>
<td>( \text{ht (m)} )</td>
<td>+0.53NS</td>
</tr>
<tr>
<td>( \text{bh (m)} )</td>
<td>+0.33NS</td>
</tr>
<tr>
<td>( \text{crd (m)} )</td>
<td>+0.94**</td>
</tr>
<tr>
<td>( \text{crl (m)} )</td>
<td>+0.53NS</td>
</tr>
</tbody>
</table>

Spearman correlation analysis (e.g. Crawley 2007)

*a* For dbh, bd and ht, \( n = 14 \), NS not significant at 5 %, * significant at 5 %, ** significant at 1 % and *** significant at 0.1 %

Table 6  Mean prediction errors of previously developed BGB models

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>Wood density</th>
<th>BGB (kg tree⁻¹)</th>
<th>MPE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( \text{Pred.} )</td>
<td>( \text{Obs.} )</td>
<td>Mean ± STD (kg tree⁻¹)</td>
</tr>
<tr>
<td><em>A. marina</em> (<em>n</em> = 10)</td>
<td>Common, Komiyama et al. (2005)</td>
<td>( \rho = 0.648^a )</td>
<td>126.7</td>
<td>100.5</td>
</tr>
<tr>
<td></td>
<td>Species-specific, Comley and McGuinness (2005)</td>
<td>–</td>
<td>38.4</td>
<td>100.5</td>
</tr>
<tr>
<td><em>S. alba</em> (<em>n</em> = 10)</td>
<td>Common, Komiyama et al. (2005)</td>
<td>( \rho = 0.508^a )</td>
<td>86.6</td>
<td>273.2</td>
</tr>
<tr>
<td><em>R. mucronata</em> (<em>n</em> = 14)</td>
<td>Common, Komiyama et al. (2005)</td>
<td>( \rho = 0.814^a )</td>
<td>109.9</td>
<td>166.0</td>
</tr>
<tr>
<td></td>
<td>Species-specific, Tamai et al.(1986)</td>
<td>–</td>
<td>75.0</td>
<td>166.0</td>
</tr>
<tr>
<td></td>
<td>Species-specific, Kairo et al. (2009)</td>
<td>–</td>
<td>60.8</td>
<td>166.0</td>
</tr>
</tbody>
</table>

*a* Wood density based on global wood density database (Zanne et al. 2009; Chave et al. 2009)

\(b\) Two-tailed \(t\)-tests, NS not significant at 5 %, * significant at 5 %, ** significant at 1 % and *** significant at 0.1 %
belowground stilt roots) for this species. Obviously the excavation procedure for *R. mucronata* should be modified to accommodate separation of tree BGB into root components.

The strong and statistically significant relationships seen between basal diameter (bd), dbh and crown diameter (crd) and total tree BGB suggest that these variables may be important predictors in tree BGB models. It is worth mentioning that crd as a predictor variable may be of particular interest since the technology for assessment of biomass is advancing. Wannasiri et al. (2013) and Hirata et al. (2014), for example, used high resolution data based on Lidar and QuickBird, respectively, and estimated biomass of mangroves by using crd as predictor variable. Besides, tree height (ht) is usually an important predictor variable in biomass models (e.g. Chave et al. 2014). For our data, however, the relationships between this variable and tree BGB were relatively weak for *A. marina* and *S. alba*, yet stronger for *R. mucronata*.

When the common model developed by Komiyama et al. (2005) was tested on our data, tree BGB were over-estimated for *A. marina* and under-estimated for *S. alba* and *R. mucronata*. Since differences in forest structure, soil, salinity and climate may influence the results, it is generally not surprising that large prediction errors appear when this model is applied outside the data range from where it was developed. A common model is also supposed to work for all relevant tree species, but the data used by Komiyama et al. (2005) did not include *A. marina* (which was one of the target species for the test on our data). Excavation procedures may also have influenced the prediction errors. However, since Komiyama et al. (2005) partly applied full excavation we do not believe that the excavation procedure is a major factor here.

The tested species-specific models (Comley and McGuinness 2005; Tamai et al. 1986; Kairo et al. 2009) all significantly under-estimated tree BGB. The most likely explanation for such under-estimations is loss of biomass due to the excavation procedures applied when these models were developed. For *A. marina*, Comley and McGuinness (2005) applied the “root ball method”. Irrespective of tree size; they limited excavation to a radius of 2 m from the subject tree. Since we in the present study sampled roots as far as 16 m from the tree base, it is quite obvious that models based on data from “root ball method” generally under-estimate tree BGB, and that the under-estimation increases with tree size. Similarly, when Tamai et al. (1986) and Kairo et al. (2009) developed their *R. mucronata* models they did not excavate the belowground stilt roots. Since we during field work observed that a significant proportion of the tree BGB originated from the belowground stilt roots, it is not surprising that the models developed by Tamai et al. (1986) and Kairo et al. (2009) under-estimated tree BGB.

According to Chave et al. (2005, 2014) and Komiyama et al. (2005) the prediction quality of biomass models is improved by including wood density as predictor variable.

However, various sources of information on wood density, including the GWD database (Zanne et al. 2009; Chave et al. 2009), show that species-specific wood density values are variable and that the reasons for such variation is not well documented. Wood density of *A. marina*, for example, varies from 0.520 to 0.732 in the GWD database. Wood density values for the three studied mangrove species based on sites from Tanzania and Africa are in general lacking in the database. In addition to differences in wood density between sites, within-tree differences are likely to be present (e.g. Nock et al. 2009; Santini et al. 2012). It is important that such differences are understood and taken into account when developing models for prediction of biomass. To our knowledge such issues have hardly been investigated for mangroves.

Biomass and carbon quantification are imperative for the implementation of reducing emission from deforestation and forest degradation (REDD) programs. To engage in such programs, Tanzania like other participating countries, need reliable assessment tools for biomass quantification in various forest types including mangroves. This is of particular importance for Tanzania since the country started the first national forest inventory in 2009 (URT 2010). Therefore, more research on mangroves is needed, not only on basic issues such as wood density, but also on the development of local tree BGB models.

**Conclusions**

The present study applied an excavation procedure involving root sampling when quantifying tree BGB for *A. marina* and *S. alba*. This procedure has never been applied to mangroves previously, but seemed to work adequately. Within a given budget, the
procedure facilitates more trees to be included in a sample compared to if all roots are excavated. DF-ratios varied between species, trees and root components. Therefore, species-, tree- and root component-specific DF-ratios were applied in conversion of fresh to dry weight biomass. For *A. marina* and *S. alba* trees, a significant proportion of total tree BGB is stored in the root crown. Future studies should therefore ensure inclusion of root crown in accounting for total tree BGB. Tests of previously developed models on our data revealed large prediction errors, partly due to differences in site conditions and partly due to incomprehensive excavation procedures applied when these models were developed. Local tree BGB models for mangroves should therefore be developed.

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PAPER TWO

Tree basic density, biomass estimation and associated uncertainties: A case of three mangrove species in Tanzania

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Tree basic density, biomass estimation and associated uncertainties: A case of three mangrove species in Tanzania

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Abstract

Focusing on three dominant mangrove species in Tanzania; Avicenia marina (Forssk.) Vierh., Sonneratia alba J. Smith and Rhizophora mucronata Lam., this study determined tree basic density (BD) and assessed sources of BD variations. In addition, it examined accuracy of different tree aboveground biomass (AGB) determination methods. The study covered four sites along the coasts of Tanzania where a total of 120 trees were destructively sampled for aboveground basic density (AGBD), AGB and volume. Among
them, 30 were excavated for belowground basic density (BGBD). The study found an overall mean tree AGBD of 0.60 ± 0.00 (SE) g cm\(^{-3}\), 0.54 ± 0.01 (SE) g cm\(^{-3}\) and 0.69 ± 0.01 (SE) g cm\(^{-3}\) for \textit{A. marina}, \textit{S. alba} and \textit{R. mucronata}, respectively. Similarly, the overall mean tree BGBD was 0.57 ± 0.02 (SE) g cm\(^{-3}\), 0.32 ± 0.01 (SE) g cm\(^{-3}\) and 0.53 ± 0.02 (SE) g cm\(^{-3}\) for \textit{A. marina}, \textit{S. alba} and \textit{R. mucronata}, respectively. The study also showed that BD varied between tree species, among individuals of the same species and between tree components. Sampling for BD therefore should take into account all sources of variations. The species mean AGBD and BGBD respectively may be applied as predictor variables for both above- and belowground biomass estimation in Tanzania. BD may also be useful as a conversion factor. If appropriately determined and applied, BD may contribute to accurate tree AGB estimates.

**Introduction**

Mangroves represent about 0.39% of global forest cover (FAO, 2010) and comprise up to 70 mangrove tree species, out of which 14 are growing naturally along the Eastern Coast of Africa (Saenger et al., 1983; Tomlinson, 1986; Aksornkoae et al., 1992). \textit{Avicenia marina} (Forssk.) Vierh., \textit{Sonneratia alba} J. Smith and \textit{Rhizophora mucronata} Lam. are abundant in Tanzania (Luoga et al., 2004; Nshare et al., 2007).

Mangroves are important for biological, ecological, economic and protection reasons (Kristensen et al., 2008; Spalding et al., 2010; Nagelkerken et al., 2012; Zhang et al., 2012). Besides, although mangroves cover relatively small areas, they hold large quantities of carbon per unit area stored in aboveground biomass (AGB) and belowground biomass
(BGB) (Donato et al., 2011). Despite their importance, mangroves are threatened by
deforestation and forest degradation, which led to a loss of 35% of the World’s mangrove
cover between 1980 and 2000 (Valiela et al., 2001; Langner et al., 2007).

Given the valuable services offered by mangrove ecosystems, their sustainable
management is therefore imperative. Unfortunately most of the services offered by
mangroves are non-market, immaterial services, implying that, in the absence of effective
legal protection against land use change and wood extraction, few measures are available
that may help to protect them. One potential instrument, however, is the Reducing
Emissions from Deforestation and forest Degradation (REDD+) initiative. REDD+ is a
system of financing mechanisms and incentives aimed at mitigating climate change by
reducing deforestation and forest degradation through sustainable management of
forests, conservation and enhancement of carbon stocks (Angelsen and Hofstad, 2008;
UNFCCC, 2011). Participating countries in REDD+ projects are required to produce
accurate estimates for their forest carbon stocks and changes through robust
Measurement Reporting and Verification (MRV) schemes.

The Inter-governmental Panel on Climate Change (IPCC) emphasises that all carbon
estimates prepared for MRV should be accompanied by an appropriate measure of
uncertainty while at the same time minimising all known sources of uncertainty (IPCC,
2006). Based on previous studies, uncertainties are likely to occur at each of the following
stages of biomass quantification: (i) sampling design, (ii) field measurements, (iii) tree level
estimates, (iv) selection of biomass model and (v) selection of basic density values when
used as a biomass predictor variable (Ketterings et al., 2001; Chave et al., 2004; Henry et al., 2010; Clark and Kellner, 2012). Basic density (BD) is defined as oven-dry mass divided by fresh volume expressed in tons m$^{-3}$, kg m$^{-3}$ or g cm$^{-3}$ (Williamson and Wiemann, 2010; Wiemann and Williamson, 2012).

Biomass can be quantified in different ways, but most commonly by applying a biomass model to forest inventory data leading to single tree or stand level estimates. Development of biomass models requires destructive sampling of trees. Selected sample trees are felled and partitioned into various tree components, e.g. stem, branch and; twig and leaf. The merchantable part of the tree, i.e. stem and branch defined by a minimum top diameter (IPCC, 2006), is then crosscut into billets, which can be measured for fresh weight and/or fresh volume over bark. Thus, tree AGB estimates from which carbon stock is derived may be determined in two different methods. First, direct AGB determination method involving determining fresh weight which is then converted to dry weight using dry to fresh weight ratio (DF-ratio) or second, indirect AGB determination method involving determining fresh volume which is then converted to dry weight using BD. The latter method is often suggested for sampling large trees because the former is labour intensive and costly (Brown, 1997; Picard et al., 2012).

For both methods however, the non-merchantable part of the tree has to be determined for fresh weight, which is converted to dry weight using DF-ratio. Merchantable and non-merchantable dry weights are then summarized to get total tree dry weight. The total tree dry weight may be used in the development of biomass models, which can be applied for
prediction of tree biomass based on forest inventory data, leading to tree and stand estimates. Tree and stand level estimates from forest inventory data may alternatively be determined by first using a relevant volume model for prediction of tree merchantable fresh volume, and then applying BD and biomass expansion factor (BEF), or biomass conversion and expansion factor (BCEF) (IPCC, 2006). In such case, BD converts merchantable tree volume to dry weight while BEF accounts for the non-merchantable biomass. On the other hand, BCEF convert merchantable tree volume to dry weight and account for non-merchantable tree biomass.

The DF-ratio and BD are determined from sub-samples extracted from sample trees (Brown et al., 1997; Picard et al., 2012). However, the accuracy of determining tree AGB from volume using BD is unknown. Extraction of sub-samples from sample trees for determination of BD without knowledge on how BD varies between species, among individuals of the same species and between sites may introduce uncertainties when such values are applied for volume to biomass conversion factor or predictor variable. Such uncertainties may also be propagated in measurement of tree sections for determination of merchantable volume. Literature on BD and its variation for mangrove species is scarce and the sources of variation are hardly documented. Adedeji et al. (2013), however, reported BD variations from pith to bark and along stem for Rhizophora racemosa GFW Meyer in Nigeria.

The common practice in estimating biomass is firstly to select a relevant biomass model, and secondly for models requiring BD as a predictor variable, to search for relevant BD values in literature (e.g. Jones et al., 2014) or in the global wood density (GWD) database (Chave et al., 2009; Zanne et al., 2009). This practice may add noise or produce biased
results. The GWD database, for example, is a collection of BD values reported by studies implemented for various purposes, especially studies on wood strength and mechanical properties (Chave et al., 2009; Zanne et al., 2009). Accordingly, the database may include values based on very small samples and limited geographical areas, making the generality and representativeness of BD values poor.

To minimise propagation of uncertainties in subsequent stages of biomass estimation at stand or landscape levels, it is important that uncertainties in tree or sub-tree biomass estimates are identified, quantified and minimised. Focusing on the three dominant mangrove species in Tanzania, A. marina, S. alba and R. mucronata, our study therefore aimed: (i) to determine BD and assess their inter- and intra-species variations, and (ii) test the hypothesis that, during destructive sampling, an indirect method of determining tree AGB (from volume using BD as a conversion factor) yields as accurate estimates as does the direct method (actual weighing). In testing this hypothesis, we applied BD values from the current study as well as relevant values from the GWD database.

**Methods**

**Study area**

In Tanzania, mangrove forests cover about 158,100 hectares (MNRT, 2015) and include ten different species, namely A. marina, B. gymnorhiza, Ceriops tagal (Perr.) C. B. Rob., Heritiera littoralis Dryand., Lumnitzera racemosa Willd., Pemphis acidula J.R. & G. Forst., R. mucronata, S. alba, Xylocarpus granatum Koen. and Xylocarpus moluccensis (Lamk.) Roem. These species also appear in Kenya and Mozambique (Tamooh et al., 2008;
Fatoyinbo *et al.*, 2008; Mohamed *et al.*, 2009). The present study was carried out at four sites along the coastline of Tanzania. The sites included Pangani (5° 38' S, 38° 54' E to 5° 40' S, 38° 53' E), Bagamoyo (6° 20' S, 38° 50' E to 6° 33' S, 39° 06' E), Rufiji (7° 38' S, 39° 16' E to 7° 55' S, 39° 24' E) and Lindi (10° 02' S, 39° 39' E)-Mtwara (10° 23' S, 40° 23' E). Climate in the study area is influenced by north-east monsoon winds blowing from October to March and south-east monsoon winds blowing from April to October. Average annual rainfall varies from 879 mm (Rufiji) to 1240 mm (Pangani) while average annual temperatures range from 25.7 °C (Lindi) to 27.0 °C (Rufiji).

*Plot sampling, measurements of standing trees and tree selection*

Generally site conditions in mangrove forests vary across and not along the sea or river shores. To cover as much variation as possible, we established 37 transects running from the edge of the sea or river across the entire expanse of the mangrove vegetation. Within each transect, one to four circular plots were established, the first plot being located close to the edge of the sea/river (for details, see Njana *et al.*, 2015). The remaining plots were distributed along the transect line, the intervals ranging from 150 to 250 m, depending on the total extension of the mangrove forest. A total of 120 plots were established using a nested plot design. Within the 2 m radius we measured diameter at breast height (dbh) for all trees with dbh ≥ 1 cm and total tree height ≥ 2 m while within the 10 m radius we measured dbh for all trees with dbh ≥ 5 cm. For *A. marina* and *S. alba* trees, dbh was determined at 1.3 m above soil surface while for *R. mucronata* trees dbh was measured at 0.3 m above the highest stilt root.
Within each plot, one tree was selected for destructive sampling; making a total of 120 trees (40 for each of the three species, *A. marina*, *S. alba* and *R. mucronata*). Among the 120 trees sampled for aboveground basic density (AGBD), belowground basic density (BGBD), AGB and aboveground fresh volume, 30 (10 for each of the three species) were excavated for determination of tree BGBD. Fifteen trees (5 for each species) were sampled at each of the sites in Pangani and Lindi-Mtwara, and 45 trees (15 for each species) were sampled at each of the sites in Bagamoyo and Rufiji.

The sample trees were selected subjectively but we ensured adequate representation of each of the three species across sites and diameter range. In addition to allocation of equal numbers of trees to each of the three tree species (i.e. 40), the selection of trees was based on strata defined by five dbh classes; 1–10, 10.1–20, 20.1–30, 30.1–40 and > 40 cm. The strata were established based on previous studies on mangrove structure in the country (Mattia, 1997; Luoga *et al.*, 2004; Nshare *et al.*, 2007). In the selection of trees for excavation (30), the feasibility of belowground sampling was also considered to make excavation less destructive. The sampling procedures are detailed in Njana *et al.* (2015).

For all sample trees of *A. marina* and *S. alba* we measured dbh, basal diameter/diameter at stump height (dsh, diameter 15 cm aboveground level), total tree height (ht), crown diameter (crd) and bole height (bht, height from ground level to first branch). Crown length (crl) was determined as the difference between ht and bht. For *R. mucronata* we measured the same parameters, but bd was measured at the same level as the highest stilt root, also ht and bht were measured from the highest stilt root. Three *R. mucronata* sample trees were multi-stemmed. For these trees, diameters of individual stems (dbh$_i$)
were combined and a surrogate for dbh was determined as \( \text{dbh} = \sqrt{\sum (dbh_i)^2} \) (e.g. Zhou et al., 2007). Mean diameters of trees harvested for AGB estimation were 22.8 cm (1.1 – 70.5 cm), 19.3 cm (1.1 – 63.6 cm) and 18.0 cm (1.4 – 41.5 cm) for A. marina, S. alba and R. mucronata, respectively. For excavated trees the mean diameters were 17.6 cm (3.0 to 38.6 cm) for A. marina, 17.1 cm (6.5 to 33.8 cm) for S. alba and 17.5 cm (1.4 to 32.6 cm) for R. mucronata. Details are provided in Njana et al. (2015).

**Destructive sampling**

Sampling aimed to generate data for determination of tree AGBD, BGBD, AGB and aboveground fresh volume. Aboveground tree components included stem, branch, and twig and leaf, while belowground tree components included root crown and root.

Using a chainsaw, sample trees were cut at 15 cm above soil surface (A. marina and S. alba) and immediately above the highest stilt root for R. mucronata. After felling a tree, the aboveground part was separated into three components; (i) stem, (ii) branch (≥ 5 cm diameter) and (iii) twig (< 5 cm diameter) and leaf for trees with dbh ≥ 15 cm. Separation of twig and leaf was time consuming and therefore this was only done for 10 out of the 40 trees for each of the three species. Stems and branches were cross-cut into billets. Fresh weights of large billets (dbh ≥ 5 cm) were determined using spring balance (to the nearest 0.1 kg) while those from small trees (dbh < 5 cm) were determined using a digital balance (to the nearest 0.01 kg). The length of billets ranged from 0.14 to 2.22 m depending on the form of stem or branch. For trees partitioned into twig and leaf, their fresh weights were determined separately while in all other cases, we recorded an aggregate fresh weight of twigs and leaves.
Furthermore, for each sample tree with dbh ≥ 15 cm, the cross-cut billets (> 5 cm thick) were recorded for mid-diameter (cm) and length (m) in order to determine merchantable volume. By merchantable volume we mean the volume of the tree including stem and branch to a fixed top diameter of 5 cm. The number of trees with diameter ≥ 15 cm were 22 (A. marina), 12 (S. alba) and 21 (R. mucronata).

From each sample tree we extracted three sub-samples from stems, two from branches and two from twigs for determination of BD and DF-ratio. All sub-samples included bark (Fearnside, 1997; Somogyi et al., 2007). Sub-samples from all aboveground tree components except for stems, were extracted from randomly selected locations. For the stem, sub-samples were extracted at 0%, 40% and 70% of total tree height (e.g. Githomi and Kariuki, 2010). Total tree height ranged from 3.1 to 30.6 m for A. marina, from 3.1 to 28.1 m for S. alba and from 0.8 to 32.2 m for R. mucronata.

BGBD on the other hand was determined through excavation of root crown and roots. For A. marina and S. alba the belowground part consisted of root crown and roots (see Figure 1); and root crown, aboveground stilt roots and belowground stilt roots for R. mucronata (see Figure 2). Details on excavation procedures are provided in Njana et al. (2015). For all the three species, after excavation of the different belowground parts, sub-samples from root crown were collected by slicing from top down wards so as to secure an appropriate vertical representation.
The dashed lines indicate cut-off points between root crown and main cable roots and between main cable roots and side cable roots.

In addition, sub-samples were extracted from randomly selected locations along the length of side or main cable roots (A. marina and S. alba). For R. mucronata in addition to sub-samples from root crown, sub-sample were also collected from randomly selected locations on above and belowground stilt root.

After extraction, sub-samples were immediately determined for fresh weights using a digital balance (to the nearest 0.01 g) followed by labelling and packing for further measurements in laboratory.
Figure 2 R. mucronata tree root system, the dashed lines indicate cut-off points between root crown and stilt roots.

Laboratory procedures

In the laboratory, sub-samples were soaked in distilled water and fresh volume determined by water displacement (Brown, 1997). Subsequently, sub-samples were oven-dried to constant weight at 105 °C and their dry weight determined by a digital balance (Picard et al., 2012).

Determination of BD, DF-ratio, tree AGB and volume

For each tree component sub-sample, BD was determined as oven-dry weight (g) per fresh volume (cm$^3$). DF-ratio was determined as the ratio of sub-sample dry to fresh weight. Exploratory analysis of covariance (ANCOVA) for DF-ratios, where dbh served as a
covariate, revealed that the DF-ratios varied significantly between aboveground tree components and over tree size ($p < 0.05$). In general, DF-ratios varied from 0.28 to 0.66 for *A. marina*, from 0.22 to 0.69 for *S. alba* and from 0.33 to 0.71 for *R. mucronata*.

Total observed fresh weight of each aboveground component was obtained by summation. Since crown materials were partitioned into twig and leaf for only 10 trees (for each of the three species) among the larger trees (dbh $> 15$ cm), we initially computed species-specific twig to leaf ratio based on the 10 observations for each species, which was used to partition the aggregate weight of twig and leaf component into individual twig and leaf weights for trees not partitioned into that level. Then total observed tree AGB was calculated as sum of the product of tree- and component-specific fresh weight and DF-ratio:

$$A\text{GB}_{h, st} = \sum_{i=1}^{n} (FW_{hi, st} * DF_{h, st}) + \sum_{b=1}^{n} (FW_{hi, br} * DF_{h, br}) + \sum_{t=1}^{n} (FW_{hi, tw} * DF_{h, tw}) + \sum_{l=1}^{n} (FW_{hi, le} * DF_{h, le})$$

where $n = $ total number of billets/twig bundles/leaf weights for a given aboveground tree component, $s = $ stem, $b = $ branch, $t = $ twig, $l = $ leaf, $h = $ $h^{th}$ tree, $i = $ $i^{th}$ sub-section, $A\text{GB}_{h, st} = $ observed total tree aboveground dry weight (kg), $FW_{hi, st}$, $FW_{hi, br}$, $FW_{hi, tw}$ and $FW_{hi, le}$ are stem, branch, twig and leaf fresh weights (kg), respectively, and $DF_{h, st}$, $DF_{h, br}$, $DF_{h, tw}$ and $DF_{h, le}$ are stem, branch, twig and leaf DF-ratios, respectively.

The volume of individual billets was computed using Huber’s formula (e.g. West, 2009). Merchantable volume was calculated as the sum of the volumes of all billets for each tree.
component (stem, branch). We applied tree- and component specific BD values to convert merchantable volume to biomass. Tree-specific and species-specific mean BD values were also tested. In addition, we applied species-specific BD values from the GWD database.

The estimated tree AGB was calculated as follows:

\[
AGB_{est} = \sum_{i=1}^{n_i} \left( FV_{hi} \times BD_{hi} \right) + \sum_{i=1}^{n_b} \left( FV_{hb} \times BD_{hb} \right) + \sum_{i=1}^{n_t} \left( FW_{hi} \times DF_{hi} \right) + \sum_{i=1}^{n_l} \left( FW_{hl} \times DF_{hl} \right)
\]

where \( n = \) total number of billets/twig bundles/leaf weights for a given aboveground tree component, \( s = \) stem, \( b = \) branch, \( t = \) twig, \( l = \) leaf, \( h = h^{th} \) tree, \( i = i^{th} \) sub-section, \( AGB_{est} = \) estimated total tree aboveground dry weight (kg), \( FV_{hi} \) and \( FV_{hb} \), are stem and branch fresh volume (m\(^3\)), respectively, and \( BD_{hi} \) and \( BD_{hb} \) are stem and branch DF-ratios, respectively. Other abbreviations are as defined previously.

**Statistical data analysis**

Data was analysed using R software (R Core Team, 2013). We initially analysed BD variation between species at tree level followed by determination of inter- and intra-tree BD variances. To analyse inter-tree BD variation, BD values were summarised by calculating tree level mean AGBD and BGBD. Trees per hectare (N) and basal area (G) (m\(^2\) ha\(^{-1}\)), dbh class (10 cm classes) and study site were included in the analysis as inter-tree BD variation determinants. The potential determinants were selected based on previous studies (e.g. Zhang et al., 2011; Auty et al., 2014).
Variation in BD between tree species was determined using linear mixed-effect model (LMM) procedures (Gałecki and Burzykowski, 2013), where species served as a fixed-effects variable. LMMs extend ordinary linear regression models (i.e. fixed) by incorporating random effects, which account for correlation between observations within the same group (Pinheiro and Bates, 2000). The use of LMM was motivated by the hierarchical structure of data used in this study. Since tree BD observations were nested within site, site was considered as a random-effects variable:

\[
BD_{ijk} = (\beta_0 + \alpha_k) + \beta_1 \ast species_{ijk} + \beta_2 \ast dbh_i + \varepsilon_{ijk},
\]

where \(BD_{ijk}\) is a basic density (g cm\(^{-3}\)) (AGBD or BGBD) value of tree \(i\) for species \(j\) in site \(k\), \(\beta_0, \beta_1\) and \(\beta_2\) are fixed-effects parameters, \(\alpha_k\) is a random-effects parameter for site \(k\), \(dbh_i\) is the diameter of tree \(i\) and \(\varepsilon_{ijk}\) is the error term of tree \(i\) for species \(j\) in site \(k\), which is assumed to be normally distributed with mean 0 and variance \(\sigma^2\). Model fitting was done using \textit{lme} function in \texttt{nlme} package in R. Significance of species in explaining variation of BD was determined by \(F\)-tests. Post-hoc tests were done using \textit{glht} function in \texttt{multcomp} package in R.

Preliminary analysis showed that N, G and dbh class were approximately linearly related with tree BD. Therefore for each of the three species, the influence of these variables, together with site, on BD was determined using LMM. In this case N, G, dbh class and site served as fixed-effects variables:
\[ BD_{ijl} = (\beta_0 + \alpha_i) + \beta_1 * N_{ijl} + \beta_2 * G_{ijl} + \beta_3 * dbh\ class_{ijl} + \beta_4 * site_{ijl} + \epsilon_{ijl} , \]

where \( BD_{ijl} \) is a basic density (AGBD or BGBD) value of tree \( i \) for species \( j \) in plot \( l \), \( \beta_0, \beta_1, \beta_2, \beta_3 \) and \( \beta_4 \) are fixed-effects parameters, \( \alpha_i \) is a random-effects parameter for plot \( l \) and \( \epsilon_{ijl} \) is the error term of tree \( i \) for species \( j \) in plot \( l \). \( \alpha_i \) and \( \epsilon_{ijl} \) were assumed to be normally distributed with mean 0 and a variance \( \sigma^2 \). Model fitting was done as described earlier.

Generally among the analysed determinants of tree BD, dbh class, site and species had significant effects on tree AGBD and that preliminary analysis revealed nonlinear relationship between tree AGBD and dbh while for BGBD this was not the case. Therefore AGBD was modelled as a function of dbh (fixed-effects variable) using the nonlinear mixed-effects modelling approach. Species, site and plot were considered as random-effects variables leading to the following overall model:

\[ BD_{ijk} = (\beta_0 + \alpha_0_{ijk}) * dbh_i^{(\alpha_1 + \alpha_2)} + \epsilon_{ijk} \]

where \( \alpha_0_{ijk} \) and \( \alpha_{ijk} \) respectively are coefficient and exponent random-effects parameters for \( i^{th} \) tree and \( j^{th} \) species. Other variables and parameters are as defined previously.

For the developed models, we computed root mean squared error (RMSE (%)) (Chai and Draxler, 2014; Walther and Moor, 2005) and mean prediction error (MPE (%)) (Chai and Draxler, 2014; Walther and Moor, 2005) as measures of goodness of fit;

\[ RMSE(\%) = \left( \frac{\sqrt{\sum (e_{ijk}^2)/n}}{MB_{obs}} \right) * 100 \]
\[
MPE(\%) = \left( \frac{\sum e_{ijk}}{MB_{obs}} \right) * 100
\]

where \( e_{ijk} \) = residuals, i.e. difference between predicted and observed biomass (kg), \( n \) = sample size, \( MB_{obs} \) = mean observed biomass (kg).

We also determined variation in BD between tree components (intra-tree variation) using LMM, in this case tree component was treated as a fixed-effects variable. Subsequently, BD variation within tree components was carried out. For stem, the analysis considered variation along stem (i.e. intra-tree variation) using data from the three different sampling heights, i.e. 0%, 40% and 70% of total tree height while for other tree components, this involved variation in BD for observations in each tree component. Since the studied mangroves are uneven-aged with varying total tree heights, there are differences in stem absolute sampling heights. To allow cross comparisons, we computed the stem absolute sampling heights \((absht)\) for all the three sampling levels and sample trees, which were then used in the analysis as source of variation. Since BDs were nested within sample trees and sample trees nested within site, the analysis was done using LMM by treating stem absolute sampling height as a fixed-effects variable (stem) and site and tree as random-effects variables (all components):

\[
BD_{mijk} = (\beta_0 + \alpha_{kij}) + \beta_1 * absht_{mijk} + \beta_2 * dbh_{ijk} + \epsilon_{mijk}
\]

where \( BD_{mijk} \) is a stem basic density value at position \( m \) within tree \( i \) for species \( j \) in site \( k \), \( \beta_0 \) and \( \beta_1 \) are fixed-effects parameters, \( \alpha_{kij} \) is a random-effects parameter for tree \( i \) belonging to species \( j \) in site \( k \) and \( \epsilon_{mijk} \) is the error term at position \( m \) within tree \( i \) for
species $j$ in site $k$. $\alpha_{kj}$ and $\epsilon_{mijk}$ were assumed to be normally distributed with mean 0 and a variance $\sigma^2$. Model fitting and post-hoc tests were done as described earlier.

Tree AGB estimation using BD as a conversion factor was analysed by comparing estimated and observed tree biomass where measures of precision, including standard deviation (STD), confidence interval (95% CI, mean $\pm t$*standard error of a mean (SE)) and relative precision (RP, i.e. $t$*SE*100/mean), were calculated separately for observed and estimated tree AGB. Tree AGB estimated using BD were considered precise when they showed lower STD, CI and lower value of RP than their corresponding values for observed tree AGB. We also computed percentage Mean Prediction Error (MPE (%)) as a measure of accuracy. Positive MPE (%) values and significantly different from zero signified over-estimation of tree AGB (i.e. positive bias). Similarly, negative MPE (%) values and significantly different from zero indicated under-estimation of tree AGB (i.e. negative bias). Conversely, non-significant MPE (%) values implied unbiased estimations hence accurate (Walther and Moore, 2005, IPCC, 2003). Tree AGB determined through weighing was considered as observed values and assumed to have been determined without error.

Results

Basic density (BD) values and variations

Basic density (BD) values for aboveground and belowground tree components as well as overall for the three mangrove species are summarised in Table 1. The results revealed that the BD values varied considerably between and within species. For example, tree mean AGBD ranged from 0.54±0.01 (SE) g cm$^{-3}$ ($S. alba$) to 0.70±0.01 (SE) g cm$^{-3}$ ($R. mucronata$) while for tree BGBD the overall mean ranged from 0.30±0.01 (SE) g cm$^{-3}$ ($S.$
*alba* to 0.54±0.02 (SE) g cm\(^{-3}\) (*A. marina*). Within species, large variations were noted for twig BD (0.35 – 0.73 g cm\(^{-3}\)) and overall tree mean AGBD (0.38 – 0.58 g cm\(^{-3}\)) for *S. alba*. Similarly, belowground stilt root BD (0.12 – 0.63 g cm\(^{-3}\)) and overall tree mean BGBD (0.32 – 0.59 g cm\(^{-3}\)) for *R. mucronata* exhibited large variation. The standard deviation (STD) within species was generally low, e.g. STD of tree AGBD was less than 0.05 for *A. marina*.

Results based on LMM revealed a significant variation of tree AGBD \(F_{(2, 112)} = 195.41, \ p < 0.001\) and BGBD \(F_{(2, 23)} = 29.34, \ p < 0.001\) between species. Post-hoc tests for multiple comparisons indicated that all pairwise comparisons were significantly different at the 0.1% level, except for the BGBD of *A. marina* and *R. mucronata*, which were not significantly different \(p > 0.05\).
Table 1 Descriptive statistics on distribution of tree aboveground (AGBD) and belowground basic density BGBD (g cm$^{-3}$) for the three mangrove species.

<table>
<thead>
<tr>
<th>Basic density/ Component</th>
<th>A. marina</th>
<th>S. alba</th>
<th>R. mucronata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean±SE$^1$</td>
<td>STD</td>
</tr>
<tr>
<td>AGBD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Twig</td>
<td>38 (72)</td>
<td>0.59±0.01</td>
<td>0.05</td>
</tr>
<tr>
<td>-Branch</td>
<td>27 (50)</td>
<td>0.59±0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>-Stem</td>
<td>40 (119)</td>
<td>0.60±0.00</td>
<td>0.05</td>
</tr>
<tr>
<td>Overall</td>
<td>40</td>
<td>0.60±0.00</td>
<td>0.03</td>
</tr>
<tr>
<td>BGBD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Root crown</td>
<td>10 (10)</td>
<td>0.61±0.02</td>
<td>0.07</td>
</tr>
<tr>
<td>-Root</td>
<td>10 (19)</td>
<td>0.45±0.02</td>
<td>0.08</td>
</tr>
<tr>
<td>-Aboveground stilt root</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>-Belowground stilt root</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Overall</td>
<td>30</td>
<td>0.57±0.02</td>
<td>0.07</td>
</tr>
</tbody>
</table>

$^1$SE = Standard error of a mean; Note: Since basic density (BD) varies between trees, the BD average values represent weighted mean using tree AGB for AGBD and BGB for BGBD as weights, n = number of sample trees and number in the brackets indicate total number of sub-samples extracted from the trees.
When considering sources of variations (Table 2), number of trees per hectare was a significant source of variation in tree aboveground basic density and their monotonic relationship was negative (*A. marina*). For *S. alba* and *R. mucronata*, basal area (m² ha⁻¹) significantly influenced aboveground basic density and their relationship was strong and positive. Similarly the relationship between tree AGBD and dbh class was strong and positive and that BD varied significantly between site (*S. alba* and *R. mucronata*, Table 2). In all other cases, the effect of determinants both on AGBD and BGBD were not significant. Despite site being a non-significant source of variation in AGBD for *A. marina* however, AGBD varied from 0.59±0.01 (SE) g cm⁻³ (Pangani) to 0.63±0.01 (SE) g cm⁻³ (Lindi-Mtwara) and BGBD varied from 0.53±0.01 (SE) g cm⁻³ (Rufiji) to 0.55±0.04 (SE) g cm⁻³ (Bagamoyo). Similar variation was observed for *S. alba* and *R. mucronata*.

### Table 2 Inter-tree basic density (BD) variation for three mangrove species

<table>
<thead>
<tr>
<th>Sources of variations</th>
<th>Category</th>
<th><em>A. marina</em></th>
<th><em>S. alba</em></th>
<th><em>R. mucronata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>r</td>
<td>df</td>
</tr>
<tr>
<td>N (trees ha⁻¹)</td>
<td>AGBD</td>
<td>1, 30</td>
<td>7.48⁺</td>
<td>-0.23NS</td>
</tr>
<tr>
<td></td>
<td>BGBD</td>
<td>1, 1</td>
<td>1.33NS</td>
<td>0.30NS</td>
</tr>
<tr>
<td>G (m² ha⁻¹)</td>
<td>AGBD</td>
<td>1, 30</td>
<td>0.28NS</td>
<td>-0.18NS</td>
</tr>
<tr>
<td></td>
<td>BGBD</td>
<td>1, 1</td>
<td>0.20NS</td>
<td>0.44NS</td>
</tr>
<tr>
<td>dbh class (cm)</td>
<td>AGBD</td>
<td>4, 30</td>
<td>1.42NS</td>
<td>0.18NS</td>
</tr>
<tr>
<td></td>
<td>BGBD</td>
<td>3, 1</td>
<td>1.59NS</td>
<td>0.48NS</td>
</tr>
<tr>
<td>Site</td>
<td>AGBD</td>
<td>3, 30</td>
<td>0.91NS</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>BGBD</td>
<td>3, 1</td>
<td>0.76NS</td>
<td>-</td>
</tr>
</tbody>
</table>

Note: r = spearman correlation, NS = Not Significant at 5%; *, ** and *** significant at 5%, 1% and 0.1%, respectively.

Results summarised in Table 3 and Figure 3 demonstrates that, the variation in AGBD between dbh was significant. All parameter estimates were significant and the models fitted well to data as
indicated by the low MRSE (%) and MPE (%). Site and species as random-effects variables improve the goodness of fit however, while site level parameter estimates were not significant species level parameter estimates were significant.
Table 3  Tree mean aboveground basic density prediction models for the three mangrove species.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Model form</th>
<th>n</th>
<th>Parameter estimates</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>Model ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common/Fixed-effects</td>
<td>$BD_{ijk} = (\beta_0 + \alpha_{ij}) \cdot dbh_{i}^{1/3} + \epsilon_{ijk}$</td>
<td>120</td>
<td>$\hat{\beta}_0$</td>
<td>0.50453*</td>
<td>14.3</td>
<td>+1.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\hat{\beta}_1$</td>
<td>0.06076*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\delta_{0,0}$</td>
<td>0.06076</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\delta_{1,0}$</td>
<td>0.06076</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\epsilon_{ijk}$</td>
<td>0.06076</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\epsilon_{ijk}$</td>
<td>0.06076</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Species-specific/Random-effects

- A. marina

$BD_{ijk} = (\beta_0 + \alpha_{ij}) \cdot dbh_{i}^{1/3} + \epsilon_{ijk}$

<table>
<thead>
<tr>
<th>n</th>
<th>Parameter estimates</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>Model ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>$\hat{\beta}_0$</td>
<td>0.56839*</td>
<td>5.5</td>
<td>-0.1</td>
</tr>
<tr>
<td></td>
<td>$\hat{\alpha}_{ij}$</td>
<td>0.1907*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\epsilon_{ijk}$</td>
<td>0.1907*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- S. alba

$BD_{ijk} = (\beta_0 + \alpha_{ij}) \cdot dbh_{i}^{1/3} + \epsilon_{ijk}$

<table>
<thead>
<tr>
<th>n</th>
<th>Parameter estimates</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>Model ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>$\hat{\beta}_0$</td>
<td>0.36774*</td>
<td>9.0</td>
<td>+0.1</td>
</tr>
<tr>
<td></td>
<td>$\hat{\alpha}_{ij}$</td>
<td>0.10787*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\epsilon_{ijk}$</td>
<td>0.10787*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- R. mucronata

$BD_{ijk} = (\beta_0 + \alpha_{ij}) \cdot dbh_{i}^{1/3} + \epsilon_{ijk}$

<table>
<thead>
<tr>
<th>n</th>
<th>Parameter estimates</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>Model ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>$\hat{\beta}_0$</td>
<td>0.57748*</td>
<td>5.3</td>
<td>-0.2</td>
</tr>
<tr>
<td></td>
<td>$\hat{\alpha}_{ij}$</td>
<td>0.05535*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\epsilon_{ijk}$</td>
<td>0.05535*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3 Relationship between tree aboveground BD and diameter at breast height (dbh) \((n = 40)\). The curves illustrate the tree aboveground basic density prediction models for the three species.

For intra-tree BD variation, the results showed that tree component was an important source of variation as BD varied between tree components. This was particularly evident for \textit{R. mucronata} where BD varied significantly both for above- \((p < 0.001)\) and belowground tree components \((p < 0.001)\) (Table 4). Post-hoc tests for multiple comparisons showed that twigs had significantly lower BD compared to stems and branches for \textit{R. mucronata}. Similarly, for \textit{R. mucronata} BD varied significantly between aboveground and belowground stilt roots and root crown. Additionally, for \textit{A. marina}, the root BD was significantly lower than root crown BD.

The results also showed that within trees, BD varied with sampling heights along stem (Figure 4). The variation was significant for \textit{S. alba} \(F_{1, 114} = 7.80, p < 0.001\) but not for the other two species. For other tree components, BD varied significantly among twigs \((p < 0.05)\) and branches \((p < 0.01)\) for \textit{A. marina}, among roots \((p < 0.01)\) for \textit{S. alba} and among belowground stilt roots \((p < 0.01)\) for \textit{R. mucronata}. In all other cases the among tree component variation was insignificant \((p > 0.05)\).
Table 4 Intra-tree basic density (BD) variation for three mangrove species.

<table>
<thead>
<tr>
<th>Sources of variations</th>
<th>Category</th>
<th>A. marina</th>
<th></th>
<th>S. alba</th>
<th></th>
<th>R. mucronata</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>df</td>
<td>F</td>
<td>df</td>
<td>F</td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Tree component</td>
<td>AGBD</td>
<td>2, 65</td>
<td>0.94</td>
<td>NS</td>
<td>2, 58</td>
<td>6.83</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>BGBD</td>
<td>1, 9</td>
<td>99.65</td>
<td>***</td>
<td>1, 9</td>
<td>2.38</td>
<td>NS</td>
</tr>
</tbody>
</table>

Note: For aboveground basic density the tree components include stem, branch and twig; for belowground basic density they include root crown and root, NS = Not Significant at 5%; *, ** and *** significant at 5%, 1% and 0.1%, respectively.

Figure 4 Distribution of basic density (BD) over absolute sampling height (absht); solid black dot, solid gray dot and plus respectively represents stem BD at 0%, 40% and 70% of total tree height.
Accuracy and precision of biomass estimation using BD as a conversion factor

The use of tree- and component-specific BD resulted in unbiased tree AGB estimates as indicated by the non-significant mean prediction errors (MPEs) for the three species (Table 5). Generally uncertainties in tree AGB estimation increased from the use of tree- and component-specific BD, where estimates were quite accurate (low MPE) to the use of BD from the GWD database, where estimates were less accurate, i.e. higher MPE for all the three species (Table 5). For example, the use of BD from the GWD database resulted into negative bias for S. alba while for R. mucronata it resulted into positive bias. Results presented in Figure 5 showed that observed and estimated tree AGB were generally in agreement with one another. When tree- or species-specific mean BD values were applied however, disagreement was noted for larger values of tree AGB. For A. marina, precision of tree AGB increased from the use of tree- and component specific BD (low 95% CI, STD and RP) to the use of BD from the GWD database (high 95% CI, STD and RP) although contrary results were observed for S. alba and R. mucronata.
Table 5 Accuracy and precision of tree aboveground biomass (AGB) estimation using basic density (BD) as a conversion factor.

<table>
<thead>
<tr>
<th>Species</th>
<th>Basic density applied</th>
<th>$n^1$</th>
<th>Total single tree AGB observations</th>
<th>Total single tree AGB estimates</th>
<th>MPE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>CI (kg)$^2$</td>
<td>STD</td>
<td>RP (%)$^3$</td>
</tr>
<tr>
<td>A. marina</td>
<td>Tree- and component-specific mean from this study</td>
<td>22</td>
<td>761.5±259.5</td>
<td>621.0</td>
<td>34.1</td>
</tr>
<tr>
<td></td>
<td>Tree-specific mean from this study</td>
<td>22</td>
<td>761.5±259.5</td>
<td>621.0</td>
<td>34.1</td>
</tr>
<tr>
<td></td>
<td>Overall species-specific mean from this study</td>
<td>22</td>
<td>761.5±259.5</td>
<td>621.0</td>
<td>34.1</td>
</tr>
<tr>
<td></td>
<td>GWD database species-specific mean</td>
<td>22</td>
<td>761.5±259.5</td>
<td>621.0</td>
<td>34.1</td>
</tr>
<tr>
<td>S. alba</td>
<td>Tree- and component-specific mean from this study</td>
<td>12</td>
<td>536.3±181.6</td>
<td>321.0</td>
<td>33.9</td>
</tr>
<tr>
<td></td>
<td>Tree-specific mean from this study</td>
<td>12</td>
<td>536.3±181.6</td>
<td>321.0</td>
<td>33.9</td>
</tr>
<tr>
<td></td>
<td>Overall species-specific mean from this study</td>
<td>12</td>
<td>536.3±181.6</td>
<td>321.0</td>
<td>33.9</td>
</tr>
<tr>
<td></td>
<td>GWD database species-specific mean</td>
<td>12</td>
<td>536.3±181.6</td>
<td>321.0</td>
<td>33.9</td>
</tr>
<tr>
<td>R. mucronata</td>
<td>Tree- and component-specific mean from this study</td>
<td>21</td>
<td>611.4±167.7</td>
<td>392.1</td>
<td>27.4</td>
</tr>
<tr>
<td></td>
<td>Tree-specific mean from this study</td>
<td>21</td>
<td>611.4±167.7</td>
<td>392.1</td>
<td>27.4</td>
</tr>
<tr>
<td></td>
<td>Overall species-specific mean from this study</td>
<td>21</td>
<td>611.4±167.7</td>
<td>392.1</td>
<td>27.4</td>
</tr>
<tr>
<td></td>
<td>GWD database species-specific mean</td>
<td>21</td>
<td>611.4±167.7</td>
<td>392.1</td>
<td>27.4</td>
</tr>
</tbody>
</table>

$^1$ Includes only trees with diameter ≥ 15 cm; $^2$ 95% confidence interval i.e. mean ± t·SE; $^3$ Relative precision (RP) = t·SE/mean; $^* =$ significant at 5%, $^{**} =$ significant at 1% and $^{***} =$ significant at 0.1%, otherwise non-significant (NS).
Figure 5 Observed (direct method) versus estimated (indirect method) tree AGB for A. marina (left panel), S. alba (middle panel) and R. mucronata (right panel). Note: A = Tree- and component-specific mean BD, B = Tree-specific mean BD, C = Overall species-specific mean BD and D = GWD database species-specific mean BD. Dashed black lines represent 1:1 relationship between observed and estimated values.

Discussion

This study reports tree AG- and BGBD values for three mangrove species in Tanzania. To our knowledge this is the first study to report BGBD for the three mangrove species. For a given species, it may be expected that different studies would yield similar values of tree BD. Komiyama et al.
(2005) reported a tree BD value similar to our study for *R. mucronata* (0.7±0.03 (STD) g cm$^{-3}$). However, Komiyama *et al.* (2005) and Jachowski *et al.* (2013), respectively, reported BD values of 0.48±0.05 (STD) g cm$^{-3}$ and 0.41±0.04 (STD) g cm$^{-3}$ for *S. alba*, the BD values reported in both studies are different from each other but also different from the values reported in our study.

The tree BD values reported in our study are also different from those reported in the GWD database (Chave *et al.*, 2009; Zanne *et al.*, 2009), where the values vary considerably. For example, tree BD values for *A. marina* vary from 0.52 to 0.73 g cm$^{-3}$ while for *S. alba* they vary from 0.39 to 0.63 g cm$^{-3}$. The variation of these values is beyond the 95% confidence interval of the tree AGBD values in our study for *A. marina* (0.58) and *S. alba* (0.52 – 0.56). Among other factors, the variation of BD noted between different studies may be due to differences in site conditions, BD determination methods, sampling, sample size and the purpose for which the studies were undertaken. For instance, many BD values reported in databases were prepared to describe wood mechanical properties and may therefore be based on small sample sizes, probably originating from very few sites, thus making generality of the estimates poor. The variation in tree BD between studies limits the reliability of results generated using such values as conversion factors for biomass estimation or as predictor variables.

We also found variation in BD at species level which varied between trees and between tree components, and in some cases the variation was significant (Tables 2 and 3, Figure 3). Factors responsible for the between tree and between tree component variation may be associated with variation in number of trees per hectare, basal area, tree size and site (Table 2) and life strategies. Differences in genetic make-up, climatic and growth conditions may also explain variation in BD between trees. Within trees, for example, BD variation along stem may be due to the proportion of wood versus bark and heart wood versus sap wood variation, cell walls and growth rate. In line with
our findings, Saintini et al. (2012), found different wood density values at different sites for *A. marina*. In our study, however, BD values were not significantly different between sites for *A. marina*. Saintini et al. (2012) reported that, growth rate of *A. marina* were positively correlated with xylem vessel size and BD and concluded that, high wood density was associated with large xylem vessels and thick fibre walls.

The strong and positive relationship between tree AGBD and dbh suggest that, tree AGBD may be predicted using dbh as a predictor variable which is readily made available through forest inventory (Table 3 and Figure 3). Accordingly, models for prediction of tree-specific mean AGBD (Table 3) may be applied to generate the tree mean BD values. Based on indicators for goodness of fit, we recommend the species-specific/random-effects to common/fixed-effects models. In addition to applying such values as co-predictor variable for modelling both species-specific and multi-species tree AGB thereby improving predictive accuracy of tree biomass, they may also be applied in evaluating predictive accuracy of existing models (e.g. Chave et al., 2004; Chave et al., 2005; Komiyama et al., 2005). Where BD models or tree level BD data are lacking however, species-specific modelling of tree biomass is not possible although for multi-species AGB and BGB models respectively, species mean AGBD and BGBD may be applied contrary to the current practice of using AGBD for modelling BGB (e.g. Komiyama et al., 2005). Whether authors developed common AGB models using tree or species level BD or both is not clear in literature (e.g. Chave et al., 2005; Chave et al., 2014). If tree biomass both tree and species level BD values are mixed up in the modelling, they are likely to lead into confounding effects, while tree level BD account for tree variation species level account for species variation. This therefore needs to be avoided.
The variation in BD between and within tree components observed in our study generally showed the importance of implementing an appropriate sampling strategy for determination of BD for the purpose of biomass estimation. The nature of variation in BD with sampling heights along the stem (Figure 4) for example suggests that, sampling for BD should ensure BD variation is sufficiently accounted for. Sampling for BD at a fixed tree height, e.g. coring or disc extraction at 1.3 m (e.g. Williamson and Wiemann, 2010, Olale et al., 2011), for trees of different sizes is likely to guarantee BD variation with dbh yet however, such sampling ignore BD variations between and even within tree components.

We also tested the accuracy and precision of indirect AGB determination (i.e. determine volume and convert volume to dry weight using BD as a volume to biomass conversion factor). Direct or indirect methods may be employed during destructive sample to generate data for the purpose of modelling (Brown, 1997; Picard et al., 2012). The use of indirect method is particularly recommended for large trees as a means to reduce cost (Brown, 1997). The results showed that, both methods yield consistent and unbiased estimates of tree AGB when applying tree- and component-specific AGBD values (Table 5 and Figure 5).

The relatively large and significant MPEs leading to biased estimates obtained when applying species-specific AGBD from the GWD database suggests that, BD sourced from the GWD database may lead into biased local biomass estimates (S. alba and R. mucronata, Table 5). This calls for inclusion of all sources of variation in determination of BD as a volume to dry weight conversion factor and that, BD from the GWD database need to be used with caution. The level of uncertainty due to the use of BD as a conversion factor may be propagated into subsequent stages of biomass estimation, for example when such estimates are used in model development (e.g. Henry et al.,
Both uncertainty due to BD and the model itself affect the tree level and finally landscape estimates. The same is likely to be the case when landscape volume estimates is converted into biomass using BD (IPCC, 2006; Somogyi et al., 2007).

Based on the “conservative principle” (i.e. the risk of over- and under-estimation should be minimised) (Grass et al., 2008), during destructive sampling the study recommend the use of direct method in biomass estimation. When it is not practical to apply the direct method, an indirect method of biomass estimation may be applied as an alternative. The following considerations are essential in order to minimise uncertainties in biomass estimation; when applying the direct method, sampling must take into account the variation of DF-ratios. On the other hand, tree- and component-specific BD values should be applied for an indirect method of biomass estimation. Moreover, for an indirect method we recommend working with a number of observations as large as 30, in order to obtain normally distributed residuals and unbiased estimates.

Conclusions

The study found that, tree BD varied between species and within species. Within species, BD varied both between trees and tree components. Sampling for BD therefore should take into account all sources of variations. BD may be useful as a conversion factor and if properly determined and applied, yield accurate biomass estimates. The species mean AGBD and BGBD respectively may also be applied as a predictor variable for tree AGB and BGB in Tanzania. Findings from this study contribute to our understanding of different sources of uncertainties in biomass determination for modelling AGB and serves as an important guideline when planning destructive sampling. Improved accuracy of biomass and carbon stock estimates is essentially needed in order to support management and conservation of mangroves through the REDD+ initiatives.
Acknowledgements

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Conflict of interest statement

None declared.

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Above- and belowground tree biomass models for three mangrove species in Tanzania: A non-linear mixed-effects modelling approach

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Above- and belowground tree biomass models for three mangrove species in Tanzania: a nonlinear mixed effects modelling approach

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Abstract

• Key message Tested on data from Tanzania, both existing species-specific and common biomass models developed elsewhere revealed statistically significant large prediction errors. Species-specific and common above- and belowground biomass models for three mangrove species were therefore developed. The species-specific models fitted better to data than the common models. The former models are recommended for accurate estimation of biomass stored in mangrove forests of Tanzania.

• Context Mangroves are essential for climate change mitigation through carbon storage and sequestration. Biomass models are important tools for quantifying biomass and carbon stock. While numerous aboveground biomass models exist, very few studies have focused on belowground biomass, and among these, mangroves of Africa are hardly or not represented.

• Aims The aims of the study were to develop above- and belowground biomass models and to evaluate the predictive accuracy of existing aboveground biomass models developed for mangroves in other regions and neighboring countries when applied on data from Tanzania.

• Methods Data was collected through destructive sampling of 120 trees (aboveground biomass), among these 30 trees were sampled for belowground biomass. The data originated from four sites along the Tanzanian coastline covering three dominant species: Avicennia marina (Forssk.) Vierh, Sonneratia alba J. Smith, and Rhizophora mucronata Lam. The biomass models were developed through mixed modelling leading to fixed effects/common models and random effects/species-specific models.

• Results Both the above- and belowground biomass models improved when random effects (species) were considered. Inclusion of total tree height as predictor variable, in addition to diameter at breast height alone, further improved the model predictive accuracy. The tests of existing models from other regions on our data generally showed large and significant prediction errors for aboveground tree biomass.

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O. M. Bollandsås: Supervising the work including providing technical guidance on data analysis and commenting on the manuscript.
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**Conclusion** Inclusion of random effects resulted into improved goodness of fit for both above- and belowground biomass models. Species-specific models therefore are recommended for accurate biomass estimation of mangrove forests in Tanzania for both management and ecological applications. For belowground biomass (*S. alba*) however, the fixed effects/common model is recommended.

**Keywords** *Avicennia-Sonneratia-Rhizophora* · Carbon · Fixed and random effects

1 Introduction

Mangroves are forests found in the tropical and subtropical coastlines between 30° south and north of equator (FAO 2007). In Africa, there are mangroves both at the western and eastern coasts. At the eastern coast of Africa, 14 mangrove species are growing naturally, and 10 among these are found in Tanzania. *Avicennia marina* (Forssk.) Vierh., *Sonneratia alba* J. Smith, and *Rhizophora mucronata* Lam. are the three most dominant mangrove species in Tanzania (MNRT 1991; Luoga et al. 2004; Nshare et al. 2007).

Mangroves provide a range of goods and services of biological and economic importance. In addition, mangroves store large amounts of carbon per unit area (Donato et al. 2011; Murray et al. 2011) and are therefore also important for climate change mitigation (UNEP 2014). Although mangroves in many countries are legally protected, for example in Tanzania, Kenya, and South Africa (FAO 2007), mangroves suffer from deforestation and forest degradation (Wang et al. 2003).

A climate change mitigation strategy under the United Nations Framework Convention on Climate Change (UNFCCC), aiming at Reducing Carbon Emissions from Deforestation and Forest Degradation (REDD+), offers an opportunity for conservation and management of mangroves. Successful implementation of REDD+ relies on the capabilities of participating countries to routinely and reliably monitor changes of carbon stocks and associated greenhouse gas emissions through establishment of a Monitoring, Reporting and Verification (MRV) system (Hewson et al. 2013). In line with this, Tanzania has, under the National Forestry Resources Monitoring and Assessment (NAFORMA) program, established a national grid of permanent sample plots, which will be monitored for biomass and carbon over time (URT 2010). For Tanzania to be able to report carbon stocks at tier 2 or 3 (IPCC 2003), the development of country-specific biomass models is therefore imperative.

Biomass models, based on allometric theory, relating easily measurable tree variables such as diameter at breast height (dbh) and total tree height (ht) to biomass, are considered to be the most efficient tools for tree level biomass prediction (Brown 1997; IPCC 2007; Chave et al. 2014). The tree variables used as model input are obtained through forest inventories (Husch et al. 2003; URT 2010). Development of biomass models requires destructive sampling of trees. Above- and belowground fresh weights of the trees are measured in field, and subsequently, dry weights are determined by using the dry to fresh weight ratio (DF ratio) derived from oven-dried subsamples. Aboveground biomass usually refers to stem, branch, and foliage, while belowground biomass refers to all live roots down to 2 mm in diameter (IPCC 2006).

Many models for prediction of both above- and belowground biomass of mangrove forests have been developed previously. A review by Komiyama et al. (2008) identified 13 species-specific and two common (i.e., multi-species) models for prediction of aboveground biomass of mangroves, while nine species-specific models and one common model were identified for belowground biomass. Additional studies on mangroves that developed models for prediction of biomass not present in this review also exist (e.g., Kairo et al. 2009; Kauffman and Donato 2012; Sitoe et al. 2014). With the exception of the models developed by Kairo et al. (2009) in Kenya and Sitoe et al. (2014) in Mozambique, most of the models have been developed for mangroves in Asia. The relatively few existing models for belowground biomass may be associated with the labor-intensive nature of sampling belowground biomass for mangrove tree species (Njana et al. 2015).

No biomass models have been developed for mangroves of Tanzania, yet numerous models have been developed based on data from other regions and some from neighboring countries in Africa. If these models are applied to quantify biomass of mangroves in Tanzania, they would be used beyond their spatial validity. Since mangrove trees may respond differently to different environmental conditions, this could also result into morphological and architectural differences between trees originating from different sites. Furthermore, it is also important that models are used within valid ranges in terms of species and tree size (dbh and ht). Models calibrated on data from other regions are more likely to violate these requirements. For example, the aboveground model by Chave et al. (2005) is based on mangrove data from a limited geographical area (French Guiana and Guadeloupe); thus, the model does not represent mangroves found in Africa and it does not include any dominant species found in Africa. Similarly,
the aboveground biomass models from mangroves in Kenya and Mozambique are both based on data from one site, and they have limited sample size (e.g., n = 5, Kairo et al. 2009; n = 31 for six species, Sitoe et al. 2014) and tree size ranges (dbh up to 42 cm, Sitoe et al. 2014). Trees with dbh > 40 cm are likely to be found in Tanzania (e.g., Mattia, 1997). Therefore, if such models are applied in Tanzania, they are likely to provide biased estimates since the tree sizes are beyond size range of the model data.

Even though models should in principle not be used outside their geographical area and tree size ranges, this is sometimes necessary due to lack of local models. However, if no suitable data exist for testing, the user remains unaware of the nature of the prediction errors. Thus, model tests on real data are preferable, but this is of course seldom possible since suitable data would mostly be collected for calibrating local models, which renders the use of the alien model unnecessary. However, Njana et al. (2015) tested selected existing belowground biomass models on relevant data from Tanzania, both common (Komiyama et al. 2005) and species-specific (Tamai et al. 1986; Comley and McGuinness 2005; Kairo et al. 2009). The results revealed large prediction errors for both the common (26–63 %) and species-specific (55–63 %) models. These results support the development of new biomass models for Tanzanian mangrove forests.

The main objective of this study was therefore to develop tree biomass prediction models for the dominant mangrove species in Tanzania. Specifically, the study aimed to (1) provide basic information on the distribution of biomass between tree components and the root-to-shoot ratio, (2) develop both common and species-specific models for above- and belowground biomass, (3) develop models for aboveground biomass components (stem, branch, leaf, and twig), and (4) assess the predictive accuracy of the existing models and of those developed here in predicting the aboveground biomass of mangroves. A mixed modelling approach was applied.

2 Materials and methods

2.1 Study area

In Tanzania, mangroves grow naturally along the coastline between the borders to Kenya in the north and Mozambique in the south. Mangroves cover about 158,100 ha of Tanzania (MNRT 2015) and include 10 different species, namely *A. marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal* (Pers.) C. B. Rob., *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Pemphis acidula* J.R. & G. Forst., *R. mucronata*, *S. alba*, *Xylocarpus granatum* Koen., and *Xylocarpus moluccensis* (Lamk.) Roem. These species are also found in Kenya and Mozambique (Tamooh et al. 2008; Fatoyinbo et al. 2008; Mohamed et al. 2009). All mangroves in Tanzania are declared as forest reserves and managed by the Tanzania Forest Service Agency under the Ministry of Natural Resources and Tourism (URT 2002). The study was carried out at four sites: Pangani, Bagamoyo, Rufiji, and Lindi-Mtwara (Table 1) covering the northern, middle, and southern parts of the coastal belt of Tanzania.

2.2 Tree sampling and measurement procedures

Site conditions in mangrove forests usually vary perpendicular to the shorelines of the sea/rivers. To cover as much variation as possible, we established nested sample plots of 2- and 10-m radii along 37 transects running from the shorelines across the entire extension of the mangrove vegetation. For each transect, the first plot was located close to the shoreline, while the remaining plots were located at distances varying from 150 to 250 m depending on the total extension of the mangroves. For some transects, it was not possible to establish all plots because of impenetrable mangrove vegetation or inaccessibility due to rivers/streams. Therefore, the number of plots sampled within transects varied from one to four. In total, we measured 120 plots. Fifteen plots were measured in Pangani and Lindi-Mtwara, respectively, while 45 plots were measured in Bagamoyo and Rufiji, respectively (Njana et al. 2015).

Within 2-m radius of each plot, we measured dbh for all trees with dbh ≥ 1 cm and total tree height ≥ 2 m, while within 10-m radius, we measured dbh for all trees with dbh ≥ 5 cm. For *A. marina* and *S. alba* trees, dbh was measured at 1.3 m above soil surface, while for *R. mucronata* trees, dbh was measured at 0.3 m above the highest stilt root.

In each plot, one tree was selected subjectively for destructive sampling, while ensuring an adequate representation of all the three species across sites, and diameter ranges from the sample plot. In total, 120 trees were sampled for aboveground biomass (40 for each of the three species), and among these, 30 were sampled for belowground biomass (10 for each of the three species). Among the sites, 15 trees (five for each species) were sampled in Pangani and Lindi-Mtwara, respectively, while 45 trees (15 for each species) were sampled in Bagamoyo and Rufiji, respectively (Njana et al. 2015). One *S. alba* sample tree had hollow and sandy sections, and since our focus was to develop models predicting biomass of healthy mangrove trees, this tree was excluded during modelling.
Before the sample trees were cut, we measured dbh, basal diameter (bd, diameter 15 cm above ground level for A. marina and S. alba or immediately above the highest stilt root for R. mucronata) using a diameter tape. We also measured ht, crown diameter (crd), and bole height (bht, height from ground level to first branch) (Fig. 1). Total and bole tree height was determined using a Suunto hypsometer. Crown length (crl) was determined from the difference between ht and bole height.

Three R. mucronata sample trees were multi-stemmed. For these trees, diameters of individual stems (dbh) were combined and a surrogate for dbh was determined as $\text{dbh} = \sqrt{\sum \text{dbh}_i^2}$ (e.g., Zhou et al. 2007) while we used the heights of individual stems to determine basal area-weighted mean heights that were used as surrogate for ht. Table 2 summarizes statistics for plot (i.e., for trees ≥5 cm) and sample tree variables.

Using a chainsaw, trees were cut 15 cm above ground level for A. marina and S. alba, while R. mucronata trees were cut immediately above the highest stilt root (URT 2010) (see Fig. 1). After felling, the aboveground part for tree with dbh ≥ 15 cm was partitioned into (i) stem, (ii) branch (≥ 5 cm), and (iii) twig and leaf, and among these, 10 trees for each of the three species were further partitioned into twig and leaf. Stem and branch were cross-cut into billets and their corresponding fresh weights determined using a spring balance measuring weight to the nearest 0.1 kg. Fresh weights of small trees (<5 cm) were determined using a digital balance. Saw dusts from the chainsaw were not included in the fresh weight. For the large trees partitioned into twig and leaf, fresh weights were determined separately for each component. For all other trees, the aggregate fresh weights, i.e., twig plus leaf, were recorded.

For determining belowground biomass of A. marina and S. alba trees, we first excavated the root crown and then selected two main cable roots from the root crown and two side cable roots from each of the two main cable roots, including their respective pneumatophores, for full excavation. The root selection included one small and one large main and side cable root, respectively, so as to cover as wide ranges of root sizes as possible.
possible. Fresh weights as well as root basal diameter of all excavated roots were determined. These measurements were later used to develop side and main cable root regression models, which were applied to predict biomass of roots not excavated (for details on excavation and biomass determination procedures, see Njana et al. 2015). For *R. mucronata*, fresh weights were determined through harvesting of all aboveground stilt roots followed by complete excavation of all belowground stilt roots. Finally, the total belowground fresh weight was determined by summarizing weights of root crown and above- and belowground stilt roots.

For each tree, three subsamples were extracted from the stem, two from the branches, and two from the twigs. The weight of the subsamples for the aboveground tree components ranged from 0.05 to 4.5 kg. All subsamples were extracted at random locations except for the stem subsamples, which were extracted at 0, 40, and 70 % of the total tree height. The fresh weight of all subsamples was determined immediately after extraction using a digital balance (to the nearest 0.01 g). This was followed by labelling and packing for further measurements in laboratory. In total, the numbers of stem, branch, and twig subsamples were 119, 50, and 72, respectively, for *A. marina*; 118, 39, and 68, respectively, for *S. alba*; and 117, 46, and 72, respectively, for *R. mucronata*.

### 2.3 Laboratory procedures and dry weight determination

In the laboratory, subsamples were oven-dried to constant weight at 105 °C and their dry weight determined by a digital balance. DF ratio of subsamples (unit less) was determined as oven dry weight (kg) per fresh weight (kg). Exploratory analysis of covariance (ANCOVA) with dbh as a covariate revealed that the DF ratio varied significantly between above-ground tree components and with tree dbh (*p*<0.05). In general, DF ratio varied from 0.28 to 0.66 for *A. marina*, 0.22 to 0.69 for *S. alba*, and 0.33 to 0.71 for *R. mucronata*. Since only 10 trees for each of the three species among the larger trees (dbh≥15 cm) were partitioned into twig and leaf, we initially computed species-specific twig to leaf ratio based on the 10 observations for each species which was used to partition the

---

**Table 2** Statistical summary of plot variables, sample tree variables, and tree biomass for different tree components

<table>
<thead>
<tr>
<th>Item</th>
<th><em>A. marina</em></th>
<th><em>S. alba</em></th>
<th><em>R. mucronata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean±STD</td>
<td>Min</td>
</tr>
<tr>
<td><strong>Plot variables</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N (no. ha⁻¹)</td>
<td>40</td>
<td>622±402</td>
<td>0</td>
</tr>
<tr>
<td>G (m² ha⁻¹)</td>
<td>40</td>
<td>15.3±10.8</td>
<td>0</td>
</tr>
<tr>
<td><strong>Sample tree variables</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bd (cm)</td>
<td>40</td>
<td>26.9±18.1</td>
<td>1.7</td>
</tr>
<tr>
<td>dbh (cm)</td>
<td>40</td>
<td>22.7±15.6</td>
<td>1.1</td>
</tr>
<tr>
<td>ht (m)</td>
<td>40</td>
<td>12.6±6.3</td>
<td>3.1</td>
</tr>
<tr>
<td>bht (m)</td>
<td>40</td>
<td>6.2±4.7</td>
<td>0.8</td>
</tr>
<tr>
<td>crd (m)</td>
<td>40</td>
<td>6.0±4.2</td>
<td>0.7</td>
</tr>
<tr>
<td>crl (m)</td>
<td>40</td>
<td>6.5±2.9</td>
<td>1.2</td>
</tr>
<tr>
<td><strong>Sample tree biomass data</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LeafB (kg tree⁻¹)</td>
<td>22</td>
<td>37.5±24.5</td>
<td>6.4</td>
</tr>
<tr>
<td>TwigB (kg tree⁻¹)</td>
<td>22</td>
<td>100.7±63.7</td>
<td>15.7</td>
</tr>
<tr>
<td>BranchB (kg tree⁻¹)</td>
<td>22</td>
<td>204.0±246.8</td>
<td>2.2</td>
</tr>
<tr>
<td>StemB (kg tree⁻¹)</td>
<td>22</td>
<td>404.8±359.3</td>
<td>73.7</td>
</tr>
<tr>
<td>AGB (kg tree⁻¹)</td>
<td>40</td>
<td>447.0±579.9</td>
<td>0.5</td>
</tr>
<tr>
<td>BGB (kg tree⁻¹)</td>
<td>10</td>
<td>100.5±93.7</td>
<td>2.1</td>
</tr>
</tbody>
</table>


*a* The statistical summary for plot variables include only trees with dbh>5 cm

*b* Since only tree with dbh>15 cm were partitioned into different aboveground tree components, the sample (*n*) is less than the expected 40 for each of the three species
aggregate twig and leaf component into twig and leaf for trees not partitioned into that level. Then, total tree aboveground biomass was calculated as the product of tree- and component-specific fresh weight and DF ratio:

\[
\text{AGB}_h = \sum_{i=1}^{n_t} (\text{FW}_{hit} \times \text{DF}_{ht}) + \sum_{i=1}^{n_t} (\text{FW}_{hit} \times \text{DF}_{ht}) + \sum_{i=1}^{n_t} (\text{FW}_{hit} \times \text{DF}_{ht}) + \sum_{i=1}^{n_t} (\text{FW}_{hit} \times \text{DF}_{ht})
\]

where \( \text{AGB}_h \) = observed total tree aboveground dry weight (kg) of the \( n \)th tree, \( n = \) total number of billets/twig bundles/ leaf weights for a given aboveground tree component, \( s = \) stem, \( b = \) branch, \( t = \) twig, \( l = \) leaf, \( i = \) ith subsection, \( \text{FW}_{hit} \), \( \text{FW}_{hit} \), and \( \text{FW}_{hit} \) are stem, branch, twig, and leaf fresh weights (kg), respectively, and \( \text{DF}_{ht} \), \( \text{DF}_{ht} \), \( \text{DF}_{ht} \), and \( \text{DF}_{ht} \) are stem, branch, twig, and leaf DF ratios, respectively.

Belowground dry weight determination for \( A. \text{marina} \) and \( S. \text{alba} \) involved conversion of fresh weight of excavated root components using species-, tree-, and component-specific DF ratios. From excavated sample root dry weight data, regression models for prediction of dry weight of unexcavated roots were developed and dry weights of unexcavated roots were predicted (for details, see Njana et al. 2015). Therefore, total root dry weights comprised excavated and unexcavated (i.e., predicted) root dry weights. Total tree belowground dry weight, i.e., belowground biomass, was derived as the sum of root and root crown dry weight. For \( R. \text{mucronata} \), tree belowground dry weight was obtained by converting total tree fresh weight to dry weight using tree-specific DF ratios. This was the case because for this species, tree belowground fresh weight was not distinguished into root components. Statistical summary for sample tree dry weights are presented in Table 2.

2.4 Model specification

Model specification involves selection of functional form as well as selection of predictor variables. Initially, we tested various functional forms; however, power functional form was the best. Power functions have been widely used to model biomass of mangrove trees (e.g., Tamai et al. 1986; Komiyama et al. 2005; Kairo et al. 2009; Ray et al. 2011; Patil et al. 2014). In this study, two variants of power functions with an additive error term (\( \varepsilon \)) were considered (model forms Model form 1 and Model form 2):

\[
B_i = \beta_0 \times (\text{dbh}_i)^{\beta_1} + \varepsilon_i \quad \text{(Model form 1)}
\]

where \( i \) represent \( i \)th observation, and \( B_i \) represent aboveground biomass, leaf biomass, twig biomass, branch biomass, or stem biomass. Model form Model form 1 represents biomass as a function of \( \text{dbh}_h \), while model form Model form 2 represents biomass as a function of both \( \text{dbh}_h \) and \( \text{ht}_h \), while the betas (\( \beta \)) are model parameters.

Diameter at breast height (dbh) is highly correlated with biomass (\( B_i \)). However, also \( \text{ht}_h \) is highly correlated with biomass and could be a useful variable in biomass models to reflect that trees reach their maximum height at an earlier stage than maximum diameter. This means that models depending on dbh only may overpredict biomass of large trees because the biomass increase per unit increase in diameter is reduced when trees approach maximum height. Thus, \( \text{ht}_h \) represents additional information not reflected by dbh (e.g., Chave et al. 2005).

2.5 Nonlinear mixed effects (NLME) modelling

2.5.1 Nonlinear mixed effects models

Three important assumptions for regression modelling are normality, homoscedasticity (if residual variance increases as a function of \( \text{dbh} \)), and independency of residuals. Results and conclusions based on regression analysis are only reliable if these assumptions are met (Ritz and Streibig 2008; Zuur et al. 2009). For biological data, however, such assumptions may be difficult to meet. Non-normal residuals, for example, may be due to outliers, while lack of independency of residuals may occur due to the structure of data itself (Zuur et al. 2009). Non-normal and heteroscedastic residuals may be dealt with by transformation (Ritz and Streibig 2008; Zuur et al. 2009), although this leads into change of the original scale and introduces bias (O’Hara and Kotze 2010; Packard 2009).

NLME modelling is one way to confront challenges encountered in conventional regression approaches since it relaxes regression assumptions and take into account the complex nature of biological data (Pinheiro and Bates 2000; Zuur et al. 2009). Within the mixed effects model framework, parameters may also be allowed to vary by grouping variables(s) (Ritz and Streibig 2008). NLME models may generally be expressed as follows (Lindstrom and Bates 1990; Vonesh and Chinchilli 1997; Pinheiro and Bates 1998):

\[
y_{ij} = f(x_{ij}, \lambda_j; \beta_j, \alpha_j) + \varepsilon_{ij}
\]

where \( i \) = \( i \)th observation, \( j \) = \( j \)th random-effect variable, \( y_{ij} \) = response variable for observation \( i \) and random-effect variable \( j \), \( x_{ij} \) = predictor variable for observation \( i \) and random-effect parameters.
variable $j$, $\lambda_j$ = random-effect variable for $j$, $\beta$ = fixed effects parameters, $\alpha_j$ = random effects parameters, and $\varepsilon_{ij}$ = error term, which is assumed normally distributed with a mean of zero.

Our data originated from four different sites and comprised three different species, where one tree was destructively sampled from each sample plot spatially distributed along transects. Since our data structure is hierarchical and the biomass–dbh relationship is nonlinear (Fig. 2), tree biomass was modelled using the NLME modelling approach in order to preserve the original scale.

Biomass models based on mixed effects modelling frameworks have also previously been developed (e.g., Moore 2010; Li et al. 2011; Xu et al. 2014). The mixed effects modelling provides a statistical capability where fixed- (i.e., populations average) and random effects (i.e., group specific) parameters may be estimated simultaneously (West et al. 2007). Under the mixed effects modelling framework, models including fixed effects parameters may therefore be regarded as common or multi-species models, while those including random effects may be regarded as species-specific models.

### 2.5.2 Modelling procedures

Model development was carried out using the R software version 3.1.2 (R Core Team 2014) using the NLME function in the NLME package (Pinheiro et al. 2015). In order to specify which parameter to be treated as solely fixed effects and which one as both fixed and random effects, we initially tested each parameter as both fixed and random effects parameters against prospective random effects variables. Prospective random effects variables included species ($j$) and site ($k$). The influence of random effects variable(s), individually or in combination on a given parameter, was evaluated using Akaike information criteria (AIC). Accordingly, $\beta_0$ (model forms 1 and 2) and $\beta_2$ (model form 2) were considered as solely a fixed effects parameter, while $\beta_1$ was considered as both fixed and random effects parameters. Model forms 1 and 2 were then re-specified to include a random effects parameter ($\alpha_{jk}$) (model forms Model form 3 and Model form 4):

$$B_{ijk} = \beta_0 \times (\text{dbh}_{ijk})^{\beta_1+\alpha_{jk}} + \varepsilon_{ijk} \quad \text{Model form 3}$$

$$B_{ijk} = \beta_0 \times (\text{dbh}_{ijk})^{\beta_1+\alpha_{jk}} \times (h_{ijk})^{\beta_2} + \varepsilon_{ijk} \quad \text{Model form 4}$$

Site did not result into significant random parameters ($\beta_1$), so relevant parameters estimated were not reported. Three sets of biomass models were developed: (i) above-ground biomass models, (ii) belowground biomass models, and (iii) aboveground tree component (leaf, twig, branch, and stem) biomass models. Both model forms 3 and 4 were fitted for total aboveground biomass, while only model form 3 was fitted for belowground biomass and aboveground tree component biomass. Model form 4 was not considered for belowground and aboveground tree components due to limited number of observations (Harrell 2001; Roxburgh et al. 2015).

During explorative data analysis, we observed that residual variances ($\sigma^2(\varepsilon_{ijk})$) were heteroscedastic. Consequently, we assumed heteroscedasticity, and residual variances were modelled as a function of dbh using varPower function in R (Pinheiro and Bates 2000; Ritz and Streibig 2008; Zuur et al. 2009);

$$\sigma^2(\varepsilon_{ijk}) = \sigma^2 \times \left(\text{dbh}_{ijk}\right)^{2\phi}$$

where $\phi$ = variance function coefficient. We initially also tested other functions in R (varExp, varIdent, varConstPower, and varComb). However, the varPower function appeared to be the best.

The effects of the variance function were evaluated using AIC. The variance function is implicitly part of the mixed effects model but is not explicitly stated; therefore, the variance functions are not reported in the results (Smith et al. 2014; de Miguel et al. 2014). Since one tree was sampled from each plot and the distance between plots ranged from 150 to 250 m, observations between plots were considered spatially independent; thus, no correlation structure was assumed.

During tests for random and variance function effects, model parameterization was done by using
maximum likelihood (ML), while we for the final models used restricted ML (REML) (Lindstrom and Bates 1990; Pinheiro and Bates 2000). The models were evaluated using root mean squared error (RMSE (%)) and mean prediction error (MPE (%)) (Chai and Draxler 2014; Walther and Moore 2005) as measures of goodness of fit while model selection was done using AIC:

$$\text{RMSE}(\%) = \left( \frac{\sum (e_{ijk}^2)}{MB_{obs}} \right)^{\frac{1}{2}} n \times 100$$

$$\text{MPE}(\%) = \left( \frac{\sum (e_{ijk})}{n} \right) \times 100$$

$$\text{AIC} = n \times \left( \ln \left( \frac{\sum (e_{ijk}^2)}{n} \right) + 2 \times (p + 1) + C \right)$$

where $e_{ijk}$ = residuals, i.e., difference between predicted and observed tree biomass (kg), $n$ = sample size, $MB_{obs}$ = mean observed tree biomass (kg), ln = natural logarithm, $p$ = number of parameters, and $C$ = constant.

RMSE (%) represents a measure of accuracy and MPE (%) a measure of bias. A model with lower RMSE (%) than the reference model implied the model to be more accurate than the reference model and vice versa. Similarly, MPE (%) values significantly different from zero implied biased aboveground biomass predictions, i.e., under- or overpredictions; otherwise, they implied unbiased aboveground biomass predictions. The commonly used model selection criterion $R^2$ was not considered since its use has been criticized (e.g., Johnson and Omland 2004; Sileshi 2014).

### 2.6 Evaluation of predictive accuracy of existing biomass models

Based on a literature review, relevant existing aboveground biomass models were selected and tested on our data to determine their predictive accuracy. The selected models ensured representation of various regions and included four common and eight species-specific biomass models (Table 3). RMSE (%), MPE (%), and AIC served as model evaluation criteria. After computation of these criteria, the existing models were ranked in descending order based on AIC. The existing models were ranked without stratification into model type or predictor variable included since AIC as a model selection criteria is capable of detecting such differences (Burnham et al. 2011).

### 3 Results

#### 3.1 Distribution of biomass into different tree parts

The three mangrove species considered in this study stored between 49 % ($R. mucronata$) and 72 % ($S. alba$) of aboveground biomass in the stem, while the rest in descending order was stored in branch, twig, and leaf (Fig. 3). On average, about 41 % of the total tree biomass is stored in the root system (Fig. 4). Figures 3 and 4 show that $S. alba$ had relatively higher stem biomass and higher root biomass compared to the other species. The root-to-shoot ratios for $A. marina$, $S. alba$, and $R. mucronata$ were 0.38, 1.29, and 0.62, respectively, with an overall mean of 0.70. Generally, the root-to-shoot ratio depicted a decreasing trend from lower to higher dbh classes.

#### 3.2 Biomass models

All parameter estimates for the above- and belowground biomass models were statistically significant (Table 4). For the aboveground biomass fixed effects models (FE1, FE2), inclusion of ht as a predictor variable was important since RMSE decreased from 42.6 to 38.4 %, which is equivalent to a decline of about 10 %. Based on AIC as model selection criterion, the fixed effects model FE2 is better than model FE1. For the aboveground biomass random effects models, inclusion of ht resulted in lower RMSE (%) and MPE (%) values for $A. marina$ (models RE1 and RE4) and $S. alba$ (models RE2 and RE5), while mixed results were observed for $R. mucronata$ (models RE3 and RE6).

The evaluation of the aboveground biomass models (Table 5) showed that inclusion of ht as predictor variable (model form 4) generally improved predictive accuracy, i.e., provided lower MPE values. The results also showed that the random effects models with ht as a predictor variable were more accurate than the fixed effects models.

For the belowground biomass models (Table 4), the goodness of fit statistics, i.e., RMSE (%) and MPE (%), improved when using random effects for $A. marina$ (model RE7) and $R. mucronata$ (model RE9) compared to the fixed effects model (model FE3), while the opposite was observed for $S. alba$ (model RE8).

The $\beta_0$ parameter estimates of the aboveground tree components biomass models were statistically non-significant ($p>0.05$) except for the stem biomass model (Table 6). All other parameter estimates were statistically significant ($p<0.05$). MPEs were slightly lower than 10 % for the leaf, twig, and branch biomass models, while MPE was slightly higher than 10 % for the stem model. The stem biomass model had lower RMSE (%) values compared to all the other component models.
Using paired t test, comparisons of observed total tree aboveground biomass with total tree aboveground biomass predicted the tree components common/fixed effects models showed that the prediction errors were non-significant for *A. marina* (*n* = 23, MPE = −6.5 %, *p* > 0.05) and *S. alba* (*n* = 17, MPE = 3.9 %, *p* > 0.05), while they were significant for *R. mucronata* (*n* = 21, MPE = 16.0 %, *p* < 0.05).

### Table 3: Existing aboveground biomass mangrove models selected for evaluation of prediction accuracy

<table>
<thead>
<tr>
<th>Model type</th>
<th>Model</th>
<th>n</th>
<th>R²</th>
<th>RMSE</th>
<th>dbh (cm)</th>
<th>Location</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common</td>
<td>AGB=3.254 × exp(0.065 × dbh)</td>
<td>31</td>
<td>0.89</td>
<td>4.244</td>
<td>0.5–42</td>
<td>Sofala bay, Mozambique</td>
<td>Sito et al. (2014)</td>
</tr>
<tr>
<td>Common</td>
<td>AGB=1.3799 × dbh^{0.955} × ht^{−0.687}</td>
<td>100</td>
<td>0.98</td>
<td>–</td>
<td>–</td>
<td>India</td>
<td>Ray et al. (2011)</td>
</tr>
<tr>
<td>Common</td>
<td>AGB=0.0509 × ρ(dbh^{2} × ht)</td>
<td>84</td>
<td>0.96</td>
<td>–</td>
<td>dbh_{max}=42</td>
<td>French Guiana and Guadeloupe</td>
<td>Chave et al. (2005)</td>
</tr>
<tr>
<td>Common</td>
<td>AGB=0.251 × ρ × dbh^{2.46}</td>
<td>104</td>
<td>0.98</td>
<td>0.085</td>
<td>5.0–48.9</td>
<td>Thailand and Indonesia</td>
<td>Komiya et al. (2005)</td>
</tr>
<tr>
<td><em>A. marina</em></td>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=0.3404 × dbh^{2.0273}</td>
<td>110</td>
<td>0.94</td>
<td>–</td>
<td>–</td>
<td>Mumbai, India</td>
<td>Patil et al. (2014)</td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=exp(0.2540+0.9140 × log(dbh))</td>
<td>10</td>
<td>0.31</td>
<td>1.340</td>
<td>8¹</td>
<td>Gazi Bay, Kenya</td>
<td>Kairo et al. (2009)</td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=0.1036 × dbh^{2}+0.5402 × dbh+(−1.5674)</td>
<td>–</td>
<td>0.94</td>
<td>–</td>
<td>2.1–12.1</td>
<td>Taiwan</td>
<td>Kuo (2008)</td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=0.308 × dbh^{2.11}</td>
<td>22</td>
<td>0.97</td>
<td>0.023</td>
<td>dbh_{max}=35</td>
<td>Darwin, Australia</td>
<td>Comley and McGuinness (2005)</td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=0.0825 × ρ×(dbh^{2} × ht)^{0.89966}</td>
<td>345</td>
<td>0.95</td>
<td>–</td>
<td>dbh_{max}=323</td>
<td>Palau</td>
<td>Kauffman and Donato (2012)</td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=exp(0.6715+0.1473 × log(dbh))</td>
<td>10</td>
<td>0.01</td>
<td>0.580</td>
<td>10¹</td>
<td>Gazi Bay, Kenya</td>
<td>Kairo et al. (2009)</td>
</tr>
<tr>
<td><em>R. mucronata</em></td>
<td>Species-specific</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=0.0311 × ρ×(dbh^{2} × ht)^{1.00741}</td>
<td>73</td>
<td>0.95</td>
<td>–</td>
<td>dbh_{max}=39.5</td>
<td>Palau</td>
<td>Kauffman and Donato (2012)</td>
</tr>
<tr>
<td>Species-specific</td>
<td>AGB=exp(−0.1811+0.6590 × log(dbh))</td>
<td>5</td>
<td>0.83</td>
<td>1.050</td>
<td>5¹</td>
<td>Gazi Bay, Kenya</td>
<td>Kairo et al. (2009)</td>
</tr>
</tbody>
</table>

Units of measurement: total aboveground biomass, kilogram; diameter at breast height, centimeter; total height (ht), meter; basic density, gram per cubic centimeter

AGB total aboveground biomass, dbh diameter at breast height, ht total height, ρ basic density, n sample sizes

¹ The figure refer to the fixed age of planted mangrove trees which is surrogate to dbh

---

**Fig. 3** Distribution of biomass between aboveground tree components. *Am* = *A. marina* (*n* = 23), *Sa* = *S. alba* (*n* = 17), and *Rm* = *R. mucronata* (*n* = 21).

**Fig. 4** Distribution between above- and belowground biomass. *Am* = *A. marina* (*n* = 10), *Sa* = *S. alba* (*n* = 10), and *Rm* = *R. mucronata* (*n* = 10). Note: AGB = total aboveground biomass, BGB = total belowground biomass.
3.3 Evaluation of predictive accuracy of existing aboveground biomass models

The predictive accuracy of the existing aboveground biomass models was evaluated by testing them on our data (Table 7). Judged by AIC, the common model developed by Chave et al. (2005) was the best for prediction of aboveground biomass for A. marina and S. alba, while the common model developed by and Komiyama et al. (2005) was the best for R. mucronata (Table 7). Except for the model developed by Chave et al. (2005) applied for S. alba and R. mucronata, MPE (%) values for all tested models were significantly (p<0.05) different from zero.

When ranking the models developed in this study based on AIC, the common (fixed effects) model was the best in prediction of aboveground biomass for A. marina while the species-specific (random effects) models were the best for the other two species (Table 7). The MPE (%) values of all the species-specific (random effects) models were low and non-significant. For the common (fixed effects) models, the MPE (%) values were low for A. marina and relatively high for S. alba and R. mucronata. However, only the MPE (%) value of common model for S. alba was significantly different from zero.

The models developed by Kairo et al. (2009) and Sitoe et al. (2014), both from eastern Africa, were the poorest performing models as demonstrated by very high RMSE (%) and MPE (%) values (Table 7). These models were also characterized by remarkable disagreement between observed and predicted biomass values (Fig. 5).
The distributions of the aboveground biomass components were quite similar for *A. marina* and *R. mucronata*, while for *S. alba*, the proportion of stem biomass was higher than for the two other species (Fig. 3). Although on average 41% of tree biomass was stored belowground, *S. alba* stored the largest proportion belowground (Fig. 4). The main reason for the relatively large proportion of belowground biomass for *S. alba*, as compared to *A. marina*, is probably due to the large pneumatophores of this species (Njana et al. 2015). This is also in line with the high root-to-shoot ratio for this species. Apparently, *S. alba* has more belowground biomass than aboveground biomass (1.29 root-to-shoot ratio). Variation of distribution of biomass into different tree components between species and a declining trend in root-to-shoot ratios over dbh classes demonstrate the strategies of trees as they grow; at early stages, more biomass is distributed in the belowground for anchorage and stabilization in the soft substrate, while at later stages, more of the biomass is distributed to the aboveground part in support of physiological processes for growth. The distribution of biomass observed in this study is not unique for mangrove alone as

### Table 5 Mean prediction errors (MPE (%)) of the aboveground biomass models over site, dbh class, and ht class

<table>
<thead>
<tr>
<th>Parameter</th>
<th>n</th>
<th>MPE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pangani</td>
<td>15</td>
<td>−4.4</td>
</tr>
<tr>
<td>Bagamoyo</td>
<td>45</td>
<td>7.3</td>
</tr>
<tr>
<td>Rufiji</td>
<td>45</td>
<td>−9.5</td>
</tr>
<tr>
<td>Lindi-Mtwara</td>
<td>15</td>
<td>20.8</td>
</tr>
<tr>
<td>dbh class (cm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.0–10.0</td>
<td>45</td>
<td>12.8</td>
</tr>
<tr>
<td>10.1–20.0</td>
<td>20</td>
<td>−3.2</td>
</tr>
<tr>
<td>20.1–30.0</td>
<td>20</td>
<td>−4.7</td>
</tr>
<tr>
<td>30.1–40.0</td>
<td>24</td>
<td>−1.4</td>
</tr>
<tr>
<td>40.0</td>
<td>10</td>
<td>2.0</td>
</tr>
<tr>
<td>ht class (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.0–5.0</td>
<td>24</td>
<td>10.2</td>
</tr>
<tr>
<td>5.1–10.0</td>
<td>36</td>
<td>25.2</td>
</tr>
<tr>
<td>10.1–15.0</td>
<td>29</td>
<td>4.7</td>
</tr>
<tr>
<td>15.1–20.0</td>
<td>14</td>
<td>−15.1</td>
</tr>
<tr>
<td>&gt;20.0</td>
<td>16</td>
<td>−3.2</td>
</tr>
</tbody>
</table>

n sample sizes

### Table 6 Aboveground tree component biomass models

<table>
<thead>
<tr>
<th>Component</th>
<th>Model form</th>
<th>Model category</th>
<th>Model type</th>
<th>n</th>
<th>Parameter estimates</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>AIC</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>3</td>
<td>Fixed effects</td>
<td>Common</td>
<td>55</td>
<td>0.91766NS</td>
<td>0.64173</td>
<td>2.0549</td>
<td>62.1</td>
<td>367.8 CFE1</td>
</tr>
<tr>
<td>Twig</td>
<td>3</td>
<td>Fixed effects</td>
<td>Common</td>
<td>55</td>
<td>0.83391NS</td>
<td>0.65931</td>
<td>0.23032</td>
<td>8.7</td>
<td>496.9 CFE2</td>
</tr>
<tr>
<td>Branch</td>
<td>3</td>
<td>Fixed effects</td>
<td>Common</td>
<td>55</td>
<td>0.05140NS</td>
<td>0.05060</td>
<td>0.27769</td>
<td>78.0</td>
<td>598.5 CFE3</td>
</tr>
<tr>
<td>Stem</td>
<td>3</td>
<td>Fixed effects</td>
<td>Common</td>
<td>55</td>
<td>0.24370NS</td>
<td>0.11111</td>
<td>0.13711</td>
<td>49.9</td>
<td>641.2 CFE4</td>
</tr>
</tbody>
</table>

SE standard error of a parameter estimate, NS not significant at 5 %, n sample sizes

*a* Significant at 5 %

*b* Significant at 1 %

*c* Significant at 0.1 %
Our study presents above- and belowground biomass models based on data from three dominant mangrove species in Tanzania, i.e., *A. marina*, *S. alba*, and *R. mucronata*. No similar models have previously been developed in the country, and only a few models have been developed in Africa or are based on data from Africa. The existing biomass models from Africa (Kairo et al. 2009; Sitoe et al. 2014) are based on limited sample sizes and data from only one site. Our biomass models however are based on data from a range of sites along the coastline of Tanzania, covering a size range beyond data used in developing the existing aboveground biomass models both in Africa (e.g., Kairo et al. 2009; Sitoe et al. 2014) and beyond (e.g., Comley and McGuinness 2005; Chave et al. 2005; Komiyama et al. 2005; Kuei 2008; Patil et al. 2014).

**Table 7** Predictive accuracy of existing aboveground biomass models and models developed in this study

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>Model type</th>
<th>Predictor variables</th>
<th>n</th>
<th>RMSE (%)</th>
<th>MPE (%)</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. marina</em></td>
<td>Chave et al. (2005)</td>
<td>Common</td>
<td>dbh, ht, ρ</td>
<td>40</td>
<td>41.5</td>
<td>−19.0</td>
<td>425.8</td>
</tr>
<tr>
<td></td>
<td>Comley and McGuinness (2005)</td>
<td>Species-specific</td>
<td>dbh</td>
<td>40</td>
<td>45.7</td>
<td>−22.7</td>
<td>429.6</td>
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<tr>
<td></td>
<td>Patil et al. (2014)</td>
<td>Species-specific</td>
<td>dbh</td>
<td>40</td>
<td>65.6</td>
<td>−36.8</td>
<td>458.4</td>
</tr>
<tr>
<td></td>
<td>Komiyama et al. (2005)</td>
<td>Common</td>
<td>dbh, ρ</td>
<td>40</td>
<td>104.8</td>
<td>36.9</td>
<td>498.0</td>
</tr>
<tr>
<td></td>
<td>Ray et al. (2011)</td>
<td>Common</td>
<td>dbh, ht</td>
<td>40</td>
<td>118.0</td>
<td>−62.7</td>
<td>507.4</td>
</tr>
<tr>
<td></td>
<td>Kuei (2008)</td>
<td>Species-specific</td>
<td>dbh</td>
<td>40</td>
<td>132.4</td>
<td>−80.2</td>
<td>514.7</td>
</tr>
<tr>
<td></td>
<td>Sitoe et al. (2014)</td>
<td>Common</td>
<td>dbh</td>
<td>40</td>
<td>151.2</td>
<td>−94.0</td>
<td>525.3</td>
</tr>
<tr>
<td></td>
<td>Kairo et al. (2009)</td>
<td>Species-specific</td>
<td>dbh</td>
<td>40</td>
<td>157.3</td>
<td>−95.1</td>
<td>528.4</td>
</tr>
<tr>
<td></td>
<td>This study</td>
<td>Common</td>
<td>dbh, ht</td>
<td>40</td>
<td>29.3</td>
<td>−1.6</td>
<td>395.9</td>
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<tr>
<td></td>
<td>This study</td>
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<td>dbh, ht</td>
<td>40</td>
<td>31.4</td>
<td>1.6 NS</td>
<td>401.6</td>
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<tr>
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<td>dbh</td>
<td>40</td>
<td>40.6</td>
<td>1.6 NS</td>
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<td></td>
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<td>2.8 NS</td>
<td>421.5</td>
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<tr>
<td></td>
<td>This study</td>
<td>Common</td>
<td>dbh</td>
<td>40</td>
<td>40.6</td>
<td>1.6 NS</td>
<td>419.5</td>
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<td><em>S. alba</em></td>
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<td>dbh, ht, ρ</td>
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<td>1.6 NS</td>
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<tr>
<td></td>
<td>Kauffman and Donato (2012)</td>
<td>Species-specific</td>
<td>dbh, ht, ρ</td>
<td>39</td>
<td>62.8</td>
<td>−40.4</td>
<td>406.3</td>
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<td>87.6</td>
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<td>Sitoe et al. (2014)</td>
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<td>154.8</td>
<td>−94.0</td>
<td>472.7</td>
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<td>Specific</td>
<td>dbh</td>
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<td>162.3</td>
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<td>13.7 NS</td>
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Existing models and models from this study are ranked separately and according to AIC in descending order.

NS not significant at 5 %, n sample sizes

a Two-tailed t-tests

b Significant at 5 %

c Significant at 1 %

d Significant at 0.1 %
Accordingly, our belowground biomass models are based on data size range beyond those reported in existing studies (e.g., Comley and McGuinness 2005; Komiyama et al. 2005; Kairo et al. 2009). In addition, our belowground biomass models are based on data generated using comprehensive procedures for quantifying tree belowground biomass involving root sampling (*A. marina* and *S. alba*) and complete root excavation (*R. mucronata*) (Njana et al. 2015).

![Graphs showing observed and predicted aboveground biomass for existing models and for models from this study. Note: Dashed gray lines represent 1:1 relationship between observed and predicted values. AGB = total aboveground biomass, BGB = total belowground biomass.](image-url)
Our models are based on a nonlinear mixed-modelling approach. Ordinary nonlinear regression is commonly used to develop biomass models. Such models, however, may violate regression assumptions of homoscedasticity and independence of residuals, which are difficult to meet for biological data. Sampling for biomass model development often results in hierarchical data. Chave et al. (2005) and Komiyama et al. (2005) for example developed common biomass models using data originating from more than one site, such data form hierarchical data structure stratified by site and species. Observations originating from the same species and/or site are likely to be more correlated hence lack of independence. A model based on non-independent observations is characterized by autocorrelated errors and therefore violate key assumptions of independence in regression (Ritz and Streibig 2008). Ignoring lack of independence tends to give imprecise parameter estimates (ibid.). The mixed effects modelling comprising both fixed and random effects that we applied in this study is a useful statistical tool in modelling hierarchical data (Ritz and Streibig 2008; Zuur et al. 2009).

Our study showed that the aboveground biomass models improved when random effects modelling was applied and when ht as an additional predictor variable was considered (Tables 4 and 5). In model development, it is important that models are properly specified and that the structure of the data is taken into account. Our study illustrate that common model including ht generally performed well across study site, species, dbh, and ht classes by resulting into decline in MPE (%) and that their corresponding random effects/species-specific further improved predictive accuracy (Table 5). This supports the role of random effects in explaining unexplained sources of variation which is only possible within the mixed modelling framework. In line with our results, Chave et al. (2005) reported that the inclusion of ht into a common mangrove biomass model reduced the standard error of aboveground biomass from 19.5 to 12.5 % for mangrove trees, while other authors reported that random effects improved predictive power of biomass models for non-mangrove trees (e.g., Fu et al. 2014; Xu et al. 2014).

Despite models including ht being better, in most forest inventories, due to many reasons such as costs, trees are not frequently measured for ht. In such cases, users are obliged either to use models including dbh as the only predictor variable or initially estimate ht using relevant models and subsequently apply biomass models based on both dbh and ht as predictor variables. However, ht prediction models for mangroves are lacking in Tanzania and the rest of Africa.

Basic density (BD) is another predictor variable which could have potentially improved predictive accuracy particularly for the common biomass model (Komiyama et al. 2005; Chave et al. 2005). However, our models did not include BD as an additional predictor variable for two reasons; firstly, BD may vary between species and between species-specific tree components and between tree size. Therefore, applying BD determined based on comprehensive sampling in modelling tree biomass may improve model predictive accuracy. Since BD is never determined in forest inventories however and that no BD prediction models exist for mangrove species, such biomass models would be better yet with limited application. Secondly, for common biomass models, BD serves as species distinguishing factor whereby species mean BD values may be used as opposed to the use of species- and tree-specific BD values. The mixed modelling approach used in this study is robust in distinguishing species.

The tests of existing models on our data generally showed large and significant underpredictions for aboveground biomass (Table 7). The underpredictions were as large as 90 % for some of the models (Kairo et al. 2009; Sitoe et al. 2014). Generally, predicted and observed biomass agreed quite well for small tree sizes, while the underpredictions increased with tree size (Fig. 5). Similar tests on belowground biomass for mangroves in Tanzania (Njana et al. 2015) showed prediction errors (underprediction) as high as 60 % when models by Komiyama et al. (2005) (common model), Comley and McGuinness (2005) (species-specific model), and Kairo et al. (2009) (species-specific model) were applied. Plausible explanations for the observed prediction errors could be the application of the models beyond data ranges (size), geographical locations, and differences in forest structure and architecture. For the belowground biomass, an additional explanation could also be inadequate excavation procedures applied when some of these models were developed (see Njana et al. 2015). Any application of the already existing above- and belowground biomass models to mangroves of Tanzania is therefore not recommended.

In the modelling, we applied species as random effects, which resulted into improved predictive accuracy of both the above- and the belowground biomass models, except for belowground biomass for S. alba where the models did not fit well to data (Table 4). This may be due to higher variances of BGB for this species (see Fig. 2). The contribution of random effects in improved predictive accuracy suggests that the biomass allometry varies by species. Therefore, the random effects/species-specific models should be applied since they are superior to the fixed effects/common models. For S. alba, however, the fixed effects model is recommended for belowground biomass. Since both the above- and the belowground biomass models performed fairly well across sites, the models may be applied across sites in Tanzania. However, the use of the models beyond species considered in this study is not recommended.

Aboveground tree component biomass estimates derived using models may be essential in describing forest structure (e.g., Camacho et al. 2011), determining forest productivity (e.g., Cox and Allen 1999; Kairo et al. 2008), and understanding ecosystem functions through quantification of carbon
stocks and sequestration (e.g., Chen et al. 2012; Pandey and Pandey 2013) which are potentially relevant for climate change mitigation strategies. For example, the leaf biomass estimated from relevant models may provide useful information on nutrient cycling while the above- and belowground biomass models may be applied to generate tier 3 carbon stock estimates for carbon monitoring, reporting, and verification in REDD+ programs. The models may also be applied to the NAFORMA data for basic scientific ecological studies and for management decision-making. Since biomass estimates are essential for both ecological and management applications, the models (total AGB, BGB, and tree component models) from this study are expected to provide ecologists with the needed information and to support management of mangroves in Tanzania and elsewhere as deemed relevant. The aboveground tree component biomass models that we developed generally gave low prediction errors (<10 %) (Table 6). In addition, estimates based on tree components were additive (in agreement with the direct tree aboveground estimates). Therefore, we recommend the use of the developed aboveground tree component common models in deriving aboveground component-specific biomass estimates for utilization and ecological purposes, and the individual estimates may safely be added up.

5 Conclusions

The biomass models reported in this study are based on comprehensive data and modelling approach. The above- and belowground biomass models improved when random effects were considered. Therefore, random effects/species-specific models are generally recommended. For estimation of belowground biomass for S. alba however, the fixed effects/common model is recommended. Based on our results, we discourage species-specific or site-specific model development for data entailing more than one species or site, instead we encourage the use of a mixed modelling approach which is robust for such data sets. The aboveground tree component biomass models may also be applied since they yield unbiased and additive estimates. Based on goodness of fit statistics, both the above- and the belowground biomass models developed in this study are the best available and provide an important tool for accurate estimation of biomass and carbon stock stored in mangrove forest in Tanzania for both management and ecological applications. Our models should be used within the range of data from which they were developed, and their use outside this data range should be done with caution.

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PAPER FOUR

Carbon storage in mangrove forests of Tanzania

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Carbon storage in mangrove forests of Tanzania

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Abstract

As carbon reservoir, mangroves play an important role in regulating global climate. Using new biomass models developed for mangroves of Tanzania, this study aimed to (i) determine species composition, (ii) determine national estimates of aboveground carbon (AGC), belowground carbon (BGC) and total carbon (TC) stocks, and (iii) assess variation of carbon stock by stand type (pure versus mixed-species). Nine species were recorded for mangrove forests of Tanzania, among them Avicennia marina (Forssk.) Vierh (32%), Rhizophora mucronata Lam. (31%) and Ceriops tagal (Perr.) C. B. Rob. (20%) were dominant. Results showed that, AGC,
BGC and TC were 33.5 ± 5.8 Mg C ha\(^{-1}\) (53% of TC), 30.0 ± 4.5 Mg C ha\(^{-1}\) (47% of TC) and 63.5 ± 8.4 Mg C ha\(^{-1}\) respectively. Since mangroves cover about 158,100 ha along the coast of the Tanzanian mainland, a total of 10.0 millions Mg C (i.e. 37.2 millions Mg CO\(_2\)e) is stored by mangrove forests of Tanzania. Estimates from this study were comparable with estimates reported previously. Carbon storage varied by stand type where pure stands had slightly lower carbon stock compared to mixed-species stands although they were not significantly different (\(p > 0.05\)). Findings from this study showed that mangroves store large quantities of carbon, therefore they need to be managed sustainably. Results from this study should be considered to be more accurate than estimates reported previously by NAFORMA (AGC = 11.5 Mg C ha\(^{-1}\), BGC = 3.2 Mg C ha\(^{-1}\) and TC = 14.7 Mg C ha\(^{-1}\)), thus may serve as national estimates for REDD+ programmes and support management of mangroves in Tanzania.

**Key words:** Above- and belowground biomass, NAFORMA (National forest resources monitoring and assessment), REDD+, Species composition

1. Introduction

As carbon reservoirs, mangroves play an important role in regulating global climate and providing other ecosystem goods and services (Nagelkerken *et al*., 2008; Donato *et al*., 2011; Alongi, 2012; Zhang *et al*., 2012; Komiyama, 2014). Like other forests, if properly managed, mangroves act as carbon sinks by absorbing CO\(_2\) from the atmosphere through the process of photosynthesis and storing it in above- and
belowground carbon pools. This therefore makes them important in climate change mitigation strategies. On the other hand, deforestation and forest degradation result into emissions of \( \text{CO}_2 \) which contribute to climate change, loss of carbon sequestration capacity and possibly loss of tree species. Deforestation and forest degradation occur mainly in the tropics, jointly they contribute about 12% of total annual anthropogenic emissions of \( \text{CO}_2 \) (van der Werf et al., 2009).

In Tanzania, mangrove declined from 109,593 ha in 1990 to 108,138 ha in 2000 (Wang et al., 2003) which is equivalent to deforestation rate of 145.5 ha per year. The annual deforestation rate is likely to be higher than that due to uncertainties of Landsat imageries applied by Wang et al. (2003). Anthropogenic factors are the main causes for decline of mangrove covers in Tanzania (Bryceson, 1981; Semesi, 1992; Wang et al., 2003; Mangora, 2011) and in different parts of the world (FAO, 2007).

Initiatives to manage mangroves sustainably exist. For example, in Tanzania mangroves are legally declared as forest reserves (MNRT, 1991; URT, 2002). National Forest Policy also clearly states that, foster management of forest resources including mangroves aims to improve both forest conditions and livelihoods (URT, 1998). Management planning of mangrove forests is an important step towards achieving their sustainable management. Information on quantity and quality of mangrove forest resources is an essential input in the planning process. In Tanzania management plans for mangrove forests have been developed (MNRT, 1991; Semesi,
1992), such plans however are out-dated. Updating or development of new management plans is therefore argent.

There are discussions going on under the United Nations Framework Convention on Climate Change (UNFCCC) on the possibility for developing countries to receive financial benefits for Reducing Emissions from Deforestation and Forest Degradation; forest conservation, sustainable management of forests and enhancement of forest carbon stocks (REDD+). It is expected that REDD+ will reduce the current trend of deforestation and forest degradation. Initiatives, such as REDD+, are considered important because of their potential to provide low-cost options to mitigate global greenhouse gas (GHG) emissions (Kindermann et al., 2008; Angelsen and Hofstad, 2008; UNFCCC, 2011).

Countries participating in the REDD+ initiative however are required to estimate their carbon benefits through a Monitoring, Reporting and Verification (MRV) systems. Carbon stocks estimates are organised into three hierarchical tiers (IPCC, 2003). For tier 1, estimates are based on IPCC default values while for tier 2 estimates are based on regional or country specific values. For tier 3 on the other hand, estimates are based on country- and forest specific values. The Inter-governmental Panel on Climate Change (IPCC) emphasises that all estimates prepared for MRV should be accompanied by an appropriate measure of uncertainty while at the same time minimising all known sources of uncertainty (IPCC, 2006).
Tanzania envisages participating in the implementation of REDD+ and has already carried out her first national forest inventory through the National Forest Resources Assessment (NAFORMA) program (URT, 2010). The permanent sample plots established under NAFORMA will be re-measured over time to provide data on the carbon stock changes.

NAFORMA results have recently been reported (MNRT, 2015). Among others, results included estimates of aboveground carbon (AGC) and belowground carbon (BGC) stocks of 11.5 Mg C ha\(^{-1}\) and 3.2 Mg C ha\(^{-1}\) (total carbon (TC) of 14.7 Mg C ha\(^{-1}\)), respectively, for mangroves in the country. Due to lack of biomass models for mangroves in Tanzania, AGC was estimated by estimating stem volume which was then converted into AGB (stem) using basic density (MNRT, 2015). Similarly, BGB was estimated using a root to shoot ratio. The same basic density and root to shoot ratio were applied for all species and tree sizes. In estimating volume, a generic model was applied. This suggests that estimates of AGC and BGC reported by NAFORMA (2015) are likely to underestimate the carbon stored in mangroves of Tanzania because other parts comprising AGB were not included.

Various methods may be employed to quantify forest carbon stock. The most common and accurate approach involves the use of biomass models. The biomass models may be considered accurate because they relate biomass and easily measurable tree parameters (e.g. diameter at breast height, measured through forest
inventories) based on allometric theory (Small, 1996; Niklas, 2006). AGB and BGB models based on data from Tanzania for three dominant mangrove species have recently been developed (Njana et al., 2015a). The use of these models to quantify carbon stocks will provide relatively more accurate information necessary for REDD+ and sustainable management of mangroves in the country.

Applying biomass models, a number of studies on mangroves have reported AGB and BGB. A review by Komiyama et al. (2008) includes 23 studies reporting AGB and BGB. Biomass and carbon stocks for mangroves are also reported in other studies (e.g. Wang et al., 2013; Abino et al., 2014; Ajonina et al., 2014; Kauffman et al., 2014; Liu et al., 2014 and Sitoe et al., 2014). Only few among such studies have been carried out in Africa (e.g. Steinke et al., 1995 (South-Africa), Slim et al., 1996 (Kenya), Sitoe et al., 2014 (Mozambique), and Ajonina et al., 2014 (Cameroon)). For studies carried out in Africa, Steinke et al. (1995) and Slim et al. (1996) reported AGB only while Sitoe et al. (2014) and Ajonina et al. (2014) reported both AGB and BGB. Among these studies, biomass estimates varied considerably between stands of different species. For example, Slim et al. (1996) reported AGB of 249 Mg ha\(^{-1}\) (primary forest) and 40 Mg ha\(^{-1}\) (primary forest) for \textit{Rhizophora mucronata} Lam. and \textit{Ceriops tagal} (Perr.) C. B. Rob. stands in Kenya, respectively. The AGB estimates reported by Slim et al. (1996) in Kenya for \textit{R. mucronata} were also different from those of Suzuki and Tagawa (1993) in Japan, who reported AGB of 108 t ha\(^{-1}\).
(primary forest) for the same species. This variation presumably reflects that biomass and carbon stock among others are influenced by site conditions and forest structure. Using the NAFORMA data, the present study aimed to provide national estimates of carbon stored in mangrove forests of Tanzania (mainland). Specifically, this study aimed to (i) document species composition of mangrove forests in the country, (ii) determine national estimates of above- and belowground biomass and carbon stocks, and (iii) assess variation of carbon stock between stand types (pure versus mixed-species).

2. Study area and Methods

2.1 Study area

Mangroves grow naturally along the coastline of Tanzania. The coastal climate is influenced by north-east winds which blow from October to March while south-east monsoon winds, blow from October to March and April to October. Annual mean rainfall ranges from 879 mm along the central to 1240 mm along the Northern and Southern ends of the Tanzanian coastline. Mean annual minimum temperatures range from 26.1 °C to 27.0 °C. The spring tidal ranges from 2 to 4 m (Richmond, 1997). From Northern to Southern Tanzania, the national forest inventory covered a total of eight mangrove sites (Figure 1).
2.2 Data

National carbon stock estimates for mangroves in Tanzania were generated using NAFORMA data collected in 2012/2013. Among others, the inventory aimed to provide sound baseline information on forest resources and establish a long term monitoring system for forest resources (URT, 2010).
2.3 NAFORMA sampling design

The forest inventory data were generated using double sampling for stratification. The sampling involved two consecutive phases; the first phase involved overlaying a dense grid of clusters on the map of Tanzania mainland at distances of 5 km x 5 km between clusters (URT, 2010; Tomppo et al., 2014; MNRT, 2015). Based on predicted volume growing stock (m$^3$ ha$^{-1}$), accessibility and slope, the country was divided into 18 strata (Tomppo et al., 2014). During the second phase, samples were systematically selected from first phase sample with different sampling intensities in each of the 18 strata. Higher sampling intensity was applied to strata with high variation and predicted growing stock while low sampling intensity was applied to strata with low variation and low predicted growing stock. The second phase sample was the one actually measured in the field. Based on the sampling design, a total of 3,420 clusters with 32,660 plots were adopted. The distance between clusters varied from 5 km to 45 km (Tomppo et al., 2014). For each cluster plots spaced 250 m apart varied from 6 to 10 depending on estimated difficulty to access the plot.

Based on the described sampling strategy, a total of 24 clusters were inventoried within mangrove forests. The 24 clusters included a total of 88 plots distributed as follows: Tanga (1 cluster (1 plot)), Bagamoyo (2 clusters (11 plots)), Ilala (1 cluster (1 plot)), Mkuranga (2 clusters (7 plots)), Rufiji (10 clusters (43 plots)), Kilwa (6 clusters (21 plots)), Lindi (2 clusters (3 plots)) and Mtwara (1 cluster (1 plot)). Figure 2 illustrates cluster plots configuration.
2.4 NAFORMA sampling unit and inventory procedures

Individual plots were regarded as sampling units (URT, 2010). Plot clustering aimed to increase efficiency the forest inventory. Circular fixed area nested plot designs were applied. The nested plots included 1, 5, 10 and 15 m radius concentric plots (Figure 3). In uneven-aged forest stands like mangroves, the stem density of small trees is much higher than the density of large trees. Therefore, to make the sampling design as efficient as possible, small trees were measured within small plots (small radii) and large trees were measured within large plots (Figure 3). As a consequence, the nested plot design implied that the number of trees measured in different size classes was almost the same, irrespective of their frequencies in the population.

Figure 2: NAFORMA Cluster design (plot = gray circles)
Within each plot, trees were measured for diameter at breast height (dbh, 1.3 m above soil surface) and identified to species level (URT, 2010). For *R. mucronata*, dbh was measured at 0.3 m above the highest stilt root. The minimum dbh of trees measured within each nested concentric circle are specified in Figure 3. For all sample plots, slope was recorded. Radius were corrected for slope when slope exceeded 5%.

![Figure 3: layout of NAFORMA concentric sample plot.](image)

2.5 Statistical data analysis

Species composition of mangrove forests was determined based on recorded species during the forest inventory. Statistical data analyses were performed using Excel and R software (R Core Team, 2014). Tree aboveground biomass (AGB) and belowground biomass (BGB) were computed using models reported by Njana et al. (2015a) for mangroves of Tanzania. The models include common (multi-species) (Models 1 and 2) and species-specific (Models 3 - 8) for three dominant mangrove
species namely *Avicennia marina* (Forssk.) Vierh, *R. Mucronata* and *Sonneratia alba* J. Smith. However, Tanzanian mangroves have a total of different nine species.

With lack of biomass models for the rest of the species, species-specific or common biomass models reported elsewhere (e.g. Chave et al., 2005; Komiyama et al., 2005; Komiyama et al., 2008) could be applied in AGB and BGB biomass estimation. However, using data from Tanzania, Njana et al. (2015a) and Njana et al. (2015b) evaluated models reported in literature and concluded that such models resulted into large prediction errors. Applying the "conservativeness principle" (i.e. when accuracy of estimates cannot be achieved, the risk of over- or under-estimation should be minimised, Grassi et al. (2008)), the species-specific models reported by Njana et al. (2015a) were therefore applied to relevant species while the common models were applied to species not covered. Here we assumed that, the common model based on the three species represents average characteristics of the mangrove species in the country. As recommended by Njana et al. (2015a), in quantifying tree BGB for *S. alba* we applied the common BGB model instead of species-specific model.

The common models applied to quantify AGB and BGB were:

\[ AGB = 0.25128 \times dbh^{2.24034}, \ n = 119, \ RMSE = 42.6\% \ \text{and} \ \text{MPE} = -0.6\% \ \text{……….. (Model 1)} \]

\[ BGB = 1.42040 \times dbh^{1.59666}, \ n = 30, \ RMSE = 89.6\% \ \text{and} \ \text{MPE} = -18.2\% \ \text{……….. (Model 2)} \]
While species-specific models were:

_A. marina_

\[ AGB = 0.25128 \times \text{dbh}^{2.24351}, \quad n = 40, \quad \text{RMSE} = 41.3\% \text{ and } \text{MPE} = 2.8\% \text{ ........... (Model 3)} \]

\[ BGB = 1.42040 \times \text{dbh}^{1.44260}, \quad n = 10, \quad \text{RMSE} = 16.8\% \text{ and } \text{MPE} = 1.5\% \text{ ........... (Model 4)} \]

_S. alba_

\[ AGB = 0.25128 \times \text{dbh}^{2.21727}, \quad n = 39, \quad \text{RMSE} = 34.2\% \text{ and } \text{MPE} = 2.8\% \text{ ........... (Model 5)} \]

\[ BGB = 1.42040 \times \text{dbh}^{1.65760}, \quad n = 10, \quad \text{RMSE} = 95.1\% \text{ and } \text{MPE} = -32.1\% \text{ ........... (Model 6)} \]

_R. mucronata_

\[ AGB = 0.25128 \times \text{dbh}^{2.26026}, \quad n = 40, \quad \text{RMSE} = 40.5\% \text{ and } \text{MPE} = -6.6\% \text{ ........... (Model 7)} \]

\[ BGB = 1.42040 \times \text{dbh}^{1.68979}, \quad n = 10, \quad \text{RMSE} = 38.7\% \text{ and } \text{MPE} = 1.6\% \text{ ........... (Model 8)} \]

Plot level AGB and BGB were derived from individual trees estimates by summation and subsequently up-scaled to per hectare estimates (Mg ha\(^{-1}\)). Total tree biomass (TB) was then obtained by summation of AGB and BGB pools. Aboveground carbon (AGC, Mg C ha\(^{-1}\)) and belowground carbon (BGC, Mg C ha\(^{-1}\)) stocks were determined from AGB and BGB using a carbon fraction of 0.47 for AGB and 0.39 for BGB (Kauffman and Donato, 2012; Abino et al., 2014). Total carbon (TC, Mg C ha\(^{-1}\)) stock was finally obtained as the sum of AGC and BGC.

Greenhouse gas inventories (and emissions) are often reported in units of carbon dioxide (CO\(_2\)) equivalents (CO\(_2\)e). Therefore, carbon stock estimates were converted
to CO$_2$e. Consequently, carbon estimates were multiplied by a molecular weight of 3.7 (Kauffman and Donato, 2012).

In carbon assessment, uncertainties are unavoidable and should be reported (IPCC, 2006; Kauffman and Donato, 2012). Among others such uncertainties may be due to biomass models and measurements (Chave et al., 2004). Therefore uncertainty in both above- and belowground carbon pool estimates were reported using 95% CI and the corresponding percentage uncertainty ($\frac{95\% \text{ CI half width}}{\text{mean}} \times 100$) (ibid). For TB and TC both based on summations and 95% CI half-width ($95\% \text{ CI}_i$) for the total estimates were computed as follows:

\[ 95\% \text{CI}_t = \sqrt{\sum (95\% \text{CI}_i)^2}, \]

where $95\% \text{ CI}_i$ is 95% CI for $i^{th}$ carbon pool.

Number of trees (N, tree ha$^{-1}$) and basal area (G, m$^2$ ha$^{-1}$) based on inventoried trees were also computed using standard formulas (Hill, 1973; Curtis and Marshall, 2000; West, 2009). Information of N and G is essential in interpretation of carbon stock estimates.

Variation of carbon stock by stand type was determined by initially clustering plots into pure and mixed-species stands. This was achieved using species enumerated in each plot. Subsequently, carbon stock estimates together with other structural parameter were subjected to analysis of variance (i.e. between and within stand types).
using \textit{lme} function in \texttt{nlme} package. Species/species composition was treated as random-effects.

3. Results

3.1 Species composition

Based on NAFORMA data (88 plots), a total of 1942 trees (dbh $\geq$ 1 cm) were measured, whereby nine mangrove species were recorded. This included \textit{Avicennia marina} (Forssk.) Vierh (Acanthaceae), \textit{Bruguiera gymnorrhiza} (L.) Lam. (Rhizophoraceae), \textit{Ceriops tagal} (Perr.) C. B. Rob. (Rhizophoraceae), \textit{Heritiera littoralis} Dryand. (Malvaceae), \textit{Lumnitzera racemosa} Willd. (Combretaceae), \textit{Rhizophora mucronata} Lam. (Rhizophoraceae), \textit{Sonneratia alba} J. Smith (Lythraceae), \textit{Xylocarpus granatum} Koen. (Meliaceae) and \textit{Xylocarpus moluccensis} (Lamk.) Roem. (Meliaceae). Weighed by basal area, \textit{A. marina} (32%), \textit{R. mucronata} (31%) and \textit{C. tagal} (20%) were the dominant species.

3.2 Tree above- and belowground biomass and carbon stocks

Tree biomass and carbon storage estimates are summarised in Table 1. Given that mangrove forests cover about 158,100 ha, a total of 10.0 millions Mg C (i.e. 37.2 millions Mg CO$_2$) is stored by mangroves of Tanzania.
Table 1: National biomass and carbon stock estimates for mangroves

<table>
<thead>
<tr>
<th>Parameter</th>
<th>n</th>
<th>95% CI</th>
<th>STD</th>
<th>Min.</th>
<th>Max.</th>
<th>Uncertainty (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGB (Mg ha(^{-1}))</td>
<td>88</td>
<td>71.3 ± 12.4</td>
<td>59.1</td>
<td>0.4</td>
<td>282.7</td>
<td>9</td>
</tr>
<tr>
<td>BGB (Mg ha(^{-1}))</td>
<td>88</td>
<td>77.0 ± 11.6</td>
<td>55.6</td>
<td>2.1</td>
<td>254.1</td>
<td>8</td>
</tr>
<tr>
<td>TB (Mg ha(^{-1}))</td>
<td>88</td>
<td>148.3 ± 17.0</td>
<td>81.1</td>
<td>2.9</td>
<td>441.1</td>
<td>12</td>
</tr>
<tr>
<td>AGC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>33.5 ± 5.8</td>
<td>27.8</td>
<td>0.2</td>
<td>132.9</td>
<td>9</td>
</tr>
<tr>
<td>BGC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>30.0 ± 4.5</td>
<td>21.7</td>
<td>0.8</td>
<td>99.1</td>
<td>8</td>
</tr>
<tr>
<td>TC (Mg C ha(^{-1}))</td>
<td>88</td>
<td>63.5 ± 7.3</td>
<td>35.3</td>
<td>1.2</td>
<td>192.5</td>
<td>12</td>
</tr>
<tr>
<td>AG-CO(_2e) (Mg CO(_2e) ha(^{-1}))</td>
<td>88</td>
<td>123.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BG-CO(_2e) (Mg CO(_2e) ha(^{-1}))</td>
<td>88</td>
<td>111.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T-CO(_2e) (Mg CO(_2e) ha(^{-1}))</td>
<td>88</td>
<td>235.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results showed that, AGC contributed about 53% of total carbon stock while the rest was stored belowground (47%). The distribution of carbon storage into above- and belowground carbon pools varied with dbh class (Figure 4). The percentage of AGC increased with dbh class while BGC declined with dbh class.

Figure 4: Distribution of AGC (gray) and BGC (dark gray) across dbh class for mangroves. I, II, III, IV and > IV represents 1.0 – 10.0, 10.1 – 20.0, 20.1 – 30.0, 30.1 – 40.0 and > 40.0 cm respectively.
The overall distributions of N, G, AGC and BGC and their corresponding structural parameters over dbh classes are summarised in Figure 5. Number of trees per hectare (N) declined steeply from smaller to larger diameter classes, whereas for other stand parameters the decline is less steep and the contributions of the two smallest diameter classes are similar, indicating that even for AGC and BGC the contribution of the 1.0-10.0 cm class is considerable.

Figure 5: Overall distribution of various forest stock parameters across dbh classes. Black, dark gray, gray, light gray and white bars respectively represent 1.0 – 10.0, 10.1 – 20.0, 20.1 – 30.0, 30.1 – 40.0 and > 40.0 cm.

Among the recorded nine recorded mangroves species, *A. marina* contributed the highest share of total AGC followed by *R. mucronata* and *C. tagal* (Figure 6).
Conversely *R. mucronata* followed by *C. tagal* and *A. marina* stored the highest proportion of total BGC. Similarly, *R. mucronata* followed by *A. marina* and *C. tagal* contributed the highest proportion of total carbon.

![Figure 6: Distribution of AGC and BGC by species; Av = *A. marina*, Bg = *B. gymnorrhiza*, Ct = *C. tagal*, Hl = *H. littoralis*, Lr = *L. racemosa*, Rm = *R. mucronata*, Sa = *S. alba*, Xg = *X. granatum* and Xm = *X. moluccensis.*](image)

3.3 Variation of carbon storage by stand type

Based on the NAFORMA data, seven among the nine recorded mangrove species existed as pure stands while *B. gymnorrhiza* and *L. racemosa* never appeared as pure stand. In addition to existing as pure stands, the seven species also co-existed with
other species. For example, among the 45 inventoried mixed-species stand plots, 11 were composed of *A. marina* and *C. tagal*. Results showed that, pure stands had slightly lower carbon stock compared to mixed-species stands although they were not significantly different (*p* > 0.05).

Table 3: Carbon storage by mangrove stand type

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pure stand (n = 43)</th>
<th>Mixed-species stand (n = 45)</th>
<th>Test on variations</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (Trees ha⁻¹)</td>
<td>4947</td>
<td>3662</td>
<td>0.014</td>
</tr>
<tr>
<td>G (m² ha⁻¹)</td>
<td>10.8</td>
<td>13.3</td>
<td>2.840</td>
</tr>
<tr>
<td>AGC (Mg C ha⁻¹)</td>
<td>29.6</td>
<td>37.2</td>
<td>2.333</td>
</tr>
<tr>
<td>BGC (Mg C ha⁻¹)</td>
<td>26.0</td>
<td>33.8</td>
<td>3.202</td>
</tr>
<tr>
<td>TC (Mg C ha⁻¹)</td>
<td>55.7</td>
<td>71.0</td>
<td>3.040</td>
</tr>
</tbody>
</table>

4. Discussion

A total of nine species were recorded for mangroves in Tanzania. There are 50 to 70 mangrove species worldwide (Lugo and Snedaker, 1975; Saenger et al., 1983; Tomlinson, 1986; Aksornkoae *et al.*, 1992), with Asia followed by Africa being considered most diverse (FAO, 2007). About 14 mangrove species are found along the East coast of Africa while only seven occurs naturally along the West Coast of Africa (FAO, 2007). Existing studies showed that, *A. marina*, *B. gymnorrhiza* and *R. mucronata* are frequently distributed along the Eastern and Southern coasts of Africa (FAO, 2007; Sitoe *et al.*, 2014; Hoppe-Speer *et al.*, 2015). With the exception of *B. gymnorrhiza*, the species that are dominant at the Eastern and Southern coast of Africa were also dominant in Tanzania. The dominance and perhaps wide distribution of *A. marina* may be attributed to the ability of this species to tolerate a wider range of salinity than *R. mucronata* and *S. alba* (Ball and Pidsley, 1995; Joshi and Ghose,
2003). *X. moluccensis* recorded in the national forest inventory was not reported in existing studies (MNRT, 1991). Moreover, *Pemphis acidula* J.R. & G. Forst. which was observed by Njana et al. (2015c) was not recorded in national forest inventory suggesting that both species may be less frequent species and with limited spatial distribution.

In this study, we report tier 2 AGC, BGC and TC and the estimates. Since carbon stocks were estimated using biomass models for *A. marina*, *S. alba* and *R. mucronata* (Njana et al., 2015a), partly uncertainties to the carbon stock estimates may be due to application of biomass models to unrepresented species. However the uncertainty is not as large as application of species-specific models based on data from elsewhere since we assumed that, the three species (about 66% of total basal area) represent average population characteristics of mangrove species in the country.

Although reported biomass and carbon estimates vary considerably, our estimates fall within the range of estimates reported elsewhere (Table 4). For example, AGB (*A. marina* and *S. alba* stands) and AGC (*A. marina* stand) estimates reported by Ray et al. (2011) and Patil et al. (2014) respectively for mangroves of India are similar to estimates reported in this study.

Despite that, Biomass and carbon estimates from this study are different from some previously reported estimates. This may be explained by a number of reasons
including differences in species composition, average tree size, geographical locations, soils and climatic conditions. Other factors may include methods applied to determine biomass and application of biomass models beyond data range. For example, AGB and BGB reported by Abino et al. (2014) (Philippines) and Ajonina et al. (2014) (Gabon) are higher than values reported in this study. Generally estimates reported by Abino et al. (2014) and Ajonina et al. (2014) are based on stands composed of species not found in Tanzania. Both studies applied Komiyama et al. (2005)’s model to quantify biomass, although tested on data from Tanzania the model tended to over-predict AGB of large trees (Njana et al., 2015a). Besides, with the exception of *S. alba* and *X. granatum*, Komiyama et al. (2005)’s model is not based on data from species found Philippines and Gabon (Abino et al., 2014; Ajonina et al., 2014). Therefore the difference in estimates between those reported in this study and those reported previously may be due to application of biomass models beyond data range.

Carbon stock estimates from our study were higher than those reported by NAFORMA (MNRT, 2015) for mangroves of Tanzania although both are based on the same data set. Most likely this is a consequence of differences in biomass estimation procedures applied between the two studies. NAFORMA estimated AGB from stem volume using a basic density of 500 kg m$^{-3}$. Volume was estimated using a generic model. Equally, BGB was estimated using a root to shoot ratio of 0.28 across species and tree sizes. The basic density applied by NAFORMA as a volume
to biomass conversion factor for mangroves was lower than recently reported values for mangrove species of Tanzania, in addition the values varied significantly by species (Njana et al., 2015c). The standard procedure in estimating AGB from volume requires that the non-merchantable part of tree biomass (branch, twig and leaf) is accounted for using the biomass expansion factor (Somogyi et al., 2007). Njana et al. (2015a) reported that, stem biomass accounted for 55% of total AGB while the remaining was attributed to other parts. The root to shoot ratio also varies between species (Komiyama et al., 2014; Njana et al., 2015a).

Comparing carbon stored by mangroves with other forest types we found that, AGC was about 54.3 ± 5.8 (SE) Mg C ha\(^{-1}\) for montane forests (; Shirima et al., 2015) and 16 – 40 Mg C ha\(^{-1}\) for miombo woodlands of Southern Africa (Ryan et al., 2011; Shirima et al., 2011; Kalaba et al., 2013; Zahabu and Jambia, 2013; Lupala et al., 2014; Shirima et al., 2015). According to Ryan et al. (2011), about 8.5 Mg C ha\(^{-1}\) was stored belowground in miombo woodlands. Generally, our estimates for mangroves were higher than those reported for miombo woodlands.

The distribution of carbon into above- and belowground stocks suggests that both AGC and BGC are equally important as carbon storage media. The distribution of AGC and BGC over dbh class may be associate with strategies of mangrove trees as they grow; at early stages more carbon is distributed in the belowground for anchorage and stabilization in the soft substrate while at later stages more carbon is
Table 4: Comparison of biomass and carbon stock for mangroves

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>Species composition</th>
<th>Model source</th>
<th>AGB (Mg ha(^{-1}))</th>
<th>BGB (Mg ha(^{-1}))</th>
<th>AGC (Mg C ha(^{-1}))</th>
<th>BGC (Mg C ha(^{-1}))</th>
<th>TC (Mg C ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wang et al. (2013)</td>
<td>China</td>
<td>A. marina</td>
<td>†Comley and McGuinness (2005)</td>
<td>40.0</td>
<td>20.4</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Abino et al. (2014)</td>
<td>Philippines</td>
<td>Avicenia officinalis, S. alba and X. granatum</td>
<td>†Komiyma et al. (2005)</td>
<td>297.2</td>
<td>103.9</td>
<td>-</td>
<td>-</td>
<td>188.5</td>
</tr>
<tr>
<td>Castanêda-Moya et al. (2013)</td>
<td>Florida</td>
<td>Mixed-species</td>
<td>†Smith and Whelan (2006)</td>
<td>100 – 162</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ray et al. (2011)</td>
<td>India</td>
<td>A. marina and S. alba</td>
<td>†Ray et al. (2011)</td>
<td>65.3 – 109.1</td>
<td>15.3 – 25.2</td>
<td>-</td>
<td>-</td>
<td>34.6 – 57.6</td>
</tr>
<tr>
<td>Patil et al. (2014)</td>
<td>India</td>
<td>A. marina</td>
<td>†Patil et al. (2014)</td>
<td>-</td>
<td>-</td>
<td>34.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ajonina et al. (2014)</td>
<td>Gabon</td>
<td>Avicenia germinas, Canecarpus erectus, Languncularia racemosa, Rhizophora harrisonii, Rhizophora mangle and Rhizophora racemosa</td>
<td>†Komiyma et al. (2005)</td>
<td>341.0</td>
<td>151.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sitoe et al. (2014)</td>
<td>Mozambique</td>
<td>A. marina, B. gymnorrhiza, C. tagal, R mucronata, X. granatum and H. littoralis A. marina</td>
<td>†Sitoe et al. (2014), †Komiyma et al. (2005)</td>
<td>58.4</td>
<td>64.7</td>
<td>28.0</td>
<td>25.2</td>
<td>-</td>
</tr>
<tr>
<td>Kairo et al. (2009)</td>
<td>Kenya</td>
<td>A. marina and B. gymnorrhiza</td>
<td>†Kairo et al. (2009)</td>
<td>11.7</td>
<td>9.67</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Steinke et al. (1995)</td>
<td>South Africa</td>
<td>A. marina</td>
<td>†Steinke et al. (1995)</td>
<td>19.8 – 74.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>This study</td>
<td>Tanzania</td>
<td>A. marina, B. gymnorrhiza, C. tagal, H. littoralis, L. racemosa, R mucronata, S. alba, X. granatum and moluccensis</td>
<td>†Njana et al. (2015a)</td>
<td>71.3</td>
<td>77.0</td>
<td>33.5</td>
<td>30.0</td>
<td>63.5</td>
</tr>
</tbody>
</table>

†AGB and BGB determined using biomass model; ††AGB determined indirectly using generic stem volume model, volume estimates were then converted to dry weight using basic density and BGB was determined using root to shoot ratio.
distributed to the aboveground part in support of physiological processes for growth (Njana et al., 2015a).

Carbon storage in mangroves varied by stand types, mixed-species stands stored higher quantities of carbon than pure stands. This suggests that, mixed-species stands are supported by resource rich environment that allow multiple species co-existence which subsequently improves stand productivity. In line with our results Chapman and Feller (2011) reported that A. germinans (L.) L. seedlings grew better in litter of Rhizophora mangle L. and vice versa. Therefore species mixing should be considered in afforestation and rehabilitation of mangroves for enhanced productivity.

There are many challenges with regard to management and conservation of mangroves. Such challenges include lack of adequate information on the role of this ecosystem. As a result mangroves worldwide have received little attention leading to their continued decline over time (Wang et al., 2003; FAO, 2007; Chen et al., 2009; Giri et al., 2011). Mangora et al. (2011) argued that challenges in conservation of mangroves in Tanzania include policy failure, weak or dysfunctional state institutions while Liu et al. (2014) observed that management of mangroves in China was challenged by vague and not enforceable laws. Findings from this study shows that, mangroves of Tanzania (10.0 millions Mg C (37.2 millions Mg CO₂) and elsewhere around the world (Abino et al., 2014; Liu et al., 2014) store large quantities of carbon. These results therefore should stimulate dialogues and influence decisions geared towards sustainable management of mangrove forests through REDD+ initiatives. Carbon stock estimates reported in this study are more accurate than stocks reported
previously by NAFORMA. Therefore they may serve as national estimates for REDD+ programmes.

5. Conclusions

Based on NAFORMA data, nine species were recorded for mangroves of Tanzania. Among them *A. marina, R. mucronata* and *C. tagal* were dominant. We found that, mangroves store large quantities of carbon both above- and belowground, implying that they have important functions in climate change mitigation strategies. Mangroves therefore need to be managed sustainably. Carbon stock estimates reported in this study are more accurate than stocks reported previously by NAFORMA. Therefore they may serve as national estimates for REDD+ programmes and support management of mangroves in Tanzania through REDD+ initiatives. Motivation for sustainable management of mangroves should however go beyond the carbon agenda since in addition to storing and sequestering carbon, mangroves are also important for coastal protection. Results from this study may also be applied as baselines for monitoring of mangrove forests. Based on NAFORMA data, this study provides national level estimates. Mangrove site specific estimates on carbon are also important for reporting tier 3 under the REDD+ thus should be considered in future studies.

Acknowledgements

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