FACULTY OF SCIENCE
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PhD thesis

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Management tools and potential of Dry Miombo woodland in carbon cycling

The case of Gangalamtumba Village Land Forest Reserve in Iringa, Tanzania

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Contents

Dedication

This thesis is dedicated to people of Mfyome village for their commitment in conserving their forest, not only for their own benefit but also for the benefit of future generations.

Acknowledgements

This PhD study was supported by the Danish International Development Assistance (DANIDA) through Enhancing Research Capacity (ENRECA) project No. 725, titled "Participatory forest management for rural livelihoods, forest conservation and good governance in Tanzania". The said financial support is highly appreciated. I am deeply indebted to my main supervisor associate Professor Thorsten Treue for a wonderful moral support and supervision throughout the PhD study. Thank you for taking care of my worries and helping me to calm down during the time of panic! For being flexible and considerate you have made my studies an enjoyable experience hence attaining successfully the expertise needed. Technical and professional guidance from my project supervisor associate Professor Henrik Meilby is highly acknowledged and appreciated. You have been always insisting about "making sketches" if things turned out to be unclear and complicated. I will never forget that! My profound gratitude also goes to Professor Yonika M. Ngaga, team leader of the ENRECA project in Tanzania for moral and logistical support during my three months of field work in Tanzania.

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Preface

This PhD thesis is intended to fulfil the requirements for a PhD degree at the Faculty of Science, University of Copenhagen in Denmark. The presented work was carried out at Gangalamtumba Village Land Forest Reserve in Iringa Rural District in Tanzania, Sokoine University of Agriculture in Morogoro, Tanzania, the Dendrochronology section at the National Museum of Denmark, the Department of Food and Resource Economics, the Danish Centre for Forest, Landscape and Planning, and at the Laboratory for Wood Biology and Xylarium in the Royal Museum for Central Africa in Belgium. All Ph.D. Courses were completed at the Faculty of Science, University of Copenhagen in Denmark.

The thesis consists of an introductory part and five papers:

PAPER I:

Mwakalukwa, E. E; Meilby, H and Treue, T. (2014). Floristic composition, structure and species associations of dry Miombo woodlands in Tanzania. *ISRN Biodiversity* 2014:1-15. Article ID 153278, http://dx.doi:10.1155/2014/153278.

PAPER II:

Mwakalukwa, E. E; Meilby, H and Treue, T. (2014). Basic density of trees and shrubs from dry miombo woodland in Tanzania (Manuscript).

PAPER III:

Mwakalukwa, E. E; Meilby, H and Treue, T. (2014). Volume and aboveground biomass models for dry Miombo woodland in Tanzania. *International Journal of Forestry Research* 2014:1-11. Article ID 531256, http://dx.doi.org/10.1155/2014/531256.

PAPER IV:

Mwakalukwa, E. E; De Ridder, M; Meilby, H; Treue, T; Trouet, V and Beeckman, H. (2014). Modelling diameter growth of *Brachystegia spiciformis* in dry Miombo woodland in Tanzania (Manuscript).

PAPER V:

Mwakalukwa, E. E; Meilby, H and Treue, T. (2014). Carbon storage and sequestration in a dry Miombo woodland area in Tanzania (Manuscript).

Ezekiel Edward Mwakalukwa,
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Abstract

Tools to support sustainable management of dry Miombo woodlands and precise assessment of carbon storage and sequestration potential are in most cases lacking in Tanzania. Accordingly, using Gangalamtumba Village Land Forest Reserve as a case study area located in Iringa region, this thesis aims to develop management tools and generate information that will enhance our understanding of the actual and potential contribution of dry Miombo woodlands in carbon cycling. This is done through a detailed assessment of floristic composition, structure, species associations and through development of models for wood basic density, volume, biomass and growth. The overall research objective was thus to enhance the basis for good woodland management planning including exploring the extent to which dry Miombo woodlands in Tanzania store and sequester C from the atmosphere. Correct identification of 88 plant woody species belonging to 29 families assisted the selection of a total of 44 important species of trees (28) and shrubs (16). These species were harvested for the determination of basic wood density values and to develop wood basic density models for specific species and for groups of species, namely trees, shrubs and combined. Aboveground volume and biomass models for specific species and species groups were also developed. Growth models of the important species, *Brachystegia spiciformis* Benth. as influenced by three external factors; rainfall, soil fertility, and competition were also developed to assist planning of sustainable harvesting levels. Finally, an application of data on forest structure, wood basic densities for trees and shrubs, and the developed models describing aboveground biomass and growth were used in assessing C stocks and sequestration potential of the woodland based on selected scenarios. Generally, the models appear robust and can thus be used in planning sustainable management of the woodlands. The developed models estimate that the dry Miombo woodland of Gangalamtumba Village Land Forest Reserve stores substantial amounts of C; 68.64 Mg C ha^{-1} both in above- and below-ground soil carbon pools. Assuming that other species' production are equal to *B. spiciformis*, which is the most dominant species in the study area, the estimated C sequestration potential of the dry Miombo woodlands was found to vary from 0.42 ± 0.03 Mg C ha^{-1}year^{-1} to 1.39 ± 0.08 Mg C ha^{-1}year^{-1}, depending on scenario. Considering the vast areas covered by dry Miombo woodlands, sustainable management of this vegetation type clearly holds potential in preventing emissions of large amounts of C currently locked up in this ecosystem.

1.0. Introduction

Dry forests account for about 42% of the total land mass in the tropics (Miles et al., 2006). Timberlake et al. (2010) defined dry forest and woodland as "vegetation dominated by woody plants, primarily trees, the canopy of which covers more than 10% of the ground surface, occurring in climates with a dry season of three months or more". In Africa, dry forests cover about 17.3 million km^2 in 31 countries and occupy an area between the rainforests in the Congo basin and the open woodlands of western, eastern and southern Africa including Miombo woodlands (Timberlake et al., 2010; Frost, 1996). It is estimated that about 505 million people derive their livelihoods in dry forest areas through crop farming which is mainly rain fed, livestock rearing as well as through gathering of timber and non-timber forest products (Timberlake et al., 2010).

The term "Miombo" is derived from *Muyombo*, a name the Nyamwezi people around Tabora Region in Tanzania have given to *Brachystegia*, a tree genus common to this woodland (Dykstra, 1983). Miombo is a generic name that describes woodland ecosystems dominated by trees in the genera *Brachystegia, Julbernadia* and *Isoberlinia* of the family Fabaceae and sub-family Caesalpinioideae (Campbell et al., 1996). Species of the closely related genera *Julbernadia* and *Brachystegia* often make up 80% of the trees, with important hardwood timber species such as *Pterocarpus angolensis* and *Afzelia quanzensis* being codominant in local areas (Lawton, 1982). The woodlands (Figure 1) form the most dominant and extensive dry forest formation in the eastern, central and southern Africa with an estimated area of 3.6 million km^2 (Campbell et al., 1996; Frost, 1996; Byers, 2001). The woodland covers large proportions of the area of 11 countries from South Africa, Angola, Zimbabwe, Botswana, Namibia, Zambia, the Democratic Republic of Congo, Burundi, Malawi, Mozambique and Tanzania (Campbell et al., 1996; Ryan et al., 2011). White (1983) divided Miombo woodlands into dry and wet Miombo based on the rainfall. Dry Miombo woodlands occur in areas receiving less than 1000 mm rainfall annually, while wet Miombo occurs in areas receiving 1000 mm rainfall or more annually. In this thesis the emphasis is on dry Miombo.

In Tanzania Miombo woodlands comprise up to 54% of the 38.8 million hectares of the Tanzanian forests (Figure 1). They occupy the southeast and the central plateau of the north, with a non-Miombo corridor 500 km long and 60-120 km wide separating these areas (Figure 2). Dry and Wet Miombo woodlands contribute 19% and 35% of the total Miombo woodland area in Tanzania, respectively (Chamshama and Vyamana, 2010). In the dry Miombo areas, vegetation is floristically impoverished and the canopy height is less than 15 m (Frost, 1996). The species most commonly found are *Brachystegia spiciformis*, and *B. boehmii*. Other dominant deciduous species include *Julbernardia globiflora*. This type of woodland is said to cover about 1.21 million km^2 and occurs in southern Malawi, south, central and northern Mozambique, southern Zambia and Zimbabwe. In Tanzania, the main concentration of this vegetation type is found in the western zone (Tabora, Rukwa, Katavi and Kigoma regions) and in the southern zone (Iringa, Njombe, Lindi, Mtwara and Ruvuma regions). The woodland also occurs in the northern part of the country (Abdallah and Monela, 2007; Timberlake et al., 2010; Giliba et al., 2011).

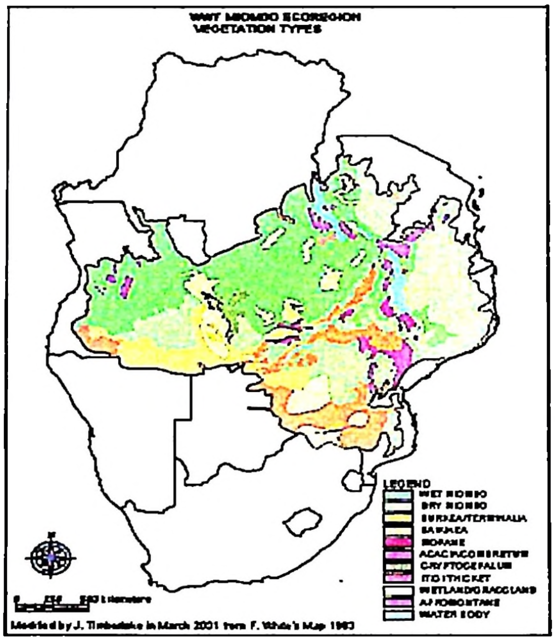

Figure 1: Miombo ecoregion vegetation types (Source: Byers, 2001)

In wet Miombo areas, the vegetation is floristically rich and the canopy height is greater than 15 m (Frost, 1996). The vegetation includes nearly all of the characteristic Miombo species. The most commonly found are *Brachystegia floribunda*, *B. glaberrima*, *B. longifolia*, *B. wangermeeana*, *Julbernardia paniculata*, *Isoberlinia angolensis* and *Marquesia macroura*. This type of woodland is said to cover about 1.36 million km^2 and occurs near the coast in central and northern Angola, northern Zambia, southern Democratic Republic of the Congo, western Tanzania, central and northern Malawi and with small extents in northern Mozambique and Burundi (Abdallah and Monela, 2007; Timberlake et al., 2010).

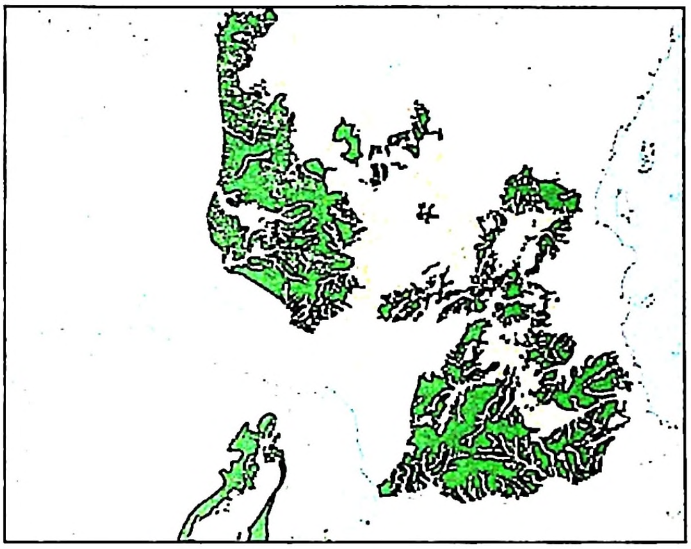

Figure 2: Distribution of drier Miombo woodland (green colour) in Tanzania and North Eastern Zambia. The gray part indicates non-dry Miombo woodlands (Source: Kindt et al., 2011)

Miombo woodlands are important sources of wood for construction as well as energy including charcoal, which is a main a source of energy for about 15 million urban dwellers. They also serve as a land bank and it has been suggested that about 40 million people inhabit areas covered or formerly covered by Miombo woodlands (Campbell et al., 1996). Given the large areas covered the woodlands are presumably also globally important for C sequestration although very few comprehensive studies to document C stocks across existing carbon pools have been conducted (Grainger, 1999; Frost, 1996; Munishi et al., 2010). In Tanzania Miombo woodlands form an integral part of the rural landscape and play a crucial role in providing rural communities with a wide range of products and services necessary for their livelihoods (Kajembe et al., 2002). Examples of the products accrued from Miombo woodlands include; medicines, charcoal, firewood, food (game meat, fruits, honey), fibres, construction and craft materials, whereas services include; cultural and spiritual values, local climate regulation, erosion and hydrological control, grazing area, wildlife habitat (and therefore hunting grounds) and catchment values. Miombo also supports agricultural production by being used for crop production and is also a source of energy for curing tobacco (Abdallah, 2001; Sauer and Abdallah, 2007).

Despite its contribution to livelihood of people through provision of various products and services, tropical dry forest Miombo woodlands in particular are threatened largely because of unplanned human activities (Miles et al., 2006). Campbell et al., (2007) reported that where Miombo woodlands dominate they suffer annual losses of about 1.4 million ha through deforestation and forest degradation. In Tanzania it is estimated that between 130,000 and 500,000 ha of forests are destroyed annually (URT, 1998). Currently statistics indicate that the deforestation rate in Tanzania is about 400,000 ha annually (FAO, 2010). These losses give rise to concern about the future capacity of these forests to provide the expected ecosystem services such as biodiversity conservation, provision of water services, regulation of the micro climate and carbon storage/sequestration.

2.0. Research objectives

A major challenge facing many developing countries including Tanzania is how to go about stopping or reducing the high rates of deforestation while at the same time meeting the needs of wood resources by their often fast growing population. This situation is further complicated due to a lack of precise data on the resources and of management tools to support sound ways of managing these resources. For proper decision-making (i.e policy development, forest management planning), accurate data on species composition, stems/ha, basal area/ha, volume/ha, diameter increments of the species and patterns of utilisation levels are vital. Proper decision-making can only be fully achieved if suitable tools (i.e. density models, volume models, biomass models and growth models) are available that are valid for specific sites and for specific species or groups of species. Unfortunately, many of the forest resources in Tanzania including dry Miombo woodlands which support livelihoods of the majority of people in the country lack proper management interventions. To some extent this is not only due to a lack of sound ecological data and accurate management tools to guide in decision making about the resources, but also due to lack of economic incentives in managing these resources and law enforcement (URT, 2007).

This thesis aims to enhance our understanding of the current condition of Tanzanian dry Miombo woodlands, develop accurate management tools to guide decision making and planning for sustainable utilisation of the woodlands, and assess the contribution of dry Miombo woodlands in carbon storage and sequestration. The latter is envisaged to provide an improved basis for inclusion of dry Miombo woodlands in the emerging carbon credit market mechanism through the Reducing

Emission from Deforestation and Forest Degradation (REDD+) scheme. In particular, information is needed to quantify the extent to which Tanzania as a country have achieved in sustainable management of the once used to be open access areas by devolving the ownership and management responsibilities to the local communities living around these areas through its strategy of Participatory Forest Management. Furthermore, information is needed to quantify the extent to which these woodlands have contributed to the storage and sequestration potential of C from the atmosphere. This is pursued through development of a range of tools needed for assessment of above-ground C stock and sequestration and a detailed assessment of existing C pools and sequestration potentials of the woodland using Gangalamtumba Village Land Forest Reserve located in Iringa Region as a case study area.

Specifically this study aims to;

i) assess the current forest conditions in terms of structure, species richness and species composition, and classify existing plant communities as influenced by edaphic and topographic factors (Paper I),

ii) develop wood basic density models for tree and shrub species and determine basic density values for species commonly found in the dry Miombo woodlands as inputs in quantification of biomass and hence carbon stocks of the woodland (Paper II),

iii) develop volume and above-ground biomass models of tree and shrub species for accurate estimation of above-ground biomass and hence C stocks of the woodland (Paper III),

iv) quantify growth of trees and develop diameter growth models relating growth to climatic, edaphic and topographic factors as well as competition from surrounding vegetation to be used in sustainable management of the woodlands, (Paper IV), and

v) quantify the existing C stocks and sequestration potentials of the woodland (Paper V).

Core research questions addressed in this study are: 1) what are the bases for good woodland management planning, and 2) to what extent does dry Miombo woodlands in Tanzania store and sequester C from the atmosphere?

3.0. Conceptual framework

Tools for sustainable management framework and enhancement of the carbon storage potential of the dry Miombo woodlands as conceptualised in this study is as presented in Figure 3. For proper management of any forest/woodland reserve, sound ecological data which describe the general conditions of the forest/woodland and how it is affected/shaped by the existing environmental conditions is important. Furthermore, it is important to use the available accurate management tools in making proper decision about the resource. Data on species composition and their distribution in a given area of forest/woodlands due to the influence of different environmental factors (e.g. elevation, slope, soil characteristics) and different levels of human activities, provide a basis for management interventions either focusing on the entire forest/woodland or a particular species, certain plant communities or particular patches in the forest. Generally, a successful intervention depends not only on the availability of sound ecological data but also on the appropriate management policies for that resource and good management plans which in turn depend on the availability of sound data and managent tools. An example is the ongoing debate about the inclusion of natural forests as one of many options for climate change mitigation through Reducing Emissions from Deforestation and Forest Degradation (REDD+).

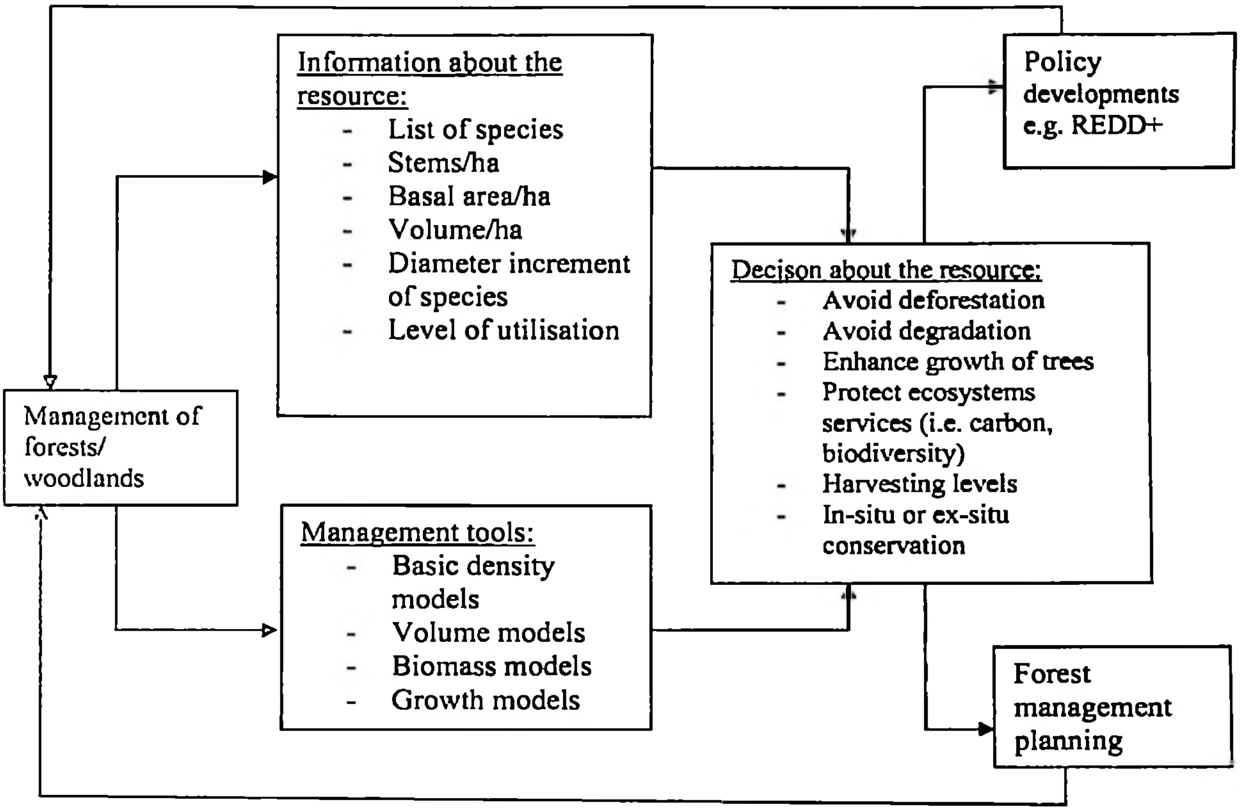

Figure 3: Management tools in support of sustainable management of forets/woodlands. The arrows indicate the flow of information.

4.0. Selection of the case study area

4.1.1. Country information

Tanzania's mainland has a total area of about 94.5 million hectares of which 88.6 million hectares are covered by landmass and the rest is inland water. Tanzania currently is the home to approximately 46 million people. More than 80% of Tanzanians live in rural areas in more than 14,000 villages. The majority of Tanzanians (about 59%) depend on natural resources for their livelihood. The major energy sources for both rural communities and urban dwellers are fuel wood and hydropower. Agriculture dominates the economy, accounting for about 50% of gross domestic product (GDP) as well as employment and income for most Tanzanians.

Forest resources in Tanzania include forests, woodland and grasslands. The exact coverage of forests and woodlands in Tanzania is not known. The figures reported in the literature are very contradicting (URT, 1998; Wily and Dewees, 2001; URT, 2006; Chamshama and Vyamana, 2010). However it has been estimated that about 50% of the total land area is forest and woodland, 40% is grassland and shrub and only 3% of the country is covered by dense closed forest. It has been estimated that the country's forest area has declined from 44.3 million hectares in 1938 or 50% of total land area to 33.1 million hectares in 1987 or 43% of total area. Current official statistics show that the country has a total area of 34 million hectares of forestland out of which 16 million hectares are reserved forests, 2 million hectares are forests in National Parks and the rest, 16 million hectares (47% of all forestland), are unprotected forests mostly Miombo woodlands lying on general land (URT, 1998; 2006). In general, the vast majority of Tanzania's forests (around 96%) are comprised of savanna woodlands of which most fall under the Miombo category (Wily and Dewees, 2001).

Forests and woodlands in Tanzania have been under de jure state control since the colonial era until the approval of the new National Forest Policy of Tanzania in 1998 (Abdallah and Monela, 2007). The new Forest policy and its subsequent Forest Act of 2002 recognize the role of community involvement in sustainable forest management and utilization (URT, 1998; 2002). This initiative came after the government realized that the past conservation approaches, which aimed to bring more forests under state tenure and protection as reserves or parks, had failed to bring unplanned deforestation under control (URT, 1998).

Current statistics show that, through Participatory Forest Management (PFM) arrangements, about 2.3 million hectares of these formerly unprotected forests/woodlands have now been placed under the authority of more than 1,400 village governments through Community Based Forest Management (CBFM) arrangements (URT, 2008). CBFM is one form of PFM where village governments get ownership to forestland and products from forests within their village land once they have demarcated and declared the area in question a village land forest reserve and have a management plan for this endorsed by the Tanzania Forest Service. Out of more than 300 declared village land forests reserves, 64 (830,000 ha or 35% of the total area under CBFM) have already been gazetted, i.e. formally recognized by the central government as part of the country's permanent forest estate, and a large proportion of these forests (200,000 ha or 24% of the gazetted area) is found in Iringa region which also includes the study area of this thesis. Most of these forests are managed in the absence of detailed management plans, suggesting that detailed surveys have not been undertaken during the implementation of PFM (URT, 2011).

4.1.2. Study site

The study was conducted at Gangalamtumba Village Land Forest Reserve located in central-southern Tanzania (7°35' S, 35°35' E), about 30 km northwest of Iringa Municipality, the administrative capital of Iringa Region (Figure 4). The forest forms part of Mfyome village which is located in the ward of Kiwele about 24 km from Iringa town. The altitudinal range is 850-1,300 m and the total forest area is 6,065 ha. Average rainfall data for the period of 50 years (1960-2009) from the nearby meteorological station (Nduli airport) located about 30 km from the forest, indicates that the area receives an average annual precipitation of 616.6 ±119.7 mm (mean ± sd) with a minimum and maximum of 447.7 mm and 1,084.8 mm, respectively. July receives very little rain, on average 0.1 mm, compared to other months while January is the wettest receiving on average 133.9 mm. GVLFR is a production forest, which is managed by the village under CBFM. This arrangement started in 2002. By-laws enacted by the village government and endorsed by the district government guide the forest management and establish exclusive rights including rights of the village to harvest, own and dispose of forest products. Day-to-day forest management is performed by an Environmental Committee (EC) which is established through direct election among all members of the village above 18 years of age. The EC is under supervision of the village government. The selection of GVLFR was based on the fact that it is a production forest from which wood products are extracted for commercial as well as subsistence purposes. Since the focus of this study was on dry Miombo areas, the rainfall received by GVLFR was also a criterion. Another reason was that the condition of the forests was relatively 'good', i.e. used but not 'degraded' which allowed for studying the species diversity and structure and for comparison with other studies of 'intact' dry Miombo.

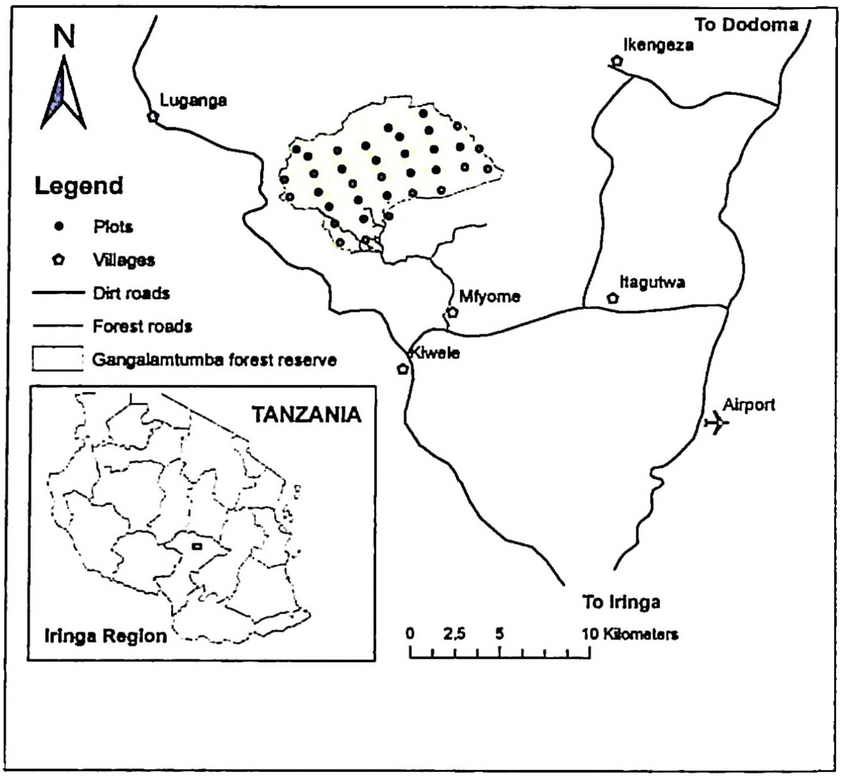

Figure 4: Map of Tanzania showing the location of study area in Iringa region.

5.0. Materials and methods

Inventory work was carried out in August, 2009. From a randomly selected starting point, 35 nested circular sample plots of 5 m, 15 m and 20 m radii (Figure 5) were established along transect lines laid down across the entire forest of 6,065 ha. The distances between transect lines and between plots within transect lines were about 2 km (Figure 4). In each plot both trees and shrub species were identified and measured for diameter at breast height (Dbh). Specifically seedlings and saplings for trees and shrubs < 5cm diameter were identified, counted and measured within the 5 m radius plots, and adults ≥ 5cm diameter were identified and measured within the 15 m radius plots. Stumps were assessed within the 20 m radius plots and measured for diameter at a height of 20 cm above-ground. Soil samples were collected from five locations at a distance of 10 m from the centre of each plot in four cardinal directions (North, East, South, West and at the centre of the plot) to a depth of 0-15 cm and 15-30 cm, respectively. A total of 70 composite soil samples were collected with a total of 35 samples from each depth interval. Also separate soil samples for soil bulk density determination were collected from each plot using a soil core device with an inner diameter of 5 cm and a length of 5 cm. Samples of deadwood were measured within the 15 m radius plots while samples of grasses and herbs and surface litter were collected from 50 cm × 50 cm plots located at a distance of 10 m from the centre of the plot in eight cardinal directions.

Species identification relied on the knowledge of local botanists but was also confirmed by an experienced botanist from the Herbarium at Lushoto Silviculture Research Centre, under the Tanzania Forest Research Institute (TAFORI). For species which could not be identified in the field together with those successfully identified in the field were taken to the TAFORI Herbarium at Lushoto for identification or confirmation. Species identification was completed in March 2011. Other measurements taken within the plots were elevation (m) using GPS, plots location using GPS, and slope (%) using a Suunto clinometer.

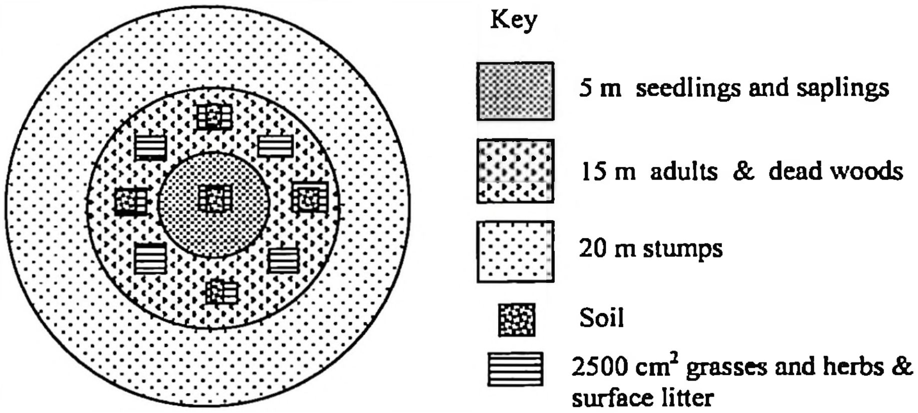

Figure 5: Concentric circular shapes of nested sample plots used in survey of Miombo woodlands vegetation and collecting data for six carbon pools in the study area.

In addition, the field survey conducted in August 2009 and August-October, 2010 involved harvesting of 142 individuals (28 tree species) and 57 individuals (16 shrub species) from the same 35 permanent circular sample plots but with a radius of 50 m established across the 6,065 ha in the study area (Figure 4). Among the harvested tree individuals were the two dominant species namely *Brachystegia spiciformis* and *Combretum molle*. *Dalbergia arbutifolia* was among the dominant shrubs; therefore also included in the list of harvested species for volume and biomass modelling. Selected species was based on two criteria; their dominance (wide availability in the forest) and their economic potential to the local people. *Brachystegia spiciformis* and *Combretum molle* are used mainly as sources of energy in terms of fire wood and charcoal. With low calorific value and high production of smoke, *Dalbergia arbutifolia* is often used in beekeeping activities. Before they were felled, each individual tree/shrub was measured for stump diameter (at 20 cm height above-ground), diameter at 50 cm above-ground, diameter 1.3 m above-ground (Dbh), diameter 2 m above-ground, crown width in four cardinal directions (North, South, West, and East), height to first branch and total height. Branches and twigs with a diameter < 5 cm were first removed and weighed and then sub-samples were taken and weighed again in the field. The remaining parts including branches and stems > 5 cm, were divided into smaller sections of not more than 2 m in length and measured for length and diameter at the two ends and at the middle of each section. Thereafter five discs, each 2-3 cm thick, were extracted from the sections using importance sampling with probability proportional to volume (Valentine et al., 1984; de Gier., 2003).

In addition, separate samples of 40 stem disks from *Brachystegia spiciformis* trees were cut at breast height for growth assessment using tree ring analysis (Figure 6). The 40 trees had a mean diameter of 21.3 cm (range 1.2-54.3 cm) and mean height of 10.1 m (range 2.0-17.2 m). Additionally, a separate plot with a radius of 7.5 m was established around each sampled tree of *Brachystegia spiciformis* for assessing the competition effect from the neighbouring trees. Each tree within this plot was also identified and measured for diameter at 20 cm above-ground, Dbh and distance (m) to the sampled tree. Climatic data from the two nearby meteorological stations of Nduli Airport and Tosamaganga, located about 30 km away from the study area, were obtained from the Tanzania Meteorological Agency headquarters in Dar es Salaam. The collected datasets were then used in the preparation of the five papers which form the core of this thesis.

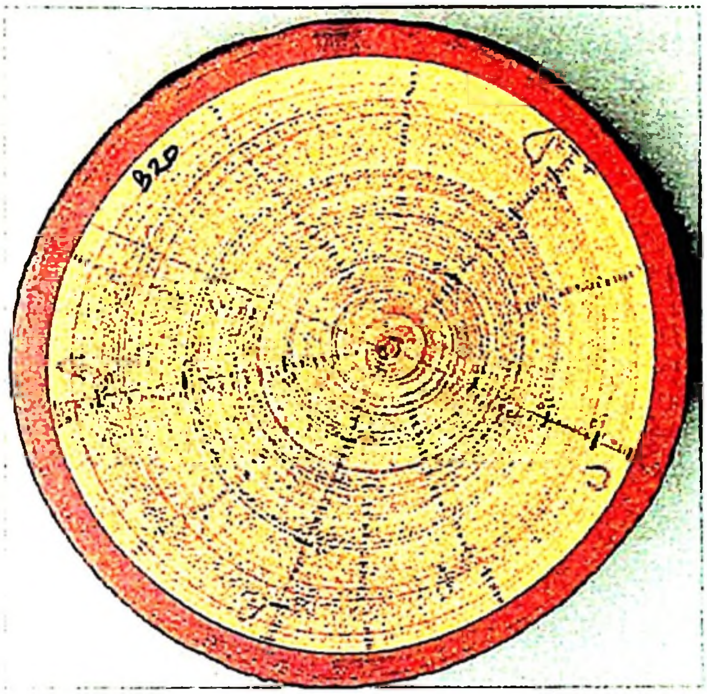

Figure 6: A stem disc of *B. spiciformis* showing four marked radii which were measured to obtain data used for growth modelling.

6.0. Main findings and discussion

This research used a case study approach to generate useful baseline information that will enhance our understanding of the production contributions and potentials of dry Miombo woodlands in C storage and sequestration in Tanzania. To fully understand these two contributions a detailed assessment of the forest condition and application of relatively accurate biomass and growth models was necessary. Therefore this study started out by characterizing the current woody species diversity of the forest (Paper I). This was followed by quantifying wood basic densities, which, among others, could inform wood biomass models (Paper II). New volume and biomass models using representative samples of species from the forest was developed in Paper III. Growth models for one dominant species, *Brachystegia spiciformis* collected in the same site was developed in Paper IV. Finally, the data and models were applied to estimate C stocks in six major C pools including trees, and shrubs as well as assessing the C sequestration potential of dry Miombo woodlands using the models developed under a range of different scenarios (Paper V).

Generally, the results showed that the case forest is in a good condition as indicated by the high basal area and growing volume despite on-going human activities in the forest e.g. charcoal making and firewood collection (Paper I). A total of 88 species belonging to 29 families identified in this study is an indication that species richness and diversity in GVLFR is relatively high in comparison with the findings reported by studies from other dry Miombo areas in the country and elsewhere (Williams et al., 2008; Banda et al., 2008; Shirima et al., 2011; Njana, 2008; Isango, 2007; Chamshama et al., 2004). These results appear to confirm earlier observations that by involving local communities in management of forests found close to their villages has to some extent positive effects in protecting and hence helping the condition of the forests to improve (Blomley et al., 2008; Treue et al., 2014). Both elevation and soil fertility levels in the study area influence the growth and formation of tree species communities and associations significantly. This finding is in agreement with other studies done elsewhere (Kubota et al., 1998: Munishi et al., 2007) and it is important particularly for the designing of management strategies of the forest. Although substantial amount of species has been identified (88 species), there is a possibility that rare species were not captured using the systematic approaches employed in this study. Therefore, by the use of the methods applied in this study together with opportunistic sampling focusing on different microhabitats should be considered during surveys in order to cover as much variation as possible so as to capture the likely forgotten species in the present study or other areas with similar conditions.

Wood basic densities are key variables when estimating tree biomasses (Paper II). However, only few studies have reported wood basic density estimates for tree species found in Miombo woodlands or other vegetation types in Tanzania (Bryce, 1967; Malimbwi et al., 1994; Munishi and Shear, 2004; Mwampamba, 2009). Wood basic densities of the 44 species reported in this study adds to the existing database of species found in Tanzania and hence increases the applicability of the existing volume equations to be used in estimation of forest biomass and hence C stocks of the woodlands. The developed basic density models in the current study will serve as tools for estimating wood densities for species found in similar vegetation types. However, efforts to report actual density values of the remaining species from destructive sampling would therefore be useful for accurate estimation of Carbon stocks potential of the woodland.

The new volume and biomass models for individual species and for broader species groups (shrubs, trees and both) provide a comprehensive range of tools to estimate the standing volume, aboveground biomass and C stock of dry Miombo vegetation in Tanzania (Paper III). Since the number of sample trees and shrubs for the general model is relatively large and includes a large number of species (44) compared to site specific models reported elsewhere (Malimbwi et al., 1994; Chamshama et al., 2004), these models are likely to be quite robust and can presumably be applied in similar sites with only a limited increase of bias compared to locally calibrated models. Although modelling the volume and biomass of shrubs turned out to be challenging, possibly due to the large variation of wood density and shapes of stems and crowns characterising this group, the new models are the first of their kind for dry Miombo woodlands. This means that they can improve the accuracy of wood biomass estimations and, hence, C stocks of this vegetation type (c.f. Chaturvedi and Raghubanshi, 2012). In most cases, shrubs have been neglected in the estimation of total woodland C stocks despite their high contribution in total stem densities (Paper I). Further research on measures that could be used to improve volume and biomass estimates for shrubs would therefore be useful.

For sustainable management of the woodlands, growth characteristics of the vegetation need to be understood (Paper IV). This is required to determine sustainable harvesting levels. However, due to the scarcity of long-term high quality data from permanent sample plots, very limited information about growth rates of tree species found in these forests is available (Borota, 1991; Schwartz et al., 2002; Elifuraha et al., 2008; Zahabu, 2008; Isango, 2009). By using tree ring analysis that go > 50 years back in time, the current study presents twelve diameter growth models of *Brachystegia spiciformis* as influenced by site, climate and competition (Paper IV). Results show that rainfall has a strong positive effect on the growth of *B. spiciformis* trees while competition had a marked negative impact. The study indicates that Miombo woodland vegetation depends both on early rains and the rains that fall during the core of the growing season. These results are in agreement with other studies reported from dry forests and Miombo woodlands elsewhere (Trouet et al., 2006; 2010). The newly developed diameter growth models can be used in assisting sustainable management and extraction levels of Miombo woodland resources as well as in estimating C sequestration potential of *Brachystegia spiciformis* populations measured in the study area and also the forest as a whole. Since each species has different growth characteristics, more research on growth behaviour of other species other than *Brachystegia spiciformis* would be useful in order to have a wide knowledge about their growth and hence growth models of many species.

Based on results from the preceding papers, the C stock for each of the six pools; trees, shrubs, deadwood, grasses and herbs, surface litter and soil as well as the sequestration potentials of the woodlands were estimated (Paper V). The reported total C stock of 68.64 Mg C ha^{-1} is considerably lower than other estimates reported for dry tropical forest elsewhere (Ryan et al., 2011; Jaramillo et al., 2003; Chen et al., 2003; Ribeiro et al., 2013). A partial reason for this difference could be that these studies included roots and soil carbon to a depth greater than 50 cm, while the present study did not include roots or soil samples below a depth of 30 cm. However, considering the vast areas covered by dry Miombo woodlands the total amount of C stored in these woodlands is clearly tremendous. Therefore, sustainable management of this vegetation type is important to prevent emission of large amounts of C currently locked up in the Miombo ecosystem. Assuming that other species' production are equal to *B. spiciformis*, the estimated C sequestration potential of the dry Miombo woodlands was found to vary between 0.42 ± 0.03 Mg C ha^{-1}year^{-1} and 1.39 ± 0.08 Mg C ha^{-1}year^{-1} depending on the applied assumptions. These results may suggest that the C sequestration potential of dry Miombo forests is fairly high compared to other moist and dry forest formations in the tropics (Worbes and Raschke, 2012; William et al., 2008; Chaturvedi et al., 2011). It should be noted however that, these estaimates are based on growth characteristics of one dominant species

Brachystegia spiciformis only. Since the woodlands has got many species with different growth characteristics, accurate estimation of carbon sequestration potential of the woodland would therefore require quantification of growth increment of other species found in the woodlands. Therefore further research on diameter growth and hence growth models of many other species from dry Miombo woodlands should be considered.

In addition to the few limitations discussed above i.e. exclusion of roots and measuring growth of one species, the following limitations might also have contributed to the low carbon stocks and sequestration observed in the GVLFR and applicability of developed models to other similar sites; low sample size (35 plots), ignoring boulders/large stones when working with soil, and for basing volume, biomass and density models on samples that are only approximately composed (in terms of sample size) as the populations of trees and shrubs in the forest and because other forests may have quite different compositions. However, these results suggest that the woodlands deserve proper attention in reducing the risk of losing this potential.

7.0. Conclusion

This study has indicated that dry Miombo woodland of GVLFR is still in good condition despite of on-going human activities in the forest. A detailed assessment of existing plant communities and factors infuencing their formations/occurrence, give a clue for a starting point for management interventions. Additonally, the newly developed tools for density estimations, volume and biomass as well as diameter growth estimations would also contribute to the planning for sustainable managenet of the woodlands. Furthermore results from this study show that the dry Miombo woodland of GVLFR stores substantial amounts of C, both in above- and below-ground soil C pools. Thus, in addition to being a sustainably managed source of forest products for local people's livelihoods and the local economy, it contributes positively to the global efforts of mitigating climate change. Concerning the C sequestration potential, the values reported in this study were based on diameter increments of *B. spiciformis* alone and the values estimated by extrapolation are therefore likely to be greater than the true values although these are still likely to be high given the vast areas covered by Miombo woodlands. Based on the fact that *B. spiciformis* is only one of the important species of the Miombo it is concluded that there is a need to study the growth behaviour of other Miombo species so as to provide a better basis for assessing the overall C sequestration potential of the Miombo.

Therefore, based on the findings obtained by this study and their limitations, the following points are recommended for future research;

- The methods applied in this study together with opportunistic sampling focusing on different microhabitats should be considered during surveys in order to cover as much variation as possible so as to capture the likely forgotten species in the present study or other areas with similar conditions.
- This study did not cover root biomass. To fully understand the C stocks potential of the dry Miombo woodlands, allometric models and quantification of root biomass of dry Miombo woodland species should be considered.
- There is very limited knowledge about growth and hence growth models of many species from dry Miombo woodlands. Studies on their anatomy especially on identifying species with annual rings should be encouraged as this would allow for development of robust growth models for a range of species.

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List of papers

PAPER I

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Research Article

Floristic Composition, Structure, and Species Associations of Dry Miombo Woodland in Tanzania

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For the majority of forest reserves in Tanzania, biodiversity is poorly documented. This study was conducted to assess species richness (woody species), diversity, and forest structure and to examine relationships between species occurrence and topographic and edaphic factors in the Gangalamtumba Village Land Forest Reserve, a dry Miombo woodland area in Tanzania. A total of 35 nested circular plots with radii of 5, 15, and 20 m were used to collect data on woody species and soil samples across the 6,065 ha community-managed forest reserve. Stumps were measured 20 cm above ground. A total of 88 species belonging to 29 families were identified. Generally forest structure parameters and diversity indices indicated the forest to be in a good condition and have high species richness and diversity. Vegetation analysis revealed four communities of which two were dominated by the family Caesalpiniaceae, indicating large variation of site conditions and possible disturbances in the study area. The high level of diversity of woody species and the high basal area and volume indicate that the forest is in good condition, but the effect of anthropogenic activities is evident and stresses the need for proper management to maintain or enhance the present species diversity.

1. Introduction

Miombo woodland is the most widespread and dominant dry forest formation in Eastern, Central, and Southern Africa. It is characterized by an abundance of tree species in the legume subfamily Caesalpinoideae, including the three dominant genera of *Brachystegia*, *Julbernardia*, and *Isoberlinia* [1, 2]. Covering an area of about 3.6 million km^2, miombo woodland supports the livelihoods of more than 100 million rural and urban dwellers by providing a wide range of products such as firewood, charcoal, timber, and forage and services such as soil conservation and water catchment [3–5]. However, due to the rapid population growth and the high level of poverty across the Miombo region, the human pressure on its woodlands has steadily increased over the last decades, leading to increasing deforestation and forest degradation [6–8].

The effects of increasing rates of deforestation and forest degradation on biodiversity in developing countries have been thoroughly studied [9–12]. Habitat loss due to deforestation reduces not only the number of species in the ecosystem but also the number and extent of places where species coexist. Activities such as charcoal production, firewood collection for subsistence use and for tobacco curing, conversion of woodlands to farmland, and seasonal forest fires are among the major drivers of deforestation and forest degradation in the Miombo region [13–17]. It is estimated that 1.4 million ha of woodlands is lost annually in the countries where Miombo woodlands dominate, leading to a loss of carbon stocks, biodiversity, and, through soil degradation, loss of plant nutrients [4, 5]. Syampungani et al. [5, p. 151] stated that "loss of biodiversity and extinction of most of the woodland resources are imminent if the current intensive exploitation of Miombo resources continues unchecked." More specifically, FAO (2000a, cited by Syampungani et al. [5]) reported that 191 tree species in the Miombo ecoregion are endangered due

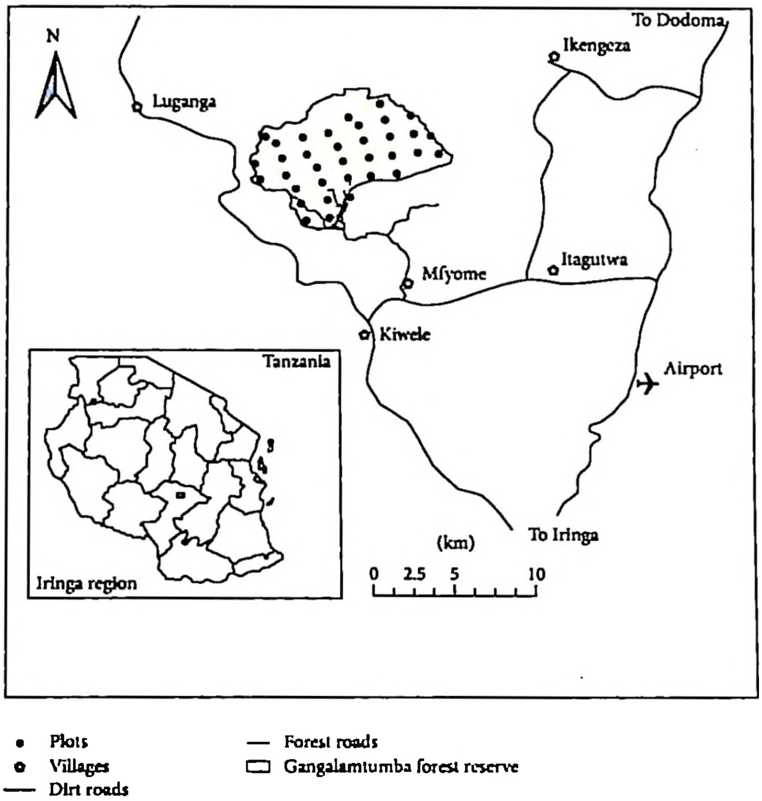

Figure 1: Map showing the location of the study area. The inserted map of Tanzania shows the location of the Iringa region.

to conversion of forest areas into agricultural lands or through charcoal production.

Gangalamtumba Village Land Forest Reserve (GVLFR) in Iringa rural district, Tanzania, which is owned and managed by the village of Mfyome, was established in 2002 under Tanzania's national participatory forest management programme and thus represents one of approximately 1500 Village Land Forest Reserves (covering some 2.4 million ha), the progressive establishment of which is intended to promote conservation of approximately 16.5 million ha of hitherto unreserved forest on general and village land [18–21]. Villages' control over Village Land Forest Reserves is conditional on their conservation/protection of these forests and the executive management is performed by an environmental/forest management committee whose members are directly elected for five-year terms by all members of the village above the age of 18 [18]. As such GVLFR is a typical example of an area which, at least until 2002, might have experienced loss of biodiversity due to increasing human activity, including charcoal production and extraction of wood for tobacco curing, giving cause for concern with respect to the maintenance of forest biodiversity [15]. The extent to which the activities have led to loss of biodiversity and deterioration of the plant community structure is so far unknown, but for the development of sustainable woodland management strategies and for planning of future management and conservation, information on these issues is urgently needed.

Although many quantitative ecological studies have been undertaken in places where Miombo dominates, its extensiveness and the large between-site variation, which is caused by climatic and edaphic factors and anthropogenic activities, appear to warrant further case studies [20, 22–29]. Ecological case studies are particularly relevant when the information generated is required for sound decision making about forest management, conservation strategies, and determination of sustainable harvesting levels. Hence, the objectives of this study were (1) to provide a detailed assessment of the current standing stock, species diversity, richness, and structure and (2) to understand the relationship between species abundance and a range of environmental and topographic factors that shape plant communities and species associations in the GVLFR.

2. Materials and Methods

2.1. Study Site. Gangalamtumba Village Land Forest Reserve is located in central-southern Tanzania (7°35′S; 35°35′E), about 30 km north of Iringa town, the administrative capital of the Iringa region (Figure 1). The forest covers 6,065 hectares and is part of the Mfyome village area, which is located in the ward of Kiwele. The forest vegetation has been described as dry Miombo woodland, similar to the dry woodland type described from other countries such as Zimbabwe and Mozambique [1]. The forest is located in a relatively flat area at an elevation of 850–1,300 metres above sea level. The region is characterised by distinct wet and dry seasons with almost no rain in the four months of June-September and about 80% of the annual precipitation falling in December-March. Average rainfall data covering the last 50 years (1960–2010) were obtained from the meteorological station at Nduli airport, which is located about 30 km from the forest, and indicate that the area receives an average annual precipitation (mean ± standard error) of 617 ± 17 mm (448–1085 mm). The mean annual temperature is 19.8°C and the average relative humidities at 06.00 and 12.00 GMT are 53.9% and 51.4%, respectively.

The GVLFR is a production forest which is managed by the Mfyome village under a community-based forest management (CBFM) arrangement established in 2002; compare above. The primary economic activity in Mfyome is smallholder agriculture, and the main economic uses of the forest are production of timber, charcoal, and firewood [20]. The woodland is also used for grazing and is an important source of subsistence products such as firewood, construction materials, fruit, mushrooms, wild vegetables, and medicinal plants [18].

2.2. *Vegetation Survey.* The field survey was conducted in July and August 2009 and involved establishment of a total of 35 permanent, nested circular sample plots distributed across the entire forest. Plots were established along transect lines and the distance between plots was approximately 2 km (Figure 1). The radii of the nested circular plots were 5 m (0.0079 ha), 15 m (0.0707 ha), and 20 m (0.1257 ha). The following parameters were recorded within each of the 35 plots: within the 5 m radius all small trees and shrubs (<150 cm tall or ≥150 cm but <1 cm Dbh) were counted and their species were identified, and medium-size trees and shrubs (≥1 cm Dbh but <5 cm Dbh) were identified and measured with respect to diameter. Within 15 m radius, the species were identified and the diameter was measured for all large trees and shrubs with Dbh ≥5 cm. Within 20 m radius, all stumps of trees and shrubs were identified to species level and measured for diameter 20 cm above ground. Initial identification of species for both standing trees/shrubs and stumps relied on the knowledge of local botanists (using local vernacular species names and features such as color of the bark, smell, and leaves) and was later confirmed by botanists from Tanzania Forest Research Institute (TAFORI) based at Lushoto Silviculture Research Station. For species that were difficult to identify in the field, samples were taken to the herbarium at Lushoto for reidentification. Other measurements taken within the plots were geographical location (UTM coordinates) and elevation (m) using GPS and slope (%) using a Suunto clinometer.

2.3. *Soil Sampling.* Soil samples were collected from five points, which were located at the centre of the plot and 10 m from the centre in the four cardinal directions (North, East, South, and West). At each point two samples were taken, 0–15 cm and 15–30 cm below the surface. The five samples taken from each depth range were mixed in the field to obtain one composite sample per depth range and plot. Thus, 70 soil samples (35 from each depth range) were collected from the 35 plots. In addition, a soil core device with an inner diameter of 5 cm and a length of 5 cm was used for extracting soil bulk density samples from the centre of each plot and at each depth. Hence, a total of 70 samples were collected for bulk density determination.

2.4. *Laboratory Analyses.* In the laboratory all soil samples were ground and passed through a 2 mm sieve to remove stones and gravel. Fine and coarse roots were also removed. Subsequently, soil samples collected at 0–15 cm depth were analysed for soil pH, soil texture, cation-exchange capacity (CEC, cmol(+)/kg), available phosphorus (ppm), and exchangeable bases (Ca^{2+}, Mg^{2+}, and K^{-}, cmol(+)/kg). Samples from both depth ranges (0–15 and 15–30 cm) were analysed for percentages of organic carbon and total nitrogen. Standard methods for soil analysis were used in order to obtain estimates for each of the mentioned variables that can be compared with results reported in the literature [30–34]. Soil pH was determined electrometrically using 10 g of soil sample diluted in 25 mL distilled water, that is, using a 1 : 2.5 ratio of soil to water. Soil texture was determined by the hydrometer method and the textural classification was done by the use of the soil texture triangle [35].

The Bray 1 method was used for the determination of extractable P for acidic soils with pH less than 7 while the Olsen method was used for soils with pH above 7 (alkaline soils). The ammonium acetate method at pH 7 was used in determination of CEC, and by the use of an atomic absorption spectrophotometer in a UNICAM 919 AA Spectrometer, all exchangeable cations (Ca^{2+}, Mg^{2+}, and K^{+}) were determined. Subsamples were finely ground into powder form (<1 mm) in an agate mortar and analyzed for total percentages of organic C and N by dry combustion (Dumas method) in a Leco CNS 2000 analyzer [33]. Samples for bulk density estimation were oven-dried at 105°C to constant weight and the weight was recorded (accuracy 0.01 g). The volume was calculated from length and cross-sectional area of the soil core, and bulk density was determined as dry weight (g) per unit volume (cm^3). Most analyses were conducted at the Laboratory of Forest Biology, Sokoine University of Agriculture (SUA), but C and N analyses were conducted at the Soil Science Laboratory at the Department of Forest and Landscape (now Department of Geosciences and Natural Resource Management), University of Copenhagen, Denmark.

2.5. *Data Analysis.* Based on the data collected the following measures were analysed: species composition was expressed through species richness and diversity measures; forest structure was expressed through stem density, basal area and volume for plant communities, species groups, and diameter classes. Total species richness was computed as the total number of species across all 35 plots. Species diversity was computed using Shannon's and Simpson's Diversity Indices

[36]. The volume of stumps was calculated as cylinder volume while total volume for standing trees was calculated using a regression equation developed for GVLFR by the authors [37, 38]: $\ln(V) = -8.4554 + 2.3236 \times \ln(\mathrm{Dbh})$ ($R^2 = 0.983$, RMSE = 0.248, Dbh range: 1.4–62 cm, $n = 104$), where V is volume (m^3/tree); Dbh is diameter at breast height (≥1 cm), RMSE is the residual standard error, R^2 is the coefficient of determination, n is the total sample size, and ln is the natural logarithm. The Importance Value Index (IVI) for each species in each plot was calculated as the sum of relative density and dominance (basal area) and expressed in percent [39]. Percentage base saturation (%BS) was determined as the ratio of total base cation concentration to CEC, while the C : N ratio was determined using the estimated elemental percentages of carbon and nitrogen [35].

Using IVI for each species, plots were classified by agglomerative hierarchical cluster analysis using Sorensen's distance measure and a group linkage method with flexible β of −0.50. The 35 plots were ordinated by nonmetric multidimensional scaling (NMS) using the PC-ORD software version 6.0 [40]. Topographic variables (elevation and slope) and edaphic variables (pH, bulk density, texture, extractable P, CEC, exchangeable base cations, %BS, C : N ratio, %C, and %N) were correlated with the NMS ordination axes. Indicator/dominant species in each cluster were determined using percentage indicator values (%IV) where values of 0 correspond to no indication and 100 is perfect indication [41, 42]. The first three to five names of these indicator/dominant species with the highest percentage indicator values (%IV), constancy, and significant indicator values ($P < 0.05$) were used to assign names to the clusters/plant community types [29, 41, 42]. The Steinhaus (Sørensen/Czekanowski) coefficient was used to assess the similarity/dissimilarity of the species compositions of the plant communities [39].

3. Results

3.1. Species Richness. Including all size categories a total of 88 species (29 plant families) of standing trees and shrubs/small trees were identified in the GVLFR (Table 1). Trees contributed 60% (21 plant families) and shrubs 40% (15 plant families) of the species. For stumps, a total of 42 species (20 plant families) of trees and shrubs/small trees, with basal diameter ranging from 2 to 50 cm, were identified. For stumps, trees contributed 76% (13 plant families) of the species while shrubs contributed 24% (10 plant families). All species represented by stumps were also represented by standing trees/shrubs. In general, tree and shrub species from the family Caesalpiniaceae contributed most (13%) to the total number of species (standing individuals), followed by those from the families Mimosaceae (10%), Rubiaceae (10%), Fabaceae (9%), and Euphorbiaceae (9%) (Table 1). Among standing trees, the greatest number of species was found in the four plant families: Caesalpiniaceae (17%), Mimosaceae (15%), Fabaceae (13%), and Combretaceae (9%), while shrubs/small trees included most species from the families Rubiaceae (26%), Euphorbiaceae (17%), and Capparaceae (9%). For stumps, tree and shrub species from the family Mimosaceae contributed most (17%) to the total number of species, followed by species from the families Caesalpiniaceae (14%), Combretaceae (10%), and Fabaceae (7%). Among species categorised as trees, the families Caesalpiniaceae (19%) and Mimosaceae (19%) contributed equal numbers of species, followed by Combretaceae (13%) and Fabaceae (9%). With respect to shrubs each of the families was represented by a single species (10%; see Table 1).

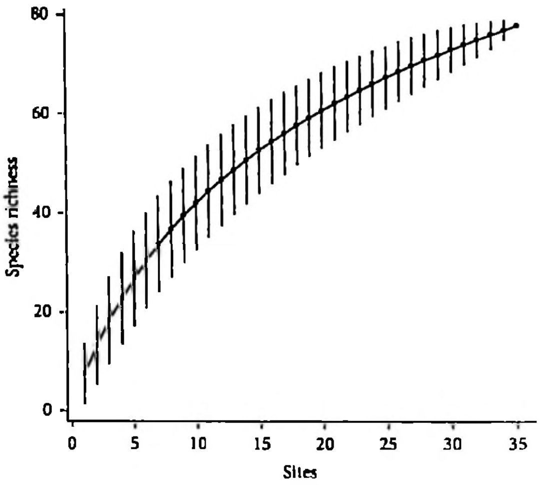

Figure 2: Species accumulation curve for large individuals (Dbh ≥5 cm) measured within circular plots with a radius of 15 m in the Gangalamtumba VLFR. Vertical lines indicate standard deviations (range 0–4.9).

When considering different size categories and including both trees and shrubs (small sizes, Dbh < 5 cm and large sizes, Dbh ≥ 5 cm), a total of 78 species (28 families) were found among large sizes, with Caesalpiniaceae (13%), Mimosaceae (12%), and Fabaceae (10%) being the most species-rich plant families, while among small sizes, a total of 69 species (27 families) were observed, with Rubiaceae (13%), Caesalpiniaceae (12%), and Mimosaceae (10%) contributing the greatest number of species (Table 1). In general the average number of species per plot was found to be 14 species (range 5–24 species per plot).

The species accumulation curve (Figure 2) shows that the 35 sites/plots used in this study were sufficient to cover much (but not all) of the variation and species diversity of the study area. At 35 plots the graph has not yet reached its asymptotic level but is starting to converge, implying that any further increase of sample size would be expected to lead to inclusion of additional rare species. However, although the sample size was small (35 plots) and does not quite capture the full woody plant biodiversity of the reserve, the results are still useful for characterizing the tree/shrub species diversity and relationships between species and site.

3.2. Species Diversity. Shannon-Wiener diversity indices for large and small individuals were found to be 3.44 and 3.26, respectively, and the Simpson index for large individuals was

Table 1: Checklist of tree and shrub species recorded in Gangalamtumba VLFR showing frequency (%), density (mean ± SE), basal area (mean ± SE), dispersion index (DI), and Importance Value Index (IVI), both for the current population of large individuals (plot size = 15 m radius; minimum Dbh = 5 cm) and for stumps (plot size = 20 m radius; minimum basal diameter = 2 cm); SH: shrub, ST: small tree, and T: tree.

S/no.	Vernacular/local name	Species/botanical name	Family	Habit/life form	Current population					Stumps			
					Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI	DI	Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI
1	Mgiha	*Dalbergia arbutifolia*	Fabaceae, subfamily Papilionoideae	ST	60	247 ± 69	1.36 ± 0.37	22.4	47.65	14	6.8 ± 4.1	0.06 ± 0.05	17.0
2	Mtono	*Commiphora africana*	Burseraceae	T	77	110 ± 23	1.59 ± 0.37	17.5	11.42	14	1.4 ± 0.6	0.01 ± 0.01	11.1
3	Miama	*Combretum molle* G. Don	Combretaceae	T	74	116 ± 27	0.69 ± 0.15	13.2	15.23	34	6.8 ± 1.9	0.05 ± 0.02	30.7
4	Mkungugu	*Acacia sp.*	Mimosaceae	T	23	40 ± 22	1.02 ± 0.54	11.1	28.73	9	2.0 ± 1.4	0.01 ± 0.01	6.5
5	Mkwee	*Brachystegia spiciformis* Benth	Caesalpiniaceae	T	37	58 ± 20	1.18 ± 0.34	11.0	17.31	26	6.1 ± 2.4	0.20 ± 0.09	30.8
6	Mkalala	*Albizia petersiana* (Bolle) Oliv.	Mimosaceae	T	40	80 ± 30	0.55 ± 0.20	8.5	27.11	6	3.6 ± 2.9	0.05 ± 0.04	9.4
7	Mlyasenga	*Combretum zeyheri* Sound	Combretaceae	T	43	60 ± 20	0.30 ± 0.11	7.4	15.97	20	2.0 ± 0.8	0.01 ± 0.01	4.7
8	Mkombivawo	*Bauhinia petersiana*	Caesalpiniaceae	SH	34	54 ± 21	0.29 ± 0.10	6.4	20.00				
9	Muguvani	*Markhamia obtusifolia*	Bignoniaceae	T	60	65 ± 13	0.38 ± 0.10	6.4	6.47	6	0.5 ± 0.3	0.0	2.3
10	Mdeke	*Hymenodictyon parvifolium* Oliv.	Rubiaceae	ST	31	50 ± 24	0.48 ± 0.24	5.8	27.49	3	0.2 ± 0.2	0.0	1.7
11	Mubwegele	*Sclerocarrya birrea* sbsp. birrea	Anacardiaceae	T	34	21 ± 6	0.61 ± 0.23	5.8	4.41	6	0.5 ± 0.3	0.01 ± 0.01	2.8
12	Mmemenamene	*Margaritaria discoidea* (Bail.)	Euphorbiaceae	SH	51	68 ± 24	0.32 ± 0.13	5.7	20.73	3	0.7 ± 0.7	0.0	0.6
13	Mkambala	*Acacia mellifera* (Vahl) Benth.	Mimosaceae	T	29	14 ± 5	0.49 ± 0.19	5.0	3.59	3	0.2 ± 0.2	0.0	0.8
14	Mugegere	*Dichrostachys cinerea* (L.) Wight & Arn	Mimosaceae	ST	31	53 ± 26	0.17 ± 0.09	4.7	30.86	29	5.9 ± 1.9	0.03 ± 0.02	17.8
15	Mbata	*Acacia seyal* Del. var. *seyal*	Mimosaceae	T	34	30 ± 10	0.19 ± 0.06	4.5	8.87	3	1.1 ± 1.1	0.01 ± 0.01	4.6
16	Mgulumo	*Lannea schweinfurthii*	Anacardiaceae	T	43	24 ± 7	0.32 ± 0.09	3.9	5.44	9	0.7 ± 0.4	0.02 ± 0.01	2.2
17	Muyombo	*Brachystegia boehmii*	Caesalpiniaceae	T	11	11 ± 7	0.19 ± 0.15	3.8	13.09	6	0.7 ± 0.5	0.01 ± 0.01	2.2
18	Mmulimuli	*Cassia abbreviata*	Caesalpiniaceae	T	34	31 ± 13	0.17 ± 0.07	3.6	13.53	9	1.6 ± 1.2	0.01 ± 0.01	4.9
19	Mdavi	*Cordia sinensis* Lam	Boraginaceae	ST	6	23 ± 23	0.11 ± 0.10	3.4	54.98	3	0.2 ± 0.2	0.0	0.6

Table 1: Continued.

S/no.	Vernacular/local name	Species/botanical name	Family	Habit/life form	Current population					Stumps			
					Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI	DI	Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI
20	Mdwendwe	*Terminalia brownii*	Combretaceae	T	17	14 ± 8	0.19 ± 0.09	3.2	11.29	3	0.5 ± 0.5	0.0	1.2
21	Mfilafila	*Diplorynchus condylocarpon*	Apocynaceae	T	31	25 ± 8	0.15 ± 0.05	3.0	6.46	6	0.5 ± 0.3	0.0	3.5
22	Mkwata	*Codyla densiflora*	Caesalpiniaceae	T	9	4 ± 2	0.33 ± 0.19	2.8	2.82	3	3.4 ± 3.4	0.04 ± 0.04	8.3
23	Mgunga	*Acacia abyssinica* (Hochst)	Mimosaceae	T	17	12 ± 7	0.14 ± 0.07	2.4	11.40	6	1.4 ± 1.2	0.01 ± 0.01	3.9
24	Mkole	*Grewia bicolor*	Tiliaceae	ST	26	21 ± 10	0.08 ± 0.03	2.1	10.78	6	0.5 ± 0.3	0.0	1.5
25	Mparapande	*Strychnos potatorum* L.f	Loganiaceae	T	23	23 ± 11	0.14 ± 0.09	2.0	13.31	6	0.7 ± 0.5	0.0	1.7
26	Kitimbwi	*Ormocarpum kirkii*	Fabaceae	SH	29	18 ± 6	0.07 ± 0.03	1.9	4.92				
27	Mtabagila	*Lonchocarpus capassa*	Fabaceae	T	26	11 ± 5	0.14 ± 0.06	1.7	5.50	3	0.2 ± 0.2	0.0	0.4
28	Muwotaponzi	*Ozoroa insignis* ssp. reticulata	Anacardiaceae	T	14	10 ± 5	0.10 ± 0.05	1.6	5.64	14	1.1 ± 0.5	0.01 ± 0.00	3.1
29	Msanzi	*Gardenia resiniflua* Hiern.	Rubiaceae	ST	9	13 ± 8	0.08 ± 0.05	1.6	12.29				
30	Mkoga	*Vitex payos*	Verbenaceae	ST	17	12 ± 5	0.11 ± 0.04	1.5	6.05	3	0.2 ± 0.2	0.0	0.2
31	Mpelemele	*Grewia forbesii* Haw. Ex Mast	Tiliaceae	ST	14	16 ± 9	0.05 ± 0.02	1.47	12.46				
32	Mnywenywee	*Dalbergia boehmii*	Fabaceae	T	14	11 ± 7	0.09 ± 0.07	1.5	12.21				
33	Mulagavega	*Albizia amara* (Roxb.) Boiv.	Mimosaceae	T	14	9 ± 5	0.04 ± 0.03	1.4	7.12				
34	Mkola	*Afzelia quanzensis*	Caesalpiniaceae	T	11	6 ± 3	0.15 ± 0.09	1.4	5.32				
35	Mugusi	*Brachystegia manga*	Caesalpiniaceae	T	20	11 ± 6	0.10 ± 0.07	1.3	8.24	6	1.8 ± 1.3	0.02 ± 0.02	2.5
36	Mwahama	*Shrebera trichoclada*	Oleaceae	T	17	11 ± 6	0.05 ± 0.02	1.2	6.97	3	0.9 ± 0.9	0.01 ± 0.01	1.5
37	Mpingo	*Dalbergia melanoxylon*	Fabaceae	T	11	11 ± 9	0.04 ± 0.03	1.2	16.55	3	1.4 ± 1.4	0.01 ± 0.01	2.6
38	Mubaya	*Strychnos innocua*	Loganiaceae	T	17	8 ± 4	0.11 ± 0.08	1.2	3.75	3	0.2 ± 0.2	0.01 ± 0.01	0.6
39	Msisina	*Albizia harveyi* Fourn.	Mimosaceae	T	14	5 ± 3	0.08 ± 0.05	1.1	3.59	3	0.5 ± 0.5	0.02 ± 0.02	1.5
40	Mlimbo	*Euphorbia cuneata* Valh.	Euphorbiaceae	ST	14	12 ± 6	0.04 ± 0.02	1.1	6.99				
41	Mwambi	*Elaeodendron buchananii*	Celasteraceae	T	3	8 ± 8	0.03 ± 0.03	1.0	20.00				
42	Mvembadanda	*Xeroderris stuhlmannii*	Fabaceae	T	14	4 ± 2	0.11 ± 0.05	0.9	1.91				
43	Mtelela	*Brachystegia bussei* Harms	Caesalpiniaceae	T	6	2 ± 1	0.12 ± 0.10	0.9	2.53				

Table 1: Continued.

S/no.	Vernacular/local name	Species/botanical name	Family	Habit/life form	Current population					Stumps			
					Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI	DI	Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI
44	Mieresi	*Premna holstii* Gürke	Verbenaceae	ST	9	8 ± 5	0.03 ± 0.02	0.9	8.99				
45	Mkongolo	*Commiphora ugogensis*	Burseraceae	T	6	1 ± 1	0.08 ± 0.06	0.8	0.97	3	0.2 ± 0.2	0.01 ± 0.01	0.9
46	Muwisa	*Boscia angustifolia* A. Rich var. angustifolia	Capparaceae	T	17	8 ± 4	0.04 ± 0.02	0.8	4.26				
47	Mnyalupuko	*Canthium pseudoverticillatum* Hien	Rubiaceae	ST	20	8 ± 4	0.04 ± 0.02	0.7	4.14				
48	Mnyaluhanga	*Bridelia scleuroneum* Muell.Arg.	Euphorbiaceae	ST	14	6 ± 3	0.04 ± 0.02	0.7	3.41				
49	Mdide	*Manilkara mochisia* (Bak.) Dubard	Sapotaceae	T	9	5 ± 4	0.02 ± 0.01	0.7	7.93				
50	Muhemi	*Erythrina abyssinica*	Fabaceae	T	6	1 ± 1	0.07 ± 0.06	0.7	1.63				
51	Msambarawe	*Vangueria infausta* Burch. Ssp. Rotundata	Rubiaceae	ST	6	8 ± 5	0.02 ± 0.02	0.6	9.25				
52	Mhehefu	*Allophylus ferrugineus* Taub.	Sapindaceae	SH	9	5 ± 3	0.02 ± 0.01	0.5	5.40	3	1.4 ± 1.4	0.01 ± 0.01	1.4
53	Mnyeng'enyeng'e	*Excoecaria bussei* (Pax)	Euphorbiaceae	ST	11	4 ± 2	0.01 ± 0.01	0.5	3.21				
54	Muganga	*Berchemia discolor*	Rhamnaceae	T	6	4 ± 3	0.04 ± 0.03	0.4	7.17				
55	Mninga	*Pterocarpus angolensis*	Fabaceae	T	6	2 ± 1	0.05 ± 0.04	0.4	2.53	3	0.9 ± 0.9	0.06 ± 0.06	2.5
56	Mtanangwe	*Ziziphus mucronata*	Rhamnaceae	T	3	4 ± 4	0.03 ± 0.03	0.4	9.00				
57	Muhekele	*Euclea divinorum* Hiern	Ebenaceae	ST	3	3 ± 3	0.01 ± 0.01	0.4	8.00	3	0.2 ± 0.2	0.0	4.9
58	Mubumila	*Cassipourea mollis* (R.E.fr.) Alstom	Rhizophoraceae	T	9	4 ± 3	0.02 ± 0.01	0.4	5.26	3	0.2 ± 0.2	0.0	0.4
59	Mkwambe	*Flueggea virosa* Willd.	Euphorbiaceae	SH	6	3 ± 2	0.03 ± 0.03	0.3	4.06				
60	Kivanga	*Zanha africana* (Radlk.) Exell	Sapindaceae	T	9	2 ± 1	0.01 ± 0.01	0.2	2.12	3	0.2 ± 0.2	0.0	0.2
61	Mninga maji	*Pterocarpus tinctorius*	Fabaceae	T	3	0	0.02 ± 0.02	0.2	1.00				
62	Mtosi	*Maerua triphylla* A. Rich.	Capparaceae	ST	3	2 ± 2	0.01 ± 0.01	0.2	6.00				
63	Mugosa	*Ehretia amoena*	Boraginaceae	ST	9	1 ± 1	0.0	0.1	0.94				
64	Mnyongamembe	*Steganotaenia araliacea*	Apiaceae	T	6	1 ± 1	0.01	0.1	1.63				
65	Mvelevele	*Vernonia amygdalina*	Asteraceae	SH	3	2 ± 2	0.01 ± 0.01	0.1	4.00				
66	Mpongolo	*Catunaregam spinosa* (Thunb.)	Rubiaceae	ST	3	1 ± 1	0.01 ± 0.01	0.1	2.00				

Table 1: Continued.

S/no.	Vernacular/local name	Species/botanical name	Family	Habit/life form	Current population						Stumps			
					Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI	DI	Frequency (%)	Density stem/ha	Basal area (m^2/ha)	IVI
67	Mboliboli	*Acacia drepanolobium* (Harms)	Mimosaceae	T	3	0	0.0	0.1	1.00				
68	Mwimakigulu	*Maerua angolensis*	Capparaceae	SH	3	1 ± 1	0.0	0.1	3.00				
69	Mnyali	*Tamarindus indica*	Caesalpiniaceae	T	6	1 ± 1	0.01 ± 0.01	0.1	0.97				
70	Mgombwani	*Combretum aculeatum*	Combretaceae	T	6	1 ± 1	0.0	0.1	0.97	3	0.2 ± 0.2	0.0	0.4
71	Msangala	*Burkea africana* Hook	Caesalpiniaceae	T	3	0	0.01 ± 0.01	0.1	1.00	3	0.2 ± 0.2	0.0	0.4
72	Mkokonza	*Opilia amentacea* Roxb.	Opiliaceae	SH	3	0	0.0	0.0	1.00	3	1.1 ± 1.1	0.0	4.2
73	Mfumbi	*Kigelia africana*	Bignoniaceae	T	3	0	0.0	0.0	1.00				
74	Mlangali	*Euphorbia candelabrum*	Euphorbiaceae	T	3	0	0.0	0.0	1.00				
75	Mpululu	*Terminalia sericea*	Combretaceae	T	3	0	0.0	0.0	1.00				
76	Mdaha	*Diospyros usambarensis* F. White	Ebenaceae	T	3	0	0.0	0.0	1.00	3	0.5 ± 0.5	0.01 ± 0.01	1.5
77	Mtundwa	*Ximenia caffra* Sond	Olacaceae	ST	3	0	0.0	0.0	1.00				
78	Mwimaperu	*Tarenna glaveolens* (S. Moore) Brem	Rubiaceae	ST	+								
79	Mwesa	*Boscia mossambicensis* Kl.	Capparaceae	ST	+								
80	Musasamulo	*Psychotria schummaniana*	Rubiaceae	ST	+								
81	Muhanza	*Senna singueana*	Caesalpiniaceae	ST	+								
82	Mtundwahavi	*Ximenia americana*	Olacaceae	ST	+								
83	Mtingiligiti	*Phyllanthus engleri* Pax	Euphorbiaceae	T	+								
84	Msada	*Vangueria madagascariensis* Gmel.	Rubiaceae	ST	+								
85	Mkunungu	*Zanthoxylum chalybeum*	Rutaceae	T	+								
86	Lukali	*Croton scheffleri* Pax	Euphorbiaceae	SH	+								
87	Kilimandembwe	*Gardenia ternifolia* K. Schum. & Thonn.	Rubiaceae	ST	+								
88	Mpela/Mbuyu	*Adansonia digitata*	Bombacaceae	T	++								
	Total (all species)				1351	1521 ± 594	13.55 ± 5.52	200		294	60 ± 30	0.72 ± 0.49	200

+ indicates species identified among smaller individuals within 5 m radius plots (Dbh < 5 cm), and ++ indicates that a large individual was identified within a 15-radius plot but was not included in the analyses of stem density, basal area, and volume as it was considered an outlier due to its tremendous size (Dbh = 340 cm).

0.05 and that of small individuals was 0.06. The following species were observed to have the greatest contributions to the Shannon-Wiener diversity index of large individuals: *Dalbergia arbutifolia* (contributing 0.30), *Combretum molle* (0.20), *Commiphora africana* (0.19), *Albizia petersiana* (0.16), and *Margaritaria discoidea* (0.14), while for smaller ones the greatest contributions were found for *Brachystegia spiciformis* (0.26), *Dalbergia arbutifolia* (0.24), *Grewia forbesii* (0.23), *Margaritaria discoidea* (0.20), and *Dichrostachys cinerea* (0.16). In terms of frequency of occurrence for standing individuals (large sizes) *Commiphora africana* was the most frequent species (77% of plots), followed by *Combretum molle* (74%) and *Dalbergia arbutifolia* (60%), while for small sizes *Margaritaria discoidea* (66%), *Markhamia obtusifolia* (65%), and *Dalbergia arbutifolia* (57%) were the most frequent species. The Importance Value Index (IVI) for large individuals (Dbh ≥ 5 cm) shows that *Dalbergia arbutifolia* (22.[illegible]), *Commiphora africana* (17.5), and *Combretum molle* (13.2) were the most important species among standing individuals, while *Brachystegia spiciformis* (30.8), *Combretum molle* (30.7), and *Dichrostachys cinerea* (17.8) appeared to be the most important among harvested individuals (stumps). These species were also found to have higher frequencies than any other harvested species observed in the GVLFR (Table 1).

3.3. Stem Density. The total mean stem density for large individuals with Dbh ≥5 cm was 1521 ± 594 stems/ha (Table 1) and that of small individuals with Dbh <5 cm (including individuals with Dbh <1 cm) was 14318 ± 6956 stems/ha. Among large individuals the most abundant species were *Dalbergia arbutifolia* (16.2% of 1521 stems/ha), *Combretum molle* (8%), *Commiphora africana* (7.2%), and *Albizia petersiana* (5.3%). Among small individuals, the most abundant species were *Brachystegia spiciformis* (13% of 14318 stems/ha) followed by *Dalbergia arbutifolia* (11%) and *Grewia forbesii* (10%). For stumps, the overall mean density was 60 ± 38 stems/ha, with *Combretum molle* (12%), *Dalbergia arbutifolia* (12%), *Brachystegia spiciformis* (10%), and *Dichrostachys cinerea* (10%) contributing the most (Table 1). Generally, the distribution of standing trees to size classes showed the usual reverse J shape, which was also approximately observed for stumps (Figure 3). However, for stumps the density of stems in the 1–10 cm diameter class was slightly lower than what would be expected if tree felling had been a random event.

3.4. Basal Area. For the GVLFR as a whole the mean basal areas for large (≥5 cm Dbh) and small individuals (<5 cm Dbh) were 13.55 ± 5.52 m^2/ha (Table 1, Figure 4) and 3.05 ± 0.02 m^2/ha, respectively. The species contributing most to the basal area of large individuals were *Commiphora africana* (12%), *Dalbergia arbutifolia* (10%), and *Brachystegia spiciformis* (9%), while those contributing most to the basal area of smaller individuals were *Dalbergia arbutifolia* (16%), *Grewia forbesii* (15%), and *Dichrostachys cinerea* (13%). The mean basal area for stumps was 0.72 m^2/ha with *Brachystegia spiciformis* contributing the greatest individual proportion (28%); 41 species made up the rest (Figure 4).

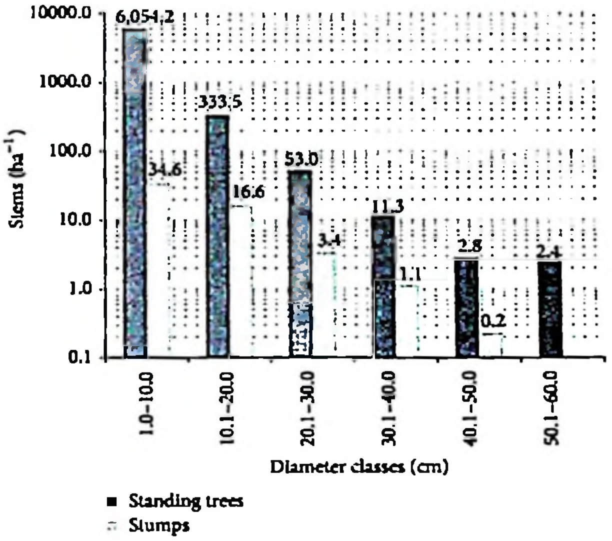

Figure 3: Density of standing trees ≥1 cm Dbh and stumps ≥1 cm by diameter class in Gangalamtumba VLFR (n = 35). NB: logarithmic scale on vertical axis.

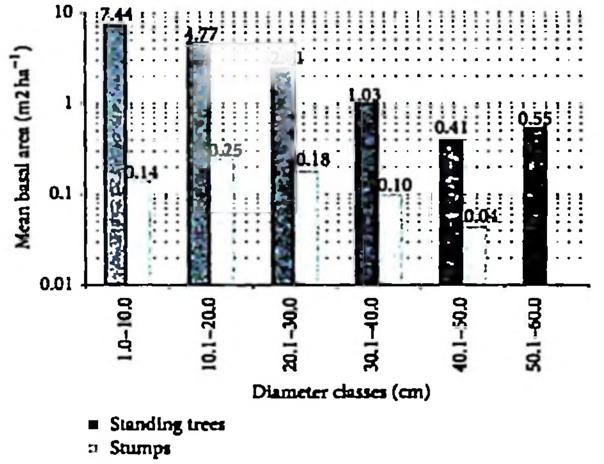

Figure 4: Distribution of basal area per hectare for standing trees ≥1 cm Dbh and stumps ≥1 cm by diameter classes in the Gangalamtumba VLFR (n = 35). NB: logarithmic scale on vertical axis.

3.5. Volume. The mean volumes for large (≥5 cm Dbh) and small individuals (<5 cm Dbh) were 92.17 ± 39.0 m^3/ha and 12.57 ± 6.35 m^3/ha, respectively (not shown in tables). The species contributing most to the volume of large individuals were *Commiphora africana* (12%), *Brachystegia spiciformis* (10%), *Acacia* sp. (9%), and *Dalbergia arbutifolia* (9%). For smaller individuals, the species that contributed most to volume were *Dalbergia arbutifolia* (16%), *Grewia forbesii* (14%), and *Dichrostachys cinerea* (13%). The mean remaining volume of stumps was found to be 0.15 ± 0.1 m^3/ha with *Brachystegia spiciformis* contributing the greatest individual percentage (28%); 41 species made up the rest.

3.6. Spatial Distribution. Dispersion indices (DI) are presented for individual species in Table 1. The dispersion index values range from 0.94, indicating almost complete spatial randomness or slight underdispersion, to 54.98, indicating considerable overdispersion, that is, a patchy or clustered distribution. Out of 77 species, excluding the single, very large *Adansonia digitata* that was considered an outlier, 64 species (83%), 9 species (12%), and 4 species (5%) were found to have DI > 1, DI = 1, and DI < 1, respectively, so the majority of species are characterised by a patchy distribution across the forest. The species with the lowest estimated DI was *Ehretia amoena* (0.94) while the highest DI was estimated for *Cordia sinensis* (54.98). The most abundant species, including *Dalbergia arbutifolia* (DI = 47.65), *Combretum molle* (DI = 15.23), and *Commiphora africana* (DI = 11.42), are strongly overdispersed.

3.7. Plant Communities and Species Association. Four plant communities were identified through cluster analysis based on the statistical significance (5%) of the observed maximum indicator values (Table 2). Only two of these plant communities were dominated by species from the family Caesalpiniaceae (Communities 1 and 24). The other two showed great variation/overlap between species of different plant families (Communities 3 and 5). The estimated Steinhaus similarity indices between pairs of plant communities varied from 32% for Communities 1 and 3 and Communities 5 and 24, to 37% for Communities 3 and 5 (not shown in tables).

The ordination diagram (Figure 5) shows that one topographic and six edaphic variables appear to be associated with the four plant communities and the species distribution in the study area. The strongest correlation with community composition was observed for elevation, followed by soil pH at 0–15 cm depth, base cation Ca^{2+} at 0–15 cm depth, percent base saturation (%BS) at 0–15 cm depth, percent clay at 0–15 cm depth, C : N ratio at 15–30 cm depth, and percent sand at 0–15 cm depth. The base cations magnesium (Mg^{2+}) and potassium (K^{+}) were not directly correlated with the community composition, but since they are included in the base saturation percentage they are indirectly related. Plant communities were ordered along the second ordination axis, which was positively correlated with pH15 ($r = 0.71$), Ca15 ($r = 0.69$), BS ($r = 0.65$), and Clay15 ($r = 0.52$) and negatively correlated with Sand15 ($r = -0.46$). Axis 1 of the ordination was positively correlated with Elev ($r = 0.85$) and CNrat30 ($r = 0.51$). As shown in Table 3 and indicated graphically in Figure 5 correlations between many of the edaphic variables are strong, particularly between pH15, Sand15, Clay15, Ca15, and BS, whereas correlation between topographic and most edaphic variables is small and nonsignificant. However, there is a significant negative correlation ($r = -0.42$) between Elev and Sand15, indicating that sandy soils are mostly found at lower elevations.

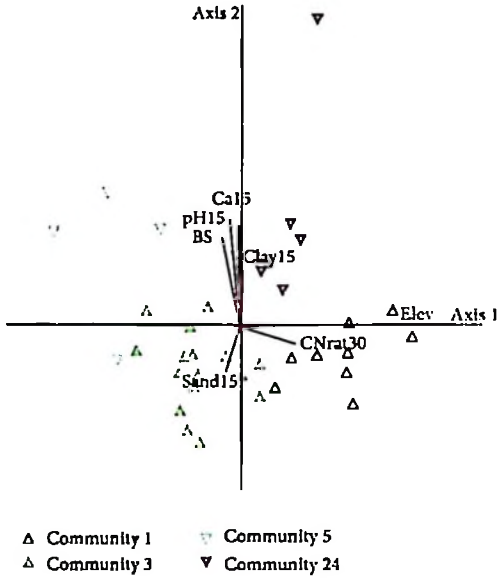

Figure 5: Compositional gradients and plant communities in NMS ordination of 35 vegetation plots for trees ≥5 cm in Gangalamtumba VLFR. Four plant communities are recognized (cf. Table 2). Community 1 = *Brachystegia spiciformis*, *Diplorynchus condylocarpon*, and *Lannea schweinfurthii* woodland; Community 3 = *Dalbergia arbutifolia*, *Commiphora africana*, and *Albizia petersiana* woodland; Community 5 = *Acacia* sp., *Acacia abyssinica*, and *Albizia amara* woodland; and Community 24 = *Bauhinia petersiana* and *Shrebera trichoclada* woodland. Elev: elevation (m); CNrat30: C : N ratio at 15–30 cm depth; Sand15: sand (%) at 0–15 cm; Clay15: clay (%) at 0–15 cm; Ca15 = Ca^{2+} (cmol(+)/kg) at 0–15 cm; pH15 = soil pH at 0–15 cm; BS: % base saturation at 0–15 cm.

4. Discussion

4.1. Species Composition. The results reported in this study show that the composition of the vegetation types found in the GVLFR, especially the dominance of species from the family Caesalpiniaceae, agreed well with previous descriptions and classifications of plant communities commonly found in miombo woodlands [1]. However, the observed dominance based on IVI of the genera *Dalbergia*, *Commiphora*, and *Combretum* contrasts with patterns usually considered common for miombo woodlands. The frequency of species in these genera was also high compared to other species observed in the GVLFR (Table 1). Similar deviations exist between the results obtained by Banda et al. [26], in the Katavi-Rukwa ecosystem, where they observed that *Terminalia* and *Combretum* were the dominant genera, and the findings of Giliba et al. [27] and Njana [43], who both noted the dominance of the two common miombo genera *Brachystegia* and *Julbernardia*. However, *Combretum* also occurred in their study areas. The results suggest that on a larger spatial scale the species diversity of miombo woodlands is very high and that the three common genera *Brachystegia*, *Julbernadia*, and *Isoberlinia* are not always dominant at the local scale.

The species richness observed in the GVLFR compares well with miombo community studies in other areas of dry miombo in Tanzania and elsewhere, which receive an average

Table 2: Plant communities and species associations in the dry Miombo woodlands of Gangalamtumba VLFR. Community numbers 1, 3, 5, and 24 represent the different plant associations: $n_{species}$: number of species (77 in total) with Dbh ≥ 5 cm; IV+: species indicator value; mean ± std. error; and BA is basal area.

Community	Associated species	Family	Habit	IV+ (%)	Constancy (%)	*P* value	Stems/ha	BA m^2/ha	Mean Dbh
Brachystegia spiciformis—*Diplorhynchus condylocarpon*—*Lannea schweinfurthii* woodland 1 ($n_{species}$ = 47, n_{plots} = 9) **Site variables (mean ± SE):** Elev = 1200 ± 20, pH15 = 6.44 ± 0.13, Ca15 = 6.04 ± 1.28, Sand15 = 72.1 ± 4.31, Clay15 = 13.7 ± 1.88, Silt15 = 14.2 ± 3.35, CNrat30 = 13.5 ± 0.5 and BS = 52.6 ± 6.5	*Brachystegia spiciformis*	Caesalpiniaceae	T	82.0	100	0.0002	164 ± 59	3.56 ± 0.77	13.8 ± 0.7
	Diplorynchus condylocarpon	Apocynaceae	T	75.9	89	0.0008	66 ± 18	0.44 ± 0.13	8.2 ± 0.5
	Lannea schweinfurthii	Anacardiaceae	T	71.9	100	0.0004	49 ± 14	0.72 ± 0.22	12.6 ± 0.9
	Boscia angustifolia	Capparaceae	T	53.6	56	0.0056	27 ± 12	0.14 ± 0.07	7.6 ± 0.6
	Euphorbia cuneata	Euphorbiaceae	ST	42.8	44	0.0200	42 ± 19	0.12 ± 0.06	6.5 ± 0.6
	Other species	—	—	—	—	—	1075 ± 574	10.07 ± 6.47	10.2 ± 0.3
	Subtotal						1423 ± 174	15.05 ± 1.78	10.9 ± 0.3
Dalbergia arbutifolia—*Commiphora africana*—*Albizia petersiana* woodland 3 ($n_{species}$ = 55, n_{plots} = 16)**Site variables (mean ± SE):** Elev = 986 ± 19, pH15 = 6.48 ± 0.09, Ca15 = 8.56 ± 1.09, Sand15 = 76.7 ± 1.56, Clay15 = 13.5 ± 1.55, Silt15 = 9.7 ± 0.96, CNrat30 = 10.6 ± 0.3 and BS = 74.4 ± 4.4	*Dalbergia arbutifolia*	Fabaceae, subfamily Papilionoideae	ST	79.3	100	0.0002	500 ± 123	2.63 ± 0.64	7.7 ± 0.2
	Commiphora africana	Burseraceae	T	54.2	94	0.0026	187 ± 40	2.72 ± 0.64	11.9 ± 0.6
	Albizia petersiana	Mimosacea	T	53.6	75	0.0200	157 ± 57	1.03 ± 0.40	8.4 ± 0.2
	Sclerocarrya birrea	Anacardiaceae	T	50.4	63	0.0186	40 ± 11	1.28 ± 0.45	16.8 ± 1.7
	Other species	—	—	—	—	—	852 ± 449	6.69 ± 3.77	8.8 ± 0.3
	Subtotal						1735 ± 166	14.35 ± 0.71	9.2 ± 0.2
Acacia sp.—*Acacia abyssinica*—*Albizia amara* woodland 5 ($n_{species}$ = 33, n_{plots} = 5) **Site variables (mean ± SE):** Elev = 986 ± 52, pH15 = 7.34 ± 0.23, Ca15 = 13.9 ± 3.3, Sand15 = 74.5 ± 6.78, Clay15 = 14.8 ± 4.7, Silt15 = 10.7 ± 2.6, CNrat30 = 10.6 ± 0.7 and BS = 96.3 ± 8.9	*Acacia sp.*	Mimosaceae	T	98.1	100	0.0002	269 ± 111	6.62 ± 2.86	17.2 ± 1.4
	Acacia abyssinica	Mimosaceae	T	59.4	80	0.0030	31 ± 9	0.60 ± 0.32	9.9 ± 0.8
	Albizia amara	Mimosaceae	T	55.2	60	0.0066	54 ± 30	0.23 ± 0.16	7.1 ± 0.8
	Grewia bicolor	Tiliaceae	ST	53.3	60	0.0106	113 ± 52	0.40 ± 0.17	7.0 ± 0.4
	Acacia seyal	Mimosaceae	T	43.3	60	0.0526	62 ± 34	0.34 ± 0.17	9.0 ± 0.5
	Other species	—	—	—	—	—	665 ± 533	5.52 ± 4.98	7.2 ± 0.4
	Subtotal						1194 ± 169	13.67 ± 3.47	10.1 ± 0.5
Bauhinia petersiana—*Shrebera trichoclada* woodland 24 ($n_{species}$ = 35, n_{plots} = 5) **Site variables (mean ± SE):** Elev = 1175 ± 25, pH15 = 7.3 ± 0.4, Ca15 = 25.4 ± 6.9, Sand15 = 52.2 ± 6.8, Clay15 = 33.1 ± 2.8, Silt15 = 14.7 ± 4.4, CNrat30 = 9.61 ± 1.3 and BS = 104.1 ± 20.4	*Bauhinia petersiana*	Caesalpiniaceae	SH	55.1	80	0.0118	192 ± 121	1.11 ± 0.50	7.5 ± 0.3
	Shrebera trichoclada	Oleaceae	T	50.5	60	0.0110	57 ± 32	0.22 ± 0.13	8.0 ± 0.5
	Manilkara mochisia	Sapotaceae	T	37.6	40	0.0332	34 ± 27	0.14 ± 0.09	6.9 ± 1.0
	Dalbergia melanoxylon	Fabaceae	T	37.0	40	0.0380	68 ± 58	0.26 ± 0.22	6.6 ± 0.3
	Ehretia amoena	Boraginaceae	ST	34.7	40	0.0344	6 ± 4	0.02 ± 0.01	7.0 ± 0.4
	Other species	—	—	—	—	—	982 ± 759	6.43 ± 4.79	9.9 ± 0.5
	Subtotal						1338 ± 137	8.17 ± 0.87	9.1 ± 0.4
	Total						1521 ± 594	13.55 ± 5.52	9.8 ± 0.1

Elev: elevation (m); CNrat30: C : N ratio at 15–30 cm depth; Sand15: sand (%) at 0–15 cm; Clay15: clay (%) at 0–15 cm; Silt15: silt (%) at 0–15 cm; Ca15: Ca^{2+} (cmol(+)/kg) at 0–15 cm; pH15: soil pH at 0–15 cm; BS: % base saturation at 0–15 cm.

TABLE 3: Pearson-correlation matrix for two topographic and eight edaphic variables† associated with the classified plant communities in the Gangalamtumba VLFR (n = 35). Applied significance levels: *5%, **1%, and ***0.1%, †not significant.

	Elev	Slope %	pH15	Ca15	K15	N15	Sand15	Clay15	CNrat30
Slope %	0.19†								
pH15	−0.13†	−0.33*							
Ca15	0.02†	−0.20†	0.83***						
K15	−0.29†	0.00*	0.10*	0.12*					
N15	0.06†	0.36*	0.10*	0.41**	0.33*				
Sand15	−0.42**	0.03†	−0.53***	−0.74***	0.06†	−0.46**			
Clay15	0.31*	−0.12†	0.51**	0.76***	−0.01*	0.47**	−0.86***		
CNrat30	0.36*	0.10*	−0.39*	−0.51**	−0.15†	−0.19†	0.40*	−0.48**	
BS	−0.24†	−0.17†	0.84***	0.91***	0.15†	0.37*	−0.58***	0.60***	−0.51**

†Elev: elevation (m); pH15: soil pH at 0–15 cm; Ca15: Ca^{2+} (cmol(+)/kg) at 0–15 cm; K15: K^{+} (cmol(+)/kg) at 0–15 cm; N15: % N concentration at 0–15 cm; Sand15: sand (%) at 0–15 cm; Clay15: clay (%) at 0–15 cm; CNrat30: C : N ratio at 15–30 cm depth; BS: % base saturation at 0–15 cm. t-value was calculated as $t = r\sqrt{(n-2)/(1-r^2)}$, where r is the Pearson-correlation coefficient and n is the total sample size.

TABLE 4: Species richness observed in other studies from dry miombo woodlands.

Plot size (ha)	Total number of plots	Total sample area (ha)	Total number of species	References
0.071	70	4.95	82	[43]
0.071	80	5.65	110	[27]
0.071	133	9.40	229	[26]
0.071	247	17.46	102	[44]
0.04	40	1.60	81	[45]
0.25	14	3.50	69	[25]
0.1	2	0.20	40	[28]
0.1	152	15.20	92 genera	[22]
0.071	35	2.47	88	This study

annual rainfall of 565–1500 mm (Table 4). Using plot sizes of 0.04–0.25 ha and sample sizes of 2–247 plots, a total number of species ranging from 40 (Dbh ≥ 10 cm) to 229 (Dbh ≥ 2 cm) have been reported from Miombo woodlands [22, 25–28, 43–45].

The high number of species reported by Banda et al. [26], Chidumayo [22], Isango [45], and Chamshama et al. [44] is likely to be a consequence of the spatial scale and coverage of these studies as they all cover large areas, include more than one site, and operate with large sample sizes. For example, Chidumayo [22] included species from both wet and dry Miombo areas in Zambia. The study by Sauer and Abdallah [15], who reported a total of 131 species occurring in the tobacco growing zone of Iringa rural district, included two forest reserves and three family-managed forests. Therefore, considering the climatic conditions in the GVLFR (617 mm of rainfall per year) and the sample size (35 plots), the species richness reported in this study can be ranked at least as high or higher than those found in the studies mentioned. The selective sampling approach, focusing on various microhabitat types, adopted by Banda et al. [26] may have contributed to the large number of species observed in their study area. Similarly, the higher number of species found by Giliba et al. [27] was probably due to the presence of riverine forest, offering site conditions favourable for many species.

The values of the Shannon-Wiener (H' = 3.44) and Simpson indices (D = 0.05) reported for large individuals in this study are within the range observed for most communities of particular life forms [36]. For example, H' usually does not exceed 5, although this maximum value varies depending on the type of the biological community sampled and the sampling approach applied (e.g., minimum diameter and size of sample units). A threshold value of 2 for H' has been mentioned as a minimum value, above which an ecosystem can be regarded as medium to highly diverse [27]. Chamshama et al. [44] reported three H' values of 3.1, 3.2, and 3.3 from Kitulangalo Miombo forest in Eastern Tanzania, while Njana [43] reported a H' value of 3.40 from dry Miombo forest in Western Tanzania. The studies by Sauer and Abdallah [15] and Giliba et al. [27] reported particularly high values of 3.46 and 4.27, respectively. This could be attributed to the very large sample sizes used in both studies and the presence of riverine forest where the chance of encountering many rare species is likely to be high. The forests examined in the mentioned studies receive an average annual rainfall of 700–1000 mm, compared to which the rainfall in the GVLFR is low (617 mm on average per year, c.f. above). The relatively high diversity found in GVLFR must therefore be attributed to other factors than climate. The soil analyses indicate that the soil fertility level in the GVLFR is relatively high, with considerable proportions of all 2 : 1 lattice clay minerals (114%) (i.e., illite, montmorillonite, and vermiculite) plus a good amount of organic matter, which may suggest that the soil has large reserves of important plant nutrients, for example, K, Mg, and Fe. The base saturation percentage (BS), which is normally used to indicate the soil fertility status (Landon, 1991), was also high, 76% on average, and with 86% of the samples (30 samples) with BS values >50% (fertile soil), and only 14% of the samples (5 samples) with BS below 50% (less fertile soil). As another indication of high soil fertility status the mean C : N ratio was 12 ± 0.43

(range 7–19) for top soil (0–15 cm) and 11 ± 0.36 (range 5–16) for subsoil (15–30 cm). In general, the values for both soil strata fall within the expected range of 8–17. Soil pH values (mean 6.7 ± 0.1, range 5.67–8.52) were also within the optimal range where all the nutrients that are most important for plant growth (Ca, Mg, K, and P) are available and accessible to plants [46]. In this study, 97% of the soil samples had pH below 8 (one sample had a pH of 8.52). Fisher and Binkley [47] noted that high pH is almost never a problem in forests as most trees do well across the full range of common pH values. Therefore, considering the low average annual rainfall compared to other forests, the relatively high fertility of the GVLFR may be the main factor creating an environment favourable to many species, thus leading to a quite high species diversity observed in this forest.

Based on the Importance Value Index *Brachystegia spiciformis* and *Combretum molle* appeared to be the most important species among harvested trees (stumps) in the study area. This result agreed very well with the large values of basal area and volume and the information obtained from local scouts and members of the village environmental committee, who said that the most frequently harvested species for charcoal making include all *Brachystegia* species found in the forest (i.e., *Brachystegia spiciformis, Brachystegia manga, Brachystegia boehmii*, and *Brachystegia bussei*). Among the *Combretum* species, the most important one (based on IVI), *Combretum molle*, is mostly used for house construction and firewood rather than for charcoal making. Apart from the *Brachystegia* species, the only other species mentioned as important for charcoal making was *Acacia mellifera*. Other species are only used in case they happen to fall when felling the preferred species during the preparation of charcoal kilns. With respect to stumps, *Brachystegia spiciformis, Brachystegia manga*, and *Combretum molle* are among the ten most abundant species in terms of density, basal area, and volume per hectare. Stumps of the other species mentioned are not commonly found, a fact which may be due to the small sample size being unable to capture sites where these species are harvested but may also be related to their limited distribution in the forest as indicated by the estimated dispersion indices (see Table 1).

4.2. Forest Structure. Species densities reported from other Miombo woodland areas in Tanzania are typically 348–1495 stems/ha for trees with Dbh >4 cm [24, 43, 45]. Compared with this the GVLFR is highly stocked as the estimated density is 2296 stems/ha for trees with Dbh >4 cm. The mean stem density of 1521 ± 594/ha for trees with Dbh ≥5 cm is also more than twice as large as values found in other studies [25–27, 44, 45, 48]. A similar pattern is seen when comparing the density of regeneration between the studies. The diameter distribution is characterised by a very clear trend of decreasing stem density with increasing diameter. The shape of the distribution is thus an inverted "J" (Figure 3), which is a common feature of natural forests with active regeneration and recruitment [49]. However, not many large trees were captured by the sample, whereas a considerable number of relatively large stumps were observed, suggesting that anthropogenic activities such as charcoal making may have affected the structure and ecological balance of the forest (see Figure 3). Since the woodlands are often hit by fire which tends to kill the seedlings (especially the late fires) and thus only few seedlings can be expected to reach larger diameter classes, lack of mature trees and the resulting lack of seeds may eventually threaten the biodiversity of the forest.

The mean basal area of 13.55 ± 5.52 m^2/ha observed in this study is slightly above the range of values typically reported from the miombo region, 7.5–12.6 m^2/ha [26, 28, 43, 44, 50]. However, the basal areas reported by Isango [45] were a bit higher (15.04–15.63 m^2/ha) than observed in this study.

The mean total volume in GVLFR was estimated at 92.17± 39.0 m^3/ha for trees with Dbh ≥5 cm. Other studies in dry Miombo woodlands have reported mean volumes of 16.7–76.03 m^3/ha [24, 44, 45, 50]. The current standing volume of GVLFR is thus slightly higher than values typically reported for forests in the Miombo ecoregion. A plausible reason for this may be that, compared to other forests, the GVLFR is still well stocked despite ongoing human activities such as charcoal making. The basal area observed for stumps was only 0.72 m^2/ha so there is no indication of intensive extraction over many years. This corresponds well with the findings of Treue et al. [20] who conclude that the estimated 0.4 m^3/ha annual extraction of woody biomass from GVLFR is considerably below its estimated annual increment of 1.5 m^3/ha and that the local forest managers seem capable of regulating the harvesting activities, which, in addition to village members' collection for subsistence uses, also included commercial charcoal production by external companies that pay a fee per bag of charcoal extracted to the village government.

4.3. Plant Communities and Species Associations. Except for *Brachystegia spiciformis*, the majority of the *Brachystegia* and *Julbernardia* species that are common to miombo woodlands elsewhere are not among the species most commonly observed in this study. A similar pattern was observed by Banda et al. [26] in the Katavi-Rukwa ecosystem where the genera that are most common in miombo woodlands, *Brachystegia, Julbernardia*, and *Isoberlinia*, were not common in their study sites. Furthermore the four plant communities distinguished in this study are comparable with those reported by other studies in Tanzania, including the work by Munishi et al. [29] in the Miombo woodlands of Rukwa basin, Chunya district, Tanzania, and the study by Banda et al. [26] in the Katavi-Rukwa ecosystem.

Elevation was noted by Munishi et al. [29] to be the most important factor shaping the species communities in their study area. This study found a similar pattern with the highest coefficient of correlation observed for elevation, suggesting that topographical variation is among the strongest determinants of community composition in dry Miombo woodlands, hence influencing the spatial distribution of species strongly. However, in our study area edaphic factors also influenced the species distribution directly. Two plant communities occurred mainly on clayey soils with high pH at intermediate elevations, one on sandy soils with low pH at low elevations and one on sandy-clayey soils at higher elevations and with neutral soil pH (Figure 5). Specifically, it appeared that the *Acacia* woodland category (Community 5) grows at low elevations around temporary streams (or at least where the ground water table is relatively high), and the *Bauhinia* woodland category (Community 24) appears mostly in places with a relatively high percentage of clay (and therefore high values of pH, Ca, and BS). By contrast it appeared that the *Dalbergia* woodland category (Community 3) is located at more sandy sites (with low values of pH, Ca, and BS), and the *Brachystegia* woodland category (Community 1) seemed to be located mostly at higher elevations where the CN-ratio is quite high. Correlations between elevation and the basic soil variables pH, Ca, and percentages of sand and clay were low (c.f. Figure 5). Thus, the results indicate that the plant communities of the dry miombo woodlands in GVLFR are not only shaped by the topographic variation (elevation) and the groundwater level but also by basic soil characteristics. The results thus confirm findings from other studies detecting effects of elevation and soil characteristics on species composition [51, 52].

5. Conclusion

Considering that the sample size used in this study was smaller than samples used in other studies in dry miombo woodlands, the results show that the species diversity in GVLFR is relatively high compared to other forest reserves. The vegetation of GVLFR is characterised by high density, basal area, and volume, and despite the scarcity of large diameter trees this indicates that the forest is in a good condition. The effect of anthropogenic activities is nevertheless evident and stresses the need for proper management, especially for economically important species preferred for charcoal making, (e.g., *Brachystegia spiciformis*), if the current species diversity is to be maintained or enhanced. A repeated future study would be needed to assess whether the current community-based management regime yields this intended outcome, but the available information and analyses allow for some optimism in this respect.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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PAPER II

Basic density of trees and shrubs from dry miombo woodland in Tanzania

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ABSTRACT

Wood basic density is a key variable in the estimation of tree biomass. However, only few studies have reported basic density estimates for tree species found in miombo woodlands or other vegetation types in Tanzania. Based on 1,004 stem disks sampled from 199 individual trees and shrubs (diameter range 1.4-62.0 cm) from Gangalamtumba Village Land Forest Reserve, Iringa rural district, Tanzania, basic densities of 44 species (wood and bark) were estimated by the water displacement method and regression models developed for three important species, *Brachystegia spiciformis* Benth (tree, N = 40), *Combretum molle* G. Don (tree, N = 41) and *Dalbergia arbutifolia* Baker (shrub, N = 37) separately, and for broader samples of trees (28 species, N = 72) and shrubs (16 species, N = 32). Diameter and height above ground were the main independent variables and in each case a range of different models were tested. The results show that for each of the life forms (trees and shrubs) the mean densities varied significantly between species ($p<0.0001$). The developed regression models can be used in estimating basic density for stem sections in cases where section volume is known but dry weight is not.

Keywords: Biomass, regression models, specific gravity, village land, water displacement method.

1. INTRODUCTION

Accurate estimation of carbon stocks for different forest ecosystems has recently received global attention as a means of assessing their potential in climate change mitigation efforts (Chave et al., 2004; Brown, 2002). Quantification of carbon involves the conversion of forest inventory data into above and/or below ground biomass estimates by the use of appropriate allometric equations specific for a given forest type (Henry et al., 2010). These equations are developed as a basis for using individual tree parameters such as diameter at breast height, wood basic density and total tree height from forest inventories to estimate tree and forest biomass. Here the three parameters are listed in the sequence also used by Chave et al. (2005) to indicate their relative importance in explaining variations in tree biomass. However, diameter at breast height and total tree height are considerably easier to measure than wood basic density and they have therefore often been used as the only explanatory variables of allometric biomass equations.

Accordingly, the inclusion of wood basic density is normally overlooked in development of allometric equations, which may result in overall poor estimation of above ground biomass (Baker et al., 2004; Henry et al., 2010), especially for forests where wood basic density varies considerably among tree species (Chave et al., 2005) or average wood basic density deviates considerably from that of the sample used for model calibration. Since forest biomass at a particular site is affected by a variety of factors including some that also influence wood basic density, e.g. stand age, species composition, climate, soil, topography, and environmental heterogeneity, the inclusion of wood basic density in site specific models has considerably reduced the uncertainty involved in estimating the spatial distribution of biomass and enabled regional-scale comparisons of tree biomass estimates (Baker et al., 2004; Fang et al., 2006; Chaturvedi and Raghubanshi, 2012). Wood basic density is considered as the most important variable in estimation of tree biomass and the best descriptor of wood functional properties and tree life-history traits (Chave et al., 2005; Henry et al., 2010; Williamson and Wiemann, 2010). Therefore, if high accuracy is required for quantification and verification of carbon storage of a particular forest, or for other management purposes, it is recommended to include wood basic density as one of the variables in modelling biomass (Chave et al., 2005). The wood basic density of a particular species and tree size can be estimated directly by destructive sampling and measurement using the water displacement method and/or by prediction using a regression equation developed from existing datasets (Olesen, 1971; Brown, 1997).

Despite its importance in accurate estimation of carbon stocks in forest ecosystems, actual data on wood basic density are wanting for about half of the 1440 tree species identified in Tanzania by the recently completed National Forestry Resources Monitoring and Assessment project (NAFORMA). For the remaining half of the species data are only available from few sites and mostly outside Tanzania (Bryce, 1967; Drichi, 1992; Malimbwi et al., 1994; Munishi and Shear, 2004; Mwampamba, 2009). The now completed work by NAFORMA has generated very useful inventory data which can be used to estimate the current and potential carbon stock of forest ecosystems in Tanzania. To this end wood basic density data and estimates can be applied in existing biomass functions that include wood density as an independent variable (see Mugasha et al., 2013; Malimbwi et al., 1994; Chamshama et al., 2004). Moreover, in cases where volume functions exist but biomass functions do not, wood basic density data can be used in biomass estimation. Accordingly, the objective of this study was to: 1) report estimates of basic density for 28 miombo tree species and 16 shrub species sampled at a study site in Iringa, Tanzania, and, based on the literature, compile wood basic densities for the 77 species encountered at the study site and; 2) develop basic density models for three dominant species (*Brachystegia spiciformis* Benth, *Combretum molle* G. Don and *Dalbergia arbutifolia* Baker) and broader models for two life form groups, trees and shrubs, found at the study site.

2. MATERIAL AND METHODS

2.1. Study site and harvesting procedures

The study was conducted at Gangalamtumba Village Land Forest Reserve (GVLFR) which is located in central-southern Tanzania (7°35' S, 35°35' E), about 30 km northwest of Iringa

Municipality, the administrative capital of Iringa Region (Figure 1). The GVLFR receives an average annual rainfall of 617 mm and the forest has been described as dry miombo woodland (Mwakalukwa et al., 2014a). Further details of the study site and sampling procedure for the selected species are described in Mwakalukwa et al. (2014b). In this paper we intend to give only a brief description of the study site and sampling strategy employed especially in collecting the stem disks.

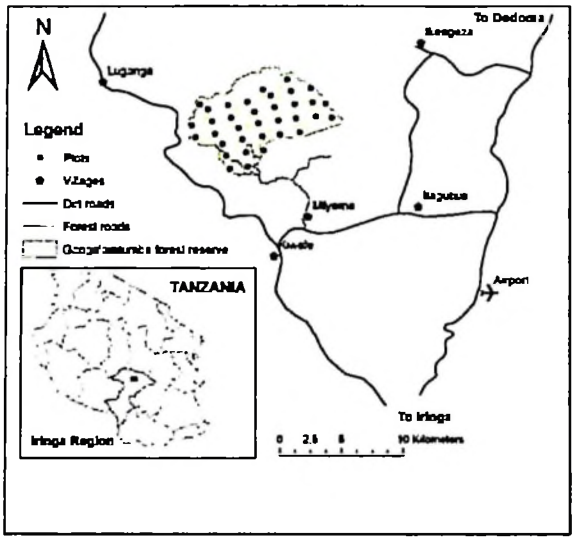

Figure 1. Map of the study area and its location in the Iringa Region.

The survey conducted in 2009 and 2010 involved harvesting of 142 individual trees (28 species) and 57 individual shrubs (16 species). The minimum and maximum diameter at breast height (Dbh) of sample trees and shrubs were 1.4 and 62.0 cm, respectively. For each tree or shrub felled, the diameter at breast height (Dbh) was measured to the nearest 0.1 cm using a diameter tape and total height was measured using a Suunto clinometer. Species were first identified by a local botanist using vernacular names in the languages Hehe and Kiswahili. Later, scientific identification was done by a botanist from the herbarium centre at the silviculture research station of Tanzania Forest Research Institute in Lushoto.

For each tree/shrub five disks with a thickness of about 2-3 cm were sampled (Figure 2). Selection of these five disks was based on importance sampling (e.g. Valentine et al., 1984 and de

Gier, 2003), implying that the selection of tree sections in which the disks were to be extracted depended on the estimated proportion of volume in each section (probability of selection proportional to volume). The sample disks were measured for fresh weight in the field and brought to the laboratory for dry weight determination. In the laboratory, all disks were oven dried at 103 ± 2 °C to constant weight. Using the water displacement method, the volume of each disk was determined (Olesen, 1971). Basic density (g/cm^3) for each disk was determined as the ratio of dry weight (g) to green volume (cm^3).

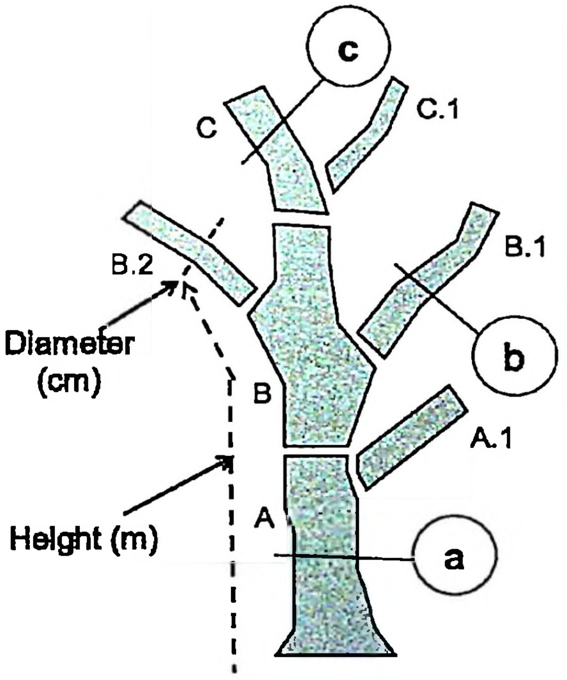

Figure 2. Example tree sketch showing the location of stem sections (un-circled letters), location where diameter was measured at the middle of each section (e.g. B.2), vertical distance (Height) that was measured between the section (e.g. B.2) and the ground and how the 5 disks (three shown, circled letters) were selected based on estimated volume.

2.2. Statistical analysis

Prior to the regression analysis, wood basic density (dependent variable) was plotted against each of the independent variables, diameter (D) measured at the middle of each section and vertical distance (H) measured between the section and the ground (e.g. Figure 2), to examine the range and shape of the functional relationship, and to assess the heterogeneity of the variance. We tested the relationships after transforming the variables. Except in the shrub dataset, diameter and height above ground were transformed to match the non-linear tendency in the data characterised by degressively decreasing basic density with increasing diameter. We selected our final models based on high adjusted R^2, low root mean squared error (RMSE), and graphical analysis of the residuals.

Several linear models with various types of transformations, including logarithmic, reciprocal, square root and cubic root transformations, were tested during development of the density models (Malimbwi et al 1994; Djomo et al., 2010; Husch et al., 2003). Finally the following general models were applied:

Model 1: $Y = a + b \times D^p + c \times H^p$

2: $Y = a + b \times D^p$

where Y is the density (g/cm^3); D is the diameter of the stem section (cm), H is the vertical distance from the ground to the middle of the stem section (m), a, b and c are regression coefficients (which may depend on species) and p is a power transformation parameter. Different values of p were tested for models 1 and 2, and it was decided that an appropriate value for the three individual species and for trees in general was $p = 0.33$, whereas $p = 1$ was a better choice for shrubs.

For species-specific density models, we used ordinary least squares estimation, assuming that errors were normally and independently distributed, whereas wood densities for groups of species, i.e. trees and shrubs, were modelled using the following general mixed linear model:

3: $Y_{ijk} = f(D_{ijk}, H_{ijk}) + \mu_i + r_j + \varepsilon_{ijk}$

where, i is species, j is tree number, k is disk number (replication within tree, five disks per tree); $f(D_{ijk}, H_{ijk})$ is either model 1 or 2, μ_i is a fixed species effect; r_j is a random effect for tree j, $r_j \sim$

$N(0,\sigma_r^2)$, and the ε_{ijk} are random errors, $\varepsilon_{ijk} \sim N(0,\sigma^2)$. Thus, species was modelled as a fixed effect and the variation between trees as a random effect. All analyses were made in R version 2.13.0 (www.r-project.org).

3. RESULTS

The mean basic densities of the 44 species sampled are presented in Table 1. These 44 species represent about 57 % of all 77 species enumerated with stems ≥ 5 cm Dbh and about 64 % of all 28 plant families encountered in the GVLFR (Appendix 1). For each of the life forms the mean densities varied significantly between species (shrubs: ANOVA, F = 20.25, df = 15, $p < 0.0001$, and trees: ANOVA, F = 124.3, df = 27, $p < 0.0001$). Mean basic densities (not weighted) for the two life forms were (mean ± std.error); shrubs: 0.708 ± 0.01 g/cm^3, and trees: 0.671 ± 0.01 g/cm^3. Average mean densities for trees ranged from (mean ± std.error) 0.347 ± 0.01 g/cm^3 for *Commiphora mossambicensis* to 0.852 ± 0.01 g/cm^3 for *Manilkara mochisia*, while for shrubs the density ranged from 0.532 ± 0.02 g/cm^3 for *Psychotria schummaniana* to 0.815 ± 0.01 g/cm^3 for *Dalbergia arbutifolia*.

The final regression models for estimating wood basic density followed the general forms specified in models 1-3, section 2.2, for all species and species groups. For the three individual species, the trees *Brachystegia spiciformis* and *Combretum molle*, and the shrub *Dalbergia arbutifolia*, the final models are presented in Table 2. The standard deviations of the residuals (RMSE) were moderate (0.042-0.066) and corresponded to about 5-8% of the average basic densities reported for the three species in Table 1. As expected the coefficients estimated for diameter were generally positive, indicating that basic density increases with increasing diameter. Presumably this is mostly a consequence of decreasing bark percentage with increasing diameter. Coefficients estimated for height above ground were generally negative, indicating that basic density decreases with height.

Among trees (Table 3) as well as shrubs (Table 4 and 5), species had a significant effect (P < 0.0001) on density. Accordingly, fixed species effects were included in models for both species groups along with effects of cubic root transformed diameter. However, height above ground turned out to have no significant effect on density in the tree dataset (Table 3) so for this group height was not included. By contrast height was significant for shrubs (P<0.0001) and therefore included in the model (Table 4).

Table. 1. Mean and standard error (SE) for wood basic density of stem disks (with bark) sampled from 44 woody species in Gangalamtumba Village Land Forest Reserve in Iringa, Tanzania.

Scientific name	Local Name (in Hehe)	Family	Individuals (plants) (N)	Samples (disks) (n)	Density Mean ± SE (g/cm^3)
Trees					
Combretum molle G. Don	Mlama	Combretaceae	41	210	0.805 ± 0.004
Brachystegia spiciformis Benth	Mkwee	Caesalpiniaceae	40	200	0.785 ± 0.004
Hymenodictyon parvifolium Oliv.	Mdeke	Rubiaceae	4	19	0.399 ± 0.02
Lannea schweinfurthii	Mgulumo	Anacardiaceae	3	15	0.584 ± 0.01
Albizia petersiana (Belle) Oliv.	Mkalala	Mimosaceae	3	15	0.819 ± 0.03
Commiphora africana	Mtono - Kijani	Burseraceae	3	15	0.375 ± 0.01
Commiphora mollis	Mtono - Mweusi	Burseraceae	3	15	0.381 ± 0.01
Brachystegia boehmii	Muyombo	Caesalpiniaceae	3	15	0.751 ± 0.01
Diplorynchus condylocarpon	Mfilafila	Apocynaceae	3	14	0.541 ± 0.03
Markhamia obtusifolia	Muguvani	Bignoniaceae	2	13	0.620 ± 0.01
Manilkara mochisia	Mdide	Sapotaceae	2	10	0.852 ± 0.01
Terminalia brownie	Mdwendwe	Combretaceae	2	10	0.807 ± 0.02
Acacia mellifera (Vahl) Benth.	Mkambala	Mimosaceae	2	10	0.847 ± 0.02
Afzelia quanzensis	Mkora	Caesalpiniaceae	2	10	0.693 ± 0.01
Acacia sp.	Mkungugu	Mimosaceae	2	10	0.749 ± 0.01
Combretum zeyheri Sond	Mlyasenga	Combretaceae	2	10	0.764 ± 0.02
Cassia abbreviata	Mmulimuli	Caesalpiniaceae	2	10	0.784 ± 0.01
Lonchocarpus capassa	Mtabagila	Fabaceae	2	10	0.768 ± 0.02
Brachystegia bussei Harms	Mtelela	Caesalpiniaceae	2	10	0.764 ± 0.02
Brachystegia manga	Mugusi	Caesalpiniaceae	2	10	0.803 ± 0.01
Sclerocarrya birrea sbsp. birrea	Mubwegele	Anacardiaceae	2	10	0.579 ± 0.02
Xeroderris stuhlmannii	Mvembadanda	Fabaceae	2	10	0.631 ± 0.01
Cassipourea mollis (R.E.fr.) Alstom	Mbumila	Rhizophoraceae	2	9	0.681 ± 0.01
Codyla densiflora	Mkwata	Caesalpiniaceae	1	5	0.719 ± 0.03
Commiphora ugogensis	Mkongolo	Burseraceae	1	5	0.410 ± 0.02
Julbernardia globiflora	Mpinati	Caesalpiniaceae	1	5	0.775 ± 0.01
Commiphora mossambicensis	Mtono - Matiti	Burseraceae	1	5	0.347 ± 0.01
Acacia seyal Del. Var. seyal	Mubata	Mimosaceae	1	5	0.755 ± 0.004
Shrubs/small trees					
Dalbergia arbutifolia	Mgiha	Papilionaceae	37	188	0.815 ± 0.01
Grewia bicolor	Mkole	Tiliaceae	4	20	0.716 ± 0.02
Canthium pseudoverticillatum Hien	Mnyalupuko	Rubiaceae	3	16	0.758 ± 0.01
Margaritaria discoidea (Bail.)	Mmemenamene	Euphorbiaceae	2	10	0.716 ± 0.02
Premna holstii Gurke	Mteresi	Verbenaceae	2	10	0.805 ± 0.02

Bauhinia petersiana	Mkombiwawe	Caesalpiniaceae	2	10	0.668 ± 0.01
Opilia amentacea Roxb.	Lukokonza	Opiliaceae	2	10	0.785 ± 0.02
Grewia forbesii Haw. Ex Mast	Mpelemele	Tiliaceae	2	10	0.691 ± 0.01
Vitex payos	Mkoga	Verbenaceae	2	10	0.613 ± 0.01
Dichrostachys cinerea (L.) Wight & Arn	Mgegele	Mimosaceae	1	5	0.682 ± 0.02
Psychotria schummaniana	Msasamulo	Rubiaceae	1	5	0.532 ± 0.02
Vangueria infausta Burch. Ssp. Rotundata	Msambalawe	Rubiaceae	1	5	0.669 ± 0.01
Ximenia caffra Sond	Mtundwa	Olacaceae	1	5	0.669 ± 0.01
Ormocarpum kirkii	Kitimbwi	Fabaceae	1	5	0.725 ± 0.02
Ehretia amoena	Mgosa	Boraginaceae	1	5	0.757 ± 0.01
Bridelia scleuroneura Muell.Arg.	Mnyaluhanga	Euphorbiaceae	1	5	0.722 ± 0.01

Table 2. Wood basic density models for three dominant species in Gangalamtumba Village Land Forest Reserve. All parameter estimates are significantly different from zero ($p<0.001$).

Species name	Disk size-diameter (cm)	Height above ground (m)	Model‡ (df)	Regression parameters†			Adj. R^2	RMSE
				a	*b*	*c*		
B. spiciformis	1.2-51.6	0.1-14.3	1 (df =197)	0.7558 (0.014)	0.0329 (0.005)	-0.0286 (0.007)	0.22	0.045
			2 (df =198)	0.7178 (0.011)	0.031 (0.005)	-	0.15	0.047
C. molle	1.3-33.0	0.1-6.7	1 (df =207)	0.7353 (0.020)	0.0753 (0.007)	-0.0685 (0.008)	0.54	0.042
			2 (df =208)	0.6192 (0.016)	0.0914 (0.008)	-	0.40	0.048
D. arbutifolia	1.4-24.7	0.1-6.6	1 (df =185)	0.7514 (0.034)	0.0812 (0.014)	-0.0757 (0.015)	0.34	0.062
			2 (df =186)	0.6214 (0.025)	0.1061 (0.014)	-	0.24	0.066

† Numbers in brackets indicate standard errors of the parameter estimates. Total number of individual stems, *N*, for each species and total number of stem disks, *n*, are listed in Table 1. Dbh is diameter at breast height, df is the number of degrees of freedom, RMSE is the standard deviation of the residuals and Adj. R^2 is the adjusted coefficient of determination.

‡ Model 1: $Y = a + bD^{0.33} + cH^{0.33}$

Model 2: $Y = a + bD^{0.33}$; where Y is density (g/cm^3), D is disk diameter in cm and H is height above ground in metres.

Table 3. Basic density model for 28 tree species in Gangalamtumba Village Land Forest Reserve.

Dbh range (cm) = 1.4-62; RMSE=0.036; σ_{ln} = 0.038; R^2_{LR} = 0.57; df = 331.

			Regression parameters†		
Parameter	Species name	Disk size-diameter (cm)	Height above ground (m)	Parameter estimate (std.error)	P-value
Coefficient (*b*)	-	-	-	0.0409 (0.005)	0.00
a(*species*)	*Cassipourea mollis*	1.9-12.3	0.2-3.9	0.6077 (0.031)	0.00
a(*species*)	*Hymenodictyon parvifolium*	1.4-38.1	0.2-5.7	0.3052 (0.024)	0.00
a(*species*)	*Manilkara mochisia*	3.0-8.7	0.6-3.3	0.7785 (0.031)	0.00
a(*species*)	*Terminalia brownii*	4.2-19.1	0.2-4.8	0.7183 (0.031)	0.011
a(*species*)	*Diplorynchus condylocarpon*	1.3-14.9	0.2-5.8	0.4859 (0.026)	0.003
a(*species*)	*Lannea schweinfurthii*	2.7-30.2	0.2-9.8	0.4904 (0.027)	0.004
a(*species*)	*Albizia petersiana*	3.4-24.4	0.3-5.6	0.7231 (0.026)	0.004
a(*species*)	*Acacia mellifera*	5.3-61.7	0.7-9.5	0.7339 (0.033)	0.004
a(*species*)	*Commiphora ugogensis*	9.4-24.0	1.5-7.9	0.3078 (0.044)	0.00
a(*species*)	*Afzelia quanzensis*	4.1-29.0	0.9-7.1	0.5953 (0.032)	0.768
a(*species*)	*Acacia sp.*	3.6-19.8	0.2-7.0	0.6620 (0.031)	0.200
a(*species*)	*Codyla densiflora*	11.3-29.6	2.4-8.1	0.6113 (0.044)	0.945
a(*species*)	*Brachystegia spiciformis*	3.1-51.6	0.1-13.6	0.6929 (0.019)	0.013
a(*species*)	*Combretum molle*	1.3-23.6	0.1-6.7	0.7013 (0.018)	0.008
a(*species*)	*Combretum zeyheri*	2.5-11.6	0.2-4.2	0.6918 (0.031)	0.050
a(*species*)	*Cassia abbreviate*	4.3-15.8	0.6-3.4	0.7021 (0.031)	0.029
a(*species*)	*Julbernardia globiflora*	3.7-15.6	3.8-8.4	0.6976 (0.043)	0.085
a(*species*)	*Lonchocarpus capassa*	1.7-32.9	0.1-10.4	0.6859 (0.031)	0.068
a(*species*)	*Brachystegia bussei*	3.8-22.9	0.8-8.9	0.6796 (0.031)	0.092
a(*species*)	*Commiphora africana*	2.6-19.9	0.2-4.7	0.2850 (0.027)	0.00
a(*species*)	*Commiphora mossambicensis*	3.3-10.2	0.5-3.1	0.2732 (0.043)	0.00
a(*species*)	*Commiphora mollis*	3.9-19.6	0.1-4.5	0.2976 (0.026)	0.00
a(*species*)	*Acacia seyal*	3.6-15.2	0.8-8.5	0.6760 (0.043)	0.188

a(*species*)	*Sclerocarrya birrea*	3.9-30.0	0.6-9.7	0.4772 (0.032)	0.003
a(*species*)	*Brachystegia manga*	4.2-22.5	0.8-11.1	0.7164 (0.031)	0.013
a(*species*)	*Markhamia obtusifolia*	2.0-4.0	0.2-3.5	0.5602 (0.030)	0.256
a(*species*)	*Brachystegia boehmii*	5.4-25.5	0.7-7.2	0.6558 (0.027)	0.215
a(*species*)	*Xeroderris stuhlmannii*	3.1-23.5	0.6-10.4	0.5390 (0.032)	0.107

[†] Numbers in brackets indicate standard errors of the parameter estimates. Letters (*a*), and (*b*) are regression parameters. RMSE is the standard deviation of the residuals; σ_{tn} is the standard deviation of the random effect of tree (between tree variation); R^2_{LR} is the likelihood ratio based coefficient of determination. Total number of individuals, *N*, and total number of stem discs, *n*, for each species are listed in Table 1, except for *C. molle* where $N = 7$ and $n = 37$, and for *B. spiciformis* where $N = 10$ and $n = 50$. These individuals were purposely selected to fill-in diameter classes, which were otherwise not represented in the dataset.

Model 2: $Y = a(species_i) + bD^{0.33}$, where Y is density (g/cm^3) and *D* is disk diameter in cm, Dbh is diameter at breast height.

Table 4. Basic density models with diameter and height for 16 shrub species in Gangalamtumba Village Land Forest Reserve. Dbh range (cm) = 1.8-21.5; RMSE=0.011; σ_{tn} = 0.006; R^2_{LR} = 0.974, df = 142.

		Regression parameters[†]			
Parameter	Species name	Disk size-diameter (cm)	Height above ground (m)	Parameter estimate (std.error)	P-value
Intercept (*a*)	-	-	-	0.7853 (0.016)	< 0.001
Coefficient (*c*)	-	-	-	-0.0213 (0.004)	< 0.001
b(diameter)	*Ormocarpum kirkii*	1.7-3.1	0.2-1.9	-0.0193 (0.001)	0.055
b(diameter)	*Opilia amentacea* Roxb.	2.4-9.3	0.1-2.7	0.0068 (0.006)	0.021
b(diameter)	*Dichrostachys cinerea*	2.9-4.3	0.5-2.2	-0.0202 (0.009)	0.940
b(diameter)	*Dalbergia arbutifolia*	1.8-24.7	0.1-6.6	0.0133 (0.004)	0.004
b(diameter)	*Ehretia amoena*	1.9-3.5	0.2-1.5	-0.0049 (0.010)	0.220
b(diameter)	*Vitex payos*	2.8-10.2	0.7-5.0	-0.0163 (0.006)	0.791
b(diameter)	*Grewia bicolor*	3.3-8.2	0.1-2.5	-0.0096 (0.005)	0.319
b(diameter)	*Bauhinia petersiana*	2.8-9.7	0.3-3.2	-0.0185 (0.006)	0.941
b(diameter)	*Margaritaria discoidea*	3.7-12.2	0.1-3.0	-0.0080 (0.006)	0.293
b(diameter)	*Bridelia scleuroneura*	3.7-7.2	0.5-3.6	-0.0025 (0.008)	0.180
b(diameter)	*Canthium pseudoverticillatum*	1.9-25.5	0.2-4.8	0.0023 (0.005)	0.040
b(diameter)	*Grewia forbesii*	3.2-8.3	0.4-1.8	-0.0164 (0.006)	0.781
b(diameter)	*Vangueria infausta*	2.7-4.3	1.1-3.0	-0.0251 (0.009)	0.619
b(diameter)	*Psychotria schummaniana*	3.9-7.9	0.2-2.7	-0.0404 (0.008)	0.095
b(diameter)	*Premna holstii*	2.6-10.5	0.1-3.8	0.0134 (0.006)	0.006
b(diameter)	*Ximenia caffra*	2.5-5.1	0.2-1.3	-0.0270 (0.009)	0.515

[†] Letters in brackets (*a*), (*b*) and (*c*) indicate regression parameters. Model 1: $Y = a + bD + cH$, where Y is density (g/cm^3) and *D* is disk diameter in cm, and *H* is height above ground in metres. Dbh is diameter at breast height; RMSE is standard deviation of the residuals; σ_{tn} is the standard deviation of the random effect of shrub (between shrub variation); R^2_{LR} is the likelihood ratio based coefficient of determination. The total number of individuals, *N*, for each species and the

total number of stem disks, *n*, are listed in Table 1, except for *D. arbutifolia* where $N = 6$, $n = 29$. These individuals were purposely selected to fill-in diameter classes which were otherwise not represented in the dataset.

Table 5. Wood basic density models with diameter only for 16 shrub species in Gangalamtumba Village Land Forest Reserve. Dbh range (cm) = 1.8-21.5; RMSE=0.011; $\sigma_m = 0.012$; $R^2_{LR} = 0.968$, df = 143.

		Regression parameters†			
Parameter	Species name	Disk size-diameter (cm)	Height above ground (m)	Parameter estimate (std.error)	P-value
Intercept (*a*)		-	-	0.6986 (0.011)	< 0.001
b(diameter)	*Ormocarpum kirkii*	1.7-3.1	0.2-1.9	0.0091 (0.014)	0.527
b(diameter)	*Opilia amentacea* Roxb.	2.4-9.3	0.1-2.7	0.0214 (0.010)	0.466
b(diameter)	*Dichrostachys cinerea*	2.9-4.3	0.5-2.2	-0.0059 (0.014)	0.441
b(diameter)	*Dalbergia arbutifolia*	1.8-24.7	0.1-6.6	0.0214 (0.006)	0.416
b(diameter)	*Ehretia amoena*	1.9-3.5	0.2-1.5	0.0213 (0.014)	0.526
b(diameter)	*Vitex payos*	2.8-10.2	0.7-5.0	-0.0142 (0.010)	0.183
b(diameter)	*Grewia bicolor*	3.3-8.2	0.1-2.5	0.0038 (0.007)	0.734
b(diameter)	*Bauhinia petersiana*	2.8-9.7	0.3-3.2	-0.0069 (0.010)	0.348
b(diameter)	*Margaritaria discoidea*	3.7-12.2	0.1-3.0	0.0026 (0.010)	0.703
b(diameter)	*Bridelia scleuroneura*	3.7-7.2	0.5-3.6	0.0043 (0.014)	0.804
b(diameter)	*Canthium pseudoverticillatum*	1.9-25.5	0.2-4.8	0.0150 (0.008)	0.709
b(diameter)	*Grewia forbesii*	3.2-8.3	0.4-1.8	-0.0012 (0.010)	0.542
b(diameter)	*Vangueria infausta*	2.7-4.3	1.1-3.0	-0.0097 (0.014)	0.337
b(diameter)	*Psychotria schummaniana*	3.9-7.9	0.2-2.7	-0.0307 (0.014)	0.054
b(diameter)	*Premna holstii*	2.6-10.5	0.1-3.8	0.0242 (0.010)	0.375
b(diameter)	*Ximenia caffra*	2.5-5.1	0.2-1.3	-0.0082 (0.014)	0.378

[†] Letters in brackets (*a*) and (*b*) indicate regression parameters. Model 2: $Y = a + bD$, where Y is density (g/cm^3) and *D* is disk diameter in cm. Dbh is diameter at breast height; RMSE is standard

deviation of the residuals; σ_m is the standard deviation of the random effect of shrub (between shrub variations); R^2_{LR} is the likelihood ratio based coefficient of determination. The total number of individuals, N, for each species and the total number of stem disks, n, are listed in Table 1, except for *D. arbutifolia* where $N = 6$, $n = 29$. These individuals were purposely selected to fill-in diameter classes which were otherwise not represented in the dataset.

4. DISCUSSION

The basic densities of wood and bark presented for 44 species in Table 1 can be used to improve the estimation of biomass and subsequently carbon content for individual species (Brown et al., 1989; Chave et al., 2003). However, given the high diversity of species in the miombo woodlands and due to lack of wood basic density values of many species in this ecosystem, average values estimated at the genus level frequently need to be applied as proxies for true individual-species estimates. Studies in neo-tropical forest indicate that 72 - 74% of the variation in wood basic density can be accounted for by genus-level estimates (Baker et al., 2004; Chave et al., 2006), so consequences for the quality of forest-level biomass estimates may be limited. Alternatively, an average basic density estimated for a mixed species group, such as trees or shrubs, or a joint average estimated for the community of woody plants (trees and shrubs), can be considered in cases where species-specific density data are not available (Brown et al., 1989; Baker et al., 2004). The basic density models developed in this study can also be of assistance in estimation of basic densities for specific species or for species groups such as trees or shrubs in cases where species-specific density data are not available. However, due to the large variation between sites with regard to species composition and the effect of site conditions on basic density, care should be taken to do this only for sites characterised by conditions similar to GVLFR. Ideally the basic density models should be validated properly for the site in question, but while this may be a manageable task for individual species it is presumably infeasible for species groups.

The comparison between the wood basic densities reported in this study for different species and the values reported by other studies conducted in miombo areas (Appendix 1), showed a weak correlation ($r = 0.42$) and linear relationship ($R^2 = 0.17$) between the two datasets. In part, the low correlation could be due to variation between sites. Another partial reason may be that many values reported in the literature were not measured on disks cut directly from trees/shrubs but on clear specimens cut from planks or boards. This implies that they contain no (heavy) knots, no (usually light) bark, and a higher percentage of heartwood than stem disks. Also, some of the values reported in the literature are presumably not basic densities including bark (dry weight per fresh volume on bark) but either basic density excluding bark (dry weight of clear specimen per fresh volume of clear specimen) or dry density of specimens (dry weight per dry volume). All of these issues could have contributed to the deviations observed. Out of 77 species recorded in GVLFR, density estimates could only be found for the exact same species in 30 cases; in 37 cases estimates were either available for the genus or for a closely related species, and in 10 cases no records were available for the exact species or for related species (Appendix 1).

The value of basic density estimates, such as those reported in this paper and in Appendix 1, partly depends on their application in biomass models. We therefore tested a few biomass models for trees and shrubs, including and not including basic density as a predictor (Table 6). It turned out that biomass estimates made using equations 1 and 2, which do not include basic density as a predictor, turned out to have a larger average percentage error than equation 3 which does include basic density as a predictor. The high average percentage error observed for equation 4 could be partly due to large deviation between the densities in the calibration sample and the GVLFR sample as none of species included in the model calibration dataset were from Africa. Moreover, the fact that equation 4 is a third-order polynomial in ln(Dbh) may also contribute to the large percentage error as this is likely to make the model very sensitive to specific characteristics of the calibration sample. The patterns observed in Table 6 seem to agree with the remark made by

Chave et al. (2005) and Henry et al. (2010) that selection of an appropriate allometric equation and the use of wood basic density for specific species tends to improve accuracy in biomass estimation and, hence, carbon content in trees.

Table 6. Biomass equations and their average percentage error showing levels of accuracy in estimating total aboveground biomass of 44 species sampled in the Gangalamtumba Village Land Forest Reserve. The percentage error was calculated as: $100\% \times (Y_{predicted} - Y_{measured})/ Y_{measured}$, where Y is the biomass of the tree.

S/No.	Equation	Avg. error (%)	Source
1.	$ln(Y) = -2.6896 + 1.9041 ln(Dbh) + 0.9377 ln(ht)$. Where: Dbh range (cm):1.4-62; N = 104; RMSE = 0.182	8.96	Mwakalukwa et al., 2014b
2.	$Y = 0.0763 Dbh^{2.2046} ht^{0.4918}$ Where: Dbh range (cm): 1.1-110; N = 167	9.75	Mugasha et al., 2013
3.	$ln(Y) = -8.8819 + 0.9497 ln(wd\, Dbh^2\, ht)$. Where: Dbh range (cm):1.4-62; N = 104; RMSE = 0.187; *wd* = wood density	7.81	Mwakalukwa et al., 2014b
4.	$Y = wd \times exp(-0.667 + 1.784\, ln(Dbh) + 0.207(ln(Dbh))^2 - 0.0281(ln(Dbh))^3)$. Where: Dbh range (cm): 5-63.4; *wd* = wood density	59.3	Chave et al., 2005

Note: Height range for species found in Table 1: 2.5-18.2 m; RMSE is standard error of the residuals; Avg. is Average; *Y* is biomass (kg); *Dbh* is diameter at breast height (cm); *ht* is total height (m); *wd* is wood density (g/cm^3).

5. CONCLUSIONS

This study for the first time provides a comprehensive pool of different models for estimating wood basic density both for selected individual species found in the dry miombo woodlands of Tanzania and for mixed species groups of trees and shrubs. The estimates and models prepared in this study include a considerable number of the species common to dry miombo and they should therefore be useful for estimation of density and woody biomass for forests with similar species composition and climatic conditions, particularly in cases where only volume estimates are available or when it is considered useful to use biomass models including basic density as a predictor.

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Appendix 1: Wood basic densities of species enumerated in the GVLFR, estimated in this study and in the literature (direct species match).

S/No.	Scientific name	Local Name (In Hehe)	Family	This study (g/cm^3)	From the Literature (g/cm^3)	Source
	Trees					
1.	*Acacia drepanolobium* (Harms)	Mboliboli	Mimosaceae		0.640	Drichi, 1992
2.	*Acacia mellifera* (Vahl) Benth.	Mkambala	Mimosaceae	0.847	0.947	Zanne et al., 2009
3.	*Acacia seyal* Del. Var. seyal	Mubata	Mimosaceae	0.755	0.750	FAO, 1969
	Acacia seyal Del. Var. seyal	Mubata	Mimosaceae	0.755	0.658	Prota, 2014a
	Acacia seyal var. fistula	Mubata	Mimosaceae	0.755	0.840	FAO, 1969
	Acacia sp.	Mkungugu	Mimosaceae	0.749		
4.	*Afzelia quanzensis*	Mkora	Caesalpiniaceae	0.693	0.945	Bryce, 1967
	Afzelia quanzensis	Mkora	Caesalpiniaceae	0.693	0.830	Hamza et al ., 2000
	Afzelia quanzensis	Mkora	Caesalpiniaceae	0.693	0.832	Hamza et al ., 2001
	Afzelia quanzensis	Mkora	Caesalpiniaceae	0.693	0.830	Hamza et al ., 2004
	Afzelia quanzensis	Mkora	Caesalpiniaceae	0.693	0.832	Mosha, 1999
5.	*Albizia amara* (Roxb.) Boiv.	Mulagavega	Mimosaceae		1.020	FAO, 1969
	Albizia amara (Roxb.) Boiv.	Mulagavega	Mimosaceae		0.677	Ishengoma et al., 2000
6.	*Albizia petersiana* (Belle) Oliv.	Mkalala	Mimosaceae	0.819	0.640	Drichi, 1992
	Albizia petersiana (Belle) Oliv.	Mkalala	Mimosaceae	0.819	0.470	Mwampamba, 2009
	Albizia petersiana (Belle) Oliv.	Mkalala	Mimosaceae	0.819	0.790	Mwampamba, 2009
7.	*Berchemia discolor*	Mujganga	Rhamnaceae		0.864	Bangura et al., 2001
8.	*Boscia angustifolia* A. Rich var. *angustifolia*	Muwisa	Capparaceae		0.640	Drichi, 1992
9.	*Brachystegia boehmii*	Muyombo	Caesalpiniaceae	0.751	0.864	Bryce, 1967
	Brachystegia boehmii	Muyombo	Caesalpiniaceae	0.751	0.740	Malimbwi et al., 1994
	Brachystegia boehmii	Muyombo	Caesalpiniaceae	0.751	0.660	Mwampamba, 2009
	Brachystegia boehmii	Muyombo	Caesalpiniaceae	0.751	0.560	Mwampamba, 2009
10.	*Brachystegia bussei* Harms	Mtelela	Caesalpiniaceae	0.764	0.694	Bangura et al., 2001
	Brachystegia bussei Harms	Mtelela	Caesalpiniaceae	0.764	0.694	Bryce, 1967
11.	*Brachystegia manga*	Mugusi	Caesalpiniaceae	0.803		
12.	*Brachystegia spiciformis* Benth	Mkwee	Caesalpiniaceae	0.785	0.817	Bangura et al., 2001
	Brachystegia spiciformis Benth	Mkwee	Caesalpiniaceae	0.785	0.801	Bryce, 1967
	Brachystegia spiciformis Benth	Mkwee	Caesalpiniaceae	0.785	0.830	Mwampamba, 2009
	Brachystegia spiciformis Benth	Mkwee	Caesalpiniaceae	0.785	0.610	Mwampamba, 2009
13.	*Burkea africana* Hook	Msangala	Caesalpiniaceae		0.945	Bryce, 1967
	Burkea africana Hook	Msangala	Caesalpiniaceae		1.020	FAO, 1969
14.	*Cassia abbreviata*	Mmulimuli	Caesalpiniaceae	0.784	0.883	Zanne et al., 2009

S/No.	Scientific name	Local Name (in Hehe)	Family	This study	From the Literature	Source
	Trees			(g/cm^3)	(g/cm^3)	
15.	*Cassipourea mollis* (R.E.fr.) Alstom	Mbumila	Rhizophoraceae	0.681		
16.	*Codyla densiflora*	Mkwata	Caesalpiniaceae	0.719		
17.	*Combretum molle* G. Don	Mlama	Combretaceae	0.805	0.758	Zanne et al., 2009
18.	*Combretum zeyheri* Sond	Mlyasenga	Combretaceae	0.764	0.650	Kamelarczyk, 2009
19.	*Commiphora africana*	Mtono - Kijani	Burseraceae	0.375	0.276	Zanne et al., 2009
	Commiphora mollis	Mtono - Mweusi	Burseraceae	0.381		
	Commiphora mossambicensis	Mtono - Matiti	Burseraceae	0.347		
	Commiphora ugogensis	Mkongolo	Burseraceae	0.410		
20.	*Dalbergia boehmii*	Mnywenywee	Fabaceae		0.790	Mwampamba, 2009
21.	*Dalbergia melanoxylon*	Mpingo	Fabaceae		1.282	Bryce, 1967
22.	*Diplorynchus condylocarpon*	Mfilafila	Apocynaceae	0.541	0.630	Malimbwi et al., 1994
23.	*Elaeodendron buchanannii*	Mwambi	Celastraceae		0.800	Prota, 2014b
24.	*Erythrina abyssinica*	Muhemi	Fabaceae		0.426	Zanne et al., 2009
25.	*Euphorbia candelabrum*	Mlangali	Euphorbiaceae		0.270	Drichi, 1992
	Euphorbia candelabrum	Mlangali	Euphorbiaceae		0.670	FAO, 1969
26.	*Hymenodictyon parvifolium* Oliv.	Mdeke	Rubiaceae	0.399	0.640	Drichi, 1992
27.	*Julbernardia globiflora*	Mpinati	Caesalpiniaceae	0.775		
28.	*Kigelia africana*	Mfumbi	Bignoniaceae		0.564	Zanne et al., 2009
29.	*Lannea schweinfurthii*	Mgulumo	Anacardiaceae	0.584	0.551	Zanne et al., 2009
30.	*Lonchocarpus capassa*	Mtabagila	Fabaceae	0.768	0.758	Zanne et al., 2009
31.	*Manilkara mochisia*	Mdide	Sapotaceae	0.852	1.076	Zanne et al., 2009
32.	*Markhamia obtusifolia*	Muguvani	Bignoniaceae	0.620	0.780	Kamelarczyk, 2009
33.	*Ozoroa insigns* ssp. reticulata	Muwotaponzi	Anacardiaceae		0.561	Bryce, 1967
	Ozoroa insigns ssp. reticulata	Muwotaponzi	Anacardiaceae		0.640	Drichi, 1992
	Ozoroa insigns ssp. reticulata	Muwotaponzi	Anacardiaceae		0.620	Drichi, 1992
34.	*Pterocarpus angolensis*	Mninga	Fabaceae		0.625	Bryce, 1967
	Pterocarpus angolensis	Mninga	Fabaceae		0.657	Hamza et al ., 2001
	Pterocarpus angolensis	Mninga	Fabaceae		0.657	Ishengoma et al., 1998
	Pterocarpus angolensis	Mninga	Fabaceae		0.510	Malimbwi et al., 1994
	Pterocarpus angolensis	Mninga	Fabaceae		0.657	Munishi and Shear, 2004
	Pterocarpus angolensis	Mninga	Fabaceae		0.590	Mwampamba, 2009
	Pterocarpus angolensis	Mninga	Fabaceae		0.710	Mwampamba, 2009
35.	*Pterocarpus tinctorius*	Mninga maji	Fabaceae		0.900	Prota, 2014c
36.	*Sclerocarrya birrea* sbsp. birrea	Mubwegele	Anacardiaceae	0.579	0.545	Bryce, 1967b

S/No.	Scientific name	Local Name (In Hehe)	Family	This study (g/cm³)	From the Literature (g/cm³)	Source
	Trees					
37.	*Shrebera trichoclada*	Mwahama	Oleaceae		0.801	Zanne et al., 2009
38.	*Steganotaenia araliacea*	Mnyongamembe	Apiaceae		0.370	Drichi, 1992
39.	*Strychnos innocua*	Mubaya	Loganiaceae		0.870	Zanne et al., 2009
40.	*Strychnos potatorum* L. f	Mparapande	Loganiaceae		0.731	Zanne et al., 2009
41.	*Tamarindus indica*	Mnyali	Caesalpiniaceae		0.865	Bryce, 1967
	Tamarindus indica	Mnyali	Caesalpiniaceae		0.875	Drichi, 1992
	Tamarindus indica	Mnyali	Caesalpiniaceae		1.050	FAO, 1969
42.	*Terminalia brownii*	Mdwendwe	Combretaceae	0.807	0.640	Drichi, 1992
43.	*Terminalia sericea*	Mpululu	Combretaceae		0.920	Prota, 2014d
44.	*Xeroderris stuhlmannii*	Mvembadanda	Fabaceae	0.631	0.817	Bryce, 1967
45.	*Zanha africana* (Radlk.) Exell	Kivanga	Sapindaceae		0.801	Bryce, 1967b
46.	*Ziziphus mucronata*	Mtanangwe	Rhamnaceae		0.640	Drichi, 1992
47.	*Acacia abyssinica* (Hochst)	Mgunga	Mimosaceae	No record		
48.	*Albizia harveyi* Fourn.	Msisina	Mimosaceae	No record		
49.	*Combretum aculeatum*	Mgombwani	Combretaceae	No record		
50.	*Diospyros usambarensis* F. White	Mdaha	Ebenaceae	No record		
	Shrubs/small trees					
51.	*Bauhinia petersiana*	Mkombiwawe	Caesalpiniaceae	0.668	0.689	Zanne et al., 2009
52.	*Bridelia scleuroneura* Muell.Arg.	Mnyaluhanga	Euphorbiaceae	0.722	0.750	Drichi, 1992
53.	*Canthium pseudoverticillatum* Hien	Mnyalupuko	Rubiaceae	0.758		
54.	*Catunaregam spinosa* (Thunb.)	Mpongolo	Rubiaceae		0.688	Zanne et al., 2009
55.	*Dalbergia arbutifolia*	Mgiha	Papilionaceae	0.815		
56.	*Dichrostachys cinerea* (L.) Wight & Arn	Mgegele	Mimosaceae	0.682	0.780	Malimbwi et al., 1994
57.	*Ehretia amoena*	Mgosa	Boraginaceae	0.757	0.440	Mwampamba, 2009
58.	*Euclea divinorum* Hiern	Muhekele	Ebenaceae		0.775	Zanne et al., 2009
59.	*Flueggea virosa* Willd.	Mkwambe	Euphorbiaceae		0.670	Drichi, 1992
60.	*Grewia bicolor*	Mkole	Tiliaceae	0.716	0.670	Drichi, 1992
	Grewia bicolor	Mkole	Tiliaceae	0.716	0.940	FAO, 1969
61.	*Grewia forbesii* Haw. Ex Mast	Mpelemele	Tiliaceae	0.691	0.450	Mwampamba, 2009
62.	*Maerua angolensis*	Mwimakigulu	Capparaceae		0.640	Drichi, 1992
63.	*Maerua triphylla* A. Rich.	Mtosi	Capparaceae		0.640	Drichi, 1992
64.	*Margaritaria discoidea* (Bail.)	Mmemenamene	Euphorbiaceae	0.716	0.803	Zanne et al., 2009
	Margaritaria discoidea (Bail.)	Mmemenamene	Euphorbiaceae	0.716	0.636	Zanne et al., 2009
65.	*Opilia amentacea* Roxb.	Lukokonza	Opiliaceae	0.785		

S/No.	Scientific name	Local Name (In Hehe)	Family	This study	From the Literature	Source
	Trees			(g/cm^3)	(g/cm^3)	
66.	*Ormocarpum kirkii*	Kitimbwi	Fabaceae	0.725	0.742	Zanne et al., 2009
67.	*Premna holstii* Gurke	Mteresi	Verbenaceae	0.805		
68.	*Psychotria schummaniana*	Msasamulo	Rubiaceae	0.532		
69.	*Vangueria infausta* Burch. Ssp. Rotundata	Msambalawe	Rubiaceae	0.669	0.689	Zanne et al., 2009
70.	*Vitex payos*	Mkoga	Verbenaceae	0.613		
71.	*Ximenia caffra* Sond	Mtundwa	Olacaceae	0.669	0.640	Drichi, 1992
72.	*Allophyllus ferrugineus* Taub.	Mlichefu	Sapindaceae	No record		
73.	*Vernonia amygdalina*	Mvelevele	Asteraceae	No record		
74.	*Cordia sinensis* Lam	Mdavi	Boraginaceae	No record		
75.	*Gardenia resiniflua* Hiern.	Msanzi	Rubiaceae	No record		
76.	*Euphorbia cuneata* Valh.	Mlimbo	Euphorbiaceae	No record		
77.	*Excocaeria bussei* (Pax)	Mnyeng'enyeng'e	Euphorbiaceae	No record		

PAPER III

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Research Article

Volume and Aboveground Biomass Models for Dry Miombo Woodland in Tanzania

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Tools to accurately estimate tree volume and biomass are scarce for most forest types in East Africa, including Tanzania. Based on a sample of 142 trees and 57 shrubs from a 6,065 ha area of dry miombo woodland in Iringa rural district in Tanzania, regression models were developed for volume and biomass of three important species, *Brachystegia spiciformis* Benth. ($n = 40$), *Combretum molle* G. Don ($n = 41$), and *Dalbergia arbutifolia* Baker ($n = 37$) separately, and for broader samples of trees (28 species, $n = 72$), shrubs (16 species, $n = 32$), and trees and shrubs combined (44 species, $n = 104$). Applied independent variables were log-transformed diameter, height, and wood basic density, and in each case a range of different models were tested. The general tendency among the final models is that the fit improved when height and wood basic density were included. Also the precision and accuracy of the predictions tended to increase from general to species-specific models. Except for a few volume and biomass models developed for shrubs, all models had R^2 values of 96–99%. Thus, the models appear robust and should be applicable to forests with similar site conditions, species, and diameter ranges.

1. Introduction

Standing volume and aboveground biomass (AGB) are the two main measures of forest stocking that are typically considered within the framework of sustainable forest management and for carbon accounting purposes [1, 2]. Accurate estimation of tree volume and forest biomass is not only crucial for assessing expected yields from commercial and subsistence harvesting. It is also important for carbon storage assessment in relation to global climate change mitigation measures [3, 4]. For this purpose, forest biomass can be applied to estimate carbon stocks and carbon fluxes when measured repeatedly, thus providing means for estimating the amount of carbon dioxide released into or removed from the atmosphere.

However, direct measurement of volume and AGB is time consuming, costly, and usually destructive by nature. Therefore, the general practice is to estimate volume and AGB from tree dendrometric characteristics such as diameter and height, using established, general, or site-specific allometric equations [1, 3, 5, 6]. The selection of an appropriate allometric equation is a key element in the accurate estimation of forest yield and stand productivity as well as carbon stocks and changes in stocks [7, 8]. Unfortunately, such equations often produce biased results when applied outside the forest area or region where they were developed. If high accuracy is required for quantification and verification of a particular forest's carbon storage or for other management purposes, it is therefore recommended to develop local biomass and volume equations or at least to harvest and measure a few trees, representing the range of tree sizes typically found in the forest, and use these to check the validity of the applied equation under local conditions [1, 9, 10].

In eastern, central, and southern Africa, where miombo woodland is the principal vegetation type, only few studies of this nature have been conducted and tools for accurate estimation of forest volume and biomass and for carbon accounting purposes are generally lacking [10–12]. In Tanzania, two studies have developed biomass models using data from a relatively dry miombo woodland site at Kitulanghalo Forest Reserve in Morogoro Region, eastern Tanzania, which receives an annual rainfall of about 900 mm year^{-1} [13, 14]. These studies were conducted on the basis of a very limited sample size (<30 trees) covering a narrow diameter range (1.1–50 cm). Recent work by Mugasha et al. [15] covers a wider range of sites (four dry and one wet miombo sites). Yet it only includes a few more trees per site in the three relatively dry miombo woodland sites, 40 trees in Manyara Region, northeastern Tanzania (854 mm year^{-1}), 40 trees in Katavi Region, western Tanzania (881 mm year^{-1}), and 40 trees in Tabora Region, western central Tanzania (771 mm year^{-1}). In addition, the number of species used in developing site-specific models was very low, for example, 10 species for the Manyara site, but the general, countrywide model had adequate species richness (>45 different species). Having included trees from wet miombo sites which have different growth habits compared to those found in typical dry miombo areas and considering the large site differences across miombo woodlands with respect to climate, soil, altitude, land form, species composition, and historical land use, there appears to be a strong need for developing models for sites that receive very little precipitation, such as the areas in Iringa Region, south central Tanzania, (617 mm year^{-1}) to increase the accuracy of predicted stand volume, biomass, and carbon stock in such site types.

Miombo woodlands consist of open, light stands of a deciduous or semideciduous nature, with up to three vegetation strata, upper canopy trees, secondary layer (including the shrub layer, <8 m tall), and herbaceous layer which consists chiefly of grasses up to 2 m tall [16]. The upper canopy trees can reach heights of 14–20 m while trees of the secondary layer may reach 8–12 m. Understory shrubs are multistemmed due to fire or stem cutting and tend to cover up to 70% of the ground. This vegetation is an important source of fuel wood for the majority of people living in miombo areas and, due to the large areas that it covers, the carbon stocks and sequestration potential of the woodland are high [17, 18]. Unfortunately, previous studies in the miombo did not include biomass models for understory species (shrubs) [13–15].

Although with some limitations due to the large number of species in tropical forests, species-specific volume and biomass models are often preferred for accurate estimation of forest volume and biomass and for carbon accounting purposes [19, 20]. This type of models has been developed for a wide range of plantation species and in temperate regions where the number of relevant tree species is lower. However, most types of tropical vegetation are characterized by dominant species, so it has been suggested to develop a database of allometric equations for selected dominant tree species which are particularly important for volume and biomass estimates as they contribute a large proportion of the biomass compared to other species [21]. In Tanzania, species-specific volume functions have been prepared for a few dominant miombo species in Tabora in the western part of the country [22, 23] and elsewhere [24]. These studies were, however, also based on a very small sample size (<27) and a narrow diameter range (<43 cm).

Wood density is a key variable in the estimation of tree biomass [25, 26]. However, none of the above studies have reported biomass models, which take into account the contribution of wood basic density in explaining the variation in tree/shrub biomass. Inclusion of wood density in biomass modelling has been shown to improve the performance of the models significantly [25, 26].

Accordingly, the objectives of this study were to (1) develop volume and AGB allometric equations for three dominant species (*Brachystegia spiciformis* Benth., *Combretum molle* G. Don, and *Dalbergia arbutifolia* Baker) and (2) develop general equations for three life form groups: trees, shrubs, and woody species in general (trees and shrubs combined). The new models will not only help increase our knowledge on total aboveground productivity of miombo woodlands but also support planning, assessment, and development of management strategies for sustainable utilization of the woodlands. Furthermore, the local biomass models developed in this paper will not only add to existing knowledge about the miombo but also support the nation of Tanzania in accurate estimation and reporting of current forest biomass stocks and their changes over time.

2. Materials and Methods

2.1. Study Site. Gangalamtumba Village Land Forest Reserve (GVLFR) is located in central-southern Tanzania (7°35′ S, 35°35′ E), about 30 km northwest of Iringa Municipality, the administrative capital of Iringa Region (Figure 1). The area of the forest is 6,065 hectares and it is managed by the Mfyome village, which is located in the ward of Kiwele. The forest can be described as dry miombo woodland and the terrain is relatively flat and located 850–1,300 metres above sea level. The average annual rainfall is (mean ± standard error) 617 ± 17 mm (range: 448–1,085 mm) and the mean annual temperature is 19.8°C. The soil texture ranges from sandy soils at low elevations to sandy clay loams at higher elevations with pH from 5.7 to 8.7. GVLFR is a production forest which allows some commercial forest activities, including charcoal production, firewood collection, and livestock grazing mainly during the dry season.

2.2. Field Sampling. The survey was conducted in August 2009 and September-October 2010 and involved harvesting of 142 individual trees (28 species) and 57 individual shrubs (16 species) from a 30 m wide boundary zone of 35 permanent circular sample plots with a radius of 50 m (0.7854 ha) that were distributed across the entire area of the GVLFR (Figure 1). Plots were located along transect lines and the distance between plots was about 2 km. The centre points of the plots are identical to those used in a survey that was previously conducted in the forest [27]. The minimum and maximum sizes of sample trees/shrubs were 1.4 cm and 62.0 cm in diameter at breast height (Dbh), respectively. For

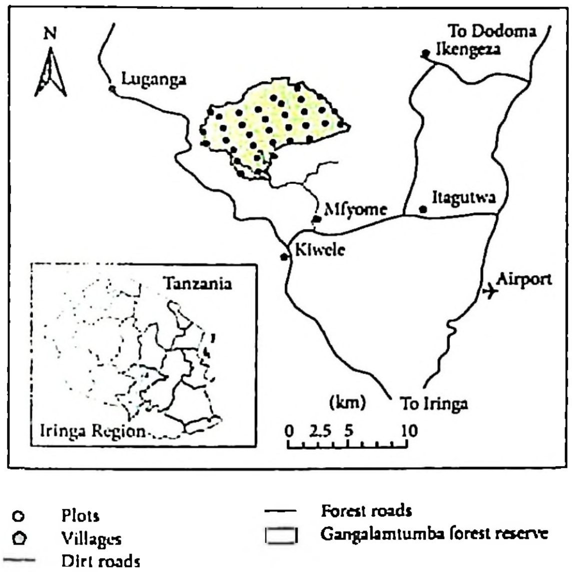


Figure 1: Map of the study area and its location in Iringa Region, Tanzania.

each tree or shrub felled, the following measurements were made: stump diameter 20 cm above ground, Dbh, crown radius in four directions (north, south, west, and east), height to first branch, and total height. Diameter was measured to the nearest 0.1 cm using a diameter tape, height was measured using a Suunto clinometer, and crown width was measured to the nearest 0.01 m by tape measure. Species were identified by a local botanist using vernacular names in the Hehe language. Scientific identification was done by a botanist from the herbarium centre at the Silviculture Research Station in Lushoto, which is part of Tanzania Forest Research Institute (TAFORI). In cases where it proved difficult to identify a species in the field, voucher specimens were collected and sent to the herbarium in Lushoto for identification.

Based on their estimated relative basal area, 44 species (both trees and shrubs) were selected as a representative sample of the most common species. This selection was meant to cover the widest possible range of diameter classes as recommended by, for example, Brown [1] and Husch et al. [3]. Furthermore, to distribute the sample across the forest, at least 3 trees and 2 shrubs were felled within each of the 35 plots. To support data quality checking and error correction, a sketch of the crown structure of each tree/shrub was prepared in the field and used for marking points of cross-cutting. Generally, the choice of upper diameter limit depends on the utilisation of the wood. In this region an important use of the wood is for charcoal production and few tree species are used for timber production. The typical top diameter applied by charcoal makers in the area appears to be 5 cm, and we therefore prepared models for total volume and biomass and for commercial volume of stems with diameter ≥5 cm.

In the field, small branches with diameter less than 5 cm were first removed, tied into bundles (piles), and weighed (fresh weight). Subsamples of these piles were selected and brought to the laboratory for dry weight determination. For each tree/shrub, five disks with a thickness of about 2-3 cm were sampled from the remaining part of the tree/shrub (≥5 cm diameter). These were used for basic density estimation and their green/fresh weight was measured in the field. Selection of the five disks was based on importance sampling, for example, [5, 28], implying that the selection of tree sections in which the disks were to be extracted depended on the estimated proportion of volume in each section (probability of selection proportional to volume). This method has been found to yield relatively good results with minimal errors and bias compared to the conventional method of sectional weight measurements in the field, which is often costly in terms of labour and time [5].

2.3. Laboratory Analyses. In the laboratory, all subsamples for twigs/branches <5 cm (crown wood) and disks extracted from stem and branch sections were oven dried at 103 ± 2°C to constant weight. Dried samples were weighed and the biomass ratio for each pile of twigs/branches was computed as the ratio of oven-dry weight to green weight [5, 13]. Green volume of the sample disks was obtained after soaking the disks in water for at least four days until they were saturated. Using the water displacement method, the volume of each disk was determined [1, 29]. Basic density ($\mathrm{g\,cm^{-3}}$) for each disk was determined as the ratio of dry weight (g) to green volume ($\mathrm{cm^3}$).

2.4. Data Preparation. For each tree, the stump volume was calculated using the cylinder formula and the volume of stem sections and branches with diameter ≥5 cm was calculated using Newton's formula. The volume of twigs/branches <5 cm in diameter was estimated using their estimated biomass and the estimated basic density [30]. Commercial volume ≥5 cm was estimated as the sum of stump volume and the volumes of stem and branch sections to 5 cm top diameter. Total volume was calculated by adding the estimated volume of branches <5 cm to the commercial volume. This dataset was used for developing volume models for each group of species: (1) *B. spiciformis*, (2) *C. molle*, (3) *D. arbutifolia*, (4) shrubs/small trees, (5) trees, and (6) all species (trees and shrubs).

Biomass (kg) was calculated as the product of density ($\mathrm{kg\,m^{-3}}$) and volume ($\mathrm{m^3}$) for stem and branch sections [5, 28]. For twigs and leaves, biomass was estimated as the product of estimated biomass ratio (dry to green weight of subsamples) and total green weight (kg) of the pile measured in the field. The total aboveground biomass for each tree was obtained as the sum of stump biomass, biomass of stem and branch sections, and biomass of twigs and leaves. The resulting dataset was used for developing biomass models for each of the six species groups mentioned above.

2.5. Statistical Analysis. Like in other studies [3, 13, 31] several linear models with different transformations were tested during the development of volume and biomass models.

Table 1: Volume and biomass equations† for estimating total aboveground and stem (≥5 cm) volume and biomass of three dominant species in the Gangalamtumba Village Land Forest Reserve. All parameter estimates are significantly different from zero ($P < 0.001$).

Species	Component	Equation†	Regression parameters			Dbh range (cm)	Adj. R^2	RMSE	Avg. error (%)
			a	b	c				
Brachystegia spiciformis ($N = 40$)	Total volume (df = 37)	3	−9.3188 (0.166)	1.9663 (0.088)	0.9118 (0.174)	1.2–54.3	0.997	0.142	1.99
	(df = 38)	4	−8.5018 (0.077)	2.4142 (0.027)	—	1.2–54.3	0.995	0.185	3.49
	Stem volume (df = 31)	3	−11.7673 (0.379)	2.0335 (0.141)	1.6858 (0.314)	5–54.3	0.990	0.209	−0.02
	(df = 32)	4	−9.8909 (0.203)	2.7460 (0.066)	—	5–54.3	0.981	0.286	2.14
	Total biomass (df = 37)	3	−2.6071 (0.149)	2.0638 (0.078)	0.7847 (0.155)	1.2–54.3	0.998	0.127	1.60
	(df = 38)	4	−1.9040 (0.068)	2.4492 (0.024)	—	1.2–54.3	0.996	0.162	2.67
	(df = 38)	6	−9.3309 (0.108)	0.9827 (0.008)	—	1.2–54.3	0.998	0.127	1.66
	Stem biomass (df = 31)	3	−5.0668 (0.343)	2.1424 (0.128)	1.5563 (0.284)	5–54.3	0.992	0.189	−0.57
	(df = 32)	4	−3.3345 (0.185)	2.8002 (0.061)	—	5–54.3	0.985	0.262	1.17
Combretum molle ($N = 41$)	Total volume (df = 38)	3	−9.0504 (0.165)	1.9212 (0.099)	0.7712 (0.183)	2.2–26.5	0.987	0.171	2.90
	(df = 39)	4	−8.5247 (0.130)	2.2972 (0.051)	—	2.2–26.5	0.981	0.204	4.24
	Stem volume (df = 30)	3	−10.3990 (0.223)	2.0420 (0.126)	1.0908 (0.193)	5–26.5	0.977	0.146	4.64
	(df = 31)	4	−9.8028 (0.277)	2.6237 (0.102)	—	5–26.5	0.954	0.206	4.98
	Total biomass (df = 38)	3	−2.4539 (0.165)	1.9685 (0.099)	0.7545 (0.183)	2.2–26.5	0.987	0.170	2.88
	(df = 39)	4	−1.9395 (0.129)	2.3364 (0.050)	—	2.2–26.5	0.982	0.203	4.20
	(df = 39)	6	−8.8347 (0.230)	0.9371 (0.168)	—	2.2–26.5	0.987	0.170	2.98
	Stem biomass (df = 30)	3	−3.7737 (0.230)	2.1112 (0.130)	1.0410 (0.199)	5–26.5	0.976	0.151	4.41
	(df = 31)	4	−3.2047 (0.275)	2.6663 (0.101)	—	5–26.5	0.956	0.205	4.66
Dalbergia arbutifolia ($N = 37$)	Total volume (df = 34)	3	−9.3147 (0.191)	1.9701 (0.059)	0.8854 (0.152)	1.8–21.5	0.991	0.144	2.04
	(df = 35)	4	−8.3253 (0.120)	2.2413 (0.051)	—	1.8–21.5	0.982	0.200	3.90
	Stem volume (df = 29)	3	−13.8803 (0.761)	2.0113 (0.246)	2.7732 (0.455)	5–21.5	0.871	0.355	12.97
	(df = 30)	4	−10.5743 (0.793)	2.7785 (0.313)	—	5–21.5	0.715	0.528	32.87
	Total biomass (df = 34)	3	−2.7097 (0.199)	1.9900 (0.062)	0.9035 (0.159)	1.8–21.5	0.990	0.150	1.22
	(df = 35)	4	−1.7001 (0.124)	2.2667 (0.052)	—	1.8–21.5	0.981	0.206	3.00

Table 1: Continued.

Species	Component	Equation†	Regression parameters *a*	*b*	*c*	Dbh range (cm)	Adj. R^2	RMSE	Avg. error (%)
	(df = 35)	6	−9.3782 (0.213)	0.9823 (0.016)	—	1.8–21.5	0.990	0.148	1.37
	Stem biomass (df = 29)	3	−7.3073 (0.776)	2.0138 (0.250)	2.8503 (0.464)	5–21.5	0.869	0.362	11.53
	(df = 30)	4	−3.9094 (0.812)	2.8023 (0.321)	—	5–21.5	0.708	0.541	30.54
	(df = 30)	6	−14.5150 (1.467)	1.2961 (0.108)	—	5–21.5	0.823	0.421	17.00

[illegible] bers in brackets indicate standard errors of the parameter estimates. Height (range): *B. spiciformis*: 2–17.2 m; *C. molle*: 2.6–9.4 m; and *D. arbutifolia*: 2.[illegible].5 m. df is degrees of freedom; RMSE is the standard error of the residuals; Adj. R^2 is the adjusted coefficient of determination; Avg. is Average. †Equation (3): $\ln(Y) = a + b\ln(\text{Dbh}) + c\ln(\text{ht})$. Equation (4): $\ln(Y) = a + b\ln(\text{Dbh})$. Equation (6): $\ln(Y) = a + b\ln(wd\text{Dbh}^2\text{ht})$; Y is volume (m^3) or biomass (kg); Dbh is diameter at breast height (cm); ht is total height (m); and wd is wood density (kg m^{-3}).

The following general model formulations with logarithmic transformation of dependent and independent variables were tested:

(1) $\ln(Y) = a + b \times \ln(\text{Dbh}) + c \times \ln(\text{Dbh}^2) + d \times \ln(\text{ht}) + e \times \ln(\text{ht}^2)$,

(2) $\ln(Y) = a + b \times \ln(\text{Dbh}^2\,\text{ht})$,

(3) $\ln(Y) = a + b \times \ln(\text{Dbh}) + c \times \ln(\text{ht})$,

(4) $\ln(Y) = a + b \times \ln(\text{Dbh})$.

For species-specific volume and biomass models, we used ordinary least squares estimation, assuming that errors were normally and independently distributed, whereas models for groups of species (i.e., trees, shrubs, and both groups combined) were prepared using the following mixed linear model formulation:

(5) $\ln(Y)_{ij} = f(\text{Dbh}_{ij}, \text{ht}_{ij}) + v_i + \varepsilon_{ij}$.

In all models, Y is volume ($\text{m}^3\,\text{tree}^{-1}$) or biomass ($\text{kg}\,\text{tree}^{-1}$); Dbh is diameter at breast height (cm) and ht is total height of the tree/shrub (m); a, b, c, d, and e are model parameters; and ln is the natural logarithm. In model 5 i is species, j is tree number, $f(\text{Dbh}_{ij}, \text{ht}_{ij})$ is one of the model formulations 1–4, $v_i \sim N(0, \sigma^2_{\text{spe}})$ is a random species effect, and ε_{ij}s are random errors, $\varepsilon_{ij} \sim N(0, \sigma^2)$. Thus, for species groups, the between-species variation was modelled as a random effect.

Furthermore, to test the contribution of wood basic density in explaining the variation of biomass, the logarithmic version of the following power model $Y = \alpha \times (wd \times \text{Dbh}^2 \times \text{ht})^b$ was tested:

(6) $\ln(Y) = a + b \times \ln(wd \times \text{Dbh}^2 \times \text{ht})$, where wd is the wood basic density.

Prior to the regression analysis, dependent variables (volume and biomass) were plotted against each of the explanatory variables to examine the range and shape of the functional relationship and to assess the heterogeneity of the variance. Relationships were tested after transforming the variables. We selected our final models based on high adjusted R^2, low residual standard error (RMSE), and graphical analysis of the residuals. To assess the quality of the final models, we applied the approach also used by Chave et al. [25] and Djomo et al. [31], where the average percentage error between predicted and measured values is compared between the different equations after back-transforming to their original scale and correcting for logarithmic bias. The percentage error was calculated as

$$100\% \times \frac{Y_{\text{predicted}} - Y_{\text{measured}}}{Y_{\text{measured}}}, \quad (1)$$

where Y is the biomass or volume of the tree. The correction factor (CF) used for correcting for logarithmic bias was the one proposed by Sprugel [32], $\text{CF} = \exp(\text{RMSE}^2/2)$, which was applied to the predicted values of volume and biomass.

Finally, the average percentage error of the models prepared in this study was compared with that of ten previously published models when applied to the datasets from GVLFR. Correction for logarithmic bias was made in cases where dependent variables had been log-transformed. All analyses were made in Excel spreadsheets and R version 2.13.0 (http://www.r-project.org).

3. Results

3.1. Volume and Biomass Models. Selected models for total and stem volume and biomass of the three most dominant species are presented in Table 1. Similarly, Table 2 shows models for total and stem volume and biomass for the three species groups: shrubs, trees, and all species (trees and shrubs). The general tendency among the final models is that the fit improved when height and wood basic density were included in the model as indicated by the high adj. R^2, low residual standard error, and low average percentage error. However, the improvement of the fit achieved by including wood density was in most cases negligible and the performances of models 3 and 6 are therefore similar. As illustrated in Figure 2, the observations of total volume and biomass were nicely distributed around the values predicted by model 4 for shrubs, trees, and trees and shrubs combined and with only few outliers ending up outside (below) the

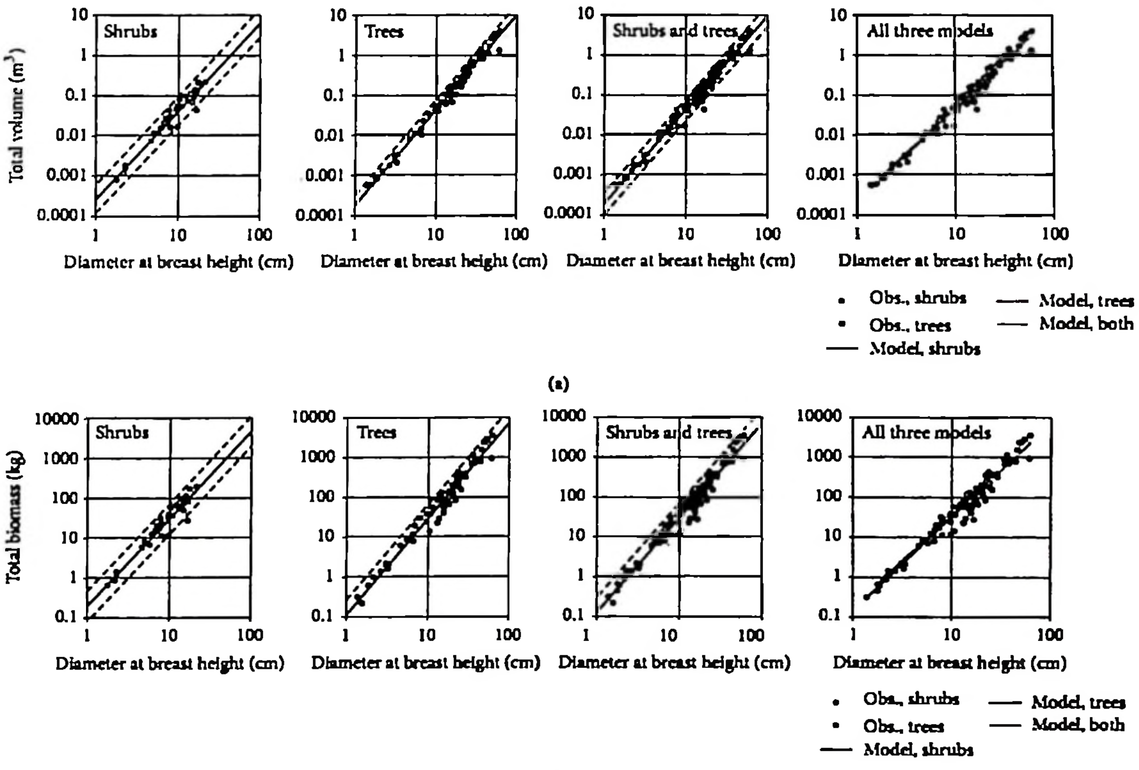
TABLE 2: Volume and biomass equations for estimating total aboveground and stem (≥5 cm) volume and biomass of shrubs, trees, and woody plants in general (shrubs and trees) in Gangalamtumba Village Land Forest Reserve. A few estimates are not significantly different from zero ($P > 0.05$). These are marked "ns."

Category	Component	Equation[1]	Regression parameters			Dbh range (cm)	R^2_{LR}	RMSE	σ_{spe}	Avg. error (%)
			a	*b*	*c*					
Shrubs (*N* = 32); 16 species	Total volume (df = 27)	3	−8.3287 (0.237)	2.2340 (0.099)	0.0507^{ns} (0.206)	1.8–21.5	0.979	0.251	0.00	18.48
	(df = 28)	4	−8.2844 (0.152)	2.2517 (2.252)	—	1.8–21.5	0.979	0.247	0.00	18.57
	Stem volume (df = 23)	3	−13.4822 (0.673)	1.7917 (0.316)	2.8547 (0.453)	5–21.5	0.865	0.533	0.00	30.34
	(df = 24)	4	−10.8001 (0.710)	2.6587 (0.299)	—	5–21.5	0.792	0.482	0.636	57.79
	Total biomass (df = 27)	3	−1.8567 (0.252)	2.2145 (0.106)	0.1591^{ns} (0.219)	1.8–21.5	0.977	0.267	0.00	21.90
	(df = 28)	4	−1.7179 (0.163)	2.2697 (0.073)	—	1.8–21.5	0.977	0.265	0.00	22.43
	(df = 28)	6	−8.6142 (0.427)	0.9417 (0.034)	—	1.8–21.5	0.968	0.266	0.184	18.93
	Stem biomass (df = 23)	3	−6.8855 (0.639)	1.9676 (0.257)	2.6083 (0.428)	5–21.5	0.916	0.390	0.276	29.50
	(df = 24)	4	−4.3236 (0.705)	2.6903 (0.296)	—	5–21.5	0.799	0.470	0.676	56.02
Trees (*N* = 72); 28 species	Total volume (df = 69)	3	−9.5238 (0.075)	1.8067 (0.040)	1.1940 (0.076)	1.4–62	0.997	0.129	0.00	1.66
	(df = 70)	4	−8.4800 (0.099)	2.3351 (0.033)	—	1.4–62	0.986	0.219	0.179	6.46
	Stem volume (df = 35)	3	−11.0643 (0.166)	1.9316 (0.079)	1.5360 (0.119)	5–62	0.994	0.162	0.00	4.55
	(df = 35)	4	−10.9307 (0.273)	3.0134 (0.093)	—	5–62	0.975	0.317	0.119	13.10
	Total biomass (df = 69)	3	−3.1399 (0.123)	1.7586 (0.057)	1.2934 (0.115)	1.4–62	0.992	0.118	0.278	2.47
	(df = 70)	4	−2.0667 (0.124)	2.3561 (0.036)	—	1.4–62	0.979	0.213	0.392	9.96
	(df = 70)	6	−9.1880 (0.101)	0.9668 (0.007)	—	1.4–62	0.996	0.131	0.052	1.32
	Stem biomass (df = 37)	3	−5.6032 (0.326)	2.1420 (0.158)	1.7090 (0.269)	5–62	0.965	0.294	0.221	6.30
	(df = 38)	4	−4.4622 (0.365)	2.9972 (0.120)	—	5–62	0.928	0.387	0.375	10.60
Combined (*N* = 104); 44 species	Total volume (df = 100)	3	−9.0339 (0.104)	1.9637 (0.053)	0.7737 (0.103)	1.4–62	0.989	0.193	0.131	6.54
	(df = 101)	4	−8.4554 (0.084)	2.3236 (0.031)	—	1.4–62	0.983	0.248	0.140	9.89
	Stem volume (df = 42)	3	−12.2617 (0.244)	2.1378 (0.127)	1.7695 (0.203)	5–62	0.977	0.271	0.153	18.50
	(df = 43)	4	−11.1929 (0.339)	3.0514 (0.115)	—	5–62	0.935	0.413	0.327	49.22
	Total biomass (df = 100)	3	−2.6896 (0.131)	1.9041 (0.064)	0.9377 (0.128)	1.4–62	0.983	0.182	0.317	8.96
	(df = 101)	4	−1.9564 (0.102)	2.3260 (0.035)	—	1.4–62	0.974	0.242	0.327	12.60

Table 2: Continued.

Category	Component	Equation[†]	Regression parameters			Dbh range (cm)	R^2_{LR}	RMSE	σ_{spc}	Avg. error (%)
			a	b	c					
	(df = 101)	6	−8.8819 (0.139)	0.9497 (0.010)	—	1.4–62	0.988	0.187	0.162	6.40
	Stem biomass (df = 42)	3	−5.9897 (0.279)	2.0894 (0.146)	1.9457 (0.238)	5–62	0.970	0.290	0.230	13.70
	(df = 43)	4	−4.8335 (0.349)	3.0979 (0.117)	—	5–62	0.924	0.383	0.488	43.10
	(df = 43)	6	−13.5156 (0.455)	1.2284 (0.032)	—	5–62	0.971	0.314	0.153	25.10

Note: numbers in brackets indicate standard errors of the estimates. Height range: shrubs 2.5–8 m; trees: 2.5–18.2 m; and combined: 2.5–18.2 m. df is degrees of freedom. RMSE is standard error of the residuals; σ_{spc} is the standard deviation of the species random effect (between-species variation); R^2_{LR} is the likelihood ratio based coefficient of determination; and Avg. is Average. [†]Equation (3): $\ln(Y) = a + b\ln(\mathrm{Dbh}) + c\ln(\mathrm{ht})$. Equation (4): $\ln(Y) = a + b\ln(\mathrm{Dbh})$. Equation (6): $\ln(Y) = a + b\ln(\mathrm{wdDbh}^2\mathrm{ht})$; Y is volume (m^3) or biomass (kg); Dbh is diameter at breast height (cm); ht is total height (m); and wd is wood density ($\mathrm{kg\,m^{-3}}$).



(a)

(b)

Figure 2: Model 4 for total volume (a) and biomass (b) of the three species groups: shrubs, trees, and shrubs and trees. First three columns: circles indicate observed values, unbroken lines show expected values, and dashed lines are 95% prediction intervals; fourth column: all three models (see legend).

95% prediction intervals. Furthermore, the graphs in Figure 2 illustrate that the differences between values predicted by models for the three life form groups are limited.

3.2. Model Performance. To some extent the overall performance of the volume and biomass models can be judged from the RMSE and R^2 values reported in Tables 1 and 2. In addition to these measures, both tables report the average percentage error after correction for logarithmic bias. As expected, species-specific models (Table 1) turned out to have lower average percentage error compared to models developed for the broader species groups (trees, shrubs, and trees and shrubs combined); see Table 2. When comparison was made between the average percentage error obtained by using species-specific models for volume and biomass prediction in the individual species datasets and the corresponding values obtained for the general, mixed species-group models (models prepared for trees applied to *B. spiciformis* and *C. molle* and models prepared for shrubs applied to *D. arbutifolia*), it emerged that the individual species-specific models produced considerably lower average percentage errors than the mixed species-group models (results not shown). A similar pattern was observed when models calibrated for trees and shrubs were applied to datasets including either trees or shrubs alone. For both volume and biomass, it emerged that model 4, which includes only one independent variable (Dbh), was characterised by larger average percentage errors than model 3 which includes two independent variables (Dbh and ht). Also, inclusion of wood basic density in the models (model 6) tended to improve the fit significantly as indicated by the high adj. R^2 and low residual standard error.

4. Discussion

The new volume and biomass models for individual species and for broader species groups (shrubs, trees, and both) provide a comprehensive range of tools for estimation of standing volume, aboveground biomass, and carbon stock of dry miombo vegetation in Tanzania. Since the number of sample trees and shrubs for the general model is relatively large and includes a large number of species (44 different species) compared to site-specific models reported elsewhere [13–15], the newly developed models are likely to be quite robust and can presumably be applied in areas with similar site conditions with only a limited increase of bias compared to locally calibrated models.

Not surprisingly, the species-specific volume and biomass models were superior to models prepared for species groups in terms of average percentage error. Similarly, models prepared for individual species groups (trees and shrubs separately) were superior to models prepared for the combined dataset including both trees and shrubs. Thus, the precision and accuracy of the predictions tends to increase from general (all species, trees, and shrubs) to species-specific (single species) models.

To assess the increase in accuracy achieved in GVLFR by the new models, 10 different previously published volume and biomass models for miombo woodlands were tested on the datasets prepared in this study. The models include five volume functions and five biomass functions and the calculated average percentage error obtained for each combination of model and dataset is shown in Table 3. In each case, model predictions were corrected for logarithmic bias, except for models 8, 9, and 16, for which no residual standard deviation (RMSE) was provided, and models 12, 13, 14, and 15 which are power models. When comparing the average percentage errors obtained for our models with those of the existing models, it turned out that both our species-specific models (Table 1) and species-group models (Table 2) yielded relatively low average percentage errors compared to the existing models. However, based on the average percentage errors, it also appeared that models 8, 9, 10, and 11 produced the most accurate estimates of volume for shrubs and, similarly, that models 9 and 10 yielded the lowest average percentage errors for volume in the combined dataset (trees and shrubs). Except for models prepared for the shrub species group (Table 2), which are characterised by relatively high average percentage errors, models prepared in this study produced better estimates of biomass with lower average percentage errors than the existing models. In part, this is a consequence of calibrating and testing our models on the same dataset, but it may also be related to the fact that the diameter ranges of the datasets applied in this study are considerably broader than those of the datasets used for calibrating the existing models from the literature. Mugasha et al. [15] observed a similar pattern of improved accuracy and precision of the predictions when comparing site-specific models to a general model. However, as shown in Table 3 models 14 and 15 (biomass) seem to work very well on the shrub dataset and the *C. molle* (tree) and *D. arbutifolia* (shrub) datasets as they are characterised by relatively low average percentage errors.

Considering the high species diversity found in the miombo woodlands, the variation of species composition from site to site, and the impact of site conditions on the shape of trees, the use of mixed-species regression models calibrated on data from sites with similar site conditions and species composition is a logical choice. By contrast, general allometric equations developed in other regions with different species composition should be used with caution and only if local mixed-species models are not available. Locally abundant species would usually not be represented in the databases used for development of such general allometric models and they therefore may not accurately reflect the true biomass of trees in a given forest area [1, 31, 33]. Therefore, the use of site-specific models is recommended to ensure that high precision is achieved in quantification of woodland resources [15].

The large percentage errors observed for the shrub dataset are presumably caused by the large variation of physical shapes characterising this category of woody plants. The dataset included 16 different shrub species, and some of them are characterised by very special stem and crown shapes and very low (or high) wood basic densities. This could explain the large variation observed in the volume and biomass for stems.

The value of species-specific models as a way to minimise variation and increase the accuracy of models should not go unmentioned. However, as explained, the high diversity of species in miombo woodlands and in most other tropical forest types combined with frequent challenges of correct botanical identification enhances the cost of preparing species-specific models with a view to improve the accuracy of standing volumes and biomass estimates at the forest level. Mixed-species models are, therefore, still useful but they should be applied with due consideration of the improved quality of volume/biomass estimates that can be obtained by the application of species-specific models.

Table 3: Average error in percent of measured values as observed for previously published volume and biomass equations for miombo woodlands when applied to species-specific and mixed-species datasets prepared in this study. Models developed in this study are included for comparison. Symbols: Y is volume (m^3) or biomass (kg); Dbh is diameter at breast height (cm); ht is total height (m); BA is basal area (cm^2); and N is sample size.

Model[†]	Source	Name of species	Average error in percent for the datasets prepared in this study					
			B. spiciformis	*C. molle*	*D. arbutifolia*	Shrubs	Trees	Combined
Model (3) = total volume $\ln(Y) = a + b\ln(\text{Dbh}) + c\ln(\text{ht})$	This study		*1.99*	*2.90*	*2.04*	*18.48*	*1.66*	*6.54*
(7) $\log_{10}Y = -3.85 + 2.49\log_{10}\text{Dbh}$ $N = 27$, Dbh: 8–40 cm	Abbot et al. [24]	*Brachystegia boehmii*	−10.73	21.76	12.01	29.98	8.44	15.34
(8) $\log_{10}Y(\text{litres}) = -1.2875 + 2.8436\log_{10}\text{Dbh}$ N = unknown, Dbh: 5–43 cm	Temu [22]	*Brachystegia spiciformis*	−6.03	17.12	0.12	2.82	10.48	7.45
(9) $Y = 0.092\text{Dbh}^{2.59}$ $N = 25$, Dbh: 6–61 cm	Malimbwi and Temu [23]	*Pterocarpus angolensis*	−21.16	4.45	−6.86	−1.11	−4.45	−3.64
(10) $\log_{10}Y = -4.22 + 2.76\log_{10}\text{Dbh}$ $N = 51$, Dbh: 5–40	Abbot et al. [24]	Mixed species (17 spp.)	−15.36	8.77	−5.7	−2.66	1.06	−0.20
(11) $Y = 0.0001\text{Dbh}^{2.032}\text{ht}^{0.66}$ $N = 17$, Dbh: 8–43 cm	Malimbwi et al. [13]	Mixed species (13 spp.)	−20.91	−1.94	−11.0	−7.45	−12.82	−11.26
Model (3) = total biomass $\ln(Y) = a + b\ln(\text{Dbh}) + c\ln(\text{ht})$	This study		*1.60*	*2.88*	*1.22*	*21.90*	*2.47*	*8.96*
(12) $Y = 0.06\text{Dbh}^{2.012}\text{ht}^{0.71}$ $N = 17$, Dbh: 8–43 cm	Malimbwi et al. [13]	Mixed species (13 spp.)	−38.56	−23.44	−30.61	−20.51	−8.07	−11.68
(13) $Y = 0.0263\text{Dbh}^{1.585}\text{ht}^{1.762}$ $N = 30$, Dbh: 1.1–50 cm	Chamshama et al. [14]	Mixed species (20 spp.)	−28.17	−33.17	−36.28	−41.81	−16.29	−24.46
(14) $Y = 0.1027\text{Dbh}^{2.4798}$ $N = 167$, Dbh: 1.1–110 cm	Mugasha et al. [15]	Mixed species (49 spp.)	−24.21	4.52	−6.81	8.85	21.19	17.39
(15) $Y = 0.0763\text{Dbh}^{2.2046}\text{ht}^{0.4918}$ $N = 167$, Dbh: 1.1–110 cm	Mugasha et al. [15]	Mixed species (49 spp.)	−20.38	−1.27	−11.09	−3.35	15.57	9.75
(16) $\log_{10}Y = -0.535 + \log_{10}\text{BA}$ $N = 191$, Dbh: 3–30 cm	Brown [1]	Mixed species (not indicated)	−50.02	−30.29	−35.91	−19.27	−19.04	−19.26

[†] For each model, the range of diameters in the material forming the basis for the model is specified.

5. Conclusion

This study for the first time provides a comprehensive pool of different allometric equations for estimating total and stem volume and biomass, for (i) selected individual species and (ii) for mixed-species groups found in the dry miombo woodlands of Tanzania. Since most of the models have higher R^2, lower RMSE, and lower average percentage error than the existing equations, these new models should be useful for providing reliable estimates of volume and biomass for forests with similar species composition and site conditions (soil and climate). Furthermore, the new models can be applied at all levels from the species-specific, individual-tree level to the stand level. Modelling the volume and biomass of shrubs turned out to be challenging, possibly due to the large variation of wood density and shape of stem and crown characterising this group. Further research on measures that could be used to improve volume and biomass estimates for shrubs would therefore be useful.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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PAPER IV

Modelling diameter growth of *Brachystegia spiciformis* in dry Miombo Woodland in Tanzania

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Abstract

Miombo woodlands cover vast areas in East and Southeast Africa and are important sources of wood products for rural and urban populations in the region. However only limited information is available on growth of Miombo tree species, which hampers efforts to assess sustainable extraction levels. Therefore the objectives of this study were to (1) assess whether *Brachystegia spiciformis* Benth., a species commonly used for charcoal production in the Miombo woodland areas, forms annual tree rings, (2) estimate the diameter increment of *B. spiciformis* using growth ring measurements, and (3) develop local diameter growth models for *B. spiciformis* using growth ring series. Stem disks were cut at 1.3 m above ground from 40 sample trees that were felled in Gangalamtumba village land forest reserve located in Iringa Rural District, Tanzania. Data on soil, elevation, slope, and competition were also collected. Competition was assessed for 25 of the sample trees by measuring all trees with diameter > 5 cm within a radius of 7.5 m around the sample trees. Several models describing the effects of factors such as site/soil quality, climate and competition on growth of *B. spiciformis* were tested. The percentage of silt was used as a proxy of site quality, total basal area (m^2ha^{-1}) as a measure of competition, and the rainfall in October and December as measures of climate. Results show that tree rings *of B.spiciformis* from dry Miombo woodlands were annual based on successfully crossdated sample of 35 stem disks. The estimated mean annual diameter increment of *B. spiciformis* was 1.93 ± 0.14 mm year^{-1} (mean ± SE). Among the four categories of explanatory variables tested either alone or in combination, climate (rainfall) was shown to have a strong positive effect on growth of *B. spiciformis* while competition had a marked negative impact. Based on the fact that *B. spiciformis* is only one of several important Miombo woodland species, we conclude that analysing the growth of other Miombo species is needed to support sustainable management of Miombo woodlands.

Key words: Allowable cut, Increment, Growth rate, Growth models,Tree rings

1. Introduction

Miombo woodland is the most widespread forest vegetation type in eastern, central and southern Africa including Tanzania. Most households in the region depend on wood and charcoal as sources of energy, and most of it is extracted from Miombo woodlands (Clarke et al., 1996). Unfortunately growth models for assisting in achieving sustainable management and extraction levels of Miombo woodland resources are scarce or missing (Schwartz et al., 2002), the main reason being that limited information is available on the growth of most tree species found in the Miombo woodlands. Such information is important for understanding forest dynamics, for estimating cutting cycles, and for developing growth and yield models that can support sustainable management of forests and woodlands in the region (Brienen and Zuidema, 2006). On a global scale, information about age and growth rate of trees is important in the effort to understand forest reources' potential to sequester and store carbon to mitigate climate change (Lloyd and Farquhar, 2011).

Over the years many approaches have been used to assess diameter increment of trees found both in temperate and tropical regions. Repeated diameter measurements of trees in permanent sample plots (PSPs) have a long history as a means of obtaining information on age and growth of trees from both regions (Bormann and Berlyn, 1981). However, the use of this data source is hampered (in many cases) by limited availability of data as many permanent plots in Miombo woodland are still young and regular monitoring has not always been conducted (Borota, 1991; Isango, 2009; Zahabu, 2008). The reliability of data collected from PSPs may also be questionable as it depends on the type of equipment used to take measurements, i.e. diameter tape, verneer calliper or dendrometers, as well as the availability of qualified manpower and funds to support the whole process (Biondi, 1999; Elifuraha et al., 2008).

As a consequence of this, results obtained using permanent plots tend to vary considerably and may appear contradictory. For example, Malimbwi et al., (1994) estimated a Mean Annual Increment (MAI) of 7.4 m^3/ha/year for Kitulanghalo forest reserve in Morogoro, eastern Tanzania, while in the same area, Malimbwi et al., (2005) estimated an MAI of 2.4 m^3/ha/year for the three-year period 1996-1999. For the same forest, Zahabu, (2008) reported three quite different values of MAI measured for three consecutive years between 2005 and 2008, namely 7.7, 11.8 and 2.56 m^3/ha/year. After crosschecking with measurements made the following year, the extreme value of 11.8 m^3/ha/year was suspected to be due to measurement errors. Alternatively, the large variation between years may partly reflect fluctuations in annual rainfall.

As an alternative to overbark measurements in PSPs, tree ring analysis has a long and well established history as a means of obtaining information on age and growth of trees from temperate regions (Bormann and Berlyn, 1981; Rozendaal and Zuidema, 2011). However, due to the widespread assumption that tropical trees generally lack annual rings, little research has been done on the use of tree ring measurements for assessment of the growth of tropical trees (Lieberman *et al*, 1985; Vetter and Wimmer, 1999; Worbes, 2002). Since the formation of annual rings is species and site specific and depends on local climatic conditions, several studies from tropical and subtropical regions have examined whether annual growth rings can be observed in particular species (Rozendaal and Zuidema, 2011). For example some studies have reported the formation of annual rings in *Brachystegia spiciformis* Benth, one of the most common and dominant tree species in the Miombo woodlands (Grundy, 2006; Trouet et al., 2006; 2010; Syampungani et al., 2010). Due to the long time series that can be produced by measuring growth rings, such measurements hold considerable potential as a basis for growth modelling as they can provide a precise picture of the growth of individual trees from the juvenile stage to maturity, including how growth has been negatively or positively affected by climatic and edaphic factors or competition from the neighbouring trees (Vanclay, 1994; Husch et al., 2003; Sapkota and Meilby, 2009). Hence the use of tree rings in growth modelling holds obvious advantages over the common method of using PSPs. Compared to PSPs the only major disadvantages of using growth ring measurements is that samples are usually small and what is a representative sample at the time of sampling might not be a representative sample of the forest as it was in the past. In this study we use 40 stems disks collected from *Brachystegia spiciformis* trees to develop growth models in support of the sustainable management of forest resources in the dry Miombo woodlands of Tanzania. Thus the objectives of this study were to i) assess whether *Brachystegia spiciformis* Benth forms annual tree rings, ii) estimate diameter increment of *B. spiciformis* using growth ring measurements, and iii) develop local diameter growth models for *B. spiciformis* including the effects of site, soil, competition and climate.

2. Material and methods

2.1 Study site

The study was conducted in Gangalamtumba Village Land Forest Reserve (GVLFR) (located between 7°30'23"S; 35°32'7"E and 7°35'10"S; 35°38'57"E) about 30 km North of Iringa Municipality, the administrative capital of Iringa Region in south-central Tanzania (Figure 1). The forest forms part of Mfyome village, which is located in the ward of Kiwele about 24 km from Iringa town. The altitudinal range is 850-1,300 m and the total forest area is 6,065 ha.

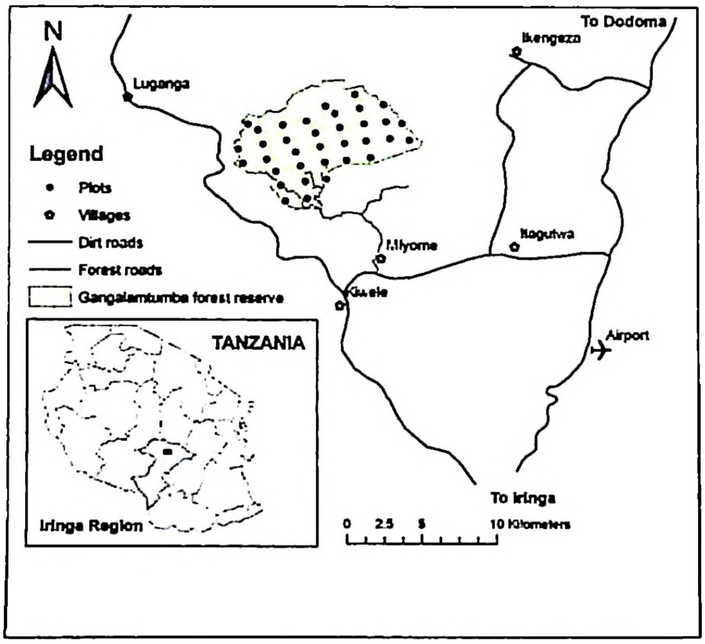


Figure 1. Map of Tanzania showing the location of the study area in Iringa region.

2.2 Species description and ecology

Miombo ecosystems are characterised by three dominant genera of tree species, *Brachystegia*, *Julbernardia* and *Isoberlinia*. A total of 17 species of *Brachystegia* occur in Zambia, 1 in Kenya, 6 in south-eastern Tanzania and 11 in western Tanzania with *Brachystegia spiciformis* Benth. being the most common species in regions where dry Miombo woodland is the principal vegetation type (Frost, 1996). *B. spiciformis* is a member of the family Fabaceae, sub-family Caesalpinioideae, and is a medium-sized deciduous tree that reaches heights of 8-25 m (max. 28 m). It grows in savanna (altitude: 0 -2350 m) and in open and closed woodlands of Southern and Eastern Africa, mostly in Tanzania, Zambia, Zimbabwe and Mozambique. The species needs an annual rainfall of at least 500 mm and a mean annual temperature of 19-20 °C to thrive. *B. spiciformis* tolerates a wide range of soils but grows best on moist and deep red soils and poorly on dry and shallow soils (Frost, 1996). The trees are heavily branched and the crown is usually large compared to the total height. The wood of *B. spiciformis* has a coarse texture, irregular and interlocked grain and no characteristic odour or taste. The pale brown and heavy wood is not durable and is therefore unsuitable for furniture and buildings. However, *B. spiciformis* wood is widely used for fuel, both in the form of charcoal and as firewood. In the study area *Brachystegia spiciformis* is one of the most important sources of charcoal and firewood for domestic use and for commercial purposes, such as tobacco curing. *B. spiciformis* is also used for beehives, and sometimes for boats and in low grade building construction (Bryce, 1967; USDA, 2010). Anatomically, the growth ring boundaries of *B. spiciformis* are marked by the presence of terminal parenchyma, a common characteristic of the subfamily Caesalpinioideae (Bryce, 1967; Trouet *et al.*, 2006; Grundy, 2006). This terminal parenchyma appears as a band of parenchymatous cells, commonly composed of a maximum of five rows of cells that form a continuous layer which is often visible on transverse surfaces as a fine light-coloured band.

2.3 Data collection

2.3.1 Trees selection and extraction of stem disks

Forty stem disks of *B. spiciformis* were obtained from sample trees that were harvested by the first author in GVLFR, mainly for development of biomass and volume functions (Mwakalukwa *et al.* 2014a). To cover a wide range of tree sizes the 40 trees were selected using a diameter-stratified approach where 2-4 trees were sampled in each 5 cm diameter class (0-55 cm). All trees were sampled within 20-50 m from the centre of circular sample plots (radius 15 m, n = 35) that were established across the 6,065 ha forest (cf. Figure 1). The plots were located along parallel transect lines established at a fixed distance of about 2 km from each other. The sample plots were used to assess stand structure and species composition of all trees and shrubs with a diameter at breast height (Dbh) of at least 5 cm (Mwakalukwa et al., 2014). In the field, each sample tree was first identified and measured with regard to total height and Dbh before it was felled. Height was measured using a graduated pole with centimetre graduation (trees shorter than 2 m) or a Suunto clinometer (taller trees) and diameter was measured with a diameter tape (accuracy 1 mm). The geographical coordinates of each sample tree, including the altitude, were measured using a GPS device. The fourty (40) stem disks were cut at 1.3 m above ground. Seventeen (17) of these disks were collected in August 2009, 16 disks in August 2010 and 7 disks in October 2010. The 40 trees had a mean diameter of 21.3 cm (range: 1.2-54.3 cm) and a mean height of 10.1 m (range 2-17.2 m). All sample disks have been incorporated in the Xylarium of the Royal Museum for Central Africa in Tervuren, Belgium, with registration numbers Tw61476 - Tw61515.

2.3.2 Growth factors

Access to water was expected to be an important factor limiting growth. Hence, local topographical variation was assumed to influence the duration of the annual period where a tree would be able to grow. Accordingly, we used elevation and slope of the terrain as proxies for basic growth conditions. In each plot, elevation (m above sea level) was recorded using GPS and slope (in %) was measured using a Suunto clinometer. Also, in each plot soil samples were collected at five locations, one at the centre of the plot and four that were located 10 m from the centre in the four cardinal directions (North, East, South and West). Soil samples were collected from the depth range 0-15 cm and the five samples were mixed thoroughly in the field to obtain one composite sample per plot (Mwakalukwa et al., 2014b). Two sets of climate data from meteorological stations located about 30 km from the study area were obtained from Tanzania Meteorological Agency in Dar es Salaam. Rainfall data for 1943-1974 were available from Tosamaganga village, and data on rainfall and temperature for 1960-2009, and relative humidity for 1975-2009, were available from Nduli airport, which is located about five kilometres from Iringa town. To assess the effect of competition on growth, a separate circular sample plot with a radius of 7.5 m was established around the sample trees. Due to time constraints this was only done for 25 of the 40 sample trees. Each tree (> 5 cm Dbh) within the plots was identified and its diameter at breast height (1.3 m) and distance (m) to the sample tree were measured.

2.4 Laboratory analyses

2.4.1 Soil analysis

In the laboratory, composite soil samples were analysed for soil texture. All samples were first ground and passed through a 2 mm sieve to remove stones and gravel. Next a subsample was analysed for soil texture using the hydrometer method. Three soil fractions, Sand, Silt and Clay, were examined and results expressed in per cent (Dewis and Freitas, 1970).

2.4.2 Growth ring measurements

Following the method used by Trouet *et al.*, (2001, 2010), transverse surfaces of all stem disks were sanded and polished (grain 80 to 1200) in order to maximise growth ring detectability. After polishing, each disk was analysed microscopically (stereo microscope) under oblique lighting conditions in order to identify and register the presence of wedging rings. For each sample disk, ring widths were measured along four perpendicular radii from pith to bark using LINTAB equipment (accuracy 0.01 mm) and TSAP-Win software (Rinn, 2003). The LINTAB equipment is connected to the computer where measured values are stored by the TSAP-Win software for further processing. These data were later used to build a site chronology after successful completion of the crossdating process.

2.4.3 Bark measurements

In order to assess the increment of trees over bark, the thickness of bark has to be determined. Therefore, Bark thickness for all 40 stem disks sampled was measured using a vernier calliper (accuracy 0.01 inches) at 16 positions around the circumference of each stem disk. The 16 positions were determined by drawing lines, from pith to bark, separated by 45° angles. Bark thickness was measured at all points where the lines crossed. Double bark thickness for each stem disk was then calculated as the average of the 16 measurements multiplied by 2. The resulting dataset was used for establishing a relationship between Dbh and bark thickness for the estimation of diameter increment over bark.

2.5 Statistical analyses

2.5.1 Crossdating of growth ring series

Cross-dating of growth ring series obtained from measurement of 40 stem disks of *B. spiciformis* was performed visually by comparing ring-width series within tree (disk) using the four radii and between trees using the average series based on the four radii as in Trouet *et al.* (2001; 2006). Statistical measures such as mean sensitivity, t-values and *Gleichlaufigkeitskoeffizient* (GLK) were used to identify problems in measurements and for verification of the cross-dating. Rainfall data collected from Nduli airport located about 30 km from the study site were also employed in the crossdating process. Out of 40 stem disks measured, 30 stems disks were available for the development of the site chronology. Ten disks were excluded during the development of the site chronology because of crossdating problems (5 disks) or because they were too young/small with only 8-15 annual rings (5 disks). All analyses were perfomed using the TSAP-Win software (Rinn, 2003).

2.5.2. Diameter increment of B. spiciformis

Based on the crossdating results, growth ring series from 35 disks (including 5 disks from small trees) were available for estimating annual diameter increment of *B. spiciformis*. Statistical parameters such as mean, standard error, and minimum and maximum ring width (mm) were computed using Excel and the statistical software package R version 2.13.0 (www.r-project.org).

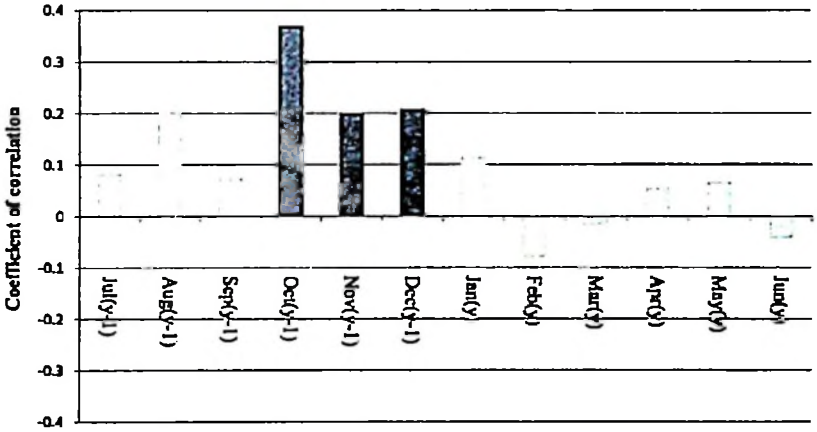
2.5.3 Growth modeling

Estimating and modelling diameter increment requires that growth can be determined reliably for time intervals of known duration, thus in practice requiring that growth rings are annual. Unfortunately, for 5 of the 40 stem disks proper cross-dating proved impossible and thus only 35 stem disks (including 5 disks from small trees) were used in the analysis. For these 35 disks, a total of 2773 annual rings were measured and available for growth modelling. The number of annual rings observed in each stem disk ranged from 8 to 242, and the material thus covered a wide range of tree ages. For each stem disk, diameter under bark was calculated as twice the sum of the annual ring widths (average of four radii) from pith towards bark. Diameter increments for each stem and year were calculated as differences between estimated diameters in successive years. First modelling was done using diameter under bark as the only explanatory variable and later other factors such as climate, site factors (elevation, slope and soil) and competition were included. Model formulation and variable selection are discussed below.

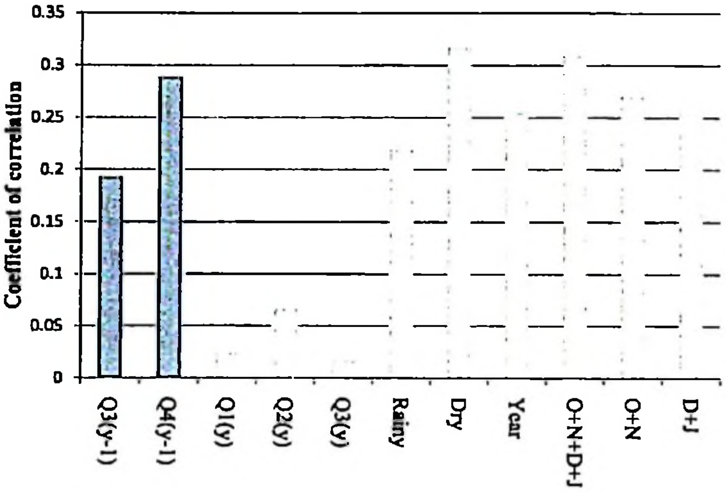
2.5.3.1 Climate

The most recent and complete climate dataset was the one from Nduli airport but this dataset only covered the years from 1960. Therefore, in order to make use of the fact that rainfall data from the meteorological station in Tosamaganga village were available from 1943, twelve monthly linear regressions were prepared using data from 1960-1974 where rainfall had been measured at both stations. The twelve regressions related monthly rainfall at the Tosamaganga station to monthly rainfall at the station in Nduli airport. Subsequently, these regressions were used to estimate rainfall for Nduli airport in the years 1943-1959. This way, a complete set of rainfall estimates for the years 1943-2009 became available for growth modelling. Temperature and relative humidity were not used in this study due to large percentages of missing data and because the data series were relatively short (first years were 1960 for temperature and 1975 for humidity) and could not be extended further back in time by relating the series to observations made at other stations.

Using Dendroclim2002 software (Biondi and Waikul, 2004), the average standardised growth index series (see section 2.5.1 above) was correlated with monthly and quarterly rainfall for the months starting from July of the previous year to June of the current year (12 months, 4 quarters), so as to identify the most useful rainfall variables to be included in growth modelling. Based on coefficients of correlation between periodic rainfall and the mean site chronology (Figure 2), the following climate variables were selected for growth modelling: October of the previous year (Rain10, r = 0.37), November of the previous year (Rain11, r = 0.20), and December of the previous year (Rain12, r = 0.21). Among the quarterly rainfall variables, the following quarters were selected: third quarter (July–September) of the previous year (RainQ3, r = 0.19), and fourth quarter (October–December) of the previous year (RainQ4, r = 0.29).



a) Monthly rainfall variables (1942-2009). Variables (e.g.): Aug(y-1) and Aug(y) are rainfall in August of the previous and the present year, respectively.



b) Quarterly rainfall variables (1942-2009). Variables (e.g): Q3(y-1) and Q3(y) are rainfall in quarter three (July–September) of the previous and the present year, respectively. Rainy - is sum of rainfall during rain season of November and December; Dry - sum of rainfall during dry season of May, June, July, August, September and October; Year – sum of rainfall of the year from May of previous year to April of current year; O+N+D+J – sum of rainfall in October, November, December and January; O+N – sum of rainfall in October and November (pre-rainy season); D+J – sum of rainfall during the core of rainy season of December and January.

Figure 2. Coefficients of correlation between mean chronology (growth indices) and rainfall variables. Used in selection of the most useful rainfall variables for growth modelling. Significant variables are shaded black while for non-significant variables are in gray.

2.5.3.2 Site factors

Elevation (m) and terrain slope (%) within each plot, were applied as proxies of basic site conditions such as access to water (depth of ground water table and runoff) and exposure. Soil texture variables were applied as supplementary indicators of growth conditions. Sand was considered a poor indicator of soil fertility and therefore the two fine-particle soil fractions, clay and silt, were chosen as proxies for soil quality. In addition, based on soil classification using the soil texture triangle (Brady, 1974), dummy variables were also introduced for each of the relevant soil classes.

2.5.3.3 Competition

Three competition indices: total basal area (tba), basal area greater than the subject tree (bag) and Hegyi's (1974) distance-weighted size ratio competition index (CI) were selected for studying the influence of competition on tree growth. Total basal area (m^2ha^{-1}) was estimated on the basis of basal areas of all trees (> 5 cm) rooted within the 7.5 m radius plot established around the 25 subject trees that included 14 individuals felled in August 2009, and 11 felled in August 2010. Basal area of trees larger than the subject tree (m^2ha^{-1}) was also calculated within the 7.5 m radius plot. The competition index (CI) by Hegyi (1974) was calculated as $CI_i = \Sigma(D_j/D_i)/L_{ij}$ (Husch *et al.*, 2003), where D_i is Dbh of the subject tree (i) in cm, D_j is Dbh of the competitor (j) in cm, and L_{ij} is distance between the subject tree and the competitor in m.

For competing trees surrounding the sample trees, the only data available were those from the plot survey, and competition measures could therefore only be estimated correctly for the year of felling. Based on the low rainfall in GVLFR, we assumed that tree growth is slow and therefore changes in competition are also likely to be slow. We therefore expected estimates of competition measures obtained for the year of felling to be decent proxies of competition for at least some years prior to felling. To enable development of models including effects of competition as well as effects of climate, and to avoid estimating sets of parameters that would only be valid for the year of felling, we therefore decided to make use of the same competition index estimates across a range of years. The final models were prepared using data from the latest 5 years but to test the stability of the parameter estimates, we expanded the dataset in steps of one year up to a maximum of 15 years. This trial was conducted by including the two independent variables: Dbh (mm) and tba (m^2ha^{-1}). Dbh of the previous year was computed by subtracting diameter increment under bark (mm) from current Dbh.

2.5.4 Selection and formulation of growth models

The basic growth equation applied in this study was the model described by Zeide (1993); $\Delta d = aD^b \exp(cD)$ and the corresponding log-transformed model; $\ln(\Delta d) = a + b\ln(D) + cD$, where D is diameter under bark (mm), Δd is diameter increment under bark (mm), and *a*, *b*, and *c* are model parameters. Since we aimed to prepare models that include effects of site, soil, climate and competition but can also be used in practice by users with different needs, we included these factors individually and in various combinations in modelling the growth of *B. spiciformis*. Four groups of equations were tested:

a). Group one: models with diameter under bark, soil and site factors.

Model 1: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D)$

2: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_3(\text{soil})$
3: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_4(\text{site})$
4: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_3(\text{soil}) + a_4(\text{site})$

b). Group two: models with Dbh, soil, site and competition.

Model 5: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition})$
6: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_4(\text{soil})$
7: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_5(\text{site})$
8: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_4(\text{soil}) + b_5(\text{site})$

c). Group three: models with diameter under bark, soil, site and climate.

Model 9: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_5(\text{climate})$
10: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_3(\text{soil}) + a_5(\text{climate})$
11: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_4(\text{site}) + a_5(\text{climate})$
12: $\ln(\Delta d) = a_0 + a_1\ln(D) + a_2(D) + a_3(\text{soil}) + a_4(\text{site}) + a_5(\text{climate})$

d). Group four: models with Dbh, soil, site, climate and competition.

Model 13: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_6(\text{climate})$
14: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_4(\text{soil}) + b_6(\text{climate})$
15: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_5(\text{site}) + b_6(\text{climate})$
16: $\ln(\Delta d) = b_0 + b_1\ln(\text{Dbh}) + b_2(\text{Dbh}) + b_3(\text{competition}) + b_4(\text{soil}) + b_5(\text{site}) + b_6(\text{climate})$

where: $\ln(\Delta d)_{it} = f(D_{it}, \text{soil}_i, \text{site}_i, \text{climate}_t) + r_i + \varepsilon_{it}$ was the general form of the mixed linear model used for modelling logarithmic diameter increment $\ln(\Delta d)$ as a function of diameter under bark (D), soil, site and climate factors for all models in groups one and three, whereas: $\ln(\Delta d)_{it} = f(\text{Dbh}_{it}, \text{climate}_t, \text{soil}_i, \text{site}_i, \text{competition}_i) + \varepsilon_{it}$ was the general form of the ordinary linear models estimated using robust regression estimators (Huber's method) and applied for modelling logarithmic diameter increment $\ln(\Delta d)$ as a function of diameter over bark (Dbh), soil, site, climate and competition for all models in groups two and four. Furthermore, the letters; $a_0 - a_5$ and $b_0 - b_6$ are regression coefficients; i is tree number; t is year; r_i is a random tree effect ($N(0,\sigma^2)$) and the ε_{it}s are random errors. The final models were selected after testing different alternatives, starting with complete models including all variables (site, soil and climate) and gradually reducing them until all parameters were significant at the 5% level. In some cases, no significant effects remained that distinguished the resulting model from models already tried, hence reducing the final number of models.

2.5.5 Auxiliary models for diameter increment prediction

Since growth was measured under bark and Dbh is normally measured over bark, it was considered necessary to prepare models relating bark thickness and diameter under bark to Dbh. In addition, a model relating height and Dbh is useful when predicting volume or biomass. All 40 observations of average bark thickness and diameter under bark were used in preparing these models. Double-logarithmic linear models were used in modelling bark thickness, diameter under bark, and height as functions of Dbh. The general form of the models was:

Model 17: $\ln(Y) = a + b \ln(\text{Dbh})$

where Y is average bark thickness (mm), diameter under bark (mm) or height (m); Dbh is breast height diameter over bark (mm or cm), letters a and b are model parameters and ln is the natural logarithm. All regression analyses were carried out using the mixed model procedure (package lme-methods REML and ML) found in R software version 2.13.0 (www.r-project.org).

3. Results

3.1 Annual nature of growth in B. spiciformis

Based on cross-dating results using mean series from each of the 30 trees (excluding five young/small trees with 8-15 annual rings) a single average site chronology was prepared (Figure 3), the length of which was limited to the range where a minimum of four trees was included. Pearson correlations between the (30×30-30)/2 = 435 pairs of individual-tree chronologies varied around a mean of 0.11 (SD 0.21). The mean Gleichläufigkeit of all such pairs was 0.55 (SD 0.10) and for 69% of the chronology pairs the Gleichläufigkeit exceeded 0.5, the value expected for independent series, thus indicating a reasonable level of similarity between the growth patterns of individual trees. Moreover, the mean Gleichläufigkeit of the 30 individual-tree chronologies and the precipitation in 12-month periods from July of the previous year to June of the current year was 0.56 (range 0.41-0.77, SD 0.10, SE 0.02), which is significantly different from 0.5 ($P<0.01$, t-test). Thus, the observed agreement across the 30 individual-tree chronologies and between these and the precipitation series suggest that growth rings of *B. spiciformis* in GVLFR are annual.

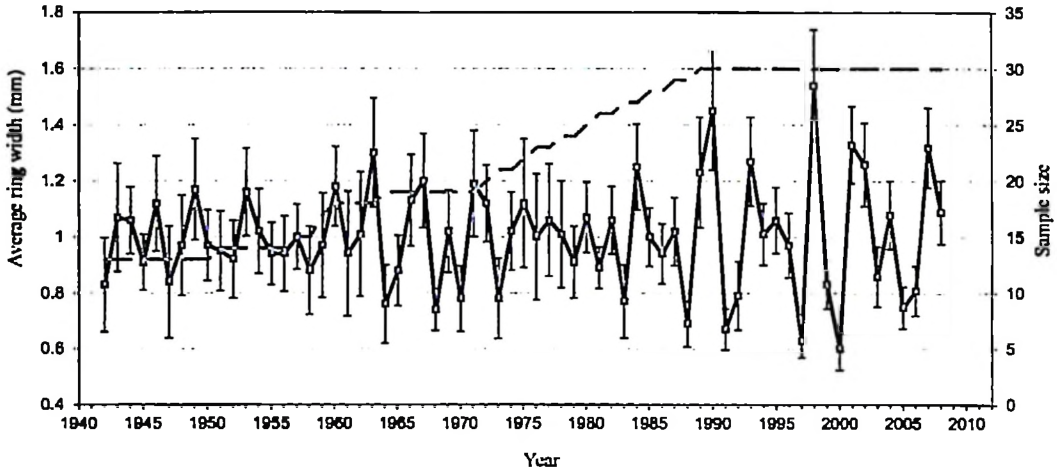


Figure 3. Unbroken line: Site chronology (mean ± standard error) based on 30 *B. spiciformis* trees sampled in the GVLFR. Dashed line: Sample size.

3.2 Average diameter increment

For the overall sample of *B. spiciformis* trees (n = 40) the average diameter increment was found to be 1.90±0.12 mm (mean±SE), whereas an average diameter increment of 1.93±0.14 mm was observed for the reduced sample of 35 trees, not including those for which proper crossdating had proven impossible. The highest average diameter increments were observed for trees with a breast height diameter of 150-200 mm. Average Dbh, average bark thickness and diameter under bark of the 35 cross-dated trees (mean±SE) were 198±26 mm, 7.9±0.8 mm, and 153±21 mm, respectively. The minimum and maximum values were equal to those presented for the total sample of 40 trees in Table 1.

Table 1. Summary of data† used for estimating diameter increment of *Brachystegia spiciformis* in Gangalamtumba village land forest reserve.

	Increm. (mm/year)	Dbh (mm)	Bark (mm)	Diam. (mm)
Minimum	0.62	12	0.8	7
Maximum	3.67	543	17.5	433
Mean	1.90	213	8.4	165
Std. error	0.12	25	0.8	20
N	40	40	40	40

† Abbreviations and symbols: Increm. = average diameter increment, Dbh = diameter at breast height (over bark), Bark = average bark thickness, Diam. = diameter under bark,

3.3 Selected growth factors

A summary of factors included in modelling the diameter increment of *Brachystegia spiciformis* is presented in Table 2. For the 67-year period (1942-2008) where precipitation data were available from the nearby meteorological stations at Nduli airport and Tosamaganga (see above), the average annual precipitation was 607±16 mm (mean±standard error) with a minimum of 312 mm in 1949 and a maximum of 1085 mm in 1967. With an average rainfall of only 0.1 ± 0.01 mm, July was the driest month of the year, whereas December had the highest average rainfall (135 ± 9 mm). The minimum and maximum values listed in Table 2 for elevation (m), slope (%) and soil texture (sand, clay and silt) indicate that the data-material covers a wide range of basic site conditions.

Table 2. Summary of data† used for modelling the diameter growth of *Brachystegia spiciformis* in Gangalamtumba village land forest reserve.

	Tba (m^2/ha)	Elevation (m)	Slope (%)	Sand (%)	Clay (%)	Silt (%)	Rain10 (mm)	Rain11 (mm)	Rain12 (mm)	RainQ3 (mm)	RainQ4 (mm)
Minimum	3.55	1019	6	32.2	5.4	5.2	0	0	2.8	0	8
Maximum	23.25	1288	49	88.2	39.9	38.0	41.9	157.1	357.8	10.3	421.7
Average	8.89	1159	19	69.6	16.5	14.0	3.8	27.0	136.0	1.0	166.8
Std.error	0.80	17	3	3.6	2.5	2.0	0.9	3.7	10.3	0.3	11.7
N	25	17	17	17	17	17	67	67	67	67	67

† Abbreviations and symbols: tba= total basal area, Rain10, Rain11 and Rain12 = Rainfall in October, November and December of the previous year, respectively, RainQ3 and RainQ4 = Rainfall in the third quarter (July-September) and fourth quarter (October-December) of the previous year, Std.error: standard error, n: sample size: 40 trees in total, 25 trees with competition measures, 17 plots with site and soil data, 67 years with rainfall data (19423-2008).

3.4 Growth models

Parameter estimates for twelve final growth models are presented in Table 3. The general pattern is that all parameters of the twelve models, except some of the intercepts, were significantly different from zero at the 5% level. Moreover, with the exception of parameter estimates for silt, all parameter estimates bear the expected signs. Compared to the basic models including diameter only, additional independent variables included only led to small reductions of the residual standard error (RMSE).

Elevation and slope were included as proxies of site quality but resulted in very little improvement in terms of RMSE. Therefore, models 3, 4, 7, 8, 11, 12, 15 and 16 are not included in Table 3.

Similar observations were made for models including soil category dummy variables. Such models proved inferior to models including continuous soil texture variables (here: silt) and, moreover, the parameter estimates were difficult to interpret. Hence, they were not included in the final set of models in Table 3. By contrast, significant improvements of the model fit was observed in the reduced dataset when competition (tba) was included as an additional element in the model (Models 5, 6, 13a, 13b, 14a and 14b in Table 3). Compared with the other types of competition indices tested, tba turned out to be superior both in terms of R^2 and significance of the parameter estimates. Model 5 (in Table 3) with tba as a measure of competition was therefore selected for testing the stability of the parameter estimates when including growth observations from an increasing number of years (5-15), assuming that the competition remained unchanged. Figure 4 shows the resulting variation of RMSE, the parameter estimates and the standard errors of the estimates. Within the range of years examined, RMSE remains stable and, if anything, indicates a slight improvement of the fit by including the most recent 6-8 years. The parameter estimates are relatively stable, implying that (i) five years appears to be sufficient to almost eliminate the effect of year-to-year variation of growth and that (ii) there is no indication that competition changes so fast that this is in conflict with our wish to smoothen the effects of year-to-year variation by including growth observations from a number of recent years. However, Figure 4 also shows that the standard errors of the estimates decrease very slowly, indicating that as the number of years increases, the year-to-year climate variation caused increasing variation of the dependent variable, but this is compensated for by the increasing number of degrees of freedom.

Table 3. Diameter growth models[†] for *Brachystegia spiciformis* in Gangalamtumba village land forest reserve. Models not including competition (tba) are mixed models with tree as a random factor, whereas the parameters of models including competition were estimated using ordinary least squares.

Model	The final structure of the model with parameter estimates	n	N	R^2	RMSE	σ_{tn}
1.	$\ln(\Delta d) = -0.08915^{ns} + 0.19902 \ln(D) - 0.00318(D)$ (0.097) (0.024) (0.0003)	35	2773	0.048‡	0.691	0.377
2.	$\ln(\Delta d) = 0.37096 + 0.19428 \ln(D) - 0.00316(D) - 0.03056(silt)$ (0.152) (0.024) (0.0003) (0.008)	35	2773	0.053‡	0.691	0.313
5.	$\ln(\Delta d) = -1.70640^{ns} + 0.6925 \ln(Dbh) - 0.0050(Dbh) - 0.0332(tba)$ (1.064) (0.258) (0.001) (0.013)	25	125	0.210§	0.556	-
6.	$\ln(\Delta d) = -0.30650^{ns} + 0.4987 \ln(Dbh) - 0.0044(Dbh) - 0.0353(silt) - 0.0427(tba)$ (1.09) (0.252) (0.001) (0.011) (0.013)	25	125	0.263§	0.491	-
9a.	$\ln(\Delta d) = -0.28008 + 0.22444 \ln(D) - 0.00309(D) + 0.00868(Rain10) + 0.00046(Rain12)$ (0.128) (0.037) (0.001) (0.002) (0.0002)	35	1561	0.036‡	0.699	0.362
9b.	$\ln(\Delta d) = -0.29529 + 0.22125 \ln(D) - 0.00293(D) + 0.02138(RainQ3) + 0.00054(RainQ4)$ (0.128) (0.037) (0.001) (0.009) (0.0002)	35	1561	0.033‡	0.700	0.360
10a.	$\ln(\Delta d) = 0.20099^{ns} + 0.21790 \ln(D) - 0.00337(D) + 0.00874(Rain10) + 0.00043(Rain12) - 0.02889(silt)$ (0.190) (0.036) (0.001) (0.002) (0.0002) (0.008)	35	1561	0.042‡	0.699	0.315
10b.	$\ln(\Delta d) = 0.17036^{ns} + 0.21526 \ln(D) - 0.00322(D) + 0.02069(RainQ3) + 0.00052(RainQ4) - 0.02786(silt)$ (0.191) (0.036) (0.001) (0.009) (0.0002) (0.008)	35	1561	0.040‡	0.700	0.316
13a.	$\ln(\Delta d) = -2.42670 + 0.8116 \ln(Dbh) - 0.0055(Dbh) + 0.0017(Rain12) - 0.0364(tba)$ (1.034) (0.251) (0.001) (0.001) (0.013)	25	125	0.249§	0.490	-
13b.	$\ln(\Delta d) = -2.36900 + 0.8044 \ln(Dbh) - 0.0055(Dbh) + 0.0012(RainQ4) - 0.0361(tba)$ (1.030) (0.250) (0.001) (0.0004) (0.013)	25	125	0.241§	0.502	-
14a.	$\ln(\Delta d) = -1.00820^{ns} + 0.6236 \ln(Dbh) - 0.0050(Dbh) + 0.0017(Rain12) - 0.0386(silt) - 0.0459(tba)$ (1.043) (0.241) (0.001) (0.001) (0.010) (0.013)	25	125	0.318§	0.473	-
14b.	$\ln(\Delta d) = -0.90610^{ns} + 0.6051 \ln(Dbh) - 0.0049(Dbh) + 0.0013(RainQ4) - 0.039(silt) - 0.0452(tba)$ (1.021) (0.236) (0.001) (0.0004) (0.01) (0.012)	25	125	0.312§	0.511	-

[†] Symbols: n is number of groups (trees, sample size), N is number of observations (growth rings), RMSE is residual standard error within single stems, σ_{tn} is the standard deviation of the random effect (between trees), the symbol "‡"indicates likelihood ratio based coefficients of determination while "§" indicates adjusted R^2; numbers in brackets are standard errors of the parameter estimates of which those that are not significant at the 5% level are marked "ns". $\ln(\Delta d)$ is the diameter increment under bark (mm), D is diameter under bark (mm), Dbh is diameter over bark (mm), Rain10 and Rain12 = Rainfall in October and December of the previous year (mm), respectively, RainQ3 and RainQ4 = rainfall in third quarter (July-September) and fourth quarter (October-December) of the previous year (mm), and tba = total basal area (m^2/ha).

Finally, it emerged that in models including rainfall there was no clear difference between using monthly rainfall for October and December (Models 9a, 10a, 13a, 14a) and quarterly rainfall for the third and fourth quarters of the year (Models 9b, 10b, 13b, 14b) as these alternatives yielded similar results in terms of R^2 and RMSE.

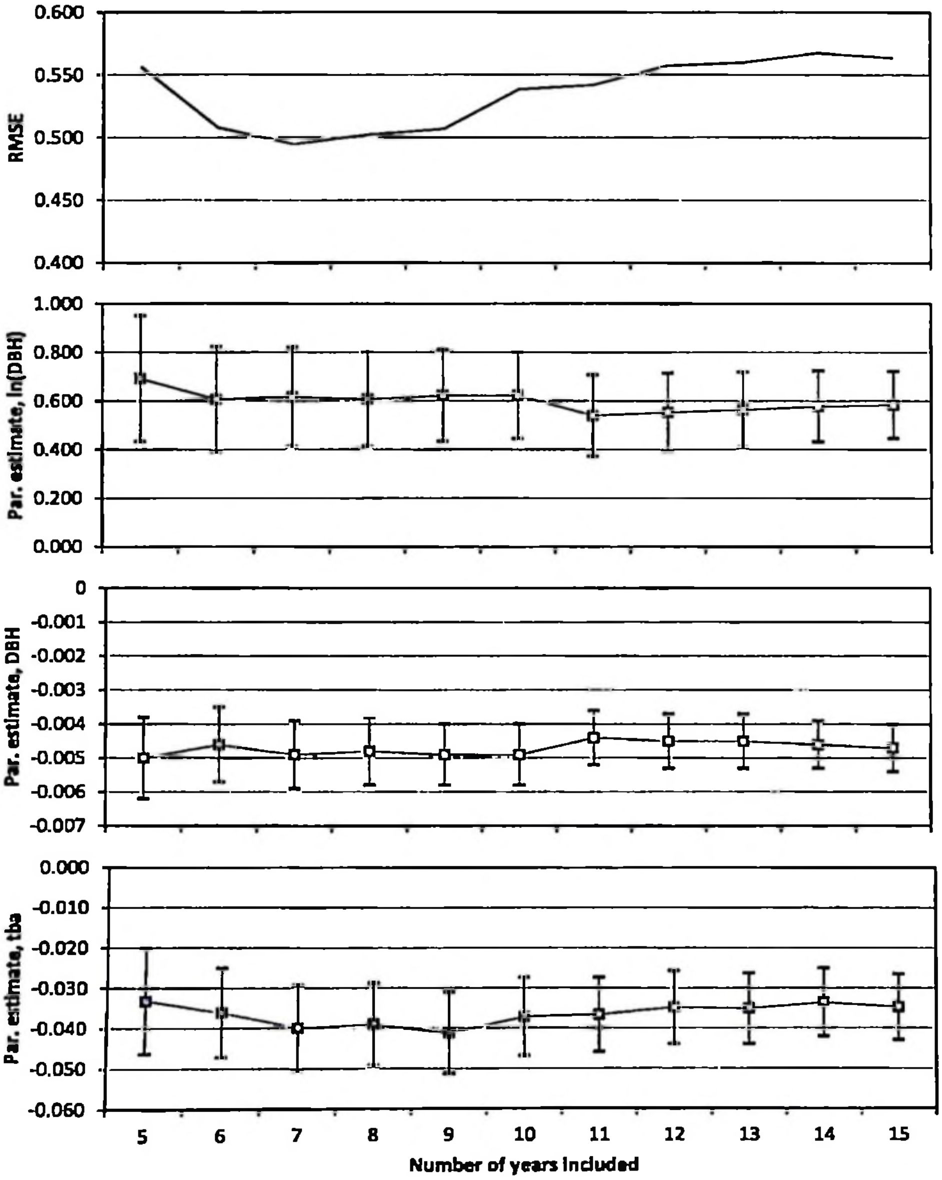


Figure 4. Root mean squared error (RMSE) and variation of parameter estimates (b_1-b_3) for model 5: $\ln(\Delta d) = b_0 + b_1\ln(\mathrm{Dbh}) + b_2\mathrm{Dbh} + b_3\mathrm{tba}$, assuming unchanged competition (tba) and including the latest 5-15 years of growth up to the time when trees were felled in 2009 and 2010. Error bars indicate standard errors of the estimates.

3.5 Auxiliary models and predicted diameter increment

To predict diameter increment of *B. spiciformis* as influenced by diameter, soil texture, climate and competition, it is necessary to determine bark thickness and diameter under bark. These were estimated using auxiliary models developed from Model 17 with diameter over bark (Dbh) as the independent variable. The final models are presented in Table 4. All three models provide a very good fit, and in all cases the coefficients of determination (R^2) exceed 94%. In addition, all parameters were significantly different from zero ($Pr>|t|<0.001$). Predicted diameter increments of *B. spiciformis* trees as influenced by diameter (Model 1), soil texture (Model 2), climate (Model9) and competition (Model 5) are shown in Figure 5. The results show that within the ranges of soil conditions (silt percentage), climate (Rain10 and Rain12) and competition (tba) observed within the 35 plots, the predicted diameter increment ranges from 0.5-1.0 mm/year, (when the maximum silt percentage of 38% is applied in Model 2), to 3-3.5 mm/year (when maximum rainfall values of 41.9 mm for October and 357.8 mm for December are applied in Model 9). Generally diameter growth of *B. spiciformis* follows the typical pattern of increasing growth when trees are small and decreasing growth when they grow older and thicker.

Table 4. Models[†] relating bark thickness, diameter under bark (mm) and total tree height (m) of *Brachystegia spiciformis* in GVLFR to diameter at breast height.

Model	**Model specification**	**Regression parameters**		**df**	**RMSE**	**R^2**
		a	*b*			
17a.	*ln*(Bark thickness, mm) = *a* + *b* *ln* (Dbh, mm)	-1.6536 (0.139)	0.7155 (0.027)	38	0.186	0.946
17b.	*ln*(Diam. under bark, mm) = *a* + *b* *ln*(Dbh, mm)	-0.77697 (0.067)	1.09414 (0.013)	38	0.090	0.994
17c.	*ln*(Height, m) = *a* + *b* *ln*(Dbh, cm)	0.89606 (0.056)	0.49119 (0.019)	38	0.132	0.942

[†] Symbols: Numbers in brackets are standard errors of the parameter estimates; df is the number of degrees of freedom; RMSE is the root mean square error, and R^2 is the coefficient of determination.

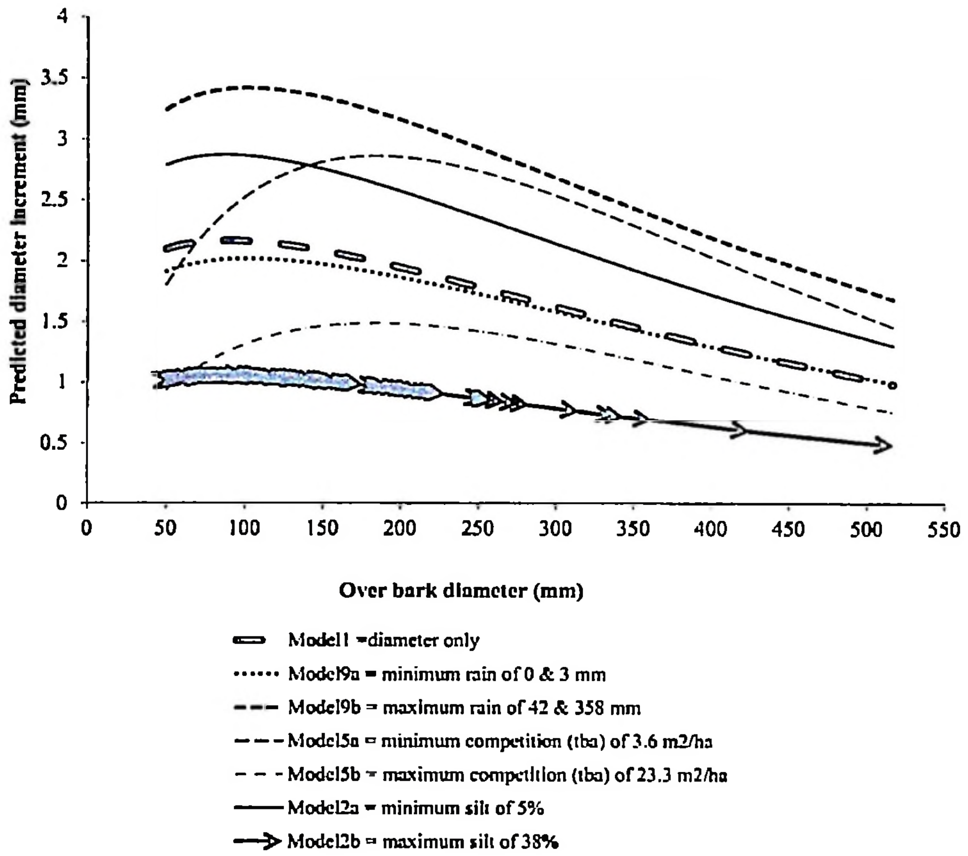


Figure 5. Predicted diameter increment (mm/year) of *B. spiciformis* trees as influenced by diameter, soil (per cent silt), climate (rainfall in October and December, mm) and competition (total basal area, tba, m^2/ha).

4 Discussion

To the best of our knowledge this study is the first to prepare a range of different diameter growth models for the important Miombo tree species *B. spiciformis*. The final models include effects of basic site conditions, as indicated by soil texture, rainfall, and competition measured as total basal area within a radius of 7.5 m. The intention with this range of model alternatives is to provide users with suitable tools whatever the type of input data available and whatever the purpose of the analysis, hence hopefully contributing to sustainable management of the woodlands. For example, Model 1 (Table 3) with diameter as the only independent variable is a basic model that can always be used. This model uses diameter under bark and since the variable normally measured on standing trees is diameter over bark, Models 17a and 17b presented in Table 4 were developed as tools for estimating diameter under bark. These models explain 95-99% of the quadratic variation (R^2) so conversion between over-bark and under-bark diameters can be done with only negligible loss of precision. However, it should be noted that bark thickness is influenced by factors such as humidity, frequency of fire, growth rate and temperature, and just like the growth models the conversion models may therefore be inaccurate outside the study area.

The average diameter increment of *B. spiciformis* of 1.9 mm/year is similar to those reported for *Afzelia quanzensis* and *Pterocarpus angolensis* ($\Delta d = 2.1$ and 2.3 mm/year, respectively) based on PSPs in Ichembe and Sikitiko forest reserves in Tanzania (Borota, 1991). However, it is considerably lower than observed for *B. spiciformis* trees in dry Miombo woodlands of western Zambia where the estimated mean annual ring width was 2.44-3.25 mm/year (Trouet *et al.*, 2006). A partial explanation for this may be that the study area in Zambia receives more rain (mean annual rainfall: 880 mm) than our study area (mean annual rainfall: 607 mm).

Since growth is influenced by a range of other factors, including the quality of soil, competition with surrounding vegetation, and climatic factors such as temperature and rainfall, the diameter increment expected for a given trunk diameter varies considerably. The observed effects of these factors on growth of *Brachystegia spiciformis* is discussed below.

4.1 Effects of competition on growth

The small variation of parameter estimates of models including competition observed when calibrated on datasets of varying temporal depth (Figure 4) appears to indicate that competition among trees has remained stable for many years. The likely reason for this is that the dynamics of dry Miombo is slow since all species grow very slowly. An additional reason may be that the natural mortality of larger individuals is low although fires are frequent. The fact that human impacts were limited in the past might also have contributed to the stability. The stability of the model fit statistics, R^2 (not shown) and RMSE, confirms that the competition measures remain (approximately) valid for many years. The negative sign of the parameter associated with tba is an indication that growth of *B. spiciformis* trees is affected negatively by sharing resources (light, water and nutrients) with other trees within the applied range of 7.5 m. As shown in Figure 5 the larger the value of tba, the slower the growth of the tree. It is worth noting that, for all models including competition, the estimated coefficient of tba remained remarkably stable with a value of about -0.04 and with standard errors of about one third of this value. By contrast, the strengths of other competition measures tested, i.e. basal area greater than the subject tree (bag) and the distance-weighted size ratio (CI), were much lower. While tba is a measure of two-sided, symmetric competition, bag and particularly CI emphasize one-sided, assymetric competition. The fact that tba was considerably more influential than bag and CI suggests that the growth of *B. spiciformis* in the study area is mainly affected by the density of the forest (two–sided / symmetric competition) while the relative size of the tree compared to others (one-sided / asymmetric competition) is of less importance. One reason for this could be that the majority of the sample trees were considerably taller than the surrounding trees; hence lack of sunlight was not a problem to them. Another potential reason is that because of the dry conditions in the study area the basal area is generally low and the forest is quite open, suggesting that the main limiting factor for growth of *B. spiciformis* trees is not light but access to water. In addition, as a consequence of the dry conditions, many trees do not grow very tall. Therefore the depth of tree crowns is limited (2-4 metres) for most trees and the shade cast by the crowns is therefore not dense enough to really hamper the growth of smaller trees.

4.2 Effects of site/soil on growth

Across all the tested models including soil texture, either in the form of continuous variables describing fractions such as clay and silt or as dummy variables for particular soil texture classes, the percentage of silt appeared to be the strongest indicator of tree growth. Immediately, the negative sign of the parameter estimates of silt are surprising, but it emerges that silt and clay percentages are both positively correlated with elevation (silt: r=0.38, P=0.03; clay: r=0.31, P=0.07), whereas sand percentage is negatively correlated with elevation (r=-0.42, P=0.01), indicating that soils with the highest Cation Exchange Capacity and water retention capacity are found at higher elevations, whereas poorer soils are found in depressions and valleys. However, since the precipitation in the area is very low, sites offering the best conditions for growth may be found in depressions where the ground water table is likely to be closer to the surface and, most likely, silt therefore acts as a proxy for plot location. Models including silt percentage (Table 3) exhibited only small variation of the associated parameter estimate with values that were generally about -0.03. This stability is presumably a consequence of the fact that silt percentage is the only model element describing basic site characteristics and is almost uncorrelated with the other variables in the models.

4.3 Effects of climate on growth

The positive sign of all parameter estimates associated with rainfall implies that growth generally increased with increasing rainfall (Figure 5). The rainfall of two individual months, October and December of the year before the growth season, had significant influence on growth. This indicates that Miombo woodland vegetation depends both on early rains and the rains that fall during the core of the growing season (Trouet *et al.*, 2006). In the study area the month of October is dry in most years but in some years the rainfall is 20-40 mm, and the correlation with the rainfall in November (r = 0.34, n = 67) is high. The rainfall in December is considerably greater (up to 200-300 mm in some years), thus explaining the smaller values of the parameter estimates characterising this month, and the variation of rainfall is greater than for any other month of the year. Finally the coefficient of correlation between rainfall in December and total rainfall of the entire growth season (October-June) is high (r = 0.65, n = 67). In the models, the rainfall in October therefore seems to act mainly as an indicator of the duration of the rainy season, whereas December is a strong indicator of the amount of water available to the trees (range 2.8 - 357.8 mm, n = 67) during the growth season. However, considering the possible effects of climate change it is comforting to note that these trees are able to exploit the rain whenever it comes. The performance of models including monthly and quarterly rainfall were similar. The reason for this presumably is that most of the months included in the quarters considered either had no rainfall at all or had rainfall that was highly correlated with the rainfall of the individual months used in the models, as exemplified above for October/November and for December and the whole growth season. Similar results on the influence of rainfall on tree growth have been reported elsewhere in the tropical region (Brienen and Zuidema, 2005).

5 Conclusion

This study provides a comprehensive set of individual tree growth models for estimating the diameter increment of the important Miombo species *B. spiciformis*. Apart from models with diameter as the only independent variable, models were also prepared that included effects of site (soil texture), climate and competition. In general, climate (rainfall) had a strong positive effect on growth while competition had a marked negative impact on the growth of *B. spiciformis* trees. For model users the choice between the models will depend on application, objectives and data availability. Based on the fact that *B. spiciformis* is only one of the important species of the Miombo we conclude that there is a need to study the growth of other Miombo species to support sustainable management of this forest type.

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PAPER V

Carbon storage and sequestration in a dry Miombo woodland area in Tanzania

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Abstract

There is a growing need both politically and academically for knowledge on carbon storage and sequestration potentials of forest ecosystems and their contribution to the global carbon balance. This study assessed carbon stocks and sequestration potential of a 6,065 ha dry Miombo woodland site in Iringa Rural District, Tanzania. The carbon stock for each of the six pools; trees, shrubs, deadwood, grasses and herbs, surface litter and soil were estimated. In addition the aboveground carbon sequestration potential was estimated by applying biomass and diameter growth models developed for *Brachystegia spiciformis* Benth to a dataset of trees and shrubs with diameter > 5 cm measured from 35 circular plots across the forest. Assuming a 50% carbon share of biomass, the results show that the carbon stock for trees was 24.71 Mg C ha^{-1}, shrubs 10.88 Mg C ha^{-1}, deadwood 0.59 Mg C ha^{-1}, grasses and herbs 0.58 Mg C ha^{-1}, and surface litter 2.47 Mg C ha^{-1}. Soil carbon was estimated separately for two depth ranges: 0-15 cm and 15-30 cm below the surface. These soil strata contributed 21.25 Mg C ha^{-1} and 8.22 Mg C ha^{-1}, respectively. The total carbon (C) stock of the six pools was found to be 68.64 Mg C ha^{-1}. Based on the 35 sample plots, the estimated carbon sequestration potential of *B. spiciformis* trees alone varied between (mean ± std. error) 0.06 ± 0.02 Mg C $ha^{-1}year^{-1}$ (with the maximum silt percentage observed, 38 %) and 0.19 ± 0.05 Mg C $ha^{-1}year^{-1}$ (with maximum rainfall in October, 42 mm, and December, 358 mm). At the forest level, assuming that other species' production are equal to *B. spiciformis*, the estimated carbon sequestration potential varied from 0.42 ± 0.03 Mg C $ha^{-1}year^{-1}$ to 1.39 ± 0.08 Mg C $ha^{-1}year^{-1}$. Considering the vast area covered by dry Miombo woodlands in Tanzania and in ten other countries in South-Eastern Africa, the carbon storage and sequestration potential in this ecosystem is clearly tremendous, which underscores the importance of conserving them.

Key words: *B. spiciformis*, Biomass, Carbon pools, Climate change, Deforestation, REDD+

1. Introduction

There is a growing need for information about carbon cycling in forest ecosystems and its contribution to global climate change mitigation (Lorenz and Lal, 2010). Dryland forests, especially the Miombo woodlands in East, Central and Southern Africa, are some of the forest ecosystems for which the carbon cycle is still poorly understood (Grace et al., 2006; Williams et al., 2007; Ciaiset al., 2011). Covering a total area of about 3.6 million km^2 in the 10 countries where Miombo woodlands dominate they suffer annual losses of about 1.4 million ha through deforestation and forest degradation (Campbell et al., 2007). Given the large areas covered by Miombo woodlands and considering the heavy disturbances affecting them (Mayaux et al., 2004; Kituyi et al., 2005), detailed studies are needed to understand their CO_2 exchange with the atmosphere and suggest appropriate mitigation measures (FAO, 2006; Munishi et al., 2010).

Covering about 15% of the global land area, it is estimated that tropical forests account for 27% of the global terrestrial carbon stock in biomass and soils (Dixon et al., 1994; Grace 2004; Robinson, 2007; Lewis et al., 2009). However, recent studies have suggested that through deforestation, tropical forests are contributing about 6-17% of total greenhouse gas emissions to the atmosphere (van der Werfet al., 2009; Baccini et al., 2012). Burning and clearing of land for agriculture are among the major causes of these carbon emissions, transferring about 0.9-2.2 PgC per year to the atmosphere (Geist and Lambin, 2002; Houghton, 2010; Fisher, 2010; Baccini et al., 2012). Finding a way to prevent this loss and sustain the carbon stored in tropical forests, has been a challenge and will presumably remain so for many years.

The United Nation's scheme for Reducing Emissions from Deforestation and Forest Degradation (REDD+), which includes conservation and sustainable management of forests as well as the enhancement of forest carbon stocks in developing countries, was initiated in the attempt to provide a solution to the problem (Mountinho et al., 2005; Miles and Kapos, 2008; Funder, 2009). This scheme is intended to compensate countries for avoided deforestation. However, for a country to benefit from the REDD+ mechanism, an accurate quantification system is required such that verifiable emission levels may be reported to the United Nations Framework Convention for Climate Change (UNFCCC, 2009). Among others, this requires the determination of reference levels including reliable ground data on forest carbon stocks and changes in stocks (Henry et al., 2011). Due to the limited number of studies emphasising carbon stocks in Tanzanian forests, such reference data are generally lacking (Munishi and Shear, 2004; Munishi et al., 2010; Shirima et al., 2011). Lack of reference data is thus becoming a challenge for the country to benefit from the REDD+ scheme as a measure for curbing the possibly escalating deforestation rate (Makundi, 2001).

Previous studies on carbon stocks in Miombo woodlands focused on major carbon pools such as trees (Munishi et al., 2010), trees and herbaceous vegetation (Shirima et al., 2011), trees and soil (William et al., 2008), grasses (Chidumayo and Kwibisa, 2003) and tree stems, saplings, roots and soil (Ryan et al., 2011). However, little is known about the importance of other carbon pools, including shrubs, surface litter and deadwood (FAO, 2006) despite their possible importance in areas where Miombo woodlands is the dominant vegetation type. Also little is known about the capability of Miombo vegetation to sequester carbon from the atmosphere due to lack of increment data for most tree species found in Miombo woodlands. Thus a quantification of carbon stored in these pools and an estimation of the sequestration potential of the entire forest will allow for a better understanding of the extent to which carbon can be lost to the atmosphere or sequestered by the vegetation. Similarly, reference data on all carbon pools from relatively undisturbed sites are needed to shed light on the full potential of degraded dry Miombo woodlands as carbon sinks. Finally, such reference data forms a partial basis for developing better conservation strategies.

The objectives of this study were thus to quantify organic carbon in living and dead organic matter, namely trees, shrubs, herbaceous plants (grasses and herbs), surface litter, deadwood and soil to a depth of 30 cm in a dry Miombo woodland site in Iringa, Tanzania. Furthermore the study seeks to estimate the sequestration potential of dry Miombo woodland. Specifically the study aimed to: 1) quantify the amount of carbon stored above ground in the vegetation: trees and shrubs with Dbh ≥1cm and herbaceous vegetation (grasses and herbs), 2) quantify the amount of carbon stored in dead organic matter: deadwood and surface litter, 3) quantify the amount of organic carbon stored below ground: soil carbon in the depth ranges 0-15 cm and 15-30 cm, and 4) estimate carbon sequestration potential of *Brachystegia spiciformis* Benth trees and the forest as a whole.

2. Material and methods

2.1 Study site

Gangalamtumba Village Land Forest Reserve (GVLFR) is located in central-southern Tanzania (latitude 7°35'South; longitude 35°35'East), about 30 km north of Iringa Municipality, the administrative capital of Iringa Region (Figure 1). The forest covers 6,065 hectares and forms part of Mfyome village which is located in the ward of Kiwele about 24 km from Iringa town. The forest is located in a relatively flat area at 850-1,300 m above sea level, which in the 50-year period from 1960 to 2009 received an average annual rainfall (mean ± standard error) of 617 ±17mm (range: 448-1085 mm). The vegetation of this forest can be described as dry Miombo woodland and the soil is relatively fertile. The annual mean temperature is 19.8°C and the Relative Humidity at 0600 GMT and 1200 GMT are 53.9 and 51.4 %, respectively.

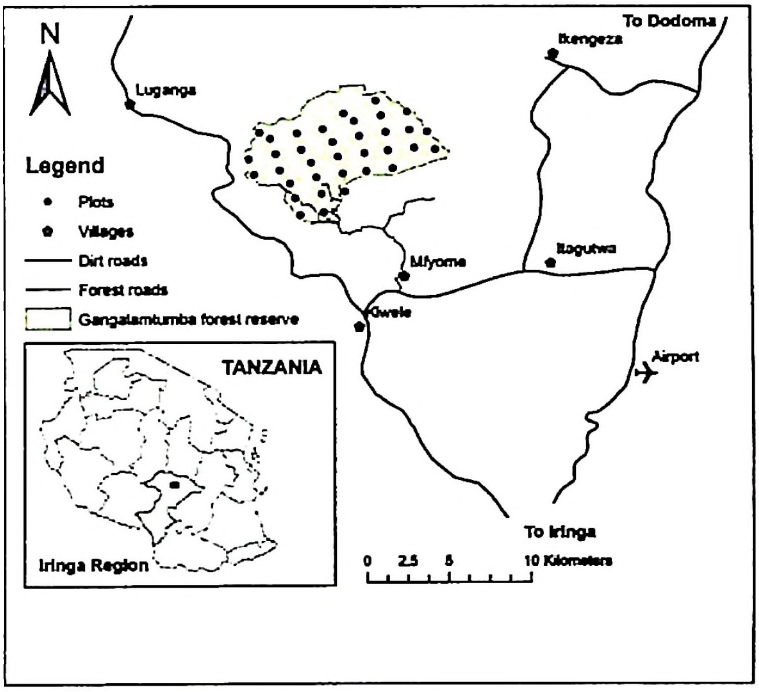

Figure 1. Map of Tanzania showing the location of study area and sample plots in the Iringa region.

The forest has been under decentralized management by the Village Environmental Committee under the Village Government since 2002 and formed part of studies into the socio-economic and biophysical effects of participatory forest management in Tanzania (Lund and Treue, 2008; Ngaga et al. 2013; Treue et al. 2014; Lund et al. 2014). These studies generally conclude that the estimated annual growth equals or exceeds the estimated annual outtake of woody biomass.

Accordingly, this particular forest presents a case of what is possible and has in fact been achieved in terms of Miombo forest conservation through sustainable utilization.

2.2 Field sampling

2.2.1 Trees and shrubs

The field survey was conducted in July and August 2009 and involved establishment of 35 nested circular sample plots with radii of 5 m (0.0079 ha) and 15 m (0.0707 ha) across the 6,065 ha forest (Mwakalukwa et al., 2014a). Plots were established along transect lines and the distance between plots was approximately 2 km. For the two carbon pools, trees and shrubs, the following parameters were assessed in each plot: Within the 15 m radius, all trees and shrubs with Dbh ≥ 5 cm were measured and identified to species level, and within the radius of 5 m all saplings (trees and shrubs, ≥1 cm and < 5 cm Dbh) were counted, measured and identified to species level. Identification of species relied on the knowledge of local botanists but was also confirmed by experienced botanists from Tanzania Forest Research Institute (TAFORI) based at Lushoto Silviculture Research Station. Most of the botanical identification work was done in March 2010 but additional work was carried out in March 2011. For species that were difficult to identify in the field, samples were taken to the herbarium at Lushoto Silviculture Research Station for re-identification. In this study, tree and shrub categories were defined on the basis of the botanical description or habit of the species. Plots were used for estimating carbon sequestration potential of *B. spiciformis*, the most common and dominant tree species in the study site, and the entire woodland area.

2.2.2 Dead wood

This study considers dead wood to include all non-living woody biomass not contained in the surface litter or soil carbon pools, either lying or standing on the ground within a radius of 15 m from the plot centre. Fallen branches and downed logs were collected and tied together into piles. Their fresh weight was measured in the field using a spring balance and sub-samples were taken from each pile. The fresh weight of sub-samples was measured in the field and the dry weight was measured at the laboratory. Subsequently ratios of dry to fresh weight were calculated and used in estimation of the total dry mass of deadwood.

2.2.3 Herbaceous vegetation and surface litter

Nine square sub-plots with a size of 0.5 m × 0.5 m were laid out. One of these sub-plots was located at the centre of the circular plot and eight were located 10 m from the centre in eight cardinal directions, North, Northeast, East, Southeast, South, Southwest, West and Northwest. All standing herbaceous vegetation (grasses and herbs) rooted within the sub-plots was cut at the ground level, the fresh weight was measured by digital kitchen balance in the field, and the material was packed in paper bags. The square sub-plots were also used for collecting surface litter specimens. All surface litter objects < 2.5 cm in size/length found above the mineral soil were collected, packed in paper bags and measured for fresh weight by digital kitchen balance in the field. Sampling was done carefully to prevent contaminating the material with mineral soil. All materials were brought to the laboratory as it was not possible to prepare composite samples in the field.

2.2.4 Soil sampling

Five soil samples were extracted in each depth interval (0-15 cm and 15-30 cm). One of the samples was located at the centre of the plot and four were located at a distance of 10 m from the centre in four cardinal directions, North, East, South and West. The samples were taken within the square 0.5 m × 0.5 m sub-plots where herbaceous vegetation and surface litter were collected. All samples were mixed thoroughly in the field in order to prepare a single composite sample per depth range and plot, and sub-samples were taken for determination of total organic carbon. A total of 70 composite soil sub-samples (35 at a depth of 0-15 cm and 35 at a depth of 15-30 cm) were collected from the 35 plots. In addition, a soil core device with an inner diameter of 5 cm and a length of 5 cm was used for soil bulk density sampling in each depth range, 0-15 and 15-30 cm. These soil cores were extracted at the centre of each plot. Hence, two samples were collected per plot, yielding a total of 70 soil samples for bulk density determination.

2.3 Laboratory analysis

In the laboratory, all deadwood samples collected were oven-dried at 103 ± 2 °C to constant weight, and their oven-dry weight measured. For herbaceous samples and surface litter, all samples were examined in detail, and mineral materials were removed. Samples were then dried to constant weight at 50 ± 2 °C and their oven-dry weight recorded. Next, the 9 samples per plot were ground to a particle size < 2 mm and 10 % of each sample was taken and mixed thoroughly with material from the eight other samples using the grinder. This way, one composite sample was prepared for each plot, yielding a total of 35 composite samples for herbaceous materials and 35 composite samples for surface litter. These samples were ground to a particle size <1 mm (c.f. Reuter et al., 1997 in McKenzie et al., 2000) to allow adequate mixing and sub-sampling for chemical analysis. The finely ground powder from each sample plot was analysed for total carbon using the dry combustion method (Dumas method) in a Leco CSN 2000 analyzer (Matejovic, 1993).

Soil samples were passed through a 2 mm sieve to remove stones and gravel. Fine and coarse roots were removed too. Afterwards, subsamples of 10 g were ground in an agate mortar to a final particle size < 1 mm and analysed for total organic carbon by the dry combustion method (Dumas method) using the same equipment as for herbaceous vegetation and litter. Soil samples extracted for bulk density determination were oven dried at 103 ± 2 °C to constant weight and the dry weight was recorded. The bulk density (gcm^{-3}) was determined as the ratio of dry weight to volume of the soil core, which was calculated as the product of length and cross-sectional area.

The fine fraction bulk density is critical when converting soil nutrient and carbon measurements to a mass-per area basis for nutrient budgets and carbon balance studies (Maynard and Curran, 2008, p.864). Since the usual practice is to analyse for soil nutrients and organic carbon and nitrogen for the fraction of particles <2 mm it was necessary to determine the bulk density of this fraction. This was calculated as the ratio of weight to volume of fine soil (<2 mm) and expressed in the unit gcm^{-3}. The weight of fine soil was determined by measuring the weight of fine and coarse particles/stones (>2 mm) separately after sieving, while the volume of fine soil was determined by subtracting the volume of stones from the total volume of the soil core. The volume of stones (>2 mm) was calculated by dividing the weight of stones (>2 mm) by a standard bulk density estimate for stones (the particle density), 2.65 gcm^{-3} (Landon, 1991, p.77). Most soil analyses were conducted at the Laboratory of Forest Biology, Sokoine University of Agriculture (SUA), Tanzania, but analyses of organic carbon and nitrogen were conducted at the Soil Science laboratory at the Department of Forest and Landscape (now the department of Geosciences and Natural Resource Management), University of Copenhagen in Denmark.

2.4 Statistical analyses

2.4.1 Trees and shrubs

As a basis for assessing carbon stocks and sequestration potentials in living trees and shrubs the woody biomass of these pools was estimated using biomass equations developed by the authors based on data from the same study site (Mwakalukwa et al., 2014b):

For trees: $ln(B, kg/tree) = -2.0667 + 2.3561 \times ln(Dbh, cm)$ ....(1)

$R^2 = 0.979$, RMSE = 0.213, Dbh range: 1.4-62 cm, n = 72.

For shrubs/small trees: $ln(B, kg/tree) = -1.7179 + 2.2697 \times ln(Dbh, cm)$ ....(2)

$R^2 = 0.977$, RMSE = 0.265, Dbh range: 1.8-21.5 cm, n = 32.

For *B. spiciformis*: $ln\ (B,\ kg/tree) = -2.6071 + 2.0638\ ln\ (Dbh,\ cm) + 0.7847 ln\ (Ht,\ m)$ ....(3)

$R^2 = 0.998$, RMSE = 0.127, Dbh range: 1.2-54.3 cm, n = 40;

Where *B* is biomass; *Dbh* is diameter at breast height (1.3 m above ground level); *Ht* is height; RMSE is the root mean square error of the residuals; R^2 is the coefficient of determination; n is the total sample size and *ln* is the natural logarithm. For all living trees and shrubs, the carbon content was estimated as 50% of biomass (Gibbs et al., 2007; Shirima et al., 2011). The estimation of carbon stocks was done separately for each plot and the results were averaged and expressed in Mg C per hectare.

To estimate the annual growth and carbon sequestration of individual trees and the overall population of trees and shrubs in the GVLFR, we applied models relating total height, bark thickness and diameter under bark to diameter at breast height (on bark) in combination with growth models describing annual diameter increment as influenced by diameter, soil texture (Silt %), competition (total basal area) and rainfall. The growth models were developed by the authors using tree ring data for a dominant tree species, *Brachystegia spiciformis*, in the same forest (Mwakalukwa et al ... *in prep* (b)):

Bark thickness: $ln(Bark\ thickness,\ mm) = -1.6536 + 0.7155\ ln\ (Dbh,\ mm)$ ....(4)

$R^2 = 0.946$, RMSE = 0.186, df = 38.

Diameter under bark (mm): $ln(D,\ mm) = -0.77697 + 1.09414\ ln(Dbh,\ mm)$ ....(5)

$R^2 = 0.994$, RMSE = 0.090, df = 38.

Total tree height (m): $ln(Height,\ m) = 0.89606 + 0.49119\ ln(Dbh,\ cm)$ ....(6)

$R^2 = 0.942$, RMSE = 0.132, df = 38.

$ln(\Delta d,\ mm) = -0.08915^{*} + 0.19902\ ln(D,\ mm) - 0.00318(D,\ mm)$ ....(7)

$R^2 = 0.048$, RMSE = 0.691, n = 35, N = 2773.

$ln(\Delta d, mm) = 0.37096 + 0.19428\, ln(D, mm) - 0.00316(D, mm) - 0.03056(silt, \%)$ ....(8)

$R^2 = 0.053$, RMSE $= 0.691$, $n = 35$, $N = 2773$.

$ln(\Delta d, mm) = -0.28008 + 0.22444\, ln(D, mm) - 0.00309(D, mm) + 0.00868(Rain10, mm)$
$+0.00046(Rain12, mm)$ ....(9)

$R^2 = 0.036$, RMSE $= 0.699$, $n = 35$, $N = 1561$.

$ln(\Delta d, mm) = -1.70640^{*} + 0.6925 ln(D, mm) - 0.0050(D, mm) - 0.0332(tba, m^2ha^{-1})$ ....(10)

$R^2 = 0.210$, RMSE $= 0.556$, $n = 25$, $N = 125$.

Here *ln(Δd)* is the diameter increment under bark, *D* is diameter under bark, *Rain10 and Rain12* = Rainfall in October and December of the previous year, respectively, and *tba* = is total basal area. n is the number of groups (sample size); and N is the number of observations/growth rings.

Using the *Dbh* measured in the field; tree height estimated using the regression of height on *Dbh* (model 6) and the biomass (model 3), the initial total aboveground biomass and carbon (50% of biomass) of *B. spiciformis* trees were estimated for each individual. Then, using the growth models (7-10) and conversion between over-bark and under-bark diameters (Model 5), an updated diameter estimate was calculated and applied to estimate new tree height, total aboveground biomass and carbon for each tree one year later. By calculating the increments of biomass and carbon from year to year and summing up estimates for all trees within each of the 35 plots, plot-level estimates of the above ground biomass increment per year (Mg $ha^{-1}year^{-1}$) and carbon sequestration potential of *B. spiciformis* (Mg C $ha^{-1}year^{-1}$) were obtained. Finally, the plot-level results were averaged to obtain a forest-level estimate. A similar analysis was conducted for the forest as a whole using biomass models 1-3 for the respective categories of woody plants and assuming that models 4-10 developed for *B. spiciformis* were also valid for other species. Statistical analysis was carried out in R software version 2.13.0 (www.r-project.org) and Excel spreadsheets.

2.4.2 Deadwood, litter and herbaceous vegetation

For deadwood, total dry mass was computed as the product of the total weight measured in the field (kg) and the ratio of oven-dry to field weight estimated for subsamples. The final results were then converted into carbon by multiplying total dry mass with a carbon percentage of 50%, c.f. above. For grasses and herbs (herbaceous vegetation), the average dry mass per unit area (kg m^{-2}) for each of the 35 plots was computed on the basis of the average dry mass of grasses and herbs from the 9 sub-plots (0.25 m^2 each) sampled within each plot. After converting the estimate into Mg ha^{-1}, the average dry mass for each plot was converted into carbon using the carbon percentage estimated for a composite sample of herbaceous vegetation from all 9 sub-plots. The final result (Mg C ha^{-1}) was computed as the average of the carbon densities estimated for the 35 plots. The same procedure was applied for determination of the average carbon density of the surface litter.

2.4.3 Soil

Root biomass and organic carbon contents for the soil fraction ≥2 mm (stones) were ignored (Vesterdal et al., 2002). Soil organic carbon (SOC) contents (Mg C ha^{-1}) for the fine soil (<2 mm) was estimated for each of the two soil strata, 0-15 cm and 15-30 cm below the surface, and was calculated as $SOC_i = p_i \times (1-s) \times d_i \times C_i \times 100\ Mg\ cm^2\ ha^{-1} g^{-1}$ where p_i is the bulk density (g cm^{-3}) of the fine soil fraction, s is the relative volume of the coarse particle fraction ≥2 mm, d_i = 15 cm is the thickness of stratum i, C_i is the C concentration in layer i, and the coefficient $100\ Mg\ cm^2\ ha^{-1} g^{-1}$ is included to convert the unit of measurement from g cm^{-2} to Mg ha^{-1}.

3. Results

3.1 Carbon stocks in GVLFR

Results for the six carbon pools assessed in the forest are presented in Table 1. For trees and shrubs/small trees a distinction was made between individuals with Dbh <5 cm and >5 cm. This was done to enable comparison with other studies. The greatest contributions to total carbon density of the forest were those of living trees and the upper 15 cm of the soil; the smallest contributions (1 % each) were those of deadwood and herbaceous vegetation.

Table 1. Mean carbon densities with standard errors for six carbon pools in GVLFR (n=35). Numbers in brackets indicate the range of values observed.

Type of Carbon pool	Category	Dbh (cm) mean ±stderror [range]	C density (Mg C ha^{-1}) mean± std.error [range]	Share %
1. Trees				
	≥5 cm Dbh	10.88±0.19 [5-59]	23.55±1.88 [2.60-46.89]	
	1-5 cm Dbh	2.98±0.07 [1-4.9]	1.16±0.21 [0 -5.14]	
	All ≥1cm Dbh	9.8±0.18 [1-59]	24.71±1.83 [4.36- 46.96]	36
2. Shrubs/small trees				
	≥5 cm Dbh	7.60±0.11 [5-23.8]	7.39±1.11 [0 - 28.93]	
	1-5 cm Dbh	2.49±0.05 [1-4.9]	3.49±0.59 [0 -13.33]	
	All ≥1 cmDbh	5.5±0.10 [1-23.8]	10.88±1.23 [0.02- 31.63]	16
3. Herbaceous vegetation (Grasses and Herbs)	-	-	0.58±0.05 [0.27-1.61]	1
Above ground, living Sub-total			*36.17±2.10* *[6.19-60.54]*	*53*
4. Deadwood	-	-	0.59±0.07 [0-1.68]	1
5. Surface litter	-	-	2.47±0.15 [0.63-4.71]	4
Above ground, dead Sub-total			*3.01±0.19* *[0.63 – 6.29]*	*4*
6. Soil				
	Depth 0-15 cm	-	21.24±0.84 [11.3-31.64]	31
	Depth 15-30 cm	-	8.22±0.38 [3.81-13.98]	12
Belowground Sub-total			*29.46±1.01* *[18.73 – 43.93]*	*43*

Grand total	-	-	***68.64 ± 2.58*** ***[33.12 – 99.76]***	***100***

3.1.1 Carbon stocks in trees

The results for mean carbon density of trees (Table 1) show that the largest proportion (95%) of the tree carbon density was found in trees with Dbh ≥5 cm. As shown in Figure 2 trees with diameters between 10 and 30 cm contribute a large proportion of the total carbon density of trees. The three most dominant species with Dbh ≥5 cm; *Commiphora africana* (16%), *Brachystegia spiciformis* (13%) and *Acacia* sp. (11%) stored as much as 40% of the tree carbon. The remaining 60% of the tree carbon was accounted for by 47 other species. Similarly, for trees with Dbh ≥1 cm, the largest proportions of tree carbon were observed for *Commiphora africana* which contributed 15%, *Brachystegia spiciformis* (12%), and *Acacia* sp. (11%), thus making up a total of 38%. The remaining 62% were distributed to the other 47 species.

3.1.2 Carbon stocks in Shrubs

The estimated mean carbon density for shrubs is presented in Table 1. As for trees, the largest proportion (68%) of the shrub carbon density was found in individuals with Dbh ≥5 cm. However, as shown in Figure 2 a considerable part of the total shrub carbon density is stored in shrubs with diameter <10 cm, whereas for trees the majority of the carbon is found in individuals with diameter ≥10 cm. The three shrub species with Dbh ≥5 cm that stored the largest amounts of carbon were *Dalbergia arbutifolia* Baker (40%) followed by *Hymenodictyon parvifolium* Oliv. (16%) and *Margaritaria discoidea* (Bail.) G.L. Webster (9%). Thus, altogether the three species accounted for 65% of the shrub carbon, while the remaining 35% was distributed among 24 other species. For all shrubs with Dbh ≥1 cm, the four most important species were *Dalbergia arbutifolia* contributing 35%, *Hymenodictyon parvifolium* (11%), *Dichrostachys cinerea* (L.) Wight & Arn (9%), and *Margaritaria discoidea* (8%). The four species thus contributed a total of 63% of the shrub carbon while the remaining 37% was distributed among the other 23 species.

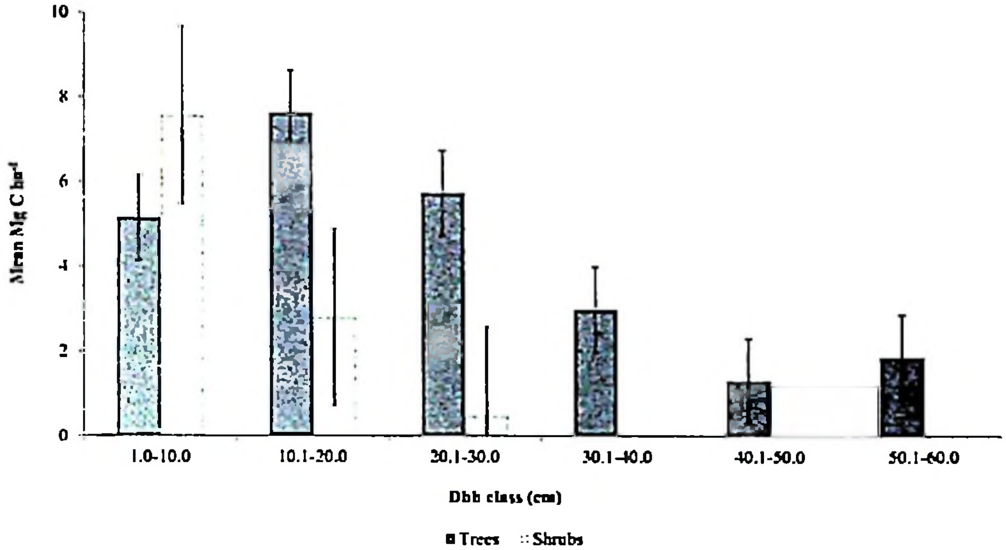

Figure 2. Distribution of mean carbon density for trees and shrubs with Dbh ≥ 1cm by diameter class (n = 35). Error bars indicate standard errors.

3.1.3 Carbon stocks in other pools

Mean carbon densities of the remaining five carbon pools: herbaceous vegetation, deadwood, surface litter and soil (0-15 cm and 15-30 cm strata) are also presented in Table 1. For herbaceous vegetation the mean carbon concentration was 45.75 ± 0.52 % (n=35) and for litter the mean carbon concentration was estimated at 44.45 ± 0.43 % (n=35). With regard to the distribution of carbon across plots a large proportion of the total carbon observed for herbaceous vegetation was found within 4 plots (23%) and the remaining 77% was distributed across 31 plots. A similar observation was made for deadwood where 28% of the total carbon was found within 4 plots. For surface litter, 23% of the carbon was observed within five plots. For soil the largest proportion (72%) of the soil carbon was found within the top 15 cm while the carbon density in the stratum below (15-30 cm) was less than half and contributed only 28% (Table 1). In general, the distribution of carbon in the 0-15 cm stratum across the 35 plots was remarkably uniform, except for 6 plots which exhibited very low values (11.3 – 15.9 Mg C ha^{-1}). By contrast, in the deeper soil stratum (15-30 cm), 11 plots contributed considerably more (41% in total) than the remaining 24 plots (59%). Finally, the soil carbon density of the top layer (0-15 cm) contributed considerably more (31%) to the total carbon density of the forest than the bottom layer (15-30 cm) which contributed only 12%.

When the six pools were combined in three major carbon pools; above ground carbon in living biomass, above ground carbon in dead materials and below ground carbon (soil to 30 cm depth), it emerged that above ground carbon in living biomass contributed slightly more than half (53%) of total carbon, followed by below ground carbon (43%) and lastly above ground dead materials with only 4% (Table 1). Stumps contributed only 2% of the above ground carbon density of dead materials (not shown). Trees and shrubs with stump diameters of 10-30 cm were found to contribute a large proportion of the total carbon density of stumps. The largest shares of the total carbon density of stumps were contributed by *Brachystegia spiciformis* (30%), *Dalbergia arbutifolia* (9%), *Albizia petersiana* (Belle) Oliv. (8%), *Combretum molle* (7%) and *Pterocarpus angolensis* (7%). Altogether the stumps of these species thus contributed 61%, while the remaining 39% were accounted for by 37 other species.

3.2 Carbon sequestration potential of GVLFR

The estimated carbon sequestration potential of *B. spiciformis* is shown in Table 2. Although extrapolation beyond the species *B. spiciformis* is obviously disputable, Table 2 also includes results calculated for the forest as a whole under the assumption that the growth of all other species is similar to that of *B. spiciformis*. At the forest level, the average carbon sequestration potential of *B. spiciformis* varied from 0.06 ± 0.02 Mg C $ha^{-1}year^{-1}$ (model 8b with silt = 38%) to 0.19 ± 0.05 Mg C $ha^{-1}year^{-1}$ (model 9b with rainfall = 42 mm in October and 358 mm in December). When assuming that all 77 species of the forest grow exactly as *B. spiciformis*, the average carbon sequestration potential of the GVLFR was found to vary between 0.42 ± 0.03 Mg

C $ha^{-1}year^{-1}$ (model 8b with silt = 38%) and 1.39 ± 0.08 Mg C $ha^{-1}year^{-1}$ (model 9b with rainfall = 42 mm in October and 358 mm in December).

Table 2. Average carbon sequestration potential (Mean ± std.error) of ***Brachystegia spiciformis*** for all plots (n=35) and for all species (77 species) within all plots assuming that the growth of these species is similar to *B. spiciformis*. The estimates are based on growth models (7-10) presented in the statistical analyses section. Different scenarios are applied, using minimum and maximum values of silt, rainfall and total basal area.

Model no. and scenario[†]	Species included	No. of Plots	Individuals (n)	Dbh range (cm)	Dbh average (cm)	Basal area (m^2ha^{-1})	Carbon sequestration (Mg C $ha^{-1}year^{-1}$)		
							Mean	Min	Max
7 Diameter alone	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.11±0.03	0	0.82
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	0.88±0.05	0.19	1.50
8a Silt min. 5.24%	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.15±0.04	0	1.10
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	1.16±0.07	0.26	2.00
8b Silt max. 38%	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.06±0.02	0	0.40
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	0.42±0.03	0.09	0.73
9a Min. rain. 0 & 2.8 mm	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.11±0.03	0	0.78
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	0.81±0.05	0.18	1.42
9b Max. rain. 42 & 358mm	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.19±0.05	0	1.33
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	1.39±0.08	0.31	2.42
10a Min. Compet. 3.6 m^2ha^{-1}	*B. spiciformis* (1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.15±0.04	0	1.05
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	1.05±0.06	0.20	1.90
10b Max. Compet. 23.3 m^2ha^{-1}	*B. spiciformis*(1)	35	135	5-51.7	13.8±0.74	1.18±0.34	0.08±0.02	0	0.54
	All (77)	35	2133	5-59.0	9.8±0.1	13.55±5.52	0.54±0.03	0.10	0.98

[†] **Symbols: Min. is minimum, Max.is maximum, Compet. is competition.**

4. Discussion

4.1 Carbon storage potential of GVLFR

4.1.1 Carbon stocks in trees

This study found a mean total carbon density for trees with Dbh ≥5 cm of 23.6 ±1.9 Mg C ha^{-1}. Other studies in dry Miombo woodlands have reported mean values between 14.7 Mg C ha^{-1} and

29.9 Mg C ha^{-1} for trees with Dbh ≥5 cm (Ribeiro et al., 2013; Shirima et al., 2011; Ryan et al., 2011; Munishi et al., 2010; William et al., 2008; Chamshama et al., 2004; Woomer, 1993; Frost, 1996, p.24 [using a carbon concentration of 50%]). It thus appears that the observed value of total carbon density for dry Miombo woodland in GVLFR lies within the range of values typically observed in the Miombo ecoregion. However, unlike the cited studies the estimated value only represents a single life form, namely trees (no shrubs), so the carbon density obtained in this study appears to be slightly higher than the values reported by other studies of the Miombo. When the carbon density estimated for shrubs with Dbh ≥5 cm is added (see Table 1), a total value of 30.9 ± 2.1 Mg C ha^{-1}is obtained for GVLFR. This high carbon density may be attributed to a good stocking state of the forest but differences related to the choice of biomass functions or applied sampling approaches cannot be ruled out, and the estimated standard error implies that a 95% confidence interval for the mean would range from 28 to 33 Mg C ha^{-1} so actually the estimate does not appear to differ significantly from the results reported by other studies.

4.1.2 Carbon stocks in shrubs

To the best of our knowledge no studies conducted in the Miombo region have reported separate values of biomass or carbon for shrubs. Based on a study in the Nhambita area in central Mozambique, Ryan et al. (2011) reported a carbon density value of 1.1 Mg C ha^{-1} for all saplings with Dbh<5 cm, regardless of whether they were shrubs or trees. Lufafa et al. (2008) reported total above-ground carbon stock values (living biomass) for shrub communities in a semiarid area in Senegal which ranged from 0.93 to 1.40 Mg C ha^{-1} with an overall mean of 1.12 Mg C ha^{-1}. Based on the results in Table 1 the estimated carbon stock in GVLFR for all trees and shrubs with Dbh in the range 1-5 cm would be 4.65 Mg C ha^{-1}, i.e. considerably higher than the above estimates. In fact, in this study shrubs turn out to have a very significant contribution (10.88 ± 1.23 Mg C ha^{-1}) to the total carbon density of the woodlands (16%, cf. Table 1). It should be noted however, that due to the large variation characterising the forest, the standard error is high but still a 95% confidence interval would not include values of about 1 Mg C ha^{-1}.

4.1.3 Carbon stocks in herbaceous vegetation

Estimates in the literature of the above-ground carbon density of herbaceous vegetation in relatively undisturbed, mixed-aged stands of Miombo woodland range from 0.02 to 1.83 Mg C ha^{-1}, with most of the values reported being less than 0.92 Mg C ha^{-1} (Ribeiro et al., 2013; Frost, 1996 p.26, assuming the same average carbon concentration as in this study: 45.75 %, n = 35). The value of 0.59 ± 0.05 Mg C ha^{-1} obtained in this study is comparable to these estimates but also to that of Shirima et al. (2011), who estimated a value of 0.65 Mg C ha^{-1} for herbaceous vegetation in Miombo woodlands of Nyanganje and Kitonga forest reserves in the Eastern Arc Mountains, Tanzania. Using the same carbon concentration as in the present study (45.75%) mean values ranging from 0.37 Mg C ha^{-1} to 0.64 Mg C ha^{-1} can be derived from biomass estimates for grassy vegetation in dry Miombo woodlands in Lusaka, Zambia (Chidumayo and Kwibisa, 2003). From a dry Miombo site of Niassa National Reserve in Mozambique which receives an average annual rainfall of 900 mm, Ribeiro et al. (2013) reported an average carbon density of 2.03 Mg C ha^{-1} for grasses. The GVLFR estimate is also in agreement with carbon densities commonly found for herbaceous vegetation in semiarid savannas and dry forests, which usually vary between almost zero during the dry season and about 2.29-6.86 Mg C ha^{-1} (assuming a carbon concentration of 45.75%) during the peak of the growth season (Tiessen et al., 1998). The relatively low value observed in this study could be attributed to the presence of dense tree cover as there was no evidence of fire in the plots during the survey in 2009. The fact that the forest is used for grazing and the study was conducted in the dry season might have contributed to the low value. Moreover, based on visual impression from the field it was evident that the ground vegetation cover was low in many of the surveyed plots.

4.1.4 Carbon stocks in deadwood

Only one study by Ribeiro et al. (2013) reported carbon stocks for deadwood in dry Miombo woodlands. They estimated a carbon stock of 0.06 Mg C ha^{-1}. Compared to other dry tropical forests, the value of 0.59 Mg C ha^{-1} (including stumps) estimated in this study is far lower than the values reported by Jaramillo et al. (2003) from dry forest in Mexico which ranged from 13 to 17 Mg C ha^{-1} and by Delaney et al. (1998) from dry forests in Venezuela which were 1.22-3.37 Mg C ha^{-1} (assuming a carbon concentration of 51% as used by Jaramillo et al., 2003). The low carbon density observed for deadwood in GVLFR is likely to reflect the high utilization level of the deadwood by local people living around the forest reserve, who depend on the forest as one of their main sources of energy in the form of firewood and charcoal (see Lund and Treue, 2008 for details on the decentralized management regime). Another reason for the small amounts of deadwood might be fire which occasionally sweeps through the area as also observed by Ribeiro et al., (2013) in their study area and, when it does, removes much of the deadwood. Thus the results suggest that in this area deadwood is not an important carbon pool compared with standing trees and shrubs and the uppermost 30 cm of the soil.

4.1.5 Carbon stocks in surface litter

Only few studies in dry Miombo woodlands have assessed the carbon potential of surface litter. Ribeiro et al., (2013) reported a mean value of 0.06 Mg C ha^{-1} from dry Miombo woodlands in Mozambique, Woomer (1993) reported a mean value of 3.82 Mg C ha^{-1} from dry Miombo woodlands in Zimbabwe while Jaramillo et al. (2003) reported a mean value of 4.56 Mg C ha^{-1} (assuming a carbon concentration of 41.11%) from tropical dry forest in Mexico. Using the same carbon concentration as Jaramillo et al. (2003), the following carbon estimates were obtained for dry Miombo woodlands of Chakwenga, Zambia: 1.07 Mg C ha^{-1}, Marondera, Zimbabwe: 1.33 Mg C ha^{-1} and Nylsvley, South Africa: 0.72 Mg C ha^{-1} (Frost, 1996). Thus, the mean carbon density of 2.47 Mg C ha^{-1} estimated in this study falls within the range of values reported by other studies conducted in dry tropical forest. At any rate, although the estimated standard error of the estimate is low in this study (0.29 Mg C ha^{-1}), the amount of litter is highly sensitive to the frequency and intensity of fire so the relative variation between sites is likely to be high.

4.1.6 Carbon stocks in soil

Reported soil carbon stocks of dry Miombo woodlands (to a depth of 50 cm) range from 16 to 140 Mg C ha^{-1} (Woomer, 1993; Williams et al., 2008; Ryan et al., 2011; Ribeiro et al., 2013). The result obtained in this study, 29.46 Mg C ha^{-1} for soil carbon to a depth of 30 cm, falls within this range and also compares well with the studies by Lufafa et al. (2008) and Woomer et al. (2004), who reported mean values to a depth of 40 cm of 17 and 21 Mg C ha^{-1}, respectively, from a semiarid area in Senegal.

The total carbon stock of 68.64 Mg C ha^{-1} estimated in this study is considerably lower than other estimates reported for dry tropical forest in the literature, e.g. 110 Mg C ha^{-1} for dry Miombo woodlands in Mozambique (Ryan et al., 2011); 141 Mg C ha^{-1} for Mexican tropical dry forest (Jaramillo et al., 2003) and 204 Mg C ha^{-1} for open Eucalypt forest savannas of Northern Australia (Chen et al., 2003). However, these studies included roots and soil carbon to a depth greater than 50 cm, while the present study did not include roots or soil samples below a depth of 30 cm. Moreover, the literature does include examples of carbon stock estimates similar to those obtained in this study. For instance, Woomer et al. (1993) reported a total carbon stock of 48 Mg C ha^{-1} including roots and soil carbon for dry Miombo woodlands in Zimbabwe and Ribeiro et al. (2013) reported a total carbon stock of 67 Mg C ha^{-1} including trees, dead trees, grasses, litter, herbaceous and soil carbon for dry Miombo woodlands in Mozambique.

4.2 Carbon sequestration potential of GVLFR

Although growth models were only available for one of the important tree species of the dry Miombo, *Brachystegia spiciformis*, the study indicated a considerable carbon sequestration potential. In the study area the basal area of *B. spiciformis* was 1.18 m^2ha^{-1} or 8.7% of the total basal area estimated at 13.55 m^2ha^{-1}. In spite of this, the carbon sequestration potential of *B. spiciformis* was as much as 0.06-0.19 Mg C $ha^{-1}year^{-1}$, depending on scenario (Table 2). If all basal area of the forest was equally productive, this would correspond to a carbon sequestration potential of 0.42-1.39 Mg C $ha^{-1}year^{-1}$ depending on scenario (Table 2), which is rather high and greater than the potential estimated for other dry forests (Worbes and Raschke, 2012; William et al., 2008; Chaturvedi et al., 2011). In Worbes and Raschke's (2012) study area, which receives an average precipitation of 1400 mm, they reported that the estimated carbon sequestration potential of the tree layer was 1.7-2.1 Mg C $ha^{-1}year^{-1}$ in different stands. By contrast, from tropical dry forest sites of N'hambita, Mozambique which receives a mean annual rainfall of 690 mm and Kotwa, India which receives a mean annual rainfall of 865 mm, the average carbon sequestration potential of the tree layer were estimated at 0.7 Mg C $ha^{-1}year^{-1}$ and 0.05 Mg C $ha^{-1}year^{-1}$, respectively (William et al., 2008; Chaturvedi et al., 2011).

Immediately, our results may suggest that the carbon sequestration potential of dry Miombo is high compared to other dry forest formations in the tropics. However since growth differs between species, and *B. spiciformis* is one of the largest trees in the forest, develops a relatively dense and deep canopy, and since a lot of other species are shorter-stature, short- and open-crowned species and their diameter increments unknown, our estimates are likely to exceed the true carbon sequestration potential of the dry Miombo woodland. Yet, even if the carbon sequestration potential on dry Miombo is only 0.42 Mg C $ha^{-1}year^{-1}$, corresponding to this paper's lower estimate c.f. above, the vast areas covered by this forest type underscores its climate change mitigation potential.

5. Conclusion

Results from this study show that the dry Miombo woodland of GVLFR stores substantial amounts of carbon, both in above- and below-ground carbon pools. A total of 68.64 ± 2.58 Mg C ha^{-1} (mean ± std. error) was estimated of which trees, shrubs and top-soil (0-15 cm) accounted for 36%, 16% and 31%, respectively. Considering the vast areas covered by dry Miombo woodlands, sustainable management of this vegetation type is clearly important to avoid emission of large amounts of carbon currently stored in this ecosystem. Making use of the 35 plots surveyed the study also examined the carbon sequestration potential of Miombo woodland vegetation, including the effects of soil fertility, climate and competition. Based on the fact that *B. spiciformis* is only one of the important species of the Miombo we conclude that there is a need to study the growth behaviour of other Miombo species so as to provide a better basis for assessing the overall carbon sequestration potential of the Miombo. The values reported in this study were based on diameter increments of *B. spiciformis* alone and the values estimated by extrapolation may therefore exceed the true values although these are still likely to be high given the vast areas covered by Miombo woodlands. From a REDD+ point of view, even degraded Miombo forest appears to hold substantial potential as the carbon stored in shrubs and the top-soil is already significant and may be doubled through improved forest governance, e.g. through decentralized management, which establishes tangible incentives to let trees mature before they are harvested.

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