Dissertationes Forestales 313

Tree growth dynamics and ecological recovery in Kitulangalo miombo woodlands, Morogoro, Tanzania

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Academic dissertation

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This research focuses on stand dynamics and ecological recovery in miombo woodlands, Morogoro, Tanzania. The study uses the Kitulangalo Permanent Sample Plots (PSPs) to analyse tree species' site-specific growth, regeneration dynamics, and stand development using empirical and modeling approaches. The high number of tree species in miombo necessitated the formulation of three species groups involving 1) trees that grow relatively rapidly to be dominants in top canopy layers 2) trees that stay mainly in the lower and middle canopy levels and 3) trees that grow slowly but persistently and may eventually rise to dominant and codominant canopy positions applied in studies I and III. Study III also applies three harvesting alternatives, which align with the recommended harvesting practices for these woodlands.

Diameter increment varied with the change in basal area growth across species groups, reaching a maximum of 3.2 cm (group 1) during 2008-2016. Density-dependent mortality and ingrowth also varied with species group as higher mortality rates dominated the lower and middle canopy layers due to asymmetrical competitions. Fencing the plots prompted thick grass cover. The drop in the total number of regeneration stems and the simultaneous increase in the number of main stems in fenced areas and dense plots indicated a self-thinning process induced by competition. This is linked to multi-stem regeneration undergoing a morphological transformation into single-stem saplings (main stems) and eventually becoming small trees. Harvesting intensity, density-dependent mortality, and ingrowth regulated stand basal area and therefore stand growth and development during the simulation. Stand structural development was dominated by species groups 1 and 2, indicating sustainability in species composition and structures. Stand development was affected by the addition of new stems of each species in each simulation year.

Miombo stands have demonstrated the potential to attain a steady-state condition over the medium-term under-regulated stand conditions and silvicultural treatments. The developed models, treatments, and harvesting alternatives may be limited in application to Kitulangalo and similar lowland miombo woodlands in Tanzania. Future studies concerning stand conditions, silvicultural treatments, and harvesting alternatives are vital for a better understanding of stand dynamics in miombo woodlands in Tanzania.

Keywords: Forest disturbance, tree growth and stand dynamics, regeneration dynamics, silvicultural treatment, harvesting alternative, miombo woodlands

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LIST OF ORIGINAL ARTICLES

This dissertation is based on the following articles (denoted by Roman numbers):

I Elisha E. Njoghomi, Sauli Valkonen & Kristian Karlsson. (**In press**). Analysing species site-specific tree growth dynamics, mortality, and ingrowth in miombo woodlands, Tanzania. **Accepted at** *Southern Forests: A Journal of Forest Science.*

II Elisha E. Njoghomi, Sauli Valkonen; Kristian Karlsson, Markku Saarinen; Wilson A. Mugasha, Celestino Balama, Rogers E. Malimbwi & Pentti Niemistö (2020). Regeneration dynamics and structural changes in miombo woodlands at Kitulangalo Forest Reserve in Tanzania. *Journal of Sustainable Forestry.* https://doi.org/10.1080/10549811.2020.1789478

III Elisha E. Njoghomi, Sauli Valkonen & Wilson A. Mugasha. (Author version Manuscript to be submitted to a Journal for peer review). Simulation of Stand dynamics for Kitulangalo Forest Reserve in Tanzania

AUTHOR CONTRIBUTION

Article I: Elisha Njoghomi and Sauli Valkonen conceptualized the research, Elisha Njoghomi analysed the data in cooperation with the coauthors, including the development of the models in R software to which Kristian Karlsson made a key contribution, Elisha Njoghomi wrote the original manuscript and incorporated the inputs of all authors.

Article II: Elisha Njoghomi and Sauli Valkonen developed the study framework. Rogers Malimbwi and Pentti Niemistö coordinated the fieldwork at Kitulangalo Forest Reserve in Morogoro, Tanzania trough INFORES-Tanzania project. Elisha Njoghomi performed data collection and analysis in cooperation with the coauthors, including the development of non-linear and generalized linear models to which Markku Saarinen and Kristian Karlsson made key contributions. Elisha Njoghomi wrote the original manuscript. Sauli Valkonen, Wilson Mugasha, Celestino Balama, Markku Saarinen, and Kristian Karlsson revised the article.

Article III: Elisha Njoghomi provided the research idea, performed simulation calculations, and wrote the original manuscript. Sauli Valkonen and Wilson Mugasha revised the manuscript.

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1. INTRODUCTION

1.1 Characterization of miombo woodlands

Miombo is the vernacular name to describe deciduous open-canopy woodlands dominated by three closely related tree genera, *Brachystegia*, *Julbernardia,* and/or *Isoberlinia*, belonging to the legume family (Fabaceae, subfamily Caesalpinioideae) (Williams et al. 2008). Their natural range extends across Eastern, Central, and Southern Africa (Trouet et al. 2010), in Mozambique, Malawi, Zambia, D.R Congo, Angola, Namibia, Zimbabwe, and some parts of South Africa (Syampungani et al. 2009)

About 100 million people around Eastern, Central, and Southern Africa depend on miombo woodlands for various forest products and services such as bioenergy, building poles, timber, foods, and medicinal plants (Syampungani et al. 2009). In Tanzania, miombo woodlands are estimated to account for about 93% of the forested land, making it a dominant forest type (NAFORMA 2015).

Generally, miombo woodlands are characterized by the cohabitation of hundreds of tree and shrub species but are dominated by only a few canopy species. The miombo understorey consists of highly variable herbaceous and grass cover (Campbell BM (1996), Chidumayo and Kwibisa 2003), which is affected by variability in annual rainfall (Chidumayo 1997). The climate of miombo is purely semi-arid (Malmer and Nyberg 2008) and its soils are heavily leached (Strømgaard 1992). The rain season prevails between November and April, while the dry season from May to October (Abdallah et al. 2012).

The increased demands for agricultural lands and bioenergy resources (Abdallah et al. 2012, Luoga et al. 2005) have resulted in severe deforestation (Masanja 2013, Nyakata 2014), consequently threatening the sustainability of miombo woodlands. The unsustainable management planning of this vast resource is due to limited and fragmented knowledge, lack of reliable data and tools for modeling vegetation dynamics in miombo woodlands. A detailed understanding of stand dynamics from individual species to landscape-level is therefore essential for sustainable management planning to enhance perpetual production of ecosystem services (Lowore 2006). Tree growth and overall forest dynamics have been scarcely studied in Tanzanian miombo woodlands (Chidumayo 2019, Chiteculo and Surovy 2018, Trouet et al. 2010). Understanding stand dynamics at multiple scales, from individual trees and gaps and small patches to stand level is essential for predicting tree growth and future development of the miombo stands

1.2 Tree regeneration strategies and stand dynamics in miombo woodlands.

Miombo woodlands are believed to have evolved alongside humans in sub-Saharan Africa (Muvengwi et al. 2020). The persistent fire occurrences, harsh climatic conditions, and herbivory have resulted in evolutionary strategies in tree species regeneration (Matowo et al. 2019, Pienaar et al. 2015), which contribute to spatial and temporal vegetation dynamics. The growth dynamics of only a few dominant tree species have previously been studied (Chiteculo and Surovy 2018, Njoghomi 2011, Trouet et al. 2010). The climatic and associated phenological variation in miombo woodlands (Trouet et al. 2010, Wagner et al. 2016) strongly influence the growth dynamics of miombo tree species (Njoghomi 2011). While some species cease their diameter growth during the dry season, other species with strong adaptive features, such as long taproot systems (Luoga et al. 2004), can utilize underground water sources for growth during the dry season (Njoghomi 2011). Asymmetrical competition caused by dominant top canopy species, however, tends to impede the growth of the understorey bushes and small tree species. Valkonen et al. (2008) pointed out that the gaps created by natural tree mortality in different canopy layers reduce competition for growth resources among the trees of different species and sizes in the stand, thus enhancing growth variation within the stand Some species have adapted by the formation of thick bark (Holdo 2005) or by developing an effective tap root system before quickly shooting up beyond the fire risk zone (Luoga et al. 2004). The main regeneration strategy of miombo species is through coppices and suckers (Piiroinen et al. 2008, Ryan and Williams 2011, Syampungani et al. 2015). This type of regeneration occurs when the upper part of the stem is removed through cutting or other mechanical injuries (Luoga et al. 2004).Disturbed miombo trees can produce massive numbers of coppices and suckers (Chidumayo 1988, Njoghomi et al. 2020), but their recruitment is likely to be restricted by low survival due to harsh climatic conditions, annual fires, herbivory, and density-dependent tree mortality (Neelo et al. 2013, Weiskittel et al. 2011). The individual effect of the disturbance agents such as animal grazing, fire, and drought (Bognounou et al. 2010) towards the reduction of the number of individual stems is, however, poorly known particularly for regeneration and tree growth of miombo woodlands of Tanzania. Shades created by the top canopy species can also restrict the recruitment of other light-demanding species in dense stands, thus favouring shade-tolerant species (Higgins et al. 2000). However, the high tree species diversity complicates the study of tree regeneration dynamics and the resulting vegetation changes in their entirety for the miombo woodlands (Mwakalukwa et al. 2014)

The contemporary dynamics of miombo woodland structure and composition (Masanja 2013, Mbwambo et al. 2008, Muvengwi et al. 2020) are strongly influenced by ongoing deforestation activities and other forms of disturbances due to pests and diseases, windstorms, and fires (Ryan and Williams 2011), animal damage and other environmental factors. The main driving forces of deforestation in miombo include wood extraction, shifting agriculture, increased bioenergy demands, fires, landscape fragmentation through urbanization, commercial agriculture, and climate change (Bond et al. 2010, Mwakalukwa et al. 2014, Syampungani et al. 2009).

Deforestation and natural mortality play an important role in the miombo dynamics by changing forest cover, stocking, plant species diversity, composition, and distribution. In the within-stand context, individual-tree mortality due to senescence, diseases, and selective logging tend to create canopy gaps allowing the sunlight to reach the forest floor, thus stimulating seed germination and growth (Schwartz and Caro 2003). Also, these disturbances can affect radial tree growth and therefore other stand parameters such as volume and biomass. Declining live stand biomass affects both the overall functioning of the ecosystem and the conservation of biodiversity and hence ecosystem resilience and therefore the abundance and perpetual supply of ecosystem services for the well-being of the human community (Ribeiro et al. 2015). Understanding stand dynamics from individual trees, gaps, and small patches, cohorts to stand level is crucial for predicting tree growth and stand development, a necessity for the sustainable planning and management of miombo woodlands.

2. AIMS AND STRUCTURE OF THIS DISSERTATION

The general objective of this study was to develop an understanding of the tree and stand growth dynamics and ecological recovery of miombo woodlands in Tanzania. The study is composed of three specific sub-studies (I, II & III) to address the following specific questions.

I. What are the main drivers of tree growth, mortality, and in-growth/recruitment in miombo stands (I)?

II. What are the impacts of fencing, thinning, soil tilling treatments and stand density on regeneration dynamics and recovery in miombo woodlands (II)?

III. What are the alternative pathways for maximizing stand growth, wood production and ecological recovery in miombo woodlands (III)?

In the following, the three articles (I-III) are referred to as studies. In the first study (I), I used results based on empirical data and modeling to analyse the site-specific growth, mortality and in-growth of tree species at Kitulangalo Forest Reserve (KFR). In the second study (II), with the use of results based on empirical data and modeling, I evaluated the impacts of silvicultural treatments and stand conditions on regeneration dynamics in KFR. This study further elucidates the causes and severity of regeneration damage, stem vigour and rate of colonization of the empty subplots using empirical data. Thirdly (study III), I predicted the future stand development of KFR sites using a whole-stand simulation system focusing on stand density, basal area growth, volume, and accumulation of above-ground biomass and carbon.

3. MATERIALS AND METHODS

3.1 Study areas

3.1.1 Geography, climate and soils

This study was conducted at Kitulangalo Forest Reserve (KFR) in the Morogoro region, Tanzania. KFR is located at -6^0 52’S and 37^0 38’N at an altitude of 300 m above sea level and spans a total of 1700 ha (Figure 1). Most of the area of KFR (1200 ha) is owned and managed by the Tanzania Forestry Services Agency (TFS), while the rest (500 ha) belongs to the Sokoine University of Agriculture (SUA), which uses it for training and research purposes. The reserve is surrounded by four villages, Maseyu, Gwata, Lubungo, and Ujembe, having an estimated total population of 5280 according to the 2012 National Census in Tanzania.

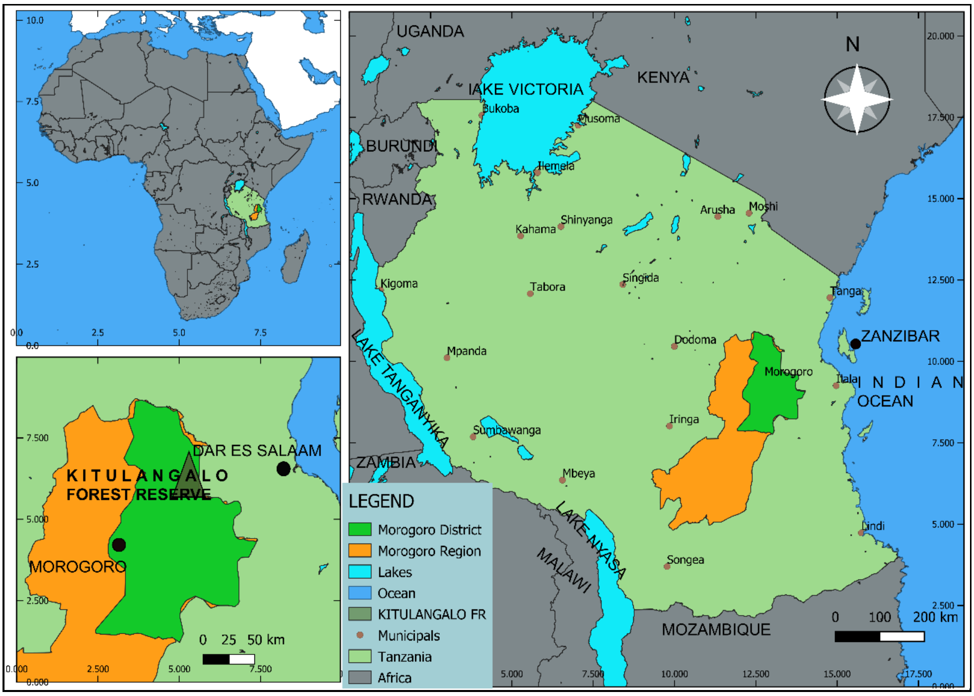

Figure 1. The location of the study area at Kitulangalo Forest Reserve in Morogoro District in Tanzania.

The vegetation at KFR is classified as dry miombo woodlands with an average annual precipitation of 500 -750 mm. The climate of the study area is semi-arid, with some transitional characteristics of the coastal mosaic woodland species. The vegetation cover at KFR consists of three main canopy layers whereby the top canopy cover is dominated by *Julbernardia globiflora* and *Brachystegia species*. The middle and lower canopy layers are, however, dominated by various short and medium-sized multi-stem trees such as *Combretum* species, *Dalbergia* species, *Commiphora* species. The riverine area on the other features some evergreen species such as Malinkara species (*Malinkara mochisia*, *M.descolor),* and *Maytenus species* (Luoga et al. 2000).The dry season ranges from 4 to 7 months, with a mean annual monthly temperature range of 21 to 25 °C (Petro et al. 2005). Degradation threats to KFR have been attributed to its vicinity to Morogoro and Dar es Salaam, the major cities with their huge charcoal demands, and its neighbourhoods, to local communities with poor livelihood alternatives.

3.1.2 Experimental design and measurements

Two experimental stands were established in February 2007 in miombo forests at Kitulangalo Forest Reserve approximately 500 m apart from each other on the land of the Sokoine University of Agriculture Training Forest (SUATF) and the Tanzania Forest Service (TFS). The two stands were subjectively selected. The experimental design represented a split-plot approach consisting of three hierarchical levels (stand, block, and plot). Each stand had two blocks: one fenced to keep cattle and other large mammals out, and the other unfenced. Each block had three main sample plots, each of which 30 x 30 m (0.09 ha) in size. Hence, the total size of each block was 30 x 90 m (0.27 ha). The 12 plots situated in the two stands (6 per stand) covered a total area equivalent to 1.08 ha. For regeneration inventory, a grid of 25 circular subplots with a radius of 1.1 m was established on each main sample plot, thus each experimental stand contained 150 regeneration subplots.

Silvicultural treatments were randomly drawn for each main sample plot within the blocks. We studied the effect of thinning on stand dynamics (study I), and that of fencing and soil tilling on regeneration (study II). Thinning was used to create gaps in the canopy, decrease inter-tree competition, and remove less economically valuable and undesirable tree species, e.g., *Diplorhynchus condylocarpon* and *Combretum collinum*, to promote the growth of economically more valuable species. The thinning out was between 10 to 20% of the stand basal area on the plots. Furthermore, thinning was applied to promote coppicing and suckering from the cut stumps, while the soil tilling treatment as a means to stimulate regeneration through enhanced germination from the seed bank as well as through suckering/sprouting from the side-roots wounded in the process of tilling. Measurements were carried out in 2007, 2008, and 2016 for monitoring tree growth (study I) and regeneration (study II).

3.2 Conceptual framework of the study

This study was motivated by the lack of knowledge on tree growth and stand temporal dynamics of miombo as well as the need for more reliable empirical data and appropriate modelling approaches in order to develop tools to predict the present and future development of miombo woodlands sustainably in Tanzania. According to the input data and information flow in the conceptual framework of this study (Figure 2), the models can be grouped into four types: 1) regeneration dynamic models, 2) stand attribute models, 3) stand development models, and 4) whole stand matrix system models based on the empirical permanent sample plot (PSP) data.

Regeneration dynamic models were used to evaluate the impact of treatments and stand density, basal area, grass cover and initial number of regeneration stem conditions as explanatory variables to study the dynamics in several regeneration subplots. Stand attribute models were used to study height-dbh and crown-width relationships with species groups and measurement times serving as explanatory variables. Respectively, the tree-level stand development models used species groups and basal area to predict the diameter increment of the trees. The species groups, density-dependent tree mortality and ingrowth, harvesting alternatives, and the stand development models were used as supporting information and tools in the development of the whole stand matrix system. The four model groups aimed to generate comprehensive information regarding the growth and stand dynamics of miombo, which is essential for the sustainable development of KFR and other similar forests in Tanzania

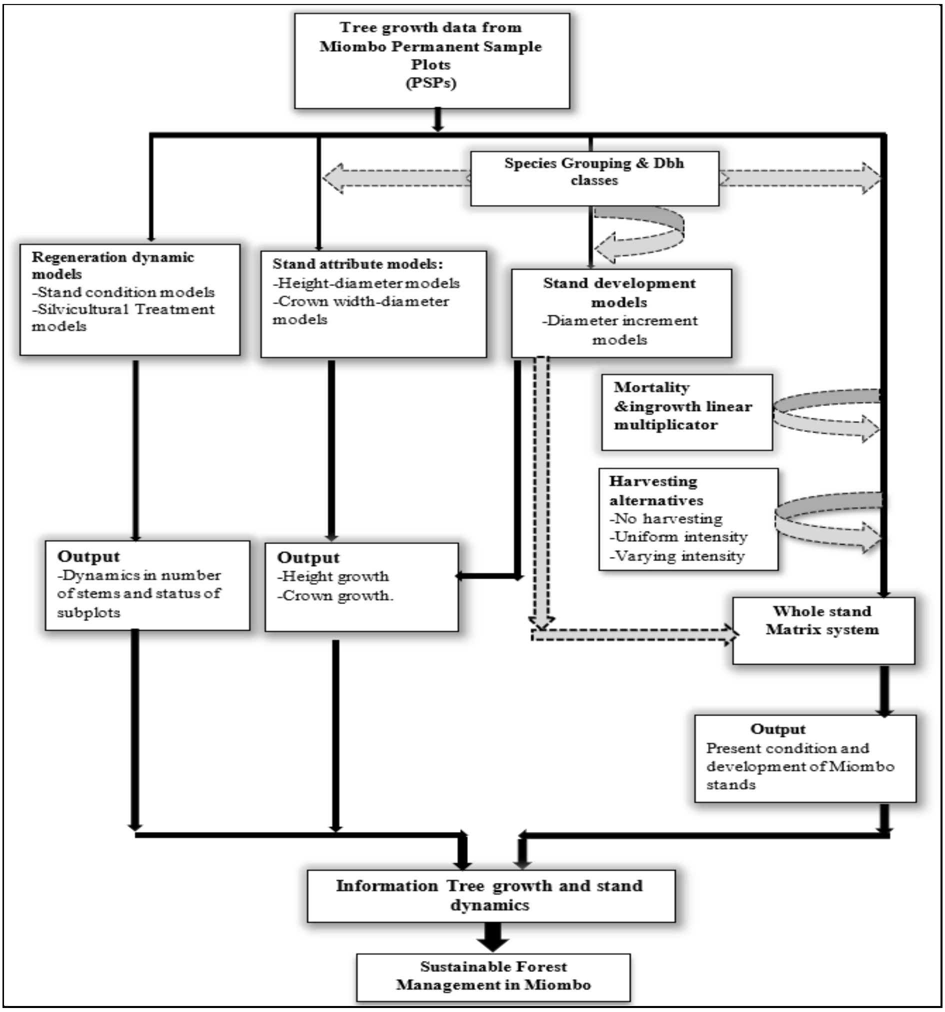

Figure 2. Conceptual framework of this study. Bold lines indicate the information flow while the dotted lines and curves indicate the use of the model outputs as inputs in the other models.

In contrast to other forest ecosystems in sub-Saharan Africa, the miombo woodland ecosystem is considered a sub-climax to evergreen or semi-evergreen forests (Frost 1996, Nduwamungu et al. 2008) where stand dynamics are strongly influenced by man-made fires and large herbivores (Geldenhuys and Golding 2008). The repeated occurrences of forest fires, animal herbivory, and other human-induced disturbances change the vegetation structure and composition at varying distribution, intensity, and frequency.

Larger cycle dynamics is a type of forest dynamics caused by infrequent, large-scale stand-replacing disturbances such as highly destructive forest fires and windstorms (Starfield et al. 1993, Turner and Dale 1998). This type of disturbance may result in an even-aged stand replacing the old vegetation. Small cycle dynamics, on the other hand, can be due to senescence mortality and regeneration in canopy gaps. Large cycle dynamics can, however, be superimposed on small cycle forest dynamics. This is described as a dichotomic conceptual model of forest dynamics originally designed for boreal forests (Shorohova et al.

2009). The results of this dissertation can be viewed within the framework of this conceptual model (Figure 3). Stand dynamics evolve through small-scale disturbances caused by density-dependent mortality of individual trees and tree groups, applied silvicultural treatments (fencing, thinning, soil tilling and control) and regeneration through canopy gaps (study I and II), and through harvesting practices (study III) representing three alternatives (no harvesting, uniform intensity, varying intensity).

These disturbances manifest as small cycles as they occur at the individual tree, plot, and stand levels. The naturally complex stand structures in miombo forests imply that encouraging continuous-cover forestry (CCF) (Pommerening and Murphy 2004) through selective harvesting could be a way forward towards enhanced sustainability and productivity in miombo woodlands.

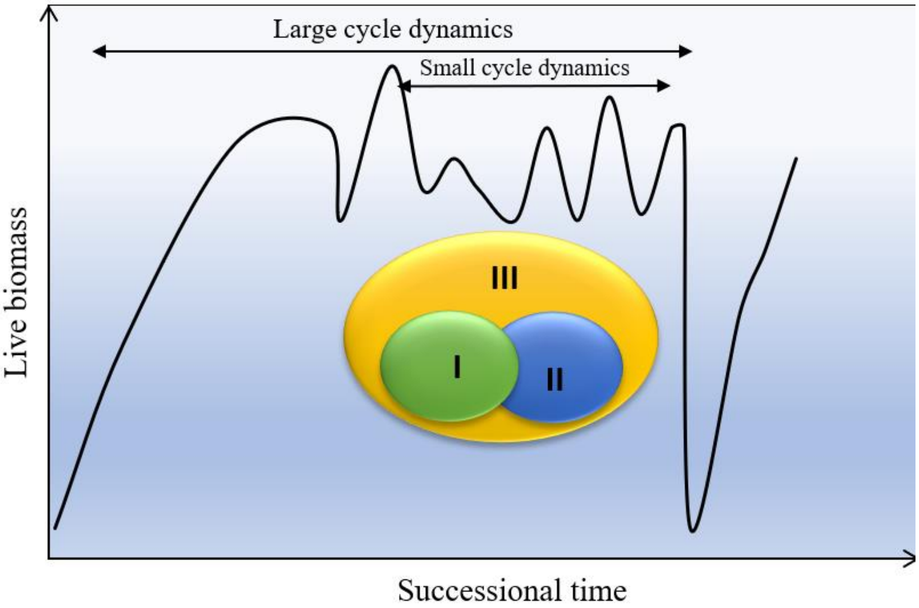

Figure 3: The framework of the dichotomic conceptual model of forest dynamics and how the sub-studies of this study are positioned in this framework (redrawn from Kuuluvainen 2016). The width of the cycle represents the length of a period. The simulation study (III) deals with the stand dynamics for the medium-length period from establishment up to 99 years into the future, while studies I and II describe shorter periods (9 years) of stand development within the long simulation period.

3.3 Methods and model developments (study I)

3.3.1 Measurements and analysis

In the sample plots, stem diameters larger than 5 cm were measured for all trees at breast height (DBH at 1.3 m), and thereafter identified with both local and botanical names. The height (*h*, m) and crown-width (*Crw*, dm) were measured from sample trees (every 10th tree was selected as a sample tree). The initial stand inventory of the sample plots was conducted in February 2007 and the final inventories were done in May 2016. All newly emerged trees, which had reached the diameter of 5 cm between the measurement time points, were measured and recorded as in-growth (recruitments). The dead trees were measured in the final inventory. Tree mortality and in-growth were analysed as changes between the two measurements. Stand growth was considered as the difference between the final and initial values of a given parameter. Negative increments were considered correct because of the complicated bark characteristics of miombo trees, which involve peeling-off. Species grouping was applied according to the canopy position and growth characteristics of the trees as explained in study I.

3.3.2 Diameter increment models

This study embarked on a tree-level modelling approach (Weiskittel et al. 2011) to estimate the eight-year diameter increments of the stand trees. The increments were also converted on an annual basis. Before constructing the models, regression analysis was performed to determine the relationship between stem diameter and diameter increments for our data. A clear non-linear relationship was found between the stem diameters and diameter increments during the eight-year period 2008-2016. Therefore, the eight-year diameter increments were modelled using the 2008 measurement instead of the initial dataset (2007), which was excluded due to some measurement errors in the data. Due to the hierarchical data structure, mixed non-linear modelling was used where the experiment hierarchy (stand, block, plot) were included as random effects and the explanatory factors, i.e., species group (1, 2 &3) or local basal area (sum of BA for all trees around a subject tree within 8 m radius) as fixed effects. The models were created using *nlme* function in R software (Pinheiro and Bates 2000). The species-specific models were developed for the two dominant species, i.e., *Julbernardia globiflora* and *Combretum molle* at our sites. The best-fit and model performance was used to evaluate the best models (for more detail, see study I).

3.3.3 Height-diameter and crown-width-diameter relationship models

Individual tree-level height-diameter and crown-width-diameter relationship models are generally very important in predicting stand growth and yield (Mehtätalo et al. 2015, Weiskittel et al. 2011) both in natural forests and plantations (Sharma et al. 2017). However, for miombo woodland, the applicability of these relationships is rather poor for estimation of the mean stand height and crown-width because the crown top dimensions of the miombo species are difficult and laborious to measure (Mugasha et al. 2019, Valkonen et al. 2008). In this study, the exploration of tree height and crown-width against stem diameter (DBH) indicated a non-linear relationship. The species groups and inventory time point (initial and final measurement) were used as fixed effects while experimental hierarchy (stands/ plots) formed the random part of the models. A model formulation based on Näslund (1936) in (Pukkala 1989) was applied to establish the relationship between height-diameter using *nlme* function in R software (Pinheiro and Bates 2000). Both models were fitted using the Maximum Likelihood estimation method. The complexity of the models with double effects enables height and crown-width prediction at each level (measurement number) and shape (species group characteristic). The best-fit and model performance was used to evaluate the best models (for more detail, see study I).

3.4 Methods and model developments (study II).

3.4.1 Measurements and analysis

For small trees (the minimum height of 20 cm and DBH < 5 cm) in the circular regeneration sub-plots, the height (cm) and species names were recorded, and additionally, the DBH (cm) measured if the tree´s height exceeded 130 cm. Measurement protocol involved a 1.1m stick which was moved clockwise around the subplot with the first-touched stem, first-measured and identified. This process aimed to ensure that the same stems recorded in the first measurement are measured during the following measurement. The number of seedlings was recorded as the total number of stems (N_{tot}) or the total number of main stems (N_{main}). For subplots with clusters of stems with similar height (same species), the height (h) of one main stem was recorded, the rest of the similar stems were counted and treated as the total number of the main stems (N_{main}). The change (mortality) in the total number of stems (dN_{tot}) and main stems (dN_{main}) was quantified as the difference between the stem number values of the initial and final inventories. The cause and severity of pest/herbivore damage and the vigor of the seedlings were also assessed. The change in percentage grass cover, stem colonization of empty plots, or withdrawal from previously inhabited subplots were visually assessed in the final inventory.

3.4.2 Regeneration dynamic models

The modeling of the regeneration dynamics focused on studying the changes to the already established seedlings, coppices, and sprouting roots in the stands rather than predicting the aspect of seeding (Weiskittel et al. 2011). Regeneration data in this study contained silvicultural treatment and stand conditions information that potentially affects the development of the stems. This study used the dataset between 2007 and 2016 as its initial and final time points of measurement. The temporal change in stem number was modeled in two ways: by applying linear mixed effect modeling (R computer software) making use of stand conditions and a generalized linear mixed modeling approach (SPSS computer software) using experimental treatments.

In the first case, the change in the number of stems (dN_{tot} and dN_{main},) was modeled against the factors fencing (F), grass cover (C), stand basal area (G), the initial total number of stems (N_{tot}) and number of main stems (N_{main}). In the second case, a generalized linear mixed-effect model was used to predict the change in the number of stems (dN_{tot} and

dN_{main}) as a function of silvicultural treatment (fencing, thinning, soil tilling, control) and measurement time, accounting for hierarchy and interaction respectively. Finally, the number of stems per unit area (N_{tot} and N_{main}) was modeled where site, stand density (N), and stand basal area (BA) were selected as explanatory factors.

3.5 Methods and model development (study III).

3.5.1 Measurements and analysis

The initial dataset collected in 2007 was used as the input data for the simulation study (study III*)*. The species groups and diameter classes formulated in the study I were applied. The diameter increment model (study I) was slightly modified to fit the matrix model context better and incorporated into the developed simulation system involving a nine-year interval (2007 to 2016). The local basal area (BA around a subject tree within a 5 m radius) was replaced by the stand basal area (BA, m^2 ha^{-1}).

3.5.2 The whole stand simulation system

To simulate stand dynamics, the so-called matrix model system was used, which was modified from the models developed by Martin Bollandsås et al. (2008) and Yahya et al. (2012). A multiplicator coefficient (factor) for mortality and ingrowth was formed to incorporate density-dependence into those elements. The temporal growth of a tree to the next diameter class was predicted directly by the diameter increment model (Forest development model). Three harvesting alternatives were formulated based on harvesting regulations in the Tanzanian Forest Act (2002). The first option involved no harvesting, i.e., when a forest is considered protected. Other prescriptions involved: 1) a minimum harvestable diameter, DBH 24 cm for *Dalbergia melanoxylon* (and other related species), and 2) prescribed minimum harvestable DBH of 40 cm for *Julbernardia globiflora* (dominant in KFR). In illegal harvesting, however, generally, all trees of a reasonable diameter are removed according to market demand. This study, therefore, applied three harvesting alternatives: 1) no harvesting; 2) uniform intensity where all trees with a DBH ≥ 40cm (all species groups) are harvested; and 3) varying intensity where only trees with a DBH ≥ 24 cm are harvested from species group 2 and those with a dbh ≥ 40cm from groups 1 and 3 respectively.

The simulation involved two harvests at 36-year intervals (i.e., t_0+36 and t_0+72). Harvesting for charcoal includes trees of all sizes, even those which are much smaller (assumed starting age of at least 10 years), and therefore a longer period is usually required to replace the existing stock. For selective timber harvesting, however, where the minimum harvestable volumes were calculated based on the already matured stems, a shorter rotation of 36 years was assumed to capitalize on the faster growth of younger trees. Based on diameter increments by (Njoghomi 2011), the harvested diameters could be replaced by a substantial number of new upgrowing stems during the 36-year interval.

The development of the Kitulangalo stand was simulated over 99 years by using nine-year intervals based on the dataset 2007-2016. The diameter increment model predicts the upgrowth of trees based on the predicted stand basal area in the previous year. Recursive simulation runs produced a sequence of stand development as estimates of stand density (N stem ha^{-1}), basal area (m^2 ha^{-1}), stand volume (m^3 ha^{-1}), above-ground biomass (AGB), and associated carbon store bound in the tree stem biomass.

4. RESULTS AND DISCUSSION

4.1 Drivers of tree growth, mortality, and in-growth in miombo (I)

Based on empirical results, the trees in miombo forests were quite unevenly distributed among the three main species groups. The dominating species were *Julbernardia globiflora* (29.9%) and *Combretum molle* (21.3%). The frequency proportion of species Group 1 increased by 6.9% during the observation period, with species Group 2 falling by 6.1%. Most of the remaining common species showed a relative decrease. The mean ingrowth (38 ± 2.0 stems ha^{-1}) in species group 1 (50%) and 2 (41%) was greater than mean mortality (18.5 ± 9.6 stems ha^{-1}) (in species group 1: 27%, group 2: 59%). Species group 3 had the lowest ingrowth (9%) and mortality (14%) at the end of the study. The dynamics in species composition and stand structure is thought to be enhanced by spatial variation in canopy gaps (Lembani et al. 2018, Syampungani et al. 2016) and the resulting asymmetrical competition towards the middle and lower-canopy species. Eliminating grazing animals and fire influenced the ingrowth dynamics by promoting thick grass cover which induced severe competition with the regeneration and smaller saplings(Kraaij and Ward 2006, Ribeiro et al. 2015), but their effects were apparently minimal to the growth of the matured trees during the study period.

The model results for the eight-year diameter increments varied with species group across dbh classes. The highest values of 3.2 and 3.9 cm were recorded in species group 1 and *Julbernardia globiflora* models respectively. The highest predicted diameter increment values for species group 2 and 3 models during the eight years were 0.8 cm and 0.7 cm respectively.

A separate model for *Julbernardia globiflora* (dominant species model) showed the highest diameter increments of 3.8 cm due to minimum variation between individuals of this species. Also, the general species group models and *J. globiflora* diameter increment model showed an extended zone of maximum growth (10-30 cm dbh) compared to groups 2 and 3 with maximum growth attained at dbh between 5 and 20 cm. Higher increment values for species group 1 and *J. globiflora* models were attributed to the small variation that existed between the *J. globiflora* individuals.

Similar increment rates were previously reported by (Njoghomi 2011) and (Elifuraha et al. 2008) for the Kitulangalo forest. The local basal area at a radius of 8m around a tree was applied to account for the influence of stand density and its variation within the stand (Contreras et al. 2011, Valkonen et al. 2008). The very light thinning treatment which involved the removal of plot basal area ranging between 11-20m^2 ha^{-1} had little influence on diameter increment. The ingrowth rate was relatively high, especially compared to the mortality rate, which tends to imply that Kitulangalo stands are recovering and progressing towards more sustainable structures. The impact of eliminating animal grazing and annual fires by protecting the plots and was expressed as a thick grass cover in the fenced plots than unfenced ones. The presence of thick grass cover induced rigorous competition and thus caused higher mortality rates for regenerants and ingrowth, especially in the lower and middle canopy species group more than in the top canopy species groups. Higher canopy species such as *J. globiflora, Pterocarpus angolensis* and *Brachystegia species* are considered more adapted to hash growing conditions in miombo than the middle and lower canopy species.

The height-diameter and crown width-diameter relationship models showed that tree height and crown width were rather closely correlated varying with stem diameter. That is a general characteristic for forest trees, but a novelty nonetheless as trees in miombo woodlands are considered highly variable especially with regards to crown shape. The statistical models were constructed and used to demonstrate the general magnitude of change during the very short observation period. The measurement of the canopy characteristics and especially change between two measurements turned out to be even more difficult than expected due to the complex tree and canopy forms of miombo.

4.2 Impact of silvicultural treatments and stand conditions on regeneration dynamics and recovery in miombo woodlands (II)

The empirical distribution in the number of seedlings and sapling stems, stem height, and species composition varied with the applied hierarchy of the experiment (stand, plot, and regeneration subplot). The fencing treatment also induced significant changes during the monitoring period. Of the variables used to indicate density, the total number of stems (N_{tot}) included all individual stems on a subplot whereas the number of main stems (N_{main}) represented the number of clusters of regeneration of similar height and species on a subplot.

There was an overall significant decrease in the total number of stems (N_{tot}) from 29761 to 19059 stems ha^{-1} (r= 0.40, p = 0.0001) and a slight increase in the number of main stems (N_{main}) from 9270 to 11054 stems ha^{-1} (r= 0.58, p= 0.0001) during the study period. The decrease in N_{tot} was larger in fenced than unfenced plots. The highest mean stem height (100-199 cm) was also observed in the fenced plots. The rate of colonization of previously empty subplots with new stems was, however, greater on the fenced plots (13% vs. 8 %) at the end of the study. Models describing the number of stems per unit area (both N_{tot} and N_{main}) showed that the number of stems with DBH > 5 cm increased. The initial number of seedlings and saplings, stand basal area, and grass cover influenced the change in the total number of stems negatively (Piiroinen et al. 2008, Syampungani et al. 2015). All regeneration models showed promising results using the nine-year (2007 to 2016) rather than the eight-year (2008 to 2016) interval data. Model results describing the change in the number of stems ($dN_{tot}$and dN_{main}) agreed with the empirical results indicating an overall decrease in the total number of stems (N_{tot}) and a slight increase in the number of main stems(N_{main}). Models describing the number of stems per unit area (N_{tot} and N_{main}) showed that the number of regenerants increased with stand density for bigger trees. The initial number of stems, basal area, and grass cover negatively affected the change in the total number of stems implying competition induced by bigger trees and surface vegetation (Piiroinen et al. 2008, Syampungani et al. 2015). Luoga et al. (2004) argued that miombo has the potential of producing a greater number of seedlings and suckers but very few can develop into saplings and small trees, let alone to maturity.

The decrease in the total number of stems and a simultaneous increase in the number of main stems in the fenced areas indicated a self-thinning process within the regeneration clusters induced by competition from grass and herbs (fencing). The prolonged droughts and severe competition induced by thick grass cover and asymmetrical competition in miombo stands result in a continuous die-back and therefore morphological changes in the multi-stems regenerants into single stems saplings through self-thinning (main stems) (Luoga et al. 2004, Zida 2007). Eliminating forest disturbances by fencing promoted thick grass cover, which in turn induced severe competition killing tender regeneration. Although we did not test the independent effect of the animal grazing and annual fires on the regeneration dynamics (Bognounou et al. 2010), it was considered that the effectiveness of applied silvicultural treatments such as thinning, soil tilling, and control on promoting miombo regeneration depends on the degree of protection of the miombo stands against animal grazing (fencing), destructive fires, and other disturbances (Chidumayo 1988).

4.3. Pathways for maximizing stand growth, wood production, and ecological recovery in miombo woodlands (III)

A single tree-diameter increment model (Weiskittel et al. 2011) provided the basis for developing a functional simulation system in this study. The model predicting diameter growth was attributed to species grouping, initial stem diameter and stand basal area explaining 38% (R^2=0.38) of the variation in diameter increments for species groups. The applied harvesting alternatives and the harvesting cycles aligned with the prescribed harvesting regimes, which recommend a rotation of 50 years for timber species and 90 for other purposes, e.g., charcoal production (Ishengoma et al. 2016) in miombo woodlands in Tanzania (Lovett 2003). The effect of harvesting alternatives on the upgrowth of trees to larger diameter classes, stand density, basal area, volume, and biomass varied across species groups. The use of a “varying intensity” harvesting alternative lowered the stand basal area compared to other harvesting alternatives, which led to a greater number of stems graduating into larger diameter classes. The effect of asymmetrical competition from the dominating top canopy species limited growth in species groups 2 and 3 causing a greater number of stems to remain in the same diameter classes. The variation can be attributed to their morphological, anatomical, and phenological characteristics (Chidumayo 1987, Ryan and Williams 2011), which limit their growth. Density-dependent mortality, ingrowth, and initial stand basal area were found to be the key elements that increased the sensitivity of the stand to changes in density, basal area, and thus stand growth.

The initial stand density constituted 170 stems ha^{-1} (41%) from the top canopy species group 1, 157 stems ha^{-1} (39%) from group 2, and 81stems ha^{-1} (20%) from species group 3. The structural and compositional changes in stand density varied with the addition of stems in each species group in each simulation year across harvesting alternatives. The proportion of stem numbers added into the stand in each simulation period was also affected by ingrowth and mortality rate across the dbh classes. The “no harvesting” treatment prompted swift growth in the stand basal area above 18 m^2 ha^{-1}, but negatively affected ingrowth and smaller trees through increased mortality. Without harvesting, the stand was able to stabilize after a few decades with a higher number of matured stems and fewer smaller stems compared to other alternatives. The “varying” and “uniform intensity” harvesting alternatives resulted in a higher number of lower and middle diameter stems compared to bigger ones (dbh > 25cm). By reducing stand basal area, harvesting in effect stimulated a higher number of ingrowth and diameter growth of smaller trees, thereby increasing the total number of stems compared to the “no harvesting” treatment.

Overall, the stand diameter distributions followed the positively skewed, i.e., reversed J-shaped diameter distribution at the end of the simulation period (Isango et al. 2007).

The species group 1 dominated the stands across all harvesting alternatives by 53% of the total number of stems, while the proportions were 27% and 19% of stems originating from species groups 2 and 3, respectively.

The stand development in basal area (BA), volume (V), and accumulation of above-ground biomass (AGB) carbon also varied with harvesting alternatives across species groups. The parameters were calculated using stem-diameter-based allometric equations (Malimbwi et al. 1994). Of all harvesting alternatives, "no harvesting" resulted in the largest basal area (18.7 m^2 ha^{-1}), net volume growth (83 m^3 ha^{-1}), and stem biomass (49 t C ha^{-1}) in 99 years, which was dominated by species group 1 because of bigger diameter trees compared to other groups. Generally, simulation of stand dynamics under harvesting alternatives with "varying intensity" and "uniform intensity" tends to arrive at relatively similar steady-state stand conditions in terms of density, basal area, volume, and accumulation of above-ground biomass carbon after 99 years (Hofstad et al. 2015, Mugasha et al. 2016). Despite the relative similarities in the stand attributes achieved through the applied harvesting alternatives, the use of "varying intensity" harvesting can be considered ecologically friendly for wood production through stand density, volume growth, and biomass accumulation in miombo woodlands. Varying harvesting intensity, however, creates variation in canopy gaps, which can induce growth variation among tree species in each canopy profile (Syampungani et al. 2020). Managing miombo stands with selective harvesting also follows the principles of Continuous-Cover Forestry (CCF) (Pommerening and Murphy 2004, Pukkala et al. 2014), which is based on selective harvesting and gap creation for enhancing wood production (Valkonen et al. 2008), ecological recovery and increased provision of ecosystem services.

5. CONCLUSIONS

- The observed stand structural dynamics indicated that proper management of miombo stands could lead to quick recovery through the processes of tree and stand growth and in-growth.
- Managing stand basal area and volume growth at appropriate levels is key for enhancing diameter increment, in-growth, and regeneration, and reducing tree mortality, which ultimately affects stand growth and yields in miombo stands.
- Proliferation of grass in the absence of grazing and fire may tend to discourage the emergence of new seedlings, coppices, and suckers in the long run.
- Periodical complete protection from grazing and prescribed fires coupled with selective harvesting provide new pathways for improving miombo regeneration and growth.
- This study has demonstrated a high degree of resilience and positive response to careful selective harvesting in lightly degraded, recovering Kitulangalo forest.
- The development of research approaches and infrastructure for miombo is still at the very beginning, along with the research infrastructure as a whole. Further studies involving the impacts of silvicultural treatments on tree

growth are vital for a better understanding of miombo dynamics for sustainable management.

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