MINDAYE TESHOME LEGESE

DECISION SUPPORT TOOLS FOR THE MANAGEMENT IN A DRY AFROMONTANE FOREST IN ETHIOPIA

A thesis submitted to the Forest Science Program of the Federal University of Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

Adviser: Carlos Miquelino Moreira Eleto Torres Co-Advisors: Evaldo Muñoz Braz Patricia Povoa de Mattos

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Assent:

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Mindaye Teshome Legese Author

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To my mother

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ABSTRACT

LEGESE, Mindaye Teshome, D.Sc., Universidade Federal de Viçosa, July 2023. **Decision support tools for the management in a Dry Afromontane Forest in Ethiopia.** Advisor: Carlos Miquelino Moreira Eletto Torres. Co-advisors: Evaldo Muñoz Braz and Patricia Povoa de Mattos.

Ethiopia is one of the tropical countries endowed with diverse forest formations. These forests provide large amounts of wood that can be used for furniture, construction, and domestic energy consumption. However, the gap between the supply and demand of wood is huge and increasing. This growing demand could be met by the sustainable production of wood from the existing natural forests. This requires up-to-date information on forest structure, diameter growth rate, standing volume, cutting cycle, and minimum logging diameter of trees. Unfortunately, such information is not available for trees from the Chilimo Dry Afromontane Forest in Ethiopia. To address this gap, this study aimed to i) develop a nonlinear mixed-effects model for predicting Juniperus procera tree height (chapter one); ii) develop mixed-species allometric equations to quantify stem volume and biomass of trees from the Chilimo Dry Afromontane Forest (chapter two), and iii) ensuring sustainable wood harvesting from J. procera trees in the Chilimo Dry Afromontane Forest (chapter three). For the first chapter, a total of 1,215 height and diameter measurements were recorded on 101 sample plots. The bestfitting base model was selected after a comparison of fourteen models. We also included the sample plot as a random effect in non-linear mixed effect modeling. The effect of adding stand variables on height prediction performance was also evaluated. The bias, root mean square error, and AIC were computed and used as the model evaluation criteria. We found that the Michaelis-Menten model best represented the height-diameter allometry of J. procera trees. The best mixed-effects model (M1) improved the height prediction performance with the RMSE and bias values of 2.692 and 0.043, respectively. The addition of the quadratic mean diameter and stem density slightly improved the prediction performance of the best-mixed effects model. The calibration response revealed that the systematic selection of the three largest diameter trees in a sample plot is the best sampling alternative to estimate the random effects and predict the height of J. procera trees from the new plots or stands. For the second chapter, we used a total of 194 sample trees from seven dominant tree species (Juniperus procera, Podocarpus falcatus, Allophylus abyssinicus, Olea africana ssp. Cuspidata, Olinia rochetiana, Rhus glutinosa, and Scolopia theifolia). Various volume and biomass equations were fitted using robust linear and nonlinear regression models. Model comparison indicated that the best

model to estimate stem volume was $ln(v) = -9.909 + 0.954 ln(dbh^2ht)$, whereas the best model to estimate biomass was $ln(b) = -2.983 + 0.949 ln(\rho dbh^2 ht)$. These equations explained over 85 % of the variations in the stem volume and biomass measurements. The mean density and basal area of trees with dbh ≥ 2 cm were 24.4 m² ha⁻¹ and 631.5 stems ha⁻¹, respectively. Based on the newly developed equations, the forest has on average 303.0 m³ ha⁻¹ standing volume of wood and 283.8 Mg ha⁻¹ biomass stock. The newly developed allometric equations derived from this study can be used to accurately determine the stem volume, biomass, and carbon storage in the Afromontane forests in Ethiopia and elsewhere with similar stand characteristics and ecological conditions. By contrast, the generic pan-tropical and other local models appear to provide biased estimates and are less appropriate for dry Afromontane forests in Ethiopia. For the third chapter, we established 165 plots (each 400 m²) in the forest and collected vegetation data. We also conducted growth ring measurements on 12-disc samples from J. procera trees. We determined the diameter growth rate, the current and mean annual increments, the minimum logging diameter, and the cutting cycle. By using the stand projection table, we estimated the harvestable volume of wood by combining four minimum logging diameters and five cutting cycles. The findings revealed that J. procera tree species has a mean density of 183 stems ha⁻¹, a total basal area of 12.1 m² ha⁻¹, and 98.9 m³ ha⁻¹ standing volume of wood. The population exhibited an inverted J-shape diameter distribution pattern. The mean annual diameter growth rate ranges between 0.50 and 0.65 cm yr⁻¹, with an overall mean of 0.59 cm yr⁻¹. The current annual increment occurred at 50 years when trees reached 30 cm in diameter, while the mean annual increment occurred at 90 years when trees attained 50 cm in diameter. After evaluating various scenarios, we found that a minimum logging diameter of 40 cm and a cutting cycle of 15 years provided the highest harvestable volume of wood (22 m³ ha⁻¹) and volume increments (1.4 m³ ha⁻¹ yr⁻¹). Additionally, this scenario allows for the harvesting of 9% of the standing J. procera trees while maintaining a larger proportion (91%) of the existing standing trees in the forest. Based on our findings, we concluded that the Chilimo Dry Afromontane Forest is well stocked and has a substantial amount of harvestable wood volume, which could help Ethiopia meet its growing national wood demand. Our study provides valuable information for policy makers to formulate regulations for wood harvesting from J. procera trees in Chilimo forest.

Keywords: Wood production. Forest structure. Allometeric equations. Dendrochronology. Mixed models.

RESUMO

LEGESE, Mindaye Teshome, D.Sc., Universidade Federal de Viçosa, julho de 2023. Ferramentas de apoio à decisão para o manejo em uma Florestas Seca Afromontana na Etiópia. Orientador: Carlos Miquelino Moreira Eleto Torres. Coorientadores: Evaldo Muñoz Braz e Patricia Póvoa de Mattos.

A Etiópia é um dos países tropicais dotados de diversas formações florestais. Estas florestas fornecem grandes quantidades de madeira que podem ser utilizadas para mobiliário, construção e consumo doméstico de energia. No entanto, a diferença entre a oferta e a procura de madeira é enorme e está a aumentar. Esta procura crescente poderia ser satisfeita através da madeira produzida de forma sustentável a partir das florestas naturais existentes. Para tal, é necessária informação actualizada sobre a estrutura da floresta, a taxa de crescimento, o volume, o ciclo de corte e o diâmetro mínimo de corte das árvores. Infelizmente, essa informação não está disponível para a Floresta Afromontana de Chilimo, na Etiópia. Para colmatar esta lacuna, este estudo teve como objetivo i) desenvolver um modelo não linear de previsão da altura das árvores de Juniperus procera com efeitos mistos (capítulo um); ii) desenvolver equações alométricas de espécies mistas para quantificar o volume do tronco e a biomassa das árvores da floresta seca de Chilimo Afromontane (capítulo dois), e iii) assegurar a exploração sustentável da madeira das árvores de J. procera da floresta seca de Chilimo Afromontane (capítulo três). Para o primeiro capítulo, um total de 1.215 medições de altura e diâmetro foram registradas em 101 parcelas estabelecidas aleatoriamente. O modelo básico de melhor ajuste foi escolhido após uma comparação de quatorze modelos. Foi efetuada a amostragem da parcela como um efeito aleatório na modelagem não linear de efeitos mistos. O efeito da adição de variáveis florestais no desempenho da previsão de altura também foi avaliado. O bias, a raiz quadrada do erro médio e o AIC foram calculados e usados como critérios de avaliação do modelo. O modelo de Michaelis-Menten representou melhor a alometria altura-diâmetro de árvores de J. procera. O melhor modelo de efeitos mistos (M1) melhorou o desempenho da predição da altura com os valores de RMSE e bias de 2,692 e 0,043, respectivamente. A adição do diâmetro médio quadrático e da densidade do caule melhorou ligeiramente o desempenho de previsão do modelo de efeitos mistos. A calibração revelou que a seleção sistemática das três árvores de maiores diâmetros em uma parcela amostral foi a melhor alternativa de amostragem para estimar os efeitos aleatórios e prever a altura das árvores de J. procera das novas parcelas ou florestas. Para o segundo capítulo, usou-se um total de 194 árvores de amostra de sete espécies de árvores dominantes (Juniperus procera, Podocarpus falcatus, Allophylus abyssinicus, Olea africana ssp. Cuspidata, Olinia rochetiana, Rhus glutinosa, e Scolopia theifolia). Diversas equações de volume e biomassa foram ajustadas usando modelos de regressão lineares e não lineares robustos. A comparação de modelos indicou que o melhor modelo para estimar o volume do caule foi $ln(v) = -9.909 + 0.954 ln(dbh^2ht)$, enquanto o melhor modelo para estimar a biomassa foi $ln(b) = -2.983 + 0.949 ln(\rho dbh^2 ht)$. Essas equações explicaram mais de 85% das variações nas medidas de volume e biomassa do caule. A densidade média e a área basal das árvores com DAP ≥ 2 cm foram 24,4 m² ha⁻¹ e 631,5 fustes ha⁻¹, respectivamente. Com base nas equações desenvolvidas, a floresta teve em média 303,0 m³ ha⁻ ¹ de volume e 283,8 Mg ha⁻¹ de estoque de biomassa. As equações alométricas desenvolvidas derivadas deste estudo podem ser usadas para determinar com precisão o volume do caule, a biomassa e o armazenamento de carbono nas florestas afromontanas na Etiópia e em outros lugares com características de povoamento e condições ecológicas semelhantes. Em contraste, os modelos pantropicais genéricos e outros modelos locais parecem fornecer estimativas tendenciosas e são menos apropriados para florestas secas afromontanas na Etiópia. Para o terceiro capítulo, estabeleceu-se 165 parcelas (cada 400 m²) na floresta e coletamos dados de vegetação. Também realizou-se medições de anéis de crescimento em amostras de 12 discos de árvores J. procera. A taxa de crescimento do diâmetro, os incrementos anuais atuais e médios, o diâmetro mínimo de corte e o ciclo de corte foram determinadas. O volume de madeira explorável combinando quatro diâmetros mínimos de corte e cinco ciclos de corte foram estimados. Os resultados revelaram que a árvore J. procera tem uma densidade de 183 hastes há⁻¹, uma área basal total de 12,1 m² há⁻¹ e um volume em pé de 98,9 m³ há⁻¹. As árvores seguiram um padrão de distribuição de diâmetro em forma de J invertido. A taxa média anual de crescimento do diâmetro varia entre 0,50 e 0,65 cm por ano, com uma média geral de 0,59 cm por ano. O máximo incremento corrente anual ocorreu aos 50 anos, quando as árvores atingiram 30 cm de diâmetro, enquanto o incremento médio anual ocorreu aos 90 anos, quando as árvores atingiram 50 cm de diâmetro. O diâmetro mínimo de corte de 40 cm e um ciclo de corte de 15 anos forneciam o maior volume de madeira explorável (21 m³ há⁻¹) e incrementos de volume (1,4 m3 há⁻¹ anno⁻¹). Além disso, este cenário permite a colheita de 9 % das árvores de J. procera enquanto mantém uma proporção maior (91%) das árvores em pé existentes na floresta. Com base em nossas descobertas, concluímos que a Floresta Afromontana Seca de Chilimo é bem abastecida e possui uma quantidade substancial de volume de madeira que pode ser colhida, o que poderia ajudar a Etiópia a atender sua crescente demanda nacional de madeira. Nosso estudo fornece informações valiosas para os formuladores de políticas formularem regulamentos para a colheita de madeira de árvores J. procera na floresta de Chilimo.

Palavras-chave: Produção madeireira. Estrutura da floresta. equações alométricas. Dendrocronologia. Modelo misto.

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General introduction

Tropical forests are home of more than a half of the Earth's biodiversity, contains about 40% of global terrestrial carbon, and have an essential influence on the global climate system (BACCINI; WALKER; CARVALHO; FARINA *et al.*, 2017; DEVARAJU; BALA; NEMANI, 2015; DI MARCO; WATSON; CURRIE; POSSINGHAM *et al.*, 2018; LEWIS; EDWARDS; GALBRAITH, 2015; MOHAMAD, 2022; PILLAY; VENTER; ARAGON-OSEJO; GONZÁLEZ-DEL-PLIEGO *et al.*, 2022; SULLIVAN; TALBOT; LEWIS; PHILLIPS *et al.*, 2017). These forests cover about 7% of the land surface and are habitat to more than half of the world's biotic species (GALLERY, 2014). Tropical forests help rural food security through different non-timber forest resources (food, medicines, and fibers) collected as a sustainable livelihood (FAO, 2020b; ROBERTS; BOIVIN; KAPLAN, 2018). Furthermore, these forests provide fuelwood for an estimated 2.4 billion rural people in less developed countries and the main material for the houses of at least 1.3 billion people worldwide (RAMETSTEINER; WHITEMAN, 2014). According to a recent study, a large number of people in developing countries depend on forests as a source of income, livelihoods, and well-being (FAO, 2018; ROBERTS; BOIVIN; KAPLAN, 2018).

Ethiopia has a total land area of 1.12 million hectares of which about 15.5% (17.35 million hectares) is covered by forests including plantations, woodlands, and high forests (BEKELE; TESFAYE; MOHAMMED; ZEWDIE *et al.*, 2015; FRANKS; HOU-JONES; FIKREYESUS; SINTAYEHU *et al.*, 2017). The forests in Ethiopia exhibit a higher complexity in terms of structure and composition, resulting from the diverse biophysical, social conditions, and disturbance history (TEKETAY; LEMENIH; BEKELE; YEMSHAW *et al.*, 2010). These forests provide wood for construction, furniture, household energy, and wood-based industries (TEKETAY, 2001a). The economic contribution of these forests (including the direct and non-direct use values) to the national GDP (Gross domestic product) was estimated at 18.8% in 2012/13 (NUNE; KASSIE; MUNGATANA, 2013). It was also estimated that 92,000 ha⁻¹ of the forest is lost annually (MOGES; ESHETU; NUNE, 2010) due to agricultural expansion (both subsistence and commercial), fuel-wood, illegal logging, and forest fire (BEKELE; TESFAYE; MOHAMMED; ZEWDIE *et al.*, 2015).

The Dry evergreen Afromontane forest is widely dispersed in central, south-eastern, eastern, northern, and southern highlands of Ethiopia (FRIIS; DEMISSEW; BREUGEL, 2010). This forest has ecological significance, being the largest remnant forests in the country which provides habitat for many endangered species and stores a large amount of carbon (BEKELE,

1994; GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a; GIRMA; SOROMESSA; BEKELE, 2014). These forests also support the livelihoods of many people by providing diverse forest products (ASFAW; LEMENIH; KASSA; EWNETU, 2013; GOBEZE; BEKELE; LEMENIH; KASSA, 2009; SHIFERAW; LIMENIH; GOLE, 2019). These forests are also endowed with various native timber tree species such as *Juniperus procera*, *Podocarpus falcatus, Olea hochstetteri*, among others (e.g. DE VLETTER, 1991; DESALEGN; TEKETAY; GEZAHGNE; ABEGAZ, 2012). Nevertheless, there is a huge gap between the supply and demand for wood products in Ethiopia (MEFCC, 2017). For example, the wood consumption in 2013 reached a total of 124 million m³ in Ethiopia. Projections indicate that within the next two decades, the demand for wood products will rise by around 27%, reaching an annual consumption of 158 million m³ by 2033. During this period there will be a 4.4 million m³ gap in the supply of wood which will be required to meet the growing needs of Ethiopia's economy (MEFCC, 2017). This indicates the urgent need to establish large scale plantation forests, expand forest industry, and adopt sustainable harvesting practices of wood from existing natural forests and wood lands.

Forest management planning requires understanding of the current stand structural conditions, i.e., basal area, standing wood volume, and tree density of the forest that will be managed, and a long term evaluation of the forest resources after management interventions have been applied (BETTINGER; BOSTON; SIRY; GREBNER, 2016). This requires detailed information about the forest stand's characteristics. Various forest management tools have been developed for different tree species to generate basic information such as the diameter growth pattern, diameter distribution, stem volume, and biomass and carbon stock (e.g., CANETTI; BRAZ; DE MATTOS; BASSO, 2021; CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO *et al.*, 2014; MUGASHA; BOLLANDSÅS; EID, 2013; SCOLFORO; SCOLFORO; THIERSCH; THIERSCH *et al.*, 2017; TESHOME; TORRES; SILESHI; DE MATTOS *et al.*, 2022). These tools are indispensable to determine the potential of a given forest stand and make informed forest management decisions.

In Ethiopia, forest resource management efforts have been constrained by the lack of fundamental tools that can provide accurate estimates of basic information such as the diameter growth rate, standing volume of wood, the total height of trees, stand productivity and other essential information's (TEKETAY; LEMENIH; BEKELE; YEMSHAW *et al.*, 2010). This had an impact on the efforts to develop a sustainable plan for managing and utilizing the natural forests in Ethiopia. These problems entail the need to develop appropriate and site-specific management tools for the diverse trees from the natural forests of Ethiopia. In this study, we

developed decision support tools for the management of *Juniperus procera* trees from the Chilimo Dry Afromontane Forest. The output of this study will specifically help forest managers and researchers by providing site-specific information about the potentials in the Chilimo Dry Afromontane Forest and timber harvesting possibilities. Furthermore, it will enable policy makers to formulate a timber harvesting regulation and ensure domestic wood production.

Objectives

General Objective

The general objective of this study is to develop forest management tools that will guide timber harvesting decisions in the Chilimo Dry Afromontane Forest in Ethiopia.

Specific Objectives

- To develop a mixed-effects height prediction model for the *Juniperus procera* tree from the Chilimo Dry Afromontane Forest
- To develop mixed species allometric equation to quantify the stem volume and tree biomass for the dominant trees from the Chilimo Dry Afromontane Forest
- To ensure sustainable wood harvesting from *Juniperus procera* trees from the Chilimo Dry Afromontane Forest in Ethiopia

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Literature review

Ethiopia is a mountainous country that spans between 3° and 15° N latitude and 33° to 48° E longitude (EMA, 1988). It is bordered by Sudan to the West, Djibouti to the east, Eritrea to the north and southeast, Somalia to the southeast, and Kenya to the south. Ethiopia is the most populous country (over 120 million people) in Eastern Africa and the second most populous in the entire continent after Nigeria. The population is estimated to be growing at a rate of 2.7 percent per annum on a fixed land area of 1.1 million km² (CSA, 2017).



Figure 1: Map of Africa and Ethiopia with regional states

Ethiopia is an ecologically diverse country, with altitudes ranging from 125 meters below sea level in the Dallol to 4,620 meters above sea level on Rasdashen (EMA, 1988). The prevailing marked contrasts in altitudes and the geographic position close to the equator and the Indian Ocean enable the country to experience large spatial variations in temperature and precipitation (FAZZINI; BISCI; BILLI, 2015). The climate of Ethiopia is mainly influenced by the seasonal migration of the Intertropical Convergence Zone (ITCZ), atmospheric circulation as well as by the complex topography of the country. Landscapes experience a variety of climates from desert climates to equatorial mountain types. The climate in the highlands (over 1800 m) is moderate and the annual precipitation ranges between 800 to

2200 mm. The lowlands are hot with annual rainfall ranging between 200 and 800 mm (TEDLA; LEMMA, 1999). Agriculture is the main economic activity, accounting for 45 % of GDP. Of the total area, 60 % is reported to be suitable for agriculture. The main products are teff (*Eragrostis tef*), sorghum (*Sorghum* bicolor (L.) Moench), barley (*Hordeum vulgare*), field peas (*Pisum sativum*), chickpeas (*Cicer arietinum* L.), niger seed (*Guizotia abyssinica*), linseed (*Linum usitatissimum*), enset (*Ensete ventricosum*), cotton (*Gossypium herbaceum*), and coffee (*Coffee arabica*). Small-holder farming is predominant, accounting for more than 90 % of the agricultural area and 95 % of total area under crop (TEDLA; LEMMA, 1999).

Ethiopia plays a crucial role as a center of genetic diversity for a variety of crops (EGZIABHER, 1991). It is one of the eight centers in the world where crop plant diversity is exceptionally high, and where various crops, such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), sorghum (*Sorghum bicolor* (L.) Moench), and field peas (*Pisum sativum*), were domesticated (ENGELS; ENGELS; HAWKES; HAWKES *et al.*, 1991). The flora of the country comprises about 6,500 - 7,000 species of higher plants, of which about 12% are endemic (EGZIABHER, 1991). Historical evidence suggests that over 40 % (between 450,000 and 500,000 km²) of the land area was once covered with high forests (HUFFNAGEL, 1961). However, currently only 15.5% (17.35 million ha) of the land area is covered with forests (BEKELE; TESFAYE; MOHAMMED; ZEWDIE *et al.*, 2015; FRANKS; HOU-JONES; FIKREYESUS; SINTAYEHU *et al.*, 2017). These forests provide wood for construction, furniture, household energy, and wood-based industries (TEKETAY, 2001b)..

Despite this fact, much of the original forest in the highlands was lost due to the population growth which in turn resulted in extensive wood harvesting for house construction and energy, agricultural expansion (shifting cultivation, large-scale investment, and the spread of sedentary agriculture), resettlement and livestock grazing (BEKELE; TESFAYE; MOHAMMED; ZEWDIE *et al.*, 2015; RUSS, 1979). The deforestation rate was estimated at 92,000 ha⁻¹ yr⁻¹ in Ethiopia (MOGES; ESHETU; NUNE, 2010). There has been a considerable effort by the government to reverse the loss of forests. The government clearly articulated the significance of forest destruction in the Climate Resilient Green Economy (CRGE) document and recommended, as viable solutions, the use of fuel-efficient stoves; sustainable forest management, increasing afforestation, and reforestation activities; and promoting the rehabilitation of degraded lands (FDRE, 2011).

Natural vegetation of Ethiopia

The natural vegetation of Ethiopia showed higher complexity in structure and composition resulting from the diverse biophysical, social conditions, and disturbance history (TEKETAY; LEMENIH; BEKELE; YEMSHAW *et al.*, 2010). Various efforts have been made to classify the natural vegetation types of Ethiopia (e.g. CHAFFEY, 1979; FRIIS; DEMISSEW; BREUGEL, 2010; LOGAN, 1946). According to a study by FRIIS; DEMISSEW e BREUGEL (2010) the natural vegetation of Ethiopia is classified as (1) desert and semi-desert scrubland, (2) Acacia-Commiphora woodland and bushland, (3) wooded grassland of the western Gambela, (4) Combretum-Terminalia woodland and wooded grassland, (5) Dry evergreen Afromontane forest and grassland complex, (6) Moist evergreen Afromontane forest, (7) Transitional rainforest, (8) Ericaceous belt (9) Afroalpine belt, (10) the riverine vegetation, (11) Freshwater lakes, lake shores, marshes, swamps, and floodplains vegetation, and (12) saltwater lakes, lake shores, salt marshes and pan vegetation. Here, we provide specific details for the major natural forest vegetation types (Figure 2).



Figure 2: Natural vegetation types of Ethiopia following Friis et al. (2010)

Dry evergreen Afromontane Forest and grassland complex

This is a very complex vegetation type occurring between 900 and 3200 m altitudinal range (EGZIABHER, 1991) and has an average annual temperature and rainfall of 14-25°C and 500-1500 mm, respectively (TEKETAY, 2001b). It is widely distributed in central, south-eastern, eastern, northern, and southern highlands (FRIIS; DEMISSEW; BREUGEL, 2010). It is dominated by both coniferous and broadleaved species i.e., *Juniperus procera*, *Podocarpus falcatus*, *Olea hochstetteri*, *Prunus africana*, *Apodytes dimidiata*, *Allophylus abyssinicus*, *Ficus sur*, and others (e.g. GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019b; SIRAJ, 2019). This forest is the habitat for many wild animals including leopard, Menelik's bushbuck, warthog, Bohor reedbuck, olive baboon, and hyenas (see HUN GIRMA; MAMO; ERSADO, 2012; SOROMESSA; KELBESSA, 2013).



Photo: Dry Afromontane Forest. Source: the author (2017)

Despite this fact, it is one of the heavily deforested and degraded vegetation types due to its location in areas suitable for settlement and agriculture (LEMENIH; BONGERS, 2011). The highlands of Ethiopia where this forest is dominantly found were inhabited by humans for millennia and heavily threatened by agricultural expansion, free grazing, illegal logging, fuelwood collection, illegal settlements inside the forest, and fire (BEKELE; TESFAYE; MOHAMMED; ZEWDIE *et al.*, 2015; RUSS, 1979). Historical evidence showed that commercial exploitation in the form of concessions began in this forest type (RUSS, 1979). The logging practices in this forest type were not supported by the knowledge of the population structure, growth rate, minimum logging diameter, and cutting cycles of specific tree species (AMENTE; HUSS; TENNIGKEIT; YEMSHAW, 2010; RUSS, 1979). Instead, individual businessmen were granted concessions by the government and harvested whatever they thought profitable. This unregulated practice, coupled with the population growth in the highlands, severely degraded the forest, resulting in the selective logging of commercially important timber tree species.

Moist evergreen Afromontane Forest

This vegetation type is found in the humid regions of the Southwestern and Southeastern highlands of Ethiopia, at elevations ranging between 1000 and 2600 m (BEKELE, 1993; FRIIS; DEMISSEW; BREUGEL, 2010; SENBETA; DENICH, 2006). The area has an average annual temperature of 15 - 20°C and receives annual rainfall ranging from 700 to 2500 mm, with rainfall occurring for 10 months each year (SENBETA; DENICH, 2006; TEKETAY, 2001b). This vegetation type is characterized by a high level of diversity in terms of its species composition, structure, and habitat types. A study conducted by SENBETA e DENICH (2006) in five forest fragments reported a woody plant density ranging from 9,309 to 69,130 individuals per hectare, basal area ranging from 46 to 54 m² per hectare, number of species ranging from 146 to 374, and number of families ranging from 57 to 91. It is also recognized as the natural habitat of the wild coffee (*Coffee arabica*) populations (SENBETA; DENICH; BOEHMER; WOLDEMARIAM *et al.*, 2007).



Photo: Moist Afromontane rainforest. Source: the author (2010)

The most frequent tree species are Aningeria adolfi-friendercii, Podocarpus falcatus, Trilepisium madagascariense, Olea welwitschii, Albizia gummifera, Milletia ferruginea, Polyscias fulva, Schefflera volkensii, Schefflera abyssinica, Bersama abyssinica, Mimusops kummel, Syzygium guineense, Sapium ellipticum, and several others (e.g. GOLE, 2003b; LULEKAL; KELBESSA; BEKELE; YINEGER, 2008; SENBETA; DENICH, 2006). It is an important source of timber and non-timber forest products including Cororima (Aframomu corrorima), Ginger (Zingiber officinale), black pepper (Piper nigrum), Turmeric (Curcuma longa), coffee (Coffee arabica), wild edible foods, medicinal plants, and honey. It is home to various wild animals including lion, leopard, black leopard, black common jackal, wild dog, wild cat, bush pig, giant forest hog, warthog, colobus monkey, olive baboon, grey duiker, bushbuck, and various bird species (SENBETA; DENICH, 2006).

According to ABEBE e HOLM (2003b), this forest type also experienced commercial selective logging in the past. The commonly harvested tree species were *Aningeria adolfi-friederici, Antiaris toxicaria, Cordia africana, Morus mesozygia*, and *Ekebergia capensis*. The harvesting was carried out through concessions granted to individual businessmen (mainly foreigners) and a few government factories, using traditional axes. The applied harvesting method severely affected the forest. Similar to other forests, they are constantly at risk from settlement and agricultural expansion, commercial tea plantations, modifications of the forest due to the management of coffee, illegal logging, wildfires, and forest grazing (GOLE, 2003a; LULEKAL; KELBESSA; BEKELE; YINEGER, 2008; SOROMESSA; KELBESSA, 2013).

Combretum-Terminalia woodland and wooded grassland

This vegetation type is predominantly found in the Northwestern, Western, and Southwestern parts of the country, at altitudes ranging from 500 to 1900 m (AWAS, 2007; FRIIS; DEMISSEW; BREUGEL, 2010; LEMENIH; KASSA, 2011). It comprised diverse species of *Acacia, Boswellia,* and *Commiphora,* which are valued for their commercial gum and resin products (TADESSE; DESALEGN; ALIA, 2007). The products from these tree species, such as frankincense and gum Arabic are crucial to supporting the livelihoods of the local communities and contribute significantly to the national economy (ESHETE; TEKETAY; HULTEN, 2005; LEMENIH; BONGERS, 2011). Ethiopia ranks as the second-largest producer and exporter of gum and resin (LEMENIH; KASSA, 2011). The export of gum and resin accounts for approximately 0.54 to 0.73 % of Ethiopia's total export revenue. There has been a steady increase in the production, export volume, and revenue earnings from gum and resin-bearing trees (LEMENIH, 2005; LEMENIH; KASSA, 2011), which can be attributed to the growing involvement of private enterprises in the production, processing, and exportation processes.

The gum and resin business are estimated to employ about 25,000 - 35,000 individuals annually at the national level. The average annual cash income per person from tapping, gum, resin collection, and cleaning and grading was estimated to be 172 USD and 165 USD, respectively (LEMENIH; KASSA, 2011). Improper tapping and overharvesting, overgrazing by livestock, increasing forest fire, and conversion to other land use by commercial farmers (such as sesame and cotton producers), and smallholder farmers due to government-led resettlement programs are among the major challenges facing this forest type (ESHETE;

TEKETAY; HULTEN, 2005; GEBREHIWOT; MUYS; HAILE; MITLOEHNER, 2002; LEMENIH; FELEKE; TADESSE, 2007). Additionally, the lack of regeneration and recruitment of *B. papyrifera*, the major resin-bearing tree species, is the other challenge in this forest type (GROENENDIJK; ESHETE; STERCK; ZUIDEMA *et al.*, 2012).



Photo: Combretum-Terminalia broadleaved woodland. Source: the author (2012)

Acacia-Commiphora woodland and bushland

This vegetation type is mainly found in the southern, eastern parts of the country as well as in the central Rift Valley with an altitudinal range between 900 and 1900 m (FRIIS; DEMISSEW; BREUGEL, 2010). The dominant trees and shrubs in this forest are known for their drought-resistant qualities and small and deciduous leaves. For example, WORKU; TEKETAY; LEMENIH e FETENE (2012) documented a total of 64 woody species belonging to 23 families and 31 genera from Borana in Southern Ethiopia. The most common tree species are Acacia senegal, A. seyal, A. tortilis, Balanites aegyptiaca, Boswellia microphylla, B. neglecta, B. rivae, Commiphora africana, C. boranensis, C. cilliata, C. monoica, C. serrulate Maytenus senegalensis and Ziziphus mucronata (TEKETAY, 2001b). This woodland is rich with gum and resin-producing Acacia, Boswellia, and Commiphora species which are the sources of foreign currency as they are exported to more than 40 countries (LEMENIH, 2005). It is also the natural habitat for various wild animals such as oryx, zebra, hartebeest, kudu, and gazelle, and has become a popular destination for tourists and recreational activities. Despite its significance, this woodland faces several challenges, including agricultural expansion, overgrazing, unsustainable fuelwood collection, and charcoal production. It is threatened by subsistence and commercial agricultural expansion, drought, free grazing by livestock, wildfire, bush encroachment, and invasive tree species.



Photo: Acacia-Commiphora small-leaved woodland (Source: Adefires Worku 2006)

Forest management practices

The concept of natural forest management is not new in Ethiopia. Several efforts have been made to develop, conserve and manage forest resources (TEKETAY; LEMENIH; BEKELE; YEMSHAW *et al.*, 2010). Most of the management practices mainly dealt with preventing further degradation and deforestation, as well as restoring degraded lands. Here, we presented the prominent forest development and management measures that have been practiced in Ethiopia:

Plantation forest development as a buffer to natural forests

This is one of the earliest forest management interventions in Ethiopia dates to the turn of the nineteenth century, during the reign of Emperor Menelik II (1888-1892). Historical records indicate that modern plantation forestry began during this period, with the introduction of various fast-growing exotic tree species, such as *Eucalyptus* spp., *Acacia spp.*, and *Pinus* spp. aimed at addressing the shortage of fuel and construction wood in Addis Ababa and nearby towns (RUSS, 1979). Consequently, large areas of plantation forests in the form of peri-urban plantations, catchment protection plantations, smallholder plantations, industrial plantations, and farm forests have been established through government-led programs. According to a recent study (FAO, 2020a), plantation forests covered a total area of 1,200,000 ha in Ethiopia. The plantation forests mainly consist of exotic and indigenous trees such as *Eucalyptus* spp., *Cupressus lusitanica, Pinus patula, Grevillea robusta, Juniperus procera,* and other tree species (BEKELE, 2011). The plantations were usually established from potted seedlings at a density ranging between 1600 and 4444 seedlings ha⁻¹ (BEKELE, 2011). The productivity of planted trees varies considerably depending on site factors, the intensity of applied silvicultural

treatments (e.g. thinning), and the rotation cycle (ÖRLANDER, 1986; PUKKALA; POHJONEN, 1990). For example, Orlander stated that the productivity of Eucalyptus varies between 40 and 55 m³ ha⁻¹ y⁻¹ for stands managed for 5-10 years, and about 30 m³ ha⁻¹ y⁻¹ for stands managed over 10 years rotation cycle. Similarly, the productivity of *Pinus patula* and *Cupressus lusitanica* also varies between 18 and 25 m³ ha⁻¹ y⁻¹ for stands managed for a 20 to 25 years rotation cycle.

Participatory Forest Management (PFM)

Natural forests and woodland resources are considered state property in Ethiopia. The communities who live around the forest were considered as outsiders and not involved in the management of the forest resources (GOBEZE; BEKELE; LEMENIH; KASSA, 2009; LEMENIH; BEKELE, 2008). The government is responsible for the management and protection of natural forests. This non-participatory approach leads to the destruction and deforestation of large areas of natural forests in different parts of the country (AMENTE, 2006a; LEMENIH; BEKELE, 2008). The prevailing problem forced the government to introduce participatory forest management (PFM), an alternative forest management approach that aimed to reduce deforestation and forest degradation without compromising the local community interest (ALEMAYEHU, 2007).

PFM is a collaborative forest management approach in which the government and the local communities agreed to protect, manage, and partially utilize the natural forest resources on a sustainable basis (GOBEZE; BEKELE; LEMENIH; KASSA, 2009). NGOs introduced Participatory Forest Management (PFM) in Ethiopia during the mid-1990s, intending to reduce deforestation and degradation while also enhancing community access to and utilization of natural forests. The PFM approach involved the development of site-specific management plans, which were collaboratively prepared by the state forest agency and the communities engaged in PFM (GOBEZE; BEKELE; LEMENIH; KASSA, 2009). Forests under Participatory Forest Management are expanding in area coverage in Ethiopia. A more recent report revealed that the total area of natural forest under PFM has now reached 2 million hectare (EFCCC, 2020). There is evidence that demonstrates the contribution of PFM in reducing deforestation and forest degradation and enhancing the social and economic importance of forests (GOBEZE; BEKELE; LEMENIH; KASSA, 2009).

Area exclosures for forest regeneration

Area exclosures have been recognized as the practice of excluding degraded land from grazing, cultivation as well as cutting trees and shrubs (MENGISTU; TEKETAY; HULTEN; YEMSHAW, 2005). This practice has become very common in Ethiopia, due to the impressive improvement observed in productivity and the reduction of soil erosion. Furthermore, it is the cheapest and fastest rehabilitation mechanism (BIRHANE; TEKETAY; BARKLUND, 2006), to foster native plant restoration (BIRHANE, 2006; MEKURIA; VELDKAMP, 2012; MENGISTU; TEKETAY; HULTEN; YEMSHAW, 2005), increasing carbon storage (MEKURIA; VELDKAMP; HAILE, 2009), reducing soil erosion (MEKURIA; VELDKAMP; HAILE; GEBREHIWOT *et al.*, 2009), improving soil properties (ABAY; TEWOLDE-BERHAN; TEKA, 2020; MEKURIA, 2013), and improving biomass production (MEKURIA; VELDKAMP, 2012; REDA; KEBEDE; KAHSAY; GEBREHIWOT, 2020). In the last three decades, thousands of hectares of degraded forests and communal lands were closed from human and livestock intervention in various parts of Ethiopia.

Major challenges of the management practices

Despite the various forest management efforts mentioned, the natural forests are unsustainably used and products are sold on informal markets (MEFCC, 2018). The natural forest resources have suffered from a lack of proper management plans. Most of the natural forests were freely accessed by local communities and converted to agricultural lands, grazing lands, and settlements (BEKELE; TESFAYE; MOHAMMED; ZEWDIE et al., 2015). The most commercially attractive timber trees were selectively logged with very few restoration efforts in the past (ABEBE; HOLM, 2003b). The logging practice was not based on the knowledge of the population structure, growth rate, and rotation cycle of tree species (AMENTE; HUSS; TENNIGKEIT; YEMSHAW, 2010; RUSS, 1979). More recently, the government initiated a new intervention to legalize timber harvesting on one-third of the existing natural forests under the concession of public forest enterprises and existing PFM schemes (MEFCC, 2018). However, reliable information on the exact proportion of forests to be harvested, the standing stock, growth rate, population structure, minimum cutting diameter, cutting cycle, and other essential information is lacking (TEKETAY; LEMENIH; BEKELE; YEMSHAW et al., 2010). Above all, decision support tools such as volume equations, growth, and biomass models, harvesting regulations, and management plans are lacking for the management of natural forests and commercially important tree species in Ethiopia.

Dendrochronology: Definition and application in the tropics

The term dendrochronology is derived from the Greek word "dendro," meaning tree, and "chronology," meaning knowing the age (FRITTS; SWETNAM, 1989; SPEER, 2010; TOUCHAN; HUGHES, 1998). Dendrochronology is the scientific discipline that focuses on the study of tree ring formation (SPEER, 2010). It is an interdisciplinary field that applies its theory and techniques to various areas of research, including ecology, archaeology, climatology, geology, hydrology, and atmospheric sciences (FRITTS, 1991; LEWIS, 1995; SPEER, 2010). The diverse applications of dendrochronology make it a valuable area of study that enhances our understanding of the natural world.

There used to be doubts regarding the applicability of dendrochronology in the tropics (e.g. LIEBERMAN; LIEBERMAN; HARTSHORN; PERALTA, 1985; WORBES, 1995). This was mainly due to the assumption that the lack of seasonality in temperature prevented trees from forming annual growth rings. However, the formation of growth rings has been reported for various tree species in the tropics (BRIENEN, 2005; ESHETE; STÅHL, 1999; GOURLAY, 1995; ROZENDAAL; ZUIDEMA, 2011; VERHEYDEN; KAIRO; BEECKMAN; KOEDAM, 2004; WORBES, 2002). In contrast to temperate conditions, the annual growth rings are induced by the seasonality in rainfall patterns (annually occurring dry periods) as well as flooding in tropics (WORBES, 1995; WORBES; JUNK, 1999). According to WORBES (1995), a dry period of 2 to 3 months and less than 60 mm of precipitation are sufficient to induce annual growth rings in tropical trees. Generally, tree ring analysis can be used to study the lifetime growth patterns, determine the ages of trees, estimate a minimum age for cutting, annual wood formation, productivity, the points of growth reduction, reconstruct the climate, and improve the management of trees (e.g. BRIENEN; ZUIDEMA, 2006; COURALET; SASS-KLAASSEN; STERCK; BEKELE et al., 2005; GEBREKIRSTOS; MITLÖHNER; TEKETAY; WORBES, 2008; MATTOS; BRAZ; DOMENE; SAMPAIO et al., 2015; ROZENDAAL; ZUIDEMA, 2011; WORBES; STASCHEL; ROLOFF; JUNK, 2003).

Techniques to identify trees for dendrochronology study

Dendrochronological studies usually begin with a thorough analysis of the wood anatomy of potential tree species. However, not every tree species is appropriate for dendrochronology due to variations in the visibility, annual nature, and other critical characteristics of their tree rings, which depend on the species, age, and environmental conditions (SCHÖNGART, 2008). Overall, any long-lived tree or shrub that produces a distinguishable annual growth ring that is cross-datable can be used for a dendrochronological study (COOK; KAIRIUKSTIS, 2013; WORBES, 1995). The fundamental process in dendrochronology is to determine the yearly formation of a growth ring. To determine this, various methods have been developed such as counting the rings of trees with a known age (e.g. COURALET; SASS-KLAASSEN; STERCK; BEKELE *et al.*, 2005; WORBES, 1995), phenological observations, cambial wounding, a correlation between ring widths and climate data, and radiocarbon dating (DE MIRANDA; HIGUCHI; TRUMBORE; LATORRACA *et al.*, 2018; STAHLE, 1999; WORBES, 1995). The procedures involved in conducting a dendrochronology study are presented in Figure 3.



Figure 3: Schematic diagram of a dendrochronology study. The Chilimo Dry Afromontane Forest (1), *J. procera* trees (2), disc sample from *J. procera* tree (3), sanding process in the laboratory (4), growth ring boundaries in the cross-sectional area (5), growth ring boundary marking (6), LINTAB tree ring measuring equipment (7), and growth ring measurement (8).

Dendrochronology and forest management

Tropical forest management is constrained by the lack of reliable information about the growth of trees which is a basis for determining the commercial tree volumes and cutting cycles (INGA; DEL VALLE, 2017; ROSA; BARBOSA; JUNK; DA CUNHA *et al.*, 2017). The growth pattern of trees or a group of trees is considered the basis for planning sustainable forest management (SCHÖNGART, 2008). This information can be obtained either from repeated measurements in permanent sample plots (PSPs) or from tree ring analysis (BRIENEN; ZUIDEMA, 2006; CONDIT; HUBBELL; FOSTER, 1993). According to BIONDI (1996) repeated forest inventories enables to quantify the growth of individual trees and provide a complete picture of growth dynamics. The information collected through this approach can help to determine the growth, recruitment, and mortality of trees. Nevertheless, conducting repeated forest inventories can be costly due to the labor-intensive nature of the process. These inventories require periodic measurements, usually at 5 to 10-year intervals, which can also be challenging to adjust to the annual growth rate of trees (CLARK; CLARK, 2001; INGA; DEL VALLE, 2017).

Tree ring analysis is a fast and reliable tool to estimate the individual tree age, and determine the lifetime growth rates of trees, in turn improving the understanding of forest dynamics, and thus helping to develop adequate forest management systems (BIONDI, 1996; BRIENEN; ZUIDEMA, 2006; GROENENDIJK; BONGERS; ZUIDEMA, 2017; ROSA; BARBOSA; JUNK; DA CUNHA et al., 2017). This approach involves harvesting or coring trees to collect wood samples for data generation. The growth information generated by this approach will help to determine the long-term growth pattern of trees and develop growth models (BRIENEN; ZUIDEMA, 2006; CANETTI; DE MATTOS; BRAZ; NETTO, 2017; ROZENDAAL; BRIENEN; SOLIZ-GAMBOA; ZUIDEMA, 2010), to reconstruct competition and forest dynamics (CANETTI; DE MATTOS; BRAZ; RICKEN et al., 2016; DE MATTOS; AGUSTINI; ALVAREZ, 2010), to estimate the diameter growth, minimum logging diameters, and cutting cycle of trees (DE MIRANDA; HIGUCHI; TRUMBORE; LATORRACA et al., 2018; MATTOS, 2008), to accurately determine the age and radial growth of trees (BRIENEN, 2005; MARTÍNEZ-RAMOS; ALVAREZ-BUYLLA, 1998; METSARANTA, 2020), to assess biomass production and carbon sequestration (MBOW; CHHIN; SAMBOU; SKOLE, 2013; SANOGO; GEBREKIRSTOS; BAYALA; VILLAMOR et al., 2016) and many other applications. In general, tree ring analysis is the most effective alternative method for determining the lifetime growth rate of trees in a relatively short period of time. This approach can aid in making informed decisions regarding forest management and gaining a better understanding of forests dynamics (e.g. COURALET; SASS-KLAASSEN; STERCK; BEKELE *et al.*, 2005).

Dendrochronology and long-term research Plots in Ethiopia

Dendrochronological research is feasible in only a few sub-Saharan African countries, and Ethiopia is among them (WILS; SASS-KLAASSEN; ESHETU; BRÄUNING *et al.*, 2011). Several dendrochronological studies have been carried out using different tree species in Ethiopia (Table 1). From the dendrochronological investigations, four major types of growth ring patterns have been identified namely: anatomically not distinct rings, multiple rings per year, annual rings, and multiple missing rings (WILS; SASS-KLAASSEN; ESHETU; BRÄUNING *et al.*, 2011). This complex tree ring formation in Ethiopia is associated with differences in precipitation patterns (such as unimodal versus multimodal) and relatively small-scale variations in tree sensitivity to water availability. The lists of dendrochronological studies and the studied tree species are presented in Table 1.

No	Trees	Forest type	References
1	Acacia Seyal		
2	Acacia tortilis		Gebrekirstos et al., 2008 and
3	Acacia senegal	Acacia-Commiphora	2009
4	Balanites aegyptiaca	woodland	
5	Boswellia neglecta		Mokria et al., 2017
6	Acacia etbaica		Eshete and Sta°hl 1999
7	Olea europaea		Siyum et al., 2019
8	Juniperus procera		Siyum et al., 2019
			Wills et al., 2011
			Sass-Klaassen et al., 2008
		Dry Afromontane Forest	Couralet et al., 2005
9	Prunus africana	Dry Anomontane rolest	Krepkowski et al., 2011
10	Ekebergia capensis		Braunning et al., 2014
11	Celtis africana		Krepkowski et al., 2011
12	Croton macrostachyus		Bräuning et al., 2014
13	Podocarpus falcatus		Krepkowski et al., 2011

Table 1: Dendrochronological studies and the studied trees in Ethiopia

			Siyum et al., 2019
14	Boswellia Papyrifera	Combretum terminalia	Tolera et al., 2013
		woodland	
15	Cupressus lusitanica	Plantation forest	Gebregeorgis et al., 2018
16	Pinus patula		Krepkowski et al., 2011

Most of the dendrochronological studies in Ethiopia were mainly focused on the climate growth relationships (e.g. ESHETE; STÅHL, 1999; GEBREGEORGIS; ZEWDIE; WILS; ROBERTSON et al., 2018; GEBREKIRSTOS; MITLÖHNER; TEKETAY; WORBES, 2008; MOKRIA; GEBREKIRSTOS; ABIYU; VAN NOORDWIJK et al., 2017; SIYUM; AYOADE; ONILUDE; FEYISSA, 2019a), river flow reconstruction (MOKRIA; GEBREKIRSTOS; ABIYU; BRÄUNING, 2018), age and growth dynamics (ABIYU; MOKRIA; GEBREKIRSTOS; BRAEUNING, 2018; COURALET; SASS-KLAASSEN; STERCK; BEKELE et al., 2005; KREPKOWSKI; BRÄUNING; GEBREKIRSTOS; STROBL, 2011; MOKRIA; TOLERA; STERCK; GEBREKIRSTOS et al., 2017; SIYUM; AYOADE; ONILUDE; FEYISSA, 2019b; TOLERA; SASS-KLAASSEN; ESHETE; BONGERS et al., 2013). The majority of the dendrochronological research has focused on selected trees from Acacia-Commiphora and Combretum-Terminalia woodlands, with only a limited number of studies from the Dry Afromontane forests, a predominant forest type in the highlands of Ethiopia. Specifically, none of the existing studies on the dry Afromontane forests have aimed to determine the minimum logging diameter, cutting cycle, and the productivity diameter class of commercially important timber tree species. The lack of such information could have implications for the sustainable management and utilization of trees from the Dry Afromontane Forest in Ethiopia.

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Chapter I: Mixed-effects height prediction model for *Juniperus procera* tree from the Chilimo Dry Afromontane Forest

1 Introduction

Tree height is an important variable for modeling and understanding the vertical structure of the forest stand, stand development over time, and the estimation of biomass, timber volume, and site productivity (BURKHART; TOMÉ, 2012; CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO *et al.*, 2014; EFCCC, 2020; FELDPAUSCH; LLOYD; LEWIS; BRIENEN *et al.*, 2012). However, measuring tree height is often fraught with errors (HUNTER; KELLER; VICTORIA; MORTON, 2013). Generally, measuring the height of standing trees is difficult in closed-canopy forests with tall and irregularly shaped crowns (HOLDAWAY; MCNEILL; MASON; CARSWELL, 2014; HUNTER; KELLER; VICTORIA; MORTON, 2013). The observed difficulties can be effectively addressed through the development of height-diameter models (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015).

Earlier studies have described the differences in height-diameter relationships among species, stands, and geographic regions (BANIN; FELDPAUSCH; PHILLIPS; BAKER *et al.*, 2012; CALAMA; MONTERO, 2004; FELDPAUSCH; BANIN; PHILLIPS; BAKER *et al.*, 2011; IMANI; BOYEMBA; LEWIS; NABAHUNGU *et al.*, 2017). In recent work, SILESHI; NATH e KUYAH (2023) provided evidence contradicting that notion and showed that most of the variability in the height-diameter relationship is a statistical artifact arising from measurement errors, small sample sizes, sampling biases and failure to capture the size-frequency distribution. Therefore, it is crucial to consider these arguments while trying to understand the height-diameter relationship of trees. Moreover, the use of additional predictor variables such as basal area, stem density, dominant height, the relative position of trees, and quadratic mean diameter have been widely recognized to enhance the accuracy of height prediction under different site conditions (RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021; TEMESGEN; V GADOW, 2004; TEMESGEN; ZHANG; ZHAO, 2014). These predictor variables will enable us to avoid the need to establish separate height-diameter relationships for each stand (CURTIS, 1967).

The basic data used to develop height-diameter models are usually collected from trees in randomly established plots within a forest stand. The data derived from such plots are clustered (trees within plots) and are usually correlated (DORADO; DIÉGUEZ-ARANDA; ANTA; RODRÍGUEZ *et al.*, 2006). When a model is fitted to correlated data using the ordinary least squares (OLS) method, the confidence intervals for the model parameters may be estimated incorrectly (ERCANLI, 2015). Recent studies (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; OGANA; ERCANLI, 2022; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021; TEMESGEN; ZHANG; ZHAO, 2014) have demonstrated that the mixed-effect modeling approach allows modeling the data collected from clustered structures and accounts for the lack of independence between observations. This approach can also help to incorporate tree height-diameter variability arising from differences in forest type, location, sample plots, and species that the OLS approach does not consider. Mixed effects models provide opportunities to simultaneously estimate both fixed effects and subject-specific (random-effects) parameters (PINHEIRO; BATES, 2000).

Various local and generalized height prediction models have been proposed for different tree species in temperate (e.g., RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021; SHARMA; VACEK; VACEK; KUČERA, 2019) and tropical forests (KEARSLEY; MOONEN; HUFKENS; DOETTERL *et al.*, 2017; LIMA; GÖRGENS; ELIAS; DE ABREU *et al.*, 2021; MUGASHA; MAUYA; NJANA; KARLSSON *et al.*, 2019). These models are designed to enable practitioners to estimate the height of trees and hence the biomass, timber volume, and site productivity of a forest without destructive sampling. On the other hand, very few efforts have been made to develop height prediction models for trees in Afromontane forests. A few models exist for some forests and trees in Ethiopia (ASRAT, ZERIHUN; EID, TRON; GOBAKKEN, TERJE; NEGASH, MESELE 2020; SEBRALA; ABICH; NEGASH; ASRAT *et al.*, 2022; SISAY; THURNHER; BELAY; LINDNER *et al.*, 2017). However, the existing models are not adequate for general use given the diversity of tree species and the geographic coverage of Ethiopia. Therefore, it is crucial to develop more height prediction models for the native tree species of Ethiopia.

In this study, we developed models that could be used to predict the height of *J. procera* Hochst. ex Endl. trees in the dry Afromontane Forest in central Ethiopia. Height prediction models do not exist for *J. procera*, although it is one of the commercially important native species in Afromontane forests across Africa and the Arabian Peninsula. The objectives of this research were (1) to evaluate the prediction performance of different local height-diameter models and select the best model for *J. procera* trees in Chilimo dry Afromontane Forest; (2) to develop a mixed effect model and analyze the plot level prediction performance; (3) to evaluate the contribution of including stand variables on the prediction performance of the best model; and (4) to determine the best sampling alternative for calibrating the best mixed-effects and generalized mixed-effects model.

2 Materials and Methods

2.1. Study area

The data used in this study were collected from the Chilimo and Menagesha Suba Dry Afromontane Forests (Figure 1). The Chilimo forest is geographically located from 38°05' to 38°15' E and 9°00' to 10°10' N, at an altitudinal range of 1,700-3,200 m (TESFAYE, MEHARI A; GARDI, OLIVER; BEKELE, TESFAYE; BLASER, JÜRGEN 2019). The area experiences a unimodal pattern of rainfall distribution occurring from May to November, with July having the highest peak. The mean annual temperature ranges between 15 and 20 °C, and its average annual precipitation ranges between 1000 and 1264 mm (TESFAYE, MEHARI A; GARDI, OLIVER; BEKELE, TESFAYE; BLASER, JÜRGEN 2019).



Figure 1: Map of the study areas overlaid with the distribution map of dry Afromontane forests following Friis et al. (2010).

The major soil types around the study areas are Vertisols, Luvisols, and Cambisols (SOROMESSA; KELBESSA, 2013). The soils are reddish-brown, gravely and shallow at higher altitudes, while at lower sites, they tend to become dark-gray and deep (SOROMESSA; KELBESSA, 2013; TESFAYE; BRAVO; RUIZ-PEINADO; PANDO *et al.*, 2016). According to MAMMO; KEBIN; CHIMIDI e IBRAHIM (2019), the surface soil (0-20 cm) in Chilimo forest has higher levels of total nitrogen, available phosphorus, and potassium, as well as a higher percentage of organic matter. Menagesha Suba forest is located between 38°28' E and 38°36' E to 8°56' N and 9°02' N with an altitude ranging between 2200 and 3385 m (LEMI; ESHETE; SEID; MULUGETA *et al.*, 2023). The area receives on average 1056 mm of rainfall per year, and the average monthly temperature ranges from 6 to 22 °C. The rainfall pattern is bimodal, with a long rainy season from June to September and a short rainy season between April and May (DUGUMA; HAGER; GRUBER, 2009). The data collected from the Menagesha suba Dry Afromontane Forest was used for calibration.

2.2. Data collection

We conducted a forest inventory in 2018 in the Chilimo and Menagesha Suba forests. We used a systematic random sampling technique for vegetation data collection. A total of 131 sample plots (20 m \times 20 m), 101 in Chilimo and 30 in Menagesha suba forest, were established along transect lines. The first transect was aligned parallel to the edge of the forest, and the others were laid out at 500 m intervals along the transect lines. The first sample plot was located randomly, and the subsequent plots were established at 300 m intervals. In each sample plot, the diameter at breast height (dbh) and total height (ht) of all trees with dbh ≥ 2.0 cm were measured using a diameter tape and Vertex IV ultrasonic hypsometer (Haglöf Sweden AB, Långsele, Sweden). The local names of all trees were recorded and identified to the species level in the field following the Flora of Ethiopia and Eritrea (EDWARDS; TADESSE; DEMISSEW; HEDBERG, 2000; EDWARDS; TADESSE; HEDBERG, 1995; HEDBERG; EDWARDS; NEMOMISSA, 2003; HEDBERG; FRIIS; EDWARDS, 2004; HEDBERG; HEDBERG; EDWARDS, 1989). Those species which were not identified in the field, their specimens were collected, pressed, and identified at the National Herbarium, Addis Ababa University. The collected data were used to compute the quadratic mean diameter (Dg), basal area (G), dominant height (hd) (the average height of the 100 tallest trees per hectare) and diameter (Dd) (the diameter for the average height of the 100 tallest trees per hectare), and the number of trees per hectare (N). The diameter and height of 1215 individual J. procera trees were extracted from the inventory data and used to develop a height prediction model. Descriptions of the dataset are presented in Table 1.

Variables	Fitting	dataset (N° of plots	= 101)	Calibrat	Calibration dataset (N^{o} of plots = 30)			
	Mean	Min.	Max.	Std	Mean	Min.	Max.	Std	
Dbh	21.10	2.00	121.20	18.45	14.3	2.00	71.00	12.70	
ht	13.55	2.00	43.22	7.76	9.90	1.60	28.00	6.20	
G	11.27	0.01	87.60	15.89	2.00	0.01	16.90	4.40	
Ν	484.48	25.00	2750.00	773.37	606.80	21.00	1149.00	365.80	
hd	10.71	2.00	38.67	6.77	4.60	1.40	14.00	2.50	
Dd	18.47	2.53	71.70	13.12	9.10	2.00	25.90	6.50	
Dq	16.23	2.00	79.80	13.81	5.40	2.00	23.90	6.10	

Table 1: The summary statistics of the fitting and calibration datasets.

where dbh = diameter at breast height (cm), ht = total height (m), N = stand density (trees ha⁻¹), G = basal area (m² ha⁻¹), Dq = quadratic mean diameter (cm), hd = dominant height (m), and Dd = dominant diameter (cm), Min = minimum, Max = maximum, and Std = standard deviation.

2.3. Juniperus procera Hochst. ex. Endl.

We chose *J. procera*, commonly known as the African Pencil Cedar, as the target species in this study because of its value as a native timber tree. It is an evergreen coniferous tree that grows up to a height of 40 m and a diameter of 3 m (POHJONEN; PUKKALA, 1992). This species was once regarded as threatened in the IUCN red list in 2011, but it has been assessed as a species of least concern (FARJON, 2013). Its native range covers Congo, Democratic Republic of Congo, Djibouti, Eritrea, Ethiopia, Kenya, Malawi, Saudi Arabia, Somalia, Sudan, Tanzania, Uganda, Yemen, Republic of and Zimbabwe (ORWA; MUTUA; KINDT; JAMNADASS *et al.*, 2009). It is grown in plantations in its native range and elsewhere, including South Africa, France, the United Kingdom, the United States, India, and Australia (ORWA; MUTUA; KINDT; JAMNADASS *et al.*, 2009). It is also a valuable timber tree species in the East African highlands and the most preferred tree in Ethiopia (ABRHA; BIRHANE; HAGOS; MANAYE, 2018). It is adapted to high elevation climates with low precipitation characteristic of Afromontane forests, which constitute a unique forest type occurring on high African mountains (WHITE, 1983).

2.4. Statistical analysis

2.4.1. Base model selection

The relationship between tree height and diameter has been described using a variety of statistical models. Various height-diameter models have been published to describe height-diameter relationships (e.g., HUANG; TITUS; WIENS, 1992; MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; ZEIDE, 1993). Some are grounded in sound theory, while others are purely empirical in nature. The power law function is the most common one based on a number of theoretical arguments (SILESHI; NATH; KUYAH, 2023). MEHTATALO e LAPPI (2020) suggested that flexibility and parsimony (i.e., combining simplicity with high predictive or explanatory power) should be considered in addition to the parameters' obvious biological interpretability when choosing the best function. We evaluated fourteen local functions (Table 2) that have been widely used to describe the height-diameter relationships of trees from both plantation and natural forests (CHENGE, 2021; CORRAL-RIVAS; ÁLVAREZ-GONZÁLEZ; CRECENTE-CAMPO; CORRAL-RIVAS, 2014; KEARSLEY; MOONEN; HUFKENS; DOETTERL *et al.*, 2017; OGANA; CORRAL-RIVAS; GORGOSO-VARELA, 2020; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021).

No	Name	Mathematical expression	References
M1	Power	$ht = 1.3 + \beta_0 \times dbh^{\beta_1}$	Stoffel and Van Soest (1967)
M2	Näslund	$ht = 1.3 + \frac{dbh^2}{\left(\beta_0 + \beta_1 \times dbh\right)^2}$	Näslund (1937)
M3	Curtis	$ht = 1.3 + \frac{\beta_0 \times dbh}{(1 + dbh)^{\beta_1}}$	Curtis (1967)
M4	Meyer	$ht = 1.3 + \beta_0 \left(1 - exp(-\beta_1 \times dbh) \right)$	Meyer (1940)
M5	Schumacher	$ht = 1.3 + \beta_0 \exp\left(-\left(\frac{\beta_1}{dbh}\right)\right)$	Schumacher (1939)
M6	Michaelis and Menten	$ht = 1.3 + \beta_1 \times dbh / (\beta_2 + dbh)$	Bates and Watts 1980
M7	Gomperz	$ht = 1.3 + \beta_0 \exp(-\beta_1 \exp(-\beta_2 \times dbh))$	Gomperz (1825)

Table 2: Lists of candidate equations for height modeling.

M8	Logistic	$ht = 1.3 + \frac{\beta_0}{1 + \beta_1 \exp\left(-\beta_2 \times dbh\right)}$	Huang et al. (1992)
M9	Chapman-Richards	$ht = 1.3 + \beta_0 (1 - exp(-\beta_1 \times dbh))^{\beta_2}$	Richards (1959), Chapman (1961)
M10	Weibull	$ht = 1.3 + \beta_0 \left(1 - exp \left(-\beta_1 \times dbh^{\beta_2} \right) \right)$	Weibull (1951)
M11	Lundqvist Korf	$ht = 1.3 + \beta_0 \exp\left(-\beta_1 \times dbh^{-\beta_2}\right)$	Zeide 1989
M12	Ratkowsky	$ht = 1.3 + \beta_0 \exp\left(\frac{-\beta_1}{(dbh + \beta_2)}\right)$	Ratkowsky (1990)
M13	Hossfeld IV	$ht = 1.3 + \beta_0 \left[1 + \left(\frac{1}{\beta_1 \times dbh^{\beta_2}} \right) \right]$	Huang (2000)
M14	Johnson- Schumacher	$ht = 1.3 + \beta_0 \exp\left(\frac{-\beta_1}{(dbh + \beta_2)}\right)$	Zeide 1989

where dbh is the over bark diameter at breast height in cm, ht is the total tree height in m, and β_0 , β_1 , and β_2 are parameters of the height-diameter models.

We fitted all models by using the *gnls* function in R software version 3.3.2. (R Development Core Team 2021). We used bias, root mean square of error (RMSE), and Akaike information criterion (AIC) (equations 1, 2, and 3) and graphical analysis to compare the predictive performance of the models and select the best fitted model (TEMESGEN; ZHANG; ZHAO, 2014). We also applied a power type variance function (var(e) = $\sigma^2 |dbh|^{2\delta}$) to correct the observed heteroscedasticity in the residuals of all models.

$$Bias = \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)}{n} \tag{1}$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (y_i - \dot{y}_i)^2}{n - p}}$$
(2)

$$AIC = n \log\left(\frac{SSR}{n}\right) + 2p \tag{3}$$

where y_i = observed values, y_i = predicted values, \hat{y}_i = average, n = total number of observations, p = number of parameters of the equation, SSR = sum of the squares of the residuals; RMSE = root mean square of error; and AIC = Akaike information criterion.

A rank was assigned to the fit statistical values of each model (MULAMBA; MOCK, 1978). These ranks were then aggregated by adding them together to calculate the final fit rank for each model. This rank serves as an indicator of the model's performance with respect to all

the considered fit statistics criteria. Furthermore, the models' compliance with the constant variance assumption was also examined by plotting the residuals against the standardized diameter. The function mywhiskers in the package *lmfor* was utilized to plot the means of residuals in 10 relative diameters classes together with the confidence interval for individual observation (mean ± 1.96 SD) and the 95% confidence intervals for the class mean to visually detect the potential heteroscedasticity in the residuals (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). The difference between each tree's diameter and the plot mean diameter divided by the diameter's standard deviation was used to calculate standardized diameters (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015). The parameters of the best-fitted model were obtained by fitting the model with the entire dataset. Finally, the model with the lowest rank sum value and exhibited no violation of the assumption of homoscedasticity was regarded as the best base model.

2.4.2. Nonlinear mixed-effects modeling

Once the best generalized nonlinear least squares model was selected, we proceeded to expand the parameters with random effects. Here, we used a subject-specific nonlinear mixed effects model (NLMEM). The reason for this choice is that the data used in this study consisted of a hierarchical structure, i.e., trees within sample plots. Several works have shown that observations taken from the same sampling unit are highly correlated (e.g., CALAMA; MONTERO, 2004; ERCANLI, 2015; ÖZÇELIK; CAO; TRINCADO; GÖÇER, 2018) and show a clear violation of the fundamental least squares assumption of independent observation. This will lead to bias in the confidence intervals for the mean value of the parameters. To address this problem, earlier studies have proposed the use of nonlinear mixed-effects models (CALAMA; MONTERO, 2004; MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021; TEMESGEN; ZHANG; ZHAO, 2014). The random-effects parameters describe a particular cluster (sample plot), while the fixed-effects parameters reflect the population average of the data (STEGMANN; JACOBUCCI; HARRING; GRIMM, 2018). More recently, NLMEM has been widely applied in modeling height-diameter relationships (CHENGE, 2021; CICEU; GARCIA-DURO; SECELEANU; BADEA, 2020; CUI; WU; ZHANG; ZHAO et al., 2022; OGANA, 2022; XIE; WIDAGDO; DONG; LI, 2020; ZHANG; FU; SHARMA; HE et al., 2021). The parameters were estimated by using the 'nlme' function (PINHEIRO; BATES, 2022) in R software version 3.3.2. (R Core Team 2021). This allows for a comparison between the different mixed effects model forms (Table 3) and the selected base model by ANOVA to test the significance of including the random effects, as both models have the same fixed effects. Model evaluation was again performed using RMSE, bias, and AIC values.

No	Model form	Random effects
M1	$ht = 1.3 + (\beta_0 + u_{0i}) \times dbh / ((\beta_1 + u_{1i}) + dbh)$	on β_0 and β_1
M2	$ht = 1.3 + \left(\beta_0 + u_{0i}\right) \times \frac{dbh}{\beta_1} + \frac{dbh}{\beta_1}$	on β_0
M3	$ht = 1.3 + \frac{\beta_0 \times dbh}{\left(\left(\beta_1 + u_{1i}\right) + dbh\right)}$	on β_1

Table 3: The evaluated nonlinear mixed-effects models form

where ht is the height of tree, dbh is the diameter at breast height, β_0 and β_1 are the fixed effects parameters, and u_i denotes the estimated random effects.

2.4.3. Generalized mixed effects models.

The contribution of the easily measured stand variables (Table 1) to improve the predictive performance of the best mixed effect model was evaluated. First, we conducted correlation analysis to evaluate the relationship of the stand variables with the parameters of the best mixed-effects model. During the analysis, different combinations of the selected stand variables were entered as predictors in the model, and the fitting performances were evaluated using the RMSE, bias, and AIC. Then, a generalized mixed-effects model was developed using the most highly correlated stand predictor variables.

2.4.4. Calibration and random effect estimation.

Two different types of predictions can be made using the mixed effects modeling approach (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; PATRÍCIO; DIAS; NUNES, 2022). The first is a fixed effects or marginal prediction that offers predictions using only the fixed part of the model. The second is conditional prediction, which provides a more accurate prediction for a given sample plot because it uses both the random and fixed elements of the model. However, when height measurements are available from subsampled trees from a new plot or stands, it is possible to localize the random effects; this process is known as calibration or localization. In this study, we used calibration to determine the plot-specific random effects and evaluate the model's performance (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; PATRÍCIO; DIAS; NUNES, 2022; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). Based on the subsample data, the random effects \hat{b}_i were usually predicted by using the following equation (VONESH; CHINCHILLI, 1997).

$\widehat{\boldsymbol{b}} = \widehat{\boldsymbol{D}}\widehat{\boldsymbol{Z}}_{i}^{T}(\widehat{\boldsymbol{R}}_{i} + \widehat{\boldsymbol{Z}}_{i}\widehat{\boldsymbol{D}}\widehat{\boldsymbol{Z}}_{i}^{T})^{-1}\widehat{\boldsymbol{e}}_{i}$

where \hat{D} is the estimated variance-covariance matrix associated with the random effects at the plot level, \hat{R}_i is the estimated variance-covariance matrix for the error term, \hat{Z}_i is the partial derivatives matrix with respect to the random effects, and \hat{e}_i is the error matrix estimated using the fixed parameters only. The detailed procedure for random effects prediction using nonlinear mixed effects modeling is presented by CALAMA e MONTERO (2004). The calibration response of the best mixed effect and generalized mixed effects models was assessed for various sampling alternatives and sample sizes in each plot using an independent dataset (Table 1). Overall, nine different sampling alternatives (Table 4) were evaluated to determine the required number of trees for the calibration process following the procedure in CAMACHO; RIVAS; HERNÁNDEZ; DURÁN *et al.* (2022):

Table 4: The evaluated sampling alternatives for calibration response

Code	Sampling alternatives
A1.	Using selected trees with diameters near the diameter distribution quartiles (0.25,
	0.50, and 0.75 percentiles).
A2.	Using selected trees with diameters close to the first and the second quartiles (0.25)
	and 0.50) of the diameter distribution.
A3.	Using selected trees with diameters close to the first and the third quartiles (0.25 and
	0.75) of the diameter distribution.
A4.	Using selected trees with diameters close to the first and the third quartiles (0.50 and
	0.75) of the diameter distribution.
A5.	Using selected trees with diameters close to the second quartiles (0.50) of the diameter
	distribution.
A6.	Using selected trees with diameters close to the Dq, the minimum (smallest diameter),
	and the maximum (largest diameter) trees in each plot.
A7.	Using the thinnest tree in each sample plot
A8.	Using 1 - 10 randomly selected trees in each sample plot
A9.	Using 1 - 10 systematically selected thickest trees in each sample plot

We assessed the performance of the calibration alternatives using the RMSE values and compared them to the RMSE estimates generated using the best mixed-effects model when all trees in the sample plot were considered to estimate the random effects.

3. Results

3.1. Base model selection

The evaluated models demonstrated variations in their ability to predict tree height (Table 5). The parameter estimates of the evaluated models were significantly different from zero at a 5% significance level. Based on the Mulamba-Mock rank index values and an analysis of the residual graphs, the Chapman-Richards and Weibull model was found to be the best among the three-parameter models, while the Michaelis–Menten model ranked first among the two-parameter models, showing the lowest goodness-of-fit statistics values. In terms of prediction accuracy, the two-parameter Michaelis-Menten model outperformed the three-parameter Chapman-Richards and Weibull models. Therefore, we have selected the Michaelis-Menten model as a base model for further analysis due to its simplicity (parsimonious) and ease of fitting (adequate fit). Details of the model diagnostics for the evaluated local models are provided in appendices (supplementary 2 - 4).

Models	Parameters			Fit statistics				Rank			
	β_0	β_1	β_2	Bias	Rank	RMSE	Rank	AIC	Rank	Σ	Final
M1	1.802*	0.659*		0.00	1	4.39	12	6398.13	11	24	8
M2	1.346*	0.195*		0.35	12	4.32	11	6389.49	9	32	11
M3	20.891*	8.041*		0.85	13	4.77	13	6531.36	13	39	13
M4	24.905*	0.043*		0.10	7	4.17	5	6322.19	6	18	6
M5	19.99*	7.102*		0.97	14	4.91	14	6586.78	14	42	14
M6	36.437*	32.113*		0.09	6	4.16	1	6314.99	2	9	1
M7	22.083*	2.415*	0.089*	0.16	10	4.24	9	6396.07	10	29	10
M8	21.152*	6.891*	0.141*	0.23	11	4.31	10	6462.61	12	33	12
M9	26.816*	0.034*	0.914*	0.08	3	4.16	2	6318.97	5	10	3
M10	27.406*	0.044*	0.929*	0.08	3	4.16	3	6318.42	4	10	4
M11	98.175*	4.849*	-0.302*	0.08	5	4.18	8	6310.83	1	14	5
M12	31.394*	20.392*	5.819*	0.12	9	4.18	7	6335.11	8	24	9
M13	36.768*	0.031*	-0.995*	0.08	2	4.17	4	6316.97	3	9	2
M14	33.337*	20.893*	7.296*	0.11	8	4.17	6	6329.15	7	21	7

Table 5: Parameter estimates and fit statistics values for the local models.

Note: * indicates significant parameter estimates at $\alpha = 0.05$.

Figure 2a and 2b illustrate the graphical representation of the model fitting and the observed versus predicted height performance, respectively. The observed and predicted graphs

showed that the model generated accurate height prediction. The visual inspection of the standardized residuals graph shows no indication of violation of the assumption of homoscedasticity in the residual's distribution (Figure 2c). The residuals are homogenously distributed around the zero line and there is no systematic pattern in the residual's distribution.



Figure 2: Diameter and height relationships (a), observed against predicted height (b), and residuals graph (c) of *J. procera* trees using the Michaelis–Menten model. The grey dots show the residuals, the empty circles show the means of residuals in 10 relative diameter classes. The thin vertical lines show the confidence interval of one observation, and the thick vertical lines show the 95% confidence interval of class mean. The thick lines that do not cross the horizontal line at y = 0 are highlighted using red color.

3.2. Nonlinear mixed effects model

The height prediction performance of the base model was significantly improved by adding a plot-level random effect (Table 6). Model comparison using the likelihood ratio (LR) test indicated that the mixed-effects model form with random effects on β_0 and β_1 (M1) had better height prediction performances (L = -3114.98, df = 6, p < 0.0001) than the remaining mixed-effect model forms. Overall, the RMSE decreased from 4.16 in the base model without random effects to 2.69 m in the best mixed effect model (M1), and the bias decreased from 0.09 to 0.04 m. Additionally, the AIC of the model decreased from 6314.99 to 5858.75 (Tables 5 and 6).

Componente	Mixed models				
Components	M1	M2	M3		
Fixed parameters					
β_0	31.6506 (1.4959)	32.3400 (1.0469)	34.6591 (0.9960)		
β_1	23.8515 (1.6557)	25.0679 (1.2465)	28.8907 (1.6301)		
Random variance components					
std (u_{0i})	12.1889	5.4512			
std (u_{1i})	11.9283		7.7571		
$\operatorname{cor}\left(u_{0i}, u_{1i}\right)$	0.9380				
σ^2	0.8463	0.9313	0.8122		
δ	0.4145	0.4018	0.4704		
Model performance					
RMSE (m)	2.6924	2.9144	3.2499		
Bias (m)	0.0432	0.0112	-0.0566		
AIC	5858.75	6051.30	6316.07		

Table 6: Parameter estimates, standard error (in parentheses), variance components, and fit statistics values for the mixed effects height-diameter models.

where β_0 and β_1 are fixed parameters; std (u_{0i}) and std (u_{1i}) are the standard deviation of the random effects; cor is the correlation between the random effects; σ^2 : residual variance; δ : parameter of power-type variance; RMSE, bias, and AIC values are the fit statistics values from the models.

The plot-level predictions closely follow the observed values, indicating that the best mixed-effects model (M1) explains the height-diameter relationship of *J. procera* trees very

well (Figure 3a). The observed and predicted graphs showed that the model generated accurate height prediction (Figure 3b). The visual inspection of the standardized residuals plot of the best-fitted mixed effect model (M1) shows no indication of violation of the assumption of heteroscedasticity in the residual's distribution (Figure 3c). Residuals are homogenously distributed around the zero line and there is no systematic pattern in the residual's distribution.



Figure 3: Plot specific height diameter curves (a), observed against predicted height (b) and residuals distribution graphs (c) of *J. procera* trees using the mixed effect model. The lines represent the local curves, and the gray dots are the observed height-diameter data.

3.3. Generalized mixed effects model.

Among the stand variables, stem density (r = -0.38, p < 0.01) and quadratic mean diameter (r = 0.26, p < 0.04) were found to be correlated with the β_0 and β_1 parameters of the best mixed effects model (Supplementary 1). The addition of these variables into the best mixed

effects model slightly improved the RMSE by 0.01%. However, the AIC and the model bias was increased by 68% and 0.03%, respectively (Tables 6 and 7). The final generalized mixed effects model resulting from expanding the fixed effects of the best mixed effects model was:

 $ht_{ij} = 1.3 + ((\beta_0 + u_{0i}) * dbh_i + \beta_2 \times Dg) / ((\beta_1 + u_{1i}) + dbh_i + \beta_3 * tpa) \dots M11$

Table 7. Parameter estimates, standard error (in parentheses), and fit statistics of the best generalized mixed effects model.

Components	M11
Fixed parameters	
β_0	28.4695 (1.3859)
β_1	13.4697 (2.1315)
β_2	-1.3338 (0.1496)
β ₃	0.1139 (0.0383)
Random variance components	
std (u_{0i})	11.3006
std (u_{1i})	11.1352
$\operatorname{cor}\left(u_{0i}, u_{1i}\right)$	0.9510
σ^2	0.8019
δ	0.4327
Model performance	
RMSE (m)	2.6921
Bias (m)	0.0724
AIC	5860.53

where β_0 , β_1 , β_2 , and β_3 are fixed parameters; std (u_{0i}) and std (u_{1i}) are the standard deviation of the random effects, cor is the correlation between the random effects, σ^2 is the residual variance, δ is the parameter of power-type variance, RMSE, bias, and AIC are the fit statistics values.

The visual inspection of the standardized residuals graph of the generalized mixed effect model (M11) shows no indication of violation of the assumption of heteroscedasticity in the residual's distribution (Figure 4). The residuals are homogenously distributed around the zero line and there is no systematic pattern in the residual's distribution.



Figure 4. Standardized residuals graph for the generalized mixed-effects model (M11)

3.4. Calibration response

Among the systematic sample selection alternatives (A1-A9), the lowest RMSE value was obtained by measuring trees with diameters close to the quadratic mean diameter, the smallest, and the largest diameter trees (A6) in each plot using the mixed effects model (Table 8). Conversely, the thinnest tree (smallest diameter) sampling alternative (A7) consistently produced the highest RMSE values for both models. The systematic selection alternative (A9) consistently outperformed the random selection alternative (A8) when using the local mixed effect model (Figure 5). However, the opposite was observed for the generalized mixed effect model. Overall, the best result for random effect estimation was obtained by systematically measuring three trees with the largest diameters in each plot.

Ne	Subcomple	N —	Model RMSE	
INU	Subsample		Local	Generalized
A0	The best local model	1215	2.6924	2.6921
A1	Quartiles [1,2,3]	3	2.2320	2.4311
A2	Quartiles [1,2]	2	2.5344	2.9109
A3	Quartiles [1,3]	2	2.2873	2.5345
A4	Quartiles [2,3]	2	2.3376	2.6929
A5	Quartiles [2]	1	2.6680	3.1421
A6	dg, dmin, dmax	3	2.1354	2.4517
A7	Thinnest	1	2.9954	3.2069

Table 8: The RMSE values for the evaluated sampling alternatives.



Figure 5: Plots of RMSE values obtained in the calibration process for the systematic and random sampling alternatives A8 and A9. The blue dashed line represents systematic selection using the generalized mixed effect model, while the red dashed line represents random selection using the same model. On the other hand, the broken red line denotes random selection using the local mixed effect model, while the broken blue lines denote the systematic selection alternative using the local mixed effect model.

4. Discussion

In this study, we developed a height prediction model for *J. procera* trees from the dry Afromontane forests of Ethiopia. Among the evaluated local models, the Michaelis–Menten model showed the best height prediction performance and was selected as the best base model. The addition of stand variables slightly improved the prediction performance of the best model. The plot level random effects enable us to capture the variability in height-diameter relationships among the plots and provide the best height prediction. The calibration response revealed that the systematic measurement of the three largest diameter trees in a plot was the best sample size to estimate the random effects and predict the height of trees from the new plots or stands. The findings of this study will help researchers and forest managers better understand the height growth pattern of *J. procera* trees in Afromontane forests and how stand variables affect height growth.

The Michaelis–Menten model was first developed to model enzyme kinetics in chemistry (MICHAELIS; MENTEN, 1913); however, it has been widely used for modeling the

height-diameter relationship of various tree species (e.g., BARBOSA; RAMIREZ-NARVAEZ; FEARNSIDE; VILLACORTA *et al.*, 2019; FAYOLLE; PANZOU; DROUET; SWAINE *et al.*, 2016; MOLTO; HÉRAULT; BOREUX; DAULLET *et al.*, 2014; PANZOU; BOCKO; MAVOUNGOU; LOUMETO, 2021). This model has two biologically meaningful parameters that represent the maximum asymptotic height (β_0) a tree can attain and the curvature (β_1) that describes the rate of increase in height (MOLTO; HÉRAULT; BOREUX; DAULLET *et al.*, 2014). It is an asymptotic model that has been used to estimate the missing height of trees during the recent national forest inventory in Ethiopia (SEBRALA; ABICH; NEGASH; ASRAT *et al.*, 2022). Various studies have also reported that two-parameter models are generally easier to fit and are quicker to achieve convergence than the three-parameter models (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015; OGANA; CORRAL-RIVAS; GORGOSO-VARELA, 2020), which is also supported by this study.

The use of nonlinear mixed effects models in height-diameter modeling allows for the incorporation of random effects, which can account for both within and between-plot variability (e.g., BRONISZ; MEHTÄTALO, 2020; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). The plot-specific height-diameter relationships (Figure 3c) showed varying degrees of variability in the asymptote and curvature and revealed a pattern of rapid development followed by a leveling off. Generally, the nonlinear mixed effects model (M1) provided better fit statistics values than the base model (Tables 5 and 6). As expected, the incorporation of random parameters of the mixed effect model allowed us to properly capture the variability was not adequately accounted for by the base model (MEHTÄTALO; DE-MIGUEL; GREGOIRE, 2015). HUANG; WIENS; YANG; MENG *et al.* (2009) similarly pointed out that the random component of the mixed effect model enables us to account for the plot level variations arising from both known and unknown factors without the necessity of explicitly identifying or measuring them. This is one of the key strengths of the Non-Linear Mixed Effects Modeling (NLMEM) approach.

The mixed effect model result showed that the u0 parameter deviates from the population mean with a standard deviation of 12.2, indicating the variation in β_0 among the sample plots. Similarly, the parameter u1 also differed from the population fixed effects on β_1 with a standard deviation of 11.9 m, indicating the variation in β_1 among the sample plots (Table 6). This result confirmed our expectations that the maximum height and curvature varied among the sample plots. The observed variation might be associated with variations in soil properties, stand structure, altitude, and stem density. Various studies have demonstrated that differences

in site quality, stem density, elevation, the relative position of trees within a stand, precipitation, and temperature are the main drivers of the variations in height-diameter relationships of various trees (BANIN; FELDPAUSCH; PHILLIPS; BAKER et al., 2012; FELDPAUSCH; BANIN; PHILLIPS; BAKER et al., 2011; MARSHALL; WILLCOCK; PLATTS; LOVETT et al., 2012; SHARMA; YIN ZHANG, 2004; SULLIVAN; LEWIS; HUBAU; QIE et al., 2018; TEMESGEN; HANN; MONLEON, 2007; TIAN; JIANG; SHAHZAD; HE et al., 2022). For example, trees that grew in soils with fewer physical limitations grew taller than trees subjected to greater physical limitations (FELDPAUSCH; BANIN; PHILLIPS; BAKER et al., 2011). Moreover, VAN BREUGEL; HALL; CRAVEN; GREGOIRE et al. (2011) also stated that soil fertility and rainfall had significant impacts on the early growth and survival of 49 tropical tree species in Panama. Specifically, the study revealed that trees in areas with higher soil fertility and rainfall were significantly taller and had larger diameters than trees in areas with lower fertility. This suggests that soil fertility plays an important role in determining the size of trees in each area. The differences in topography can be a potential cause of the variation in the height-diameter relationship, resulting in taller trees in the valleys compared to ridges in drier areas and vice versa in wet regions (DETTO; MULLER-LANDAU; MASCARO; ASNER, 2013). In densely populated stands, trees may have to compete more for resources such as water, nutrients, and light, which can hinder their growth and result in significant height variability (GOMEZ-GARCIA; FONSECA; CRECENTE-CAMPO; ALMEIDA et al., 2015). In general, forests with several terrain attributes (i.e., soil types, topography, light conditions, and competition for resources) are likely to have greater variation in tree heights among coexisting individual tree species.

The use of additional predictor variables in height-diameter models is not uncommon, and it is often used to improve height prediction accuracy (e.g., BRONISZ; MEHTÄTALO, 2020; CAMACHO; RIVAS; HERNÁNDEZ; DURÁN *et al.*, 2022; OGANA, 2022; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). This shows that the variability in the height-diameter relationships of trees can be explained by the additional stand variables and diameter. In this study, we found that the inclusion of quadratic mean diameter and stem density slightly improved the RMSE by 0.01% (Table 6). These results suggest that they may not be the most important factors in determining tree heights. Similar findings were reported by CICEU; GARCIA-DURO; SECELEANU e BADEA (2020), who reported that the addition of stem density had little effect on the height prediction performance in their study. Tree height is primarily determined by individual tree genetics and environmental factors such as light availability and soil fertility, which might not be adequately captured by the evaluated stand

variables. For example, NEOPHYTOU; WEISSER; LANDWEHR; ŠEHO *et al.* (2016) examined how genetic variation relates to height growth in Douglas fir trees in various geographic regions. Their findings indicate a significant relationship between genetic variation and height growth in these trees.

The main purpose of calibration is to estimate the random effects for a new plot and improve height prediction (CICEU; GARCIA-DURO; SECELEANU; BADEA, 2020; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). This requires a prior measurement of height, predictor variables, and the estimation of random effects from a new plot. In the calibration process, the local mixed effect model appeared to be more flexible and appropriate for height prediction than the generalized version, which is similar to previous findings (CASTAÑO-SANTAMARÍA; CRECENTE-CAMPO; FERNÁNDEZ-MARTÍNEZ; BARRIO-ANTA *et al.*, 2013; RAPTIS; KAZANA; KAZAKLIS; STAMATIOU, 2021). This is evidenced by the fact that the RMSE values are consistently higher for the generalized mixed effects model than for the local mixed effects model (Figure 5). Furthermore, the simple model structure (i.e., without stand variables) of the calibrated mixed effect model mixed effect model (TRINCADO; VANDERSCHAAF; BURKHART, 2007).

In this study, different sampling alternatives were identified for use in estimating the random effects from the new plot and improving height prediction. Generally, the systematic selection of the three largest diameter trees from each plot (A9) was found to be the best option to estimate the random effect and predict the height of trees from a new plot or stand. This is mainly related to the fact that the height of the largest trees represents the dominant height for the plot and could be used as an additional stand variable for the model representing the site index, thereby offering additional information for estimating the random effect. This is consistent with the findings of CALAMA e MONTERO (2004), who stated that measuring the height of four trees with larger diameters in each plot was the best sampling alternative for calibration. The results from other studies also showed that using randomly selected trees closest to the second quartiles of the diameter distribution provided the best calibration result (CORRAL-RIVAS; ÁLVAREZ-GONZÁLEZ; CRECENTE-CAMPO; CORRAL-RIVAS, 2014). Similarly, OGANA; HOLMSTRÖM; SHARMA; LANGVALL et al. (2023) found that using measurements from the most extreme four trees was the best calibration alternative for several dominant tree species by taking into account various growth conditions, silvicultural practices and environmental factors in Sweden.

The choice of the sampling alternative depends on the available data for calibration and practical application of the model. If the required calibration data are available, then the calibrated local mixed-effects model using the three largest diameter tree alternatives (A9), or the second-best sampling alternative (A6) could be used. However, if the calibration data are not available, the generalized mixed effect model (M11) could be the best option because additional stand variables are included in the model. The additional stand variables will enable us to capture the natural variability among the sample plots. Moreover, if the calibration data and/or the stand variables are not available, the base model (with no random parameters) or mixed-effects model (random parameters = 0) could be used for tree height prediction (PATRÍCIO; DIAS; NUNES, 2022). Overall, the three largest diameter tree measurement alternative (A9) is advantageous since it requires less sampling effort in terms of cost and time for data collection (DORADO; DIÉGUEZ-ARANDA; ANTA; RODRÍGUEZ *et al.*, 2006). The use of the model along with the proposed sampling alternatives will ensure high accuracy in height prediction while minimizing the time and cost associated with field work.

5. Conclusions

The Michaelis–Menten model provided the best height prediction of the height-diameter relationship of the *J. procera* tree among the evaluated local models. The addition of quadratic mean diameter and stem density has little contribution to improving the height prediction performance. However, the best mixed effects model captures the between-plot variation in the height-diameter relationship and provides plot-level height prediction. The fixed effect of the mixed effects model can be used for the prediction of the mean height of *J. procera* trees for a given diameter in the Chilimo forest. The calibration response revealed that the measurement of the three largest diameter trees was the best sampling alternative to estimate the random effects and predict the height of trees for the new plots or stands. Generally, the calibrated height-diameter model developed in this study will help researchers and forestry practitioners reduce costs associated with height data collection as well as make better decision-making in stand volume and biomass estimation from different Afromontane forests in Ethiopia and elsewhere.

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7. Supplementary

Supplementary 1: Correlation between the best mixed effects model parameters and stand-level predictor variables





Supplementary 2: Height-diameter relationships using different nonlinear regression models



Supplementary 3: Standardized residuals graph of the nonlinear regression models



Supplementary 4: Observed and predicted height by non-linear regression models

Chapter II: Mixed-species allometric equations to quantify stem volume and tree biomass from the Chilimo Dry Afromontane Forest in Ethiopia

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1 Introduction

Afromontane forests constitute a unique forest type occurring on high African mountains (WHITE, 1983). They are found in Ethiopia, Cameroon, and in South Africa (GADOW; ZHANG; DURRHEIM; DREW et al., 2016; GRIMSHAW, 2001; WHITE, 1983). Although they are widely separated, Afromontane forests share a similar mix of plant species (over 4000 species, of which ~ 3000 are endemic), which are often distinct from the surrounding lowland forests (WHITE, 1983). Dry Afromontane forests are among the major natural forest types widely dispersed in the central, southeastern, eastern, northern, and southern highlands of Ethiopia (FRIIS; DEMISSEW; BREUGEL, 2010; UN-REDD, 2017). This forest type has ecological significance, being the remnant forest in different parts of the country; it provides habitat for many endangered species and stores a large amount of carbon (GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a; GIRMA; SOROMESSA; BEKELE, 2014; UN-REDD, 2017). The forest also supports the livelihoods of many people by providing diverse forest products (ASFAW; LEMENIH; KASSA; EWNETU, 2013; GOBEZE; BEKELE; LEMENIH; KASSA, 2009; SHIFERAW; LIMENIH; GOLE, 2019). However, the potentials of these forests have been impaired by severe anthropogenic disturbances, and have been heavily deforested and degraded due to their location in areas suitable for settlement and agriculture (LEMENIH; BONGERS, 2011). Hence, they require management intervention, which could help to maintain their biodiversity, productivity, and sustainability (TEKETAY; LEMENIH; BEKELE; YEMSHAW et al., 2010).

Sustainable forest management requires an accurate estimation of the important characteristics of the forest resources, i.e., stem density, basal area, the standing volume of wood, and biomass stock (ADEKUNLE; NAIR; SRIVASTAVA; SINGH, 2013; BETTINGER; BOSTON; SIRY; GREBNER, 2016). This information is fundamental for assessing the productivity of a forest stand and guiding forest management decisions (ADEKUNLE; NAIR; SRIVASTAVA; SINGH, 2013; AKINDELE; LEMAY, 2006; HUSCH; BEERS; KERSHAW JR, 2003). Quantifying the biomass stock of forests is important for commercial uses (e.g., timber, fuelwood, and fiber), for scientific studies of ecosystem productivity, energy, and nutrient flows, and for assessing the contribution of forests to the carbon cycle and climate change mitigation. In line with this, PARRESOL (2001) stated that the biomass and volume of a tree should normally be estimated through regression analysis. This author stated that selected trees would be destructively sampled and measurements of the diameter at many points along

the stem (for volume model) and weights of the components of each tree (for biomass model) would be made and related by regression to one or more traits of the standing trees.

Stem volume and biomass assessment have global interest, especially in the context of the Kyoto Protocol rules and climate change agreements (LINDNER; KARJALAINEN, 2007). Hence, developing countries involved with REDD+ (reducing emissions from deforestation and forest degradation) need to have a robust Measurement, Reporting, and Verification (MRV) system. Volume and biomass estimation models are a key element of the MRV system and enable us to properly assess the national wood, biomass, and carbon stocks. Despite this fact, information is scarce on stem wood volume and biomass in Afromontane forests in both Ethiopia and Africa in general; this is mainly due to the lack of locally developed biomass and volume estimation models.

Developing a site-specific biomass model is a key element in the accurate estimation of forest biomass, carbon stock, and fluxes (WILLIAMS; RYAN; REES; SAMBANE et al., 2008). Such information is gaining both economic and political currency in renewable energy development, carbon credit markets, and REDD + projects (NATH; TIWARI; SILESHI; SAHOO et al., 2019). Very few volume models (BERHE; ASSEFA; TEKLAY, 2013; GERESLASSIE; WORKINEH; TAKELE; ADEM et al., 2019; POHJONEN, 1991; TAKENAKA; ABEBE; TABUCHI, 2020; TESHOME, 2005; TSEGA; GUADIE; TEFFERA; BELAYNEH et al., 2019) and biomass models (ABICH; MUCHEYE; TEBIKEW; GEBREMARIAM et al., 2019; DABA; SOROMESSA, 2019; FEYISA; BEYENE; MEGERSA; SAID et al., 2018; MOKRIA; MEKURIA; GEBREKIRSTOS; AYNEKULU et al., 2018; SOLOMON; BIRHANE; TADESSE; TREYDTE et al., 2017; TESFAYE; BRAVO-OVIEDO; BRAVO; RUIZ-PEINADO, 2016; TETEMKE; BIRHANE; RANNESTAD; EID, 2019) are available in Ethiopia. These models are developed either for single tree species or mixed species by using a very small number of trees and/or the sampling does not include the larger diameter size trees in the forest. Hence, precise estimates of the standing volume of wood and biomass stock are lacking in Ethiopia's various forests.

The limited availability of models in Ethiopia has led to the use of pan-tropical models, principally CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO *et al.* (2014) and the general volume equation ($v = d \times h \times f$) where f = 0.5 (e.g., SISAY; THURNHER; BELAY; LINDNER *et al.*, 2017), to estimate tree biomass (ABERE; BELETE; KEFALEW; SOROMESSA, 2017; DIBABA; SOROMESSA; WORKINEH, 2019; ESHETU; HAILU, 2020; GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a) in different forests. The use of such a model often leads to biased biomass and volume estimates for particular species,

forests, and sites because there are variations in wood density, tree allometry, form factor, and growth stage among species (HENRY; PICARD; TROTTA; MANLAY et al., 2011; NÁVAR; NÁJERA; JURADO, 2002). Hence, it is vital to develop site and species-specific models. However, given the great diversity of species and variability within species in tropical forests, various efforts have been made to develop mixed-species biomass and volume models (e.g., ASRAT, ZERIHUN; EID, TRON; GOBAKKEN, TERJE; NEGASH, MESELE, 2020a; CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO et al., 2014; MOKRIA; MEKURIA; GEBREKIRSTOS; AYNEKULU et al., 2018; MUGASHA; MWAKALUKWA; LUOGA; MALIMBWI et al., 2016). However, minimal effort has been made to develop mixed-species equations to estimate stem volume and biomass for Afromontane forests in Africa in general and Ethiopia in particular. As a result, our knowledge of the standing volume of wood, biomass stocks, and carbon storage in Afromontane forests is limited. Therefore, the objective of this study was to develop a mixed-species stem biomass and volume estimation model and accurately estimate the standing volume of wood, biomass, and carbon stock in the Chilimo dry Afromontane Forest in Central Ethiopia. In addition, we compared the predictive performance of our newly developed model with the previously developed pan tropical and other models. We believe that these models will be useful for conservation and REDD+ projects and research in global environmental change in Afromontane forests across Africa.

2 Materials and Methods

2.1. Study site description

This study was conducted in the Chilimo forest, located 97 km west of Addis Ababa in central Ethiopia. It is located between 38° 05' - 38° 15' E longitude and 9° 00' - 10° 10' N latitude, with an altitudinal range of 1700 - 3200 m (Figure 1). This forest is one of the few remnants of dry Afromontane forests that once covered Ethiopia's Central Plateau. Currently, the forest has a total area of 4500 ha. SOROMESSA e KELBESSA (2013) recorded 213 plant species in 83 families. The main species in the canopy layers are *Juniperus procera*, *Podocarpus falcatus*, *Prunus africana*, *Olea europaea* ssp. *cuspidata*, *Hagenia abyssinica*, *Apodytes dimidiata*, *Ficus spp.*, *Erythrina brucei*, and *Croton macrostachus* (KASSA; CAMPBELL; SANDEWALL; KEBEDE *et al.*, 2009; SOROMESSA; KELBESSA, 2013). In the past, the forest was under state control, but this has weakened since 1991. Deforestation in the Chilimo forest has increased significantly despite the forest's designation as one of the National Forest Priority Areas (KASSA; CAMPBELL; SANDEWALL; KEBEDE *et al.*, 2009).

Increasing timber extraction rates, along with grazing and farming pressure, have radically reduced the forest cover (KASSA; CAMPBELL; SANDEWALL; KEBEDE *et al.*, 2009). The forest is currently managed by local forest user groups through a participatory forest management scheme (MOHAMMED; INOUE, 2014).

Figure 1: Map of the study area overlaid with the distribution map of dry Afromontane forests following FRIIS; DEMISSEW e BREUGEL (2010).



2.2. Data collection

2.2.1. Forest inventories

We employed a systematic sampling technique to collect vegetation data in February and March 2018. Overall, 161 sample plots $(20 \times 20 \text{ m})$ were established along the transect lines. The first transect was aligned parallel to the forest's edge (30 m) and others were laid out systematically at 500 m intervals. The first plot was located randomly, and the subsequent plots were established at 300 m intervals along the transect lines. First, the boundary of each plot was marked with pegs and/or plastic ropes. Then, the diameter at breast height (dbh) and the total height (ht) of all trees with $dbh \ge 2.0$ cm, which falls within the plot boundary, were measured using a diameter tape and Vertex IV ultrasonic hypsometer (Haglöf Sweden AB, Långsele, Sweden). A tree was judged to be within the plot when the center of the stem appeared to fall on or within the margins of the plot. Finally, the spatial location (latitude and longitude), elevation, and slope of each plot were measured using the Garmin GPS-72 receiver and Suunto Clinometer.

2.2.2. Tree species selection and measurement

First, we selected seven dominant tree species (*Juniperus procera*, *Podocarpus falcatus*, *Allophylus abyssinicus*, *Olea Africana* ssp. *Cuspidata*, *Olinia rochetiana*, *Rhus glutinosa*, and *Scolopia theifolia*) based on the basal area information generated from the inventory data. Second, representative sample trees were randomly chosen across the range of diameter size classes for the seven species among the fallen tree species during the asphalt road construction that passes through the Chilimo forest. Additional data were obtained from Tesfaye *et al.* (TESFAYE; BRAVO-OVIEDO; BRAVO; RUIZ-PEINADO, 2016). The selected seven dominant tree species altogether contributed over 89 % of the total basal area of the Chilimo forest.

A total of 194 trees were used to develop the stem volume and biomass model. The number of harvested trees was determined based on the relative abundance and diameter size distribution of each tree species. Hence, we sampled a larger number of trees from the abundant tree species with a larger diameter size distribution (e.g., Juniperus procera and Podocarpus *falcatus*) and a lower number of trees from the less abundant tree species. Before felling, the diameters at the ground level, 0.3 m, and 1.3 m, as well as the total height of the selected trees, were measured. These measurements were used to calculate the stump volume (parts of the stem from ground level to 0.3 m). After felling, the stem was sectioned and the total length and over-bark diameters at the lower and upper part of each section were measured. The section volume was computed using the Smalian formula, whereas the top section was computed using a cone formula (BURKHART; TOMÉ, 2012; WEST, 2015). The section volumes were summed up to estimate the total stem volume of each tree. The volume of branches and leaves was not considered in this study. The wood densities (determined at 12 % moisture content) of five tree species (Allophylus abyssinicus, Olea Africana ssp. Cuspidata, Olinia rochetiana, Rhus glutinosa, and Scolopia theifolia) recorded from the Chilimo forest were obtained from TESFAYE; BRAVO-OVIEDO; BRAVO e RUIZ-PEINADO (2016). Densities of Juniperus procera and Podocarpus falcatus were obtained from ICRAF's wood density database

(CARSAN; ORWA; HARWOOD; STROEBEL *et al.*, 2014). The stem biomass was calculated by multiplying the stem volume estimates by their basic wood densities, as done in BURKHART e TOMÉ (2012).

2.3. Data Analysis

2.3.1. Model development

The commonly used dendrometeric variables i.e., diameter (dbh), height (ht), and wood density (ρ) were used as independent predictor variables. We tested six-volume and eight biomass estimation equations (Table 1). We selected the equations from literature based on their widespread use in Ethiopia and elsewhere (BERHE, 2009; BURKHART; TOMÉ, 2012; GERESLASSIE; WORKINEH; TAKELE; ADEM *et al.*, 2019; MUGASHA; EID; BOLLANDSÅS; MALIMBWI *et al.*, 2013; PICARD; SAINT-ANDRÉ; HENRY, 2012).

Table	1:	Vo	lume	and	biomass	equat	tions	tested	in	this	study.	

Form	No	Mathematical forms	References
		Volume equations	
Lincor	M1	$ln(v) = ln(\beta_0) + \beta_1 ln(dbh) + \varepsilon$	HUSCH (1963)
Lineai	M2	$ln(v) = ln(\beta_0) + \beta_1 ln(dbh^2ht) + \varepsilon$	SPURR (1952)
Linear Nonlinear Linear	M3	$ln(v) = ln(\beta_0) + \beta_1 \ln(dbh^2) + \beta_2 ln(ht) + \varepsilon$	SCHUMACHER (1933)
	M4	$\mathbf{v} = \beta_0 \; (dbh)^{\beta_1} \; \varepsilon$	HUSCH (1963)
Nonlinear	M5	$\mathbf{v} = \beta_0 \; (dbh^2 ht)^{\beta_1} \; \mathbf{\varepsilon}$	SPURR (1952)
	M6	$\mathbf{v} = \beta_0 \ (dbh^2)^{\beta_1} (ht)^{\beta_2} \varepsilon$	SCHUMACHER (1933)
Linear		Biomass equations	
	M7	$ln(b) = ln(\beta_0) + \beta_1 ln(dbh) + \varepsilon$	HUSCH (1963)
	M8	$ln(b) = ln(\beta_0) + \beta_1 ln(dbh^2ht) + \beta_2 ln(\rho) + \varepsilon$	SPURR (1952)
	МО	$ln(b) = ln(\beta_0) + \beta_1 ln(dbh) + \beta_2 ln(ht) +$	SCHUMACHER (1933)
	1019	$\beta_3 ln(\rho) + \varepsilon$	
	M10	$ln(b) = ln(\beta_0) + \beta_1 ln(\rho dbh^2 ht) + \varepsilon$	CHAVE et al. (2014)
	M11	$\mathbf{b} = \beta_0 \; (dbh)^{\beta_1} \; \mathbf{\epsilon}$	HUSCH (1963)
	M12	$\mathbf{b} = \beta_0 \ (dbh^2 ht)^{\beta_1} \ (\rho)^{\beta_2} \ \varepsilon$	SPURR (1952)
Nonlinear	M13	$\mathbf{b} = \beta_0 \; (\rho db h^2 h t)^{\beta_1} \; \mathbf{\epsilon}$	CHAVE et al. (2014)
	M14	$\mathbf{b} = \beta_0 \ (dbh)^{\beta_1} (ht)^{\beta_2} (\rho)^{\beta_3} \ \mathbf{\varepsilon}$	SCHUMACHER (1933)

Note: ln = natural logarithm, v = stem volume (m³), b = stem biomass (kg), ht = total height (m), dbh = diameter at breast height (cm), and ρ = wood density (g cm³).

It must be noted that M1, M2, and M3 are the linear versions of the nonlinear volumes M4, M5, and M6, respectively. Similarly, among the biomass models, M1, M2, M3, and M4 are the linear versions of the nonlinear M5, M6, M7, and M8, respectively. Although the linear and nonlinear versions (e.g., M1 and M4 of the volume equations) are mathematically equivalent, they are not identical in the statistical sense (PARRESOL, 1999; SILESHI, 2014). As a result, the estimated parameters (e.g., slope) and biomass may slightly differ. Because some authors use each version when developing biomass estimation models, we opted to compare the linear and nonlinear versions and determine whether they performed differently.

Although 194 trees were initially sampled, one tree with a diameter of 98.0 cm consistently appeared as a leverage point across all models. Therefore, we excluded that tree from all analyses. Even then, we noted a variable number of outliers and leverage points depending on the model. Since the combined effect of outliers and leverage points can destabilize the coefficients of models with multiple predictors, we used robust regression (TASKINEN; WARTON, 2013) compared to ordinary least squares (OLS) regression. The model fitting was done by *rlm* and *nlrob* functions in the MASS and robustbase packages of R, respectively. These R functions fit the models by the iteratively reweighted least-squares (IRLS) method using the Tukey bisquare weighting method (RIAZOSHAMS; MIDI; GHILAGABER, 2019). We compared the performance of the different models using model selection criteria and graphical analysis of residuals. Since linear models cannot be compared directly with nonlinear models, we conducted all model comparisons on the arithmetic scale. First, we back-transformed the predictions of the linear models to the original units to allow comparison with our nonlinear model and other published equations. We used a correction factor (CF) to correct the systematic bias induced during the back-transformation of logarithmically transformed data (CHAVE; ANDALO; BROWN; CAIRNS et al., 2005; SILESHI, 2014). The CF is normally computed from the mean square of error (ε) as follows:

$$CF = EXP\left(\frac{\varepsilon^2}{2}\right) \tag{1}$$

Next, we calculated various model selection criteria in the arithmetic domain to compare linear and nonlinear models straightforwardly. For this purpose, we chose the Nash and Sutcliffe efficiency factor (NSEF), the average systematic error (Bias), the root means square of error (RMSE), the mean absolute percent error (MAPE), and the bias-corrected Akaike information criterion (AICc). We did not include the R^2 due to its well-known limitations (SILESHI, 2014). Instead, we used the NSEF, because its calculation is straightforward for both linear and nonlinear models. The NSEF formula is the same as the R^2 of linear regression, but it is applied directly to the original biomass data and the predictions from any one of the models as follows:

$$NSEF = 1 - \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2}$$
(2)

where y_i is the observed (measured) value, \hat{y}_i is the predicted value, and \bar{y} is the average of the observed value. NSEF varies from $-\infty$ to 1, with values close to 1 being the best, and negative values indicating an unacceptable model performance.

Calculating the AIC (AKAIKE, 1973) for models estimated using least square methods is tricky because AIC is formulated initially based on the negative log-likelihood from maximum likelihood estimation. Following GAGNÉ e DAYTON (2002), we calculated the AIC from the residual sum of squares (RSS) of the regression as follows:

$$AIC = n * \ln\left(\frac{RSS}{n}\right) + 2p \tag{3}$$

where n is the number of observations, and p is the number of model parameters. To correct for small sample sizes, we used the bias-corrected AIC (hereafter AICc) computed as:

$$AIC_c = AIC + \frac{2p(p+1)}{n-p-1} \tag{4}$$

Then, we computed the Akaike weights (AICw) from the AICc cohort of models as recommended by JOHNSON e OMLAND (2004). AICw indicates the probability that the model is the best among the set of candidate models, thus measuring the strength of evidence for each model. Therefore, we chose the model with AICw close to 1 as the best. For all models, the bias (%), MAPE (%), and RMSE (%) were calculated as follows in the arithmetic domain:

$$Bias(\%) = \frac{1}{R} \sum_{l=1}^{R} \frac{100}{n} \sum_{i=1}^{n} \frac{y_i - \hat{Y}_i}{Y_i}$$
(5)

$$MAPE(\%) = \frac{1}{R} \sum_{I=1}^{R} \frac{100}{n} \sum_{i=1}^{n} \frac{|y_i - \hat{Y}_i|}{Y_i}$$
(6)

$$RMSE(\%) = \frac{1}{R} \sum_{i=1}^{R} 100 \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left(\frac{y_i - \hat{Y}_i}{y_i}\right)}$$
(7)

where R is the number of resampling (200), n is the number of trees per resampling r, and yi and ŷi are the observed and predicted biomass and volume values.

We also calculated a relative measure hereafter referred to as rRMSE calculated as a ratio of RMSE to the mean values of the predicted biomass and expressed in %, i.e., 100*(RMSE/mean). This measure is sometimes called the coefficient of variation and is used for comparing models (e.g. CHIANUCCI; PULETTI; GROTTI; FERRARA et al., 2020; VONDERACH; KÄNDLER; DORMANN, 2018). The rRMSE estimates the error in estimation as a percentage of the predicted mean biomass. Since the above criteria do not reveal problems inherent in the model specification (SILESHI, 2014), we conducted various model diagnostics, including tests of normality, homoscedasticity of errors, and influence statistics (Table S1). We used the Shapiro-Wilk test to determine the normality of residuals. Tests of normality and homogeneity, alone, are not adequate (SILESHI, 2014). Therefore, we conducted additional diagnostics to check whether certain observations have undue influence on the coefficients. There are two types of outliers, i.e., those in the response variable and outliers to the predictors are called leverage points (TASKINEN; WARTON, 2013). We used residual plots of standardized residuals to detect outliers against the explanatory variables to reveal patterns and deemed values exceeding -2.0 or +2.0 as outliers that could cause serious heteroscedasticity. Since residual plots cannot reveal leverage points, we identified leverage points from the robust regression analysis (Table S1). We conducted a one-way analysis of variance (ANOVA) to test whether residuals from our best models vary with species. The percent relative standard error (PRSE) statistics were also computed to assess the reliability of the parameter estimation of a model (SILESHI, 2014). Sileshi considered that a coefficient estimate is unreliable if PRSE > 25 %.

In linear models where two or more variables were included, we also checked the variance inflation factor (VIF) to assess multicollinearity between the predictor variables (SILESHI, 2014). In nonlinear models, we checked for symmetry in estimated parameters using Hougaard's measure of Skewness (|g|). It must be noted that nonlinear regression assumes that parameters are close to linear so that the uncertainty about the value of each parameter is symmetrical. A parameter with g > 0.25 is said to be noticeably skewed, and in such cases, alternative model parameterization is strongly advised (HOUGAARD, 1985)

2.3.2. Model validation

In the analyses above, we have only examined the ability of various models to describe the data at hand, which is referred to as in-sample fit. This is sometimes confused with the predictive power of the model or its out-of-sample fit. However, models usually have a grossly inflated performance in-sample compared to their performance in follow-up studies (IOANNIDIS, 2008). The goodness of fit and model selection criteria also tend to better fit the sample data, especially when models are over-fitted (SILESHI, 2014). Therefore, we employed the Monte Carlo cross-validation technique to evaluate the biomass prediction performance of the models. The fits of the models were examined by randomly splitting the data (193 trees) into two parts, with 70% for model development and 30% for model validation; this process was repeated 200 times. The commonly used model fit statistics (Equations 5, 6, and 7) were calculated during every repetition using the randomly selected data, and finally, the average values of the 200 repetitions were computed (TEMESGEN; ZHANG; ZHAO, 2014). A model that provides smaller values of these metrics was considered the best model (Table 5). The final parameter estimates were obtained by fitting all models with the entire dataset. All of the statistical analyses were computed using the R software (R Core Team TEAM, 2013).

2.3.3. Comparison with previously published (generic) models

We compared the predictive performance of our biomass models with the previously published pan-tropical models and models from tropical dry forests in Africa (Table 2). We chose these models for comparison with our model because they are commonly used for biomass estimation in Ethiopia and elsewhere (see GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a; KENDIE; ADDISU; ABIYU, 2019; SIRAJ, 2019).

Table 2: Previously published models tested using our data set.

Mathematical form	References
$\mathbf{b} = 0.112 (\rho db h^2 ht)^{0.916}$	CHAVE et al. (2005)
$\mathbf{b} = 0.0673 (\rho db h^2 h t)^{0.976}$	CHAVE et al. (2014)
$\mathbf{b} = 0.196 (dbh)^{2.141} (\rho)^{0.625}$	TETEMKE <i>et al.</i> (2019)
$\ln(b) = -1.134 + 1.969\ln(dbh) + 0.295\ln(ht)$	\mathbf{DIOMO} at al. (2016)
$+ 1.185 \ln(\rho)$	DJOMO et al. (2010)

Note: ln = natural logarithm, b = stem biomass (kg), ht = total height (m), dbh = diameter at breast height (cm), and ρ = wood density (g cm³).

The usual criteria used for comparing local models have some limitations when comparing local with generic models. For example, R^2 is an inadequate criterion for comparing linear and nonlinear models because a nonlinear model does not have a true R^2 due to the absence of a true intercept. The RMSE is scale-dependent, and therefore, it does not help compare models in different formulations (e.g., linear vs. nonlinear). It is also hard to determine

the magnitude of RMSE in the absence of a reference point. Hence, we used rRMSE, MAPE (%), and NSEF (%) applied directly to the original data and the predictions from any one of the models.

2.3.4. Estimation of stand-level basal area, volume, biomass, and carbon stocks

The density (stem ha⁻¹) and basal area (m² ha⁻¹) were calculated for each tree species. Each tree's stem volume and biomass were calculated using the newly developed volume (M2) and biomass model (M10) in this study. The belowground (root) biomass was estimated by using a 0.20% conversion factor of the stem biomass (MACDICKEN, 1997). The total biomass (the sum of the stem and root biomass) was converted into carbon by dividing the total biomass value by 2, following the procedures in PEARSON; WALKER e BROWN (2005).

3 Results

3.1. Harvested tree species

The 194 trees used here accounted for 89 % of the total basal area in the Chilimo forest (Table 3). The diameter, total height, and wood density ranged between 6.2 and 85.0 cm, 5.6 and 27.4 m, and 0.52 and 0.82 g cm⁻³. Most of the tree species had diameters concentrated in a narrow range. For example, *Olea africana* ssp. *Cuspidata*, *Allophylus abyssinica*, *Olinia rochetiana*, *Rhus glutinosa*, and *Scolopia theifolia* had diameters less than 29 cm, while *Juniperus procera* and *Podocarpus falcatus* had diameters ranging between 11.6 and 85.0 cm. However, most tree species exhibited little variation in the wood density values (Table 3).

Table 3: Tree species used for model building and their wood density, diameter at breast height, and total height measurements.

Na	Tree areaise	N		dbh (cm)		ht (m)	
INO	Tree species	IN	ρ	$Mean \pm SD$	Range	Mean	Range
1	Juniperus procera	89	0.58	34.3 ± 17.3	11.6-85.0	16.2 ± 5.3	6.8-27.4
2	Podocarpus falcatus	15	0.52	40.6 ± 15.4	20.0-64.0	19.2 ± 4.9	11-25.6
3	Olea africana	20	0.82	14.5 ± 5.9	6.3-28.8	10.6 ± 2.1	5.9-14.5
4	Allophylus abyssinicus	15	0.59	11.3 ± 3.9	6.4-21.3	10.6 ± 3.1	7.0-17.0
5	Olinia rochetiana	20	0.66	14.9 ± 6.7	6.2-27.5	12.6 ± 2.9	7.3-19.4
6	Rhus glutinosa	15	0.61	15.6 ± 4.9	9.0-23.5	11.3 ± 3.0	6.0-17.4
7	Scolopia theifolia	20	0.64	11.8 ± 4.1	6.4-22.0	8.2 ± 1.9	5.6-13.0

Note: SD = standard deviation, N = the number of sample trees (No ha⁻¹), dbh = diameter at breast height (cm), ht = total height (cm), ρ = wood density (g cm⁻³), and Range = minimum and maximum values.

3.2. Volume estimation models

The parameter estimates, their corresponding standard errors, and the PRSE statistics of the evaluated volume models are given in Table 4. All parameters of the models were statistically significant at $\alpha = 0.001$ levels. The Monte Carlo cross-validation statistics of the models are given in Table S4. Among the models, model 2 (M2) was the best model to predict the stem volume. This model produced the lowest RMSE, MAPE, and AICc and higher NSEF values. The observed and predicted stem biomass graphs using the evaluated models are shown in Figure S1. Among the models, M2 and M6 provided the closest prediction to the observed stem volume.

No	Estim	ated parame	eters	PRSE		
	β0	β_1	β2	βο	β_1	β2
Linear mo	dels					
M1	-8.907	2.385				
M1 M2	(0.112)	(0.036)		1.25	1.5	
M2	-9.909	0.954				
	(0.095)	(0.011)		0.96	1.12	
M3	-9.883	0.962	0.925			
	(0.127)	(0.026)	(0.090)	1.29	2.72	9.7
Nonlinear	models					
	0.0015	1.751				
M4	(0.000)	(0.045)		18.15	2.55	
	0.0002	0.845				
M5	(0.000)	(0.014)		15.09	1.6	
	0.0001	0.827	0.939			
M6	(0.000)	(0.019)	(0.068)	18.02	2.35	7.28

Table 4: Parameter estimates, standard errors (in parenthesis), and PRSE statistics for the evaluated volume estimation models.

Note: the best models among linear and nonlinear models are given in bold.

The residual graphs of the evaluated models are shown in Figure 2. The residuals of linear models were randomly scattered around zero lines for all fitted values, while the residuals of nonlinear models followed a funnel shape distribution indicating non-constant variance. Furthermore, the nonlinear models tended to have more outliers than the linear models, and the parameter " β_0 " in all nonlinear models was also significantly skewed (Table S1 and S2). Taking all these into consideration, we selected M2 rather than the non-linear models for volume estimation. ANOVA did not reveal significant variation with species in residuals from M2.



Figure 2: Residual graphs for the evaluated volume models.

3.3. Stand characteristics and biomass estimation

The number of trees, basal area, and stem biomass of trees in the Chilimo dry Afromontane Forest is presented in Table 5. The average standing volume of wood was 303.0 m³ ha⁻¹ in the Chilimo forest. Overall, *Podocarpus falcatus* (43.5%), *Juniperus procera* (38.1%), *Schefflera volkensii* (7.5%), and *Schefflera abyssinica* (2.2%) were the tree species that exhibited the largest stem volume wood. Each of these species also comprised 49.1, 39.3, 6.2, and 2.1% of the total stem biomass. The measured stem biomass values were highly variable across the forest, with an average value of 283.8 Mg ha⁻¹. The estimated carbon stocks also varied between 15.3 and 989.4, with a mean value of 173.6 Mg ha⁻¹ in the Chilimo forest.

Stand characteristics	Unit	Mean	Minimum	Maximum	SD
Stand density	stems ha ⁻¹	631.5	25.0	2600.0	455.3
Basal area	$m^2 ha^{-1}$	24.4	1.5	100.9	15.1
Stem volume in the forest	$m^3 ha^{-1}$	303.0	7.5	1592.0	312.8
Stem biomass	Mg ha ⁻¹	283.8	25.5	1649.0	298.9
Belowground biomass	Mg ha ⁻¹	56.8	5.1	329.8	59.8
Total biomass	Mg ha ⁻¹	340.6	30.63	1978.8	358.7
Carbon stock	Mg ha ⁻¹	170.3	15.3	989.4	179.4

Table 5: Summary of forest inventory results, estimated stem volume (M2), biomass (M10), and carbon stocks in the Chilimo dry Afromontane Forest.

3.4. Biomass estimation models

The parameter estimates, their corresponding standard errors, and the PRSE statistics of the evaluated biomass models are given in Table 6. All parameters of the nonlinear models were significantly different from zero (p < 0.001) except parameters β_2 and β_3 of M8 and M9, which were not. The goodness-of-fit statistics based on cross-validation of the evaluated models are given in Table S4. The cross-validation statistics indicated that M9 from the linear models and M12 from the nonlinear models were the best for biomass estimation. However, the PRSE statistics have shown that some of the parameters of M8, M9, M12, M13, and M14 had PRSE > 25 %. The observed and predicted stem biomass graphs using the evaluated models are shown in Figure 3. Visual analysis of the graphs shows that except for M7 and M11, the remaining models overestimated the stem biomass (Figure S2). However, M10 provides the closest stem biomass prediction to the remaining biomass models.

Table 6: Parameter estimates, standard errors (in parentheses), and PRSE statistics for the evaluated biomass models obtained using the entire dataset.

No	Estimated parameters					PRSE				
INO	β ₀	β_1	β_2 β_3		βο	β_1	β_2	β3		
Linear	models									
M7	-2.238	2.301			1 9	15				
	(0.107)	(0.034)			4.0	1.5				
M8	-3.127	0.929	0.278*		2.0	1.2	55.0			
	(0.093)	(0.011)	(0.155)		5.0	1.2	55.9			

M9	-3.142	1.847	0.945	0.274*	2.0	20	00	57 2
	(0.123)	(0.051)	(0.083)	(0.157)	3.9	2.0	0.0	57.2
M10	-2.983	0.949			2 1	1 2		
	(0.092)	(0.011)			3.1	1.4		
Nonlii	near model	S						
M11	0.913	1.744			178	2.5		
	(0.162)	(0.044)			17.0	2.5		
M12	0.123	0.847	0.593		16.6	16	31.2	
	(0.020)	(0.014)	(0.185)		10.0	1.0	51.2	
M13	0.176	1.355	1.067	0.107	14.2	16	25.8	35
	(0.045)	(0.048)	(0.100)	(0.266)	14.2	1.0	23.8	5.5
M14	0.138	0.849			Q /	248.6		
	(0.020)	(0.013)			7.7	240.0		

Note: * indicates non-significant coefficients at $\alpha = 0.05$. The best-fit model is given in bold.

The residual graphs of the evaluated models are shown in Figure 3. The residuals of linear models were randomly scattered around zero lines for all fitted values, while the residuals of nonlinear models followed a funnel shape distribution indicating non-constant variance. Furthermore, the parameter " β_0 " in all nonlinear models was significantly skewed, and the nonlinear models tended to have more outliers than the linear models (Table S1 and S2). Moreover, the assumption of multicollinearity was not violated since none of the explanatory variables of the evaluated linear models showed a VIF value higher than 5. Taking all these into consideration, we selected M10 as the best model for stem biomass estimation.



Figure 3: Residual graphs for the evaluated biomass models.

3.5. Comparison of our models with the previously published biomass models

The stem biomass prediction and the associated fit statistics of the evaluated models are given in Table S5. The models by Chave et al. (2005 and 2014) systematically overestimated stem biomass, especially for trees with dbh > 25 cm (Figure 4), which is evidenced by systematically declining residuals (Figure 5). Conversely, the model developed by TETEMKE; BIRHANE; RANNESTAD e EID (2019) was less accurate and severely underestimated the stem biomass. Our best model (M10) and the model developed by Djomo showed the highest prediction performance (Table S5 and Figure 4). However, the model by Djomo et al. (2016) was developed for small-diameter trees (dbh < 32 cm) and is not consistent for larger trees. This indicated that our best model (M10) is the most appropriate model to accurately estimate the stem biomass of trees.

Figure 4: Comparison of biomass prediction performance by our best model and previously published biomass models. The dots in different colors represent the biomass prediction by each model and the lines represent the best-fit line.





Figure 5: Comparison of the residual plots of our best models with the generic biomass models using our dataset.

4 Discussions

Very few studies have attempted to develop stem volume equations in Ethiopia (BERHE; ASSEFA; TEKLAY, 2013; GERESLASSIE; WORKINEH; TAKELE; ADEM *et al.*, 2019; POHJONEN, 1991; TAKENAKA; ABEBE; TABUCHI, 2020; TESHOME, 2005; TSEGA; GUADIE; TEFFERA; BELAYNEH *et al.*, 2019). In this study, we developed mixed species allometric equations using 193 individuals from seven dominant species from the Chilimo forest. The selected trees contributed over 89% of the total basal area of the forest. The number and diameter size range of the sampled trees used in the present study were relatively higher than in previous biomass model development efforts in Ethiopia. For instance, TETEMKE; BIRHANE; RANNESTAD e EID (2019) used 86 trees and developed a mixed-species model for dry Afromontane forests in Northern Ethiopia. Similarly, MOKRIA; MEKURIA; GEBREKIRSTOS; AYNEKULU *et al.* (2018) and (ASRAT, ZERIHUN; EID, TRON; GOBAKKEN, TERJE; NEGASH, MESELE, 2020a) sampled 84 and 63 trees and

developed biomass models for exclosures and Dry Afromontane forests in northwestern and south-central Ethiopia, respectively.

The evaluated volume models exhibited varied stem volume prediction performance (Table S4). The dbh-only model had the highest RMSE and MAPE and the lowest NSEF values, both in the linear and nonlinear forms. This indicates that diameter alone is not a sufficient predictor for stem volume estimation. The addition of height improved the prediction performance of the model by reducing the RMSE and MAPE by 11% and 5%, respectively. This is consistent with the findings of (e.g., CHAVE; ANDALO; BROWN; CAIRNS et al., 2005; GOUSSANOU; GUENDEHOU; ASSOGBADJO; KAIRE et al., 2016; MATE; JOHANSSON; SITOE, 2015), who reported that the inclusion of height improved the predictive performance of a model. On the contrary, various studies (e.g., ASRAT, ZERIHUN; EID. TRON; GOBAKKEN, TERJE; NEGASH, MESELE, 2020b; MUGASHA; MWAKALUKWA; LUOGA; MALIMBWI et al., 2016; SEGURA; KANNINEN, 2005) have argued that the dbh-only model outperformed a volume model with height and dbh. This is mainly attributed to the difficulty of height measurement in a closed canopy tropical forest due to the complex crown form and stand condition (Sharma and Parton, 2007). In this study, the combined variable model (M2), which incorporates diameter and height, becomes the best volume model. The predictor variables of this model explained over 95% of the variances in the stem volume. Similarly, POHJONEN (1991) reported that a combined variable model (dbh and h) provided the best stem volume prediction with lower prediction error (10-12 %) for the Juniperus procera tree from the Menagesha Suba forest in Ethiopia. A combined variable function has been considered the most appropriate and preferred function for predicting the total stem volume of trees (BURKHART; TOMÉ, 2012). This is because the stem form of a tree is better explained by a combination of height and diameter than by height or diameter, alone (e.g. HUSCH; BEERS; KERSHAW JR, 2003).

Very few tree volume estimation models have been found in Ethiopia (BERHE; ASSEFA; TEKLAY, 2013; GERESLASSIE; WORKINEH; TAKELE; ADEM *et al.*, 2019; POHJONEN, 1991; TAKENAKA; ABEBE; TABUCHI, 2020; TESHOME, 2005; TSEGA; GUADIE; TEFFERA; BELAYNEH *et al.*, 2019). This study reported a mixed-species volume model developed using 193 individuals from seven tree species from the Chilimo dry Afromontane Forest. The newly developed mixed-species volume model will help to accurately estimate the standing volume of wood and ensure sustainable management efforts in dry Afromontane forests in Ethiopia. Generally, there is a high demand for wood in Ethiopia, and the country is currently importing a large amount of wood to satisfy national demand. This

enables the country to allocate a large amount of hard currency to import processed wood and wood products (MEFCC, 2018). However, there is a huge amount of harvestable wood in the natural forests that can satisfy the growing wood demand in Ethiopia (MEFCC, 2018). Accurate estimation of the standing volume of wood from the natural forests in Ethiopia is constrained by the lack of site-specific volume models. Using our newly developed stem volume model, we noted that on average, 303.0 m³ ha⁻¹ volume of wood is found in the Chilimo forest. The observed volume of wood is higher than the volume estimated from dry Afromontane forests in the Amhara region (SISAY; THURNHER; BELAY; LINDNER et al., 2017), Miombo woodlands in Tanzania (LUOGA; WITKOWSKI; BALKWILL, 2002), moist tropical forest in Nigeria (LOWE, 1997), and closed tropical broadleaf forests (BROWN; GILLESPIE; LUGO, 1989) (Table S3). This implies that a large amount of wood is available in the Chilimo forest, which can be used under a sustainable forest management scheme. Additionally, domestic wood production from the Afromontane Forest will enable the country to save the hard currency allocated to import wood and use it for other purposes. However, care should be taken to enhance the regeneration of the harvested trees, minimize damage during harvesting, and develop locally applied logging regulations (i.e., determine minimum felling diameter, annual allowable cut, harvesting techniques, and identify the harvestable species) before beginning logging in the Chilimo forest. The observed variation in stand volume might be related to the differences in the stocking, basal area, tree allometry, and disturbance level among the forests. In our study, volume data is derived from the main stem of trees (branch wood volume is not accounted for), whereas in the other studies, the total volume of trees was reported. The mean density (631.5 stems ha⁻¹) and basal area (24.4 m² ha⁻¹) in our study area were higher than the findings from Afromontane forests in the Amhara region (580 stems ha⁻¹) and Miombo woodlands in Tanzania (347.6 stems ha⁻¹ and 9.8 m² ha⁻¹). On the other hand, the Chilimo forest is one of the community-managed forests, and most trees are concentrated in the lower and medium diameter size class (97 % are < 60 cm diameter class), which indicates that the forest is regenerating and recovering from the past disturbances. It is well known that undisturbed forests with many trees accumulate more volume than disturbed forests.

Biomass models are usually developed by adopting direct and indirect methods. The direct method involves felling trees and weighting, whereas the indirect method requires species-specific volume, wood density, and biomass expansion factor (BEF) information (PICARD; RUTISHAUSER; PLOTON; NGOMANDA *et al.*, 2015). It is well known that tree biomass can be accurately determined by the direct weighting method. However, this method is time-consuming and expensive (HUSCH; BEERS; KERSHAW JR, 2003). In this study, we

determined the stem biomass by multiplying each tree's volume and respective wood density following the procedures (BURKHART; TOMÉ, 2012). This is mainly related to the shortage of time to harvest and collect the data from the study area. Uncertainty in stem biomass estimation might occur for such computations compared to the direct weighting method. Despite this fact, the biomass model based on dbh alone has shown lower efficiency compared with multiple predictor models (Table 6). A model with one predictor variable (dbh-based model) has shown poor prediction performance as evidenced by larger RMSE (37%) and MAPE (24%) values (Table S4). The addition of height and wood density improved the biomass prediction performance of the model by reducing the RMSE by 9 % and MAPE by 5%. This indicates that height and wood density enabled the capture of more variability in stem biomass from the sampled trees (CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO et al., 2014). Although the cross-validation statistics show that M9 and M12 are the best models, the PRSE statistics revealed that some parameters of M8, M9, M12, M13, and M14 had PRSE > 25 % and parameters β_2 and β_3 of M8 and M9 were not significantly different from zero. In line with this, SILESHI (2014) indicated that a coefficient estimate of a model is unreliable if PRSE is greater than 25 %. Hence, these models cannot be reliably used for biomass prediction purposes. Accordingly, we selected the combined variable model (M10) which comprised diameter (dbh), height (ht), and wood density (ρ) for biomass estimation. This model explained over 96% of the variation in the stem biomass measurements. This is consistent with various studies (e.g., CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO et al., 2014) that reported a combined variable model provided better biomass prediction than the other models.

The biomass estimated in this study (340.6 Mg ha⁻¹) was less than the biomass estimates from the South African Mistbelt forest (MENSAH; VELDTMAN; DU TOIT; GLÈLÈ KAKAÏ *et al.*, 2016) and closed-canopy tropical forests in 12 countries in Africa (LEWIS; SONKE; SUNDERLAND; BEGNE *et al.*, 2013). However, it was comparatively higher than the estimates from the moist Afromontane forest in Ethiopia (WOOD; TOLERA; SNELL; O'HARA *et al.*, 2019), the tropical rain forest in Costa Rica (CLARK; CLARK, 2000), the Montane forest in Congo (IMANI; BOYEMBA; LEWIS; NABAHUNGU *et al.*, 2017), and Mata Atlantic forest in Brazil (ALVES; VIEIRA; SCARANELLO; CAMARGO *et al.*, 2010) (Table S3). Similarly, the carbon stock (170.3 Mg C ha⁻¹) estimates in this study were higher than the estimates from humid forest in Congo (XU; SAATCHI; SHAPIRO; MEYER *et al.*, 2017) and Montane forest in Tanzania (WILLCOCK; PHILLIPS; PLATTS; BALMFORD *et al.*, 2014), but lower than the estimates from moist Afromontane forest in Ethiopia (MEWDED; LEMESSA, 2019), South African Mistbelt forest (MENSAH; VELDTMAN; DU TOIT; GLÈLÈ KAKAÏ *et al.*, 2016), tropical rainforest in Gabon (GOÏTA; MOULOUNGOU; BÉNIÉ, 2019), Brazilian Amazonia forest (LIMA; SUWA; DE MELLO RIBEIRO; KAJIMOTO *et al.*, 2012), and Montane rainforest (MUNISHI; SHEAR, 2004) in Tanzania. The observed variation might be related to the difference in the models used to estimate the biomass, the disturbance level, the species composition, and the differences in the number of larger diameter trees, which constituted a significant amount of biomass as evidenced by the findings in moist forests across the tropics (SLIK; PAOLI; MCGUIRE; AMARAL *et al.*, 2013). Differences in biomass estimates for dry and moist tropical forests have been attributed to the use of different allometric equation forms (e.g. POORTER; BONGERS; AIDE; ZAMBRANO *et al.*, 2016). The forest structure also showed a larger number of trees in the lower and middle diameter classes, which indicates that the forest was in a growth stage. Overall, the Chilimo forest has a substantial amount of biomass and carbon stocks compared with the estimates from other tropical forests in Africa. This highlights the importance of the dry Afromontane Forest for climate change mitigation and the carbon market.

Compared with our newly developed model, the mixed-species equation developed by TETEMKE; BIRHANE; RANNESTAD e EID (2019) severely underestimated the stem biomass of trees in the present study (Table S5). On the other hand, the generic pan-tropical models consistently overestimated the stem biomass of trees above dbh \geq 30 cm (Table S5 and Figure S3). Given the importance of large trees in the carbon budget, the biomass in large trees must be accurately estimated. However, the generic pan-tropical models were not able to predict biomass for the larger trees; this implies that the generic pan-tropical models are inferior to our models. This is consistent with the previous studies that reported that the CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO et al. (2014) model tended to overestimate tree biomass compared with locally developed models (DJOMO; IBRAHIMA; SABOROWSKI; GRAVENHORST, 2010; NGOMANDA; OBIANG; LEBAMBA; MAVOUROULOU et al., 2014; VAN BREUGEL; RANSIJN; CRAVEN; BONGERS et al., 2011). A possible explanation could be the difference in wood density range, tree allometry (diameter and height range), tree species composition, site quality, and climatic condition, which affect the efficiency of the compared models. For example, the database used to develop the model in (CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO et al., 2014) showed that the tree species had a wood density ranging between 0.09 and 1.12 g cm3, a diameter between 5 and 122 cm, and a total height between 1.2 and 70.7 m whereas, in this study, the database comprised relatively lower wood density values ranging between 0.52 and 0.82 g cm³, a diameter between 6.2 and 85.0 cm, and total height between 5.6 and 27.4 m. These variations could be the possible source

of uncertainty among the models used to accurately predict the stem biomass of trees. Despite this fact, the CHAVE; RÉJOU-MÉCHAIN; BÚRQUEZ; CHIDUMAYO *et al.* (2014) equation remains the commonly used model, submitted to the UNFCC and various local studies, for calculating the biomass and CO₂ emission levels from Ethiopian forests (GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a; GIRMA; SOROMESSA; BEKELE, 2014; SIRAJ, 2019; SOLOMON; PABI; ANNANG; ASANTE *et al.*, 2018; UN-REDD, 2017). In this study, we noted that the newly developed mixed-species model could accurately estimate the stem biomass compared to the frequently used pan-tropical and local models. Hence, we recommend the use of these models in the Chilimo Dry Afromontane Forest as well as other similar Afromontane forests elsewhere. However, caution should be taken to not use these models in a forest comprising different tree species, tree diameter size ranges, and climatic conditions than those in the dry Afromontane Forest considered in this study.

This study presents a new approach to estimating the stem volume and biomass from the Chilimo Dry Afromontane Forest; we consider this an important decision-support tool for the management of forests in Ethiopia. This approach enables the government or forest owners to obtain accurate information on the stand-level standing stock of wood and stem wood biomass and make utilization plans. However, this study has some limitations that a subsequent study could improve. Due to the short data collection period, we could not collect the branch and foliage data and did not use the direct weighting method to estimate the biomass of tree components. Furthermore, wood density information did not include bark density, which could be a possible source of bias in biomass estimation. Hence, we recommend including this critical component of the tree and updating the equations in future efforts.

5 Conclusions

The lack of a biomass and volume equation is a major bottleneck hindering the national carbon stock estimation endeavors and management of natural forests in Ethiopia. The newly developed mixed-species equations can be used to accurately quantify the standing volume of wood and biomass stock and enable forest managers to develop appropriate management strategies for dry Afromontane forests. This study demonstrated that a combined variable model that includes diameter, height, and wood density was the best model for stem biomass and volume estimation. The frequently used pan-tropical models systematically overestimated stem biomass for larger trees and should not be used for biomass estimation in the present study area. This study also suggested that the Chilimo Dry Afromontane Forest has a substantial amount of biomass and carbon stocks compared with the estimates from other tropical forests in Africa.

This highlights the importance of the Afromontane Forest for climate change mitigation and the carbon market. Considering the limitations of this study, we recommend further research, as well as developing tapper and height-diameter equations for trees from Dry Afromontane forests.

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7. Supplementary

Component	Models	Model form	PSW	Outliers (%)	Leverage (%)
Volume	M1	$ln(V) = ln(\beta_0) + \beta_1 ln(dbh) + \varepsilon$	0.8177	1.03	1.03
	M2	$ln(V) = ln(\beta_0) + \beta_1 ln(dbh^2ht) + \varepsilon$	0.0184	2.58	1.03
	M3	$ln(V) = ln(\beta_0) + \beta_1 \ln(dbh^2)$	0.0750	2.58	1.55
		$+\beta_2 ln(ht) + \varepsilon$			
	M4	$V = \beta_0 * (dbh)^{\beta_1} * \varepsilon$	< 0.0001	5.15	
	M5	$V = \beta_0 * (dbh^2ht)^{\beta_1} * \varepsilon$	< 0.0001	2.58	
	M6	$\mathbf{V} = \beta_0 * (dbh^2)^{\beta_1} (ht)^{\beta_2} * \varepsilon$	< 0.0001	2.58	
Biomass	M7	$ln(B) = ln(\beta_0) + \beta_1 ln(dbh) + \varepsilon$	0.6697	1.55	1.03
	M8	$ln(B) = ln(\beta_0) + \beta_1 ln(dbh^2ht) +$	0.0917	4.12	18.04
		$\beta_2 ln(\rho) + \varepsilon$			
	M9	$ln(B) = ln(\beta_0) + \beta_1 ln(dbh) +$	0.0194	3.61	13.92
		$\beta_2 ln(ht) + \beta_3 ln(\rho) + \varepsilon$			
	M10	$ln(B) = ln(\beta_0) + \beta_1 ln(\rho dbh^2 ht) + \varepsilon$	0.0690	2.58	1.03
	M11	$\mathbf{B} = \beta_0 * (dbh)^{\beta_1}$	< 0.0001	4.64	
	M12	$\mathbf{B} = \beta_0 * (dbh^2 ht)^{\beta_1} (\rho)^{\beta_2}$	< 0.0001	2.06	
	M13	$\mathbf{B} = \beta_0 * (\rho db h^2 h t)^{\beta_1}$	< 0.0001	2.06	
	M14	$B = \beta_0 * (dbh)^{\beta_1} (ht)^{\beta_2} (\rho)^{\beta_3}$	< 0.0001	5.15	
	Chave 2005		NA	4.64	
	Chave 2014		NA	3.61	
	Djomo 2016		NA	1.55	
	Tetemke 2018		NA	6.19	

Table S1. Model diagnostics: significance (P) of Shapiro-Wilk test (PSW), outliers (%), leverage points (%).

		95% Confidence limits						
Models	Parameter	Estimate	Lower	Upper	Skewness (g).			
Volume								
M4	β_0	0.0006	0.0004	0.0008	0.460			
	β_1	2.0028	1.9186	2.0870	0.046			
M5	β_0	0.0002	0.0001	0.0002	0.403			
	β_1	0.8459	0.8194	0.8723	0.040			
M6	β_0	0.0001	0.0001	0.0002	0.476			
	β_1	0.8277	0.7897	0.8656	0.005			
	β_2	0.9334	0.7996	1.0673	0.020			
Biomass								
M11	βο	0.3718	0.2467	0.4970	0.457			
	β_1	1.9830	1.8992	2.0667	0.047			
M12	β_0	0.1298	0.0880	0.1716	0.428			
	β_1	0.8453	0.8185	0.8722	0.033			
	β_2	0.6588	0.2948	1.0227	-0.008			
M13	β_0	0.1403	0.1012	0.1795	0.381			
	β_1	0.8478	0.8213	0.8742	0.039			
M14	βο	0.1173	0.0743	0.1602	0.491			
	β_1	1.6583	1.5817	1.7349	0.003			
	β_2	0.9246	0.7884	1.0608	0.018			
	β3	0.6828	0.3165	1.0492	-0.006			

Table S2. Skewness in the nonlinear parameter estimates. Values in bold are considerably skewed according to Hougaard's measure of skewness (|g|).

Variables	Site	Mean	References
	Afromontane forest Ethiopia	28.9-92.4	Sisay et al., 2017
	Miombo woodlands in Tanzania	47.0	Luoga et al., 2002
Volume	Closed tropical broadleaf forest	22.5-122.3	Brown et al., 1989
	Dense Forests in India	469.4	Chhabra et al.,2002
	Moist tropical forest in Nigeria	220.0	Lowe 1997
	Rain forest in Costa Rica	186.0	Clark and Clark 2000
	Brazilian Atlantic Forest	263.0	Alves et al., 2010
Biomass	Montane forest in Congo	290.0	Imani et al., 2017
Biomass	Closed-canopy Forests in Africa	395.7	Lewis et al., 2013
	Central Amazonia Forest	327.8	Castilho et al., 2006
	South African Mistbelt forest	358.1	Mensah et al., 2016
	Humid Forest in Congo	139.9	Xu et al., 2017
	Montane forest in Tanzania	130.0	Wilcock et al., 2014
	Primary forest in Indonesia	175.0	Stas 2014
Carbon	South African Mistbelt forest	179.0	Mensah et al., 2016
Care on	Tropical rainforest in Gabon	223.0	Goïta et al., 2019
	Brazilian Amazonia Forest	253.0	Lima et al., 2012
	Moist Afromontane Forest Ethiopia	384.4	Mewded and Lemessa 2019
	Montane rainforest in Tanzania	427.0	Munishi and Shear 2004

Table S3. Comparison of the estimated stem volume (m³ ha⁻¹), biomass (Mg ha⁻¹), and carbon stock (Mg ha⁻¹) in the Chilimo forest with other tropical forests.

Models	No	Bias (Kg)	RMSE (%)	MAPE (%)	NSEF (%)	AICc	AICw	CF
Volume models								
	M1	0.006	39.046	23.929	92.183	-380.1	0.0	1.004
Linear	M2	-0.008	27.883	18.988	95.985	-473.8	1.0	1.001
	M3	-0.007	28.285	19.125	95.862	-469.5	0.2	1.001
	M4	-0.005	38.104	29.721	92.609	-598.9	0.0	NA
Nonlinear	M5	-0.004	24.007	25.887	97.086	-627.6	1.0	NA
	M6	-0.004	24.045	25.751	97.058	-607.7	0.0	NA
Biomass mo	odels							
	M7	6.058	36.556	23.753	92.985	1807.0	0.0	1.003
. .	M8	-2.153	26.243	18.389	96.310	1692.7	0.0	1.001
Lineal	M9	-2.185	26.344	18.654	96.285	1683.6	1.0	1.001
	M10	-2.831	27.110	18.895	96.050	1699.4	0.0	1.001
Nonlinear	M11	2.302	36.001	29.302	93.190	1421.9	0.0	NA
	M12	-1.361	23.820	22.357	96.998	1273.6	0.6	NA
	M13	-2.160	23.947	24.686	96.970	1280.5	0.4	NA
	M14	-1.859	24.144	22.471	96.894	1313.1	0.0	NA

Table S4. Model comparison and selection based on Monte-Carlo cross-validation statistics.

Types	Models	Observed (kg)	Predicted (Kg)	Bias (%)	rRMSE (%)	MAPE (%)
Our best model	M10	294.87	299.01	-1.38	27.16	18.72
	Chave et al. (2005)	294.87	473.32	-37.70	70.39	73.77
Conoria modela	Chave et al. (2014)	294.87	517.21	-42.99	86.71	70.45
Generic models	Djomo et al. (2016)	294.87	315.32	-6.49	26.87	42.75
	Tetemke et al. (2018)	294.87	207.54	42.08	84.86	26.34

Table S5: Comparison of stem biomass prediction by our best model and previously published generic pan-tropical biomass models using our dataset.

Figure S1: The observed (the full circle) against predicted (the solid blue line) stem volume graphs for the evaluated models. The dashed line represents the 1:1 line (i.e., a perfect fit between the observed and predicted).



Figure S2: The observed stem biomass (the full circles) and predicted values (solid blue line) using the evaluated biomass models. The dashed line represents the 1:1 line (i.e., a perfect fit between observed and predicted).



Chapter III: Ensuring sustainable wood harvesting from *Juniperus procera* trees from the Chilimo Dry Afromontane Forest in Ethiopia.

1 Introduction

Forests are known to contribute substantially to the supply of wood for industrial and nonindustrial uses (FAO, 2020a; WEST, 2014). Over 15% of Ethiopia's total land area (~17.35 million hectares) is covered by forests including plantations, woodlands, and natural forests (BEKELE; TESFAYE; MOHAMMED; ZEWDIE et al., 2015; FRANKS; HOU-JONES; FIKREYESUS; SINTAYEHU et al., 2017). The natural forests in Ethiopia are complex in structure and composition resulting from the diverse biophysical, social conditions, and disturbance history (TEKETAY; LEMENIH; BEKELE; YEMSHAW et al., 2010). Dry evergreen Afromontane forest is among the forest types widely dispersed in the highlands of Ethiopia (FRIIS; DEMISSEW; BREUGEL, 2010). Being the largest remnant forest in the country, Afromontane forests have ecological significance, including the provision of habitat for many endangered species and storage of significant amounts of carbon (BEKELE, 1994; GEBEYEHU; SOROMESSA; BEKELE; TEKETAY, 2019a; GIRMA; SOROMESSA; BEKELE, 2014). These forests are also endowed with various native timber tree species such as Juniperus procera, Podocarpus falcatus, Olea hochstetteri, among others (e.g. DE VLETTER, 1991; DESALEGN; TEKETAY; GEZAHGNE; ABEGAZ, 2012). Nevertheless, there is a huge gap between the supply and demand for wood and wood products in Ethiopia (MEFCC 2015). This growing gap is met through unsustainable wood harvesting from the existing natural forests and plantation establishment. The country has also relied on importing various wood products from abroad. For example, on average the government spent over USD 118 million annually from 1997 to 2017 to import various wood products (TOLERA, 2021).

Selective logging is a polycyclic yield regulation system in which a portion of the growing stock above a certain dimension is harvested at short intervals (SEYDACK, 2012). Selective logging of commercially important tree species is sometimes practiced in the natural forests of Ethiopia. For example, *Aningeria adolfi-friederici, Antiaris toxicaria, Cordia africana, Morus mesozygia,* and *Ekebergia capensis* were harvested from the moist Afromontane forests in southwestern Ethiopia (ABEBE; HOLM, 2003a). Additionally, the two coniferous tree species *Podocarpus falcatus* and *Juniperus procera* were also selectively logged from various Dry Afromontane forests in Ethiopia (TESFAYE; TEKETAY; FETENE, 2002). The logging was performed by both state-owned and privately operated sawmills as well as plywood factories. Generally, the logging practice was unplanned and caused overexploitation of timber tree species and extensive forest degradation (ABEBE; HOLM, 2003a; RUSS, 1979). Consequently, the government formulated a harvesting ban on the existing natural forests. This

leads to unsustainable utilization through illegal logging from the natural forests in Ethiopia (AMEHA; NIELSEN; LARSEN, 2014). Hence, it is crucial to develop tools that can enhance the management of natural forests and ensure a continuous supply of wood, while protecting the natural forest resources in Ethiopia.

Sustainable forest management planning requires species-specific and accurate information on the structure, standing volume, biomass, and growth rate of trees from a given forest (CANETTI; DE MATTOS; BRAZ; NETTO, 2017; DE MATTOS; SALIS; BRAZ; CRISPIM, 2010; GROENENDIJK; BONGERS; ZUIDEMA, 2017; SCHÖNGART, 2008). Such information is usually obtained either from repeated measurements in permanent sample plots (PSPs) or from growth ring analysis (BRIENEN; ZUIDEMA, 2006; CANETTI; BRAZ; DE MATTOS; BASSO, 2021; CONDIT; HUBBELL; FOSTER, 1993; ROSA; BARBOSA; JUNK; DA CUNHA et al., 2017). Repeated forest inventories are an efficient technique to measure tree growth and obtain a full picture of their growth dynamics. The growth rate, recruitment, and mortality of trees can all be measured using this technique. However, it is labor-intensive, expensive, requires periodic measurements usually every 5-10 years, and can be difficult to obtain annual growth rates and monitor the entire life cycle of the tree. Furthermore, monitoring large areas can be a challenge, particularly for certain species with wider distribution (CLARK; CLARK, 2001; INGA; DEL VALLE, 2017; KERSHAW JR; DUCEY; BEERS; HUSCH, 2016). Unfortunately, Ethiopia does not have a program for permanent sample plots, which could help to address these issues. However, tree ring analysis is a fast and reliable tool to obtain the lifetime growth rate and the establishment age of trees (CANETTI; BRAZ; DE MATTOS; BASSO, 2021; GROENENDIJK; BONGERS; ZUIDEMA, 2017; ROSA; BARBOSA; JUNK; DA CUNHA et al., 2017). Such information can be used to determine the timber stock in a forest, assess the sustainability of timber harvesting for several tropical timber trees, and develop a species-specific management plan (LIGOT; FAYOLLE; GOURLET-FLEURY; DAINOU et al., 2019; LÓPEZ; VILLALBA; BRAVO, 2013; ROZENDAAL; BRIENEN; SOLIZ-GAMBOA; ZUIDEMA, 2010).

J. procera is one of the most important tree species in African montane forests, found in countries such as Sudan, Eritrea, Ethiopia, DR Congo, Malawi, and Zimbabwe as well as Saudi Arabia and Yemen (GARDEN, 2022; POHJONEN; PUKKALA, 1992). This species has significant economic and ecological importance for these nations. The wood is durable and termite resistant (POHJONEN, 1991), and is one of the most commercially exploited timber tree species in Ethiopia (see BEKELE, 1993; RUSS, 1979; TEKETAY, 1992). In the past, various studies focused on the climate growth relationship (COURALET; SASS-KLAASSEN; STERCK; BEKELE *et al.*, 2005), seed behavior and germination rate (MAMO; MIHRETU; FEKADU; TIGABU *et al.*, 2006; MAMO; NIGUSIE; TIGABU; TEKETAY *et al.*, 2011), and genetic variability among different populations of this species (SERTSE; GAILING; ELIADES; FINKELDEY, 2011). However, the basic information for calculating the timber yields including the standing stock, growth rate, minimum cutting diameter, cutting cycle, and other essential information is lacking and the available ones are outdated (TEKETAY; LEMENIH; BEKELE; YEMSHAW *et al.*, 2010). The lack of basic information constrains the development of forest management plan for sustainable wood harvesting from this tree species as well as the natural forests in Ethiopia.

Various studies reported modelling the growth of trees enables to explore the rotation age, minimum cutting diameter, age of maximum annual increment, age of thinning, and the calculation of annual allowable cut in sustainable management systems (BRIENEN; ZUIDEMA, 2006; CANETTI; DE MATTOS; BRAZ; NETTO, 2017; GROENENDIJK; BONGERS; ZUIDEMA, 2017). Therefore, the objectives of this study were to (1) determine the population structure and diameter growth rate of the *J. procera* tree; (2) develop a diameter growth model and evaluate the ideal minimum logging diameter and cutting cycle for this tree species; (3) provide the potential harvestable volume of wood through simulation by combining different minimum logging diameters and cutting cycles from Chilimo forest managed under participatory forest management scheme. This is hoped to enable forest managers and policymakers to formulate species-specific management regimes and ensure sustainable timber harvesting from the existing Dry Afromontane Forest in Ethiopia.

2 Materials And Methods

2.1. Study site description

This study was conducted in the Chilimo forest, located 97 km west of Addis Ababa in central Ethiopia (Figure 1). It is geographically located from 38°05' to 38°15' E and 9°00' to 10°10' N, at an altitudinal range of 1,700-3,200 m. The area experiences a unimodal pattern of rainfall distribution from May to September, with July having the highest peak. The average annual temperature is between 15 and 20°C, and its average annual precipitation ranges between 1000 and 1264 mm (Tesfaye et al., 2018). The major soil types around the study areas are Vertisols, Luvisols, and Cambisols (Soromessa and Kelbessa 2014). The forest is among the remnant dry Afromontane forests that once covered Ethiopia's central plateau. Chilimo forest currently covers a total area of 4,500 ha and is jointly managed by twelve Forest User Groups

(FUGs) and Oromiya Wildlife and Forest Enterprise (OFWE) under the participatory forest management scheme (AMEHA; NIELSEN; LARSEN, 2014; TESFAYE, MEHARI A; GARDI, OLIVER; BEKELE, TESFAYE; BLASER, JÜRGEN, 2019). In this arrangement, the regional government and local communities agreed to jointly protect, manage, and sustainably utilize the forest resources. Members of the forest user groups are allowed to harvest wood for the maintenance of public schools and houses (for poor and aged people), firewood and construction wood from dead and dying trees for their subsistence use, and livestock grazing (AMEHA; LARSEN; LEMENIH, 2014). Commercial harvesting is not allowed from the natural forest but from the plantation forests established surrounding the natural forest.

Figure 1: Map of the study area overlaid with the distribution map of dry Afromontane forests following FRIIS; DEMISSEW e BREUGEL (2010).



2.2. Forest Inventory

A forest inventory was conducted in 2018 in the Chilimo forest. A systematic random sampling technique was employed to collect the vegetation data. A total of 165 sample plots $(20 \text{ m} \times 20 \text{ m})$ were established along transect lines. The first transect was aligned parallel to the edge of the forest (20 m) and others were laid out at 500 m intervals. The first plot was located randomly, and the subsequent plots were established at 300 m intervals along the

transect lines. In each sample plot, the diameter at breast height (dbh) and total height (h) of all trees with dbh ≥ 2.0 cm were measured using a diameter tape and Vertex IV ultrasonic hypsometer (Haglöf Sweden AB, Långsele, Sweden). The local names of all trees were recorded and identified to the species level in the field following the Flora of Ethiopia and Eritrea (EDWARDS; TADESSE; DEMISSEW; HEDBERG, 2000; EDWARDS; TADESSE; HEDBERG, 1995; HEDBERG; EDWARDS; NEMOMISSA, 2003; HEDBERG; FRIIS; EDWARDS, 2004; HEDBERG; HEDBERG; EDWARDS, 1989). For those species difficult to identify in the field, their specimens were collected, pressed, and identified at the National Herbarium, Addis Ababa University.

All trees with a diameter ≥ 2 cm were considered to describe the structure of the forest. The density (N° ha⁻¹), basal area (m² ha⁻¹), frequency (number of plots with species presence), and Importance Value Index (IVI) for each species were calculated (Table S1). The density was calculated by converting the total number of individuals of each species per plot to equivalent numbers per hectare. IVI is the sum of the relative density, relative dominance, and relative frequency values (KENT; COKER, 1992), where relative density (%) is the density of each species as a percentage of the total density of all species, relative frequency (%) is the frequency of each species as the percentage of the total frequency of all species, and the relative dominance (%) is the basal area of each species as the percentage of the total species the relative contribution of each species in the study area and the most important species were those having the highest values (GONÇALVES; REVERMANN; GOMES; AIDAR *et al.*, 2017).

2.3. Target tree species

Among the species enumerated, *J. procera* was selected for further studies based on the basal area and diameter distribution information generated from the inventory data (Table S1). It is one of the tree species commercially exploited for timber from dry Afromontane forests (AMENTE, 2006b). *J. procera* is an evergreen tree that attains over 40 m in height and 3 m in diameter (NEGASH, 1995). The species grows within the altitudinal range between 1,700 - 3,300 m above sea level (STERCK; COURALET; NANGENDO; WASSIE *et al.*, 2010; TIGABU; FJELLSTRÖM; ODÉN; TEKETAY, 2007).

The average wood density of this species is 0.60 ± 0.07 g cm⁻³ (MOKRIA; GEBREKIRSTOS; AYNEKULU; BRÄUNING, 2015). The wood can be used for the manufacturing of lead-pencil, construction, and lining of buildings, as well as for a variety of outdoor works owing to its fine texture, straight grain, resistance to termite attack, and

workability (DESALEGN; TEKETAY; GEZAHGNE; ABEGAZ, 2012; NEGASH, 1995). Previous dendrochronological studies showed the existence of annual growth rings which are defined by the presence of large, round, and thin-walled tracheid in the lighter earlywood and small, flattened, and thick-walled tracheid in the darker latewood (MOKRIA; GEBREKIRSTOS; AYNEKULU; BRÄUNING, 2015; WILS; ROBERTSON; ESHETU; SASS-KLAASSEN *et al.*, 2009).

The *J. procera* population structure (the number of individuals per diameter class) was analyzed by constructing frequency distribution histograms using 10 cm diameter classes. First, we plotted the cumulative number of individuals against the diameter size to understand the diameter size class with management potential as well as to determine the carrying capacity of the forest (BRAZ; DE MATTOS; OLIVEIRA; BASSO, 2014; GOTELLI, 2008; WHITTAKER, 1970). In this way, we assume that the current structure is the same trajectory as the past (GOTELLI, 2008), and then represent the number limit of trees of that species in the stand with the stabilization of the curve (TIETENBERG; LEWIS, 2018). We also calculated the time of passage from one diameter size class to the other by estimating the duration of the growth phases (SOUZA; ARAÚJO; CAMPOS; NETO, 1993).

2.4. Disc sample collection for growth ring analysis

Tree ring analysis is a fast and reliable tool to obtain the lifetime growth rates of trees, determine the age, enable the understanding of the forest dynamics, and help to develop species-specific management criteria (CANETTI; DE MATTOS; BRAZ; NETTO, 2017; DE MATTOS; AGUSTINI; ALVAREZ, 2010; DE MIRANDA; HIGUCHI; TRUMBORE; LATORRACA *et al.*, 2018; GROENENDIJK; BONGERS; ZUIDEMA, 2017; ROSA; BARBOSA; JUNK; DA CUNHA *et al.*, 2017; SCHÖNGART, 2008). This approach involves harvesting or coring trees to collect samples. A total of 12 stem disc samples were collected at 1.3 m height across the range of diameter sizes (dbh \geq 40 cm) among the fallen tree species due to the asphalt road construction that passes through the Chilimo forest.

The collected disc samples were sanded with progressively finer sandpaper (from 80 to 400 grit size). Before measurement, four radii were drawn, and the ring boundaries were marked with a pencil. The ring widths were measured to 0.01 mm using LEICA MS 6 microscope coupled with a LINTAB digital measuring table associated with TSAP-Win software (RINN, 2003). The accuracy of visual cross-dating and measurement errors were further checked using the COFECHA program (HOLMES, 1983). Following the successful cross-dating, diameter growth curves were created by accumulating the ring-width increments for each tree and used

to describe the diameter growth pattern (e.g., CANETTI; BRAZ; DE MATTOS; BASSO, 2021). Additionally, the mean annual diameter increments and passage time for each diameter size class were calculated and presented using a boxplot.

2.5. Bark sample collection for over-bark diameter reconstruction

Sample trees (n = 202, diameter range 2.0 - 125.5 cm) were selected for a bark sample collection from the Chilimo forest. The trees were systematically sampled to cover the range of diameters within a forest. Overall, two bark samples were collected at 1.3 m above ground level by using a machete (we removed a small piece of bark about 10 cm in length). The bark thickness was directly measured in the field using a digital Vernier caliper.

The mean bark thickness (b) was calculated from two bark sample measurements and converted into cm. The calculated mean bark thickness was used to determine the under-bark diameter (D_{ub}) of the respective tree from the over-bark diameter (D_{ob}) measurements. The under-bark diameter was calculated by using the following formula:

$$D_{ub} = D_{ob} - b$$

We fitted the power function bark thickness prediction equation (equation 1) by considering the relation between the over-bark diameter (D_{ob}) and under-bark diameter (D_{ub}) was established. The relation between the over-bark diameter (D_{ob}) and under-bark diameter (D_{ub}) was calculated by using the following power function.

$$D_{ob} = \beta_0 \times D_{ub}^{(1+\beta_1)} + \varepsilon$$
, where $\beta_0 = 1.16$ and $\beta_1 = -0.03$ Equation 1

Where D_{ob} is the over-bark diameter (cm), D_{ub} is the under-bark diameter (cm). By using the mean bark thickness and under-bark diameter, we calculated the over-bark diameter (dbh) of a tree at any age. This conversion was required since the volume equation we used to calculate the stem volume of a tree requires the over-bark diameter (Dob) as the input variable.

2.6. Diameter growth modeling

To describe the age-diameter relationship of the tree species, we adjusted six sigmoid growth models (Table 1) that are widely used in growth modeling (BURKHART; TOMÉ, 2012). The purpose of fitting a growth model is to represent the biological development of the studied species including its juvenile, adult, and senescence phases. The models were fitted by the *nls* function in the *nlstools* package in R Software (BATY; RITZ; CHARLES; BRUTSCHE *et al.*, 2015). The best-fitted model was selected based on the Pearson correlation coefficient,

bias, and root means square of error (RMSE) values obtained from the Leave-One-Out crossvalidation (LOOCV) technique, and graphical analysis of the residual distributions. The crossvalidation technique was repeated 200 times, and statistics and errors of the model were averaged over 200 realizations following the procedures in HUY; POUDEL e TEMESGEN (2016).

Bias (%) =
$$\frac{1}{R} \sum_{r=1}^{R} \frac{100}{n} \sum_{i=1}^{n} \frac{y_i - \hat{Y}_i}{y_i}$$
 Equation 2

RMSE (cm) =
$$\frac{1}{R} \sum_{R=1}^{R} \sqrt{\frac{1}{n} \sum_{i=1}^{n} (y_i - \hat{Y}_i)^2}$$
 Equation 3

$$r_{y\hat{y}} = \frac{\sum (xi - \bar{x}) (yi - \bar{y})}{\sqrt{\sum (xi - \bar{x})^2 \sum (yi - \bar{y})^2}}$$
Equation 4

We used the height prediction model developed for *J. procera* tree in chapter one (Equation 6) and determined the total height for the reconstructed diameter at a specific age. The wood volume of trees at a given age was estimated using a volume equation developed for *J. procera* (Equation 5) from the Chilimo forest. From the calculated volume, we derived the current annual volume increment (CAIv) and mean annual volume increment (MAIv) using Equations 7 and 8 following the procedure in SCHÖNGART (2008).

$$V = 0.0004246 \, (dbh)^{1.2824861} (ht)^{1.038178}$$
 Equation 5

$$ht = 1.3 + 35.831 dbh / (31.390 + dbh)$$
 Equation 6

$$MAI_v = CGv_{(t)}/t$$
 Equation 7

$$CAI_{v} = CGv_{(t+1)} - CGv_{(t)}$$
 Equation 8

where V is the stem volume of the tree, dbh is the diameter at 1.3 m above the ground level (cm), ht is the total height (m), MAIv is the mean annual volume increment (m³), CAIv is the current annual volume increment (m³), CGvt is the cumulative volume increment at different years (cm) and t is the age (years).

Table 1: Growth functions tested to determine the diameter growth pattern of the *J. procera* tree.

No	Equations	Functional form
1.	Gompertz	$\mathbf{Y} = \beta_0 exp\big(-exp(\beta_1 - \beta_2 Age)\big)$
2.	Logistics	$\mathbf{Y} = \frac{\beta_0}{\left(1 + \beta_1 exp(-\beta_2 Age)\right)}$

3.	Johnson-Schumacher	$\mathbf{Y} = \beta_0 exp \left(-\beta_1 / (Age + \beta_2) \right)$
4.	Monomolecular	$\mathbf{Y} = \beta_0 \big(1 - \beta_1 exp(-\beta_2 Age) \big)$
5.	Chapman-Richards	$\mathbf{Y} = \beta_0 \big(1 - exp(-\beta_1 Age) \big)^{\beta_2}$
6.	Schumacher	$\mathbf{Y} = \beta_0 exp\big(-(\beta_1 /Age)\big)$
7.	Lundqvist-Korf	$Y = \beta_0 exp(-\beta_1 * A_0 e^{-\beta_2})$

where Y is the diameter at 1.30 m from the ground; "t" is the time required (age); " β_0 , β_1 , β_2 and β_3 " are model parameters (BURKHART; TOMÉ, 2012).

The age that provides the maximum average annual volume increments was defined at the point where the MAI and CAI curves met (BETTINGER; BOSTON; SIRY; GREBNER, 2016). The ideal minimum logging diameter (MLD) was defined as the diameter at the maximum CAI which can be derived from the age diameter relationship curve of the tree species. The cutting cycle which represents the mean passage time through the 10 cm diameter class until reaching the MLD was acquired by Equation 9:

$$Cutting \ cycles = \frac{Age_{(MLD)}}{(MLD*0.1)}$$
 Equation 9

2.7. The harvestable volume of wood simulation

The harvestable volume of wood potential from the *J. procera* tree population was simulated by considering different scenarios. Each scenario was defined by a combination of four Minimum logging diameters (30, 40, 50, and 60 cm) and five cutting cycles (15, 20, 25, 30, and 35 years). We also used the number of trees and volume in each diameter size class. The simulation was performed by using the diameter size class projection method using the mathematical function (Equation 10) proposed by (ALDER, 1995)

$$N_{k,t+1} = N_{k,t} + I_K - O_k - M_k - H_k$$
 Equation 10

where $N_{k, t+1}$ is the number of trees in diameter size class k in the period t+1, $N_{k, t}$ is the number of trees in class k at the period t, I_k is the ingrowth into the class k during the period, O_k is the outgrowth from class k to the subsequent classes, M_k is the mortality rate in class k, and H_k is the harvested tree during the period.

We built the matrix by simulating for 5 years (t) intervals, starting with a 15 cm dbh center class, until the steady state (structure equilibrium) was attained (BUONGIORNO; GILLESS, 2002). We used the stem volume of wood from the *J. procera* tree above the MLD

to define the harvestable volume of wood (H_k). The initial population structure ($N_{k,t}$) was obtained from the recent inventory in the Chilimo forest. The average annual diameter growth rate by diameter class was obtained from the growth ring analysis. The number of trees passing to the next classes (O_k) was calculated from the passage time between diameter classes using Equation 11.

$$o_k = \frac{t.i}{w}$$
 Equation 11

where O_k is the number of trees migrating from class k to the subsequent classes, i is the average increment of the diameter size class k, w is the interval between diameter size classes (10 cm), and t is the period considered.

The number of individuals in the first diameter size class was used as recruitment (I_k). Generally, long observation data from permanent sample plots are required to get reliable estimates of mortality rate. However, permanent sample plots are scanty in Ethiopia. Hence, we used an alternative approach suggested by LUNDQVIST (2017) to estimate the average annual mortality rate (M_i) in each diameter size class (Equation 12).

$$M_{i} = 100 \left[1 - \frac{N_{i+1}I_{i+1}}{N_{i}I_{i}} \right]^{\left(\frac{2}{(t_{i}+t_{i+1})}\right)}$$
Equation 12

where (M_i) is the annual mortality rate in the diameter class (i) in percentage, (N_i) is the number of trees in the diameter class (i), (N_{i+1}) is the number of trees in the subsequent diameter class, (I_i) and (I_{i+1}) are the mean annual diameter increment of class i, and the subsequent class in cm, (t_i) and (t_{i+1}) are the passage time from the diameter class (i) and (i+1) to the subsequent classes. The steady-state was determined by running the matrix until the volume production is relatively stabilized. The final harvesting simulation output of each scenario was regarded as the maximum harvestable volume of wood potential provided by the *J. procera* tree population from the Chilimo forest.

3 Results

3.1. Woody species composition

A total of 37 woody plant species in 30 families were recorded during this study (Table S1). The most species-rich families were *Rosaceae* (represented by three species), followed by *Rhamnacea*, *Oleaceae*, *Loganiaceae*, *Flacourtiaceae*, and *Celastraceae* each represented by two species. The remaining families were represented by one species. The top ten abundant tree species were *J. procera*, *Olea europaea* ssp. *cuspidata*, *Olinia rochetiana*, *Maytenus gracilipes*, *Podocarpus falcatus*, *Scolopia theifolia*, *Rhus glutinosa*, *Osyris quadripartita*, *Allophylus abyssinicus*, and *Dovyalis abyssinica*. The mean stem density of all tree species (dbh ≥ 2 cm) was 925 stems ha⁻¹, while the total basal area was 26 m² ha⁻¹. The lists of all tree species registered from the Chilimo forest were presented in Table S1.

3.2. Density and diameter size distribution of J. procera

The mean stem density of *J. procera* trees (dbh ≥ 2 cm) was 183 stems ha⁻¹, while the total basal area was 12.1 m² ha⁻¹, and the standing volume of wood was 98.9 m³ ha⁻¹. Overall, trees with dbh ≥ 40 cm contributed 19.3% of the mean density, 72.1% of the total basal area, and 65.4% of the total standing volume of wood. The maximum diameter of the trees was 121.2 cm while the tallest tree was 50.2 m in the forest. The population of *J. procera* showed an inverted J-shape diameter distribution pattern characterized by a higher number of individuals in the lower diameter classes (Dbh ≤ 20 cm) and a progressively declining number of trees with increasing diameter sizes (Figure 2a). The cumulative number of trees (Figure 2b) tends to stabilize after the 65 cm diameter size which shows the maximum number of individuals of the species the stand can support (stand carrying capacity). The population structure of the top ten tree species was presented in Figure S3.



Figure 2: Population structure (a), the cumulative number of trees (b), and the standing volume of wood (c) by diameter size class for the *J. procera* tree population from the Chilimo forest.

3.3. Diameter growth rates and passage time by dbh classes

The mean annual diameter growth ranges between 0.50 cm year⁻¹ and 0.65 cm year⁻¹ with an overall mean of 0.59 ± 0.24 cm year⁻¹. A Kruskal-Wallis tests also showed that there was a statistically significant difference in diameter growth rates between the different diameter size classes (*Chi-square* = 46.53, *p-value* < 0.05). The trees exhibited the lowest diameter growth rate in the lower class (0.50 cm year⁻¹) and the growth rate progressively increased with increasing diameter size and reached 0.65 cm year⁻¹ at the highest diameter size (Figure 3a). The average time required to move from one diameter class to the next higher-size class ranges between 16 and 19 years.



Figure 3: The observed average diameter growth rates (a) and passage time (b) by diameter size classes. The boxplots show the median values (solid horizontal line), 50th percentile values (box outline), and 90th percentile values (whiskers). The blue and black full circles represent the mean and individual observations.

3.4. Modeling the cumulative diameter growth

The estimated parameters and the goodness-of-fit statistics of the fitted diameter growth models are presented in Table 3. The Johnson-Schumacher model better fitted with the diameter growth data as shown by the fit statistics values (Table 3) and graphical analysis (Figure 4). This model had the lowest RMSE and Bias values. All the parameter estimates of the tested models were significantly different from zero (p < 0.001). The scatter plots observed against predicted diameter growth for the evaluated models are presented in (Figure S1). Visual comparison of the evaluated models revealed that the Johnson-Schumacher model provides the

closest prediction to the observed diameter growth than the remaining models. The residual plot shows that the residuals of Johnson-Schumacher were randomly scattered around zero lines for all fitted values except for the smaller diameter sizes (Figure 5).

Table 3: Parameter estimates and fits statistics for diameter growth estimation models using theLeave-One-Out Cross-Validation (LOOCV) technique.

No	Models	βο	β_1	β_2	r _{yŷ}	RMSE (cm)	Bias (%)	P-value
1.	Gompertz	49.371	3.418	0.037	0.9321	5.12	-0.08	< 0.001
2.	Logistics	43.987	13.104	0.065	0.9291	5.22	-0.17	< 0.001
3.	Johnson-Schumacher	94.469	76.626	14.384	0.9330	5.08	-0.03	< 0.001
4.	Monomolecular	107.600	1.023	0.0065	0.9319	5.13	-0.03	< 0.001
5.	Chapman-Richards	62.254	0.019	1.540	0.9327	5.10	0.00	< 0.001
6.	Schumacher	68.060	41.306		0.9285	4.88	0.42	< 0.001
7.	Lundqvist-Korf	294.115	10.712	0.390	0.9324	5.08	-0.03	< 0.001



Figure 4: Cumulative diameter growth curves (black lines) and the fitted models (red line). The 12 lines represent the cumulative diameter growth of individual *J. procera* trees.



Figure 5: Residuals graph for the evaluated diameter growth models

J. procera trees attained the maximum CAI in volume at 50 years of age and reached 30 cm in diameter. This diameter (30 cm) is considered the minimum logging diameter (MLD) for the *J. procera* tree from the Chilimo forest. On the other hand, trees attained the maximum average volume increment (MAI) at 90 years of age and the trees reached 50 cm in diameter (Figure 6). The estimated cutting cycle until the trees reach the MLD was 17 years.



Figure 6: Current and mean annual increment curves in volume estimates (a) and the cumulative diameter growth curve (b) for *J. procera* tree.

3.5. The potential harvestable volume of wood

The simulation analysis considering the 30 cm MLD (the diameter at the maximum CAI in volume) consistently showed the largest harvestable volume of wood and the amount decreased in the subsequent harvests and remained stable after the fifth harvesting entry (Figure 7). On the contrary, the 40, 50, and 60 cm MLD (the diameter at the maximum MAI in volume) consistently showed the lowest initially harvested volume of wood and the amount increased in the second harvest and stabilized after the fifth harvesting entry.



Figure 7: Simulation of the long-term harvestable volume of wood (m³ ha⁻¹) for the evaluated minimum logging diameters and cutting cycles. The light blue vertical line indicates the harvesting entry after which the harvesting was stabilized.

The projected harvestable volume of wood at the steady state was consistently reduced with increasing minimum logging diameters, but this value increased with increasing cutting cycle lengths (Figures 8a & c). On the contrary, the volume increment reduced with increasing cutting cycle lengths and minimum logging diameters (Figures 8b & d). Generally, the largest

harvestable volume of wood was obtained by considering the 30 cm MLD combined with 35 years cutting cycle, whereas the lowest harvestable volume of wood was obtained by considering the 60 cm MLD and 15 years cutting cycle. On the other hand, the highest volume increment was observed from 40 cm MLD and 15 years cutting cycle, while the lowest volume increment was obtained by considering the 60 cm MLD and 35 years of cutting cycles (Figure 8b).



Figure 8: The projected harvestable volume of wood (a and c) and volume increment (b and d) against the minimum logging diameters (MLD) and cutting cycles.

4 Discussions

The observed mean density of *J. procera* trees in this study (183 stems ha⁻¹) is higher than the findings from the Adelle Forest (86 stems ha⁻¹) in Bale Mountains (YOUNG; ROMME; EVANGELISTA; MENGISTU *et al.*, 2017), Wofwasha forest (92.6 stems ha⁻¹) in central Ethiopia (FISAHA; HUNDERA; DALLE, 2013), and the dense rainforest (42.04 stems ha⁻¹) in south-western Ethiopia (ABEBE; HOLM, 2003a). This suggests that the Chilimo forest presents a higher stock and has larger number of stems. The differences in anthropogenic disturbance levels and forest management practices are probably responsible for the variation

in stem density. The total basal area (12.1 m² ha⁻¹) was lower than the findings from the Wofwasha forest (FISAHA; HUNDERA; DALLE, 2013), the Adelle Forest (YOUNG; ROMME; EVANGELISTA; MENGISTU *et al.*, 2017), and the Adaba-Dodola forest (HUNDERA; BEKELE; KELBESSA, 2007). This value is, however, greater than the findings from the Arero forest (SHIFERAW; LIMENIH; GOLE, 2019) in southern Ethiopia. The harvesting of larger-diameter trees from the Chilimo forest in the past could explain the relatively lower mean basal area (EFAP, 1994; HASSEN, 2013). Previous studies reported that anthropogenic disturbances i.e. free grazing, timber extraction, and mining cause changes in species composition, tree density, and basal area (KIKOTI; MLIGO, 2015). A relatively lower amount of basal area and density of trees have been previously reported from other dry Afromontane forests which experienced anthropogenic disturbances in central Ethiopia (BEKELE, 1993; TILAHUN; SOROMESSA; KELBESSA; DIBABA, 2011).

In the Chilimo forest, the total standing volume of wood derived from *J. procera* trees $(dbh \ge 2 \text{ cm})$ was 98.9 m³ ha⁻¹. Out of this, trees with a dbh ≥ 40 cm constituted 65 % of the total standing volume of wood, highlighting the potential for timber harvesting. This is partly related to the recovery of the forest from past disturbances due to the protection by the local communities. Chilimo forest is among the natural forests managed by local forest user groups organized as cooperatives under participatory forest management schemes (Mohammed & Inoue, 2014). In this arrangement, the local government and communities agreed to jointly protect, manage, and sustainably utilize the forest resources. Various studies presented that this arrangement helps to enhance tree regeneration, accumulate biomass stock, improve livelihoods, and alleviate poverty (AMENTE, 2006a; GOBEZE; BEKELE; LEMENIH; KASSA, 2009; SIRAJ, 2019).

J. procera exhibited an inverted J-shape diameter distribution pattern in the Chilimo forest(Figure 2a). This pattern indicates a healthy regeneration process and continuous recruitment of new individuals in the smaller diameter classes, followed by gradual reduction in numbers as the trees mature within the forest. According to (YOUNG; ROMME; EVANGELISTA; MENGISTU *et al.*, 2017), a tree population with such kind of diameter distribution pattern could be considered a stable population with low conservation concern. The reason for the good regeneration might be the formation of additional microsites created due to tree harvesting in the past, facilitating the availability of light, nutrients, and moisture to the remaining trees. On the other hand, the population size of *J. procera* trees stabilized after the 65 cm diameter size class (Figure 2b). This shows that the population has reached its upper limit of growth, commonly known as carrying capacity. Beyond this point, the population is

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likely to experience a significant decline due to the higher competition for scarce resources (DEL MONTE-LUNA; BROOK; ZETINA-REJÓN; CRUZ-ESCALONA, 2004). This carrying capacity implies a diameter limit that needs to be considered for planning appropriate management intervention and ensuring a sustainable and productive forest structure.

Timber harvesting is legally prohibited from the natural forests in Ethiopia. This is primarily due to the absence of tools to regulate timber harvestings, such as diameter growth rate, minimum cutting diameter, and cutting cycles for the timber tree species. Additionally, lessons from previous conventional logging practices in Ethiopia have led to the depletion of the timber stock and severe degradation of the remnant forest (ABEBE; HOLM, 2003a). In this study, we provided the required information that enables policymakers to make informed decisions regarding the harvesting of wood from J. procera tree species. The average annual diameter growth rate varies between 0.50 cm year⁻¹ and 0.65 cm year⁻¹ with an overall mean of 0.59 cm year⁻¹. These values are within the range of the growth rate reported from commercially harvested timber tree species from a wet tropical forest in Cameron (GROENENDIJK; BONGERS; ZUIDEMA, 2017), Bolivian Cerrado (LÓPEZ; VILLALBA; BRAVO, 2013), Sinop micro-region in the Brazilian Amazon forest (CANETTI; BRAZ; DE MATTOS; BASSO, 2021), Bolivian Amazon forest (BRIENEN; ZUIDEMA, 2006), Semi deciduous forest in Cameron (WORBES; STASCHEL; ROLOFF; JUNK, 2003), Central African forest (LIGOT; FAYOLLE; GOURLET-FLEURY; DAINOU et al., 2019), from different Ecoregions in Bolivia (DAUBER; FREDERICKSEN; PEÑA, 2005). However, our diameter growth values are higher than the estimates for the same tree species from various dry Afromontane forests in Ethiopia. For instance, COURALET; SASS-KLAASSEN; STERCK; BEKELE et al. (2005) reported a mean annual growth rate of 0.40 cm year⁻¹ and 0.26 cm year⁻¹ ¹ from the Adaba-Dodola and Menagesha suba Dry Afromontane forests. Similarly, SIYUM; AYOADE; ONILUDE e FEYISSA (2019b) reported a mean diameter growth rate of 0.23 cm year⁻¹ from Hugumburda and 0.18 cm year⁻¹ from Desa'a forest in Northern Ethiopia. This variation might be related to the differences in the local environmental factors including climate, topography, soil fertility, moisture, and inherent genetic differences (e.g. KARYATI; IPOR; JUSOH; WASLI, 2017; KERSHAW JR; DUCEY; BEERS; HUSCH, 2016). Generally, the calculated average diameter growth rate by diameter classes provides the potential range of growth rates for the species.

Individual *J. procera* trees showed the maximum CAI in volume at the age of 50 years and trees attained 30 cm in diameter (Figure 6). This shows that trees attain the highest growth rate at this age and the growth declines afterward. Maintaining trees above 30 cm diameter in

the forest is considered a waste of space and income from a production forestry point of view since the trees already passed their point of maximum wood production (Figure 6). Similarly, the tree exhibited the maximum MAI in volume at 90 years (the age that provides the maximum volume production) and the trees attained 50 cm in diameter. This is consistent with the findings by Pohjonen and Pukkala (1992) who reported the maximum CAI in volume between 35 and 40 years and the maximum MAI in volume between 50 and 60 years for the same tree species from the Menagesha Suba forest in Central Ethiopia.

The 30 cm MLD (the diameter at maximum CAI) and 35 years cutting cycle provided the largest harvestable volume of wood (48 m³ ha⁻¹) and the best scenario from the wood production point of view (Table S2). However, the cutting cycle length is large, and difficult to meet the growing wood demand gap as well as the local community interest. Alternatively, the 30 cm MLD combined with the remaining cutting cycles also provided a large amount of harvestable wood and volume increments (Table S2). Nevertheless, this scenario entails harvesting a large proportion (11-22 %) of the current standing trees, including those with the most productive diameter size before they can reach their reproductive stages. This will impede seed production and the regeneration process. According to COURALET; SASS-KLAASSEN; STERCK; BEKELE *et al.* (2005), *J. procera* tree starts seed production when the diameter reaches around 25 cm. Therefore, it is crucial to strictly protect these diameter size classes in the forest while ensuring sustainable wood harvesting practices.

The 40 cm MLD and a 15-year cutting cycle resulted in the optimum harvestable volume of wood (22 m³ ha⁻¹) and volume increment (1.4 m³ ha⁻¹ year⁻¹). Additionally, this scenario allows for the harvesting of small proportion (9 %) of the standing trees while maintaining a larger proportion (91 %) of the existing standing trees in the forest. This scenario will enable wood harvesting in a short period (every 15 years) and lead to meeting the local community interest as well as the national wood demand gap. The timber volume increment presented here is higher than the findings from selected timber trees from the Brazilian Amazon Forest (BRAZ; CANETT; DE MATTOS; BASSO *et al.*, 2018; CANETTI; BRAZ; DE MATTOS; BASSO, 2021), from the Bolivian Amazon Forest (BRIENEN; ZUIDEMA, 2006). However, it is within the range of the average volume increment reported from selectively logged tropical forests (Putz et al., 2012). The initially harvested volume recovery rate was comparable with the 35% recovery rate reported by (PUTZ; ZUIDEMA; SYNNOTT; PEÑA-CLAROS *et al.*, 2012) for tropical forests, 21-36 % recovery rate from four species in Cameroon (GROENENDIJK; BONGERS; ZUIDEMA, 2017), 18- 49 % recovery rate from three canopy tree species from the semi-deciduous moist forest in Bolivia (ROZENDAAL; BRIENEN; SOLIZ-GAMBOA;

ZUIDEMA, 2010), and 18-61 % recovery rate from four timber tree species from Bolivian Amazon Forest (BRIENEN; ZUIDEMA; MANAGEMENT, 2006). Our estimates are slightly higher than the volume recovery rate reported from the Bolivian Amazon Forest (DAUBER; FREDERICKSEN; PEÑA; MANAGEMENT, 2005). The higher recovery rate can be attributed to the high densities per hectare and the relatively higher average diameter growth rates (0.59 cm year⁻¹) of *J. procera* trees compared to the Amazon species.

The 50 cm MLD (diameter at the maximum MAI) and 60 cm MLD relatively provided the lowest harvestable volume of wood and volume increments (Table S2). Only 3 - 5 percent of the total number of *J. procera* trees will be harvested and the largest proportion (95 - 97 percent) of *J. procera* trees will be maintained in the forest (Table S2). These scenarios are the least important combination from the wood production point of view and satisfy the local community interest. Trees require 90 years to reach the MLD and provide the lowest amount of harvestable volume of wood. The low diameter growth rate (\geq 60 cm dbh) and few number of trees in the preceding classes may be the cause of the low timber volume recovery. At this point, the trees have already passed their point of maximum wood production and start to show declining growth (senescence phase).

The initially harvested volume of wood was not completely recovered for the applied MLD and cutting cycles (Table S1). Generally, the recovery rate (%) increased with increasing the length of cutting cycles for all minimum logging diameters. This is consistent with the findings from the Amazon forest (BRAZ; DE MATTOS; THAINES; DE MADRON et al., 2015), a semi-deciduous moist forest in the Central African Republic (LIGOT; GOURLET-FLEURY; DAINOU; GILLET et al., 2022), and the East African tropical forest (BONNELL; REYNA-HURTADO; CHAPMAN, 2011). However, various studies (BRIENEN; ZUIDEMA; MANAGEMENT, 2006; PUTZ; ZUIDEMA; SYNNOTT; PEÑA-CLAROS et al., 2012) associated the non-recovery of the initially harvested volume of wood in the subsequent cycles with unsustainable wood harvesting. However, the first harvesting contains some old-aged trees that have been present in the forest for many decades or centuries, thus it would not be reasonable to assume a total recovery of the volume of wood that was initially cut in the succeeding short cycles (BRAZ; DE MATTOS; THAINES; DE MADRON et al., 2015; DAWKINS; PHILIP, 1998). The volume increment, or net production, in other words, is what matters most. The population structure of a tree, the cutting cycle, and the applied minimum logging diameter (MLD) all have an impact on the volume increment rate. The initial harvested volumes likely cannot be recovered within the existing short-cutting cycle lengths (which is not

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the purpose of forest management), and forest managers or policymakers need to be made aware of this.

There is a huge gap between the demand and supply of wood products in Ethiopia (MEFCC 2015). This has resulted in increased import of wood products from 17,750 cubic meter in 1997 to 128,914 cubic meter in 2017 and is expected to reach 158 million cubic meter by 2033 (TOLERA, 2021). During these periods, the country spent on average over 118 million USD per year on importing various wood products. Hence it is very important to explore an alternative to decrease the dependency on importing wood products and satisfy the evergrowing national wood demand. We found that the studied forest had a large amount of harvestable volume of wood potential based on the current structure and diameter growth rate. Our simulation analysis revealed that 22 m³ ha⁻¹ wood can be sustainably harvested from *J. procera* trees above 40 cm dbh and 15 years of cutting cycles from the Chilimo forest.

Currently, most of the existing natural forests are administered through a Participatory Forest Management approach (PFM). Evidence from recent studies showed that this approach could not be able to provide adequate income for the forest-based communities (SUTCLIFFE; WOOD; MEATON, 2012). The authors suggested the importance of searching for an alternative to increasing the income of the local communities on a sustainable basis. Hence, the findings of this study i.e., cutting cycle, minimum logging diameter, and harvestable volume of wood could be used as inputs for policymakers to develop wood harvesting regulations, modify the current PFM approach, and enhance the local community's income from the Chilimo Dry Afromontane Forest. Sustainable timber production could generate incentives for the forest managing community, generate employment for the wider community, and help Ethiopia meet its growing national wood demand and reduce import dependence. In this study, we developed a unique procedure by combining the population structure with the diameter growth rate and determining the sustainability of timber harvesting from the Chilimo Dry Afromontane Forest considering the J. procera tree population. The performance of the method could be improved by increasing the data from other Afromontane forests. Future efforts should focus on exploring the potential of other timber tree species such as *Podocarpus falcatus*, *Hagenia abyssinica, and* Olea cuspidata ssp. africana from the Afromontane forests and ensure domestic wood production.

The timber harvesting practice should be planned in detail and strictly follow the principles of the Reduced Impact Logging (RIL) method. Various studies reported that RIL enables to maintain biodiversity and carbon storage (BERRY; PHILLIPS; LEWIS; HILL *et al.*, 2010; GRISCOM; ELLIS; BURIVALOVA; HALPERIN *et al.*, 2019; MILLER; GOULDEN;

HUTYRA; KELLER et al., 2011; PUTZ; ZUIDEMA; SYNNOTT; PEÑA-CLAROS et al., 2012; SASAKI; ASNER; PAN; KNORR et al., 2016), and is promoted for timber production from tropical forests (PUTZ; SIST; FREDERICKSEN; DYKSTRA, 2008; VIDAL; WEST; PUTZ, 2016). It incorporates conducting surveys, employing directional felling, planning skid trails, and using climber-cutting methods (SIST; NOLAN; BERTAULT; DYKSTRA, 1998). Generally, RIL can reduce the overall damage to the remaining forests (BERTAULT; SIST, 1997), thereby promoting better stand development. In this study, we consistently used the average diameter growth rate for the entire simulation period. However, previous studies showed that trees exhibited a higher growth rate after logging due to the canopy opening and reduced competition (GOURLET-FLEURY; MORTIER; FAYOLLE; BAYA et al., 2013; PEÑA-CLAROS; FREDERICKSEN; ALARCÓN; BLATE et al., 2008; SCHWARTZ; LOPES; MOHREN; PEÑA-CLAROS, 2013). This would result in higher yields than projected in our simulation. Hence, it is very important to incorporate the observed growth change due to logging and update the simulation in the future. Various studies have indicated that the amount of wood that can be harvested in the future can be improved in response to the different silvicultural treatments after the initial logging i.e., the liberation of potential crop trees from lianas and girdling of inferior species, enrichment planting of the desired trees (DE GRAAF; POELS; VAN ROMPAEY, 1999; PEÑA-CLAROS; FREDERICKSEN; ALARCÓN; BLATE et al., 2008). Hence, we recommend the timber harvesting practice should be supported with various types of silvicultural treatments that enhance the growth of the remnant trees and guarantee a sustainable harvest from the Chilimo forest.

5 Conclusions

Our studies indicated that the *J. procera* tree population has adequate structure and outgrowth by diameter size class that justifies continued timber management. The Chilimo forest has great potential and should be explored for timber production. This will enable the country to partly meet the national wood demand as well as diversify the source of income for the local communities. The simulation result revealed that the initially harvestable volume of wood and volume increments was considerably varied among the evaluated minimum logging diameters and cutting cycles. Generally, the total harvestable volume of wood will decrease with increasing the minimum logging diameter. However, increasing the cutting cycle length will increase the total harvestable volume of wood but will reduce the annual increment. Among the evaluated harvesting scenarios, the 40 cm MLD and a 15-year cutting cycle have been shown to provide the highest harvestable volume of wood (22 m³ ha⁻¹) and volume increments

(1.42 m³ ha⁻¹ yr⁻¹). Additionally, this scenario allows for the harvesting of 9% of the standing *J. procera* trees while maintaining a larger proportion (91%) of the existing standing trees in the forest. The suggested management options will enable policymakers to develop appropriate monitoring regulations that guide timber harvesting from Dry Afromontane forests.

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7 General conclusion

Juniperus procera tree populations has an inverted J-shape diameter distribution pattern which indicates a healthy regeneration status in the Chilimo forest. The developed models (hypsometeric, setm volume, and biomass) enabled to estimate the missing height of trees, standing volume of wood, and biomass stock in the Chilimo forest. *Juniperus procera* has a mean density of 183 stems ha⁻¹, a total basal area of 12.1 m² ha⁻¹, and a standing volume of wood 99 m³ ha⁻¹. This indicates that the forest is overstocked and some sort of intervention, such as wood harvesting, is necessary to maintain a balanced and suatainable forest structure. Among the evaluated wood harvesting scenarios, the combination of 40 cm minimum logging diameter and 15 years cutting cycle sustainabily provided 22 m³ ha⁻¹ of wood from *Juniperus procera* tree population. This will enable the country to partly meet the growing wood demand gap through domestic wood production. Furthermore, the information generated by this study including the diameter growth rate, minimum logging diameter and cutting cycles will help policy makers to develop wood harvesting regulations for the respected tree species which is abscent in Ethiopia.

Supplementary

Table S1: Scientific name, frequency, density (No ha⁻¹), basal area (m² ha⁻¹), and IVI (Importance Value Index) of all tree species (dbh > 2 cm) from the Chilimo forest.

No	Scientific name	Frequency	Density	Basal area	IVI
1	Juniperus procera Endl.	137	182.8	10.3	47.4
2	Olea europaea L, subsp, cuspidata	109	81.3	4.0	30.2
3	Olinia rochetiana A, Juss.	108	98.5	2.4	28.0
4	Maytenus gracilipes (Welw, Ex Oliv) Exell	93	117.3	0.2	22.3
5	Podocarpus falcatus (Thunb.) Mirb.	83	73.7	1.2	20.6
6	Scolopia theifolia Gilg,	61	69.5	0.4	14.9
7	Rhus glutinosa Hochst, ex A, Rich,	65	32.5	0.4	14.5
8	Osyris quadripartita Decne	62	33.3	0.1	13.5
9	Allophylus abyssinicus (Hochst) Radlk,	50	19.6	0.6	11.4
10	Dovyalis abyssinica (A, Rich) Warp,	45	21.2	0.0	9.6
11	Nuxia congesta R,Br, ex Fresen	43	18.5	0.3	9.5
12	Maytenus addat (Loes) Sebsebe	33	12.5	0.2	7.3
13	Ekebergia capensis Sparrm,	30	5.8	0.2	6.5
14	Bersama abyssinica Fresen,	27	5.1	0.0	5.6
15	Prunus africana (Hook, f) Kalkm,	22	5.1	0.4	5.1
16	Apodytes dimidiata E, Mey, ex Arn,	19	4.1	0.2	4.2
17	Erica arborea L,	15	3.6	0.0	3.1
18	Sideroxylon oxyacanthum Baill,	14	5.0	0.1	3.0
19	Myrica salicifolia Hochst, ex A, Rich,	13	2.7	0.1	2.8
20	Buddleja polystachya Fresen,	12	3.1	0.0	2.5
21	Cassipourea malosana (Bak) Alston,	9	2.1	0.0	1.9
22	Hagenia abyssinica (Bruce) G,F, Gmel,	7	1.1	0.2	1.7
23	Calpurina aurea (Aiton) Benth,	7	1.5	0.0	1.4
24	Rhamnus staddo A. Rich.	6	1.1	0.0	1.2
25	Pavetta abyssinica Fresen	5	0.6	0.0	1.0
26	Ilex mitis (L) Radlk,	3	1.4	0.2	1.0
27	Celtis africana Burm, f.	2	2.1	0.1	0.6
28	Ficus sur Forssk,	2	1.5	0.1	0.5
29	Olea wechesteria	2	0.7	0.0	0.5
30	Schefflera abyssinica (Hochst, ex A, Rich) Harms	1	0.1	0.0	0.2

31	Dombeya torrida (G,F,Gmel) P, Bamps	1	0.1	0.0	0.2
32	Rosa abyssinica Lindley	1	0.2	0.0	0.2
33	Croton macrostachys Del,	1	0.1	0.0	0.2
34	Pittosporum viridiflorum Sims	1	0.1	0.0	0.2
35	Myrsine melanophloeos (L) R, Br,	1	0.1	0.0	0.2
36	Carissa spinarum L,	1	0.1	0.0	0.2
37	Rhamnus prinoides L'Herit.	1	0.1	0.0	0.2

MLD	CC (Years)	Variables -	Values						
(cm)			Initial	1	2	3	4	5	6
		Harvestable volume	80	25	27	22	21	20	20
	15	Increment	5.3	1.7	1.8	1.5	1.4	1.3	1.3
	15	Harvested trees	28	14	15	12	11	11	11
		Remnant trees	72	86	85	88	89	89	89
	20	Harvestable volume	80	36	34	29	28	28	28
		Increment	4.0	1.8	1.7	1.4	1.4	1.4	1.4
		Harvested trees	28	19	17	15	14	14	14
		Remnant trees	72	81	83	85	86	86	86
		Harvestable volume	80	45	39	35	34	34	34
30	25	Increment	3.2	1.8	1.5	1.4	1.4	1.4	1.4
50	23	Harvested trees	28	23	19	17	17	17	17
		Remnant trees	72	77	81	83	83	83	83
		Harvestable volume	80	53	43	41	40	40	40
	30	Increment	2.7	1.8	1.4	1.4	1.3	1.3	1.3
	50	Harvested trees	28	26	21	20	20	20	20
		Remnant trees	72	74	79	80	80	80	80
		Harvestable volume	80	62	50	48	48	48	40
	35	Increment	2.3	1.8	1.4	1.4	1.4	1.4	1.2
	55	Harvested trees	28	29	23	22	22	22	22
		Remnant trees	72	71	77	78	78	78	78
		Harvestable volume	61	18	27	27	24	22	22
	15	Increment	4.1	1.2	1.8	1.8	1.6	1.5	1.4
		Harvested trees	19	7	11	11	10	9	9
		Remnant trees	81	93	89	89	90	91	91
		Harvestable volume	61	26	35	31	29	28	27
	20	Increment	3.1	1.3	1.7	1.6	1.4	1.4	1.4
	20	Harvested trees	19	10	14	12	11	11	11
40		Remnant trees	81	90	86	88	89	89	89
10		Harvestable volume	61	33	43	37	35	35	35
	25	Increment	2.4	1.3	1.7	1.5	1.4	1.4	1.4
		Harvested trees	19	13	16	14	13	13	13
		Remnant trees	81	87	84	86	87	87	87
		Harvestable volume	61	43	48	42	41	41	41
	30	Increment	2.0	1.4	1.6	1.4	1.4	1.4	1.4
	50	Harvested trees	19	16	18	16	15	15	15
		Remnant trees	81	84	82	84	85	85	85

Table S2: Simulated harvestable volume of wood (m³ ha⁻¹), volume increments (m³ ha⁻¹ yr⁻¹), no of harvested trees (%), and remnant trees (%) for the evaluated harvesting scenarios.

		Harvestable volume	61	51	52	47	46	46	46
	25	Increment	1.7	1.5	1.5	1.3	1.3	1.3	1.3
	35	Harvested trees	19	19	19	17	17	17	17
		Remnant trees	81	81	81	83	83	83	83
		Harvestable volume	42	15	18	23	23	22	21
	15	Increment	2.8	1.0	1.2	1.5	1.6	1.5	1.4
	15	Harvested trees	10	4	5	7	7	7	6
		Remnant trees	90	96	95	93	93	93	94
		Harvestable volume	42	19	26	29	28	26	26
	20	Increment	2.1	1.0	1.3	1.5	1.4	1.3	1.3
	20	Harvested trees	10	6	8	9	8	8	7
		Remnant trees	90	94	92	91	92	92	93
		Harvestable volume	42	24	33	34	31	30	30
50	25	Increment	1.7	0.9	1.3	1.4	1.3	1.2	1.2
50	23	Harvested trees	10	7	10	10	9	9	9
		Remnant trees	90	93	90	90	91	91	91
		Harvestable volume	42	28	39	37	35	34	34
	20	Increment	1.4	0.9	1.3	1.2	1.2	1.1	1.1
	30	Harvested trees	10	8	11	10	10	10	10
		Remnant trees	90	92	89	90	90	90	90
		Harvestable volume	42	33	43	39	38	37	37
	25	Increment	1.2	0.9	1.2	1.1	1.1	1.1	1.1
	55	Harvested trees	10	9	12	11	11	11	11
		Remnant trees	90	91	88	89	89	89	89
		Harvestable volume	23	8	9	11	13	13	13
	15	Increment	1.5	0.5	0.6	0.7	0.8	0.9	0.9
	15	Harvested trees	5	2	2	2	3	3	3
		Remnant trees	95	98	98	98	97	97	97
		Harvestable volume	23	10	12	15	16	16	15
	20	Increment	1.2	0.5	0.6	0.7	0.8	0.8	0.8
	20	Harvested trees	5	2	3	3	4	4	3
		Remnant trees	95	98	97	97	96	96	97
60		Harvestable volume	23	11	18	21	21	20	20
	25	Increment	0.9	0.5	0.7	0.9	0.9	0.8	0.8
	23	Harvested trees	5	3	4	5	5	5	4
		Remnant trees	95	97	96	95	95	95	96
		Harvestable volume	23	16	22	25	23	23	22
	30	Increment	0.8	0.5	0.7	0.8	0.8	0.8	0.7
	50	Harvested trees	5	3	5	5	5	5	5
		Remnant trees	95	97	95	95	95	95	95
	35	Harvestable volume	23	18	26	27	25	25	25

Increment	0.7	0.5	0.7	0.8	0.7	0.7	0.7
Harvested trees	5	4	6	6	6	5	5
Remnant trees	95	96	94	94	94	95	95



Figure S1: Population structure of selected tree species from the Chilimo forest