Modelling tree growth rates across southern African woodlands: A hierarchical mixed-effects approach

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Abstract

Ecosystem products such as fuel, timber, food, and water, coupled with services such as regulation of the climate, mitigation of floods, and maintenance of soil fertility, provided by southern African woodlands (SAWs) play a central role in the livelihoods of millions of both rural and urban dwellers. However, the ability of these woodlands to meet future demand is threatened by their rapid deforestation and degradation. This has led to a proliferation of campaigns to champion their sustainability especially given uncertainties inherent in global change. Key to their sustainability is disentangling how fast trees grow across the region. Growth rate studies can aid policy formulations that herald management of existing woodlands. For example, if growth rates are known for a given stand, it can enable the prediction of maximum sustainable yield of fuel or timber, and how that changes with edaphoclimatic fluctuations. Although investigating growth rates is a continuing concern within sustainability science, studies focusing on the broader southern African region are still limited, leading to major uncertainties on the determinants of tree growth rates across SAWs.

Understanding tree growth rates require scientists to unravel the biophysical interactions that influence growth. This information can then be used to develop spatial-temporal predictive models. In this thesis, I combine data from permanent sample plots (PSPs), remote sensing products, and modelling techniques to contribute towards deepening our current understanding of tree growth rates and sustainable harvesting rates across SAWs. The PSP data I use is the subcontinent's largest growth dataset and spans 27 years (1991 – 2018) with 38,276 individual trees on 223 permanent sample plots (PSPs) in 8 countries across southern Africa.

Results show a mean (±SEM) diameter increment of 1.62 ± 0.3 mm yr^{-1} across the region, with a substantial site-to-site variation. The hypothesised drivers of growth rates variation such as soils and climate had little effect at the regional level, although plot-level tree basal area (a proxy for tree-tree competition) consistently reduced growth rates. Examining the determinants of growth for each species, however, revealed strong and often contrasting effects of soils, climate, tree size, and fire. A continuum of responses across species emerges, with contrasting patterns between miombo woodland dominants such as *Brachystegia* and open savanna species. In the faster-growing miombo dominant group, growth increased with stem size, on poor soils, and was less affected by reduced water availability and seasonality. The open savanna group exhibited the opposite trends, growing relatively faster on good soils and in wetter conditions. These findings challenge conventional understanding of the determinates of tree growth in savannas, and suggest distinct controls in different types of savanna, and thus distinct responses to global change. The observed widespread effect of tree-tree competition may play an important, but hitherto neglected, role in determining community composition and sustaining tree-grass coexistence. It is also likely to moderate the current increase of trees in savanna systems, suggesting the globally important C sink in African savannas is unlikely to be sustained.

When I assessed basal area increment (BAI) with the aim of estimating growth rates across unmeasured areas of SAWs, I found BAIs ranging between 0.07 and 0.7 with an estimated regional mean of 0.35 m^2/ha/year. I further found that BAI was positively related to rainy season length (RSL) but was negatively affected by climatic water deficit (CWD), with some other factors also playing a more minor role. Considering that this study covered a wide environmental gradient, the ability of the selected model to predict growth on an independent dataset with a correlation coefficient (*R*) of 0.8, a root mean square error (RMSE) of 0.01 m^2/ha/year, a RMSE-observations standard deviation ratio (RSR) of 0.7, a percent bias (PBias) of 7.8%, and a Nash-Sutcliffe Efficiency (NSE) of 0.5 between observations and predictions suggests that the model provides practical usability in predicting BAI for sustainable woodland management across unmonitored areas of SAWs. Model predictions across unmonitored areas of SAWs were found to range between 0.07 and 0.7 with an estimated regional mean of 0.35 m^2/ha/year and were consistent with previous literature. By extension, the model has demonstrated the potential to contribute towards deepening our understanding of woodland dynamics across unmonitored areas of SAWs. It is notable however that the model failed to predict with a 1:1 precision therefore, caution needs to be applied in its use. In particular, its skill can be improved by the use of higher resolution ground-based PVs and further plots. The predicted BAI across unmeasured areas can be used to support the analyses of woodland structures, estimation of carbon stocks, and overall economic assessments of woodland policies for sustainable management options.

In terms of sustainable harvesting rates, I found a mean annual increment (*G*) of 0.64 ±0.1 m^3/ha across the region. I then adopted an annual allowable cut (AAC) of 80% of the *G* to ensure sustainability in both ecological and economic terms. I found a mean AAC of 0.51 ±0.1 m^3/ha with a range of 0 – 7.4 m^3/ha/year across the region. It is notable however that the distribution of AACs is very skewed, with most in the dataset well below 1 m^3/ha/year, and a few outlier plots (4 to be specific) above 3 m^3/ha/year. At this AAC level, recovery scenarios were found to surpass the volume at the beginning of the inventory within Year 1. At the individual stem level of the 1,025 large trees studied, results show a mean annual diameter growth rate of

1.5 ±0.3 mm translating into a harvest cycle of 233 ±46 years when a widely accepted harvest size of 35 cm is used thus implying that on a given stand with 233 trees, one tree can be harvested every year. In this study, the set AAC was found to suggest that there is potential for any PSP to recover and become resilient as long as strict adherence to the AAC is followed. I, therefore, conclude that adherence to AAC is a pivotal part of good woodland management because it is the primary safeguard against under or over cutting. This is especially true because by harvesting only large trees as prescribed by the AAC, trees in smaller diameter classes are allowed to graduate to higher classes. Further, the process supports the regeneration of large trees which will in the long term ensure woodland sustainability.

Lay Summary

A cursory inspection of the literature reveals critical knowledge gaps in the understanding of tree growth rates across the broader southern African region. Growth rates are of interest because they enable us to better understand the structural dimensions of woodlands. Understanding the complexity of tree growth dynamics, especially because of the uncertainties introduced by climate and global change, is vitally important because millions of rural and urban dwellers rely on these woodlands for fuelwood, timber, food, and water. These woodlands also provide services such as regulation of the climate, mitigation of floods, and maintenance of soil fertility. The major drawback in tree growth studies is that southern Africa is a highly data-scarce region. In this thesis, my overall aim was to develop statistical models and use them to examine growth rates in measured areas, predict across unmonitored areas, and propose sustainable harvesting rates using a new dataset that has been generously made available by the Socio-Ecological Observatory for Southern African Woodlands (SEOSAW; https://seosaw.github.io/).

Models suggest that trees are growing slowly. Factors such as soils and climate that have previously been thought to be the main determinants of growth were found to have little effect at the regional level while competition for resources between trees was found to consistently suppress tree growth rates. Basal area increment, a common way of describing changes in stand density was found to be positively related to rainy season length (RSL) but was negatively affected by climatic water deficit.

In terms of sustainable harvests, findings suggest that there is potential for any given stand to recover and become resilient so long a harvest of 80% relative to mean annual growth rates is maintained. I, therefore, conclude in this thesis that a shift from the current unrestricted harvesting that is practiced over much of the region is necessary to ensure sustainability. Close monitoring and intensive management are equally essential if the productivity potential of SAWs is to be achieved.

Declaration of Authorship

I hereby declare that this thesis and the work embodied in it are my own and have not been submitted for any other degree at the University of Edinburgh or any other institution. I further certify that all material that is not my own is duly acknowledged by appropriate referencing.

Brigadier Libanda

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Acknowledgements

When I started this Ph.D., developing statistical models was nothing but a daunting task because I did not even know how to load data in R. 4 years later, I can confidently say I now know how to load data in R, and this would not have been possible without the support and guidance that I received from many people.

First, I will forever remain deeply indebted to my Supervisors Casey M. Ryan and Ed T.A. Mitchard for their expert guidance, patience, willingness to set aside time from their obvious busy schedules to respond to my emails, accommodating me in their offices, keeping me motivated, and for their overall support during my entire Ph.D. program. Undoubtedly, without the supportive environment they created, I would have given up in my first semester!

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To my family, thank you for a strong support system.

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List of Abbreviations

AAC	Annual allowable cut
AGB	Above ground biomass
AIC	Akaike information criterion
ALS	Airborne laser scanning
BA	Basal area
BAI	Basal area increment
CHIRPS	Climate Hazards Group InfraRed Precipitation with Station data
CWD	Climatic water deficit
DBH	Diameter at breast height
DJF	December - February
DRC	Democratic Republic of Congo
DS	Drought stress
EV	Explanatory variable
FAO	Food Agriculture Organization
FEWS	Famine Early Warning System
FRIM	Forestry Research Institute
G	Growth
GLMM	Generalized linear mixed model
IPCC	Intergovernmental Panel on Climate Change
ITCZ	Inter Tropical Convergence Zone
LiDAR	Light Detection and Ranging
LOSum	Length of growing season
MAI	Mean annual increment

MAP	Mean annual precipitation
MAT	Mean annual temperature
N	Soil Nitrogen
NCAR	National Centre for Atmospheric Research
NCEP	National Centres for Environmental Prediction
NIAS	Northern Institute of Applied Science
NSE	Nash-Sutcliffe efficiency
P	Soil phosphorus
Pbias	Percent bias
PCA	Principal component analysis
pH	Soil pH
POM	Point of measurement
PSP	Permanent sample plots
PV	Predictor Variable
R	Correlation coefficient
RFI	Rainfall intensity
RMSE	Root mean square error
RQs	Research questions
RSL	Rainy season length
RSR	RMSE-observations standard deviation ratio
RSS	Residual sum of squares
SADC	Southern African Development Community
SAWs	Southern African woodlands
SD	Standard deviation
SEM	Standard error of the mean

SEOSAW	Socio-Ecological Observatory for Southern African Woodlands
SLA	Specific leaf area
Spp	Species
TAFORI	Tanzania Forestry Research Institute
TSS	Total sum of squares
UNFPA	United Nations Population Fund
VIFs	Variance inflation factors
WSS	Within-cluster sum of squares
ZFC	Zimbabwe Forestry Commission

CHAPTER I

CHAPTER 1: GENERAL INTRODUCTION

1.1 Background

Southern African woodlands (SAWs) have been the subject of much systematic investigation because of their hyper-diverse ecosystem products and services. Many scientists (e.g., Campbell, 1996; Mitchard *et al.,* 2009; Ryan *et al.,* 2016; Mugasha *et al.,* 2016; De Cauwer *et al.,* 2017; Pritchard *et al.,* 2019) and policy makers (Anderson *et al.,* 2006; Dewees *et al.,* 2010) agree that the woodlands of southern Africa provide ecosystem products and services essential for the welfare of the rural majority. In Urumwa Forest Reserve, for example, Njana *et al.,* (2013) found that the woodlands provide 42% of total household income, 28% of non-monetary income, and 59% of monetary income for the rural populace. In an earlier study, Nhira and Fortmann, (1993) found it befitting to refer to the woodlands as *socio-forests* given the large populace that live in and depend on these woodlands. This name tag was also found useful later by Ryan *et al.,* (2016) and most recently by Pritchard, (2017).

SAWs also provide habitation for mammals, birds, and insects. Many rare and endangered species depend on these woodlands (Alexander *et al.,* 2010; Trytsman *et al.,* 2020; Grab and Nash, 2020). Their rich endemism is well documented with several plant species, birds, and invertebrates (Tripathi *et al.,* 2019; Darbyshire *et al.,* 2020).

The woodlands also serve as a cultural heritage and are regarded as places of spiritual importance for rural dwellers (Ribeiro *et al.,* 2021); some specified trees and sites are considered sacred and thus, conserved for cultural reasons (Morris, 1970). The significance of SAWs extends to hydrology especially because the region is the source of Africa’s fourth longest river, the Zambezi (Beilfuss, 2001). Therefore, the quality and quantity of the Zambezian waters depend on land use activities in the woodlands (Campbell, 1996). In fact, land-use activities are generally regarded as one of the key determinants of changes in any hydrological system (Huang *et al.,* 2013). The water quality of rivers, streams, or lakes may degrade following changes in land cover, land use, and the general increase in anthropogenic activities (Ngoye and Machiwa, 2004; Bai *et al.,* 2010).

The woodlands also play an important role in the carbon cycle. The role of trees in the global carbon cycle is well documented (IPCC, 2001; Taub, 2010). Carbon is a chemical element essential for life on earth. The carbon cycle involves the inter-movements of carbon among different spheres of the earth including the atmosphere, water bodies, trees (and other living things), and inanimate things (e.g., rocks and sediments). The carbon cycle is founded on the processes of photosynthesis and respiration. In general, through photosynthesis, carbohydrates are created and sequestered in trees to form biomass. These carbohydrates are later broken-down during respiration thereby releasing CO_2 back to the atmosphere. The processes of photosynthesis and respiration are described in detail by the Northern Institute of Applied Science (NIAS) and are available here: https://www.nrs.fs.fed.us/niacs/forests/carboncycle/. In recent studies, SAWs have also been shown to be powerful contributors to the global terrestrial carbon pool. For example, as part of the region, the miombo acts as an important carbon store holding ~18 – 24 Pg C (Ryan *et al.,* 2016). Further evidence suggests that taken together, tropical woodlands store 25% of global tree carbon (Pan *et al.,* 2011). It is also highly likely that tropical woodlands will become a source of carbon in the future because of ongoing woodland loss and to some extent, the effect of climate change on the capacity of the remaining woodlands to capture excess CO_2 (Mitchard *et al.,* 2018).

1.2 Statement of the problem and justification for the research

It is now well understood that while SAWs play an important role in human wellbeing and the carbon cycle, their ability to meet future demand of ecosystem products and services is threatened by external pressures such as deforestation and degradation (Nansikombi *et al.,* 2020; Rannestad and Gessesse, 2020; Sikuzani *et al.,* 2020). I use degradation here to mean human destruction of some trees, but not to the extent that the woodland is no longer classed formally as forest[1]. Degradation is especially prevalent in woodlands because millions of people depend on and live in the woodlands, not just near them as with tall trees.

Early examples of research into deforestation include Agyei, (1998) who documented that in the 1990s, global woodlands were reducing by ~15.4 million hectares per year which equates to a 0.8% annual deforestation rate. However, the rate of deforestation across SAWs greatly surpassed the 0.8% global annual figure owing to the over-dependence on fuelwood as a major source of energy (Agyei, 1998). With the aid of satellite radar data, new insight shows that the loss of SAWs aggravated by deforestation and degradation is −0.075 PgC yr^{-1} and −0.038 PgC yr^{-1} respectively (McNicol *et al.,* 2018). This is 3 - 6 times worse than previously estimated (McNicol *et al.,* 2018). The impact of degradation and deforestation on the economies of sub-Saharan countries is significant as governments and local communities risk losing a substantial source of revenue, fuel, food, medicine, and landscape/climate stabilising force in the future.

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[1] *The threshold used for 'forest' here is 10% canopy cover across most of the region (See: FAO, 2000; Wunder, 2003) thus degradation is the loss of canopy cover and happens before deforestation.*

The continued shrinkage of SAWs due to rapid degradation and deforestation may be amplified by their potential response to changes in precipitation, temperature, and fire regimes which would make them uniquely sensitive to climate and global change (Platts *et al.,* 2008; Naidoo *et al.,* 2013). This was also highlighted earlier in the work of Lesolle, (2012) who argued that the ongoing global warming will alter the phenology of certain tree species with potentially negative consequences for other ecosystem members and thus ecosystem functioning. Allen *et al.,* (2010) also observed that climate change is likely to exacerbate drought-induced mortality across the world including SAWs. All these threats call the future of SAWs into question and clearly show that the current business-as-usual trajectory of resource use, management, or the lack thereof, is unsustainable.

Growth, mortality, and regeneration rates are some of the factors that are important for the sustainability of SAWs (Muvengwi *et al.,* 2020; Njoghomi *et al.,* 2020; Njoghomi, 2021). Key among these factors is disentangling how fast trees grow as this enables modelers to predict the maximum sustainable yield of fuel or timber.

Understanding tree growth requires scientists to unravel the biophysical interactions that influence growth. Site- (e.g., precipitation, temperature, and soils) and tree-specific (e.g., species, functional traits, competition, stem damage, and diameter) variables are essential for the growth of trees (Toledo *et al.,* 2011; Bowers, 2017). Environmental variables are widely acknowledged as the main controls of tree growth especially because the reception of environmental signals is in the apical meristematic regions of tree stems (Hanover, 1980). For growth to occur, trees make their own food in the presence of water, sunlight, carbon dioxide, and soil nutrients. This process is well understood: it begins with the absorption of water from the roots by osmosis which naturally includes dissolved nutrients. The water thus transports the dissolved nutrients via the xylem to the leaves which then ‘feed’ the tree. The lack of water can, therefore, critically limit tree growth (Ryan *et al.,* 1997). In fact, many trees in drought-prone areas have been observed to experience defoliation, leaf scorch, and stunted growth when droughts occur, with such responses likely increasing chances of longer-term survival, but reducing growth in the short term (Bréda *et al.,* 2006; Sala *et al.,* 2010). In the long term, model projections show that there is a high likelihood of overall future reductions in rainfall, and climate change-driven droughts are likely to be more frequent and severe across southern Africa (Dunning *et al.,* 2018); this will potentially strain tree growth in the future.

Apart from droughts, climate change will have other cascading effects, especially because temperature slows photosynthesis at the temperatures normally experienced in SAWs (Trouet *et al.,* 2012) although may increase it during cold winters in the south, where photosynthesis might become temperature limited. Jacoby and D’Arrigo, (1997) further found evidence of this temperature effect in a tree ring study that also indicated a possible CO_2 fertilization effect which makes trees grow faster but also potentially leads to bush encroachment (Mitchard and Flintrop, 2013). Bush encroachment is a phenomenon that refers to the clampdown of grazeable grasses and herbs by encroaching tree species (Ward, 2005). This in turn threatens the livelihoods of pastoralists as it reduces the carrying capacity for livestock, and potentially also the food availability for wild herbivores. Pioneering studies to understand causes of bush encroachment have shown that removal of grass and herbs is mainly by overgrazing which allows water to percolate deeper and become available for woody plant growth (Walter, 1954). Recent understanding has also highlighted that bush encroachment can be a result of changes in fire management, land fragmentation, and rainfall (Mitchard and Flintrop, 2013; Stevens *et al.,* 2017).

Tree growth rate studies can be used to understand how fast the observed bush encroachment is happening (O'Connor, 2005; Ward, 2005; Stevens *et al.,* 2017). These studies can also aid in understanding African savanna function, and prediction of their future response to global change (Higgins *et al.,* 2000). By extension, results from tree growth studies can be used by forest managers to model future dynamics of growth. This information can then be utilised to maintain harvests and land-use conversions within the sustainable capacity of SAWs.

1.3 Aim and objectives

In this Ph.D., I aimed at using a 27-year (1991 – 2018) dataset from 223 PSPs dotted across 8 countries to assess tree growth rates across the broader southern African region. My findings will underpin management and strategic planning that aim to confine human activities within the sustainable capacity of southern African woodlands. Results will also highlight growth patterns and their dynamics at a broader scale than was previously possible. They will further give us a snapshot of future growth variations under global change and different management regimes. To achieve this aim, I developed hierarchical mixed-effects models and used them to answer the following important yet presently poorly understood research questions:

RQ1: How fast are trees growing across southern Africa and what are the main determinants of growth rates?

RQ2: How well can tree growth in unmonitored areas of southern Africa be predicted?

RQ3: How are the current dynamics of tree population structure and how can they be used in Combination with growth rates to determine sustainable harvesting rates on monitored PSPs across SAWs?

1.4 Overview of the study area

1.4.1 Structure and composition of southern African woodlands (SAWs)

Much of southern Africa is covered by savanna ecosystems (Mishra *et al.,* 2015). A savanna is a biome characterised by a mixture of woodlands and grasslands with trees being widely enough spaced that the canopy generally does not close (see Figure 1.1). This allows enough light to reach the ground thereby, supporting the flourishing of grasses and herbs (McPherson, 1997; Anderson *et al.,* 1999).

The largest biome of southern African savannas is the miombo (Mistry, 2000). This woodland type of savanna is covered mostly by trees from the legume family *Fabaceae*, and subfamily *Caesalpinioideae* (Campbell, 1996) whose renaming is detailed by Azani *et al.,* (2017). The dominance of these trees is the main distinguishing factor between the miombo and other African savannas (Gonçalves *et al.,* 2017). These woodlands cover between 2.7 and 3.6 million hectares of southern Africa (Ryan *et al.,* 2016); extending from Tanzania to the southern parts of Congo and also covering southern parts of Zimbabwe, Zambia Malawi, Angola, and Mozambique (Figure 1.1).

Southern African woodlands are generally punctuated by the occurrence of other types of savannas e.g., *Colophospermum mopane*. These are found especially in the low-lying areas of the Zambezi and Luangwa rivers (Tripathi *et al.,* 2019; Kampamba *et al.,* 2019).

Acacia is another type of savanna prevalent across SAWs, especially in Tanzania. Unlike the miombo, *Acacias* are found on nutrient-rich soils and areas with less rainfall (Campbell, 1996). Shallow wetlands (Dambos) are another distinct feature of southern African woodlands (Malaisse, 1974). These Dambos are seasonally waterlogged.

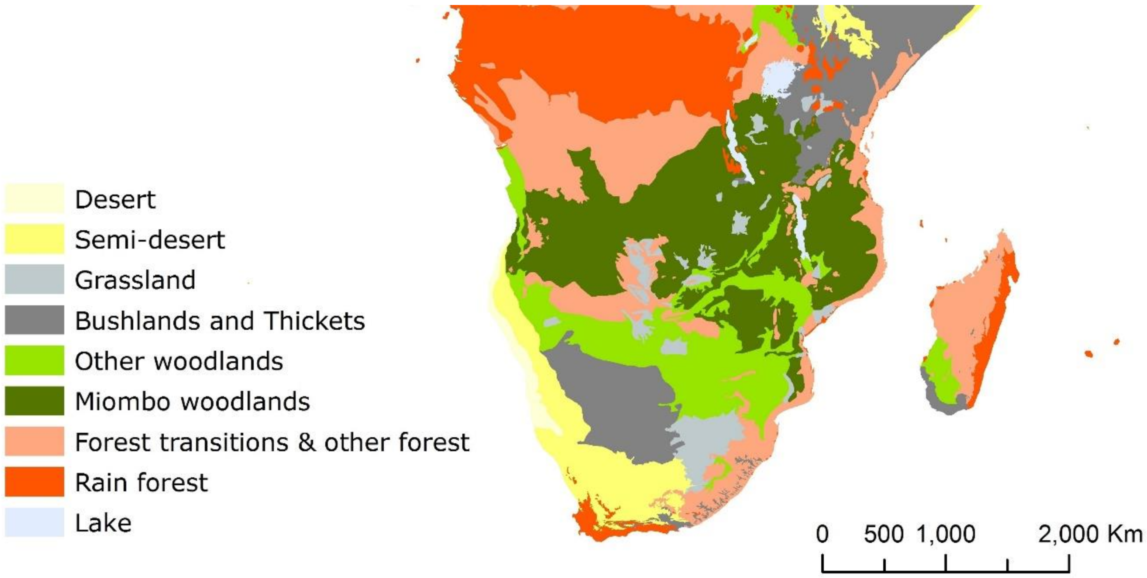

Figure 1.1: Map of vegetation across southern Africa. Modified from White, (1983)

1.4.2 Topography and climatology

Geographically, southern Africa is bounded by the Atlantic to the west and the Indian Ocean to the east. It covers the land mass from the equator to about 34º south (Reason, 2016). The topography over southern Africa (Figure 1.2) can be classified in general terms as a plateau. The highest points are observed over Lesotho, north-central parts of Namibia, Mount Moco area in Angola, and Kilimanjaro in Tanzania.

Much of the landmass in Mozambique is below 500 m making the country’s land area and parts of south-eastern Tanzania the lowest altitudes in the region (Reason, 2016).

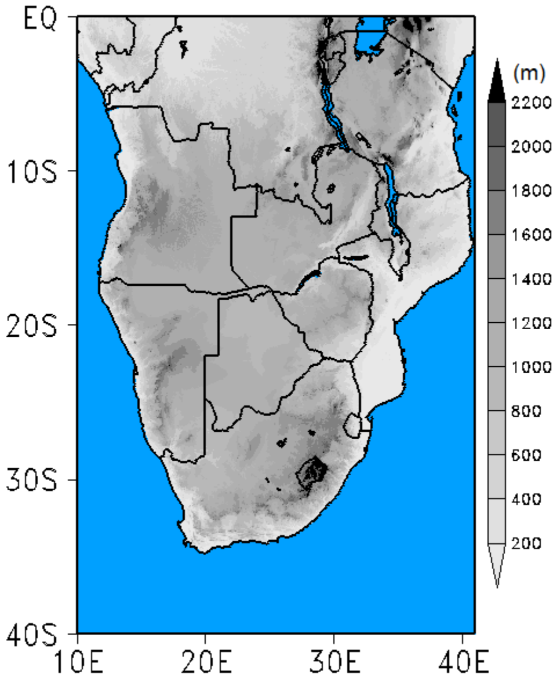

Figure 1.2: Topographical map (m) of southern Africa based on 15-arcsecond resolution (~500 m) SRTM15 Plus dataset (Becker *et al.,* 2009).

Southern Africa experiences a bimodal climate with distinct dry and wet seasons (Reason, 2016; Ryan *et al.,* 2016). The region is characterised by large variations of rainfall at both spatial and temporal scales (Mason and Joubert, 1997). *Generally,* the wet season commences at the end of October/beginning of November which coincides with the transitioning of the Inter-Tropical Convergence Zone southwards and it lasts until April of the following year when the ITCZ retreats northwards (Goddard and Graham, 1999). The ITCZ is a seasonally occurring low-pressure zone characterised by the convergence of the north-eastern trade winds, south-eastern trade winds, and the Congo air mass (Libanda *et al.,* 2016). The oscillating of the ITCZ northwards in April marks the close of the rainy season and the beginning of a cool and dry season which lasts from May to August when a hot season begins and lasts until November just before a new rainy season is ushered in (Reason, 2016).

Precipitation regimes across the region are also greatly influenced by the El Niño Southern Oscillation (ENSO). Overall, the region experiences drier than normal conditions when an El Niño event is in progress while wetter than usual conditions are associated with La Niña events (Richard *et al.,* 2000; Gore *et al.,* 2020). During the period 1991 – 2018, the highest precipitation amounts were received northwards towards the Equator (Figure 1.3a) while the highest temperatures were experienced in the desert areas of the Kalahari (Figure 1.3b). Although precipitation and temperature data for longer time frames is obtainable, the 1991 – 2018 period was chosen to reflect the timeframe for which tree growth rates data are available.

On average, the lowest temperatures are experienced during June/July while the highest temperatures are observed in September/October (Xulu *et al.,* 2020). However, given the little cloud cover during June/July (usually less than four oktas[2]), maximum temperatures are not very different from those experienced during September/October (Reason, 2016). In general, temperatures begin to rise around August until March the following year when they begin to drop. Average maximums are usually 25 to 30°C, except along coastal areas where cold air advection leads to temperatures of ~15°C (Reason, 2016).

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[2] *A unit used in expressing the extent of cloud cover, equal to one eighth of the sky.*

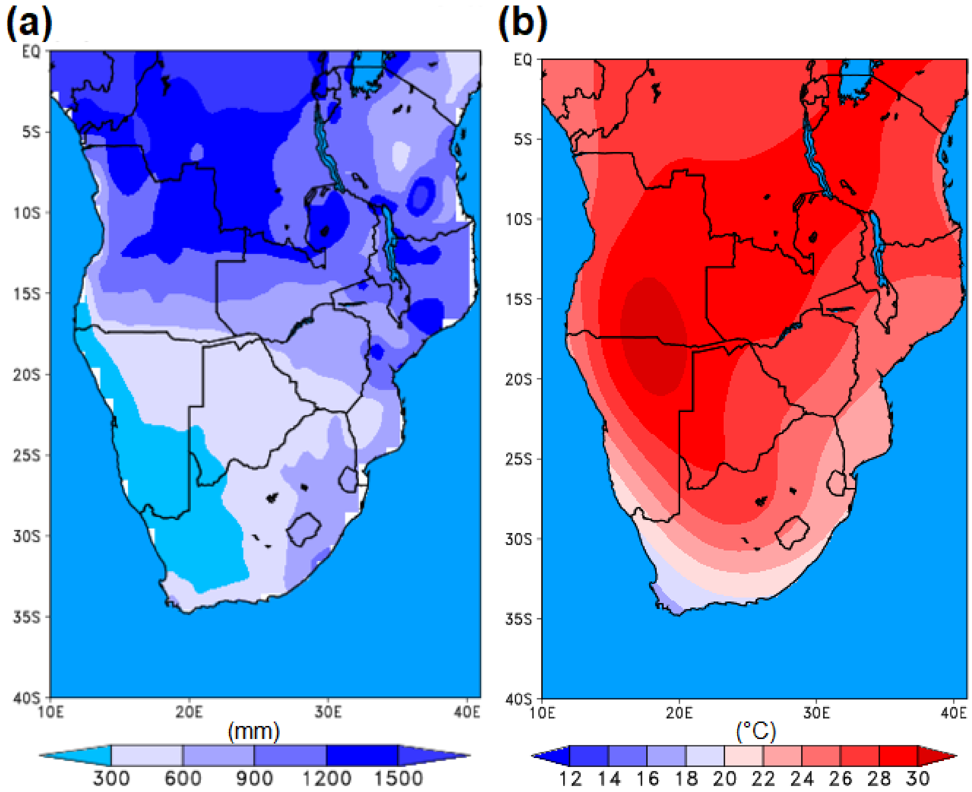

Figure 1.3a: Mean monthly precipitation (mm); **3b** mean monthly temperature (ºC) for the period 1991 – 2018 averaged over longitude 10ºE to 41ºE and latitudes 40ºS to the Equator; based on Kalnay *et al.,* (1996).

Exploratory analyses of how PSPs and sites sample environmental space indicate that while most PSPs have mean annual precipitation (MAP) ranging from 800 – 1000 mm and consistent with regional-level MAP, a few of them are generally drier with MAP well below 500 mm (Figure 1.4A). PSP level mean annual temperature (MAT) was also found to be consistent with regional-level MAT although some PSPs were observed to be generally colder (Figure 1.4B). To understand the infiltration and permeability to be expected at each PSP, the percentage of soil sand content present in the top 30 cm of the soil was explored and it was found that most PSPs average 55 – 65% with very few of them outside this range (Figure 1.4C). Further, fire disturbance was observed to be very variable from one PSP to another (Figure 1.4D).

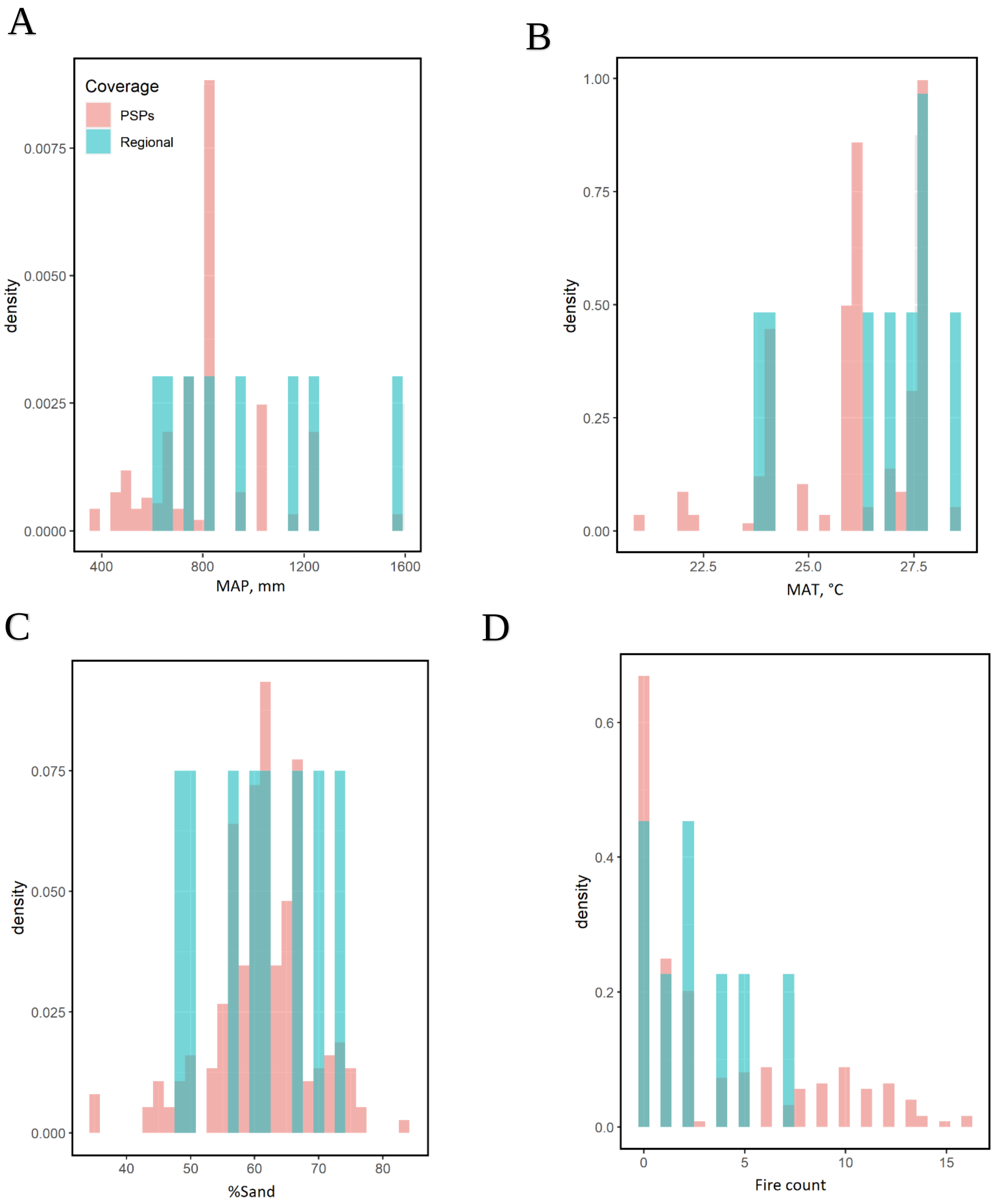

Figure 1.4: Environmental conditions across each PSP for **A)** MAP, mean annual precipitation **B)** MAT, mean annual temperature **C)** %sand and **D)** fire count. The red colour indicates PSP-level data while the blue colour shows regional averages.

Precipitation data was sourced from Funk *et al.,* (2015); temperature data was sourced from Harris *et al.,* 2020; Soil data was sourced from Hengl *et al.,* (2017); and fire count is based on Giglio *et al.,* (2015)

1.4.3 Description of study sites and sampling strategy

To study tree growth rates, different approaches can be used e.g., tree rings and repeated plot measurements (Stahle *et al.,* 1999; Sibona *et al.,* 2017). Tree rings are usually circular and are developed in the cross-section of woody plants on an annual cycle (Marcelo-Peña *et al.,* 2020). It is worth noting, however, that some studies have shown that in some regions in the tropics and depending on genera, tree rings may not be discernible or are not annual (Détienne, 1989). For this reason and based on data availability, I used the repeated plot measurement approach in this thesis. Further, I chose this approach because repeated plot measurements give insights into the structure and function of ecosystems that would otherwise be difficult or impossible to assess (Shugart *et al.,* 2010). Repeated plot measurements also provide an understanding of the dynamics of local and global woodlands (Pretzsch, 2009) in the face of a changing climate (IPCC, 2007). For example, through the use of plot data, a relationship, significant at the *α* 5%, was established for the first time between leaf attributes and the growth rate of trees grown under natural conditions in Australia (Prior *et al.,* 2004). Repeated plot measurements also provide data for comparative analyses with remote sensing techniques while at the same time providing useful information on what is necessary to be captured in models. This is evident from a recent study that used plot-based measurements to assess light detection and ranging (LiDAR) accuracy (Sibona *et al.,* 2017). Results showed that plot-based measurements improve airborne laser scanner (ALS) approximations. Plot measurements also play a central role in timber inventories whose end goal is to determine, with precision, the value of standing trees in any given plot. Depending on the purpose or geographical location, these plots vary in shape and size. However, the common ones are square and circular (Bonham, 2013).

To unravel patterns of growth rates, the repeated plot measurements used in this Ph.D. project are courtesy of SEOSAW, which is an acronym of Socio-Ecological Observatory for Southern African Woodlands (The SEOSAW Partnership, 2021). SEOSAW is an ongoing project whose main goal is to understand the response of southern African woodlands to global change. SEOSAW is founded on the premise of several hypotheses. For instance, it is hypothesised that the structure and ecosystem services provision of southern African woodlands is a result of an increase in extreme meteorological events, an upward trend in CO_2 concentrations, a change in fire regimes, and an increase in population, therefore, resource use. However, before SEOSAW, there was no regional network of plot-based measurements to provide evidence of these changes across southern African woodlands. The lack of a regional network hampered the validation of model predictions against plot-based datasets. For the first time, SEOSAW brought scientists (with their datasets) together and thus, constructed a regional network with 2269 plots in 11 countries across southern Africa. Some of this data (see Figure 1.5 for the spatial spread of plots) have been used in this Ph.D. project to explore variations of tree growth rates.

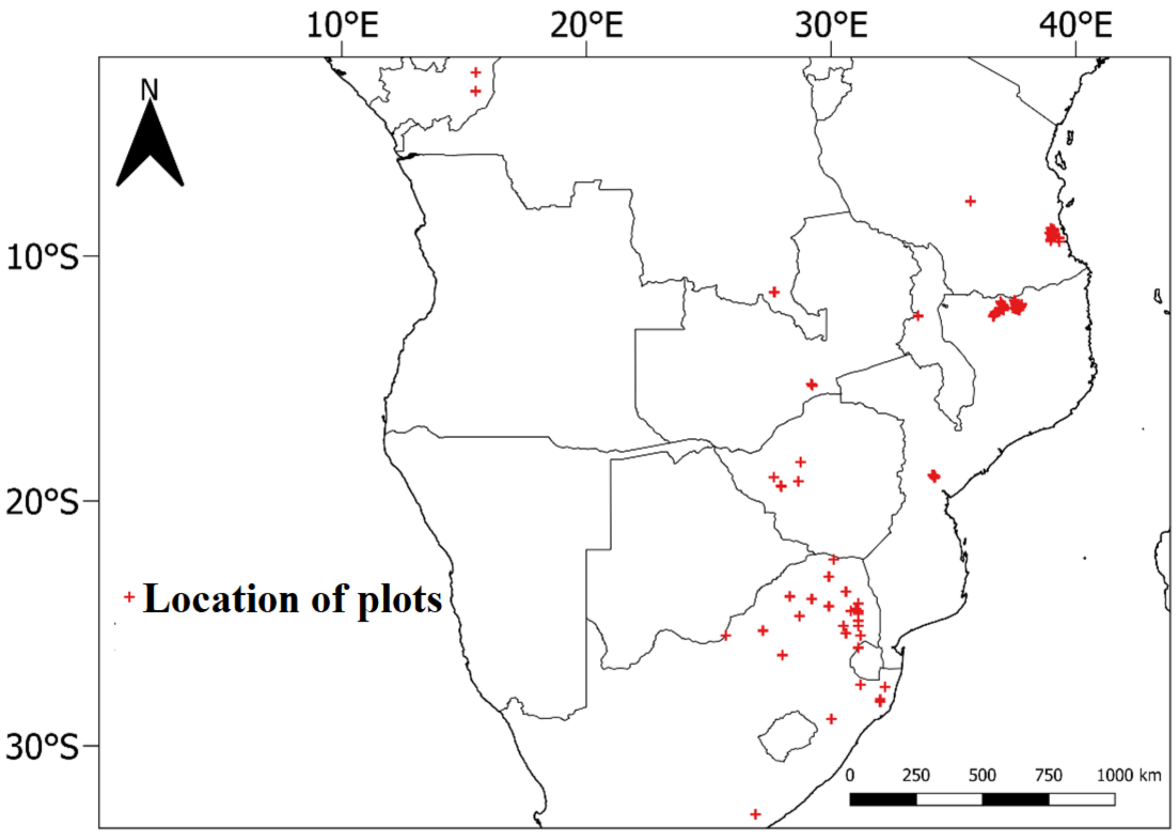

Figure 1.5: Geographical spread of the 223 permanent sample plots (PSPs) used in this study

To thoroughly capture the hierarchical nature of the dataset, I grouped the PSPs (Figure 1.4) into sites. In general, I considered all PSPs geographically located next to each other to be a single site as they experience similar climatic and edaphic conditions. This process resulted in the following 11 sites:

1) *Bateke, Congo:* The Bateke site in the central region of Congo is a protected reserve that was established in 1951 (King, 2008). This site has a forest cover of around 20% with the surrounding landscape being grassland or savannas with patchy tree cover.

Like most African savannas, the soils of this site have low fertility and are generally hundreds of meters of sand thus having very little ability to hold water. The patches where forests have been for a long time have better soils therefore, local communities utilize these patches of evergreen forests for agricultural activities. River valleys are mainly dominated by gallery forests. The topography can best be described as a plateau although hills and steep valleys are common features. The area has an equatorial climate and experiences annual temperatures of ~25ºC with mean annual precipitation of ~2800 mm (Walters, 2012). A detailed description of this site is given in the work Nieto-Quintano *et al.,* (2018). The data from this site were collected as part of a fire experiment, with early and late burn treatments applied to the plots: this was considered in this analysis.

2) *Katanga, DRC*: The Katanga site is on an 800-ha protected area of upper-Katanga (Muledi and Shutcha, 2016). Since its establishment in 2003, the site has been protected from fire and fuel-wood collection. On the Koppen-Geiger climate classification system (Geiger, 1954), the region is classified as humid sub-tropical (Cwa) with mean annual rainfall of 1200 mm and mean annual temperature of ~23ºC. Although the site is mainly a plateau, termite mounds, similar to those found in Nhambita are common. Baert *et al.,* (2009) documents that the soils across this region are mostly haplic and xanthic Ferralsols with low pH and nutrient content. The vegetation is mostly a mixed tropical dry woodland with a canopy height of 14 meters on average (Muledi and Shutcha, 2016). The dominant tree species are *Brachystegia spiciformis, Julbernardia, and Marquesia macroura*.

3) *Kilwa, Tanzania*: The Kilwa site is located in Kilwa District, south-eastern Tanzania. The annual average precipitation is 821 mm and the mean annual temperature is ~28ºC. The site is characterised by three main vegetation types: savanna, woodland, and dense woodland/forest (McNicol *et al.*, 2018). The vegetation type is mainly miombo woodlands with scattered areas characterised by coastal forests (Lilleso *et al.,* 2014; Kalonga *et al.,* 2017).
4) *Iringa, Tanzania*: The Iringa site was established by the Tanzania Forestry Research Institute (TAFORI; Mugasha *et al.,* 2016). Overall, the forest covers an area of 97 Km^2 of which the greater part (90 Km^2) is characterised by miombo woodlands with *Brachystegia, Julbernardia, Diplorhynchus, and Condylocarpon* being the dominant tree species. Summer temperatures are mostly ~29ºC and drop to ~12ºC in the winter. The region generally experiences dry-miombo-woodlands precipitation with an annual average of 629 mm (Shelukindo *et al.,* 2014).
5) *Kamatupa, Zambia*: The Kamatupa and Kankumba PSPs are located in Rufunsa ~110 KM east of the capital city of Zambia (Lusaka). Other literature (e.g., Chidumayo, 2013) may refer to the location as Chongwe, this is because districts were recently re-demarcated. The geography of the site is characterised by hills and punctuated by dambos (Chidumayo, 2013). The area is mostly underlain by schists, quartzites, and gneiss (Kashimu, 2010). Many studies have documented that soils from basement rocks are generally of low nutrient status (Bell, 1982; Chidumayo, 2013; Olakunle, 2015). It can therefore be inferred that this site is of nutrient-poor soils. Generally, the annual rainfall over the site averages 822.9 mm. Like most areas in the region (e.g. Kenneth Kaunda International Airport Meteorological Station), the site

receives its main rains from November – March (Hachigonta *et al.,* 2008; Libanda *et al.,* 2018). Temperatures are usually mild to hot averaging ~21ºC on annual scales (Chidumayo, 2013). The most dominant tree species on these sites include *Boehmii, Jubernardia globiflora, Isobelina anglensis,* and *Brachystegia manga.* Most of these trees are of known age as they are mainly regrowth following a clearing that occurred in 1971/72 and 1981/82. Details of this clearing are provided in the work of Chidumayo, (2013).

6) *Chimaliro, Malawi*: The Chimaliro site is a forest reserve located in Kasungu and Mzimba districts of Malawi (Abbot *et al.,* 1998). The establishment of the site was speared headed by the Malawi Department of Forestry (http://www.dof.gov.mw/) through its research branch i.e., the Forestry Research Institute (FRIM; https://www.frim.org.mw/; Walker *et al.,* 2004). The area experiences three distinct seasons: cool dry (May to August), hot (August to November), and wet (November – March; Libanda *et al.,* 2017). The mean annual precipitation over the area is ~1000 mm and is thus, a type of wet miombo woodlands (White, 1983). The woodland is generally open with 20 – 60% canopy cover and a grass understory (Walker *et al.,* 2004). The dominant species are *Julbernardia paniculate* and the genus *Brachystegia.* The common soils, especially across low-lying areas of the site are clay loam alluvium whereas higher elevation areas are generally covered by Lithosol soils (Abbot *et al.,* 1998).
7) *Nhambita, Mozambique*: The Nhambita site is in Gorongosa district of Sofala province. On the Koppen-Geiger climate classification system, Nhambita is classified as a tropical savanna (Aw) climate (Geiger, 1954). Nhambita receives its main wet season from November to March in which ~82% of the

precipitation is received (Ryan *et al.,* 2011). The soils are mainly sandy, low in nutrients, and derived from metamorphic, migmatitic gneiss, and granite rocks (Tinley, 1977; Ryan, 2009). Although the soils are mainly sandy, fertile loamy soils are common on termite mounds. Tinley, (1977) estimated that these moulds are at least one per hectare. *Caesalpinioideae, Acacia* and *Combretum* are the most common tree species in Nhambita. Like most woodlands, trees do not form a closed canopy at this site. This, therefore, encourages the flourishing of a continuous grass layer. The PSPs in Nhambita were established in 2004 under the principal lead of Professor Mat Williams of the School of Geosciences, University of Edinburgh. The PSPs were established as part of The Nhambita Community Carbon Project (Ryan, 2009).

8) *Niassa, Mozambique*: Niassa is a forest reserve geographically located in the northern part of Mozambique. The reserve is documented to be one of the largest conservation areas across southern African countries (Ribeiro *et al.,* 2008; Ribeiro *et al.,* 2017). Like most parts of Mozambique, Niassa is a low land at 200 – 600 meters above sea level. Geiger, (1954) classifies the climate of the Niassa region as tropical sub-humid. The annual average precipitation over the area is 900 mm (Ribeiro *et al.,* 2008). In the summer, the average temperature is 30ºC which plummets to ~20ºC in the cooler months of May, June, and July. In a study on the vegetation of Africa, White, (1983) identified *Brachystegia spiciformis, Boehmii,* and *Julbernardia globiflora* as the most dominant tree species in Niassa.
9) *Hwange, Zimbabwe*: All the PSPs (i.e., Kazuma, Fuller, Ngamo, Umzibani, Gwaai, and Gwaampa) at this site are generally located in the North-western

part of the country in Matebeleland. The soils are mostly nutrient-poor and have been likened to the Kalahari sand in previous literature. This type of soil has supported the dominance of *Baikiaea plurijuga, Pterocarpus angolensis, Guibourtia coleosperma, Brachystegia boehmii, Bukea Africana*, and *Amblygonocarpus andongensis* tree species (Campbell, 1996). The region can best be described as dry (White, 1983; Abdallah and Monela, 2007; Gonçalves *et al.,* 2017) with mean annual rainfall of only 650 mm. The rainfall pattern is similar to that of the Kamatupa site i.e., main rains received from November to March. Mean temperatures in the summer average 30ºC and plummet to ~10ºC in the cooler months of June and July (Campbell, 1996).

10) *Savanna, South Africa*: The South African PSPs were grouped into two sites based on their location and following the most recent classification of the terrestrial biomes in the country (Siyavula, 2019). All plots geographically located in the western parts of Limpopo, the northern parts of the Northern Cape and Free State, KwaZulu Natal, and the Northwest Province were classified as Savanna. This classification is generally characterised by hot and wet summers with little or no rain in the winter; soils are generally sandy.
11) *Grassland, South Africa*: all PSPs that are geographically located on the Highveld, with very variable mean annual precipitation (400 mm to 2000 mm) and soils characterised by rich fertile upper layers were classified as Grassland. The occurrence of frost in the cold winters is common. On this site, vegetation cover is mostly grass with scattered trees usually on riverbeds or hilly ground.

1.5 Definition of key terms

To clearly establish the position taken in this thesis, terms that are used repeatedly have been defined hereunder:

1) *Tree:* This is perhaps the most frequently used word in this thesis. Its use is meant to mean a plant whose shade is enough to sit in (Palgrave, 2002) and this includes any woody stem (e.g., lianas, baobabs, and climbers) with a diameter at breast (DBH) ≥5 cm;
2) *Diameter at breast height (DBH):* This is one of the most widely used dendrometric measurements and in this thesis, it is used to refer to the diameter of a tree trunk at 1.3 meters from the ground (Feldpausch *et al.,* 2011).
3) *Growth:* According to Atwell *et al.,* (2019) trees have six organs which can be grouped into vegetative (i.e., leaves, stems, and roots) and reproductive (i.e. flowers, fruits, and seeds) structures. Tree growth is used in this work to mean the increase in size of the vegetative structures, specifically, the diameter at breast height of the stem;
4) *Explanatory (EVs) and Predictor variables (PVs):* Traditionally, statistical modelling has been used for many years to develop and test theories in terms of explaining causality or prediction. Although it is expected that the difference between explaining and predicting should be obvious, Shmueli, (2010) contends that conflation between the two is common. In this work, to clearly illustrate the differences between modelling for an explanatory versus a predictive goal, the same variables have been named differently. EVs are

used when testing for causal hypotheses while PVs are used when predicting new growth rates;

5) *Fixed effects:* These are variables that are hypothesised to affect tree growth. This terminology is used interchangeably with EVs or PVs depending on the modelling goal as discussed in point 4;
6) *Random effects:* These are grouping variables;
7) *Indet:* This is used to denote unidentified species names i.e., species indeterminate (Sigovini *et al.,* 2016);
8) *Permanent sample plot (PSP):* These are marked areas that are remeasured over several years and the unique dataset generated is used to develop growth-and-yield models among other ecological inquiries. The models are then used to support sustainable woodland management decisions (Mesh, 2012; The SEOSAW Partnership, 2020);
9) *Basal area*: This term is used to quantify the total cross-sectional area of all stems on a permanent sample plot (PSP) at breast height, and is generally expressed in this thesis as per unit of land area (McElhinny *et al.,* 2005);
10) *Uneven-aged management:* This term is used to refer to the practice of managing a woodland by occasionally harvesting selected individual stems from any given PSP while preserving its natural form (Valkonen *et al.,* 2020);
11) *Biological diversity*: Whenever I use this terminology, I refer to the variety of life forms in any given PSP with a focus on the number of tree species (Guiguindibaye *et al.,* 2020);
12) *Competition:* I use competition in this thesis to refer to the everyday struggle between and among trees to obtain resources such as nutrients, sunlight, water, and general growing space (Zhang *et al.,* 2020);

13) *Deforestation:* While there are different definitions of deforestation, I use it in this thesis to mean the conversion of land use from woodland to non-woodland whether internationally or not (Doggart *et al.,* 2020).

1.6 Outline of the thesis

In Chapter 1, I introduce the research subject matter, its scope, and the overarching goal of the thesis. For peer-reviewed publication, and to allow a reader with limited time to dip into a self-contained study, I present Chapters 3 – 5 as standalone research papers, with their own research questions, materials used, experimental design, and statistical techniques used to analyse the data.

In Chapter 2, I aim at giving a systemic overview of the determinants of tree growth rates across the world and highlighting research gaps that will be filled by this thesis.

In Chapter 3, I aim at:

(i) quantifying growth rates of woodland trees across the sub-continent;

(ii) Investigating the sources of variation in tree growth rates;

(iii) Identifying fast and slow-growing species, and separating the effect of location from species identity i.e., are some species fast growing because they only occur in resource-rich environments?

In Chapter 4, I aim at addressing the data limitedness of the sub-continent by:

(i) Developing and validating a suitable model based on observed data;

(ii) Using the validated model to predict tree growth rates in unmeasured areas.

In Chapter 5, I aim at contributing to sustainable woodland management by using growth rates to determine an annual allowable cut (AAC) for timber species across southern African woodlands (SAWs).

In Chapter 6 I look back and bring everything together by giving the overall concluding remarks to the thesis, highlighting the key findings and recommendations.

1.7 Chapter summary

SAWs are under increasing external pressure from resource depletion, agricultural production, degradation, and climate change (Platts *et al.,* 2008). This thrusts their future into obscurity and uncertainty. Renewed interest in finding sustainable methods that will confine human activities to the sustainable capacity of SAWs has thus, been widely heralded with emphasis being placed on moving away from focussing only on the present and drifting towards understanding how they will potentially change in the future. The aim of this project is to contribute meaningful information on how fast trees have been growing in SAWs, together with discovering the factors that influence growth rates. My findings will underpin management and strategic planning that aim to confine human activities within the sustainable capacity of SAWs. Results will also highlight growth patterns and their dynamics at a broader scale than was previously possible. They will further give us a snapshot of potential future growth variations when management practices are instituted.

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CHAPTER II

CHAPTER 2: CLIMATIC AND BIOTIC CONTROLS OF TREE GROWTH: A SYSTEMATIC REVIEW

Abstract

There is a recognised need to understand what factors are associated with trees growing faster or slower, in order to increase both our ecological understanding of how the environment interacts with tree growth, but also to examine the potential influence of disturbance and climate change on longer-term tree health and ecosystem stability. The principal objective of this study was to investigate the current understanding of tree growth and identify research gaps, in advance of later chapters that use a novel widespread field dataset. Literature included here is not restricted to southern African woodlands (SAWs); other study areas outside southern Africa have also been considered to provide a holistic view. The evidence from this study suggests that while mean tree diameter growth rates vary across the world, over SAWs, they range from ~0.16 to ~0.66 cm/year. Five parameters are repeatedly identified as key drivers of tree growth across SAWs. In order of their importance, these parameters are: (1) mean annual precipitation (MAP), (2) Stem size, (3) December – February precipitation (DJF), (4) Species (spp), and (5) Mean annual temperature (MAT). While these factors are repeatedly mentioned as key drivers, scant data exists therefore, not all studies were data-supported and understanding of tree growth modulators across the subcontinent remains poorly resolved.

Keywords: tree growth rates, growth determinates, sustainability, southern Africa,

2.1 Introduction

Scientific evidence suggests that trees are among the most important natural resources required for human survival. They furnish us with oxygen (Nowak *et al.,* 2007), food (Östlund *et al.,* 2004), medicine (Eldeen *et al.,* 2005), shelter (McArthur, 1991), timber, fuel, and a horde of other products too numerous to mention. As global population projections for 2050 reach 9 billion (Vira *et al.,* 2015), matters of food security, nutrition, access to medicine, and shelter will dominate both scientific and policy inquiries. Trees play a central role in all these matters. Further, trees' role in taking in carbon, and thus limiting the impact of climate change, is understood to be vital (IPCC, 2018). It, therefore, follows that it is vitally important to humanity to understand how they grow and what drives their growth.

Trees are known to grow up to heights unreached by any other living organism on earth. The coastal redwood *Sequoia sempervierns* include the tallest known tree with a height of 115.6 meters and a diameter at breast height (DBH) of 8.9 m (Royal Forestry Society, 2015). In Africa, the *Entandrophragma excelsum (Meliaceae)* which is generally found in the valleys of Kilimanjaro, is one of the tallest trees reaching heights of 59.2 to 81.5 meters and 1.24 to 2.55 m diameter (Hemp *et al.,* 2017).

Like any other plant, trees need sunlight, nutrients, and ordinarily, water to grow. The leaves and overall crown of any given tree are especially useful in using sunlight, water, and nutrients for photosynthesis while the roots provide the transport mechanism for the absorption of water and nutrients from the soil. Several other parts of trees contribute to their growth. For example, the bark is known to protect trees from pests, insects, and fungal infections which can impede tree growth (Hadj

Taieb *et al.,* 2020; Boland and Woodward, 2021). This was also highlighted in the work of Nguyen *et al.,* (2016) who studied incidents of fungal diseases in 16 tree species on 209 permanent sample plots (PSPs) across 6 European countries. They found that fungal pathogens exert cascading consequences on the overall function of trees potentially embedding growth.

The Phloem is another part of trees that plays an important role in their growth. This tissue transports photosynthates to all parts of the tree as required during translocation (Crafts and Crisp, 1971; Oparka and Cruz, 2000; Turgeon and Wolf, 2009; Chen *et al.,* 2012; Sevanto, 2014).

Taken together, tree growth is significantly affected by the environment they grow in. If any given environmental factor does not meet the ideal standard, a tree’s growth gets limited e.g., trees that are not adapted to water-stressed environments cannot survive in deserts areas. In fact, most tree growth challenges are caused by environmental stress such as too little water, higher/lower than required temperatures, etc.

Although extensive research has been carried out on the theoretical process of tree growth, understanding precursor conditions that actually lead to trees growing around the world is still a developing field. The main objective of this review is to assess the current understanding of what controls tree growth. This synthesis is therefore critical as it will also identify gaps that will be filled by chapters that follow.

2.2 Methodological approach and sources of data

Literature searches were done by adapting the pragmatic sampling procedure used by Evans and Brown (2017) who employed Scopus (www.scopus.com) to examine the response of Boreal-Temperate Forest Ecotone to climate change. Scopus is an online abstract and citation database that houses peer-reviewed literature and web sources of quality standing. It contains >70 million records across over 20,000 journals. The metadata data used in this study were retrieved from Scopus using The University of Edinburgh's Affiliation ID.

In the first step, to construct a robust pool of authoritative peer-reviewed literature and establish the current understanding of what controls tree growth around the world, I did not limit the search to SAWs. Therefore, the only terms that I used in the Scopus online database were: ‘tree growth rates’. This search returned 81, 014 articles. I did a within-results search to limit them to articles that were highly cited. I then perused their titles and abstracts and picked the most relevant to inform the context that I used in the introduction and section 2.3 of this Chapter.

In the second step, I combined the terms ‘southern Africa’, with an ‘AND’ operator to ‘tree growth’. To capture both pioneering and recent understanding of what controls tree growth, I chose ‘Published: All years to present’. This search returned 364 articles with 1953 being the year of the first publication and 2018 the year of the most recent publication. To ensure that other relevant literature was not left out, I repeated the search but without the ‘southern’ terminology. This search returned 1,645 articles. I then screened the results with a bias towards (1) capturing articles whose study sites were in southern Africa, and (2) articles whose findings highlighted what controls tree growth. It is important to note that the two criteria used here did not require a study’s sole aim to be tree growth determination rather that they contain results that highlight what precisely controls tree growth.

To ensure that the search was exhaustive, the third and last step involved targeted searches with ‘tree growth’ AND [name of a country in southern Africa], where I listed all countries in turn. This resulted in 3 new findings for Tanzania, 3 all duplicates for Malawi, 1 new and 3 duplicates for Zambia, 1 new paper for Lesotho, 3 new and 3 duplicates for South Africa, 3 new and 3 duplicates for Angola, 4 new and 5 duplicates for Mozambique, 1 duplicate for Swaziland, 3 duplicates for Botswana, and 2 duplicates for Zimbabwe.

2.3 Results and discussion

2.3.1 Overview of studies on tree growth rates across the world

With the continued upward trend of global temperatures (IPCC, 2001a), climate change studies across myriad disciplines have become widespread. There is a large volume of published studies (e.g., Körner, 2012; Körner *et al.,* 2016) describing the role of temperature on tree growth rates and consequent dynamics of woodlands. Much of the literature shows that rising temperatures will impact the growth and spatial distribution of trees. Mcmahon *et al.,* (2010) investigated linkages between forest growth and temperature by using a new dataset covering 22 years and sourced from 55 temperate forest plots. All the plots used had well-documented land-use histories and therefore, their findings of accumulated biomass that exceeded expected natural growth among more recent measurements were attributed to changes in temperature. Figure 2.1 shows the accelerated growth of the plots that were censused and their increased biomass gain.

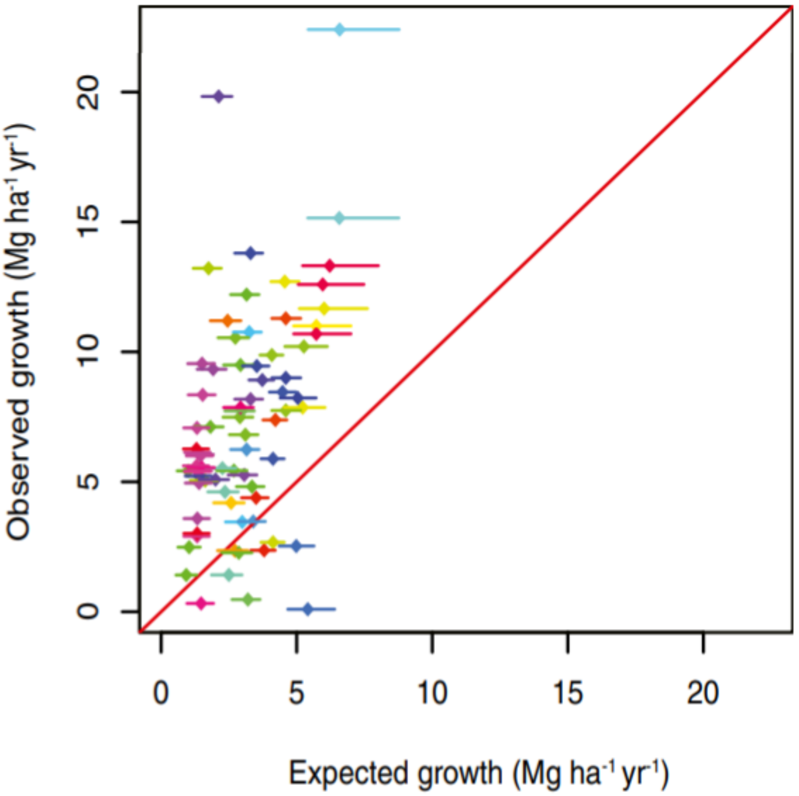

Figure 2.1: Observed versus expected annual biomass change (Mg ha^{-1} yr^{-1}) showing accelerated growth i.e., faster/increased biomass gain. Different colours of diamonds represent plot censuses while lines show 95% confidence limits. The red diagonal line represents the 1:1. *Source:* Mcmahon *et al.,* (2010)

In line with many studies that investigate the impacts of climate change on tree growth dynamics, Pretzsch *et al.,* (2014) used the oldest existing experimental forest plots in Central Europe to investigate tree growth (Figure 2.2). Their research was concentrated on Norway spruce (*Picea abies*) and European beech *(Fagus sylvatica)*. These taxa were chosen because they dominate much of Central and Eastern Europe covering about 30% of the total landmass which equates to 14 × 106 ha. These plots have been under continuous site observations since 1870 and the surveillance has been on individual tree-basis. Their findings indicate that comparing current growth rates and those observed in 1960, Central Europe's dominant species (Norway spruce and European beech) have significantly accelerated individual tree growth, stand volume growth, and stock accumulation. The observed acceleration of growth ranged from 32 to 77% with tree growth, 10 – 30% with stand volume growth, and 6 to 7% with stock accumulation.

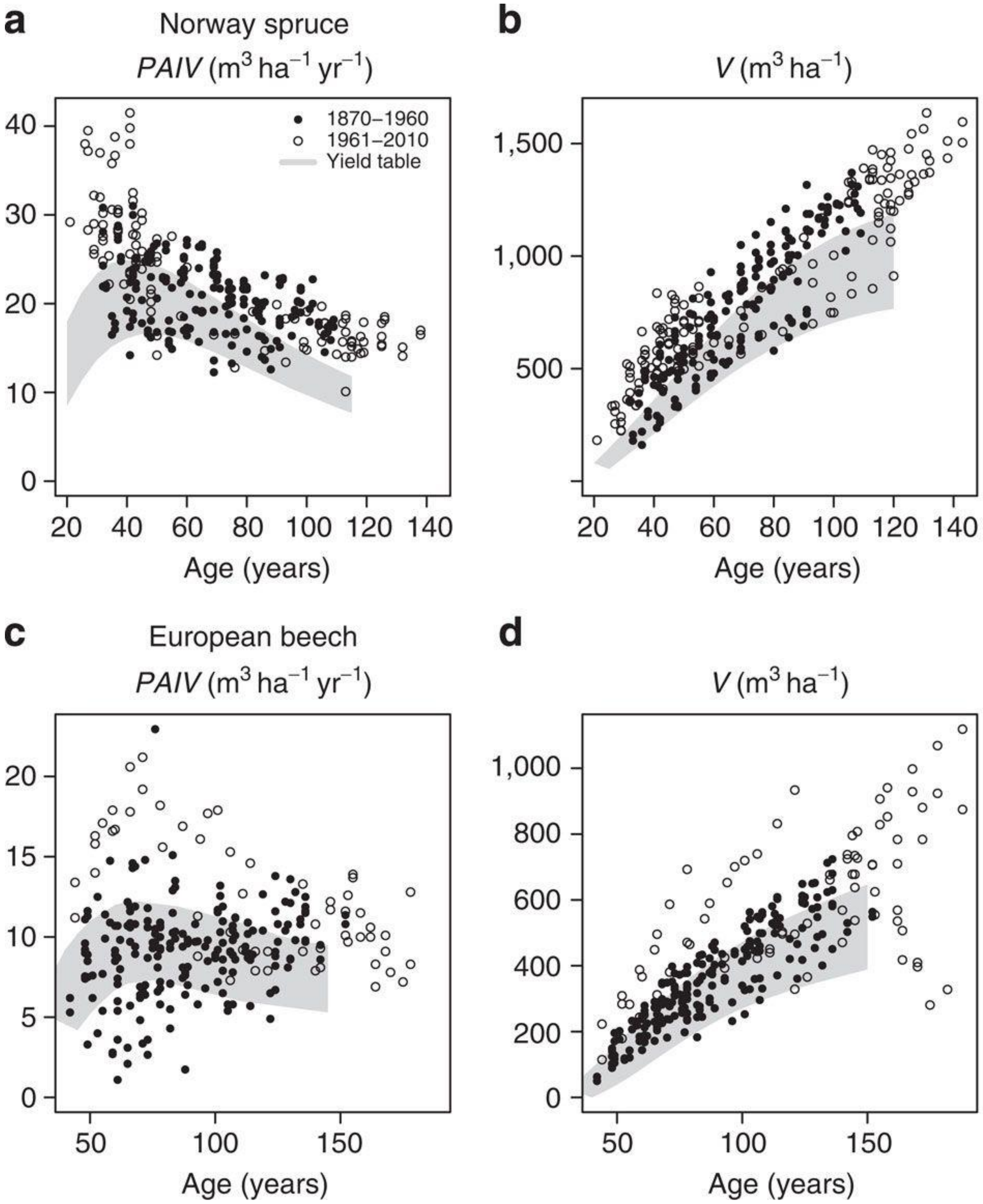

Figure 2.2: Observed versus expected stand growth for **(a)** Norway spruce; **(b)** Norway spruce wood standing stock volume (V in m^3 ha^{-1}); **(c)** European beech **(d)** European beech wood standing stock volume (V in m^3 ha^{-1}) for the period 1870 – 2010. *Source:* Pretzsch *et al.,* (2014). PAIV, Periodic Annual Volume Increment

Attempts have also been made to predict tree growth rates from other factors. Among them, studies of functional traits as proxies for predicting individual tree growth seem to be an expanding field. Existing research (e.g., Violle *et al.,* 2007; Adler *et al.,* 2014) recognises the critical role played by seed mass, specific leaf area (SLA), and wood density in predicting individual tree growth. However, recently, Paine *et al.,* (2015) closely examined the relationship between functional traits and individual tree growth and found that these traits (seed mass, SLA, and wood density) are weak predictors. In this study, Paine *et al.,* (2015) used 27, 352 trees, consisting of 278 species from 27 different sites around the world. Data collected from these sites (Figure 2.3) was used to investigate correlations between traits and growth. Their results showed that functional traits are unsuitable for predicting tree growth over broad regions.

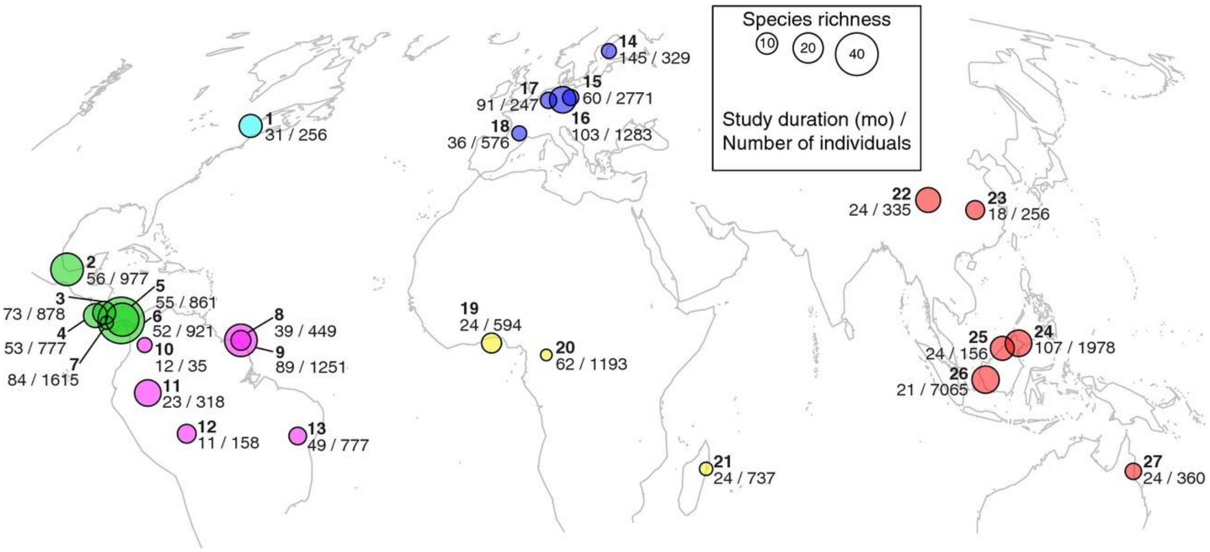

Figure 2.3: Geographical location of study sites. Different colours represent differences in biogeographic regions and the size of the points are with respect to the number of species studied at each site. Site numbers are given in bold whereas the duration (months) and the number of individuals monitored are given in plain text. *Source:* Paine *et al.,* (2015).

Other studies on growth rates around the world that were reviewed to inform this paper include a comparative analysis of growth rates in Northwestern Russia and Sweden (Angelstam *et al.,* 2016), growth rates of maple trees in Vermont (Berg *et al.,* 2018), growth rates of tropical rainforests in Costa Rica (Clark *et al.,* 2015), and growth rates of tropical trees in Panama (Condit *et al.,* 1993).

2.3.2 Statistical distribution of tree growth literature across southern Africa

Of the 364 articles, ~54% of tree growth rates literature across SAWs shows that Scientists use repeated plot measurements (Figure 2.4). This involves examining tree growth in permanent sample plots (PSPs; De Cauwer *et al.,* 2017; Green *et al.,* 2017). To enable easy remeasurements, all trees in the PSPs are tagged with permanent metal tree tags, and the census is repeated, generally on an annual basis although some studies prefer 5-year intervals (Lewis *et al.,* 2011). The PSPs are established in different shapes and sizes but are generally, circular, square, or rectangular. The point of measurement (POM) of tree diameter widely used is 1.3 meters above the ground and is commonly referred to simply as diameter at breast height (DBH; Lewis *et al.,* 2011). The minimum DBH threshold widely accepted across SAWs is ≥5 cm although in some countries e.g., Mozambican woodlands where bigger trees are common, a higher (≥10 cm) threshold is accepted (Campbell, 1996). The data that are collected are then used to calculate and project tree growth.

At ~40%, the use of growth rings is the second most common method of studying tree growth across SAWs (Figure 2.4). Growth rings are usually circular and are developed in the cross-section of woody plants on an annual cycle (Marcelo-Peña *et al.,* 2020). It is worth noting, however, that some studies have shown that in some regions in the tropics and depending on genera, growth rings may not be discernible or are not annual (Détienne, 1989).

With 5 and 1.3% respectively*,* modelling techniques and ecological succession/Chronosequence studies constitute the least common methods used across southern African woodlands (Figure 2.4).

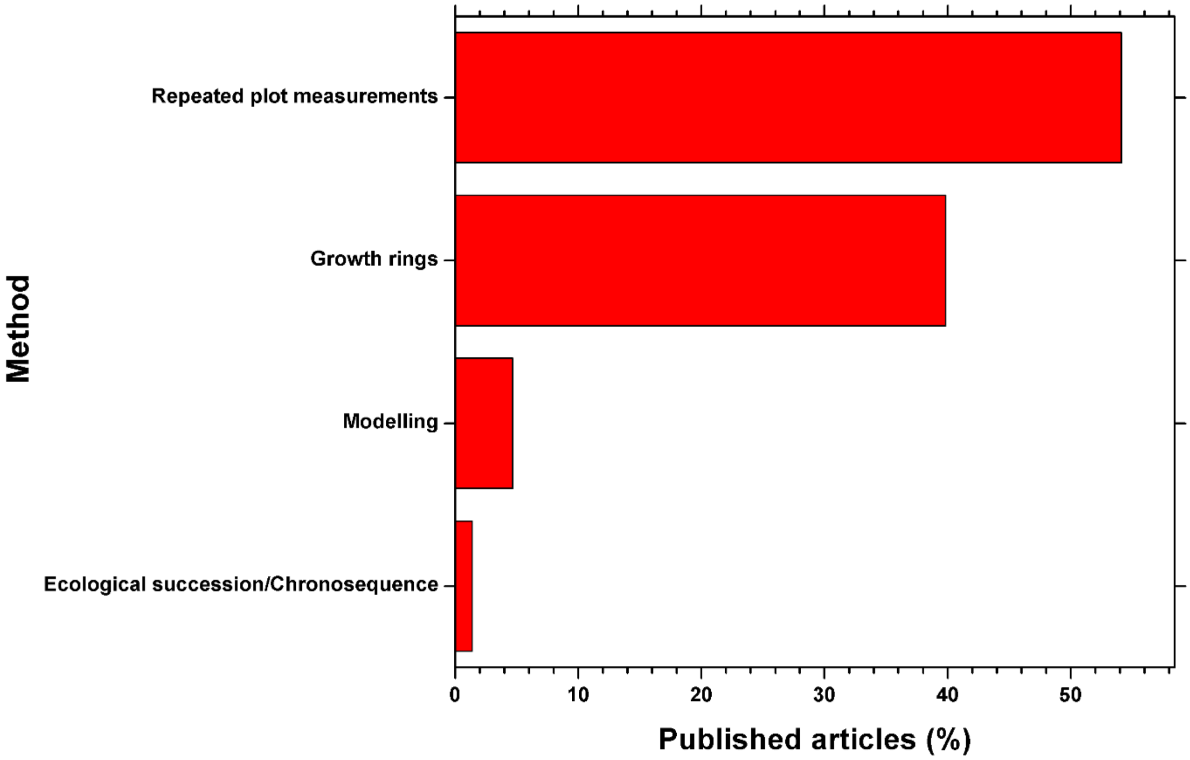

Figure 2.4: Methodological approaches used in tree growth rate studies across SAWs. Ecological succession/chronosequence studies are done on sites that may differ in age but are located on similar environmental conditions (e.g., soil types and climate). Modelling generally relates to projections of growth and development of woodlands. Growth rings are developed in the cross-section of woody plants on an annual cycle. Studies that use repeated plot measurements depend on diameter at breast height (DBH) measurements. This data is based on systematic literature searches in the Scopus online database for the period 1953 - 2020

Although there are big annual variations, there is generally a rapid increase in the number of peer-reviewed papers on tree growth rates across southern Africa over recent decades (Figure 2.5). This increase can be attributed to the runaway resurgence of deforestation (Kapekele, 2006) and degradation (Ahrends *et al.,* 2010) across much of the region, as well as an increase in funding for science and training of scientists. This naturally necessitates the need for studies that make meaningful contributions to the sustainability of the woodlands. It is worth noting that from 1993 to 1998, there were no studies that particularly focussed on the controls of tree growth rates while the highest number of publications was recorded in 2017.

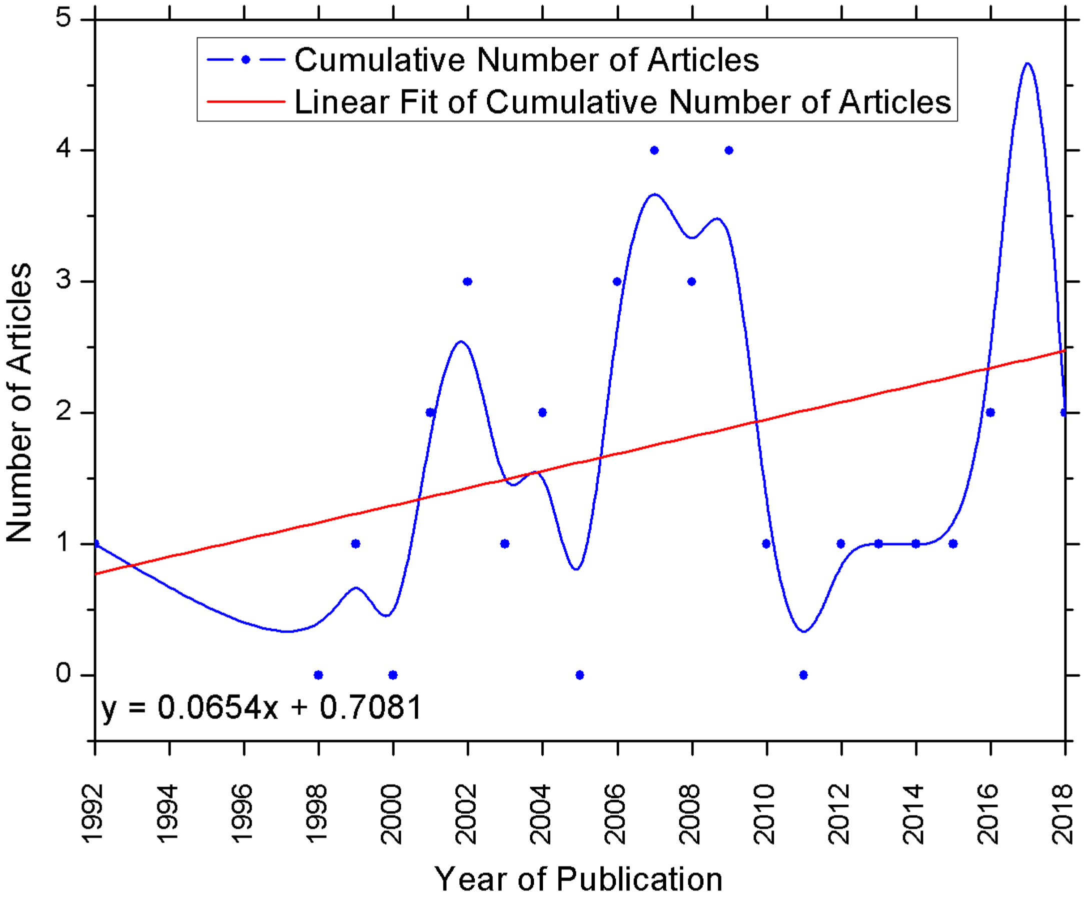

Figure 2.5: Cumulative number of articles published across southern Africa for the period 1992 –2018

An analysis of the geographical distribution of the case-study areas by the number of tree growth rate studies for each country found that, at 38%, most of the studies were done in South Africa, followed by Zambia (18%). At 2%, there is generally a dearth of studies in Malawi and Madagascar (Figure 2.6).

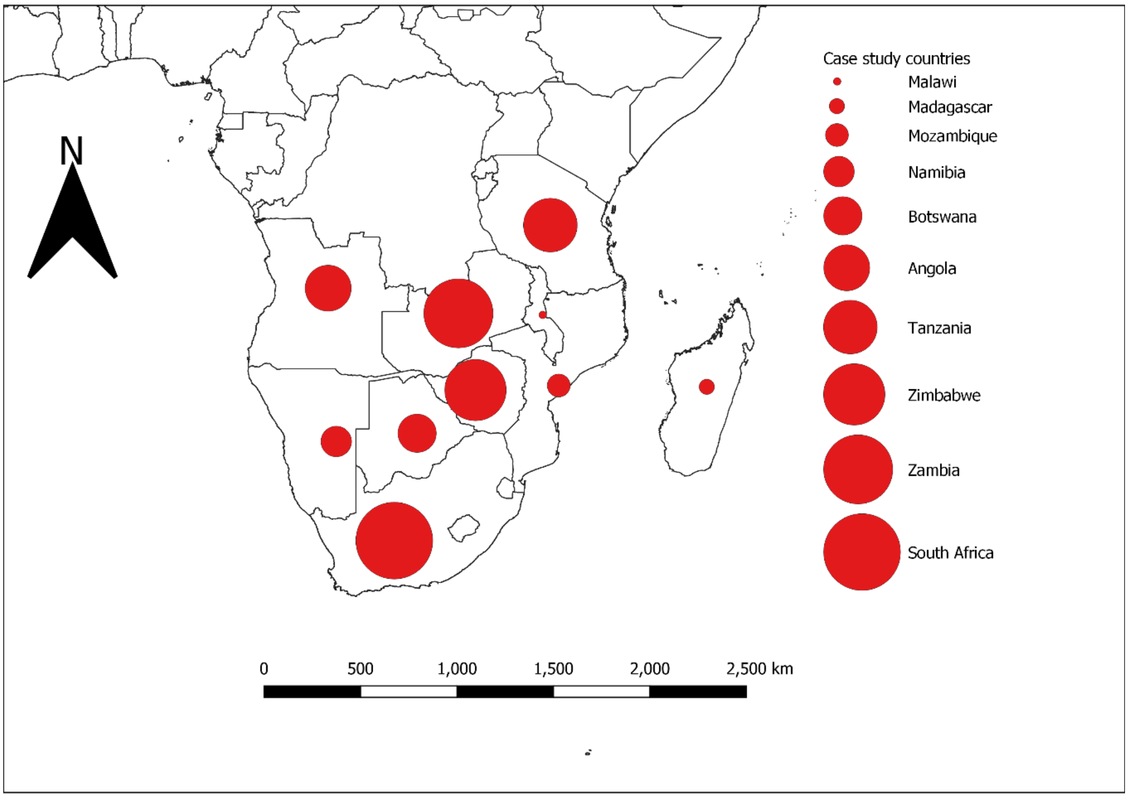

Figure 2.6: Spatial distribution of case-study areas by number of studies per country

2.3.3 Overview of studies on growth rates across Africa

Overall, the studies found a wide variety of growth rates from site to site and country to country. The emphasis seems to be placed on timber species, understandably so because of their high demand. For instance, in an attempt to understand the productivity potential of *Pterocarpus angolensis*, a timber tree generally found in natural mixed forests across southern Africa, DBH increment was studied as part of the indicators of productivity at 217 permanent plots (De Cauwer *et al.,* 2017). Results indicated that over 50 years, mean annual growth rates were 0.51cm per year. Similar results were found when *Pterocarpus angolensis* was studied in the

Rukwa Region of Tanzania (Schwartz *et al.,* 2002). In Schwartz *et al.,* (2002), the average tree ring width for 10 adult trees was studied and results showed that mean tree growth rates were 0.49 cm/year.

Growth rates of *Brachystegia spiciformis* were studied at three sites in the woodlands of Mongu, Zambia (Trouet *et al.,* 2006). These sites are geographically located within a 25 km radius of Mongu which is bounded by longitudes 23.1ºE and latitude 15.4ºS. Results showed that annual growth rates were 0.24 cm, 0.26 cm, and 0.32 cm, for sites 1, 2, and 3 respectively – so considerably slower than for *Pterocarpus angolensis*, but these sites are considerably drier.

In the miombo woodlands of Tanzania, Mugasha *et al.,* (2016) used individual tree diameter growth models to analyse growth rates using data from 117 plots in the Iringa and Manyara regions (Figure 2.7). This data spanned a period of 13 years from 1997 to 2009 and it consisted of 4,758 observations of individual tree growth with 141 species. Their methodological approach was model-based clustering which led to the selection of models with few independent variables, and which were in agreement with expected biological characteristics in the region. Therefore, biological behaviour was the main criteria used to select the models. Given that the models performed in accordance with expected biological behaviour, it was concluded that they are suitable for the development of decision-support tools for growth studies and forest management in the miombo woodlands. Once again, growth rates were mostly between 0/0.2 and 0.5 cm/year, though with more variation for small trees.

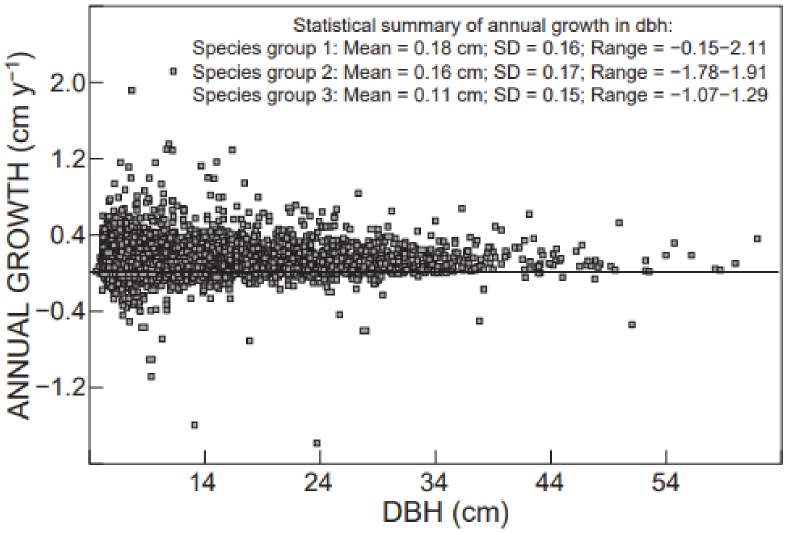

Figure 2.7: Annual growth (cm y^{-1}) over diameter at breast height (DBH;n = 4 758) showing that most trees grow between 0 and 0.5 cm yr^{-1}. Low growth rates for the largest trees could be an indication of the age effect. The species groups are included as Supplementary Material 2.1. *Source:* Mugasha *et al.,* (2016)

The academic literature on the impacts of the environment on growth rates has revealed interesting findings. Lacy and Shackleton, (2014) document that understanding growth rates and management of trees is one way of mitigating some of the potential impacts of climate change. In their study, they compared growth rates of indigenous street and garden trees in Grahamstown, South Africa. Results showed that street trees grew approximately 30% slower than trees in gardens. They attributed the slow growth of urban trees to the adverse environment in which they grow. In particular, they cited increased soil compaction, therefore, low rainfall infiltration as a major constraining factor. Conclusively, they documented that the environment (e.g., rainfall and soil) are important explanatory variables for tree growth.

Therrell *et al.,* (2007) examined the growth rate dynamics of *Pterocarpus angolensis* at 9 sites across southern Africa and found that although the diameter increments were in the range reported by previous studies in the region, they were generally lower at all the 9 sites. They further documented a positive significant relationship between annual diameter increments and mean seasonal rainfall.

Further reading on growth rates across Africa included the works of Clark and Clark, (1999) who modelled growth rates of tropical rainforest trees, Groenendijk *et al.,* (2014) who examined the growth rates, among other traits, of 22 commercial tree species in Central Africa and Stahle *et al.,* (1999) who studied Zimbabwean timber trees.

Conclusively, even though there are differences in methodological approaches, results indicate that generally, mean tree growth rates across southern African woodlands range from ~0.16 to ~0.66 cm/year (Table 2.1). The only study that reported growth rates outside this range is that of Van Holsbeeck *et al.,* (2016) who documented growth rates as high as 0.80 cm/year in Kavango (Namibia) and attributed their fast growth to age-diameter relations citing faster growth when trees are still young (as was the case in Kavango) and slowing down at a later stage.

2.3.4 Current understanding of what controls tree growth

Analyses of the literature confirm that tree growth is influenced by myriad factors (Table 2.1). Some of these include seasonal rainfall, soil moisture (González-Muñoz *et al.,* 2014; Chitra-Tarak *et al.,* 2015; Chidumayo, 2015; Rohner *et al.,* 2017) length of the rainy season, length of the dry season, relative humidity, temperature, and CO_2 concentrations (Larcher, 1995; Campbell, 1996; Vinya, 2010). Overall, climate and soil properties are documented to be among the most important explanatory variables for tree growth (Lévesque *et al.,* 2016; Angelstam *et al.,* 2016). In fact, it is observed that tropical trees cease to grow at temperatures below 15ºC (Larcher, 1995), December – February (DJF) rainfall explains 10 - 30% of *Pterocarpus angolensis* radial growth (Stahle *et al.,* 1999), and annual rainfall was found to explain 70% of diameter at breast height (DBH) growth in South Africa (Shackleton, 2002).

A cursory review of the controls of tree growth rates according to major biomes of the world (Figure 2.8) indicates that in the tropical and subtropical grasslands, savannas, and shrublands, mean annual precipitation (MAP) and the December -February (DJF) are the most cited controls. However, in the montane grasslands and shrublands, reviewed literature cites species as being the major control. In the tropical and subtropical moist broadleaf forests, in the temperate broadleaf and mixed forests, and across Mediterranean forests, woodlands, and scrub, MAP is the most cited control of tree growth rates.

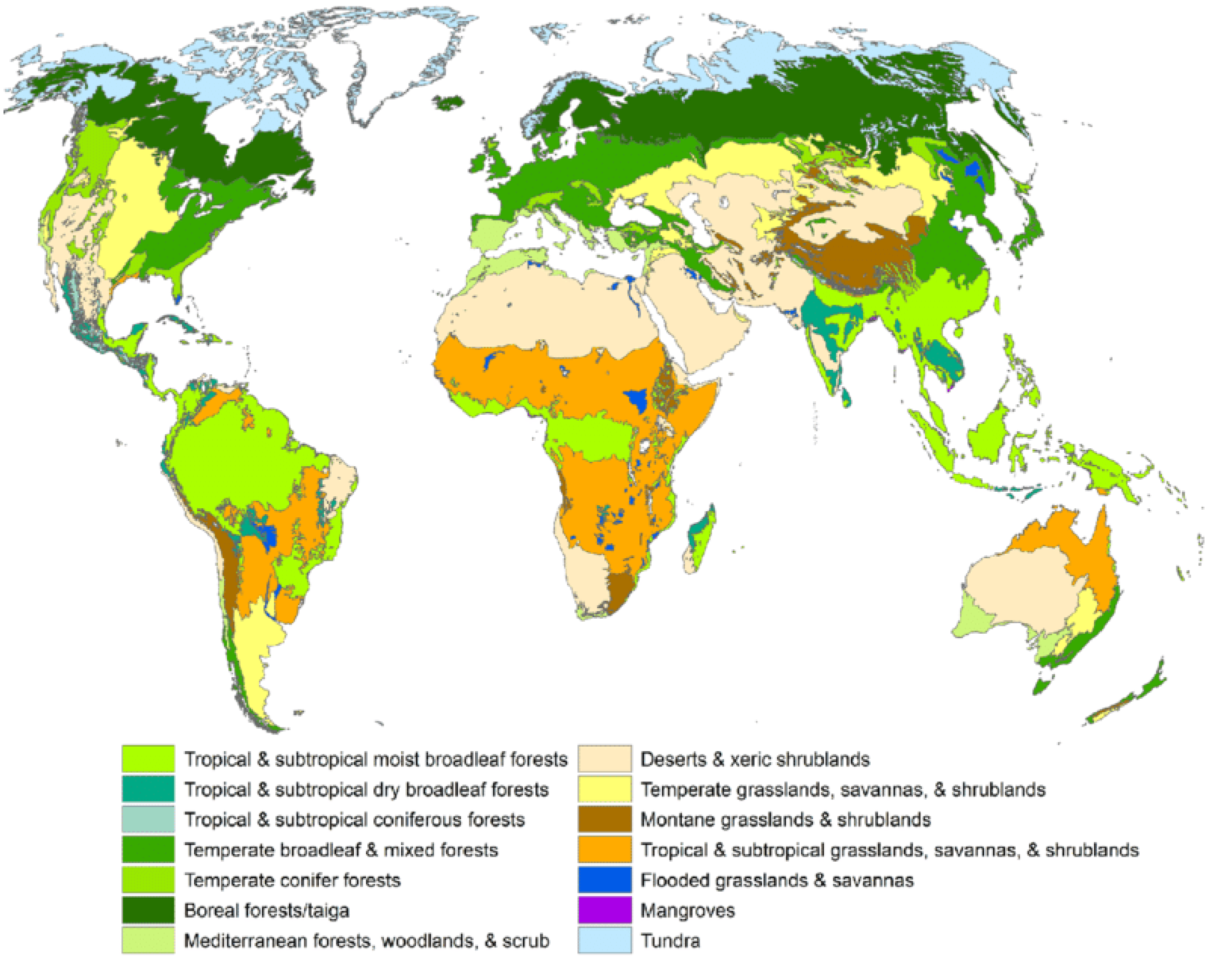

Figure 2.8: Major biomes of the world used to classify literature in Table 2.1. *Source:* Olson *et al.,* (2001)

Table 2.1: Controls of tree growth around the world arranged alphabetically by country. MAP is mean annual precipitation, DJF is December – February precipitation, SPP is species, SS is stem size, TEM is temperature, DP is dry season precipitation, and ND is not discussed. ⬆ Positive effect, ➡variable effect, X effect not discussed

Source	Country	Methods	Mean annual growth (cm/year)	Key findings						
				MAP	DJF	SPP	SS	TEM	DP	ND
Biome: Tropical & Subtropical Grasslands, Savannas, & Shrublands										
Ngugi *et al.*, (2015)	Australia	Repeated plot measurements	-	⬆			⬆			

Fichtler *et al.*, (2004)	Namibia	Growth rings	0.47	⬆				➡		
De Cauwer *et al.*, (2017)	Namibia and Angola	Repeated plot measurements and growth rings	0.51	⬆		➡	➡			
Shackleton *et al.*, (2002)	South Africa	Repeated plot measurements	0.45	⬆						
van Daalen *et al.*, (1992)	South Africa	Growth rings and C^{14} dating	0.47							X
Lacy and Shackleton, (2014)	South Africa	Growth rings	0.71 – 0.96	⬆						
Therrell *et al.*, (2007)	South Africa, Mozambique, and Zimbabwe	Growth rings	0.39 (S. Africa and Zimbabwe), and 0.4 (Mozambique)		⬆					
Schwartz *et al.*, (2002)	Tanzania	Growth rings	0.049							X
Mugasha *et al.*, (2016)	Tanzania	Repeated plot measurements	~0.16							X
Groome *et al.*, (1957)	Tanzania	Repeated plot measurements	0.59							X
Trouet *et al.*, (2006)	Zambia	Growth rings	~0.26	⬆	⬆			➡		
Chidumayo, (2015)	Zambia	Repeated plot measurements	-						⬆	
Therrell *et al.*, (2006)	Zimbabwe	Growth rings	-		⬆					
Stahle *et al.*, (1999)	Zimbabwe	Growth rings	0.4		⬆					
Biome: Montane grasslands & shrublands										
Li *et al.*, (2016)	China	Repeated measurements	-							X
Li *et al.*, (2017)	China	Repeated measurements	-			➡				
Biome: Tropical & subtropical moist broadleaf forests										
Locosselli *et al.*, (2017)	Brazil	Growth rings	0.1 – 0.66	⬆				➡		
Groenendijk *et al.*, (2014)	Central Africa	Growth rings	-			➡				
Clark and Clark, (1999)	Costa Rica	Repeated plot measurements	0.4			➡				
Clark *et al.*, (2015)	Costa Rica	Repeated plot measurements	-							X
Condit *et al.*, (1993)	Panama	Repeated plot measurements	-							X
Biome: Temperate broadleaf and mixed forests										

Huang *et al.*, (2017)	Denmark	Growth rings	-	↑			
Vaz Monteiro *et al.*, (2017)	UK	Growth rings	-	↑	→		
Berg *et al.*, (2018)	United States	Growth rings	-	↑		↑	→
Biome: Boreal forest/taiga							
Angelstam *et al.*, 2016)	Russia and Sweden	Repeated plot measurements	-	↑			→
Biome: Mediterranean forests, woodlands, and scrub							
Linares *et al.*, (2014)	Spain	Growth rings	-	↑			→
Rohner *et al.*, (2017)	Switzerland	Repeated plot measurements	-	↑			→

2.4 Research gaps and conclusion

This chapter has revealed that although there are some studies on tree growth rates across southern Africa (SAWs) that highlight key points relevant to the current contribution, they suffer from spatial data limitedness. Therefore, findings are not representative of the entire SAWs. In fact, no single study exists which adequately explored the entire subcontinent. To overcome this geographical limitation, this Ph.D. project considers the broader southern African woodlands i.e., 38,276 trees belonging to 400 species on 223 permanent sample plots (PSPs) in 8 countries.

Further, none of the studies reviewed appear to have considered finding a methodological approach that would enable the prediction of growth rates in unmonitored areas of SAWs. This general lack of methodological rigour may put in question our current understanding of SAWs and thus, ability to sustainably manage them. To cover this gap, I developed and validated a hierarchical mixed-effects model and used it to predict growth rates across a wide unmonitored environmental gradient of southern Africa.

Lastly, while studies reviewed provided insights on how fast trees grow in some parts of SAWs, no study attempted to apply the observed growth rates in determining sustainable harvesting rates. To cover this deficiency, in this Ph.D. project, I used variations in growth rates for 49 timber species across southern African woodlands (SAWs) to determine an annual allowable cut (AAC) for sustainable woodland management.

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Supplementary Material 2.1: Tree species groups, scientific names, and number of observations.

Source: Mugasha *et al.,* (2016)

Species group	Obs.	Name
1	1	*Albizia harveyi* E.Fourn.
	3	*Albizia schimperiana* Oliv.
	3	*Albizia* sp.
	22	*Bauhinia petersiana* Bolle
	87	*Brachystegia* sp.
	134	*Brachystegia bussei* Harms
	2	*Cassia abbreviata* Oliv.
	3	*Cassia* sp.
	8	*Dichrostachys cinerea* (L.) Wight & Arn.
	6	*Diospyros kirkii* Hiern
	9	*Dombeya rotundifolia* Hochst.
	1	*Ehretia amoena* Klotzsch
	9	*Ficus abutilifolia* Miquel
	4	*Kigelia africana* (Lam.) Benth.
	18	*Ozoroa mucronata* (Bernh.) R.Fern. & A.Fern.
	9	*Pappea capensis* Eckl. & Zeyh.
	21	*Pteleopsis myrtifolia* (M.A.Lawson) Engl. & Diels.
	21	*Pterocarpus angolensis* DC.
	13	*Rubia* sp.
	7	*Schrebera trichoclada* Welw.
	1	*Senegalia nigrescens* (Oliv.) (syn. *Acacia nigrescens* Oliv.
	1	*Senegalia polyacantha* (Willd.) Seigler & Ebinger (syn. *Acacia polyacantha* Willd.)
	2	*Stegnocarpus* sp.
	3	*Tarenna neurophylla* (S. Moore) Bremek.
	19	*Terminalia sericea* Burch. ex DC.
	4	*Terminalia* sp.
	1	Unknown1
	1	Unknown2
	2	Unknown3
	7	*Zanthoxylum chalybeum* Engl.
2	5	*Acacia* sp.
	3	*Afzelia quenzesis* Welw.
	4	*Albizia amara* (Roxb.) Boiv.
	3	*Albizia versicolor* Welw. ex Oliv.
	14	*Boscia salicifolia* Oliv.
	16	*Boscia* sp.
	12	*Brachystegia boehmii* Taub.
	134	*Brachystegia spiciformis* Benth.
	42	*Brachystegia microphylla* Harms
	51	*Brachystegia utilis* Burtt Davy & Hutch.
	1	*Burkea africana* Hook.
	17	*Commiphora mollis* (Oliv.) Engl.
	1	*Commiphora* sp.
	1	*Cussonia spicata* Thunb.
	3	*Cussonia zimmermannii* Harms
	3	*Erythrophleum africanum* Harms
	10	*Euphorbia candelabrum* Welw.
	6	*Faurea saligna* Harv.
	1	*Ficus* sp.
	3	*Ficus natalensis* Hochst.
	1	*Garcinia buchananii* Baker
	1	*Harungana madagascariensis* Lam. ex Poir.
	471	*Julbernardia globiflora* Benth.
	2	*Lannea* sp.
	1	*Lannea stulmanii* Engl.
	1	*Ochna holstii* Engl.
	14	*Ochna schweinfurthiana* F.Hoffm.
	2	*Rothmani fischeri* (K.Schum.)
	3	*Sclerocarya birrea* (A.Rich.) Hochst.
	4	*Sterculia quiqueloba* (Garcke) K.Schum.
	1	*Uapaca kirkiana* (Muell.Arg.)
2	4	*Vachellia nilotica* (Lam.) P.J.H.Hurter & Mabb. (syn. *Acacia nilotica* Lam.)
	1	*Vachellia seyal* (Delile) P.J.H.Hurter & Mabb. (syn. *Acacia seyal* Del.)
	3	*Xeroderris* sp.
	8	*Zyzigium* sp.
3	13	*Allophyllus africanus* P.Beauv.
	9	*Allophyllus* sp.
	2	*Annona* sp.
	7	*Azanza garckeana* F.Hoffm.
	1	*Azanza* sp.
	18	*Bauhinia pertesiana* (Bolle) A.Schmitz.
	15	*Bauhinia tomentosa* L.
	14	*Boscia angustifolia* Guill. & Perr.
	5	*Boscia mossambicensis* Klotzsch
	10	*Bridelia micrantha* (Hochst.) Baill.
	5	*Bridelia* sp.
	17	*Caesalpinia spinosa* (Molina) Kuntze
	1	*Canthium burttii* Bullock *sensu* R.B.Drumm.
	5	*Catunaregam* sp.
	8	*Clerodendrum* sp.
	26	*Combretum binderianum/collinum* Kotschy.
	153	*Combretum molle* (R.Br. ex G.Don.) Engl. & Diels
	127	*Combretum zeyheri* Sond.
	1	*Commiphora eminii* Engl.
	1	*Commiphora pilosa* Engl.
	8	*Cordia* sp.
	3	*Cussonia* sp.
	11	*Dalbergia boehmii* Taub.
	50	*Dalbergia melanoxylon* Guill. & Perr.
	104	*Dalbergia nitidula* Baker.
	11	*Dichrostachys glomerata* Chiov.
	2	*Dioscorea* sp.
	102	*Diplorhynchus condylocarpon* (Mull.Arg.)
	5	*Euclea schimperi* Hiern
	21	*Euphorbia tirucalli* L.
	1	*Flacourtia indica* Oliv.
	1	*Flueggea virosa* (Roxb. ex Willd.)
	3	*Gardenia imperialis* K.Schum.
	5	*Gardenia jovis-tonantis* (Welw.) Hiern
	6	*Grewia* sp.
	1	*Hymenaea verrucosa* Gaertn.
	42	*Lannea schimperi* (Hochst. ex A.Rich.)
	1	*Lonchocarpus* sp.
	10	*Maerua triphylla* Thunb.
	1	*Margaritaria discoidea* (Baill.) G.L.Webster
	28	*Markhamia obtusifolia* Sprague
	1	*Markhamia puberula* (Klotzsch) K.Schum.
	3	*Markhamia* sp.
	3	*Maytenus senegalensis* (Eckl. & Zeyh.).
	9	*Monotes elegans* Gilg.
	19	*Mundelia sericea* (Willd.) A.Chev.
	3	*Ormocarpum kirkii* S.Moore
	9	*Ormocarpum* sp.
	9	*Ozoroa insignis* Del.
	1	*Phyllanthus engleri* Pax.
	11	*Pleurostylia africana* Loes.
	1	*Pleurostylia* sp.
	30	*Pseudolachnostylis maprouneifolia* Pax.
	6	*Pseudolachnostylis* sp.
	9	*Rhus* sp.
	1	*Schrebera* sp.
	1	*Sclerocarya* sp.

Species group	Obs.	Name	Species group	Obs.	Name
3	1	*Strychnos innocua* Del.	3	1	Unknown5
	2	*Strychnos potatorum* L.		2	Unknown6
	20	*Strychnos* sp.		1	*Uvaria* sp.
	1	*Swartzia madagascariensis* Desv.		1	*Vernonia colorata* Willd.
	1	*Tarenna graveolens* (S.Moore) Bremek.		1	*Vernonia* sp.
	9	*Tarenna* sp.		6	*Vitex fischeri* Gürke.
	2	*Terminalia stenostachya* Engl. & Diels		3	*Ximenia americana* L.
	3	*Trachylobium verrucosum* Oliv.		14	*Ximenia caffra* Sond.
	1	*Turraea* sp.		5	*Zanha africana* Radlk.
	1	Unknown4			

CHAPTER III

CHAPTER 3: TREE-TREE COMPETITION DRIVES VARIATION IN GROWTH RATES ACROSS AFRICAN SAVANNA TREES

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Author Contribution

This study was initially suggested by CMR. The analytical design, model development, data analyses, literature searches, and manuscript writing were led by BL and CMR with inputs from all authors.

Abstract

The determinants of tropical tree growth rates remain a major uncertainty, leading to a lack of understanding of trade-offs between life-history strategies, sustainable harvesting rates, and likely responses to global change. In the savannas and dry forests that cover half the vegetated tropics, tree growth rates are very poorly known, particularly in Africa where there are few studies of the processes that influence growth rates. Here, drivers of variation in growth rates of 38,276 trees belonging to 400 species on 223 permanent sample plots (PSPs) in 8 countries across southern Africa are analysed. Results show a mean (±SEM) diameter increment of 1.62 ± 0.3 mm yr^{-1} across the region, with substantial site-to-site variation. The hypothesised drivers of growth rate variation such as soils and climate had little effect at the regional level, although plot-level tree basal area (a proxy for tree-tree competition) consistently reduced growth rates. Examining the determinants of growth for each species, however, revealed strong and often contrasting effects of soils, climate, tree size, and fire. A continuum of responses across species emerges, with contrasting patterns between miombo woodland dominants such as *Brachystegia* and open savanna species. In the faster-growing miombo dominant group, growth increased with stem size, on poor soils, and was less affected by reduced water availability and seasonality. The open savanna group exhibited the opposite trends, growing relatively faster on good soils and in wetter conditions. These findings challenge conventional understanding of the determinates of tree growth in savannas, and suggest distinct controls in different types of savanna, and thus distinct responses to global change. The observed widespread effect of tree-tree competition may play an important, but hitherto neglected, role in determining community composition and sustaining tree-grass coexistence. It is also likely to moderate the current increase of trees in savanna systems, suggesting the globally important C sink in African savannas is unlikely to be sustained.

Keywords: tree growth rates, competition, hierarchical mixed-effects models, sustainability, southern Africa, SEOSAW

3.1 Introduction

It is now well established that trees constantly engage in competition for water, light, and nutrients (Rozendaal *et al.,* 2020). Tree species, therefore, develop distinct strategies for survival with implications on overall stand growth rates, dynamics, and structure across their respective competitive environments. This is particularly widely documented in forests (Uriarte *et al.,* 2004; Lasky *et al.,* 2014; Looney *et al.,* 2016). However, the impact of competition on tree growth rates in the savannas is understudied, particularly across southern African woodlands (SAWs). The existing literature on growth rates ignores the possibility of competition in the savannas citing the generally sparse distribution of trees characteristic of such a biome (Kunstler *et al.,* 2015). Therefore, the impact of competition on tree growth rates across SAWs remains unclear. Further, most studies of tree growth rates across SAWs have only been carried out in a small number of areas. To date, no large-scale studies have been performed to investigate tree growth rates across the broader SAWs. Consequently, determinants of tree growth rates across the broader SAWs remain speculative.

While SAWs play an important role in human wellbeing and the carbon cycle, their ability to meet future demand of ecosystem products and services is threatened by external pressures such as deforestation and degradation. Early examples of research into deforestation and degradation include Agyei, (1998) who documented that in the 1990s, global woodlands were reducing by ~15.4 million hectares per year which equates to 0.8% annual deforestation rates. However, the rate of deforestation across SAWs alone surpassed the 0.8% global annual figure owing to the over-dependence on fuelwood as a major source of energy (Agyei, 1998). With the aid of radar data, new insight shows that the loss of SAWs aggravated by deforestation and degradation is -0.075 PgC yr^{-1} and -0.038 PgC yr^{-1}, respectively. This translates into 3 - 6 times worse than previously estimated (McNicol *et al.,* 2018). The impact of degradation and deforestation on the economies of sub-Saharan countries is significant as governments and local communities risk losing a substantial source of revenue in the future.

The continued shrinkage of SAWs due to rapid degradation and deforestation may be amplified by their potential response to changes in precipitation, temperature, and fire regimes which would make them sensitive to climate and global change (Platts e*t al.,* 2008; Naidoo *et al.,* 2013). This was also highlighted earlier in the work of Lesolle, (2012) who argued that the ongoing global warming is thought to alter the phenology of certain tree species thus, the observed differences in growth rates among species. This was further corroborated by Adame *et al.,* (2014) who showed differences among tree species functional groups and their importance in predicting growth rates. Sala *et al.,* (2010) and Allen *et al.*, (2010) also observed that climate change will exacerbate drought-induced mortality across the world including SAWs. All these threats call the future of SAWs into question and clearly show that the current business-as-usual trajectory of resource use, management, or the lack thereof, is unsustainable.

Growth rates, mortality rates, and regeneration rates are some of the factors that are important for the sustainability of SAWs. Key among these factors is disentangling how fast trees grow as this enables modelers to predict the maximum sustainable yield of fuel or timber.

Understanding tree growth rates requires unravelling biophysical interactions that influence them. Site- (e.g., precipitation, temperature, and soils) and tree-specific (e.g., species, functional traits, competition, stem damage, and diameter) variables are essential for the growth of trees (Toledo *et al.,* 2011; Bowers, 2017). This study aims to focus on two key aspects of the determinants of tree growth rates in savannas: firstly, the importance of water and soil nutrient resources on growth rates is analysed as these have been widely hypothesised to be the first-order controls on mature savanna tree growth rates. Secondly, the role of tree-tree competition is also examined. This has received less attention compared to tree-grass competition in savannas, but theoretical studies suggest it may be critical to shaping the non-linear transient dynamics of ecosystem structure (Calabrese *et al.,* 2010). In addition, recent empirical data suggest it may be much more important than previously appreciated, even, or especially, in sparely wooded systems. After evaluating these two aspects, “functional growth” types among the large pool of savanna species are examined. The term “functional growth” types here is used to refer to groupings of species whose growth rate responds in similar ways; such grouping has been suggested as a way forward in terms of understanding the complexity of diverse species assemblages and facilitating modelling of savanna responses to global change.

To achieve the aim of this study, a novel data set of 38,276 trees belonging to 400 species on 223 permanent sample plots (PSPs) in 8 countries across the broader southern African region is used. Further, hierarchical mixed-effects models were developed and used to answer the following presently poorly understood research questions:

i. How fast are trees growing across SAWs?
ii. What are the main determinants of tree growth rates across SAWs and how different do species respond to them?

iii. Which species are fast/slow growers across SAWs?

Findings will underpin management and strategic planning that aim to confine human activities within the sustainable capacity of SAWs. Results will also highlight growth patterns and their dynamics at a broader scale than was previously possible.

3.2 Materials and methods

Traditionally, tree growth rates have been studied using the width of annual rings in cores/discs extracted from stems (Fichtler *et al.,* 2004) or by repeated measurements of tagged trees on permanent sample plots (PSPs; Mugasha *et al.,* 2016). It is worth noting that in some regions especially within the confines of the tropics and depending on genera, growth rings may not be discernible or are not annual (Détienne, 1989). For this reason and based on data availability, the repeated PSPs measurement approach was used in this study. Therefore, data from long-term permanent sample plots were collated, explanatory variables (EVs) were extracted using coordinates for the centre of each PSP, and hierarchical mixed-effects models were developed and used to disentangle the effects of each EV on tree growth rates across the region.

3.2.1 Study area and tree measurements

The study area covers a wide environmental gradient across 8 countries stretching from the Bateke plateau in the Republic of Congo (Latitude 2.5°S and Longitude 15.4°E) to Ciskei in South Africa (32.8°S, 26.9°E). Evidently, the PSPs span a large geographical area (Figure 3.2).

The stem data used in this study were collected by the Socio-Ecological Observatory for Southern African Woodlands (SEOSAW) partners. SEOSAW's main goal is to understand the response of southern African woodlands to global change (The SEOSAW Partnership, 2021). This data consists of 38,276 individual stems belonging to 400 species across 223 PSPs in 8 countries and covers the period 1991 – 2018 with varying remeasurement intervals (Table 3.1 and Supplementary material 3.8).

Trees were marked or tagged and measured at ~1.3 m using a diameter at breast height (DBH) tapeline or callipers. The tagging/marking guaranteed easy identification during remeasurements. 95.8%, representing 36,649 individual stems were identified at the genus level while 93.2%, representing 35,676 stems were identified at the species level.

Growth calculations

Tree diameter measured on tagged or marked stems was used to calculate mean annual growth. Therefore, growth is used in this work to mean the slope of a linear line of best fit to the repeated diameter measurement data of each tree. Although several methods can be used to compute tree growth, this approach was chosen because it considers all data points thus, is unlikely to be biased by randomly high or low measurements (Sedmark and Scheer, 2012).

Trees with the following characteristics were removed from the analyses:

(i) Those that had a DBH under 5 cm, representing 7.8% of the initial dataset;

(ii) Those that were measured at different points of measurements (POMs) between census dates, representing ~0.007% of the initial dataset;

(iii) Those that died, representing 6.9% of the dataset;

(iv) 1.3% of the stems that were marked as outliers were also removed. Outliers were defined as trees having annual growth rates outside the ±1 cm/year[3]. range.

These measures ensured that growth was kept at biologically realistic rates and are consistent with previous studies (Holdo, 2006; Mugasha *et al.,* 2016).

Geographical structure

Most of the datasets consisted of a group of plots (mean = 0.7 ±0.1 Ha) in small geographical areas (mean bounding box = 2.9 ±0.2 Ha). However, the South African data had a different sampling arrangement with wide geographical coverage in the savannas and grassland areas of the country. To represent the hierarchical structure of the dataset, PSPs were grouped by sites. For the South African data, they were grouped into two meta- “sites” (Grassland and Savanna) based on Siyavula, (2019). Specifically, all PSPs that are geographically located on the Highveld, with very variable mean annual precipitation and soils characterised by rich fertile upper layers were classified as Grassland sites. All PSPs geographically located in the western parts of Limpopo, the northern parts of the Northern Cape and Free State, KwaZulu Natal, and the Northwest Province were classified as Savanna.

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[3] *±1 cm/year was chosen as a threshold based on the fact that it was later learnt that growth is 0.162 cm/year meaning any stems beyond ±1 cm/year would be way off i.e., 5 or more standard errors away from the mean*

Table 3.1: Inventory of the data used in this study. *PI,* Principal Investigator

							Measurement year	
PI	**Reference**	**Site**	**No. of plots**	**Median Plot size (ha)**	**No. of stems**	**No. of censuses**	**First**	**last**
Nieto-Quintano	Nieto-Quintano *et al.,* (2018)	Bateke, Congo	3	25	2754	2 - 3	2015	2017
Mukungwa	-	Chimaliro, Malawi	18	0.25	1945	2 - 4	1998	2004
Mugasha	Mugasha *et al.,* (2016)	Iringa, Tanzania	26	0.04	887	2 - 4	2002	2012
Muledi	Muledi *et al.,* (2020)	Katanga, DRC	3	10	5068	2 - 3	2010	2014
McNicol	McNicol (2018)	Kilwa, Tanzania	23	1	15846	2 - 3	2010	2018
Chidumayo	Chidumayo (2019)	Kamatupa, Zambia	30	0.16	192	2 - 4	1998	2001
Ryan	Ryan (2009)	Nhambita, Mozambique	7	1	3104	2 - 5	2006	2017
Ribeiro	Ribeiro *et al.,* (2017)	Niassa, Mozambique	50	0.28	1867	2 - 4	2004	2015
Zimbabwe Forestry Commission	-	Hwange, Zimbabwe	12	0.25	1718	2 - 3	1994	2015
Shackleton	Shackleton (2002)	Grassland, South Africa	13	0.084	1253	5 - 8	1991	1998
Shackleton	Shackleton (2002)	Savanna, South Africa	38	0.17	3642	2 - 7	1992	1998
Total			**223**		**38, 276**			

3.2.2 Ancillary datasets

Based on the review presented in the introduction, data on site-level environmental factors that were hypothesised to influence growth rates (soils, climate, fire) were extracted from global gridded products (Table 3.2) or calculated based on gridded data. In addition, plot-level tree basal area was calculated for each plot, as a proxy for tree-tree competition. As well as these plot-level variables, initial stem size and species were included as predictors in all models.

Table 3.2: Summary of potential explanatory variables (EVs). In the model, initial diameter was log-transformed

Level	Variable	Acronym	Unit	Resolution	Source	Mean	SD	Range	Method referenced
Stem	Initial Stem Size	Diamy0	mm	stem	This study	14.3	10.3	3.7-70.9	Holdo, (2006)
	Species	spp	count	stem	This study	400	-	-	Mugasha *et al.*, (2016)
Plot-competition	Basal Area	BA	m^{2}ha^{-1}	stem	This study	8.7	8.1	0.007-63.5	Xue *et al.*, (2012)
Plot-soil	Sand Content	Sand	%	250 m	Hengl *et al.*, (2017)	61.2	7.4	35.3-83.6	Case and Staver, (2018)
	Total Phosphorous	P	mg kg^{-1}	250 m	Hengl *et al.*, (2017)	293	129	135-897	Hengl *et al.*, (2017)
	Total Nitrogen	N	mg kg^{-1}	250 m	Hengl *et al.*, (2017)	858.6	211	564-1743	Hengl *et al.*, (2017)
	pH	pH	-	Plot	Hengl *et al.*, (2017)	6	0.3	5.4-8.1	Hengl *et al.*, (2017)
	Organic Carbon	OrgC	g kg^{-1}	250 m	Hengl *et al.*, (2017)	11.8	4.4	4.7-25	Hengl *et al.*, (2017)
	Soil Depth	SoilDepth	cm	250 m	Hengl *et al.*, (2017)	16.8	0.9	11-18	Hengl *et al.*, (2017)
Plot-fire occurrence	fire count	FC	No. of fires	Plot	Giglio *et al.*, (2015)	3.6	4.4	0-16	Giglio *et al.*, (2015)
Plot-climate	Mean Annual Precipitation	MAP	mm yr^{-1}	0.05° x 0.05°	Funk *et al.*, (2015)	904.5	221.6	358-1939	Workie and Debella, (2018)
	Rainy Season Length	RSL	days yr^{-1}	0.05° x 0.05°	Funk *et al.*, (2015)	118.5	19.2	91-172	Amekudzi *et al.*, (2015)
	Rainfall Intensity	RFI	mm d^{-1}	0.05° x 0.05°	Funk *et al.*, (2015)	7.8	2.2	2.6-10.2	Guenang and Kamga, (2012)
	Mean Annual Temperature	MAT	°C	0.5° x 0.5°	Kalnay *et al.*, (1996)	25.9	1.2	20.8-28.6	Kalnay *et al.*, (1996)
	Length of Growing Season	LOSsum	days	0.05° x 0.05°	Didan, (2015)	232.5	21	186-304	Didan, (2015)
	Climatic Water Deficit	CWD	mm	~4km	Abatzoglou *et al.*, (2018)	709.7	189	33-1321	Rozendaal, *et al.*, (2020)
	Frost	Frost	days	0.5° x 0.5°	Harris *et al.*, (2014)	2.4	6.2	0-36	Harris *et al.*, (2014)

3.2.3 Analytical approach and model development

This study employs a hierarchical mixed-effects approach because of its inherent nature to accommodate variability at more than one level (Gelman and Hill, 2007), which herein relates to the variability at the individual stem, species, plot, and site levels. The response variable was the mean diameter increment (mm/year.) from the line of best fit of the observations. EVs included all the variables hypothesised to influence growth (Table 3.2), but to reduce the collinearity of the soil and climate data, principal components of these two sets of variables were computed. The first three principal components, which had eigenvalues greater than 1 were used for soils and the first two for climate; these accounted for 86% and 75% of the variation, respectively (Supplementary Material 3.1 and 3.2). In both cases, scree plots (Supplementary Material 3.3 and 3.4) showed that the eigenvalues start to form straight lines after the chosen principal component (PC). Following the Kaiser Criterion (Braeken and Van Assen, 2017), these PCs were retained for further analyses. EVs were chosen based on their magnitude and direction. Overall, a magnitude of ≤ -4 and ≥ 4 was considered to infer that a corresponding EV is important to the calculation of any given Principal Component (Hartmann *et al.,* 2018).

Considering the retained soil axes, the first one is mainly a texture, pH, Organic Carbon, and soil depth gradient. This axis was thought of as a measure of soil hydraulic properties and fertility. The second one is a P, N, and pH gradient (soil fertility), and the last one is mainly texture, and depth (soil hydraulic properties).

Regarding the retained climate axes, the first axis comprises mean annual precipitation (MAP), climatic water deficit (CWD), length of the growing season (LOSum), and rainfall intensity (RFI). Therefore, this axis primarily measures water availability. The second one is mainly mean annual temperature (MAT), rainy season length (RSL), and RFI. This axis is similar to the first one but with MAT and it was regarded as a measure of seasonality.

The first model (model 0) was a simple one and was developed to reflect the nested structure of the data and to produce an estimate of the region-wide mean and SEM. A second, more complex model (model 1) was used to evaluate the effects of the explanatory variables (EVs). In model 1, the effect of all predictors was allowed to vary by species which were specified as random effects (random slopes and intercepts for all predictors). Plot and site were also included as random effects. To help interpret the effect of species and identify any groupings in the data, species were clustered by their random effects. The K-means approach was then used to examine the within-groups sum of squares. This approach has previously (see Dalponte *et al.,* 2015) been found useful in computing the distance between a cluster centroid and individual observations and then assigning the observation to the nearest cluster. To decide on the optimal number of clusters, the elbow method (Thorndike, 1953), which considers the total within-cluster sum of square (WSS) as a function of the number of clusters was used. The bend in the curve of the WSS was taken as an indicator of the optimal number of clusters. This led to the identification of 2 groups which explained ~64% of the point variability.

All numerical continuous EVs were centred and scaled using their means and standard deviations (Table 3.2). Models were fit using the lme4 package (Bates *et al.,* 2015) in R Programming Language (R Core Team, 2013). Models were checked for goodness-of-fit and spatial autocorrelation in residuals using the DHARMa package (Hartig, 2015). To account for non-linearity, stem size was log-transformed. However, initial analyses revealed that log- and non-log transformed growth rates had a similar effect both in magnitude and direction. Thus, the response variable was kept without log-transforming it to avoid losing its intuitive meaning.

3.3 Results

3.3.1 Observed growth rates across SAWs

The observed mean growth increment was 1.7 ±0.02 mm/year and was non-normally distributed (Figure 3.1; median: 1.4 mm/year). 89.3% of stems had positive growth rates (Table 3.3 and Supplementary material 3.8). Since only ~10.7% of the stems experienced shrinkage, all of them were retained for further analyses. Results further show that ~79.6% of the stems grew at a rate ranging from 0 – 5 mm yr^{-1}.

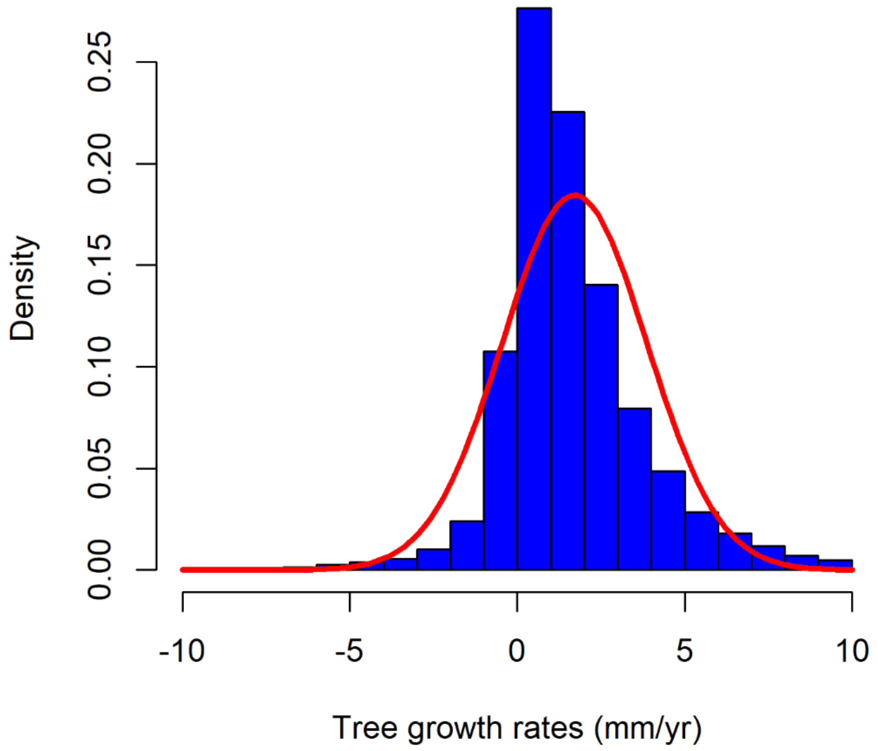

Figure 3.1: Distribution of observed tree growth rates (mm/year) across southern Africa. The red line indicates a density curve; bin width: 1 mm. The dataset contains 38,276 trees, 400 species, 223 permanent sample plots (PSPs) across 8 countries.

Table 3.3 20 most abundant species studied; Full list of all the 400 species studied is included as supplementary material 3.8. Species are arranged logically by mean annual increment. *Stems*, number of stems for each individual species; *Countries*, number of countries in which each species was present; *MAI*, stem-level mean annual increment; *SE*, standard error; *Median MAI*, median mean annual increment; *Max*, maximum mean annual increment, *Min*, minimum mean annual increment, *Neg MAI%*, stems with negative mean annual increment as a percentage of that species; *Pos MAI%*, stems with positive mean annual increments as a percentage of that species

				MAI (mm/year)						
Species	**Stems**	**Countries**	**Average census length (Years)**	**MAI**	**SE**	**Median**	**Max**	**MIN**	**Neg MAI%**	**Pos MAI%**
Julbernardia paniculata	1382	3	20	3.3	0.1	3.0	10.0	-8.0	3.6	96.4
Pterocarpus angolensis	521	7	26	2.9	0.1	2.5	10.0	-5.8	6.7	93.3
Brachystegia boehmii	1026	5	19	2.6	0.1	2.3	10.0	-6.0	7.1	92.9
Brachystegia spiciformis	541	6	21	2.3	0.1	1.8	9.7	-5.0	5.2	94.8
Julbernardia globiflora	1122	5	24	2.1	0.1	1.6	10.0	-9.8	6.9	93.1
Burkea africana	695	6	26	1.9	0.1	1.8	7.5	-8.1	5.3	94.7
Combretum adenogonium	444	1	13	1.8	0.1	1.7	6.7	-6.3	19.6	80.4
Dalbergia melanoxylon	456	4	25	1.6	0.1	1.5	8.0	-7.4	10.1	89.9
Hymenocardia ulmoides	535	1	7	1.5	0.0	1.5	8.0	-3.5	3.0	97.0
Hymenaea verrucosa	635	1	8	1.5	0.0	1.3	8.0	-9.2	3.0	97.0
Pseudolachnostylis maprouneifolia	1216	5	20	1.5	0.0	1.1	10.0	-5.6	5.7	94.3
Combretum apiculatum	2205	4	26	1.4	0.0	1.0	9.5	-7.2	11.5	88.5
Diplorhynchus condylocarpon	4727	7	26	1.4	0.1	1.1	10.0	-10.0	16.6	83.4
Combretum zeyheri	540	5	26	1.3	0.0	1.0	10.0	-10.0	8.0	92.0
Indet indet	1576	5	26	1.3	0.0	1.0	10.0	-6.2	8.1	91.9
Baikiaea plurijuga	1114	1	21	1.2	0.0	1.0	7.8	-5.0	4.0	96.0
Bauhinia petersiana	371	2	14	1.2	0.1	1.0	9.0	-4.6	14.3	85.7
Hymenocardia acida	2480	3	11	1.1	0.2	1.0	10.0	-10.0	33.0	67.0
Maytenus senegalensis	404	2	26	1.1	0.0	0.9	9.5	-9.2	6.2	93.8
Suregada zanzibariensis	577	1	8	1.1	0.0	1.0	5.5	-8.8	4.7	95.3

Based on model 0 (Table 3.4), the regional mean is estimated at 1.62 ± 0.3 mm/year, with site-level means ranging from 1 – 3 mm yr^{-1} (Figure 3.2). Much of the variation is explained at the species, site, and plot levels, respectively. The Katanga site in the Democratic Republic of Congo (DRC) has the fastest growth rates while the slowest were observed at the Bateke site of Congo, in Tanzania, Zambia, and parts of Zimbabwe.

Table 3.4: A structural summary of the two models used in this study. inc, diameter increment; AIC, Akaike Information Criterion; fixed effects: stem size, competition, fire, Hydraulic properties and soil fertility (Soil PCA1); Soil fertility (Soil PCA2); Hydraulic properties (Soil PCA3); Seasonality (Climate PCA1); Water availability (Climate PCA2)

Model	**Formula**	**AIC**	**ΔAIC**	**Akaike weight**
Model 0	inc ~ (1 | site) + (1 | plot) + (1 | species)	161341.3	49985.3	0
Model 1	inc ~ fixed effects + (1 | site) + (1 | plot) + (fixed effects | species)	111356	0	1

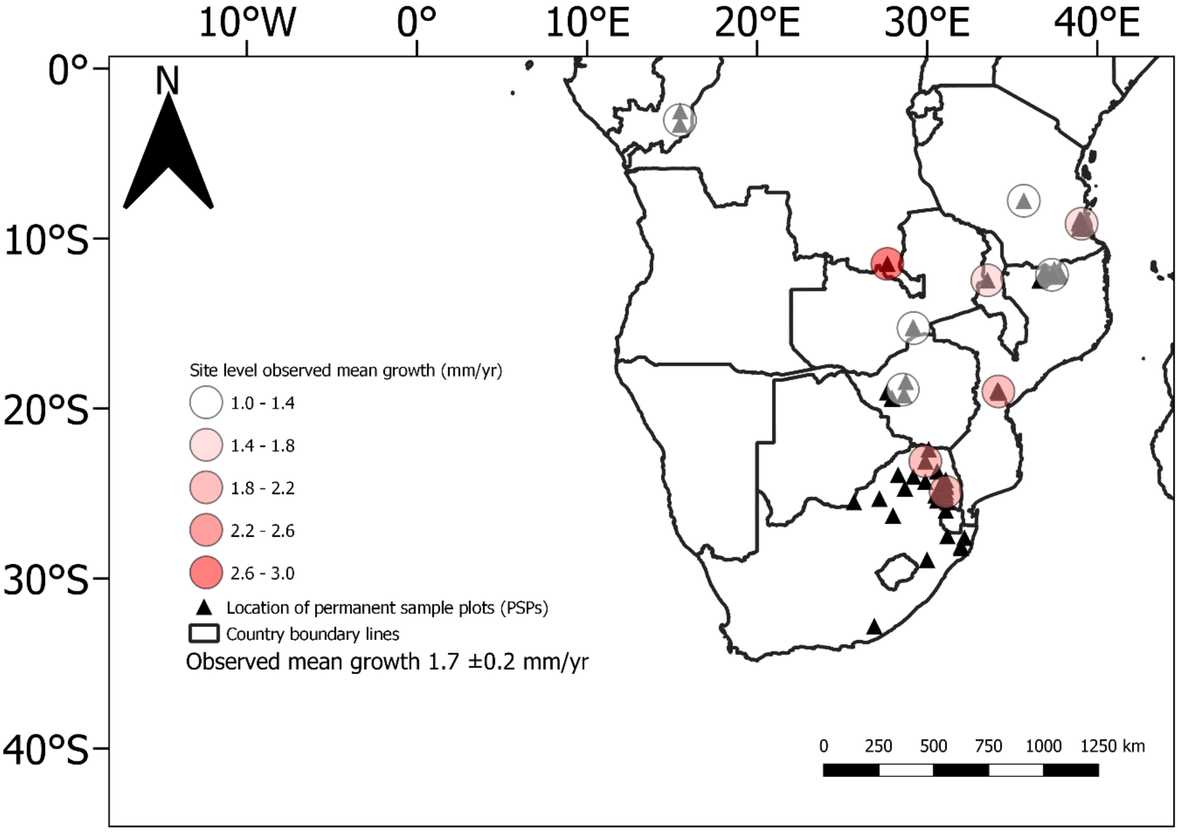

Figure 3.2: Site level observed mean annual growth rates (mm yr^{-1}) and geographical distribution of PSPs. The dataset contains 38,276 trees, 400 species, 223 permanent sample plots (PSPs) across 8 countries. The inventory period spans 27 years (1991 – 2018)

3.3.2 Determinants of growth rates across SAWs

Having accounted for stem-, plot-, and site-level attributes (Model 1; Table 3.5), results indicate that of the fixed effects, water availability is the only EV that has a positive effect on tree growth. However, it is important to note that the only effect that is significant here is plot-level basal area (BA) which is used as a proxy for tree-tree competition. It was found to have a negative effect on tree growth rates.

It is worth noting here that all fixed numerical continuous variables were standardized using their means and standard deviations (Table 3.2) before using them to drive models. Therefore, the contribution of all EVs together with residuals to the observed 1.62 ± 0.3 mm yr^{-1} mean annual growth rate implies that one standard unit of competition/BA (9.9 m^2 ha^{-1}) reduces tree growth rates by 0.2 mm $yr\text{-}^1$ (Table 3.4) which translates into a 12.3% reduction in growth. Further, it is also worth mentioning that across differently structured models, competition is the only EV that was significant. Regarding the grouping variables, much of the variance (0.57 i.e., 10.2%) is explained at the site level, followed by species (0.23 i.e., 4.2%), and plots (0.17 i.e., 3.1%) respectively.

Table 3.5: Statistical summary of model 1 with highlighted row denoting statistically significant fixed effects at the *α* 0.05. PSPs, permanent sample plots.

Fixed Effects			
	Variable	**Estimate**	**Std Error**
	Intercept	1.6	0.3
	Initial diameter	-0.0	0.1
	Competition	-0.2	0.1
	Fire	-0.0	0.1
	Hydraulic properties and soil fertility	-0.0	0.1
	Soil fertility	-0.0	0.1
	Hydraulic properties	-0.1	0.1
	Seasonality	-0.3	0.1
	Water availability	0.1	0.2
Random Effects			
Groups	**Name**	**Variance**	
PSPs	Intercept	0.2	
Species	Intercept	0.2	
	diam_y0.log	0.1	
	ba.plot	0.0	

	fire	0.1
	Hydraulic properties and soil fertility	0.0
	Soil fertility	0.1
	Hydraulic properties	0.1
	Seasonality	0.1
	Water availability	0.1
Site	Intercept	0.6
	Residual	4

To assess the effect of competition on different tree sizes, stems were divided into small (< 10 mm), medium (10 – 20 mm), and large (> 20 mm) classes. This assessment revealed interesting findings: first, competition was found to consistently reduce growth rates and it had the largest negative effect (Fig. 3.3). Second, the effect of competition was found to be largest on small trees (Fig. 3.3B), and this is consistent with previous literature elsewhere (e.g., Das, 2012).

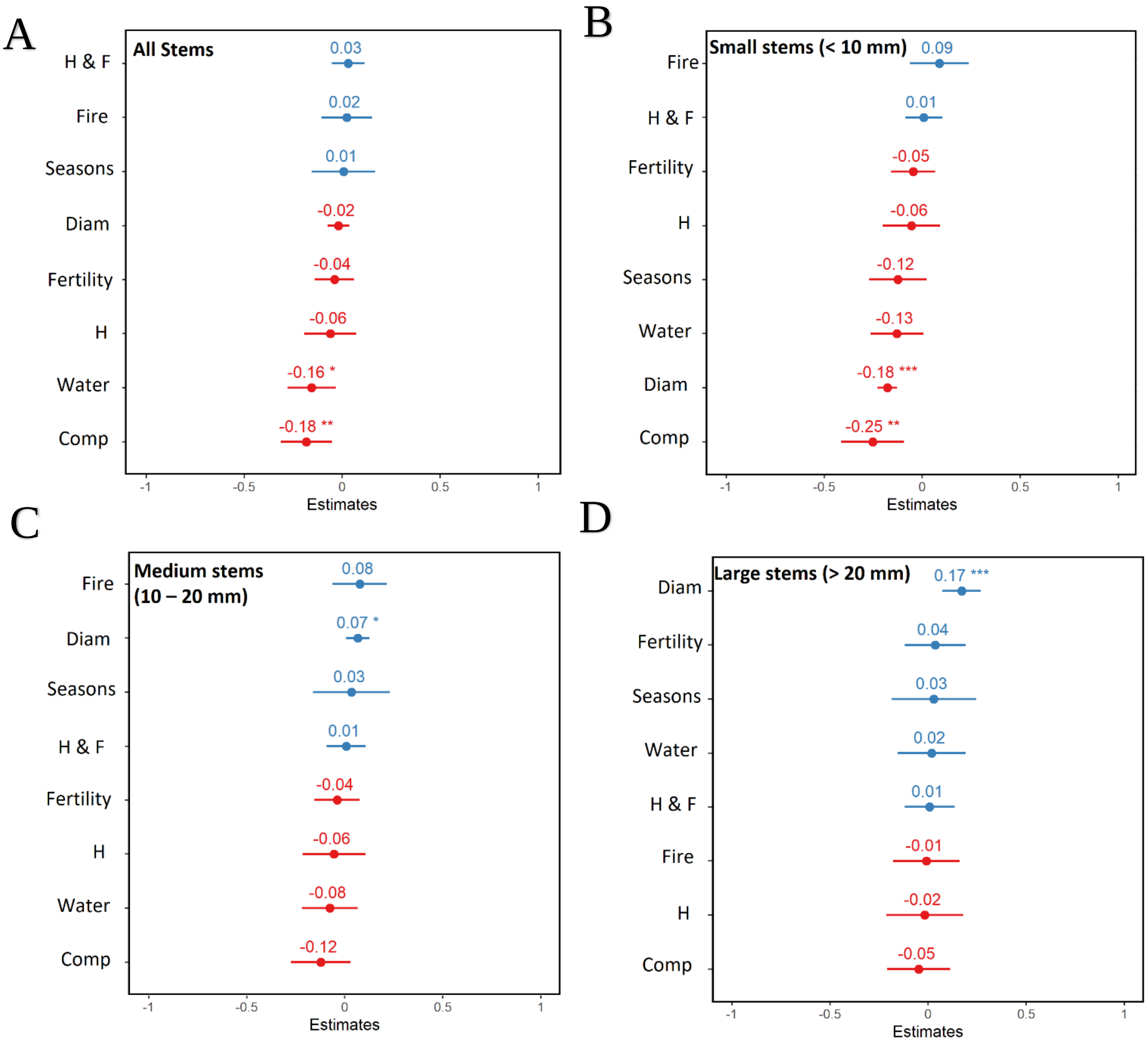

Figure 3.3: Effect of explanatory variables (EVs) on tree growth rates across differently sized stem classes for **A)** All stems **B)** small stems (< 10 mm) **C),** medium stems (10 – 20 mm), and **D)** large stems (> 20 mm). Diam, diameter at breast height (DBH); Fertility, soil fertility; H, soil hydraulic properties; H & F, soil hydraulic properties and soil fertility, Water, water availability; Season, Seasonality; Comp, basal area used as a surrogate of inter-tree competition. EVs are arranged in order

of effect size with blue symbolizing positive effect and red negative effective. Significance codes: 0 '***'; 0.001 '**'; 0.01 ‘*’

An exploration of the conditional modes of the random effects in the final model revealed noticeable variability in the response of species to EVs. Some species were observed to have similar responses in direction while others had opposite responses (Figure 3.4). Based on this observation, the effect of species was explored further to identify any possible groupings in the data.

The K-means approach was used to examine the within-groups sum of squares. To decide on the optimal number of clusters, the elbow method (Thorndike, 1953), which considers the total within-cluster sum of square (WSS) as a function of the number of clusters was used. The bend in the curve of the WSS was taken as an indicator of the optimal number of clusters. However, results showed no perfect bend (Figure 3.5), thus 2 clusters were chosen because they showed the steepest change (Figure 3.5). The absence of a perfect bend suggests that a continuum of responses across species exists and the only species that can have used for further analyses are those far apart while leaving out those at the intersection. Therefore, only the 2 clusters were studied further.

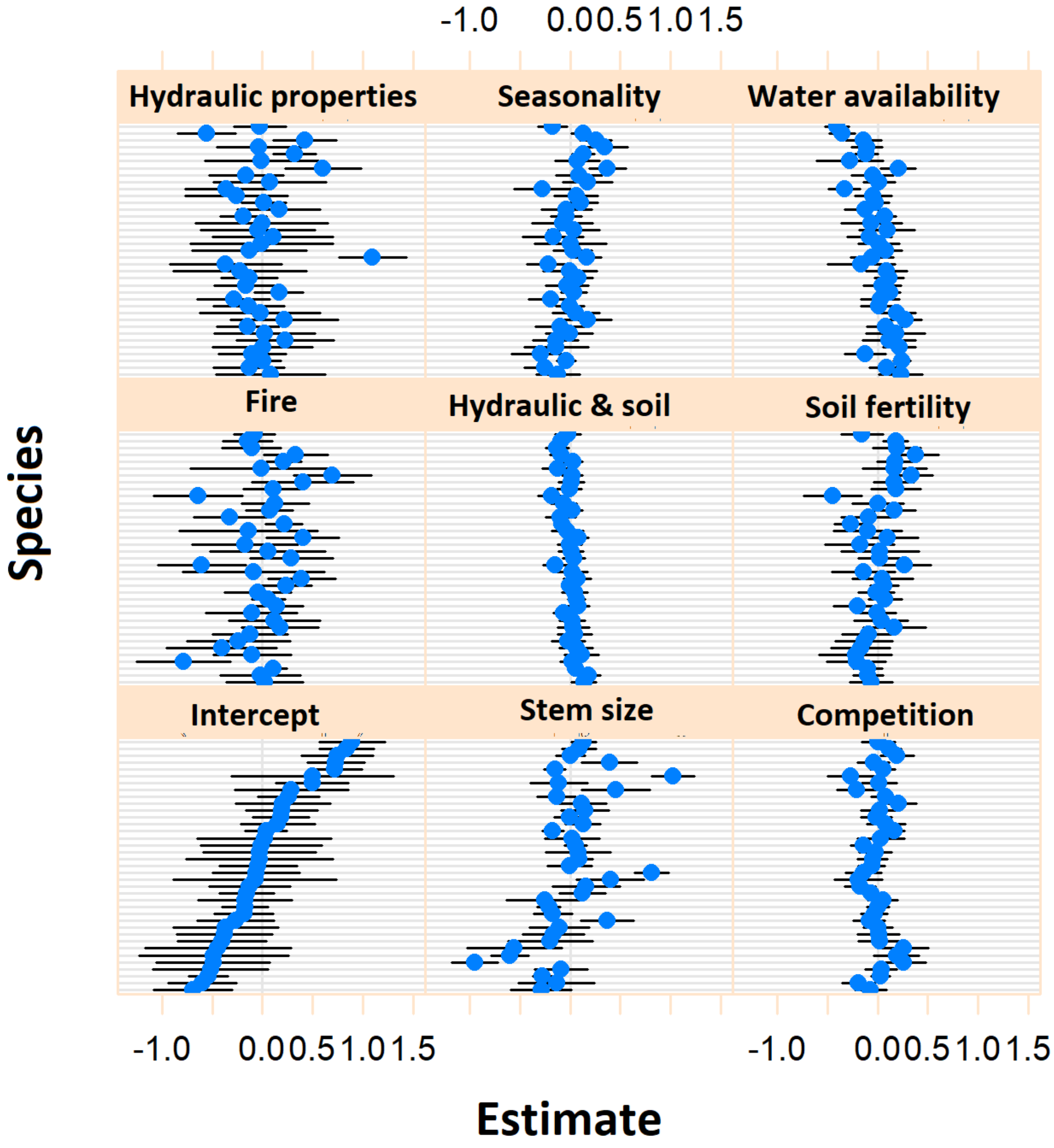

Figure 3.4: Response of species to explanatory variables showing that species respond variably to each explanatory variable. Species are not ranked in any specific order as the motivation here is to show that some species were observed to have similar responses in direction while others had opposite responses

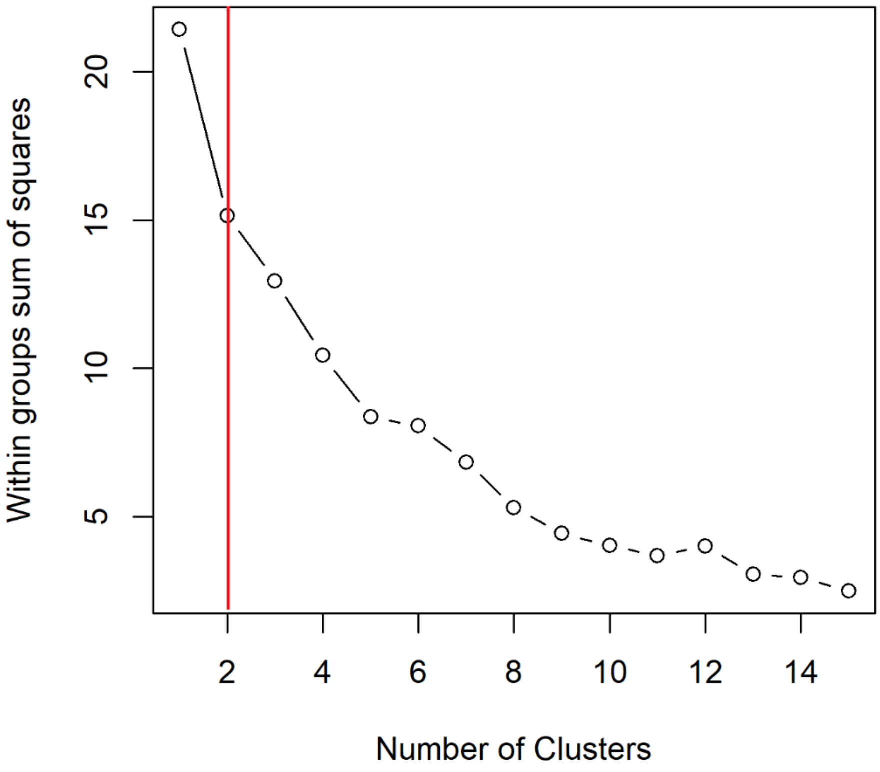

Figure 3.5: Within-cluster sum of squares for the optimal number of clusters. The red vertical line indicates the number of clusters chosen

A closer examination of the two clusters revealed that those that are generally fast growers (e.g., *Brachystegia boehmii* and *julbernardia globiflora*) are miombo woodland dominant trees and are shown in orange (Figure 3.8). Slow growers (e.g., *Annona senegalensis*) are generally open-savanna dominant species (shown in green). At the cluster level, species were found to respond variably to climate. Fast growers (miombo dominants) were observed to perform better than slower growers (savanna dominants) even under less water availability but were critically affected by more seasonality. Further, miombo dominant trees were found to generally grow faster as they increase in size while bigger trees characteristic of Savanna systems exhibited slow growth rates. The single most striking observation to emerge from this analysis is that the response of different species to competition across environmental gradients is roughly similar entailing that competition is widespread across the subcontinent.

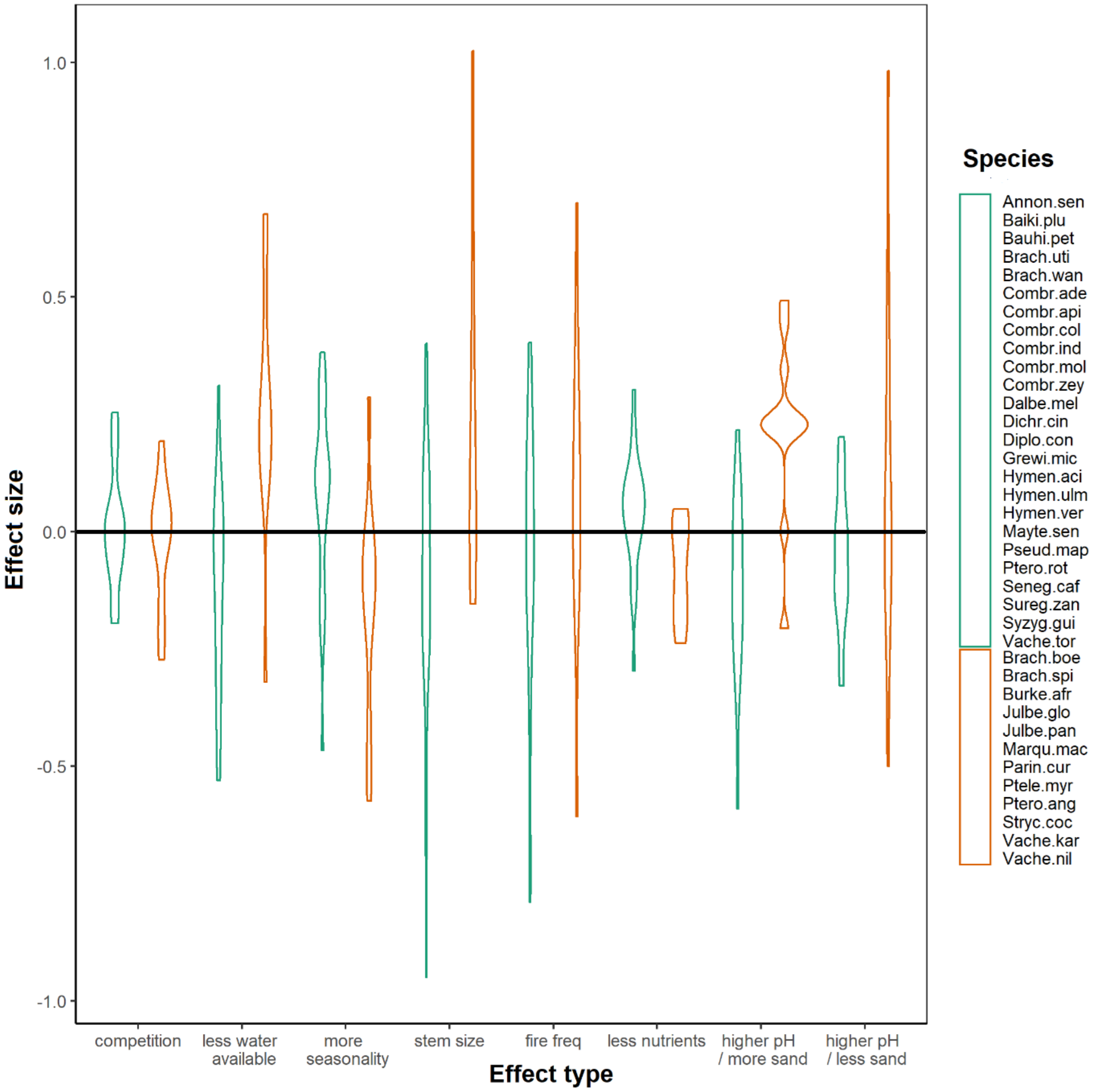

Figure 3.6: Effect type and size based on clustering of species with similar effect. Orange colour shows fast growers which are *mainly* miombo woodland dominant trees. Green shows slow growers which are *generally* open-savanna dominant species. Fast growers perform better than slower growers even under less water

availability but are critically affected by more seasonality. Strikingly, the response of all species to competition is roughly similar. The black horizontal line shows y = 0. *Annon.sen, Annona senegalensis; Baiki.plu, Baikiaea plurijuga; Bauhi.pet, Bauhinia petersiana; Brach.uti, Brachystegia utilis; Brach.wan, Brachystegia wangermeeana; Combr.ade, Combretum adenogonium; Combr.api, Combretum apiculatum; Combr.col, Combretum collinum; Combr.ind, Combretum indet; Combr.mol, Combretum mole; Combr.zey, Combretum zeyheri; Dalbe.mel, Dalbergia melanoxylon; Dichr.cin, Dichrostachys cinerea; Diplo.con, Diplorhynchus condylocarpon; Grewi.mic; Grewia macrocarpa; Hymen.aci, Hymenocardia acida; Hymen.ulm, Hymenocardia ulmoides; Hymen.ver, Hymenocardia vertus, Mayte.sen, Maytenus senegalensis; Pseud.map, Pseudolachnostylis maprouneifolia; Ptero.rot, Pterocarpus rotundifolius; Seneg.caf, Senegalia caffra; Sureg.zan, Suregada zanzibariensis; Syzyg.gui, Syzygium guineense; Vache.tor, Vachellia tortilis; Brach.boe, Brachystegia boehmii; Brach.spi, Brachystegia spiciformis; Burke.afr, Burkea Africana; Julbe.glo, Julbernardia globiflora; Julbe.pan, Julbernardia paniculate; Marqu.mac, Marquesia macroura, Parin.cur, Parinari curatellifolia; Ptele.myr, Pteleopsis myrtifolia; Ptero.ang, Pterocarpus angolensis; Stryc.coc, Strychnos cocculoides; Vache.kar, Vachellia karroo; Vache.nil, Vachellia nilotica*

3.4 Discussion

3.4.1 Observed growth rates across SAWs

One of the initial aims of the current study was to estimate growth rates of woodland trees across the sub-continent. Here, potential implications of growth rates documented in section 3.3 will be discussed before moving on to their determinants.

Findings demonstrate that individual trees are growing at 1.6 ±0.3 mm yr^{-1}. When this rate was compared to growth studies in the region (Table 3.6), it was found that at 1 significant figure, 75% of all biometry-based studies are within ±0.5 mm yr^{-1} thus, indicating good model skill. It is worth noting though that most increment-core-based studies have substantially higher growth estimates than biometry-based. Additionally, estimates found in the literature (e.g., De Cauwer *et al.,* 2017; Chidumayo, 2019; Williams, 2020) were largely for local PSPs, in one or two countries. None of the studies had a dataset large enough to estimate the regional mean growth rate. In fact, Swemmer and Ward, (2020) contend that while published growth rate data across SAWs are useful for the improvement of simulation models, they are currently inadequate to establish regional patterns thus, tree growth rates across the sub-region remains a major uncertainty. Therefore, this study provides the subcontinent's largest growth data hence the first data-supported regional estimate across a wide environmental gradient.

While the dataset used in this study provides invaluable insights on the subcontinent's growth rates and patterns, it suffers from a geographical bias with most PSPs mainly being located across eastern parts of the region and little to no data in the western parts of SAWs. Understanding tree growth rates across unmeasured areas of SAWs is, therefore, one of the region’s most pressing issues. This knowledge gap provided the motivational foundation of Chapter 4 of this thesis.

3.4.2 Determinants of tree growth rates across SAWs

The observation that plot-level tree basal area (BA), herein referred to as competition, was the only explanatory variable (EV) that was significant across all models suggests that tree-tree competition is widespread across the region. Its negative effect on tree growth rates can be attributed to limited resource availability on stands with high competition (Fernández-de-Uña *et al.,* 2015). In a recent study, Rozendaal *et al.,* (2020) found that competition reduces tree growth rates, and its effect is invariant across environmental gradients. This corroborates findings embodied in this study. Several other studies (e.g., Thomas *et al.,* 2009; Calabrese *et al*., 2010) also document the depressing effect of competition on tree growth consistent with the findings in the present study.

With regards to the relationship between species and competition, Seifert *et al.,* (2014) found great variation in species reaction to competition in South Africa. In the present study, a near-zero variation across the whole region was found entailing that while there may be localized variations, overall, competition has a negative effect on species growth rates. It is notable that while many studies have documented the negative effect of competition on tree growth rates, all of them were based on forest trees and none in savannas. Further, no study appears to have placed emphasis on the magnitude of effect. By clearly showing that 1 SD of BA (9.9 m^2 ha^{1}) reduces growth by 12.3 ±0.7% and that the response of species across the region is roughly similar, this study documents a contribution that has previously not been described. The observed widespread tree-tree competition likely plays an important role in determining community composition and sustaining tree-grass coexistence (Dohn *et al.*, 2013). It is also likely to moderate the current increase of trees in savanna systems *(*Kalwu *et al.,* 2010) and the associated carbon sink (Hubau *et al.,* 2020), with global implications for the Anthropocene carbon cycle (Babst *et al.,* 2014).

Model outputs showed that species respond variably to climate. Specifically, fast growers (miombo dominants) were found to perform better than slower growers (savanna dominants) even under less water availability but were critically affected by more seasonality. The dissimilar response of savanna and miombo dominant species to seasonality and water availability has not been previously described. These findings, therefore, shed new light on this. It is important to note that the intensity and frequency of droughts are projected to intensify (Taylor *et al.,* 2012; Zhao and Dai, 2015) implying a potential reduction in available water for tree growth in the near future. This will potentially lead to a strain on the growth of food trees which are mainly slow growers thus, thrusting the future of food security for the rural majority into further disarray. On the other hand, the observation that fast growers perform well even under less water availability suggests that they are more tolerant to drought than slow growers thus, more likely to increase in abundance relative to co-occurring slow-growing tree species. This will potentially make water availability an important dictator of southern African woodland dynamics and composition.

Although water availability was found to be insignificant in the present study, its positive effect was not surprising as it has been documented in several studies around the world (Stahle *et al.,* 1999; Shackleton *et al.,* 2002). In fact, similar findings are documented in the work of Toledo *et al.,* (2011) who used 165 1-ha sample plots to study tree growth rates across Bolivian tropical lowland forests. They found that climate is a stronger driver of tree growth than soils with an increase in rainfall leading to higher tree growth rates. Broadly, tree physiology suggests that rainfall, which furnishes soil moisture (Walter, 2018; Case and Staver, 2018), enhances tree growth. However, contrary to expectations, this study did not find a significant downward gradient of growth rates from high to low rainfall PSPs. This absence is thought to indicate that while water availability is important, the magnitude of effect in comparison to other EVs (e.g., competition) and grouping variables (e.g., site) is more important.

Regarding soils, species were again found to respond variably to them. Of interest, the effect of soils was found to be small. This find supports evidence from recent observations such as those of Muledi *et al.,* (2020) who used comprehensive soil data sampled at high spatial resolution and found very little effect of the EV on growth. In fact, they documented that only 4 of the 19 species studied had some influence from soils. In a recent detailed review of savanna growth rates, Swemmer and Ward, (2020) also found little influence of soils on growth rates – in agreement with this data-supported study. They attributed this lack of influence to the possibility that savanna trees have evolved enough to enable different species to maximize the use of available nutrients, for each soil type within each region, such that precipitation and light become the primary determinants.

Perhaps one of the most frequently asked questions in tree growth studies is whether big trees grow faster than smaller ones. This question is critical because the growth rate of an individual tree determines the growth and productivity of an entire stand over time (Binkley *et al.,* 2013). Some studies have argued that large trees generally grow faster than smaller ones. It is postulated that this happens because bigger trees generally tend to have deeper root systems than smaller ones. Therefore, during dry spells, bigger trees can find water and nutrients at greater depth. Empirical evidence further suggests that bigger trees have more resilient barks than smaller ones. Weak barks tend to easily get bruised and open up to the entry of pathogens that cause myriad infections. When this happens, trees concentrate on healing thereby, stunting growth (Tavankar *et al.,* 2018). Binkley, (2004) also adds that bigger trees grow faster than smaller ones in the same stand because they use resources more efficiently. In this work, when species-diameter interactions were considered, it was found that big trees in the higher rainfall miombo woodland generally grow fast while big open savanna trees do not. This observation re-echoes the resource limitedness of open savanna environments as well as the slow growth functional types of open savanna species.

3.4.3 Fast and slower growers across SAWs

Results at the species level indicate that stems that have the fastest increment are mainly the woodland dominants while the slower growing trees are smaller, open savanna species. Slow growth in the open savanna species can be attributed to limited resources in savanna environments and differences in functional types between woodland dominants and open savanna species. This is corroborated by Rossatto *et al.,* (2009) who studied growth differences between co-occurring forest and savanna trees and found that generally, savanna trees grew slower due to limited resources in their environments. However, when forest trees invaded the savanna, they showed faster growth despite limited resources. The study, therefore, concluded that apart from resource availability, species-specific functional type contributes to how fast a tree grows.

3.4.1 Implications of observed growth rates across SAWs

Growth rates contained in this study have crucial implications across myriad disciplines. For instance, 70% of Africa's poor live in rural areas with 90% of these livelihoods being directly or indirectly dependent on agriculture (Dione, 2007). However, Sub-Saharan Africa is projected to remain food insecure by 2050 (Onyutha, 2018). Many rural people are likely to turn to food trees for survival as they often do during drought-driven famine (Hertsgaard, 2011). With an average annual growth rate of 1.3 ±0.1 mm, most of the food trees (e.g., *Annona senegalensis*) in this dataset are savanna dominant and thus, slow growers. This, therefore, highlights a crucial need for renewed interest in conserving them if their potential to contribute to rural food security and improve nutrition is to be realized (National Research Council, 2008).

The observed slow growth of trees across SAWs will have other cascading effects on livelihoods because growth is the principal regulator of water, energy, and carbon among savanna ecosystems themselves, the hydrosphere, and ordinarily, the atmosphere (Swemmer and Ward, 2020). As such, tree growth is a key parameter for the structure and proper functioning of SAWs which provide energy, traded wood fuels, and the much-needed nutrient transfer to agricultural fields (Ryan *et al.,* 2016). When slow growth rates are coupled with overexploitation of woodland resources, the ability of SAWs to provide ecosystem products and services is thrown into disarray.

Regarding timber species, *Dalbergia melanoxylon* and *Pterocarpus angolensis* are the only fast growers that are timber species in this dataset. The use of *Pterocarpus rotundifolius* for timber has generally been discontinued due to a general lack of durability (Venter and Venter, 1996). Among the slow growers, *Baikiaea plurijuga* and *Vachellia tortilis* are the only timber species. However, other species such as *Combretum zeyheri, Suregada zanzibariensis,* and *Senegalia caffra* though not commercial timber trees, are often logged and used as fencing posts (Tropical Plants Database, 2020). While the timber-related use of these trees is apparent, the conservation of *Pterocarpus angolensis* is of utmost importance given its commercial demand especially that findings embodied in this work indicate that its regional growth rate is 2.9 ± 0.07 mm yr^{-1}. This suggests that it would generally take long for trees of this species to reach an acceptable harvesting size. Thus, calls for reinforcement of sustainable management practices.

Table 3.6: A comparative analyses of model predictions and what the literature says

Source	Country	Criteria	Method	What they found	Findings in this study using similar criteria
Williams, (2020)	South Africa	DBH >100 mm of 5 medicinal species i.e. A. *adianthifolia, B. maughamii, E. transvaalense, S. chirindensis, W. salutaris*	Biometry	B. maughamii 2.2 mm yr^{-1}	Of the 5 species, only B. maughamii is present in the data used in this study. The model predicts that this species is growing at 1.6 mm yr^{-1} thus, roughly similar to their find
Chidumayo, (2019)	Zambia	DBH ≥ 30 mm	Biometry	3.4 – 5.0 mm yr^{-1} in re-growth areas and 1.5 mm	Based on data availability, only uneven-aged old-growth stands were examined in

Source	Country	Criteria	Method	What they found	Findings in this study using similar criteria
				yr^{-1} in uneven-aged old-growth stands.	this study and at 2.1 mm yr^{-1}, the model estimate is not very different from that of Chidumayo.
De Cauwer *et al.*, (2017)	Angola and Namibia	Used both DBH measurements and growth rings to interrogate the productivity potential of *Pterocarpus angolensis* with DBH ≥ 50 mm	Biometry and Increment cores	5.2 mm yr^{-1}	The model estimate is 2.4 mm yr^{-1} thus, substantially lower than what De Cauwer *et al.*, (2017) found.
Van Holsbeeck *et al.*, (2016)	Namibia	Used increment cores	Increment cores	7.1 – 8.0 mm yr-1 in the Kavango region and 5.0 mm yr^{-1} in northern Namibia	Model prediction is 2.7 mm yr^{-1} thus, substantially lower than theirs
Mugasha *et al.*, (2016)	Tanzania	DBH ≥ 50 mm	Biometry	~1.5 mm yr-1 (average of the 3 species clusters)	Model prediction is 0.5 mm yr^{-1} thus, lower than that of Mugasha.
Therrell *et al.*, (2007)	Botswana, South Africa, Mozambique, Zambia, and Zimbabwe	Used tree rings to analyse growth of *Pterocarpus angolensis*	Increment cores	2.6 – 4 mm yr^{-1}	Model prediction is 1.5 mm yr^{-1} thus, lower than theirs
Trouet *et al.*, (2006)	Zambia	Used tree rings to study growth of *Brachystegia spiciformis* at 3 sites	Increment cores	2.4, 2.6, and 3.2 mm yr^{-1}, for sites 1, 2, and 3 respectively	Model predicts 2.2 mm yr^{-1} thus, roughly similar to theirs

Source	Country	Criteria	Method	What they found	Findings in this study using similar criteria
Schwartz *et al.,* (2002)	Tanzania	DBH ≥ 20 mm *Pterocarpus angolensis* and growth rings	Biometry and Increment cores	4.9 mm yr^{-1}	Model predicts 2.2 mm yr^{-1} thus, lower than theirs
Shackleton *et al.,* (2002)	SA	Only Bushbuckridge was studied	Biometry	4.5 mm yr^{-1}	Model predicts 2.8 mm yr^{-1} thus, lower than theirs
Stahle *et al.,* (1999)	Zimbabwe	Growth rings of *P. angolensis* were studied	Increment cores	4 mm yr^{-1}	Model predicts 2.3 mm yr^{-1} thus, lower than theirs

3.5 Concluding thoughts

This study set out to investigate tree growth rates across the broader southern African region to provide information relevant to the policy dialogue that seeks to champion sustainable utilization of the woodlands. Results show a mean diameter increment of 1.62 ± 0.03 mm yr^{-1} across the region. Of the fixed effects tested, variation was found to be mainly explained by plot-level tree basal area, a proxy for tree-tree competition. The most striking result to emerge from this study is that the effect of competition on both savanna systems and miombo dominant trees remains roughly similar and statistically significant. This is the first evidence that tree-tree competition is a widespread phenomenon in African savannas even in the presence of chronic disturbance and resource limitations.

Notably, the observed mean annual growth is relatively slow and consistent with earlier analyses in some parts of southern Africa (e.g., Chidumayo, 2019). Evidently, to meet future demand for ecosystem products and services, growth cannot be relied upon to replace harvested trees. Instead, these woodlands need much more intensive management of existing trees. Policy formulations that promote poverty alleviation have the potential to incentivize woodland conservation as this would potentially ease the pressure on the woodlands.

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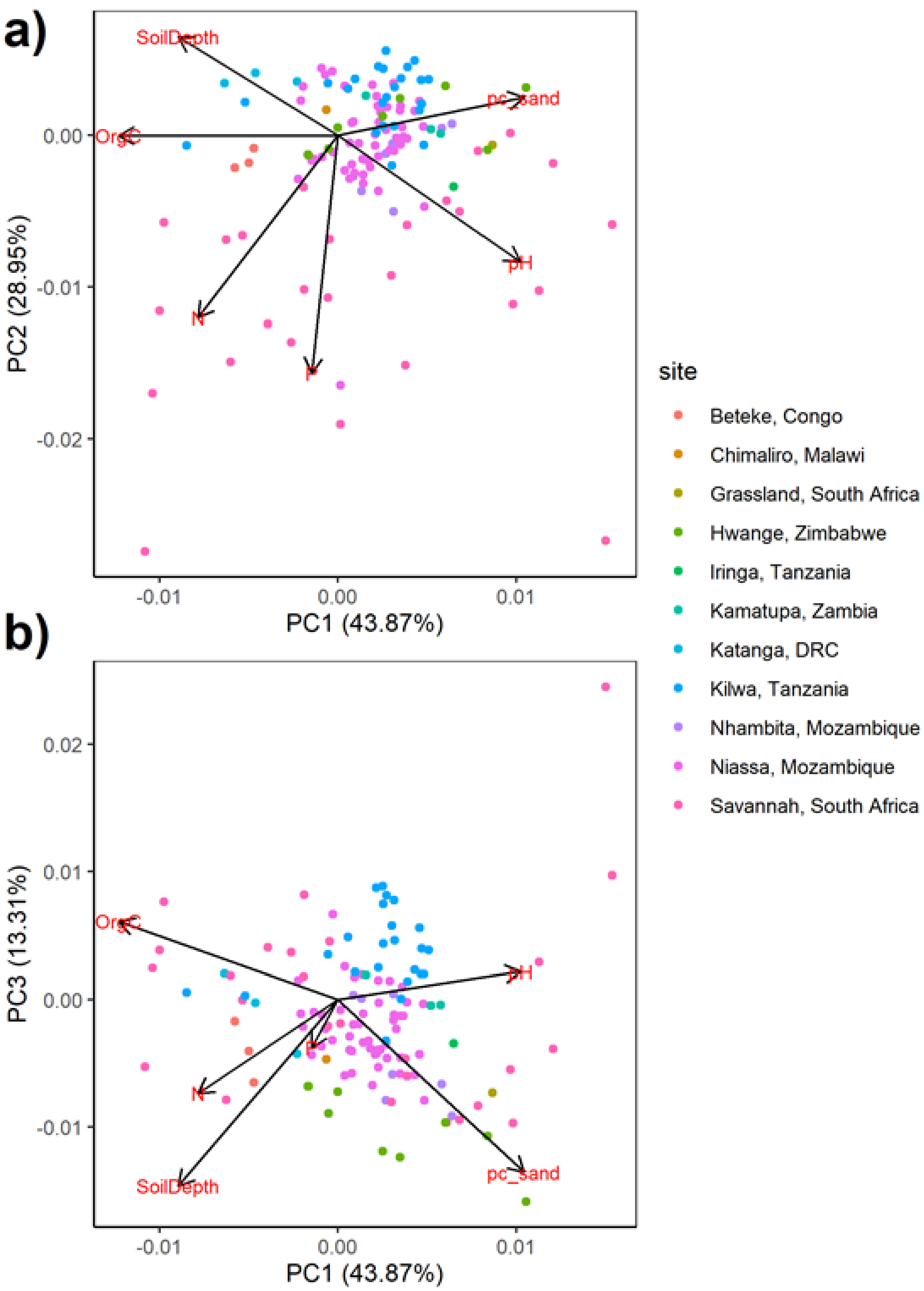
Supplementary Material 3.1: Importance of soil principal components

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Standard deviation	1.62	1.32	0.89	0.59	0.58	0.39
Proportion of variance	0.44	0.29	0.13	0.06	0.06	0.02
Cumulative proportion	0.44	0.73	0.86	0.92	0.98	1

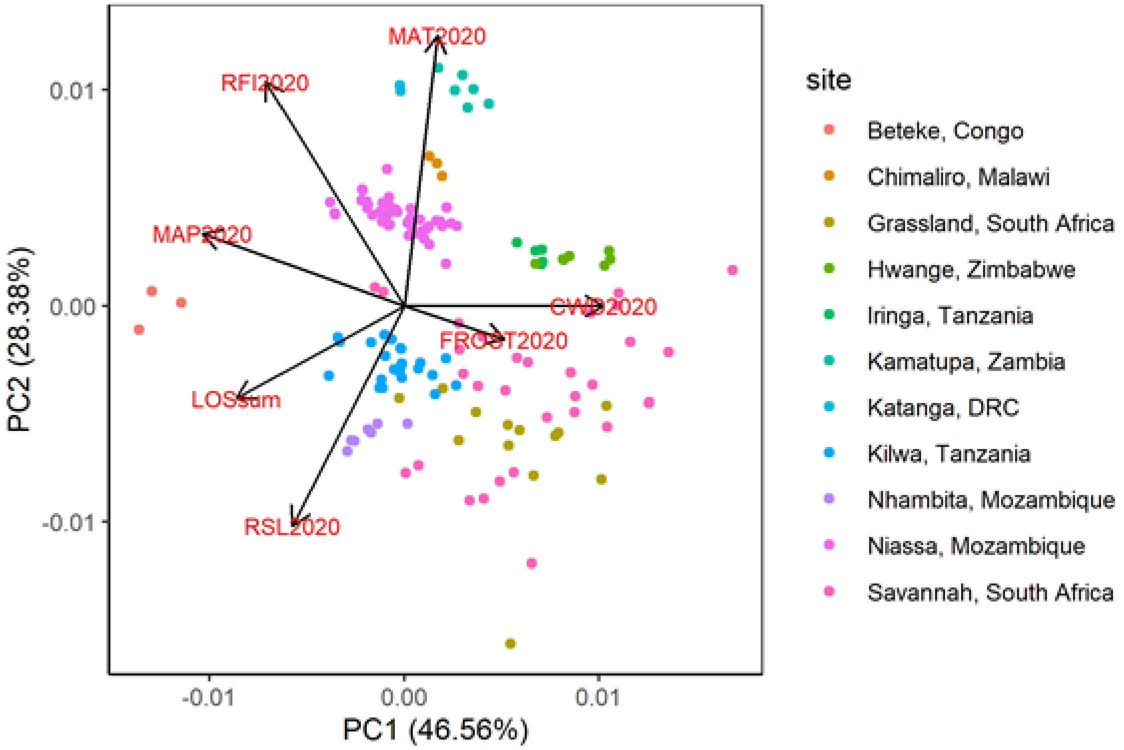
Supplementary Material 3.2: Principal components of soil explanatory variables (EVs) with **a)** showing the first and second components; **b)** first and third components. OrgC, Organic Carbon; N, Soil Nitrogen; P, Soil Phosphorus; pc_sand, %sand



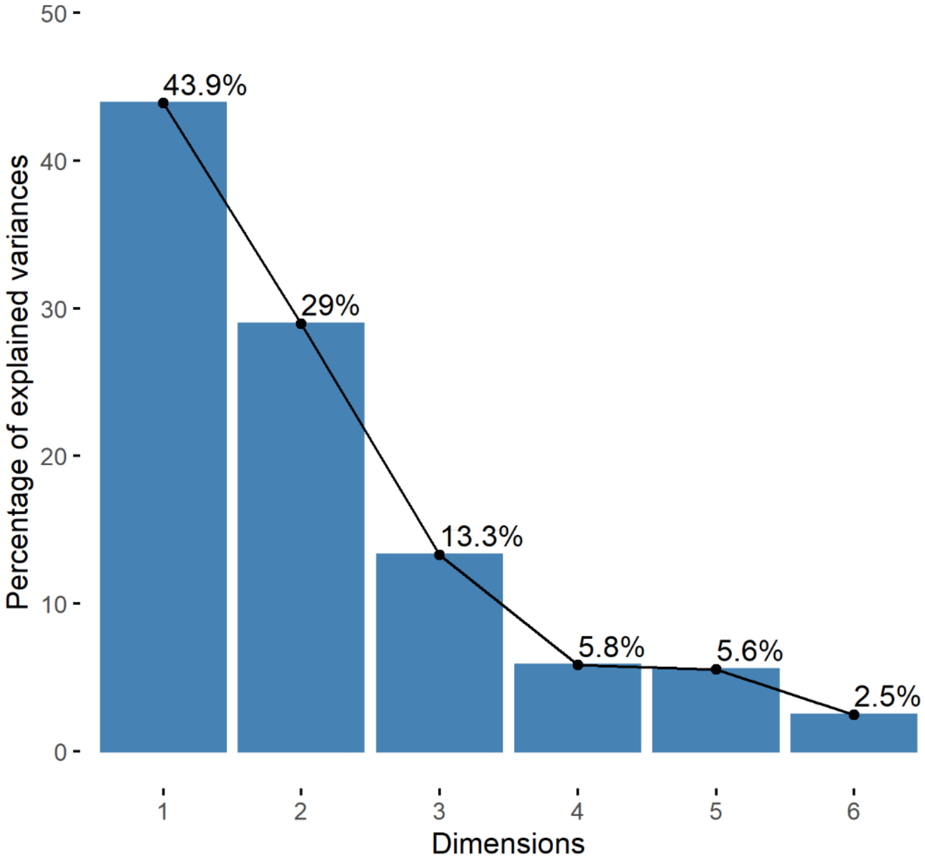
Supplementary Material 3.3: Importance of climate principal components

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Standard deviation	1.81	1.41	0.93	0.65	0.60	0.29	0.06
Proportion of variance	0.47	0.28	0.12	0.06	0.05	0.01	0
Cumulative proportion	0.47	0.74	0.87	0.93	0.99	0.99	1

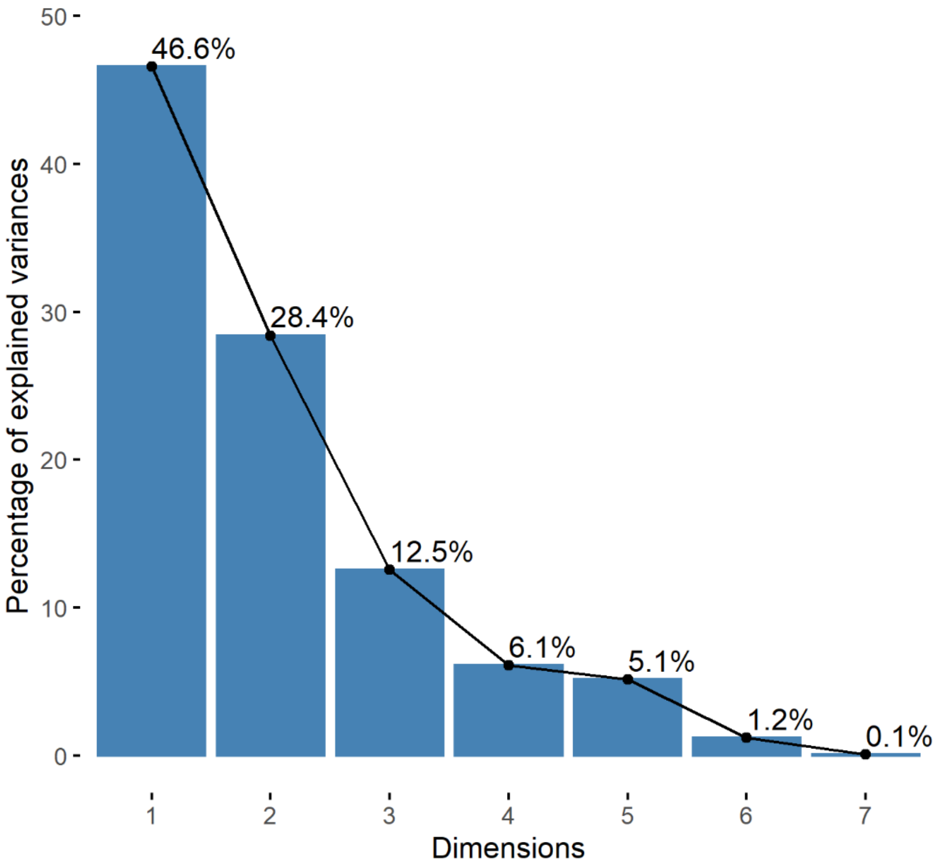
Supplementary Material 3.4: Principal components of climate explanatory variables (EVs). RSL2020, rainy season length; RFI2020, rainfall intensity; MAP2020, mean annual precipitation; LOSsum, length of the growing season; CWD2020, climatic water deficit; FROST2020, frost occurrence; MAT2020, mean annual temperature



Supplementary Material 3.5: Scree plot of soil PCAs. The first dimension is mainly a texture, pH, Organic Carbon, and soil depth gradient. The second one is a P, N, and pH gradient, and the third one is mainly texture and depth.



Supplementary Material 3.6: Scree plot of climate PCAs. The first dimension is mainly mean annual precipitation (MAP), climatic water deficit (CWD), length of the growing season (LOSum), and rainfall intensity (RFI). The second one is mainly mean annual temperature (MAT), rainy season length (RSL), and RFI.



Supplementary Material 3.7: Full list of SEOSAW Partners in alphabetical order

Anderson Muchawona[2], Caroline Lehmann[1], Charlie M. Shackleton[3], David Bauman[4], Emmanuel N. Chidumayo[5], Jonathan I. Muledi[6], Katani J. Zephania[7], Mylor N. Shutcha[6], Natasha Ribeiro[8], Paula Nieto-Quintano[1], Rebecca Stedham[9], Ricardo M. Holdo[10], Sally Archibald[11], Samuel J. Bowers[1], Steve D. Makungwa[12], Thomas K. Brade[1], Anthony M. Swemmer[13], Williams Mathew[1], Wilson A. Mugasha

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Supplementary Material 3.8: Full list of all the 400 species studied. *Stems*, number of stems for each individual species; *Countries,* number of countries in which each species was present; *MAI*, stem-level mean annual increment; *SE,* standard error; *Median MAI,* median mean annual increment; *Max,* maximum mean annual increment, *Min,* minimum mean annual increment, *Neg MAI%,* stems with negative mean annual increment as a percentage of that species; *Pos MAI%*, stems with positive mean annual increments as a percentage of that species

				MAI (mm/year)						
Species	**Stems**	**Countries**	**Average census length (Years)**	**MAI**	**SE**	**Median**	**Max**	**MIN**	**Neg MAI%**	**Pos MAI%**
Psydrax mutimushii	2	1	4	8.8	0.4	8.8	9.5	8.0	0.0	100
Syzygium congolense	1	1	2	7.5	0.6	7.5	7.5	7.5	0.0	100
Berchemia zeyheri	1	1	4	7.4	0.1	7.4	7.4	7.4	0.0	100
Albizia ferruginea	2	1	2	7.3	0.6	7.3	8.0	6.5	0.0	100
Senegalia galpinni	1	1	11	6.7	0.1	6.7	6.7	6.7	0.0	100
Elaeis guineensis	2	1	8	6.7	0.0	6.7	6.9	6.5	0.0	100
Cussonia natalensis	4	1	6	5.8	0.1	5.5	9.8	2.3	0.0	100
Terminalia gerrardii	1	1	8	5.8	NA	5.8	5.8	5.8	0.0	100
Ekebergia pterophylla	2	1	6	5.6	0.0	5.6	7.5	3.7	0.0	100
Senegalia galpinii	3	1	5	5.4	0.0	5.3	6.0	5.0	0.0	100
Sterculia quinqueloba	3	2	11	5.3	0.0	5.8	8.0	2.3	0.0	100
Terminalia indet	4	1	4	4.9	0.1	4.6	7.6	2.6	0.0	100
Albizia versicolor	16	3	21	4.6	0.1	3.9	9.8	1.3	0.0	100
Englerophytum magalismontanum	1	1	6	4.5	0.0	4.5	4.5	4.5	0.0	100
Harpephyllum caffrum	1	1	6	4.5	0.1	4.5	4.5	4.5	0.0	100
Ficus sansibarica	2	1	8	4.5	0.1	4.5	6.4	2.5	0.0	100
Marquesia macroura	248	1	4	4.4	0.1	4.5	10.0	-9.8	8.1	91.9
Croton silvaticus	7	1	4	4.2	0.1	4.1	8.5	0.8	0.0	100
Albizia antunesiana	94	3	16	4.1	0.1	3.6	9.8	-2.0	6.4	93.6

Maytenus undata	2	1	5	4.1	0.0	4.1	4.4	3.8	0.0	100
Cassine indet	1	1	7	4.1	0.0	4.1	4.1	4.1	0.0	100
Vepris nobilis	1	1	2	4.0	NA	4.0	4.0	4.0	0.0	100
Albizia adianthifolia	19	1	4	4.0	0.0	4.3	8.8	-2.0	5.3	94.7
Apodytes dimidiata	3	1	6	4.0	0.0	3.2	7.0	1.7	0.0	100
Vitex fischeri	8	1	4	3.9	0.1	3.5	10.0	1.3	0.0	100
Peltophorum africanum	27	1	7	3.7	0.0	3.3	9.7	0.0	3.7	96.3
Mundulea sericea	15	2	20	3.7	0.1	3.8	6.7	0.2	0.0	100
Ficus ingens	9	1	4	3.7	0.1	3.3	8.0	1.3	0.0	100
Pterocarpus tinctorius	168	1	4	3.6	0.1	3.4	10.0	-5.8	8.3	91.7
Grewia monticola	46	1	11	3.6	0.1	3.6	8.9	-0.4	6.5	93.5
Millettia laurentii	9	1	2	3.6	0.2	3.0	8.5	0.0	11.1	88.9
Terminalia stenostachya	30	1	11	3.6	0.1	3.6	7.9	-0.1	3.3	96.7
Commiphora glandulosa	11	2	22	3.5	0.1	2.3	9.3	0.8	0.0	100
Erythrophleum africanum	85	3	23	3.5	0.1	2.9	9.5	-0.4	1.2	98.8
Senegalia nigrescens	198	3	25	3.4	0.1	2.9	10.0	-1.5	4.0	96.0
Pavetta gardeniifolia	2	1	6	3.4	0.0	3.4	4.1	2.7	0.0	100
Zanthoxylum capense	1	1	6	3.4	0.0	3.4	3.4	3.4	0.0	100
Anisophyllea boehmii	31	1	4	3.4	0.1	2.8	9.8	-0.5	3.2	96.8
Antidesma rufescens	1	1	2	3.3	NA	3.3	3.3	3.3	0.0	100
Erythrina abyssinica	19	2	16	3.3	0.1	2.5	6.5	0.5	0.0	100
Julbernardia paniculata	1382	3	20	3.3	0.1	3.0	10.0	-8.0	3.6	96.4
Combretum microphyllum	1	1	7	3.3	NA	3.3	3.3	3.3	0.0	100
Heteropyxis natalensis	80	1	6	3.3	0.0	3.2	6.7	0.3	0.0	100
Grewia occidentalis	6	1	4	3.3	0.1	3.0	4.9	2.2	0.0	100
Securidaca longipedunculata	5	3	19	3.2	0.1	3.0	8.7	0.5	0.0	100
Rhus chirindensis	4	1	6	3.2	0.0	2.9	4.7	2.5	0.0	100
Olea africana	13	1	6	3.2	0.0	2.6	8.8	0.9	0.0	100
Pterocarpus indet	10	1	11	3.2	0.0	3.1	7.6	0.0	0.0	100
Faurea speciosa	67	1	6	3.2	0.0	3.5	6.4	-0.1	1.5	98.5
Azanza garckeana	2	1	11	3.1	0.0	3.1	4.4	1.9	0.0	100

Diospyros indet	3	2	12	3.1	0.1	1.0	8.7	-0.3	33.3	66.7
Pterocarpus rotundifolius	266	2	26	3.1	0.1	2.9	10.0	-1.3	4.5	95.5
Vitex havilandii	2	1	5	3.1	0.0	3.1	3.3	2.9	0.0	100
Cordyla africana	5	2	12	3.1	0.1	2.5	9.0	0.0	0.0	100
Grewia conocarpa	8	1	7	3.0	0.1	2.3	6.7	1.3	0.0	100
Vachellia sieberiana	1	1	4	3.0	0.1	3.0	3.0	3.0	0.0	100
Sclerocarya birrea	172	3	27	3.0	0.1	2.5	9.7	-4.5	4.7	95.3
Rhus rehmanniana	35	1	6	3.0	0.0	2.9	7.5	0.2	0.0	100
Rhus lucida	20	1	6	3.0	0.0	2.8	6.0	0.2	0.0	100
Clerodendron myricoides	2	1	5	3.0	0.1	3.0	3.9	2.0	0.0	100
Pterocarpus angolensis	521	7	26	2.9	0.1	2.5	10.0	-5.8	6.7	93.3
Rhus dentata	9	1	5	2.9	0.0	2.3	7.9	0.2	0.0	100
Vachellia robusta	152	2	25	2.9	0.1	2.6	8.7	-3.1	8.6	91.4
Vangueria esculenta	3	1	6	2.9	0.0	3.0	3.0	2.7	0.0	100
Commiphora pilosa	26	1	8	2.9	0.0	2.5	7.0	0.3	0.0	100
Terminalia sericea	188	5	26	2.9	0.0	2.6	8.3	-1.0	1.6	98.4
Senegalia campylacantha	12	1	8	2.8	0.0	1.9	7.2	0.3	0.0	100
Vachellia erubescens	12	1	6	2.8	0.0	2.9	5.3	0.6	0.0	100
Cassine transvaalensis	3	1	7	2.8	0.1	3.4	4.6	0.4	0.0	100
Elachyptera parvifolia	9	1	4	2.8	NA	1.3	9.8	-1.3	11.1	88.9
Pericopsis angolensis	132	4	19	2.8	0.1	2.5	9.8	-9.4	7.6	92.4
Dombeya rotundifolia	127	2	25	2.7	0.1	2.3	7.7	-0.4	1.6	98.4
Ozoroa sphaerocarpa	9	1	6	2.7	0.0	2.4	5.4	1.0	0.0	100
Schotia brachypetala	3	1	6	2.7	0.1	3.7	3.9	0.6	0.0	100
Bequertiodendron magaliesbergensis	40	1	6	2.7	0.0	2.7	6.6	0.4	0.0	100
Amblygonocarpus andongensis	4	2	23	2.7	0.0	2.7	4.9	0.5	0.0	100
Grewia schinzii	9	1	11	2.7	0.2	2.7	5.3	0.7	0.0	100
Senegalia ataxacantha	24	1	6	2.7	0.0	2.5	6.0	0.1	0.0	100
Ficus sycomorus	4	2	19	2.7	0.1	3.1	5.7	-1.3	25.0	75.0
Brachystegia boehmii	1026	5	19	2.6	0.1	2.3	10.0	-6.0	7.1	92.9
Psychotria capensis	4	1	6	2.6	0.1	2.3	4.2	1.5	0.0	100

Parinari curatellifolia	204	6	25	2.6	0.0	2.2	9.5	-2.8	7.8	92.2
Senegalia polyacantha	20	2	2	2.5	NA	2.0	6.5	0.0	0.0	100
Brachystegia indet	35	2	11	2.5	0.1	1.8	8.0	0.0	0.0	100
Ormocarpum kirkii	6	3	23	2.5	0.0	2.8	5.0	0.0	16.7	83.3
Cissus integrifolia	2	1	11	2.5	0.0	2.5	4.2	0.9	0.0	100
Ficus glumosa	11	1	5	2.5	0.1	2.4	5.3	0.3	0.0	100
Ceiba pentandra	1	1	2	2.5	NA	2.5	2.5	2.5	0.0	100
Lannea stuhlmannii	28	2	25	2.5	0.0	2.0	9.6	-0.1	7.1	92.9
Cussonia spicata	17	2	20	2.5	0.0	1.9	5.6	0.1	0.0	100
Vitex mombassae	22	2	22	2.4	0.0	2.0	6.5	-0.1	4.5	95.5
Millettia stuhlmannii	175	2	14	2.4	0.0	2.1	7.9	-2.5	3.4	96.6
Strychnos potatorum	6	1	11	2.4	0.1	2.3	5.9	-0.1	16.7	83.3
Loeseneriella crenata	5	1	11	2.4	0.0	2.2	3.1	2.1	0.0	100
Vachellia nilotica	335	3	27	2.4	0.0	2.1	10.0	-1.0	2.1	97.9
Piliostigma thonningii	7	3	26	2.4	0.0	2.0	8.6	0.5	0.0	100
Philenoptera katangensis	101	1	4	2.3	0.1	2.2	9.4	-7.3	8.9	91.1
Ormocarpum indet	1	1	3	2.3	NA	2.3	2.3	2.3	0.0	100
Zanthoxylum chalybeum	35	2	12	2.3	0.1	2.0	8.8	-9.0	5.7	94.3
Sterculia murex	16	1	6	2.3	0.0	1.7	6.8	0.6	0.0	100
Brachystegia spiciformis	541	6	21	2.3	0.1	1.8	9.7	-5.0	5.2	94.8
Protea gaguedi	3	2	7	2.3	0.1	2.6	4.0	0.0	0.0	100
Brachystegia taxifolia	14	1	4	2.3	0.1	2.5	4.5	0.0	0.0	100
Rhus lancea	10	1	6	2.3	0.0	2.4	5.4	-1.1	20.0	80.0
Vachellia amythethophylla	47	1	6	2.3	0.0	2.3	9.5	-3.0	10.6	89.4
Commiphora pyracanthoides	2	1	4	2.2	0.0	2.2	3.4	1.1	0.0	100
Euclea crispa	24	1	6	2.2	0.0	2.4	6.2	0.3	0.0	100
Grewia bicolor	63	1	6	2.2	0.0	1.8	8.7	-0.2	3.2	96.8
Garcinia huillensis	6	2	11	2.2	0.1	1.6	7.3	-0.6	33.3	66.7
Monotes katangensis	67	1	4	2.2	0.1	2.3	8.3	-8.5	10.4	89.6
Celtis africana	7	1	6	2.2	0.1	1.9	4.2	1.5	0.0	100
Brachystegia longifolia	8	2	14	2.2	0.0	1.9	4.8	0.8	0.0	100

Haplocoelum foliolosum	75	1	4	2.2	0.1	1.8	9.8	-9.0	17.3	82.7
Diospyros mespiliformis	57	4	27	2.2	0.1	1.7	9.0	-0.8	3.5	96.5
Lannea discolor	128	6	25	2.2	0.1	2.2	7.5	-1.2	3.9	96.1
Senegalia caffra	264	1	6	2.2	0.0	2.0	8.5	-2.8	4.9	95.1
Crossopteryx febrifuga	24	1	13	2.1	0.0	1.9	5.5	0.0	0.0	100
Ekebergia capensis	10	1	8	2.1	0.1	1.3	9.7	0.5	0.0	100
Pappea capensis	21	3	22	2.1	0.1	2.1	6.1	-4.3	19.0	81.0
Vachellia grandicornuta	100	1	6	2.1	0.0	2.0	8.0	-0.1	1.0	99.0
Brachystegia wangermeeana	280	1	4	2.1	0.1	1.8	10.0	-6.5	11.4	88.6
Senna singueana	11	3	19	2.1	0.0	2.0	4.8	0.0	9.1	90.9
Senegalia burkei	96	1	6	2.1	0.0	2.1	7.4	-0.8	6.3	93.8
Strychnos madagascariensis	61	2	26	2.1	0.0	1.9	9.8	-2.3	14.8	85.2
Julbernardia globiflora	1122	5	24	2.1	0.1	1.6	10.0	-9.8	6.9	93.1
Combretum collinum	350	5	24	2.0	0.1	1.5	9.8	-9.3	7.7	92.3
Diospyros abyssinica	8	1	4	2.0	0.1	2.4	8.8	-5.0	12.5	87.5
Afzelia quanzensis	26	3	10	2.0	0.0	1.5	8.5	-1.5	11.5	88.5
Margaritaria indet	49	1	8	2.0	0.0	1.8	10.0	-3.4	10.2	89.8
Lannea schweinfurthii	50	3	11	2.0	0.1	1.5	9.5	-1.0	6.0	94.0
Xeroderris stuhlmannii	89	2	12	2.0	0.0	2.1	6.8	-2.2	9.0	91.0
Bauhinia galpinii	10	1	6	2.0	0.0	1.7	5.3	0.1	0.0	100
Dalbergia boehmii	111	2	11	2.0	0.1	1.9	8.1	-6.8	14.4	85.6
Aganope stuhlmannii	79	2	6	2.0	0.1	1.5	8.5	-2.5	7.6	92.4
Brackenridgea zanguebarica	17	1	11	2.0	0.1	2.1	5.9	-1.1	11.8	88.2
Dichrostachys cinerea	214	6	26	2.0	0.0	1.9	6.3	-1.1	5.6	94.4
Spirostachys africana	50	2	20	2.0	0.0	1.8	5.9	-5.0	6.0	94.0
Ficus thonningii	25	1	4	2.0	0.2	1.8	9.0	-7.3	12.0	88.0
Glycine wightii	2	1	8	1.9	0.0	1.9	2.4	1.4	0.0	100
Brachystegia bussei	28	1	9	1.9	0.0	2.1	3.0	0.5	0.0	100
Vachellia tortilis	214	1	6	1.9	0.0	1.8	6.0	-0.4	0.9	99.1
Pteleopsis myrtifolia	265	2	14	1.9	0.0	1.8	9.3	-3.5	3.0	97.0
Euclea indet	3	1	6	1.9	0.0	1.3	3.5	1.0	0.0	100

Commiphora edulis	6	1	4	1.9	0.0	2.0	2.5	1.3	0.0	100
Euphorbia indet	2	1	6	1.9	0.0	1.9	3.8	0.0	0.0	100
Kirkia acuminata	28	1	8	1.9	0.0	1.9	5.2	-0.3	3.6	96.4
Burkea africana	695	6	26	1.9	0.1	1.8	7.5	-8.1	5.3	94.7
Uvariastrum hexaloboides	10	1	4	1.9	0.1	2.1	3.8	-0.5	10.0	90.0
Brachystegia allenii	37	1	11	1.9	0.0	1.5	5.9	-2.2	2.7	97.3
Trichilia emetica	5	2	25	1.9	0.1	1.6	5.7	-1.1	20.0	80.0
Euclea divinorum	17	1	7	1.9	0.0	1.7	6.0	-0.4	5.9	94.1
Senegalia davyi	49	1	6	1.9	0.0	1.3	8.8	0.0	4.1	95.9
Monotes africana	33	3	14	1.9	0.0	1.0	8.8	0.0	0.0	100
Homalium abdessammadii	2	1	4	1.9	0.0	1.9	4.5	-0.8	50.0	50.0
Zanthoxylum indet	3	1	2	1.8	NA	2.0	3.0	0.5	0.0	100
Gardenia spatulifolia	2	1	5	1.8	0.0	1.8	2.1	1.6	0.0	100
Rhus Searsia	6	1	6	1.8	0.0	1.8	3.0	1.0	0.0	100
Vachellia swazica	4	1	7	1.8	0.0	2.0	2.3	0.9	0.0	100
Philenoptera violacea	21	1	13	1.8	0.1	1.9	7.9	-9.6	28.6	71.4
Guibourtia coleosperma	16	1	21	1.8	0.1	1.2	6.0	-1.7	18.8	81.3
Hexalobus monopetalus	58	2	16	1.8	0.1	1.4	9.8	-9.8	17.2	82.8
Ximenia caffra	41	5	23	1.8	0.0	1.3	8.0	-1.7	4.9	95.1
Albizia harveyi	25	1	7	1.8	0.0	1.3	4.9	-0.7	8.0	92.0
Combretum adenogonium	444	1	13	1.8	0.1	1.7	6.7	-6.3	19.6	80.4
Cassia abbreviata	85	5	20	1.8	0.0	1.5	6.3	-2.0	8.2	91.8
Holarrhena pubescens	24	2	11	1.8	0.0	1.7	6.3	-2.0	12.5	87.5
Vitex payos	41	4	19	1.8	0.0	1.5	7.2	-3.0	2.4	97.6
Rhus leptodictya	43	1	6	1.8	0.0	1.6	4.7	-0.4	4.7	95.3
Faurea rochetiana	23	4	17	1.8	0.0	1.5	4.0	0.0	0.0	100
Ziziphus mucronata	187	4	26	1.7	0.1	1.5	9.9	-6.8	18.2	81.8
Bolusanthus speciosus	86	1	6	1.7	0.1	1.6	8.4	-1.2	1.2	98.8
Manilkara discolor	181	1	2	1.7	NA	1.0	7.5	-3.0	0.6	99.4
Rothmannia engleriana	8	2	4	1.7	0.0	1.3	7.0	-1.5	12.5	87.5
Philenoptera wankieensis	21	1	7	1.7	0.0	1.4	5.5	0.0	0.0	100

Albizia amara	4	1	15	1.7	0.0	2.0	3.2	-0.5	25.0	75.0
Zanha africana	19	2	17	1.7	0.0	0.8	7.5	0.0	0.0	100
Vachellia reficiens	67	1	8	1.7	0.1	1.4	8.5	-2.0	10.4	89.6
Coptosperma neurophyllum	4	1	10	1.7	0.0	1.5	2.4	1.2	0.0	100
Rytigynia indet	1	1	6	1.7	NA	1.7	1.7	1.7	0.0	100
Bridelia scleroneura	191	1	8	1.7	0.0	1.0	9.0	-3.5	4.2	95.8
Commiphora mollis	14	1	6	1.7	0.0	1.3	3.2	0.8	0.0	100
Commiphora merkii	11	1	6	1.7	0.0	1.8	2.4	0.6	0.0	100
Uapaca kirkiana	148	4	17	1.7	0.0	1.3	8.8	-0.3	4.1	95.9
Strychnos cocculoides	244	3	20	1.6	0.0	1.2	8.0	-2.5	5.3	94.7
Strychnos spinosa	76	5	24	1.6	0.0	1.5	6.5	-1.9	10.5	89.5
Dalbergia melanoxylon	456	4	25	1.6	0.1	1.5	8.0	-7.4	10.1	89.9
Psychotria indet	18	2	14	1.6	0.0	1.6	3.5	-0.3	5.6	94.4
Uapaca nitida	157	4	17	1.6	0.1	1.3	8.5	-9.5	11.5	88.5
Euclea undulata	11	1	4	1.6	0.0	1.6	2.8	-0.1	9.1	90.9
Diospyros lycioides	5	1	4	1.6	0.1	1.3	3.5	0.0	0.0	100
Brachystegia tamarindoides	10	1	7	1.6	0.1	1.5	5.0	-3.0	10.0	90.0
Vachellia karroo	227	1	6	1.6	0.0	1.1	9.0	-1.3	6.6	93.4
Antidesma venosum	25	1	6	1.6	0.0	1.4	6.1	-0.3	4.0	96.0
Strychnos innocua	74	4	19	1.6	0.1	1.5	6.0	-4.5	13.5	86.5
Commiphora indet	16	2	20	1.6	0.1	0.6	5.8	0.0	0.0	100
Euclea natalensis	22	1	7	1.6	0.0	1.5	4.1	0.1	0.0	100
Stereospermum kunthianum	28	1	13	1.6	0.1	1.2	4.9	-0.5	7.1	92.9
Pavetta schumanniana	11	1	7	1.6	0.0	1.1	4.2	0.3	0.0	100
Lecaniodiscus fraxinifolius	108	1	11	1.6	0.1	1.2	7.5	-1.4	13.9	86.1
Canthium inerme	9	1	5	1.6	0.0	1.7	2.3	0.3	0.0	100
Combretum mossambicense	2	1	11	1.6	0.1	1.6	1.7	1.4	0.0	100
Bobgunnia madagascariensis	160	5	19	1.6	0.1	1.2	9.0	-5.6	5.0	95.0
Brachystegia manga	35	1	11	1.6	0.0	1.2	7.6	-4.0	5.7	94.3
Balanites maughamii	3	1	5	1.6	0.0	1.9	3.0	-0.1	33.3	66.7
Brachystegia floribunda	165	1	6	1.6	0.1	1.2	8.5	-6.0	5.5	94.5

Diospyros lyciodes	3	1	6	1.5	0.0	1.3	2.2	1.2	0.0	100
Bridelia mollis	11	2	25	1.5	0.0	1.6	3.4	-1.7	9.1	90.9
Teclea nobilis	1	1	7	1.5	0.1	1.5	1.5	1.5	0.0	100
Combretum molle	283	7	26	1.5	0.1	0.9	10.0	-9.5	16.3	83.7
Ochna schweinfurthiana	101	4	17	1.5	0.1	1.0	10.0	-9.0	9.9	90.1
Hymenocardia ulmoides	535	1	7	1.5	0.0	1.5	8.0	-3.5	3.0	97.0
Allophylus africanus	30	3	16	1.5	0.1	0.9	9.0	-1.5	16.7	83.3
Ehretia indet	45	1	8	1.5	0.0	1.5	5.5	-4.0	11.1	88.9
Alloteropsis angusta	3	1	6	1.5	0.0	1.5	2.3	0.9	0.0	100
Ozoroa insignis	17	4	17	1.5	0.0	1.3	5.0	-0.4	11.8	88.2
Rhus gueinzii	2	1	4	1.5	0.0	1.5	2.9	0.2	0.0	100
Tarenna pavettoides	2	1	11	1.5	0.0	1.5	2.0	1.0	0.0	100
Hymenaea verrucosa	635	1	8	1.5	0.0	1.3	8.0	-9.2	3.0	97.0
Dalbergia armata	1	1	6	1.5	0.0	1.5	1.5	1.5	0.0	100
Entada abyssinica	2	1	4	1.5	0.2	1.5	4.7	-1.8	50.0	50.0
Boscia angustifolia	20	2	8	1.5	0.2	2.0	7.0	-9.8	20.0	80.0
Pseudolachnostylis maprouneifolia	1216	5	20	1.5	0.0	1.1	10.0	-5.6	5.7	94.3
Cussonia arborea	40	2	14	1.5	0.0	0.9	7.8	-2.3	5.0	95.0
Artabotrys brachypetalus	2	1	11	1.5	0.0	1.5	1.8	1.1	0.0	100
Bauhinia galpinni	8	1	11	1.5	0.1	1.4	2.5	0.4	0.0	100
Ficus salicifolia	3	1	6	1.5	0.0	0.7	3.5	0.1	0.0	100
Turraea nilotica	2	2	10	1.4	0.1	2.1	2.3	0.0	0.0	100
Terminalia mollis	3	1	2	1.4	NA	1.6	3.2	-0.5	33.3	66.7
Ochna indet	1	1	4	1.4	0.0	1.4	1.4	1.4	0.0	100
Dalbergia indet	6	1	11	1.4	0.1	1.5	3.0	0.0	16.7	83.3
Combretum apiculatum	2205	4	26	1.4	0.0	1.0	9.5	-7.2	11.5	88.5
Ekebergia benguelensis	23	2	16	1.4	0.1	0.8	7.3	-2.3	13.0	87.0
Commiphora tenuipetiolata	4	1	6	1.4	0.0	1.5	1.9	0.9	0.0	100
Senna petersiana	6	2	19	1.4	0.1	1.3	2.2	0.7	0.0	100
Vangueria infausta	22	2	10	1.4	0.0	1.4	5.2	-0.6	18.2	81.8
Strychnos pungens	14	2	19	1.4	0.1	1.8	7.0	-9.0	28.6	71.4

Maytenus indet	77	2	23	1.4	0.0	1.5	5.5	-3.2	13.0	87.0
Ehretia amoena	5	2	25	1.4	0.0	0.4	3.2	0.3	0.0	100
Multidentia crassa	47	2	8	1.4	0.0	1.0	5.0	-1.5	12.8	87.2
Colophospermum mopane	162	2	20	1.4	0.0	1.1	7.0	-0.4	1.9	98.1
Ficus stuhlmannii	5	1	6	1.4	0.0	0.8	4.0	0.1	0.0	100
Rhus pentheri	28	1	6	1.4	0.0	0.9	5.2	-2.0	14.3	85.7
Clerodendron glabrum	21	1	7	1.4	0.0	1.3	2.9	0.1	0.0	100
Monotes engleri	26	1	11	1.4	0.0	1.4	2.9	0.0	0.0	100
Thespesia garckeana	9	1	4	1.4	0.1	1.0	6.3	-0.8	22.2	77.8
Diplorhynchus condylocarpon	4727	7	26	1.4	0.1	1.1	10.0	-10.0	16.6	83.4
Diospyros quiloensis	51	1	7	1.4	0.0	1.0	6.2	-0.6	3.9	96.1
Gymnosporia senegalensis	19	2	8	1.4	0.0	1.0	4.5	-3.0	10.5	89.5
Grewia holstii	2	1	8	1.3	0.0	1.3	1.8	0.9	0.0	100
Brachystegia utilis	234	3	14	1.3	0.0	1.0	10.0	-4.8	4.7	95.3
Berchemia discolor	3	1	11	1.3	0.0	0.6	3.0	0.4	0.0	100
Fluggea virosa	6	1	7	1.3	0.0	1.5	2.7	-0.2	16.7	83.3
Psidium indet	4	1	7	1.3	0.0	1.4	3.0	-0.5	25.0	75.0
Combretum zeyheri	540	5	26	1.3	0.0	1.0	10.0	-10.0	8.0	92.0
Indet indet	1576	5	26	1.3	0.0	1.0	10.0	-6.2	8.1	91.9
Protea angolensis	31	1	6	1.3	0.1	0.5	6.8	-3.3	12.9	87.1
Rhoicissus revoilii	10	1	11	1.3	0.1	1.2	3.6	-2.5	20.0	80.0
Commiphora tenuispina	39	1	6	1.3	0.0	1.4	2.2	0.1	0.0	100
Margaritaria discoidea	142	2	13	1.3	0.0	1.0	8.0	-4.5	9.9	90.1
Albizia brevifolia	2	1	4	1.3	0.0	1.3	1.6	0.9	0.0	100
Hugonia orientalis	30	1	11	1.3	0.0	0.9	8.7	-4.1	6.7	93.3
Bridelia duvigneaudii	3	1	4	1.3	0.1	1.5	2.8	-0.5	33.3	66.7
Ochna puberula	6	1	4	1.3	0.1	1.0	2.8	0.3	0.0	100
Craterosiphon quarrei	2	1	4	1.3	0.1	1.3	1.5	1.0	0.0	100
Ochna leptoclada	22	1	11	1.2	0.1	0.8	7.0	-3.6	13.6	86.4
Annona senegalensis	243	5	25	1.2	0.0	1.0	9.5	-3.0	12.3	87.7
Protea caffra	8	1	6	1.2	0.0	1.5	2.6	-0.1	12.5	87.5

Rhus pyroides	24	1	6	1.2	0.0	1.1	3.4	-1.7	8.3	91.7
Baikiaea plurijuga	1114	1	21	1.2	0.0	1.0	7.8	-5.0	4.0	96.0
Hymenodictyon parvifolium	14	1	4	1.2	0.1	1.5	4.0	-1.0	14.3	85.7
Entandrophragma caudatum	9	1	14	1.2	0.1	1.5	2.2	-0.7	11.1	88.9
Terminalia sambesiaca	78	1	11	1.2	0.0	0.8	10.0	-5.1	14.1	85.9
Vachellia gerrardii	83	1	7	1.2	0.1	1.0	7.2	-1.6	15.7	84.3
Bauhinia petersiana	371	2	14	1.2	0.1	1.0	9.0	-4.6	14.3	85.7
Strychnos henningsii	4	1	11	1.2	0.2	-0.4	8.5	-2.9	50.0	50.0
Maerua angolensis	4	1	11	1.2	0.1	1.2	3.4	-1.1	25.0	75.0
Terminalia prunioides	58	1	6	1.2	0.0	0.8	6.0	-1.7	6.9	93.1
Flacourtia indica	81	3	19	1.2	0.0	1.0	5.0	-4.4	14.8	85.2
Rothmannia indet	2	1	6	1.2	0.1	1.2	3.5	-1.2	50.0	50.0
Boscia albitrunca	20	1	6	1.2	0.0	1.1	2.7	-0.2	15.0	85.0
Bridelia micrantha	8	1	9	1.2	0.1	1.0	2.0	0.9	0.0	100
Phyllocosmus lemaireanus	30	2	16	1.1	0.1	0.7	9.5	-1.3	16.7	83.3
Senegalia senegal	7	1	11	1.1	0.0	0.4	2.7	0.2	0.0	100
Diospyros fischeri	87	1	8	1.1	0.0	1.0	6.5	-2.5	11.5	88.5
Combretum indet	326	3	23	1.1	0.1	0.8	9.7	-9.8	31.3	68.7
Pleurostylia africana	4	1	9	1.1	0.0	0.8	2.8	0.0	25.0	75.0
Syzygium owariense	6	1	4	1.1	NA	0.9	2.5	0.0	0.0	100
Hymenocardia acida	2480	3	11	1.1	0.2	1.0	10.0	-10.0	33.0	67.0
Isoberlinia angolensis	12	1	3	1.1	0.0	1.0	3.9	0.0	0.0	100
Rhus refracta	1	1	3	1.1	0.0	1.1	1.1	1.1	0.0	100
Baphia massaiensis	29	1	21	1.1	0.0	0.9	3.3	-1.6	10.3	89.7
Maytenus senegalensis	404	2	26	1.1	0.0	0.9	9.5	-9.2	6.2	93.8
Ochna holstii	146	1	8	1.1	0.0	0.8	5.8	-2.3	9.6	90.4
Schrebera trichoclada	10	2	12	1.1	0.0	0.3	4.6	0.0	10.0	90.0
Pavetta edentula	15	1	5	1.1	0.0	0.7	3.4	-0.7	20.0	80.0
Kigelia africana	5	3	19	1.1	0.0	0.5	2.6	0.0	0.0	100
Bersama indet	26	2	23	1.1	0.0	1.0	5.3	-2.1	11.5	88.5
Suregada zanzibariensis	577	1	8	1.1	0.0	1.0	5.5	-8.8	4.7	95.3

Vangueria acutiloba	38	1	8	1.1	0.0	0.6	4.5	-1.2	21.1	78.9
Phyllanthus maderaspatensis	17	1	7	1.0	0.0	1.0	4.0	-2.0	11.8	88.2
Faurea saligna	95	2	10	1.0	0.0	0.8	4.4	-3.3	9.5	90.5
Commiphora schimperi	1	1	5	1.0	0.0	1.0	1.0	1.0	0.0	100
Phyllanthus indet	21	1	8	1.0	0.0	0.7	5.8	-0.4	9.5	90.5
Strychnos indet	48	2	26	1.0	0.0	0.9	5.9	-1.2	4.2	95.8
Dovyalis hispidula	1	1	7	1.0	NA	1.0	1.0	1.0	0.0	100
Mimusops indet	1	1	6	1.0	NA	1.0	1.0	1.0	0.0	100
Neonotonia wightii	2	1	2	1.0	NA	1.0	1.5	0.5	0.0	100
Croton dichogamus	2	1	2	1.0	NA	1.0	1.0	1.0	0.0	100
Combretum imberbe	11	2	25	1.0	0.1	0.6	3.8	-1.7	27.3	72.7
Combretum hereroense	100	2	25	1.0	0.0	0.5	9.3	-3.5	18.0	82.0
Markhamia obtusifolia	172	4	20	1.0	0.1	1.0	6.8	-2.5	11.0	89.0
Commiphora zanzibarica	1	1	11	1.0	0.0	1.0	1.0	1.0	0.0	100
Diospyros kirkii	88	1	11	0.9	0.0	0.7	10.0	-4.5	9.1	90.9
Euclea racemosa	10	2	22	0.9	0.1	1.3	4.5	-6.3	30.0	70.0
Vangueria madagascariensis	40	1	2	0.9	NA	1.0	5.0	-3.0	17.5	82.5
Senegalia erubescens	4	1	6	0.9	0.0	1.0	1.6	0.1	0.0	100
Gardenia jovis-tonantis	4	1	6	0.9	0.0	0.9	1.7	0.2	0.0	100
Markhamia indet	182	1	12	0.9	0.0	0.9	5.0	-3.6	13.7	86.3
Ehretia rigida	44	1	6	0.9	0.0	0.7	3.8	-0.7	18.2	81.8
Pterocarpus erinaceus	39	1	6	0.9	0.0	0.9	2.5	-0.5	5.1	94.9
Combretum binderianum	68	1	7	0.9	0.0	0.7	4.2	-2.7	11.8	88.2
Lannea schimperi	12	1	10	0.9	0.0	0.9	2.3	0.0	0.0	100
Dalbergia nitidula	79	3	17	0.9	0.0	0.7	5.3	-4.6	11.4	88.6
Rhus tenuipes	5	1	3	0.8	0.0	1.7	2.3	-1.0	40.0	60.0
Xylia torreana	6	1	11	0.8	0.1	0.6	2.2	0.0	16.7	83.3
Cassine aethiopica	14	1	5	0.8	0.0	0.7	2.5	0.0	14.3	85.7
Vitex indet	2	1	7	0.8	0.0	0.8	1.1	0.6	0.0	100
Rhus indet	2	2	20	0.8	0.1	0.8	1.0	0.6	0.0	100
Boscia salicifolia	24	2	15	0.8	0.0	0.8	4.2	-3.0	16.7	83.3

Spirostachys indet	6	1	7	0.8	0.0	0.8	2.6	-0.8	16.7	83.3
Tabernaemontana elegans	6	1	11	0.8	0.1	1.3	3.6	-3.2	33.3	66.7
Grewia flavescens	8	1	5	0.8	0.0	1.2	2.9	-1.3	37.5	62.5
Combretum celastroides	4	1	4	0.8	0.0	0.9	1.5	0.0	25.0	75.0
Uvaria kirkii	71	1	8	0.8	0.0	0.5	4.5	-2.9	18.3	81.7
Syzygium cordatum	63	1	6	0.8	0.0	0.7	6.1	-1.1	17.5	82.5
Swartzia madagascariensis	30	1	8	0.8	0.0	0.7	4.0	-0.3	10.0	90.0
Senegalia mellifera	6	1	6	0.8	0.0	0.5	1.8	0.0	0.0	100
Cordia indet	7	1	10	0.8	0.0	0.6	2.4	0.3	0.0	100
Ficus sur	7	1	2	0.8	NA	0.5	8.0	-2.5	42.9	57.1
Sterculia rogersii	74	1	6	0.8	0.1	0.6	3.1	-0.8	10.8	89.2
Tamarindus indica	27	2	11	0.8	0.0	0.5	8.1	-4.0	11.1	88.9
Uvaria lucida	78	1	8	0.8	0.0	0.7	3.5	-1.3	17.9	82.1
Catunaregam spinosa	57	3	17	0.7	0.0	0.7	5.6	-5.4	21.1	78.9
Vangueria indet	3	2	23	0.7	0.0	0.4	1.8	-0.1	33.3	66.7
Uapaca sansibarica	1	1	1	0.7	NA	0.7	0.7	0.7	0.0	100
Bridelia cathartica	26	3	17	0.7	0.1	0.7	3.5	-3.8	15.4	84.6
Grewia microcarpa	361	1	8	0.7	0.0	0.5	8.5	-2.6	12.5	87.5
Tragia brevipes	2	1	8	0.7	0.0	0.7	1.0	0.3	0.0	100
Cremaspora triflora	20	1	8	0.6	0.0	0.7	1.2	-0.1	10.0	90.0
Ozoroa engleri	1	1	4	0.6	0.0	0.6	0.6	0.6	0.0	100
Boscia indet	17	2	11	0.6	0.1	0.3	3.2	-0.7	29.4	70.6
Ozoroa paniculosa	3	1	6	0.6	0.1	0.5	1.6	-0.2	33.3	66.7
Cleistochlamys kirkii	89	1	11	0.6	0.1	0.5	5.6	-4.8	28.1	71.9
Tarenna indet	5	1	6	0.6	0.0	0.5	3.0	-2.7	40.0	60.0
Ochna pulchra	10	1	18	0.6	0.0	0.7	4.5	-3.3	30.0	70.0
Diospyros batocana	1	1	3	0.6	0.0	0.6	0.6	0.6	0.0	100
Dovyalis caffra	1	1	4	0.5	0.0	0.5	0.5	0.5	0.0	100
Salvadora angustifolia	3	1	4	0.5	0.1	1.1	1.5	-1.1	33.3	66.7
Lonchocarpus capassa	11	2	21	0.5	0.0	0.3	2.3	-0.9	27.3	72.7
Scolopia stolzii	7	1	11	0.5	0.0	0.8	2.0	-1.2	28.6	71.4

Maprounea africana	7	1	2	0.5	0.6	0.5	2.5	-2.0	28.6	71.4
Vitex madiensis	1	1	2	0.5	0.1	0.5	0.5	0.5	0.0	100
Grewia indet	1	1	6	0.5	NA	0.5	0.5	0.5	0.0	100
Garcinia buchananii	1	1	6	0.5	0.0	0.5	0.5	0.5	0.0	100
Combretum elaeagnoides	64	2	17	0.5	0.0	0.4	2.1	-0.3	4.7	95.3
Flueggea virosa	24	1	15	0.5	0.0	0.6	2.6	-3.0	16.7	83.3
Elaeodendron matabelicum	3	1	11	0.5	0.0	0.5	1.0	0.0	0.0	100
Syzygium guineense	247	6	19	0.5	0.2	0.5	9.5	-9.5	38.5	61.5
Bauhinia tomentosa	16	2	12	0.4	0.0	0.5	2.3	-3.4	12.5	87.5
Cussonia paniculata	1	1	6	0.4	0.0	0.4	0.4	0.4	0.0	100
Cussonia indet	2	1	6	0.4	0.0	0.4	0.5	0.3	0.0	100
Syzygium indet	8	1	6	0.4	0.0	0.3	1.0	-0.3	25.0	75.0
Euphorbia tirucalli	8	1	10	0.3	0.0	0.3	1.0	0.0	0.0	100
Combretum paniculatum	2	1	11	0.3	0.0	0.3	0.9	-0.2	50.0	50.0
Ormocarpum trichocarpum	22	2	25	0.3	0.0	0.9	2.1	-5.7	18.2	81.8
Bridelia ferruginea	11	1	2	0.3	0.3	2.0	5.0	-7.5	36.4	63.6
Adansonia digitata	5	1	6	0.3	0.1	0.1	1.4	-0.9	40.0	60.0
Gardenia ternifolia	1	1	4	0.3	NA	0.3	0.3	0.3	0.0	100
Olax obtusifolia	1	1	4	0.3	NA	0.3	0.3	0.3	0.0	100
Vachellia xanthophloea	2	1	6	0.3	0.0	0.3	0.3	0.2	0.0	100
Ceriops tagal	4	1	7	0.2	0.0	0.0	0.7	-0.2	25.0	75.0
Euclea schimperi	25	1	4	0.2	0.0	0.3	1.1	-2.5	20.0	80.0
Ficus indet	16	2	26	0.2	0.0	0.4	3.3	-3.0	25.0	75.0
Diospyros sinensis	31	1	11	0.2	0.1	0.2	4.6	-4.3	29.0	71.0
Xylopia parviflora	1	1	2	0.2	NA	0.0	0.5	0.0	0.0	100
Maclura africana	2	1	11	0.1	0.1	0.1	2.0	-1.7	50.0	50.0
Vachellia indet	1	1	4	0.1	0.0	0.1	0.1	0.1	0.0	100
Turraea floribunda	1	1	11	0.1	0.0	0.1	0.1	0.1	0.0	100
Uapaca pilosa	7	1	4	0.0	0.1	0.8	1.3	-3.0	28.6	71.4
Bridelia indet	1	1	3	0.0	NA	0.0	0.0	0.0	0.0	100
Sorindeia indet	1	1	5	0.0	NA	0.0	0.0	0.0	0.0	100

Annona indet	0	1	3	0.0	NA	0.0	0.0	0.0	100	0.0
Cola mossambicensis	16	1	11	-0.1	0.1	-0.2	1.5	-1.4	56.3	43.8
Ximenia americana	8	1	11	-0.1	0.0	-0.1	2.0	-1.8	50.0	50.0
Ricinodendron rautanenii	2	1	11	-0.2	0.0	-0.2	0.2	-0.5	50.0	50.0
Grewia caffra	1	1	1	-0.6	NA	-0.6	-0.6	-0.6	100	0.0
Rothmannia fischeri	2	1	5	-0.6	0.0	-0.6	0.6	-1.9	50.0	50.0
Sterculia appendiculata	2	1	11	-0.8	0.2	-0.8	3.8	-5.5	50.0	50.0
Markhamia zanzibarica	8	1	13	-0.9	0.1	0.6	1.0	-9.0	37.5	62.5
Protea indet	1	1	11	-3.6	0.1	-3.6	-3.6	-3.6	100	0.0

CHAPTER IV

CHAPTER 4: PREDICTING BASAL AREA INCREMENT ACROSS SOUTHERN AFRICA: THE ROLE OF CLIMATE AND SITE CHARACTERISTICS

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Author Contributions

The conception, analytical design, model development, data analyses, literature searches, and manuscript writing of this study were led by BL with inputs from CMR and ETAM.

Abstract

A cursory review of literature shows that no study has attempted to find a methodological approach that would enable us to predict basal area increment (BAI) in unmeasured areas of southern Africa. This general lack of methodological rigour may put in question our current understanding of southern African woodlands (SAWs) and thus, ability to sustainably manage them. Climatic and biotic factors influence BAI and represent an important yet unexploited source of predictability across unmeasured areas of SAWs. Here, I developed hierarchical mixed-effects models and used them to predict BAI across a wide unmonitored environmental gradient of southern Africa. To account for the inherent correlation among trees located within the same site, I specified site as a random effect. I then explored a large pool of Predictor Variables (PVs) and finally settled on those that are thought to have a clear hypothesis and address climate- and site-specific characteristics. I used data from 60% of 223 permanent sample plots (PSPs) across 8 countries for model fitting, while the remaining 40% were used for validation. After performing backward stepwise regression, the selected model explained 60% of BAI variance in the fitting plots and 50% in the validation dataset. Based on data for validation, various markers suggested the model had strong predictive power: I found a correlation coefficient (R) of 0.8, a root mean square error (RMSE) of 0.01 m^2/ha/year, a RMSE-observations standard deviation ratio (RSR) of 0.7, a percent bias (PBias) of 7.8%, and a Nash-Sutcliffe Efficiency (NSE) of 0.5 between observations and predictions. Overall, BAI was found to be positively related to rainy season length (RSL) but was negatively affected by climatic water deficit (CWD), with some other factors also playing a more minor role. Considering that this study covered a wide environmental gradient, the ability of the selected model to predict growth on an independent dataset with statistics shown above suggests that it provides practical usability in predicting BAI for sustainable woodland management across unmonitored areas of SAWs. Model predictions across unmonitored areas of SAWs were found to range between 0.07 and 0.7 with an estimated regional mean of 0.35 m^2/ha/year and were consistent with previous literature. By extension, the model has demonstrated the potential to contribute towards deepening our understanding of woodland dynamics across unmonitored areas of SAWs. It is notable however that the model failed to predict with a 1:1 precision and could only explain half of the variation found in the validation dataset, itself not randomly distributed across the region; therefore, caution needs to be applied in its use. In particular, its skill could be improved by the use of higher resolution ground-based PVs, and further plots. The predicted BAI across unmeasured areas can be used to support the analyses of woodland structure, estimation of carbon stocks, and overall economic assessments of woodland policies for sustainable management options.

Keywords: Basal area increment; hierarchical mixed models; stepwise selection; SEOSAW; southern African woodlands.

4.1 Introduction

Much of what we know about tree growth rates across southern African woodlands (SAWs) is based on plot measurements. However, most of the ecological problems such as how to sustainably manage SAWs are broad-scale – scales larger than available observations. The lack of extensive growth monitoring plots across the sub-continent is mainly because setting them up and carrying out repeat measurements is expensive, time-consuming, and labour-intensive (Priyadi *et al.,* 2005). Understanding tree growth rates across unmeasured areas of SAWs is, therefore, one of the region's most pressing issues. It follows that our knowledge of growth rates across unmeasured areas is dependent on how well we can use data collected from permanent sample plots (PSPs) to develop predictive models (Brassel *et al.,* 2001; Bowman *et al.,* 2012; Rohner *et al.,* 2017).

When data from PSPs is used to drive models with the aim of predicting unmeasured areas or extending an environmental-ecological relationship from PSPs to unmeasured areas, the process is termed *extrapolation*. The science of spatial extrapolation has always been pivotal to ecological inquiry (Popper, 1959; Miller *et al.,* 2004) and is made possible because the structuring of ecological processes in space and time is often found to be correlated with environmental variables (Peters *et al.,* 2004). As such, models are developed to address factors that may influence the ecophysiological aspects of individual trees. Some of these factors include (i) stem characteristics e.g., stem size and species (Mugasha *et al.,* 2016); (ii) site characteristics e.g., altitude, fire frequency, soil texture, and available water capacity (Lévesque *et al.,* 2016); (iii) climate characteristics e.g. mean annual precipitation (MAP), rainy season length (RSL), seasonal water stress, temperature, and nitrogen deposition (Linares *et al.,* 2014; Dong *et al.,* 2012). These factors interrelate with tree physiology differently in space and time. For example, actual evapotranspiration (AET) can be a useful indicator of net primary productivity because it represents the spatial-temporal variability of energy and water required by trees for biological use and growth (Lutz *et al.,* 2010).

Stem size is thought to be one of the most important predictor variables (PVs) of tree growth (Weiner *et al.,* 2009; Zhang *et al.,* 2016). In fact, strong positive correlations between stem size and growth rates over varying periods have been reported in some studies around the world (Stephenson *et al.,* 2014).

Edaphic studies (e.g. Jim, 1998; Hogberg *et al.,* 2006) show that although the optimum pH range for plant growth is 5.5 – 7.0, some trees tend to grow better in more acidic soils than others. Textural classifications of soils also play an important role in tree growth. For example, soils characterised by poor hydraulic structure and heavy compaction tend to slow tree growth by restricting root expansion, and nutrient transport from lower layers of the soil (Jim, 1998). Similar results are documented in the work of Woollen *et al.,* (2016) who observed that tree growth in Mozambique is slow because of low rainfall and poor soil conditions.

Solar radiation is another variable that underpins tree growth (Dong *et al.,* 2012) because it makes photosynthesis possible. The ability of trees to absorb radiation largely depends on their spatial location because the intensity of radiation decreases with an increase in the depth of canopies it needs to penetrate before reaching target trees which may also vary depending on slope and aspect (Rüger *et al.,* 2011). However, given the open nature of savannas, canopies are unlikely to be an important obstruction but radiation incident in these biomes can still be affected by atmospheric mechanisms such as absorption, scattering, water vapour content, pollution, and cloud coverage (Oliphant *et al.,* 2003).

Numerous studies (e.g., D'Amato *et al.,* 2004; Rozendaal *et al.,* 2020) have also proposed that tree-tree competition can be an important biotic PV of growth. In particular, large trees near stems of interest are thought to exert higher competition than small and distant trees. These observations are often interpreted as a consequence of the struggle for required resources for growth. Tree-tree competition was also found to be a crucial determining factor of individual tree growth rates across SAWs in Chapter 3 of this thesis.

Although, in theory, these variables manage to represent the general growth of trees, it is crucial to develop a modelling framework that can take into consideration multiple variables while simultaneously controlling for possible effects of multicollinearity (Pinheiro and Bates, 2000; Rohner *et al.,* 2017).

While there are many approaches to modelling tree growth, mixed-effects models (Pinheiro and Bates 2000) are among the widely used. They have previously been successfully employed to model shrub growth sensitivity to climate across the tundra biome (Myers-Smith *et al.,* 2015), to disentangle relationships between leaf area and stem growth (Kidombo and Dean, 2018), to predict tree growth in China (Ma and Lei, 2015) and to model diameter growth in the miombo woodlands of Tanzania (Mugasha *et al.,* 2016). All of these uses of mixed models show that employing them across a wide environmental gradient of a data-sparse southern Africa could yield extremely important results. This is especially true considering that many of the published studies on growth rates across southern Africa do not focus on prediction. Consequently, a fuller understanding of using factors that modulate tree growth to predict it is often lacking which hinders cost-effective and targeted sustainable woodland management.

The overarching goal of this study is to address one presently poorly understood research question: *how well can we predict basal area increment (BAI) as a function of climate and site characteristics across a data-sparse southern Africa?* Findings from this study will primarily accomplish three tasks:

(i) They will deepen our understanding of what controls BAI across the southern African region;

(ii) They will provide a modelling framework with practical usability in predicting BAI across the region;

(iii) They will provide indispensable information for input into decision-making processes that seek to promote the sustainability of southern African woodlands.

Whereas Chapter 3 of this thesis focused on individual tree growth rates, I chose to focus on plot-level BAI in this Chapter because most PVs are too coarse to predict individual tree growth rates. This Chapter, therefore, builds on Chapter 3 and adds 2 distinct points: (i) It reveals important drivers of BAI that may have been missed at the individual stem level (ii) it provides insights into tree growth rates (BAI) across unmonitored areas of SAWs.

4.2 Materials and methods

4.2.1 Growth data

Unravelling biophysical interactions that influence BAI with statistical significance is not easy. It requires large quality-controlled stem datasets covering wide environmental gradients (Rohner *et al.,* 2017). Here, 38, 276 stems belonging to 400 species on 223 PSPs in 8 countries (Figure 4.1) inventoried between 1991 – 2018 were used (The SEOSAW Partnership, 2021). Individual stems were tagged with unique identifiers to guarantee their reidentification in subsequent inventories. Apart from individual diameter at breast height (DBH) measurements, information regarding site, plot, and silvicultural interventions were also recorded were possible.

In deciding trees to be included in this dataset, the approach suggested by Dong *et al.,* (2012) which was also found useful by Mugasha *et al.,* (2016) was employed. This approach disqualifies trees with the following characteristics:

(i) Those that had a DBH under 5 cm, representing 7.8% of the initial dataset;
(ii) Those that were measured at different points of measurements (POMs) between census dates, representing ~0.007% of the initial dataset;
(iii) Those that died, representing 6.9% of the dataset.

These measures ensured that growth was kept at biologically realistic rates and consistent with previous studies (e.g., Holdo, 2006).

I calculated mean annual growth by using a linear line of best fit to basal area data at the plot level. I then took the regression line to be the average annual BAI. Although there are several methods that can be used to compute BAI, I chose this approach because it considers all data points thus, unlikely to be biased by randomly high or low measurements (Sedmark and Scheer, 2012).

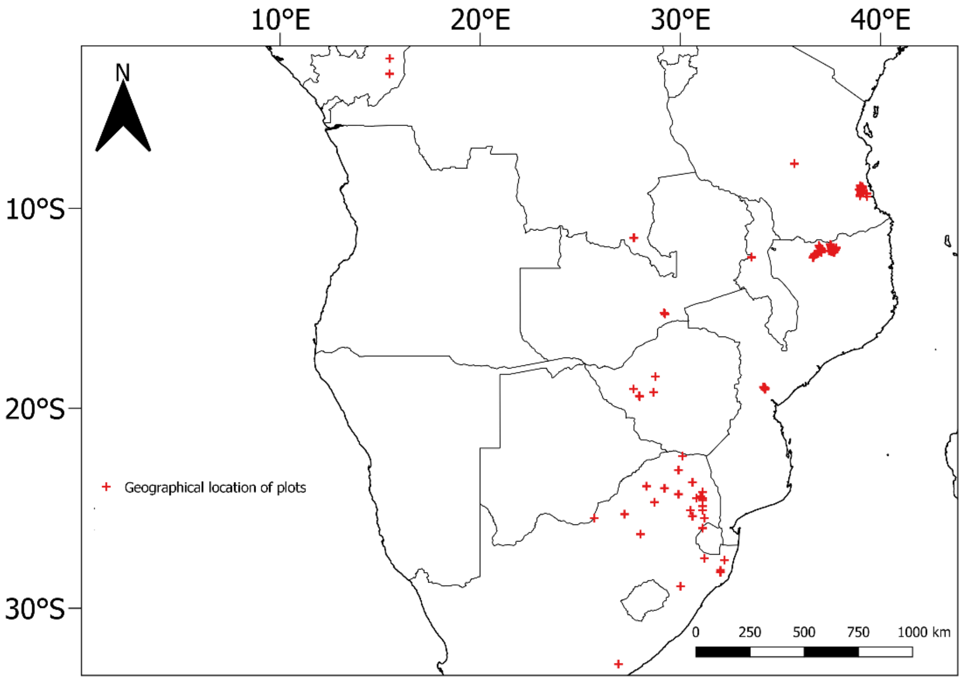

Figure 4.1: Geographical spread of the 223 permanent sample plots (PSPs) used in this study

4.2.2 Predictor variables (PVs)

The complex task of predicting BAI across unmonitored areas requires carefully disentangling the effect size and direction of each variable that is thought to drive tree growth rates. Interrogating all possible variables also presents opportunities to discover previously unsuspected variables that may be meaningful and important for tree growth. Therefore, I started by exploring a large pool of PVs before settling for a few that have a clear hypothesis and address climate- and site-specific characteristics.

Climate-related PVs

The preferred option was to use climate-related PVs collected from each PSP. Unfortunately, not all PSPs had climatological measurements covering the study period (i.e., 1991 – 2018). Those that did, the climatological stations were either far from the PSPs themselves or contained several missing values. For uniformity, I used reanalysed and/or satellite products. The use of reanalysed/satellite climatic datasets in ecological studies across southern Africa is very common. For example, Ryan *et al.,* (2017) used Tropical Rainfall Measuring Mission (TRMM) data to detect onset dates of rainfall for subsequent investigation of pre-rain green-up across southern Africa. The same product was also used by Case and Staver, (2018) in their work on African Savannas.

In this study, I used the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk *et al.,* 2015) because of its high spatial resolution (0.05º x 0.05º) which enabled the capturing of precipitation at the centre of each plot. This precipitation data was subsequently used to compute mean annual precipitation (MAP), rainy season length (RSL), and rainfall intensity (RFI).

A number of methods for computing RSL exist. For example, Hachigonta *et al.,* (2006) employed a rainfall-based criterion which was earlier used by the Famine and Early Warning System (FEWS) and documented in AGRHYMET, (1996). This approach requires the first dekad (10 days) of the rain season to accumulate a total of 25 mm followed by two dekads with a total of at least 20 mm. The onset date is then taken as the first day of the first dekad. In the work of Hachigonta *et al.,* (2008), this method was used to calculate the rainy season length for maize (Zea mays; *sensu* Chaudhury *et al.,* 2011) cultivation in Zambia. Ryan *et al.,* (2017) also used the same statistical approach to examine pre-rain green-up across tropical southern Africa. In their study, Ryan *et al.,* (2017) cautioned that this approach is designed to determine rainfall that allows determining the start of maize cultivation. Thus, the approach should be used conservatively with respect to tree water requirements. For this reason, the approach followed in this study is similar to that of Odekunle *et al.,* (2004). To implement this approach, a RSL algorithm was developed in R Programming Language (R Core Team, 2013) which regarded the onset as the first day when 8% of precipitation was recorded at the centre of each PSP and the cessation was taken to be the day when 90% of precipitation was recorded. The length of the rainy season was then taken to be the difference between cessation and onset. Many researchers (e.g., Ilesanmi, 1972; Laux *et al.,* 2008; Ndomba, 2010; Guenang *et al.,* 2012; Amekudzi *et al.,* 2015) have utilized a similar approach in studies around the world. RFI was subsequently calculated as a measure of the amount of rain that fell per time period i.e., the period for which growth data is available for any given PSP.

Climatic water deficit (CWD) which is defined as annual evaporative demand that exceeds available soil moisture (Stephenson, 2011; Lutz *et al.,* 2010) was used as a surrogate for seasonal water stress (SWS). CWD is widely used as a surrogate for seasonal water stress in studies around the world (Lutz *et al.,* 2010; Rozendaal *et al.,* 2020).

Soil-related PVs

Taken in isolation, climatic factors have been found to be insufficient predictor variables by previous studies (e.g., Jolly *et al.,* 2005). For this reason, site-related PVs were also explored. In particular, the percentage of soil sand content present in the top 30 cm of the soil at each PSP was used as a proxy for soil texture. This dataset is made freely available by the Africa Soils Information Service (Hengl *et al.,* 2015) at a 250 m resolution across the sub-Sahara African region. Soil texture provides indispensable information for understanding tree growth requirements because it shows the infiltration and permeability to be expected at each PSP. In general, fine-textured soils are expected to be less permeable than those that are coarse-textured. The choice of 30 cm depth was based on the fact that it accommodates most of the water needed by plants for their growth (Kulmatiski *et al.,* 2010; Case and Staver 2018). This dataset is given as a weight percentage of sand particles (SNDPPT) and is specified as follows: SNDPPT_sd1 which covers 0 - 5 cm, SNDPPT_sd2 5 – 15 cm and SNDPPT_sd3 15 to 30 cm. To get the 30 cm depth, weighted averaging was used.

Soil Phosphorus was also used as a measure of nutrients required for tree growth (Zavišić *et al.,* 2018; Soong *et al.,* 2020). Above-ground biomass was used as a measure of competition (Zobel and Zobel, 2002).

4.2.3 Model fitting and selection

For modelling purposes, I sectioned the final dataset into model fitting (60%) while the remaining independent dataset (40%) was used for model validation (Table 4.1). To ease the comparability of the estimated coefficients, I standardized all PVs before including them in the models (Gelman and Hill, 2006). The lme4 package (Bates *et al.*, 2015) was used for model fitting in R Programming Language (R Core Team, 2013).

For model selection, as a first step, highly correlated PVs were excluded as these often represent the same physiological processes and if included, they often introduce complications of collinearity. To do this, I employed variance inflation factors (VIFs) as suggested in the work of Zuur *et al.,* (2009). In principle, VIFs range from 1 upwards. The numerical value of each VIF gives the percentage of inflation for the variance of each coefficient. To interpret the VIF values, 1 is considered as not being correlated, values between 1 and 5 moderately correlated, and values greater than 5, highly correlated. With this in mind, I set the exclusion threshold at 4.

I then calculated square roots of VIFs for each PV in the model. Finally, I sequentially dropped all PVs with the highest VIFs until all values were < 4.

Based on VIFs, I identified a global model. To enhance model parsimony, I performed a backward stepwise regression; starting from the global model, PVs with the strongest reduction of the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) were excluded. Model selection was considered complete when exclusion of additional PVs did not reduce the AIC any further. I then used different combinations of the final PV set to specify 4 differently structured models with the aim of finding the combination with the best predictive power.

In addition to the AIC, I also used Akaike Weights (AWs) for model selection. AWs range between 0 and 1, with the total number of weights for all models in the candidate, set being equal to 1 and the highest-ranked model being taken as having the highest probability that it is the best (Symonds and Moussalli, 2011).

I considered AIC, $R^{2,}$ and Akaike Weights as sufficient measures for the selection of the most parsimonious model because they inherently include penalties for model complexity in order to achieve the best possible predictive power (Vandekerckhove *et al.,* 2015). Therefore, a follow-up with subsequent measures of parsimony such as ΔAICc, or evidence ratios was considered unnecessary. In fact, all these measures are a representation of essentially the same thing.

Table 4.1: Summary statistics of basal area increment (BAI) data. PSP, permanent sample plots

Data	**PSPs**	**Stems**	**Mean BAI ±SE (m^2/ha/year.)**	**BAI Range (m^2/ha/year.)**
Fitting	133	22,965	0.16 ± 0.01	0 to 0.8
Validation	90	15,311	0.13 ±0.01	0 to 0.64
Total	**223**	**38,276**		

4.2.4 Model evaluation techniques

Four models reached the final selection stage (Table 4.1) as discussed in section 4.2.3 paragraph 3; these include *Model 0* which was a combination of above ground biomass (AGB), soil phosphorous (P), soil depth (SD), rainy season length (RSL), climatic water deficit (CWD), the longitudinal (Lon) and latitudinal (Lat) location of each PSP; *Model 1* (AGB + P + RSL + CWD + Lon + (1 **|** site)), *Model 2* (AGB + P + RSL + CWD + Lat + (1 **|** site)), and Model 3 (AGB + P + RSL + CWD + (1 **|** site)).

After identifying the best predictive model (*Model 1.* See Table 4.2), I used several model performance metrics, both statistical and graphical to gauge predictions. First, I calculated coefficient of determination (R^2; Steel and Torrie, 1960) to quantify the proportion of the variance in the training data explained by the model. To do this, I used the *r.squaredGLMM* function in the MuMIn package (Nakagawa and Schielzeth, 2013) because of its convenience in returning the variance explained by PVs alone (Marginal R^2) and by both fixed effects (PVs) and random effects (Conditional R^2). The scale of R^2 extends from 0 to 1, with higher values (i.e., ≥ 0.5) generally considered as strong evidence for a well-performing model (Moriasi *et al.,* 2007). Mathematically, R^2 is expressed as follows:

$$R^2 = 1 - \frac{RSS}{TSS} \qquad \text{Eq. 1}$$

Where: *RSS* is the residual sum of squares and *TSS* is the total sum of squares of the data variance.

Prediction errors (i.e., Root mean square error - RMSE) were also explored. RMSE is a widely used measure of checking the reliability of model predictions. It is mathematically expressed as follows:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(X_{Obs,i} - X_{model,i})^2}{n}} \qquad \text{Eq. 2}$$

Where: X_{Obs} is observed BAI and X_{model} indicates model predictions of BAI at time and place *i.* The lower the RMSE, the better the model predictions (Moriasi *et al.,* 2007). Although RMSE is widely used, Singh *et al.,* (2005) found it problematic because there are no guidelines of what exactly constitutes a low RMSE value. This observation led to the development of another model evaluation statistic. Since it is an improvement of the RMSE, the new evaluation statistic was simply called the RMSE-observations standard deviation ratio (RSR). The RSR metric standardizes RMSE based on the standard deviation of observations. It combines both an error-index and the additional information as recommended in the work of Legates and McCabe, (1999). Mathematically, the RSR is expressed as follows:

$$RSR = \frac{RMSE}{STDEV_{obs}} = \frac{\left[\sqrt{\sum_{i=1}^{n}(Y_i^{obs} - Y_i^{sim})^2}\right]}{\left[\sqrt{\sum_{i=1}^{n}(Y_i^{obs} - Y_i^{mean})^2}\right]} \qquad \text{Eq. 3}$$

The scale of the RSR metric is optimal at 0 and denotes zero residual variation thus, perfect model predictions. Therefore, the closer the RSR is to 0, the lower the RMSE, and the better the model prediction performance (Singh *et al.,* 2005; Moriasi *et al.,* 2007). To implement the RSR metric in this study, I used the hydroGOF package (Zambrano-Bigiarini, 2020) in R Programming Language (R Core Team, 2013).

Percent bias (PBIAS) which can be thought of as an error index was used to compute the average tendency of predicted BAI to be larger or smaller than observed BAI (Moriasi *et al.,* 2007). As the name suggests, PBias is given as a percentage with 0% being the optimal value. Positive values indicate that the model overestimates observed BAI while negative values show that the model underestimates it (Gupta *et al.,* 1999). Mathematically, PBias is expressed as follows:

$$PBias = \left[\frac{\sum_{i=1}^{n} (Y_i^{obs} - Y_i^{sim}) * 100}{\sum_{i=1}^{n} (Y_i^{obs})} \right] \qquad \text{Eq. 4}$$

Where: PBias is the deviation of BAI expressed as a percentage, Y_i^{obs} is observed BAI, and Y_i^{sim} is predicted BAI.

Pearson's correlation coefficient *(R)* was used to determine the degree of collinearity between predicted and observed BAI. Mathematically, the R coefficient is given as follows:

$$R = \frac{\sum_{i=1}^{n} (x_i - \bar{x}).(y_i - \bar{y})}{\sqrt{\sum_{i=1}^{n} (x_i - \bar{x})^2}.(\sum_{i=1}^{n} (y_i - \bar{y})^2} \qquad \text{Eq. 5}$$

Where: *x* denotes observed BAI while *y* shows predicted BAI. The scale of the correlation coefficient ranges from −1 to 1 with 0 indicating that there is no relationship. However, if *R* is 1 or -1, it indicates that a perfect positive or negative linear relationship exists.

Nash–Sutcliffe model efficiency (NSE; Nash and Sutcliffe, 1970) was employed to analyse how well the plot of observed versus predicted BAI fits the 1:1 line on the validation dataset. NSE is a widely used (Moriasi *et al.,* 2007; Vis *et al.,* 2015; Förster *et al.,* 2018) normalized statistic in modelling studies and it is efficient in determining the relative size of the residual variance. Mathematically, NSE is expressed as follows:

$$NSE = 1 - \left[\frac{\sum_{i=1}^{n} (Y_i^{obs} - Y_i^{sim})^2}{\sum_{i=1}^{n} (Y_i^{obs} - Y^{mean})^2} \right] \qquad \text{Eq. 6}$$

Where: Y_i^{obs} is the *i*th observation of BAI, Y_i^{sim} is the *i*th prediction of BAI, Y^{mean} is the mean of observed BAI, and *n* is the total number of observed BAI values. The scale of NSE ranges between -∞ and 1.0 with an NSE value of 1 being the optimal value. Values between 0 and 1 are generally considered acceptable levels of model performance (Nash and Sutcliffe, 1970).

Conclusively, the strength of each PV was directly graded using the estimated parameters since they were all standardised. Thus, PVs with the largest statistically significant estimates were taken as having the greatest impact on BAI (Zhang *et al.,* 2016).

Finally, I subjected all models to a spatial autocorrelation test to check if there is a tendency for PSPs close together to have similar residuals. To do this, I used the DHARMa package (Hartig, 2015) to calculate Moran's *I* (Moran, 1950). Moran's *I* is a widely used approach because of its convenience in pinpointing the locations of spatial clusters (positive autocorrelation) and spatial outliers (negative autocorrelation).

The scale of Moran's *I* is between -1 and 1 with observed values close to zero indicating no spatial autocorrelation (Xiong *et al.,* 2019). The statistical significance of Moran's *I* is evaluated using a Z score and associated *P*-value which is generated by random permutation (Paradis *et al*., 2004). The null hypothesis used in this study was that there is zero spatial autocorrelation present in the model residuals and the alternative hypothesis was spatial autocorrelation is present.

4.3 Results

4.3.1 Model performance

Although several other climatic variables (i.e., temperature, evapotranspiration downwelling surface solar radiation, frost, length of growing season, mean annual temperature) were investigated, RSL, MAP, and CWD are the ones that were ultimately found useful in predicting BAI across unmonitored areas of SAWs. Similar to climate-related PVs, several other soil and site-related PVs were explored (i.e., available water capacity, soil Nitrogen, soil pH, Organic Carbon, Human Footprint Index, slope, topography, and fire occurrence). However, only Soil depth and P were ultimately found useful in predicting BAI across unmonitored areas of southern Africa.

Apart from Model 2, models that reached the final selection stage exhibited the same R^2 values (Table 4.2). Although there were small differences in their AICs, Model 1 was selected because apart from having the smallest AIC, it also had the lowest (i.e., 0.1) observed spatial autocorrelation value. Inarguably, the inclusion of longitude among PVs in Model 1 facilitated the reduction of spatial autocorrelation. Further, I chose Model 1 because it had the strongest Akaike Weight (0.706) which can be interpreted that there is a 70.6% chance that it really is the best-approximating model describing BAI data given the 4 models considered.

Overall, the selected model explained 60% of BAI variance based on data for fitting and 50% on validation data (See R^2 values). Further, it is important to note that the proportion of variance explained by the PVs alone (Marginal R^2) in the fitting dataset was 51% which improved to 60% when the hierarchical structure (i.e., random effects; Conditional R^2) of the data was taken into consideration (see

Nakagawa and Schielzeth, 2013). This was not surprising as random effects managed to capture site-specific effects not included among PVs.

Table 4.2: Models that reached the selection stage with highlighted row denoting final model. AGB, above ground biomass; P, soil phosphorous; SD, soil depth; RSL, rainy season length; CWD, climatic water deficit; Lon and Lat, longitude and latitude of individual permanent sample plots

Model	**Predictor Variables (PVs)**	**AIC**	R^2	**Moran's *I***	**Akaike Weights**
Model 0	AGB + P + SD + RSL + CWD + Lon + Lat	-207.8	0.6	0.1	0.289
Model 1	AGB + P + RSL + CWD + Lon	-208.9	0.6	0.1	0.706
Model 2	AGB + P + RSL + CWD + Lat	-197.5	0.5	0.4	0.002
Model 3	AGB + P + RSL + CWD	-197.3	0.6	0.5	0.002

Rainy season length (RSL) was found to be the main predictor of BAI with one standardized unit of RSL translating into a BAI increment of 0.13 m^2/ha/year (Figure 4.2). Other small effects, in order of importance, were from climatic water deficit (CWD), above-ground biomass (AGB), soil phosphorous (P), and the longitudinal location of each PSP. The relationships of these variables with BAI and among themselves are given in Supplementary Material 4.1 and 4.2 respectively.

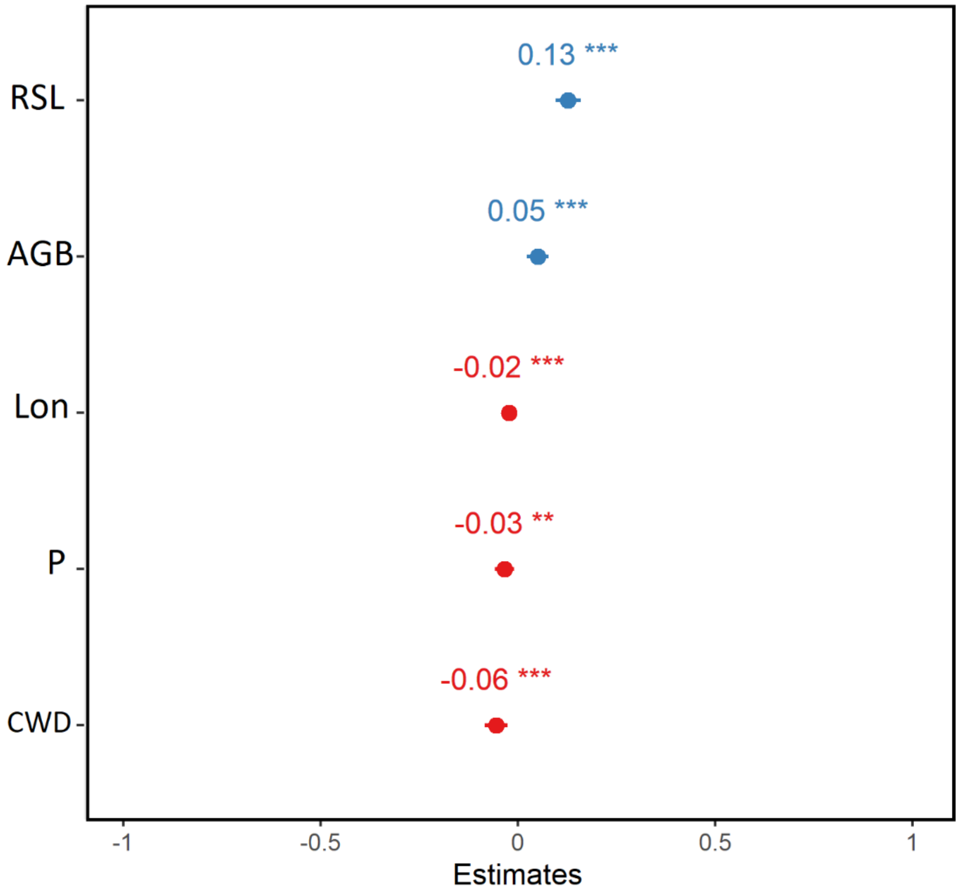

Figure 4. 2: Statistical summary of Model 1. RSL, rainy season length; AGB, above-ground biomass; Lon, the longitude of individual permanent sample plot; P, soil phosphorous; CWD, climatic water deficit. Numbers in blue (red) represent variables with positive (negative) effects. Significance codes: 0 '***'; 0.001 '**'

When the distribution of BAI data was explored further, results showed 2 clusters with low values in Niassa, Mozambique, and Kamatupa, Zambia being generally concentrated below 0.14 m^2/ha/yr while the remaining sites were observed to have well spread BAI values (Figure 4.3 and Supplementary Material 4.3, see Fig. 3.4 for the geographical location of sites). Chidumayo (2019) attributed the slow growth rates in Kamatupa, Zambia to age (years since woodland clearing) which was determined by assessing repositories of the Zambia Forestry Department. Trees at these PSPs had been clear-felled at knee height mainly for purposes of fuel (firewood/charcoal) and they had since regrown. The study found that age was the most important predictor of growth rates, and it had a significant negative effect. Exploring the effect of age on the full SEOSAW dataset would yield interesting results but this information is not readily available for most sites. It would therefore make an important addition to future research lines.

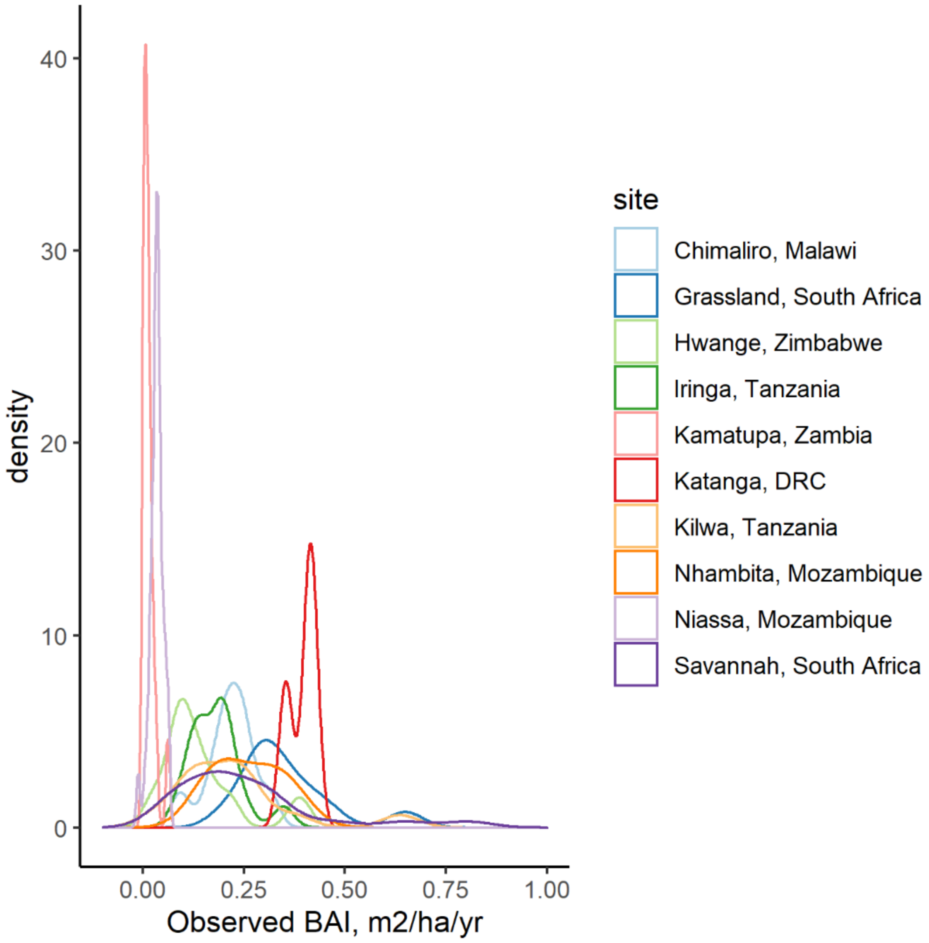

Figure 4.3: Observed basal area increment (BAI) across SAWs. Different colours indicate sites studied whose geographical locations are given in Fig. 3.4 of this thesis

To avoid strong clustering in the predictions as seen in the observed data (Figure 4.3), BAI for Niassa, Mozambique, and Kamatupa, Zambia (hereafter NK) were predicted separately from the rest of the data. This was an important step especially considering that the goal of model validation was not only to ensure that the selected predictor set was parsimonious but to also verify that the model retained sufficient information to predict a dataset not used in the fitting process.

When Model 1 was tested for robustness based on an independent dataset not used for fitting (validation dataset), results showed that at 0.8, the correlation coefficient between observed and predicted BAI for the NK data was very strong (Figure 4.4) although a drop in the full dataset was noted (Figure 4.5). It is notable however that considering all the model performance metrics (i.e., *R,* RMSE, RSR, PBias, NSE), the model performed relatively well on the full dataset as well.

Overall, these results indicate that Model 1 performed fairly well on an independent dataset although some bias is evident. Therefore, the ability of the selected model to predict growth on an independent dataset with a correlation coefficient of 0.8, a RMSE of 0.01, RSR of 0.7, PBias of 7.8%, and NSE of 0.5 (Figure 4.4) suggests that the model provides practical usability in predicting BAI for sustainable woodland management across unmonitored areas of SAWs. Regarding the observed drop in performance when the full dataset was used, these results suggest that predicting across unmeasured areas would yield better results if done closer to observed data and/or having a good distribution of PSPs. It is notable however that an inspection of random effects showed that all sites had an intercept of between -0.05 to 0.05 suggesting very little variation. Therefore, the model shows potential for further improvement especially by the use of higher resolution ground-based PVs and increasing the number of PSPs.

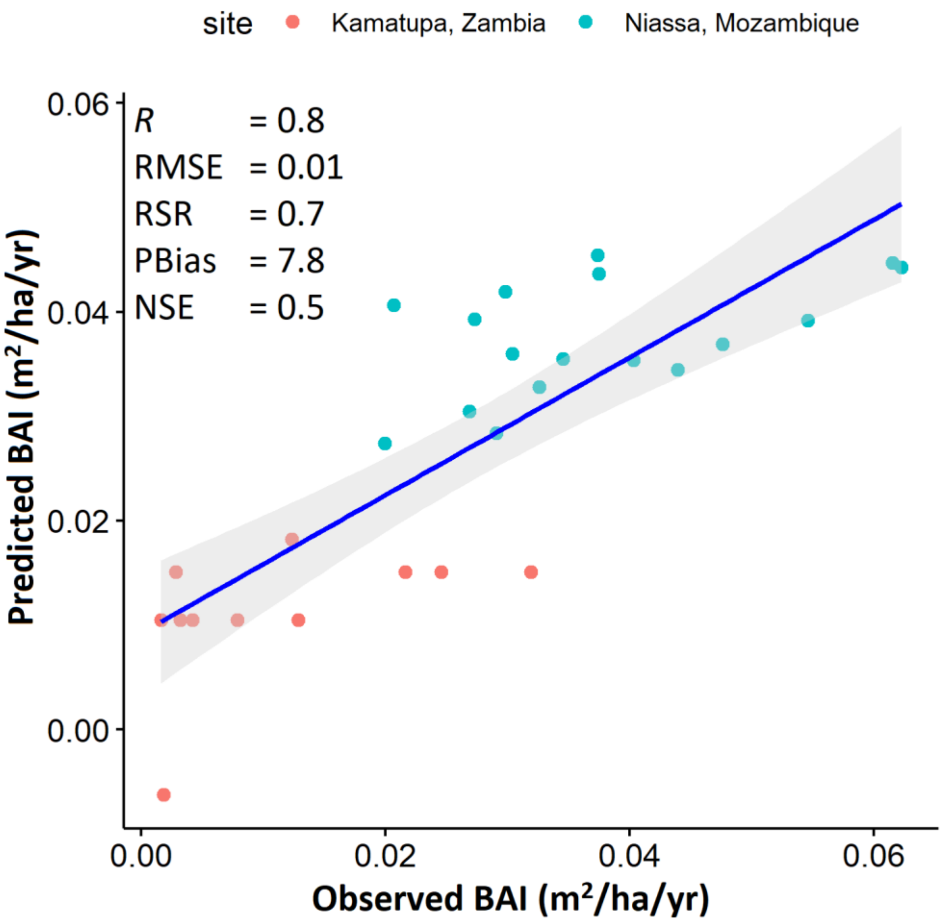

Figure 4.4: Comparison of observed and predicted BAI (m^2/ha/year.) based on data for validation covering the Niassa and Kamatupa sites. The blue solid diagonal line represents the regression. Shades of grey are the confidence interval at 95%. *R,* correlation coefficient; *RMSE*, Root Mean Square Error; *RSR,* RMSE-observations standard deviation ratio; *PBIAS,* Percent Bias; *NSE,* Nash–Sutcliffe efficiency; *BAI,* basal area increment

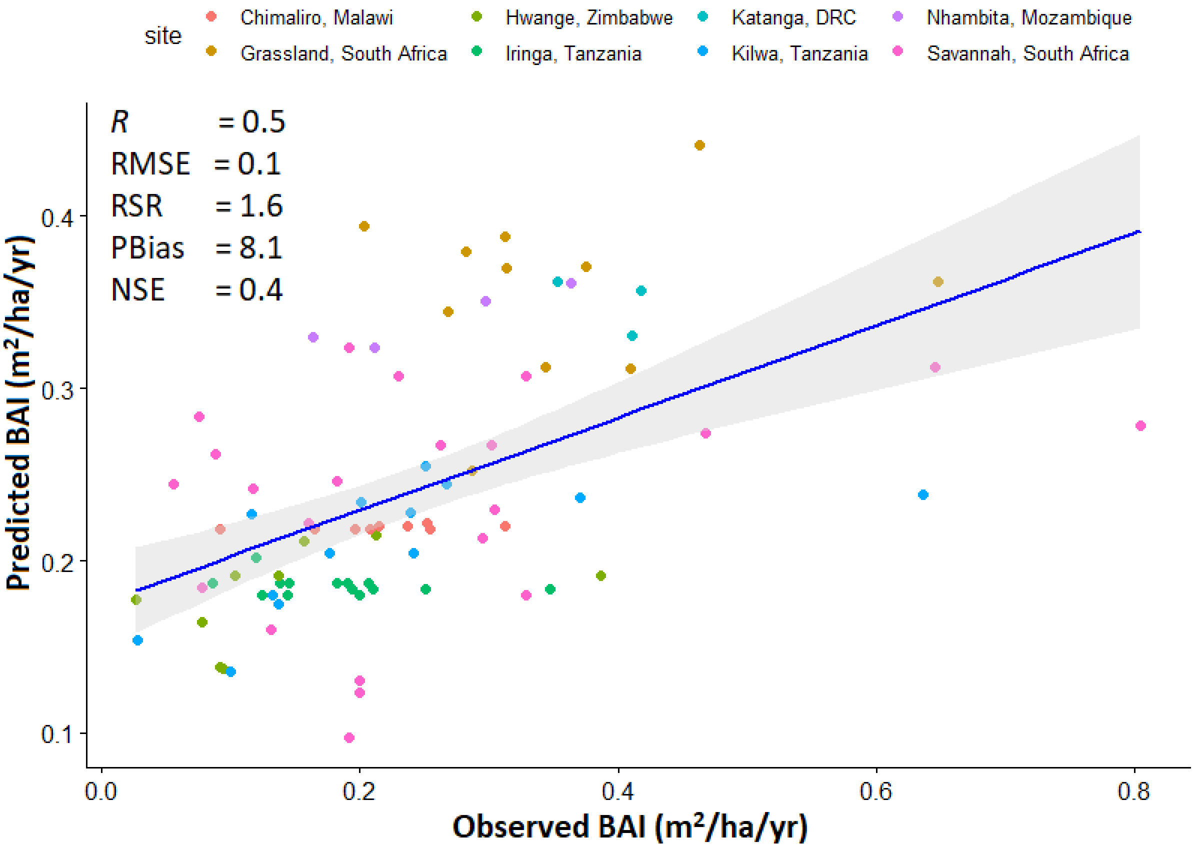

Figure 4.5: Comparison of observed and predicted BAI (m^2/ha/year.) based on data for validation covering all sites apart from Niassa and Kamatupa. The blue solid diagonal line represents the regression. Shades of grey are the confidence interval at 95%. *R,* correlation coefficient; *RMSE*, Root Mean Square Error; *RSR,* RMSE-observations standard deviation ratio; *PBIAS,* Percent Bias; *NSE,* Nash–Sutcliffe efficiency; *BAI,* basal area increment

4.3.2 Patterns of BAI across unmonitored southern Africa

Model 1 predictions of BAI across unmonitored areas of SAWs were found to range between 0.07 and 0.7 with an estimated regional mean of 0.35 m^2/ha/year (Figure

4.6). High BAI values, generally ranging between 0.5 and 0.7 m^2/ha/year, were observed in the Katanga region of the Democratic Republic of Congo and the eastern parts of South Africa. Central Mozambique, parts of eastern Botswana, and southern Malawi exhibited the lowest BAI typically ranging between 0.07 and 0.28 m^2/ha/year. Tanzania and some parts of Zambia seemed to have midlevel BAI around ~0.4 m^2/ha/year.

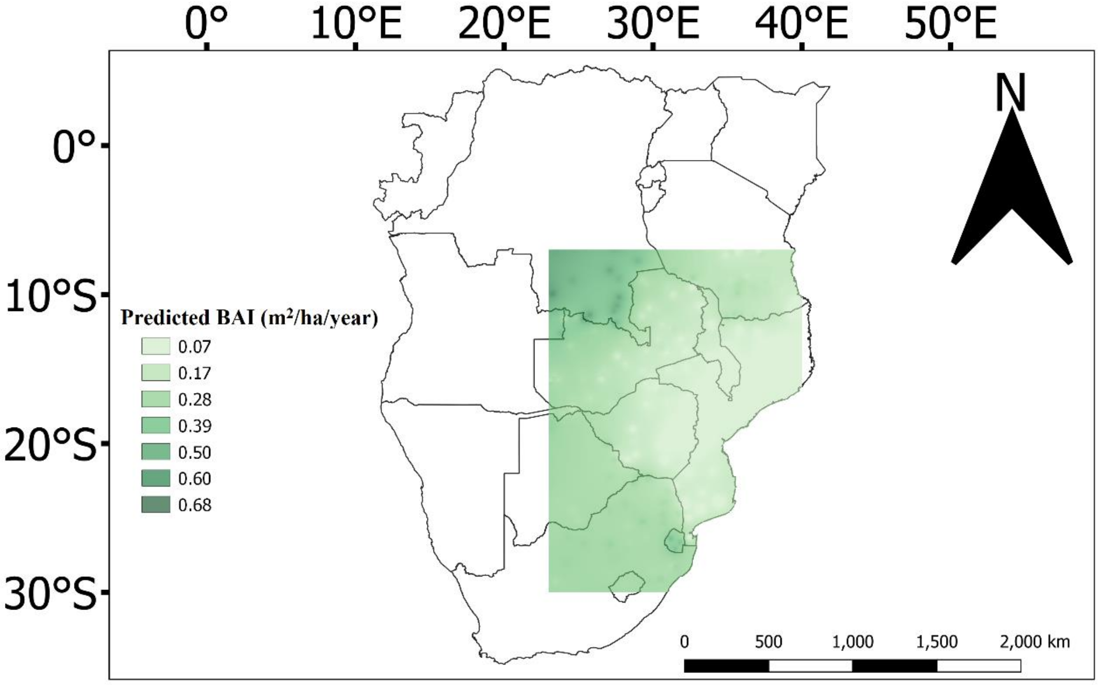

Figure 4.6: Predicted BAI (m^2/ha/year) across unmonitored areas

4.4 Discussion

This study set out to develop a hierarchical mixed-effects model that would provide insights into basal area increments (BAI) across unmonitored areas of southern African woodlands (SAWs).

Regarding the predicted BAI values of between 0.07 and 0.7 m^2/ha/year (Figure 4.4), these were found to agree with observed BAI documented in most parts of the region. For instance, Gadow *et al.,* (2016) found a maximum BAI value of 0.75 m^2/ha/year when they studied 20 different tree species in South Africa. Chidumayo, (2019) who studied growth patterns of Miombo woodlands in Zambia found a mean BAI of 0.40 m^2/ha/year in dry miombo and 0.53 m^2/ha/year in wet miombo. This find is in direct agreement with the model predictions in the present study which estimated BAI over Zambia to be ~0.4 m^2/ha/year (Figure 4.4).

Stem-level attributes such as size, species, and age have previously been named as key drivers of BAI across SAWs (Chidumayo, 2019). However, since the overarching goal of this study was to predict BAI across unmeasured areas of SAWs where stem-level attributes are unknown, they could not be used. Thus, this study relied on climate and soil predictor variables (PVs). Of these PVs, rainy season length (RSL) was found to have the largest effect on BAI. This find suggests that long rainy seasons translate into equally longer growing seasons hence the observed large effect of RSL on BAI. A similar observation was made in the tropical woodlands of Mexico (Whigham *et al.,* 1998), central Amazon (Dünisch *et al.,* 2003), and northern Brazil (Grogan and Schulze, 2012) where RSL was found to have a larger effect than mean annual precipitation.

Climatic water deficit (CWD) which was used as a surrogate for seasonal water stress was found to have a negative effect on BAI. Previous studies have found that CWD exerts detrimental effects on tree growth across the world. For example, Restaino *et al.,* (2016) reported that water deficits led to decreases in tree growth rates across all latitudes in the United States. Ledo *et al.,* (2018) who studied controls of root to shoot ratio also found that CWD has major controls on tree growth rates across the world and concluded that aridity has a major depressing effect on tree growth rates.

Soils were generally found to have an effect not significantly different from zero. The small effect of soils re-echoes the findings embodied in Chapter 3 of this thesis. Although that Chapter considered individual tree growth rates, soils were again found to have negligible effect. Swemmer and Ward, (2020) also found little influence of soils on growth rates – in agreement with the present study. They attributed this lack of influence to the possibility that savanna trees have evolved enough to enable different species to maximize the use of available nutrients, for each soil type within each region, such that precipitation becomes the primary determinant of growth rates.

The observation that above-ground biomass (AGB) which was used as a surrogate for competition exerts a positive effect on BAI is surprising and counterintuitive. However, it is notable that the effect (0.05) is small. Apart from being a proxy for competition, AGB can also be a proxy for lots of big trees, with deep roots, and the ability to acquire a lot of resources – this would then explain its positive effect. However, the uncertainty surrounding this effect provides an interesting investigative point in future research lines.

While a hyper-diverse range of PVs was explored before settling for the final set used in this study, it is notable that other PVs can be considered by future studies. Examples of variables that were not readily available for inclusion in this work are: measures of disturbance aside from fire e.g., damage caused by both animals and people (Holdo, 2006; Nasseri *et al.,* 2010; Tripathi *et al.,* 2019), detailed soil nutrient data sampled at high spatial resolution (Lévesque *et al.,* 2016; Muledi *et al.,* 2020) and infestations of pathogens (Schuldt *et al.,* 2017). All these variables can have profound implications on BAI. Although such PVs are not easy to get, they can potentially improve the predictive power of models.

It is important to note that the model documented in this work is based on the 223 PSPs and therefore, its use in predicting BAI across other regions, with different woodland structure, should be done cautiously. In particular statistical measures reported in section 4.3 of this thesis could be used to quantify model uncertainty. Further, the model identified herein can best be used to give future scenarios and to show how tree growth rates on these PSPs will potentially be influenced by future global change. Of key interest here is that RSL and CWD are the main predictors of BAI. Model projections show that future RSL will potentially become shorter while CWD is likely to be enhanced across southern Africa (Dunning *et al.,* 2018); this will potentially strain BAI in the future. Future adaptation and management strategies should therefore account for these potential changes.

4.5 Concluding thoughts

A hierarchical mixed-effects model was developed to predict basal area increment (BAI) across unmonitored areas of southern African woodlands (SAWs). A carefully selected set of predictor variables (PVs) representing climate and site-level attributes was used to drive the final model. The following conclusions can be drawn from the present study: BAI was found to be mainly influenced by rainy season length (RSL) which, as expected, exerted a positive effect. Climatic water deficit (CWD) which was used as a surrogate for seasonal water stress was found to suppress BAI. The effect of above-ground biomass (AGB) which was used as a surrogate for competition, was surprising and counterintuitive but presents an interesting line of future research.

Considering that this study covered a wide environmental gradient, the ability of the selected model to predict growth on an independent dataset with a correlation coefficient (R) of 0.8, a root mean square error (RMSE) of 0.01 m2/ha/year, a RMSE-observations standard deviation ratio (RSR) of 0.7, a percent bias (PBias) of 7.8%, and a Nash-Sutcliffe Efficiency (NSE) of 0.5 suggests that the model provides practical usability in predicting BAI for sustainable woodland management across unmonitored areas of SAWs. Additionally, with these results, woodland managers will be able to detect and delineate risk areas of impeded BAI. Furthermore, the selected model could be used to disentangle possible effects of future global change on BAI across the region. Specifically, model projections of the most important PVs could be used to drive the mixed-effects model to understand the possible effects of future global change on BAI.

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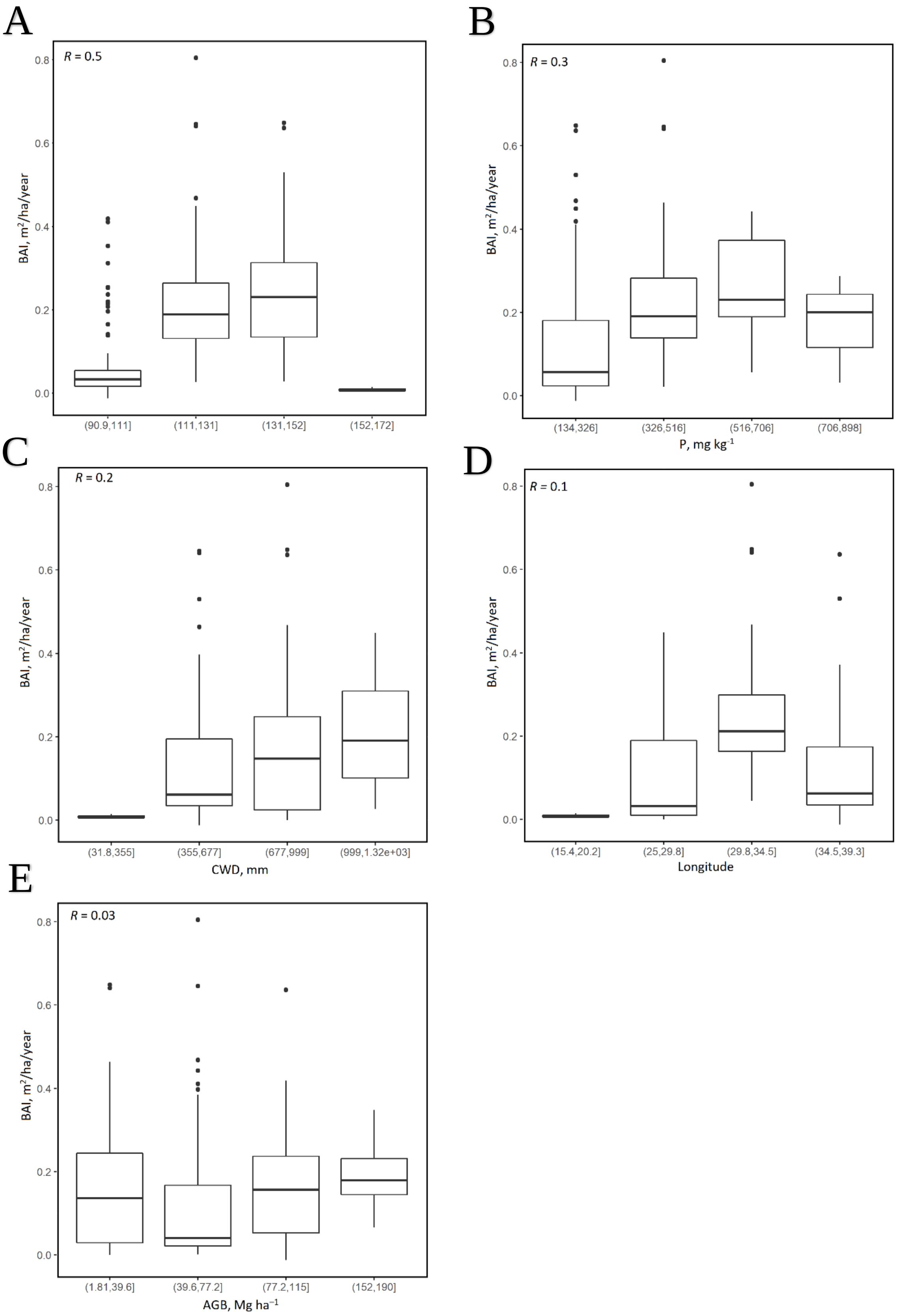
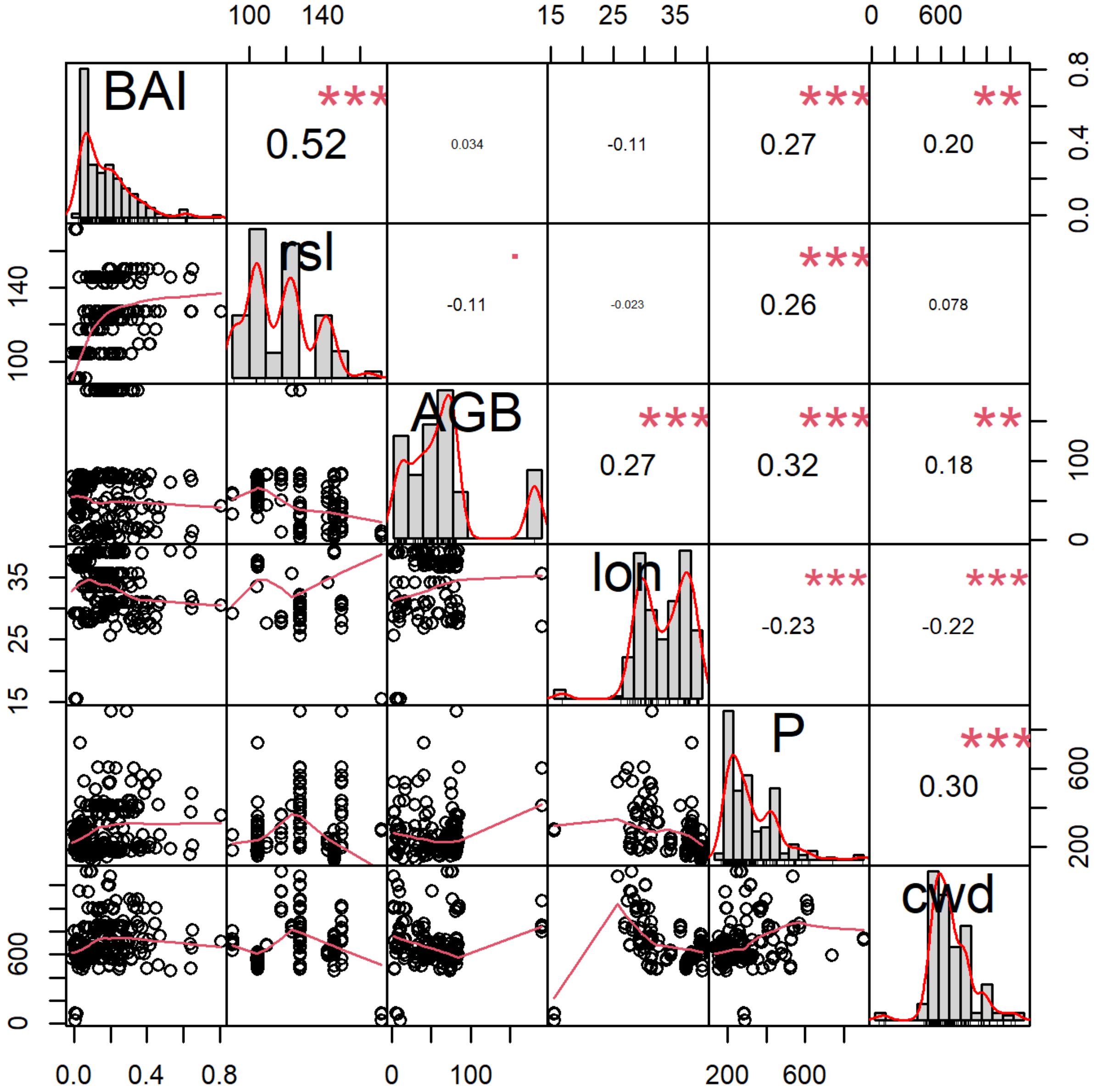
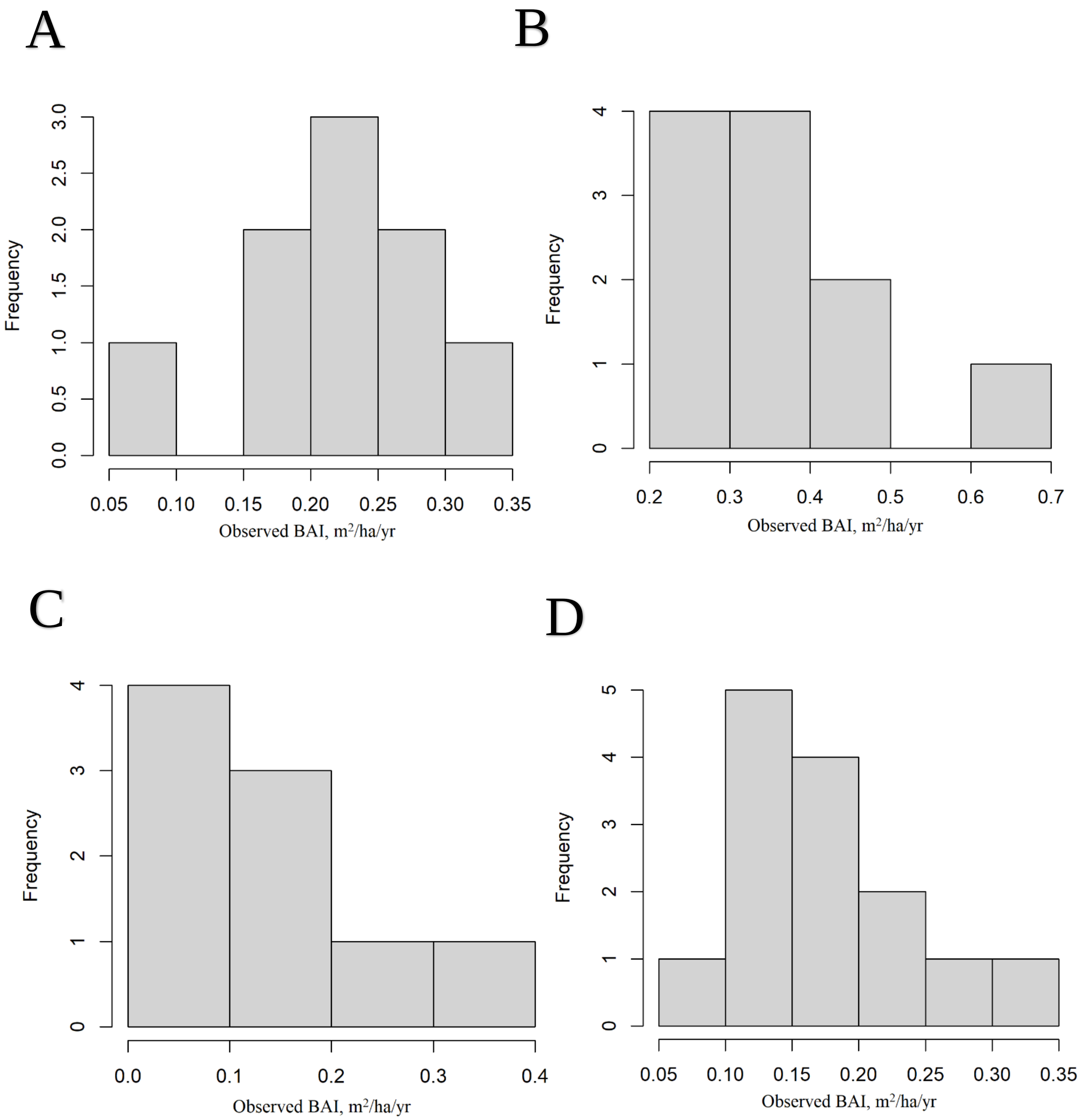
Supplementary Material 4.1: Variation of environmental variables with basal area increment (BAI) across the study region for **A)** BAI and RSL, **B)** BAI and P; **C)** BAI and CWD, **D)** BAI and Lon; **E)** BAI and AGB. RSL, rain season length; P, soil phosphorous; CWD, climatic water deficit; Lon, the longitude of individual permanent sample plots; AGB, above-ground biomass.

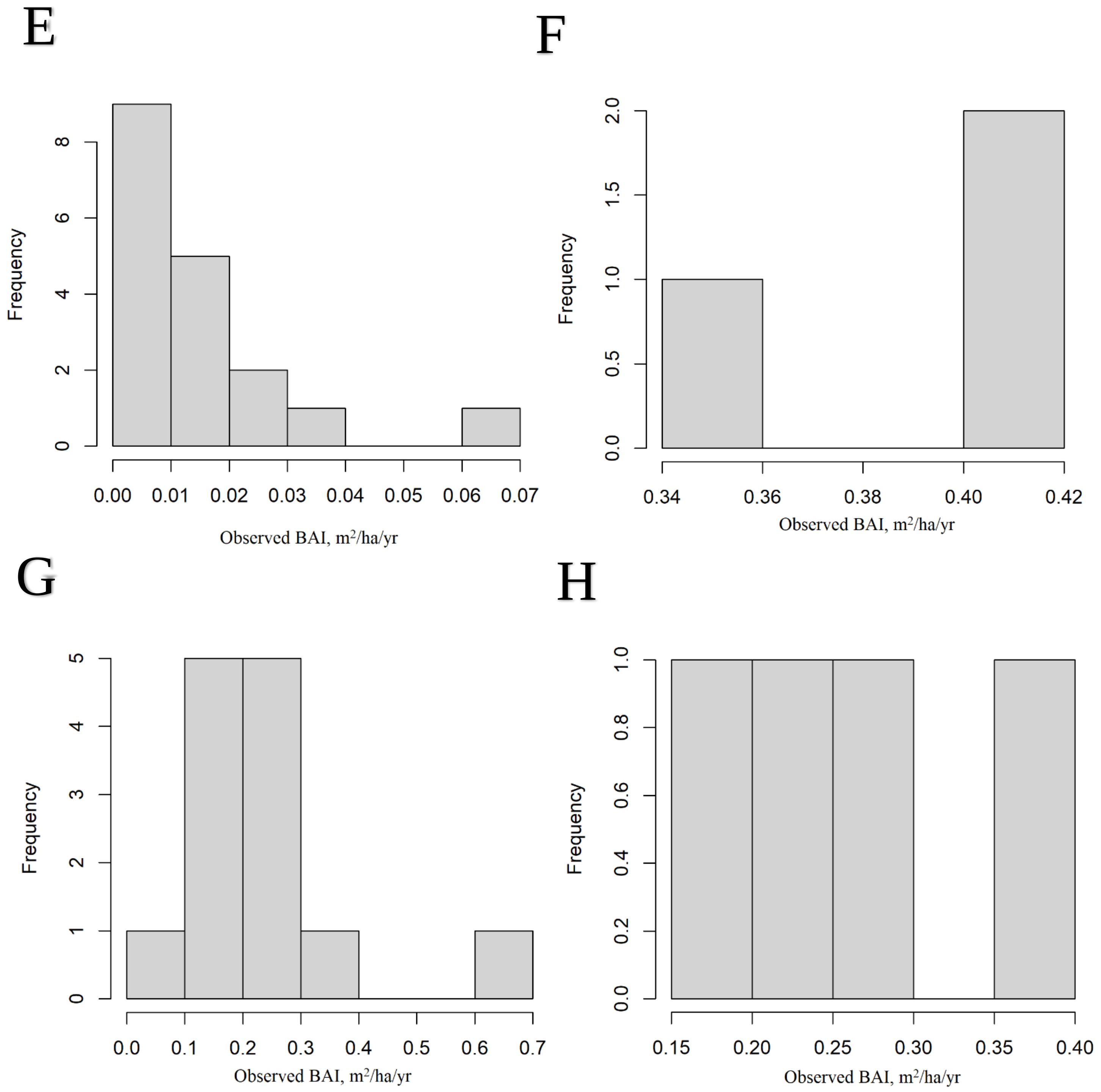


Supplementary Material 4.2: Multivariate plot representing the relationships among explanatory variables; BAI, Basal area increment, rsl, rainy season length; AGB, above ground biomass; lon, longitude of each plot; P, soil phosphorus, cwd, climatic water deficit



Supplementary Material 4.3: Observed basal area increment (BAI) across SAWs for individual sites i.e., **A)** Chimaliro, Malawi **B)** Grassland, South Africa **C)** Hwange, Zimbabwe **D)** Iringa, Tanzania **E)** Kamatupa, Zambia **F)** Katanga, DRC **G)** Kilwa, Tanzania H) Nhambita, Mozambique **I)** Niassa, Mozambique **J)** Savannah, South Africa

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Observed BAI, m²/ha/yr
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0.38
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Observed BAI, m²/ha/yr
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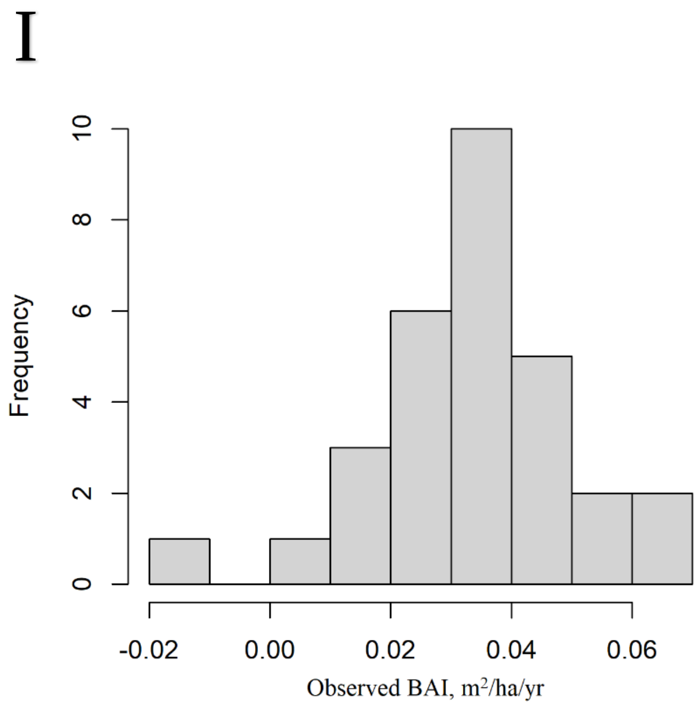
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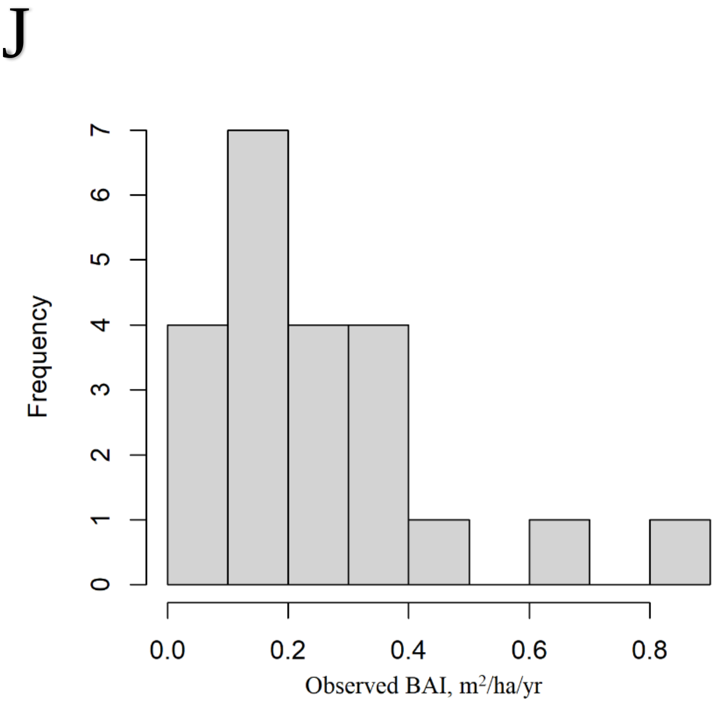
Observed BAI, m²/ha/yr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Observed BAI, m²/ha/yr

CHAPTER V

CHAPTER 5: ANNUAL ALLOWABLE CUT FOR MERCHANTABLE TIMBER SPECIES ACROSS SOUTHERN AFRICAN WOODLANDS

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Author Contributions

The conception, analytical design, model development, data analyses, literature searches, and manuscript writing of this study were led by BL with inputs from CMR and ETAM.

Abstract

Allocating an annual amount of timber that can safely be harvested without negatively impacting long-term timber stocks and ecosystem health is an important component of good woodland management. However, apart from a few countries, this practice is still limited across southern Africa due to the lack of extensive growth monitoring plots data. Here, I used a new dataset composed of 1,025 tree measurements of large stems from 49 timber species on 115 permanent sample plots (PSPs) in 7 countries inventoried between 1991 and 2018 to determine a sustainable annual allowable cut (AAC). I used allometric equations from volume models developed in Angola, Tanzania, Mozambique, and Zambia to estimate a mean annual increment (*G*). I found a *G* of 0.64 ±0.1 m^3/ha/year across the region. I then adopted an AAC of 80% of the *G* to ensure sustainability in both ecological and economic terms. I found a mean AAC of 0.51 ±0.1 m^3/ha/year with a range of 0 – 7.4 m^3/ha/year across the region. It is notable however that the distribution of AACs is very skewed, with most in the dataset well below 1 m^3/ha/year, and a few outlier plots (4 to be specific) above 3 m^3/ha/year. At the individual stem level of the 1,025 large trees, results show a mean annual diameter growth rate of 1.5 ±0.3 mm/year translating into a harvest cycle of ±years when a widely accepted harvest size of 35 cm is used – thus implying that on a given stand with 233 trees, one tree can be harvested every year. In this study, the set AAC was found to suggest that there is potential for any PSP to recover and become resilient as long as strict adherence to the AAC is followed. I, therefore, conclude that adherence to AAC is a pivotal part of good woodland management because it is the primary safeguard against under or over cutting. This is especially true because by harvesting only large trees as prescribed by the AAC, trees in smaller diameter classes are allowed to graduate to higher classes. Further, the process supports the regeneration of large trees which will in the long term ensure woodland sustainability.

Keywords: Annual allowable cut, sustainable woodland management, timber species, SEOSAW, southern Africa

5.1 Introduction

Timber is one of the most important ecosystem products extracted from southern African Woodlands (SAWs; Campbell, 1996; Ribeiro *et al.,* 2020). As of 2003, over 300, 000 people were estimated to be directly employed in the commercial timber industry with millions indirectly benefitting from the industry (Oksanen and Mersmann, 2003); considering that this is almost 20 years ago, this estimate may have quadrupled by now. Between 1993 and 2002, various wood-based products that were exported from southern African countries amounted to more than US$2 billion (FAO, 2007), and most recently (between 2015 and 2020), the Food and Agriculture Organization Statistical Database (FAOstats) documents that wood-based products that were exported from the region amounted to US$11.1 billion (FAO, 2020). China is currently the main timber importer from SAWs while Mozambique is the largest exporter to China in the region (Lukumbuzya and Sianga 2017; Ribeiro *et al.,* 2020).

It is notable however that the timber industry is marred by illegalities. In fact, poor timber harvesting (over-exploitation and destructive harvesting techniques) is one of the most repeatedly cited contributors to woodland resource loss. Ribeiro *et al.,* (2020) documents that unsustainable management practices such as over-exploitation and destructive logging techniques have contributed to worsening levels of degradation across SAWs.

Koigi, (2018) estimated that Africa loses $17 billion to illegal logging activities annually with international smuggling fuelling the trade. This subjects millions of livelihoods across the continent that depend on woodlands to displacement and endangers species endemic to the region. Intensified woodland management has elsewhere been found to have the potential of ensuring the support of future generations through wood and non-wood products. I use intensified woodland management here to mean increased management efforts in comparison to current practices (Hegan and Luckert, 2000). While intensified woodland management can be considered a very broad term, both scientists and policy makers agree that policy frameworks that curb illegal timber activities and enforce an annual allowable cut (AAC) are instrumental to this cause (Hansen and Treue 2008; Santos de Lima, 2018; EFI, 2020). In fact, in a recent study, Syampungani *et al.,* (2020) argue that the ability of the woodlands to continue providing wood- and non-wood goods and services hinge on the adoption of intensified management practices that enforce sustainable harvesting techniques such as giving enough time to woody species to regenerate by resprouting from the stump after harvesting.

Although the exact extent of woodland resource loss to poor timber harvesting practices across southern Africa is difficult to assess, *Pterocarpus angolensis, Afzelia quanzensis,* and *Milletia stuhlmannii* are some of the most sort after and thus, heavily harvested timber species across SAWs (Mate, 2014; De C auwer *et al.,* 2017; *De Cauwer et al.,* 2020). Marzoli, (2007) estimated that the three species account for 78% of harvested timber volume in Mozambique.

Pterocarpus angolensis (subfamily – *Papilionoideae*) can generally be considered as a medium-to-large tree whose heights have been found to reach 28 m in some miombo countries across SAWs (van Wyk and van Wyk, 1997; Therrell *et al.,* 2007). Some of the countries in which this reddish-brown heartwood species has been found include Malawi, Mozambique, Zambia, Zimbabwe, and Botswana. Although *Pterocarpus angolensis* is widely regarded as one of the most valuable timber species, it is also used for myriad other purposes such as traditional medicines and carving (Fichtler *et al.,* 2004; Mate, 2014).

Afzelia quanzensis (subfamily - *Caesalpinioideae*) is a medium-to-large deciduous tree whose presence is widespread across SAWs especially on elevations of up to 1800 m characterized by wet climates with mean annual precipitation of ~1000 mm (van Wyk and van Wyk, 1997; Jøker and Msanga, 2000; Mate, 2014). The height of *Afzelia quanzensis* trees is known to vary between 12 and 15 meters. Pioneering studies (e.g., Gomes e Sousa, 1966), have noted that timber extracted from *Afzelia quanzensis* is of high quality especially given its resistance against termites. The wood is also generally hard and durable making it suitable for both construction materials and furniture (Hines and Eckman, 1993). Mate, (2014) estimates that the basic density of *Afzelia quanzensis* is 0.69 g m^{-3}.

Like *Pterocarpus angolensis and Afzelia quanzensis, Millettia stuhlmannii* (subfamily – *Faboideae*) is a medium to large deciduous species whose height varies between 15 to 25 m with a crown that is best described as spreading (Mate, 2014). It is often found on rocky landscapes, bushvelds, and forests (van Wyk and van Wyk, 1997). *Millettia stuhlmannii* timber is commonly used to manufacture musical instruments, railway sleepers, furniture, and wooden floors. Its wood is moderately hard and the density is estimated to range between 0.5 and 0.8 g m^{-3} (Mate *et al.,* 2015).

In this Chapter, volume growth rates of the above three key-, together with 46 other merchantable timber species (trees saleable for commercial products; see Fig. 5.2, Bullard and Monaghan, 1999; FAO, 2002) are studied with the aim of informing woodland sustainability. To this end, the following three research questions (RQs) are parsed together:

i) In terms of volume, how fast are large stems growing across SAWs?

ii) Based on findings from RQ1, what is the average sustainable harvesting cycle across SAWs?

iii) Based on RQ1 and 2, what is the average AAC across SAWs?

5.2 Materials and methods

5.2.1 Study area and data sources

A total of 38,276 individual trees belonging to 400 species on 223 permanent sample plots (PSPs) in 8 countries were recorded at varying intervals but between 1991 and 2018 (Figure 5.1). Of these trees, I chose and studied large stems belonging to 49 key merchantable timber species (Supplementary material 3.1). I defined large trees as stems with a maximum diameter at breast height (DBH) of ≥ 35 cm, a widely accepted DBH size for harvesting (Groome *et al.,* 1957; Geldenhuys, 1996; Therrell *et al.,* 2007).

The stem data used in this study is part of a larger SEOSAW dataset. SEOSAW, which is an acronym for *Socio-Ecological Observatory for Southern African Woodlands* (SEOSAW) is a network of scientists across the globe with interests in understanding the potential response of SAWs to global change (The SEOSAW Partnership, 2021).

For the full dataset (i.e., 38,276 trees), PSP inventorying involved tagging or marking individual stems and measuring them at ~1.3 m. The tagging and/or marking ensured that stems were easily identified in subsequent inventory years. All woody life-forms with a diameter at breast (DBH) of *generally* ≥5 cm were measured. However, due to resource limitedness, height measurements were not taken.

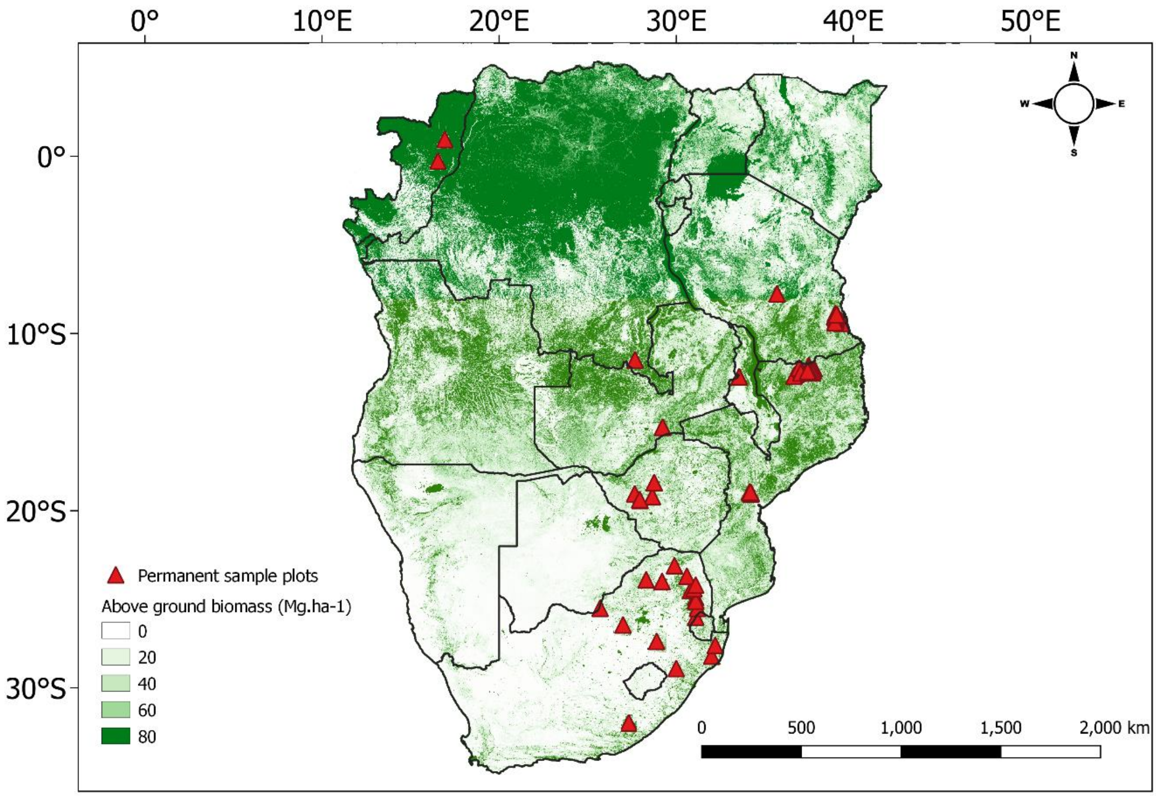

Figure 5.1: Geographical spread of PSPs inventoried. The above-ground biomass data is from Bouvet *et al.,* (2018).

5.2.2 Volume estimation

Merchantable volume (Figure 5.2) is one of the main measures of stand productivity considered crucial for woodland management (Brandeis *et al.,* 2006). Apart from its obvious use in computing potential stand yields, volume is also used in carbon storage calculations which are pivotal for global climate change studies. However, direct onsite measurement of volume is an expensive and time-consuming undertaking (Mwakalukwa *et al.,* 2014). Therefore, the general practice is to estimate volume based on allometric equations developed using onsite diameter and height measurements (Brandeis *et al.,* 2006). Given, uncertainties associated with field-measured tree heights (Wang *et al.,* 2019), I considered it necessary to use more than one volume equation in this study (Table 5.1). The first equation (Mwakalukwa *et al.,* 2014) was based on 142 individual trees inventoried in 2009 and 2010 in Iringa, central-southern Tanzania, and can be expressed as follows:

$$\ln(Y) = a + b\ln(DBH) \quad \text{Eq. 1}$$

Where, $\ln(Y)$ is the response variable i.e., the logarithmic form of volume, a and b are parameters estimated at −10.9307 ± 0.2 and 3.0134 ±0.1, respectively.

The second equation (Mate, 2014) was based on 58 individual trees inventoried in 2014 in Inhambane and Sofala Provinces located in the southern and central regions of Mozambique. This equation can be expressed as follows:

$$V = \beta_0 D^{\beta_1} \quad \text{Eq. 2}$$

Where V is the response variable (volume), β_0 and β_1 are parameters estimated at 0.001270 and 1.807100, respectively and D is the diameter at breast height.

The third equation (Banks and Burrows, 1966) was based on 91 stems measured in Zimbabwe and can be expressed as follows:

$$V = \beta_0 + \beta_1 * \mathrm{DBH}^2$$

Where: β_0 and β_1 are parameters estimated at -0.3688 and 0.001037 respectively and DBH is the diameter at breast height.

The fourth and final equation (De Cauwer *et al.,* 2020) was based on 356 individual tree inventories in Namibia and Angola. It can mathematically be presented as follows:

$$V = \exp(a + b_1 * (\ln DBH)^2 + b_2 * (\ln DBH)^3$$

Where: a, b_1, and b_2 are parameters estimated at -7.533, 0.896, and -0.110 respectively.

Although there are many other equations that can be considered, I chose these because they specifically dealt with merchantable (Figure 5.2) and not total volume. Further, they included timber species of interest in this study.

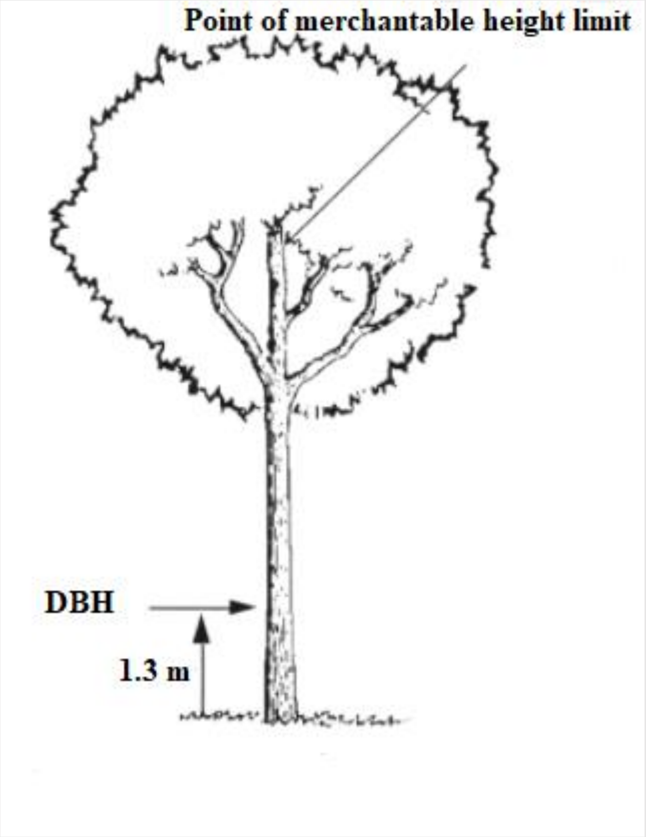

Figure 5.2: Common reference points for tree inventories and merchantable volume estimation. *Source:* Heiligmann and Bratkovich, (2016)

Table 5.1: Summary of allometric volume equations considered in this study. *n* is the number of stems on which the equations were based

Source	Species	Country	*n*
De Cauwer *et al.*, (2020)	*Pterocarpus angolensis*	Namibia and Angola	356
Mwakalukwa *et al.*, (2014)	28 different species	Tanzania	142
Mate, (2014)	*Pterocarpus angolensis, Afzelia quanzensis*; and *Milletia stuhlmannii,*	Mozambique	58
Banks and Burrows, (1966)	*Baikiaea plurijuga, Guibourtia coleosperma,* and *Pterocarpus angolensis*	Zimbabwe	91

5.2.3 Mean annual increment and harvesting cycles

I calculated mean annual increment (*G*) for each PSP using the following widely used equation (Shackleton, 1993; FAO, 1998; Luoga *et al.,* 2002; Otuoma *et al.,* 2011):

$$G = \{(I_{trees} * n) - M + R\} / n \qquad \text{Eq. 3}$$

Where, G is the mean annual increment in volume (m^3/ha/year), I_{trees} is the sum of volume increments of stems that did not die during the study period (m^3/ha), M is the sum of the volume of stems that died thus, no longer contributed to net woodland growth (m^3/ha), R is the volume of stems that were recruited during the study period (m^3/ha), n is the period of measurements in years.

I then calculated harvesting cycles by considering the mean annual increment of individual stems and how long it can take for them to reach 35 cm.

5.2.4 Annual allowable cut and offtake estimation

Regardless of what formula is used to calculate AAC, the underlying concept is that any given volume, number of trees, or area of PSP should only be cut once during the time it takes for a tree to reach the minimum diameter size for harvesting (Vanclay, 2014). The rationale for this is to give a woodland enough time to recover after harvesting. For sustainability purposes, an AAC that is considerably below the mean annual increment is preferred because the residual volume ensures sustainability. Therefore, in this study, I set AAC at 80% of the mean annual increment (Otuoma *et al.,* 2011).

Offtake was used in this work to define the number of stems in volume removed from any given PSP either through harvesting or non-anthropogenic mortality (Otuoma *et al.,* 2011; Ndegwa *et al.,* 2018). To estimate current offtake, the sum of stems in volume that did not die during the study period (m^3/ha) was considered. Considering alive stems at the beginning and end of the inventory helped to ensure that stems that died and/or were harvested got accounted for in projections.

5.2.5 Scenario modelling

To give an idea of how sustainable 80% of G as an annual allowable cut is, PSP-averaged volume projections for the next 5 years were considered. The rationale here was that by taking growth rates into consideration, different levels of annual allowable cut would have varied implications for residual PSP volume thus giving a snapshot of how the woodlands would potentially evolve in the future. It further helped to give insights into how different AAC levels impact residual volume.

The starting volume (*Volume at start*) and mean annual increment (*G*) used is the average for all the 1,025 individual large stems belonging to 49 merchantable timber (Supplementary Material 5.1) on 115 permanent sample plots in 7 countries.

5.4 Results

5.4.1 Volume estimation

With near perfect correlation coefficients (>0.9 in all cases) and small root mean square errors < 0.5 (m^3/ha) in all cases, results (Figure 5.3) of the comparative analyses among the 4 volume allometric equations (Banks and Burrows, 1966; Mate, 2014; Mwakalukwa *et al.,* 2014; De Cauwer *et al.,* 2020) indicate that they produce similar estimates and thus, any of them can be used for volume computation. Based on these results, Mate, (2014) was used in subsequent analyses. Given the close similarity in the performance of the 4 equations, the choice of Mate, (2014) was based purely on the fact that model development included the three most valuable timber species (*Pterocarpus angolensis, Afzelia quanzensis, Milletia stuhlmannii*) which are of primary interest in the present study.

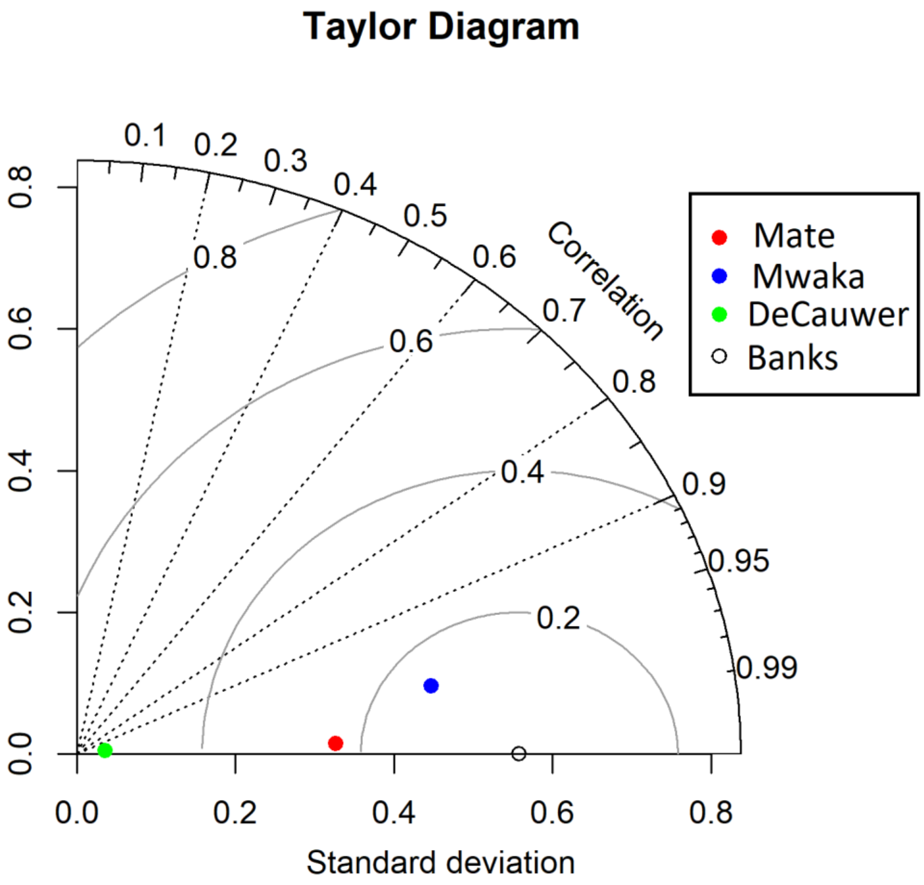

Figure 5.3: Comparative analysis of volume allometric equations for (De Cauwer *et al.,* 2020) Mate, (2014), Mwakalukwa *et al.,* (2014), and Banks and Burrows, (1966) which was set as the reference. This Taylor diagram (Taylor, 2001) has three axes: correlation coefficient (outer azimuthal curve; black solid line), standard deviation (radical distance from zero), and centred RMS difference (inner azimuthal curve)

5.4.2 Mean annual increment and harvesting cycles

Results indicate that from the overall population of 38,276 individual trees, 12,256 stems representing 32% of the dataset belonged to the 49 key merchantable timber species of interest in this study. Results further indicate that only 1,025 of the 12,256 trees met the size threshold of ≥35cm and represent ~3% of the total stem data. 62.5% of the 1,025 large stems studied belong to 7 timber species with each having ≥ 20 stems (Table 5.3).

In terms of volume, a mean annual increment (*G*) of 0.64 ±0.1 m^3/ha/year across the region was found (Figure 5.4) and was within the range reported by previous studies (Table 5.2). it is notable that most (71%) PSPs experienced mean annual increments ranging from 0 to 1 m^3/ha/year, while ~17% exhibited rates in the range of 1 – 9.3 m^3/ha/year, and the remaining ~11% had negative *G*s. Negative *G*s were a result of a given PSP having very high mortality and near-zero recruitment rates into the large stem category (i.e., stems ≥35 cm). While most of the stems were within the growth range reported in previous studies, 16 of the merchantable timber species studied exhibited very high stem-level growth rates (Supplementary material 5.1) and hence high-volume increments (Figure 5.4).

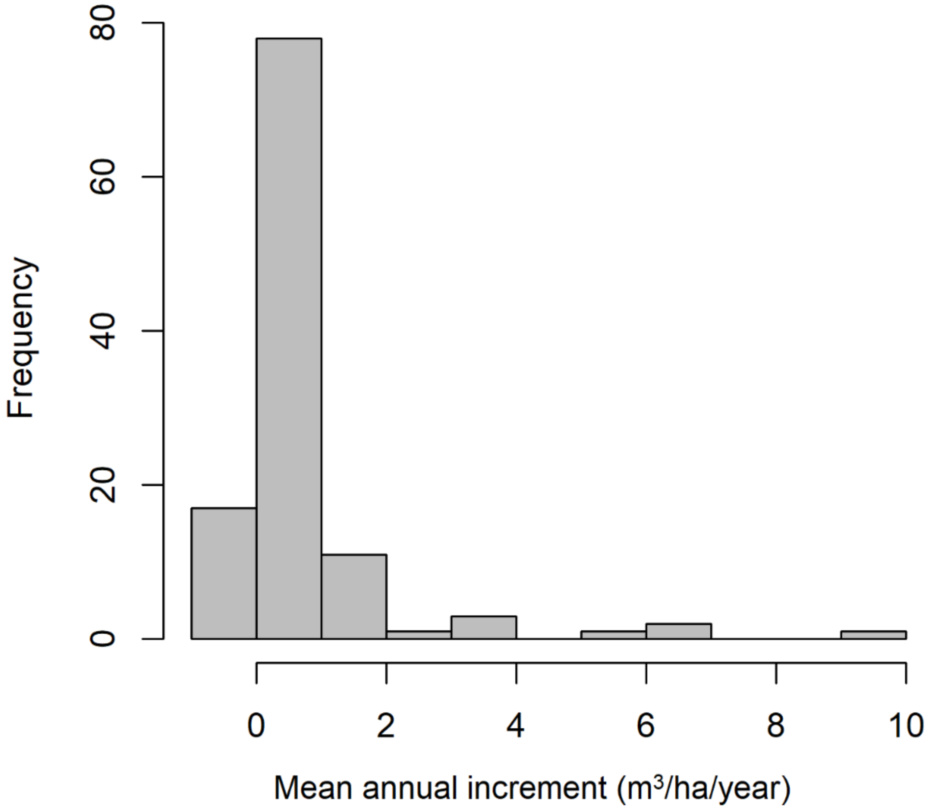

Figure 5.4: Mean annual increment (*G*) of merchantable timber species across southern African woodlands (m^3/ha/year)

Table 5.2: Mean annual increment (*G*; m^3/ha/year.) as reported by previous studies

Source	Country	Mean annual Increment m^3 $ha^{-1}yr^{-1}$
De Cauwer *et al.*, (2020)	Angola and Namibia	1.9 – 2.7
Malimbwi *et al.*, (2009)	Miombo across SAWs	0.58 to 3
Luoga *et al.*, (2002)	Tanzania	4.35
Chidumayo, (1988)	Zambia	2.0

At the individual stem level of large trees, the mean annual increment of merchantable timber species was found to be 1.5 ±0.3 mm/year (Supplementary Material 5.1). This was found to be within the range reported in previous studies (e.g., Mugasha *et al.,* 2016; Chidumayo, 2019; Rozendaal *et al.,*2020). It further translates into a mean harvesting cycle of 233 ±46 years when a widely accepted harvest size of 35 cm is used (Groome *et al.,* 1957; Geldenhuys, 1997; Therrell *et al.,* 2007).

It must be emphasised that although the majority of the stems had positive growth rates, 12 species were found to exhibit negative rates (Supplementary material 5.1). The negative growth rates can be attributed to the fact that most of these species consisted of very few surviving stems generally < 5 coupled with near-zero recruitments and high mortality rates. Therefore, when the negative and positive rates were considered, growth rates were found to average around 0.64 ±0.1 m3/ha/year across the region. The effect of negative growth rates on the regional mean was also observed at the stem level i.e., 1.5 mm/year (Supplementary material 5.1).

Of the 7 most common timber species (Table 5.3), *Pericopsis angolensis* was found to be the fastest-growing with a mean annual increment of 6.5 ±2.4 mm/year while at a rate of only 0.9 mm *Pterocarpus angolensis* exhibited the slowest growth rate (Table 5.3).

5.4.3 Annual allowable cut

Projections presented here are meant to only give a snapshot of the effect of some offtake levels (i.e., mortality and harvesting) on stand volume. Results (Table 5.3) indicate that, as expected, all offtake targets below the mean annual increment lead to increased volume. Of interest here is that within Year 1, recovery scenarios surpass the volume at the beginning of the inventory at any given offtake target. The exceedance is 0.51, 0.38, 0.26, and 0.13 (m^3/ha) for 20, 40, 60, and 80% of G respectively. To ensure sustainability in both ecological and economic terms, the

80% offtake target has been proposed in previous studies (Otuoma *et al.,* 2011) as being reasonable; the same target was therefore adopted here.

Table 5.3: Projected recovery scenarios in volume (m^3/ha) for merchantable timber species over the next 5 years for varying annual offtake levels. The growth and starting volume considered here is the average for all the 115 PSPs across southern Africa. *G* is the mean annual increment in volume (m^3/ha/year)

			Projected recovery scenarios in volume (m^3/ha)					
Offtake rate as a % of *G*	**Volume At start (m^3/ha)**	***G* (m^3/ha/year.)**	**Yr. 0**	**Yr. 1**	**Yr. 2**	**Yr. 3**	**Yr. 4**	**Yr. 5**
0	9.1	0.64	9.1	9.74	10.38	11.02	11.66	12.3
20	9.1	0.64	9.1	9.61	10.12	10.64	11.15	11.66
40	9.1	0.64	9.1	9.48	9.87	10.25	10.64	11.02
60	9.1	0.64	9.1	9.36	9.61	9.87	10.12	10.38
80	9.1	0.64	9.1	9.23	9.36	9.48	9.61	9.74
100	9.1	0.64	9.1	9.10	9.10	9.10	9.10	9.1

5.5 Discussion

The present study was designed to provide insights into sustainable harvesting rates across southern African woodlands (SAWs) with the motivation of ensuring a constant current supply of wood products while maintaining or improving future timber yields vis-à-vis annual allowable cuts (AAC). Further, AAC as a silvicultural practice and technique has the potential of supporting ecological sustainability of

SAWs as it helps with maintaining successional pathways, ecosystem functions, populations, and even carbon storage (RIW, 2013; Syampungani *et al.,* 2020). While the importance of AAC is apparent, the practice is still limited across SAWs due to the lack of extensive growth monitoring plots (Syampungani *et al.,* 2018) therefore, this study provides the sub-region's first AAC analyses thanks to a new SEOSAW dataset.

Results embodied in section 5.4 of this work indicate a *G* of 0.64 ±0.1 m^3/ha/year across the region which was found to be consistent with estimates from previous studies (Chidumayo, 1988; Luoga *et al.,* 2002; Malimbwi *et al.,* 2009; De Cauwer *et al.,* 2020).

At the stem level, a mean annual increment of 1.5 ±0.3 mm was found thus, suggesting a mean harvesting cycle of 233 ±46 years when a widely accepted harvest size of 35 cm is used (Groome *et al.,* 1957; Geldenhuys, 1997; Therrell *et al.,* 2007) – thus implying that on a given stand with 233 trees, one tree can be harvested every year. These results further indicate a rather slow recruitment cycle into the large stems category. Based on these results, an annual allowable cut (AAC) of 80% has been adopted in this work to foster more sustainable woodlands. I, therefore, argue that since SAWs are generally uneven-aged, woodland management practices where selective harvesting of individual large trees (≥ 35 cm) at the 80% of *G* is followed by the allowance of natural regeneration has the potential to sustain woodland volume, especially that within Year 1, recovery scenarios surpass the volume at the beginning of the inventory (Table 5.4). It is important to note however that the rate at which regeneration occurs is strongly affected by anthropogenic activities (Campbell, 1996) as such there is an untold need for post-harvest management practices that champion regeneration.

While the AAC described here satisfies tree conditions for harvesting, other factors such as market prices and total available timber across all plots need to be considered before actually deciding to harvest. Therefore, deciding to harvest is as important a financial matter as it is an ecological one.

Adhering to the AAC proposed here would yield several benefits apart from constant timber supply. For example, AAC promotes the biodiversity of tree species because it allows for the selection of which stems to be harvested and which ones to be left. Trees that are left to continue growing can potentially be a source of seed for reproduction and regeneration (Tachiki and Iwasa, 2010) thus, encouraging the continuance of a given species. By extension, AAC reduces the effect of tree competition among desired timber species. This is especially important for SAWs considering that results from Chapter 3 of this thesis indicate that competition is widespread in the Savannas.

While elsewhere (e.g., Bergeron *et al.,* 2017), clear-cuts have been found to be beneficial in both ecological and economic terms, these work best across even-aged stands.

However, given the uneven nature of SAWs, selective harvesting based on AAC is recommended in the present study as an optimal alternative for sustainable woodland management. Unlike clear-cuts which are generally straightforward, selective harvesting based on AAC is complex because of multiple species and age classes in the dataset. However, when ardently followed, this approach ensures that a balance among biodiversity, ecosystem function, and the economic aspects of timber production is maintained. This is because the computation of AAC is based on the concept that guarantees any given volume, number of trees, or area of PSP to only be cut once during the time it takes for a tree to reach the minimum diameter size for harvesting (Vanclay, 2014) thus, giving a woodland enough time to recover after harvesting.

It was also noted that 71% of the PSPs experienced *G* not significantly different from 0. Possible explanations for this can be argued from two fronts: first, individual stem growth of SAWs has been found to be slow in this thesis and elsewhere (e.g., Chidumayo, 2019). Second, there is currently little or no AAC adherence in most countries across SAWs. As such, selective timber harvesting generally includes small trees (< 35 cm) which reduces the likelihood of replacement and sets any given stand at risk of collapse as it inhibits natural recruitment of timber species into the large stems' category (Syampungani *et al.,* 2018).

Conclusively, to guarantee the sustainability of SAWs, policymakers will require enforcement of woodland management plans that take into account growth rates and therefore, annual allowable cuts for specific timber species of interest with strict adherence to harvesting cycles. For AAC to be an effective policy instrument, other ecological factors must be considered e.g., in some years, average *G* may not be attained thus, any attempt to enforce AAC during a lean year may result in volume stocks falling below the expected level thereby causing unexpected/undesired feedbacks (Vanclay, 2014). The time of harvesting needs to also be considered carefully because it affects the rate of regeneration; for instance, Chidumayo (1993) found that trees cut in November had a slower regeneration rate compared to those cut in July. Campbell (1996) argues that these differences can be attributed to the fact that the duration of the growing season after cutting in November is generally shorter compared to the cutting done in July, furthermore, the phenological phase of trees in November and July differs markedly. Specifically, most trees across SAWs would have used up much of their stored 'food' by

November and this ordinarily constrains growth in the season that follows whereas in July, most trees are not as active and thus, food resources kept underground remain undisturbed (Campbell, 1996). In terms of economics, demand for timber may also vary from year to year, therefore, flexibility in the AAC such as setting a 5 or 10-year allowable cut would ensure that AACs are only enforced in years that have actual demand for timber and this would help to ensure that the timber volume on each PSP remains within the 5 or 10-year volume target. Periodic reviews of timber levels together with their overall impact in both ecological and economic terms then adjusting the AAC as may be required are also strongly recommended.

5.6 Concluding thoughts

Returning to the research questions posed at the beginning of this study, it is now possible to state that at the individual stem level, large trees are growing at an annual rate of 1.5 ±0.3 mm/year translating into a harvest cycle of 233 ±46 years when a widely accepted harvest size of 35 cm is used. In terms of volume, a mean annual increment of 0.64 ±0.1 m^3/ha/year and a mean AAC of 0.51 ±0.1 m^3/ha/year with a range of 0 – 7.4 m^3/ha/year were found across the region.

Results further indicate that 71% of the PSPs experienced G not significantly different from 0 thus, suggesting slow growth and overexploitation of small trees which in turn inhibits recruitment into the large stem class and threatens natural successional pathways. However, there is potential for any PSP to recover and become resilient as long as an AAC of 80% is strictly followed.

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Supplementary material 5.1: Full list of merchantable timber species studied. Stems, number of stems for each individual species; Countries, number of countries in which each species was present; Median size, median diameter at breast height of each species; *sMAI*, stem-level mean annual increment; SE, standard error

				Measurement Years		***sMAI* (mm/year)**	
Species	**Stems**	**Countries**	**Median size (cm)**	**First**	**Last**	**Growth**	**SE**
Albizia versicolor	4	2	35.7	2006	2017	16.4	3.8
Cordyla africana	3	2	51.3	2006	2017	7.2	3.7
Pteleopsis myrtifolia	18	1	38.7	2010	2018	6.7	5.4
Pericopsis angolensis	33	3	40.4	1998	2015	6.5	2.4
Senegalia polyacantha	4	1	45.3	2010	2012	6.4	28.8
Cussonia natalensis	2	1	41.6	1992	1998	5.5	7.4
Uapaca nitida	2	2	37.8	1998	2015	4.9	0.9
Brachystegia spiciformis	135	6	44.9	1994	2015	4.8	1.7
Uapaca kirkiana	1	1	35.9	1998	2001	4.7	0.5
Julbernardia globiflora	227	5	43.7	1994	2018	4.4	1.0
Kirkia acuminata	1	1	38.2	1994	2002	4.3	0.2
Brachystegia utilis	6	1	41.1	1998	2002	3.9	7.6
Vachellia robusta	7	2	38.0	1993	2017	3.8	1.9
Brachystegia boehmii	85	4	43.0	1998	2017	3.5	1.7
Vachellia tortilis	1	1	36.0	1992	1996	3.1	1.2
Vachellia sieberiana	1	1	49.4	2010	2014	3.0	0.9
Diospyros mespiliformis	4	2	36.4	2010	2017	2.9	2.1
Brachystegia manga	7	1	36.4	2004	2015	2.9	1.5
Brachystegia bussei	1	1	39.5	2003	2012	2.9	0.3
Celtis africana	3	1	52.1	1992	1996	2.7	14.0
Brachystegia longifolia	1	1	38.2	2006	2012	2.3	0.4
Terminalia stenostachya	4	1	46.8	2006	2017	2.3	4.6
Sclerocarya birrea	47	3	43.2	1991	2018	1.7	1.2
Strychnos spinosa	3	1	41.4	1991	1998	1.6	1.0
Terminalia sambesiaca	1	1	40.3	2004	2015	1.5	0.6
Baikiaea plurijuga	47	1	37.0	1994	2015	1.0	0.5
Combretum imberbe	2	1	60.1	2006	2017	1.0	2.1
Erythrophleum africanum	21	2	43.5	2006	2017	1.0	2.4
Pterocarpus angolensis	67	5	37.8	1992	2017	0.9	0.5
Tamarindus indica	13	1	42.6	2010	2017	0.6	4.9
Ceriops tagal	2	1	43.7	2010	2017	0.6	0.1
Amblygonocarpus andongensis	1	1	41.8	1994	2002	0.5	0.2
Trichilia emetica	3	1	35.7	2006	2017	0.4	3.4
Xeroderris stuhlmannii	21	2	43.3	2006	2018	0.4	2.4
Diospyros kirkii	1	1	36.4	2004	2009	0.2	0.0
Millettia stuhlmannii	28	2	40.0	2004	2018	0.1	1.9

Burkea africana	87	3	40.5	1998	2018	-0.4	1.2
Guibourtia coleosperma	9	1	53.8	1994	2006	-0.7	7.6
Colophospermum mopane	17	2	41.3	1992	2012	-1.2	2.8
Parinari curatellifolia	6	2	44.5	1992	2014	-1.8	1.3
Afzelia quanzensis	11	1	36.7	2010	2012	-1.9	5.8
Dalbergia melanoxylon	25	2	41.3	2006	2017	-2.2	3.2
Pseudolachnostylis maprouneifolia	36	3	37.6	2006	2018	-3.1	1.4
Vachellia nilotica	3	3	36.2	1992	2017	-3.3	0.7
Senegalia nigrescens	15	3	41.1	1992	2017	-4.7	1.9
Sterculia appendiculata	1	1	83.0	2006	2017	-5.5	3.1
Combretum zeyheri	5	2	36.1	2004	2017	-6.5	2.2
Ricinodendron rautanenii	3	1	66.0	2006	2017	-12.0	15.0

CHAPTER VI

CHAPTER 6: DISCUSSION AND KEY CONCLUSIONS

6.1 Thesis overview

The overarching objective of this thesis was to deepen our understanding of tree growth rates, their determinants, and what rate of tree harvesting could be sustainable across southern African woodlands (SAWs). I addressed the following four key themes:

i) The current understanding of tree growth rates across SAWs;

ii) The importance of climatic, edaphic, and stem-level attributes in determining tree growth rates across SAWs;

iii) Maps of how tree growth rates vary across the region;

iv) Harvesting rates that have the potential to stimulate sustainability across SAWs.

Findings from these four themes were aimed at providing insights to the following broad research questions (RQs):

RQ1: How fast are trees growing across southern Africa and what are the main determinants of growth rates?

RQ2: How well can tree growth in unmonitored areas of southern Africa be predicted?

RQ3: How are the current dynamics of tree population structure and how can they be used in combination with growth rates to determine sustainable harvesting rates on monitored permanent sample plots (PSPs) across SAWs?

In this chapter, I aim at looking back and bringing together the main findings from the three empirical Chapters with a view of clearly showing how the overarching objective of this thesis has been met. Based on the findings, I will also propose potential future lines of scientific inquiry.

6.2 Unique dataset

Overall, I succeeded in meeting the objective of this thesis thanks to the collation of a unique dataset that I used in every results chapter. The dataset is courtesy of SEOSAW, which is an acronym of Socio-Ecological Observatory for Southern African Woodlands (The SEOSAW Partnership, 2021). SEOSAW is an ongoing project whose main goal is to understand the response of southern African woodlands to global change. SEOSAW is founded on the premise of several hypotheses. For instance, it is hypothesised that the structure and ecosystem services provision of southern African woodlands is a result of an increase in extreme meteorological events, an upward trend in CO_2 concentrations, a change in fire regimes, and an increase in population, therefore, resource use. However, before SEOSAW, there was no regional network of plot-based measurements to provide evidence of these changes across southern African woodlands. The lack of a regional network hampered the validation of model predictions against plot-based datasets. For the first time, SEOSAW brought scientists (with their datasets) together and thus, constructed a regional network with 2269 plots in 11 countries across southern Africa. I used some of this data in this Ph.D. project to explore variations of tree growth rates at a previously impossible scale.

Before using the data, I invested time in processing and cleaning it to make it analyses ready and to enable other researchers to use the data to answer further research questions. For example, I removed trees with the following characteristics from the whole dataset:

i) Single measurements;
ii) Those that had a DBH under 5 cm;

iii) Those that were measured at different points of measurements (POMs) between census dates;

iv) Those that died;

Following the cleaning, I developed hierarchical mixed-effects models and used the data to provide the first-ever regional estimate of tree growth rates across SAWs. I further used it to predict growth rates across unmeasured areas of the region and to estimate sustainable harvesting rates.

6.3 Results summary and implications

Returning to the objectives I set at the beginning of the thesis, it is now possible to state that I have met them all. Specifically, I have found that individual tree growth is explained mostly by tree-tree competition while BAI is mainly explained by rainy season length with soils having a very small effect on both. I have further found that AAC varies greatly by site but is mostly very small, well below 1 m^3/ha/year likely lower than is used throughout the region. Details of all these findings are included hereunder:

6.3.1 Growth rates

Southern African woodlands (SAWs) are a focus of global policy dialogues on conservation because of their high endemism (Wyk and Smith, 2001; Iannella *et al.,* 2021), incredible diversity (Madonsela *et al.,* 2018), contribution to the global carbon cycle (McNicol *et al.,* 2018; Poulsen *et al.,* 2020), and the ecosystem goods and services they provide e.g., fruits, medicinal plants, timber as well as other non-timber products (Ryan *et al.,* 2016; Mudavanhu *et al.,* 2017; Mubaya and Ndebele-Murisa, 2019). Scientific evidence shows that SAWs are currently subjected to increasing human pressure and thus, experiencing rapid changes due to deforestation (Mapfumo *et al.,* 2017), land-use change (German *et al.,* 2020), and unsustainable logging practices (Sedano *et al.,* 2020). They are also at the forefront of climate change, with large changes in temperature, rainfall, and the frequency of extreme events already occurring (Higgins *et al.,* 2000, IPCC 2013), and in places rapid bush/woody encroachment observed (O’Connor, 2005; Ward, 2005; Stevens *et al.,* 2017). It, therefore, follows that results from tree growth studies must be used by forest managers and governments to model future dynamics of growth. This information can then be utilised to ensure harvests and land-use conversions are within the sustainable capacity of SAWs, both now and in the future.

A systematic review of the literature showed that to date, much of the research on tree growth rates across southern Africa has relied on growth rings which develop in the cross-section of woody plants on an annual cycle (Trouet *et al.,* 2006; Chichinye *et al.,* 2020; Shikangalah *et al.,* 2020). Such studies have limitations, including a lack of area basis, and that some studies have shown that in some regions in the tropics, and depending on genera, growth rings may not be discernible or are not annual (Détienne, 1989). As an alternative, repeated measurements on permanent sample plots (PSPs) are used, which do not suffer from these issues and represent the second most common approach of studying tree growth rates across southern Africa (Mugasha *et al.,* 2016) as well as the basis of the datasets used in this thesis.

Previous research (e.g., Shackleton *et al.,* 2002; Trouet *et al.,* 2006; Mugasha *et al.,* 2016; De Cauwer *et al.,* 2017) has found tree growth rates across SAWs to range between 1 and 7.1 mm/year. However, it is noteworthy that although some studies on tree growth rates have been done across the region, and highlight key points relevant to the current contribution, they suffer from spatial data limitation. Therefore, their findings are not representative of the entire SAWs. In fact, no single study exists which adequately explored the entire subcontinent. To overcome this geographical limitation, this Ph.D. project considered the broader southern African woodlands i.e., 38,276 trees belonging to 400 species on 223 permanent sample plots (PSPs) in 8 countries.

Results in Chapter 3 of this thesis suggest that individual trees are growing at 1.6 ±0.3 mm yr^{-1} with site-to-site variations. At the species level, stems that exhibited the fastest increment are mainly the woodland dominants while the slower growing trees are smaller, open savanna species. Slow growth in the open savanna species can be attributed to limited resources in savanna environments and differences in functional types between woodland dominants and open savanna species.

6.3.2 Determinants of growth rates

The science is clear and the evidence is undeniable that trees constantly engage in competition for water, light, and nutrients (Rozendaal *et al.,* 2020). Tree species, therefore, develop distinct strategies for survival with implications on overall stand growth rates, dynamics, and structure across their respective competitive environments. This is particularly widely documented in forests (Uriarte *et al.,* 2004; Lasky *et al.,* 2014; Looney *et al.,* 2016). However, the impact of competition on tree growth rates in the savannas is understudied, particularly across southern African woodlands (SAWs). The existing literature on growth rates ignores the possibility of competition between trees in the savannas, citing the generally sparse distribution of trees characteristic of such a biome (Kunstler *et al.,* 2015). Therefore, the impact of competition on tree growth rates across SAWs remains unclear. Further, most studies of tree growth rates across SAWs have only been carried out in a small number of areas. To date, no large-scale studies have been performed to investigate tree growth rates across the broader SAWs. Consequently, determinants of tree growth rates across the broader SAWs remain speculative.

In Chapter 3 of this thesis, I showed that competition is the only explanatory variable (EV) that was significant across all models. This suggests that tree-tree competition is widespread across the region, and is the main universal controller of tree growth. Its negative effect on tree growth rates can be attributed to limited resource availability on stands with high competition (Fernández-de-Uña *et al.,* 2015). This is not an isolated finding: in a recent study, Rozendaal *et al.,* (2020) found that competition reduces tree growth rates, and its effect is invariant across environmental gradients. Several other studies (e.g., Thomas *et al.,* 2009; Calabrese *et al.,* 2010) also document the depressing effect of competition on tree growth consistent with the findings in the present study.

Examining the determinants of growth for each species, however, revealed strong and often contrasting effects of soils, climate, tree size, and fire. A continuum of responses across species emerges, with contrasting patterns between miombo woodland dominants such as *Brachystegia* and open savanna species. In the faster-growing miombo dominant group, growth increased with stem size, on poor soils, and was less affected by reduced water availability and seasonality. The open savanna group exhibited the opposite trends, growing relatively faster on good soils and in wetter conditions. These findings challenge conventional understanding of the determinates of tree growth in savannas, and suggest distinct controls in different types of savanna, and thus distinct responses to climate change.

The observed widespread effect of tree-tree competition may play an important, but hitherto neglected, role in determining community composition and sustaining tree-grass coexistence. It is also likely to moderate the current increase of trees in savanna systems, suggesting the globally important C sink in African savannas is unlikely to be sustained.

6.3.3 How well can tree growth in unmonitored areas of southern Africa be predicted?

Much of what we know about tree growth rates across southern African woodlands (SAWs) is based on plot measurements. However, most of the ecological problems such as how to sustainably manage SAWs are broad-scale – scales larger than available observations. The lack of extensive growth monitoring plots across the sub-continent is mainly because setting them up and carrying out repeat measurements is expensive, time-consuming, and labour-intensive (Priyadi *et al.,* 2005). Understanding tree growth rates across unmeasured areas of SAWs is, therefore, one of the region's most pressing issues. It follows that our knowledge of growth rates across unmeasured areas is dependent on how well we can use data collected from permanent sample plots (PSPs) to develop predictive models (Brassel *et al.,* 2001; Bowman *et al.,* 2012; Rohner *et al.,* 2017).

In Chapter 4 of this thesis, I developed a hierarchical mixed-effects model and used it to interrogate tree growth rates across unmeasured areas of SAWs. Whereas in Chapter 3 I examined growth rates at individual stem level, in Chapter 4, I used basal area increment (BAI) because of the coarse resolution of predictor variables (PVs). The predicted BAI values of between 0.07 and 0.7 m^2/ha/year are in agreement with observed BAI documented in most parts of the region. For instance, *Gadow et al.,* (2016) found a maximum BAI value of 0.75 m^2/ha/year when they studied 20 different tree species in South Africa. Chidumayo, (2019) who studied growth patterns of Miombo woodlands in Zambia found a mean BAI of 0.40 m^2/ha/year in dry miombo and 0.53 m^2/ha/year in wet miombo. This find is in direct agreement with the model predictions in Chapter 4 of this thesis which estimated BAI over Zambia to be ~0.4 m^2/ha/year.

Stem-level attributes such as size, species, and age have previously been named as key drivers of BAI across SAWs (Chidumayo, 2019). However, since the overarching goal of this study was to predict BAI across unmeasured areas of SAWs where stem-level attributes are unknown, they could not be used. Thus, in this study, I relied on climate and soil predictor variables (PVs). Of these PVs, rainy season length (RSL) was found to have the largest effect on BAI. This find suggests that long rainy seasons translate into equally longer growing seasons hence the observed large effect of RSL on BAI. A similar observation was made in the tropical woodlands of Mexico (Whigham *et al.,* 1998), central Amazon (Dünisch *et al.,* 2003), and northern Brazil (Grogan and Schulze, 2012) where RSL was found to have a larger effect than mean annual precipitation.

Climatic water deficit (CWD) which I used as a surrogate for seasonal water stress was found to have a negative effect on BAI. Previous studies have found that CWD exerts detrimental effects on tree growth across the world. For example, Restaino et al., (2016) reported that water deficits led to decreases in tree growth rates across all latitudes in the United States. Ledo *et al.,* (2018) who studied controls of root to shoot ratio also found that CWD has major controls on tree growth rates across the world and concluded that aridity has a major depressing effect on tree growth rates.

I found soils to generally have an effect not significantly different from zero. The small effect of soils re-echoes the findings embodied in Chapter 3 of this thesis. Although that Chapter considered individual tree growth rates, soils were again found to have negligible effect. Swemmer and Ward, (2020) also found little influence of soils on growth rates – in agreement with the present study. They attributed this lack of influence to the possibility that savanna trees have evolved enough to enable different species to maximize the use of available nutrients, for each soil type within each region, such that precipitation and light become the primary determinants of growth rates. In addition to this, the observed tree-tree competition in this thesis together with tree-grass competition intensify the competition effect on tree growth rates thus cancelling out the potential positive impact of nutrients.

With various markers showing that the BAI model in Chapter 4 had strong predictive power, we for the first time have a map of woody productivity across SAWs based on field plot data. The model further suggests that it is useful for predicting growth rates which are a significant input when determining safe harvest levels and climate change impacts.

6.3.4 Using growth rates to determine sustainable harvesting rates

Large portions of southern African woodlands (SAWs) have been degraded because of unsustainable logging practices (Kayambazinthu and Oeba, 2019: Makonese *et al.,* 2018). Allocating an annual amount of timber that can be harvested safely is pivotal for sustainable woodland management and this approach is widely used across the world as a policy instrument for woodland sustainability (Luckert and Haley, 1995; Armstrong, 2004; Debkov and Il'intsev, 2017) and the concept is used more widely still, for example in fisheries management. I designed Chapter 5 of this thesis with the aim of determining sustainable harvesting rates across southern African woodlands (SAWs). As such, I only studied large trees with diameters at breast height (DBH) ≥ 35 cm as these are the preferred trees when harvesting for timber or fuel use.

Results showed that 71% of the PSPs studied experienced growth rates not significantly different from 0 and thus, the safe harvesting rate is equally 0. Possible explanations for this can be argued from two fronts: first, individual stem growth of SAWs has been found to be slow in this thesis and elsewhere (e.g., Chidumayo, 2019). Second, there is currently little or no AAC adherence in most countries across SAWs. As such, selective timber harvesting generally includes small trees (< 35 cm) which reduces the likelihood of replacement and sets any given stand at risk of collapse as it inhibits natural recruitment of timber species into the large stems' category (Syampungani *et al.,* 2018).

At the individual stem level, large trees were found to be growing at 1.5 ±0.3 mm/year thus, suggesting a mean harvesting cycle of 233 ±46 years when a widely accepted harvest size of 35 cm is used (Groome *et al.,* 1957; Geldenhuys, 1997; Therrell *et al.,* 2007) –implying that on a given stand with 233 trees, one tree can be harvested every year. It further indicates a rather slow recruitment cycle into the large stems' category. Based on these results an annual allowable cut (AAC) of 80% relative to the mean annual increment (*G*) was adopted to foster more sustainable woodlands. In Chapter 5, I, therefore, argue that since SAWs are generally uneven-aged, woodland management practices where selective harvesting of individual large trees (≥ 35 cm) at the 80% of *G* is followed by allowance of natural regeneration has the potential to sustain woodland volume, especially that within Year 1, recovery scenarios surpass the volume at the beginning of the inventory (Table 5.4). It is important to note however that the rate at which regeneration occurs is strongly affected by anthropogenic activities (Campbell, 1996) as such, there is an untold need for post-harvest management practices that champion regeneration.

Conclusively, to guarantee the sustainability of SAWs, policymakers will require enforcement of woodland management plans that take into account growth rates and therefore, annual allowable cuts for specific timber species of interest with strict adherence to harvesting cycles. These AACs will likely be considerably smaller than current practice throughout much of the region, suggesting considerable conflict will result: but the alternative will be an inevitable degrading of the timber resources of SAWs.

6.4 Project limitations

While this project considered a hyper-diverse pool of potential tree growth rates explanatory variables (EVs), it is conceivable that future research lines could benefit from the inclusion of more EVs. For instance, statistical linkages between tree growth and rising concentrations of atmospheric carbon dioxide have been reported by many studies (e.g., Hättenschwiler *et al.,* 1997; Long *et al.,* 2005; Taub, 2010). Carter *et al.,* (2017) has also provided a detailed synthesis of how nitrogen (N) deposition is linked to tree growth among other processes. Bedison and McNeil, (2009) also found that growth is influenced by N deposition. Guan *et al.,* (2014) found that trees that have longer roots start growing even before the onset of the rainy season. A recent study also found that rainfall received during the dry season boosts tree growth in the Zambian miombo woodlands (Chidumayo, 2015). It is, therefore, argued that root depth is a driving factor of tree growth. However, to keep this project focused, manageable within the allotted time frame, and to avoid issues of collinearity between competing variables, the influence of CO_2, N deposition, and root depth on tree growth were beyond its scope. They could be a fruitful source of future investigation.

Other potential factors that can be considered by future studies include non-random plot distributions to deal with bias that may occur towards certain areas, geographies, and natural ecosystems. Further, future research lines could consider factoring in the tree tag effect i.e., studies (e.g., Picchi, 2020) have shown that there is a correlation between the level of disturbance on a PSP and tree tags with tagged PSPs generally being less disturbed than their surroundings. Further, since the PSPs used herein were set up by several people for different reasons, this could potentially introduce a bit of noise in the data although unlikely to change any of the fundamental conclusions of this thesis given the rigorous data quality control the whole set was subjected to.

Based on data availability, important explanatory variables for tree growth that have been considered in this project and that have been reported in other studies (e.g., Rohner *et al.,* 2017; Chidumayo, 2015; Bowers, 2017) include: mean annual precipitation, rainfall intensity, rainy season lengthy, length of the growing season, climatic water deficit, frost, temperature, soil properties (N, P, pH, soil depth, organic carbon, percentage of sand content), species, competition, stem size, and plot burns between inventories.

6.5 Concluding thoughts

In this thesis, I aimed at contributing to the improvement of the current understanding of tree growth rates, their determinants, and sustainable harvesting rates across southern African woodlands (SAWs). By using the subregion's largest growth rates dataset, this thesis has deepened our knowledge on tree growth rates and their determinants at a larger spatial scale than was previously possible. The thesis has also provided new insights with regard to tree growth rates across unmonitored areas of SAWs. Findings are crucial for determining current and future sustainable harvesting rates. They may also contribute towards explaining tree-grass coexistence and overall woodland community composition. Results may also be used to shed new light on the response of tree growth rates to future global change while at the same time helping in explaining the current increase of trees in savanna systems and the sustainability of the globally important C sink in African savannas.

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