EFFECTS OF CLIMATE ON PRODUCTIVITY IN TROPICAL TREE SPECIES IN WESTERN KENYA

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ABSTRACT

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The dendrochronological potential of various tropical tree species was determined and then cumulative growth trajectories for diameter and above ground biomass were created for species of sufficient sample size (n > 2). The species with the highest dendrochronological potential included *Cupressus lusitanica*, the *Eucalyptus* spp. and *Mangifera indica*. The three fastest growing species in the study, based on annual diameter increment, were *Eucalytus camaldulensis*, *Eucalyptus grandis*, and *Acacia mearnsii* . In terms of annual biomass production, the three species that grew most rapidly were *Eucalyptus camaldulensis*, *Mangifera indica*, and *Acacia mearnsii.* Growth-climate relationships were examined for *Acacia mearnsii, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalytus saligna, Mangifera indica,* and *Markhamia lutea.* Standardized basal area increments were run through a correlation analysis with climate data obtained from nearby meteorological stations to determine if any growth responses to environmental factors existed. Both positive and negative correlations between growth and climate parameters (precipitation, temperature, climate moisture index) were found for many of study species. However, correlations among species did not present a clear pattern. A majority of the precipitation correlations were positive and the temperature correlations were negative.

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TABLE OF CONTENTS

CHAPTER 3

GROWTH-CLIMATE RELATIONSHIPS OF TROPICAL TREE SPECIES IN WESTERN KENYA

CHAPTER 4

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

Global climate change has become a subject of increasing concern worldwide. With a growing world population and increasing CO_2 emissions, interest in carbon sequestration has become considerable. Thus, forests worldwide will play a major role in climate change mitigation efforts. Trees are recognized as excellent sinks for atmospheric carbon in the long term, which can lessen the effect of gases emitted from the burning of fossil fuels. Perhaps even a greater concern is that 20 per cent of annual greenhouse gas emissions are a direct result of deforestation (CIFOR, 2009). Through governmental programs now being established, land owners can be paid for choosing not to cut down their forests, based on the amount of carbon that trees on their land sequester. Although these programs are coming into place in parts of the world, tropical regions, in which trees comprise a large portion of the landscape, have few of these beneficial programs in place (CIFOR, 2009). The issue in tropical regions stems from the lack of knowledge in tropical tree ecology. In truth, little is known of how tropical trees grow or how old they really are (Worbes and Junk, 1999). Estimating the productivity of these trees thus becomes difficult. The solution to this problem is dendrochronology.

As a tool, dendrochronology can be used to calculate tree productivity on an annual basis and allow farmers to be paid accordingly. In the past, forest carbon studies have only evaluated the carbon density and the total carbon storage already in existence (Glenday, 2006). Stand development is usually measured on 5- to 10-year intervals and measurements generally take long periods of time to collect (Metsaranta and Lieffers, 2009). Dendrochronology is the key to accurately determining, in any given year, how much carbon is being sequestered by a particular tree or forest. Therefore, tropical dendrochronology studies are needed to improve forest management strategies, understand the impacts of climate on forests, provide knowledge of the forest ecology, and present valuable data related to carbon stock changes in the forest (Rozendaal and Zuidema, 2010).

This review begins with a discussion on global climate change and climate change in the tropics, reviewing the impacts on these ecosystems during the 20th century, as well as future projected impacts. This section is followed up by a description of general plant ecophysiology and how climate effects tree growth. The paper then transitions into a section covering methods used for measuring these climatic effects on tree growth, primarily through the implementation of dendrochronology. The advancement of tropical dendrochronology is discussed in the following section and the challenges faced by researchers in the field are covered. The review concludes by narrowing the focus to the study region, incorporating a description of the regional climate and how this influences the common vegetation types found in that region.

1.2 Climate change

Climate change has become an increasing concern in recent years. The number one most likely cause for the global climate change that has occurred during the 20th century is greenhouse gas emissions, such as carbon dioxide, methane, and nitrous oxide (IPCC, 2007). The increases in carbon dioxide can largely be attributed to fossil fuel emissions and land use change, e.g., deforestation. Land use change comprises 20% of the total global carbon emissions, equivalent to 1.7 billion metric tons of carbon and is the leading source of greenhouse gas emmisions (CIFOR, 2009). The increase in the other gases is due to agriculture. The already evident impacts of global climate change include increases in global average air and ocean temperatures, rising global average sea level, and large scale melting of snow and ice (IPCC, 2007).

Climate during the 21st century is projected to have significant impacts worldwide. A 0.2° C per decade increase in temperature is projected for the next two decades (IPCC, 2007). Additionally, global climate change is projected to have influence over future wind patterns, precipitation, and ice. Due to the large timescale of climatic processes, increases in temperature and rising seas levels would continue for centuries, even if emissions were to remain constant at their current levels (IPCC, 2007). Ecosystems will also be greatly impacted by global climate change. A combination of climate change, land-use change, and natural disturbances can potentially overcome the resiliency of many ecosystems (Fischlin et al., 2007). As global mean temperatures exceed 2 to 3° C above pre-industrial levels, the potential impacts on ecosystems could include increasing risk of organism extinction and changes in structure and functioning of both terrestrial and aquatic ecosystems (Fischlin et al., 2007).

Forests hold the greatest influence of current and future climate change, due to deforestation. With 56 percent of the earth's forests being located in tropical areas of the world, knowing how tropical forests will be impacted by climate change is of paramount importance (CIFOR, 2009). Evidence from a variety of study types has shown that climate change is having significant impacts on the ecology of tropical forests (Fischlin et al., 2007). The majority finding is that climate change is causing an increase in biomass and carbon storage in these forests; i.e., the forests are getting bigger (Lewis et al., 2009). However, several studies have predicted decreases in tree growth, due to increased allocation of carbon toward respiration as temperatures also increase (Clark et al., 2003; Clark, 2004; Feeley et al., 2007). The most likely cause of the increased growth in tropical forests is the increase in atmospheric CO_2, with secondary drivers including: incoming solar radiation, the direct:diffuse ratio, and nutrient deposition rates (Lewis et al., 2009).

Savannah ecosystems can have a forest cover of up to 50% and comprise a large portion of western Kenya. Interestingly, African forest ecosystems have been shown to have a larger increase in biomass when compared to forests of South America, possibly due to cooler average temperatures in Africa (Lewis et al., 2009; Philips et al., 2009). The importance of these ecosystems in regards to future carbon sequestration efforts is thus stressed. However, the impacts of climate change on tropical savannah systems are highly speculative, as limited studies have been conducted assessing these impacts (Fischlin et al., 2007). Although impacts on these ecosystems is uncertain, it is predicted that they will be especially sensitive, due to contrasting effects on the different vegetation types from CO_2 fertilization and warming temperatures.

1.3 Effects of climate on growth

Light, temperature, and water availability have the greatest impacts on the carbon balance of trees. With the growing concern of atmospheric CO_2 levels, it is vital that the general processes affecting carbon assimilation in trees is understood. Thus, this section of the paper focuses on the physiological processes of trees that control the productivity of forest ecosystems.

The availability of light greatly influences the net photosynthesis of a tree. Net photosynthesis can be defined as difference between the total amount of carbon assimilated from the atmosphere and amount of carbon lost to the atmosphere during respiration (Barnes et al., 1998). All leaves have a light-saturation point at which they reach their maximum photosynthetic rate. Some tree species have a higher tolerance for shade than others, meaning that although their maximum photosynthetic rates are lower, their respiration rates are also lower, enabling them to maintain a positive net photosynthetic rate at lower light levels (Barnes et al., 1998). In general, the less tolerant a species is to shade, the higher the concentration of chlorophyll (light absorbing pigment) in the leaves (Field and Mooney, 1986). Ultimately, higher photosynthetic rates do not always translate into high net gains of carbon. Light intensity has a large impact on whether the carbon balance is positive or negative.

Temperature has major implications on net photosynthesis of a tree. Each species has a range of optimum temperatures at which net photosynthesis is greatest. In addition, gross photosynthesis and respiration are influenced by temperature in slightly different ways, having major impacts on total carbon gain of the leaf (Berry and Bjorkman, 1980; Berry and Downton, 1982). With increasing temperature, gross photosynthesis steadily rises, but then rapidly declines. Respiration also increases with rising temperature, but does not begin to decrease until temperature well above that of gross photosynthesis, leading to net losses of carbon above a certain temperature (Barnes et al., 1998). Hence, increasing global temperatures can have negative impacts on forest productivity if that threshold is surpassed.

Water availability plays a major role in the amount of carbon being assimilated by tree leaves. Unfortunately, plants are faced with a trade-off between assimilating carbon from the atmosphere and losing water due to the difference in water potential between the leaf and the atmosphere (Barnes et al., 1998). If the plant loses too much water, the water potential of the leaves drops to a level in which the stomata are forced to close, restricting gas exchange with the atmosphere. Thus, major drought events can cause stomata to close and photosynthesis to cease. Many plant species growing in dryer ecosystems have developed adaptations to cope with poor water availability. Such adaptations include: changes in cell wall elasticity, membrane permeability, and the maintenance of positive leaf water potentials through high solute concentrations in cells (Bradford and Hsiao, 1982). An increase in precipitation would likely promote an increase in growth, with other factors constant.

1.4 Measuring the effects of climate on forest and tree productivity

1.4.1 General dendrochronology

The techniques listed in this section were originally developed for temperate regions. These techniques include sanding, crossdating (visually and statistically), and ring width measuring. Due to new challenges that have arisen from tropical dendrochronology studies, several new techniques have also been developed to aid in ring boundary determination (discussed in the following section), which is an essential first step in dendrochronological investigations.

Over the years, many different techniques have been established (Stokes and Smiley, 1996). Either full stem discs or tree cores may be used for dendrochronology. Before analysis can begin, the transverse side of each sample must be sanded in order to clearly see the anatomical structures of the wood. Typically, sanding up to a grit level of 600 is sufficient.

The goal of any dendrochronological analysis is successful cross-dating between samples by comparing the ring widths of multiple trees to find common years of suppressed growth (Yamaguchi, 1991; Speers, 2010). Therefore, the rings that are of utmost importance in cross-dating are those that are narrow, relative to their neighboring rings. Upon completion of cross-dating and ring measurement, a chronology of tree-ring widths can be constructed and compared to climate data obtained from nearby meteorological stations (Chhin et al., 2004; Chhin et al., 2008a; Chhin et al., 2008b; Chhin et al., 2010).

1.4.2 Tropical dendrochronology

In tropical regions, trees experience a short dormancy due to one or two dry periods during the year (Shorrocks, 2007). Thus the leading climatic factor limiting growth in tropical regions is moisture availability, rather than temperature (Worbes 2002; Schöngart et al., 2006; Trouet et al., 2010). Since the discovery of periodic growth rings in tropical trees species, the frequency of tropical dendrochronological studies has increased.

Several factors may be the primary cause of the dormancy period in tropical trees (Worbes, 2002), including periodic flooding (Worbes, 1985; Worbes, 1997; Dezzeo et al., 2002) and drought (Medway, 1972). In the case of extended periods of flooding, oxygen to the root system is inhibited, halting growth for a period of time. On the other hand, one or more periods of little to no rainfall throughout the year can cause leaf senescence in many species. The catalyst for dormancy may be region-dependent (e.g. rainforest flood plain vs. savannah).

Recent studies have discovered that tropical woody species under less stressful conditions produce a distinct ring boundary (Stahle et al., 1999; Worbes, 2002; Maingi, 2006; Trouet et al., 2006; Trouet et al., 2010; Verheyden et al., 2004). Ring boundaries in tropical trees are characterized by a number of different features. Most commonly, a thin band of marginal parenchyma, one to two cells thick and visible only under a microscope on a well polished cross-section of wood, reveals the true ring boundary. Other distinct anatomical features of ring boundaries include: transition from high to low vessel density, absence of apotracheal parenchyma, dark rings visible to the naked eye, and alternating dark and light bands, (Maingi, 2006).

Generally, overstory or open-grown trees are used in tropical dendroecology studies because it is difficult to age understory trees, which grow under stressful conditions, e.g., low light levels or severe nutrient competition from larger trees. Although adult trees tend to exhibit clearer and more consistent ring boundaries, juvenile (and understory) trees fail to do so (Worbes, 1988). Understory trees tend to grow more slowly than adult trees because of poor light conditions (Chazdon and Fetcher, 1984; Rozendaal and Zuidema, 2010), and frequently exhibit many tree ring anomalies such as wedging/missing rings. In addition, juvenile trees, with a more poorly developed root system, may not have access to the same water sources as fully developed canopy trees, leading to differences in response to changes in climatic conditions. However, Couralet et al. (2010) have reported some progress with aging understory species in the Republic of Congo. Using traditional cross-dating techniques they were able to determine the annual nature of growth rings in several understory species. Such results suggest that future understory tree studies may be feasible.

The rings of most tropical trees are very difficult to detect, requiring new dendrochronological techniques, in addition to traditional ones. For instance, when tropical samples are sanded, common practice is to reach a grit level as high as 1200, double that of temperate samples. Other ring boundary detection methods such as wood staining and vessel density analysis have been conducted. Wood staining for identifying lignified vs. unlignified tissues, provides a successful method for accentuating ring boundaries in some temperate species (Vazquez-Cooz and Meyer, 2002). Such procedures are starting to be used on tropical species as well. Verheyden et al. (2005) created time series of vessel features (diameter, density, etc.) for mangrove trees in eastern Kenya and used spectral analysis to detect annual and sub-annual patterns. Researchers continue to explore new analysis techniques in order to expand knowledge of tropical tree ecology.

What makes the ring boundaries so difficult to detect are the frequent anomalies that occur, such as the behavior of ring wedging, when one or more rings merge with one another, becoming locally absent for a significant distance along the circumference of the ring. For this reason, a full-stem disc is required to successfully cross-date a tree and measure the width of each ring (Worbes, 2002). Due to the difficulty of cross-dating tropical trees, many researchers find it useful to catalogue which tree species have shown promise for future dendrochronological studies (Maingi, 2006). Species that lack distinct growth ring boundaries can thus be avoided.

When tree-ring boundaries of tropical trees have been successfully identified, their periodic nature must be determined before analysis can proceed. A few common methods for determining the periodicity of growth rings within a tree species include: sampling trees of a known age (e.g. plantation trees) (Stahle, 1999), ^{14}C radiocarbon dating (Dezzeo et al., 2003), or cambial wounding (Verheyden et al. 2004). Cambial wounding requires the insertion of a sharp object into the cambium of a tree in order to create a visible wound at that location. At least several years later, the tree is then cut down or a sample is taken at the wounded region at a known time period from the wounding date and the number of rings present from the wound outward will reveal the periodic nature of the growth rings (Martin and Moss, 1997).

Knowledge of the tree-ring periodicity and measurement of the ring width allows climate-growth analyses to be performed. Many studies have shown that precipitation has a dominant effect on radial growth (Rozendaal and Zuidema, 2010). Trouet et al. (2010), compared the growth rates of *Brachystegia speciformis* in southern Africa to monthly and seasonal precipitation patterns. The trees in four of their five study sites showed positive correlations between radial growth and annual precipitation (Trouet et al. 2010). Tree-ring chronologies can also be used to infer past climate conditions (Berlage, 1931). Berlage (1931) was the first to successfully create a tree-ring chronology in the tropics, based on the species *Tectona grandis* (teak). The chronology was over 400 years long, providing insight to past climate conditions in parts of the Amazon rainforest.

1.4.3 Dendrochronological studies of Africa

Several dendrochronological studies have been conducted throughout Africa within the past several years, but a majority of them are based out of regions of Africa that exhibit a unimodal rainfall pattern (Schöngart et al., 2006; Couralet et al., 2010; Trouet et al., 2010, etc.). A unimodal rainfall distribution is characterized by a region with one distinct rainy season during each calendar year, with a distinct period of little to no rainfall in between each rainy season.

A majority of recent studies have successfully cross-dated tropical tree species. In a study conducted in Ethiopia, Gebrekirstos et al. (2008) were able to identify ring boundaries in four dominant savannah-based species, three of which were *Acacia* spp. Using ring width measurements, they were able to compare the relationship between tree growth and climate parameters and found a strong correlation between growth and precipitation (Gebrekirstos et al., 2008). In a later study, the same group of researchers were able to find strong correlations between tree growth and precipitation via stable carbon isotope ($\delta^{13}C$) ratios (Gebrekirstos et al. 2009). These ratios can be a useful tool in reconstructing past climate conditions (Gebrekirstos et al. 2009).

1.5 Study Area

1.5.1 Climate

Kenya has a wide range of climate and topography, leading to very diverse types of vegetation. It is dotted with mountain ranges and receives anywhere from 150mm to 2000mm of rain annually, based on location (Maundu and Tengnäs, 2005). The western region of Kenya, near the Lake Victoria basin, has two rainy seasons in a given year. These rainy seasons are caused by the tilt and rotation of the earth. As the earth rotates it creates systems of circulation air and where these systems meet one another is referred to as the intertropical convergence zone (ITCZ) (Shorrocks, 2007). Circulating cells of air above the earth's surface converge near the equator and send warm air rising upward creating a zone of moisture. This zone is the ITCZ. The air in each cell then moves poleward where it cools and then descends at either the Tropic of Cancer (northern hemisphere) or the Tropic of Capricorn (southern hemisphere). The air that descends in these regions is very dry, explaining the occurrence of many deserts at these latitudes (Aguado and Burt, 2004). The ITCZ shifts throughout the year, resulting in dry and wet periods.

1.5.2 Vegetation

The diverse climate of Kenya has enabled a wide range of plant species to establish themselves in many different ecological niches. About 7,000 known native plant species currently exist in Kenya (Maundu and Tengnäs, 2005). The many ecosystems ranging from desert to mountain ranges to coastal areas, allow for very different types of vegetation, such as scrubland, savannah, tropical rain forests, dry highland forests, and, afro-alpine forests and even mangrove forests (Maundu and Tengnäs, 2005).

As a result of the bi-modal rainfall pattern in the area of western Kenya, some trees form not one growth ring per year, but two. Having two growth rings per year makes dendrochronological analysis more difficult. With the common behavior of tropical trees to exhibit wedged rings as described above, keeping track of each ring can be troublesome. It may also be the case that even though the region of study experiences a bimodal rain pattern, certain tree species may still only produce one annual ring (Verheyden et al. 2004). Before dendrochronological analysis can take place, the periodicity of the rings must first be determined.

1.6 General objectives and thesis structure

Although recent efforts have amounted to a valuable step forward in tropical dendrochronology, there is still little information about the dendrochronological and dendroclimatic potential of tree species specific to western Kenya. Furthermore, little is known about the average annual growth rates (biomass and carbon sequestration) of these tropical trees. The objectives of this study are to address following questions:

1. Which Kenyan tree species have high potential for dendrochronology?

   Chapter 2 will address this question. By evaluating the study species based on the method provided in Maingi (2006), the useful species can be added to the already existing list of useful tropical trees, saving future researchers valuable time and money.

2. Of those tree species that have been identified as good candidates for dendrochronology, how much biomass are they accumulating annually?

   Chapter 2 will address this question also, after first determining which species are suitable enough for this type of analysis.

3. How is tree growth affected by climate variables?

   Chapter 3 will address this question. Dendrochronology allows us to determine accurate tree age and annual productivity. Productivity can be expressed in terms of diameter, basal area, and/or biomass increase. Biomass can be converted into carbon, providing information about the annual carbon flux in the forests of western Kenya. The availability of climate data allows correlation analysis to reveal any significant impacts that past climate has had on tree productivity.

REFERENCES

REFERENCES

Aguado, E., Burt, J.E., 2004. Understanding Weather and Climate, third ed. Pearson Education, Inc., New Jersey.

Barnes, B. V., Zak, D. R., Denton, S. R., Spurr, S. H., 1998. Forest Ecology: 4th Ed. John Wiley and Sons, Inc. New York, NY.

Berlage, H. P., 1931. Over het verband tusschen de dikte der jaarringen van djatiboomen (*Tectona grandis* L. f.) en den regenval op Java. Tectona. 24:939-953.

Berry, J., Bjorkman, O., 1980. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiology 31, 491-543.

Berry, J., Downton, W. J. S., 1982. Environmental regulation of photosynthesis. *In* R. Govindjee (ed.) *Photosynthesis, Development, Carbon Metabolism, and Plant Productivity. Vol. 2* Academic Press, New York. 580 pp.

Bradford, K. J., Hsiao, T. C., 1982. Physiological responses to moderate water stress. *In* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. (eds.), *Physiological Plant Ecology II: Water Relations and Carbon Assimilation*. Encyclopedia of Plant Physiology, Volume 12B. Springer-Verlag, New York.

Chhin, S., Wang, G. G., Tardif, J., 2004. Dendroclimatic analysis of white spruce at its southern limit of distribution in the spruce woods provincial park, Manitoba, Canada. Tree-Ring Research 60, 31-43.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2008a. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany 86, 167–178.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2008b. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. For. Ecol. Manage. 256,1692–1703.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2010. Growth-climate relationships vary with height along the stem in lodgepole pine. Tree Physiology 30, 335-345.

CIFOR, 2009. Simply REDD: CIFOR's guide to forests, climate change and REDD. Bogor, Indonesia. www.cifor.cgiar.org

Clark, D.A., 2004. Tropical forests and global warming: slowing it down or speeding it up? Front. Ecol. Environ. 2, 73–80

Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc. Natl. Acad. Sci. USA100,5852–5857

Couralet, C., Sterck, F.J., Sass-Klaassen, U., Van Acker, J., Beeckman, H., 2010. Species-Specific Growth Responses to Climate Variations in Understory Trees of a Central African Rain Forest. Biotropica 42, 503-511.

Dezzeo, N, Worbes, M, Ishii, I, Herrera, R, 2002. Growth rings analysis of four tropical tree species in seasonally flooded forest of the Mapire River, a tributary of the lower Orinoco River, Venezuela: Plant Ecology.

Feeley, K.J., Wright, S.J., Supardi, M.N.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. Ecol. Lett. 10, 461–469.

Field, C., Mooney, H. A., 1986. The photosynthesis-nitrogen relationship in wild plants. *In* T.J. Givnish (ed.), *Ecological (Biophysical) Land Classification in Canada*. Lands Directorate, Environment Canada, Ottawa.

Fischlin, A., G.F. Midgley, J.T. Price, R. Leemans, B. Gopal, C. Turley, M.D.A. Rounsevell, O.P. Dube, J. Tarazona, A.A. Velichko, 2007. Ecosystems, their properties, goods, and services. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, 211-272.

Glenday, J., 2006. Carbon Storage and emissions offset potential in an East African tropical rainforest. J. For. Eco. Man. 235, 72-83.

Gourlay, I.D., 1995. Growth ring characteristics of some African acacia species. Journal of Tropical Ecology 11, 121-140.

Hartig, T, 1853. Ueber die Entwicklung des Jahrringes der Holzpflanzen. Bot. Z. 31: 553-560, 32: 569-582.

Henry, M., Tittonell, P., Manlay, R. J., Bernoux, M., Albrecht, A., Vanlauwe, B., 2009. Biodiversity, carbon stocks and sequestration potential in aboveground biomass in smallholder farming systems of western Kenya. J. Agr. Ec. Env. 129, 238-252.

IPCC, 2007. Summary for Policymakers. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M.Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jacoby, G. C., 1989. Overview of tree-ring analysis in tropical regions. IAWA Bulletin. 10, 99-108.

Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T. A., Laurance, W. F., 2009. Changing ecology of tropical forests: Evidence and drivers. Ann. Rev. Ecol. Evol. Syst. 40, 529-549.

Maingi, J. K., 2006. Growth rings in tree species from the Tana River floodplain. J. East African Natural History. 95, 181-211

Martin, D.M., Moss, J.M.S., 1997. Age determination of Acacia tortilis (Forsk.) Hayne from northern Kenya. African Journal of Ecology 35, 266-277.

Maundu, P., Tengnäs, B., 2005. Useful Trees and Shrubs for Kenya, World Agroforestry Centre, Nairobi.

Medway, F. L. S., 1972. Phenology of a tropical rain forest in Malaya. Biol. J. Linn. Soc. 4:117-146.

Metsaranta, J.M., Lieffers, V.J., 2009. Using dendrochronology to obtain annual data for modeling stand development: a supplement to permanent sample plots. Oxford University Press, Forestry. Doi: 10.1093/forestry/cpn051.

Phillips, O.L., Aragao, L., Lewis, S.L., Fisher, J.B., Lloyd, J., 2009. Drought sensitivity of the amazon rainforest. Science 323, 1344–1347

Schöngart, J., Orthmann, B., Hannenberg, K.J., Porembski, S., Worbes, M., 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Global Change Biology. 12, 1139-1150.

Shorrocks, Bryan, 2007. The Biology of African Savannahs, New York.

Stahle, D. W., 1999. Useful strategies for the development of tropical tree-ring chronologies. IAWA j. 20, 249-253.

Speers, J. H., 2010. Fundamentals of Tree-Ring Research. University of Arizona Press, 368 pp.

Stahle, D. W., Cleaveland, M.K., Maingi, J., Munyao, J., 1995. The dendroclimatology of Vitex keniensis in Kenya. Supplement to Eos 76(46), F316, Transactions, American Geophysical Union.

Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. Forest Ecology and Management 124, 217-229.

Stokes, M.A., Smiley, T.L., 1996. An Introduction to Tree-Ring Dating. The University of Arizona Press, Arizona.

Trouet, V., Coppin, P., Beeckman, H., 2006. Annual growth ring patterns in Brachystegia spiciformis reveal influence of precipitation on tree growth. Biotropica 38, 375-382.

Trouet, V., Esper, J., Beeckman, H., 2010. Climate/growth relationships of Brachystegia spiciformis from the miombo woodland in south central Africa. Dendrochronologia 28, 161-171.

Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2004. Growth rings, growth ring formation and age determination in the mangrove Rhizophora mucronata. Annals of Botany 94, 59-66.

Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytologist 167, 425-435.

Worbes, M, 1985. Structural and other adaptations to long term flooding by trees in Central Amazonia. Amazonia. 9: 459-484.

Worbes, M, 1988. Variety in structure of annual growth zones in *Tabebuia barbata* (E. Mey) Sandw., Bignoniaceae, a tropical tree species from Central Amazonian inundation forests. Dendrochronologia. 6: 71-89.

Worbes, M., 1995. How to meaure growth dynamics in tropical trees. A review. IAWA Journal 16, 337-351.

Worbes, M, 1997. The forest ecosystems of the Amazonian floodplains. In Junk WJ (Ed), The Amazonian floodplains: Ecology of a pulsing system. Ecological Studies. 126, Springer Verlag, Berlin:223-265.

Worbes, M., Junk, W.J., 1999. How old are tropical trees? The persistence of a myth. IAWA Journal20, 255-260.

Worbes, M, 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. Dendrochronologia. 20: 217-231

Yamaguchi, D. K., 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21, 414–416.

CHAPTER 2

DENDROCHRONOLOGICAL POTENTIAL AND ANNUAL BIOMASS PRODUCTIVITY OF TROPICAL TREE SPECIES IN WESTERN KENYA

2.1 Introduction

Many tropical ecosystems are expected to largely contribute to the future of climate change and carbon dynamics (IPCC, 2008). As many tropical ecosystems exist in Africa, the continent has become an area of increasing interest for forestry related studies. Kenyan ecosystems in particular range in form from that of dry savannah forests of the north to afro-alpine vegetation in the mountain ranges, tropical rainforests, and mangrove forests near the eastern coast (Maundu and Tegnas, 2005). The region of Western Kenya, along the River Yala Basin is home to a mosaic of farmland consisting of varying degrees of tree cover (Dietz and Kuyah, 2011). Because 87% of this agricultural land contains at least 10% tree cover, it becomes a significant contributor to stabilizing and possibly increasing carbon sequestration (Zomer et al., 2009).

Currently, a need for more technical based research assessing biomass and carbon productivity of tropical trees in Kenya has arisen in order to promote climate-change adaptation and climate mitigation interventions. Knowledge of tree growth rates is necessary to understand the impacts of climate change on tropical ecosystems in Western Kenya. Issues with restricted computational facilities and lack of human resources (Hudson and Jones, 2002; Swart et al. 2002), along with insufficient climate data (Jenkins et al., 2002) have made such studies difficult (IPCC 4AR, 2007).

With sufficient climate records for a region, tree-ring analysis offers a method for annual growth rate estimates for individual tree species at the landscape level. Such data can then be used to create accurate models for estimating future carbon stocks in a landscape based on proxy climate data. In the case of developing countries, such as Kenya, the lack of manpower for inventory measurements increases the importance of these models. Countries wanting to implement reforestation carbon offset projects can inventory the landscape on a less frequent basis (i.e. every five years) and use the carbon storage models during the intervening years.

Dendrochronology has been used in a variety of tropical ecosystems, including Kenya, to create individual species growth models and the impacts of climate parameters (Tarhule and Hughes, 2002). The formation of periodic tree-rings is the key component in linking species growth characteristics with climate seasonality characteristics of the region. However, detection of tree-rings in tropical species has proven to be more difficult and the trigger for formation different than that of temperate and boreal regions. Dormancy in temperate and boreal tree species is induced by cold temperature during the winter months of the year, producing a distinct ring boundary. Dormancy in tropical species is induced by either a seasonally dry period or an extended duration of flooding in floodplain forests. In either case, cambial dormancy and ring formation in tropical trees is directly controlled by seasonal fluctuations in moisture availability (Rozendaal and Zuidema, 2010). Although dendrochronology shows good potential for understanding growth-climate relationships in the tropics, standard dendrochronoligical techniques have not always proven to be sufficient (Worbes, 1995). Tree-ring anomalies such as false or wedging rings, caused by within season climate fluctuations, have hampered research in these regions (Worbes, 2002). Consequently, tree-ring studies in Africa (Stahle et al., 1999; Stahle, 1999; Worbes and Junk, 1999; Courelet et al., 2005; Therrell et al., 2007; Gebrekirstos et al., 2008; Trouet et al., 2010), and more specifically Kenya (Martin and Moss, 1997; Verheyden et al., 2005; Maingi, 2006), are rare.

This paper assessed the dendrochronological potential of individual tree species growing in the Yala River Basin in Western Kenya and then determining annual biomass production of species with a sample size greater than two. The species included in the study are *Acacia mearnsii, Bridelia micrantha, Combretum molle, Croton macrostachyus, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Grevillea robusta, Mangifera indica, Markhamia lutea, Persea americana, Syzygium cuminii* and *Trilepisium madagascariensis.* The samples were collected from a variety of growing environments including agricultural, natural forest, and plantations.

2.2 Material and methods

2.2.1 Study area

This study was conducted on three 100 km^2 blocks of land located in the Yala River Basin of Western Kenya. These three designated areas were labeled as the lower, middle and upper Yala regions with the lower Yala region starting near Lake Victoria. The Yala River catchment, covering an area of 3351 km^2, drains into the Winam Gulf in Lake Victoria. The elevation, beginning in the lower Yala region, ranges from 1,200 m above sea level to 2,200 m above sea level in the upper Yala region. The average annual rainfall for the entire Yala Basin is 1487 mm follows a bimodal distribution. Average total annual precipitation and average mean annual temperature data is shown for each of the respective Yala blocks (lower, middle, upper) in Table 2.1. There are several major soil types present along the Yala Basin, including: acrisols, ferralsols and nitrosols (Jaetzold and Schmidt, 1982). These soil types exhibit the characteristics of good physical structure, well drained, deep to very deep and variable fertility.

The variety of soil and climatic conditions along the altitudinal gradient of the basin in conjuncture with a highly heterogeneous landscape which includes a mosaic of farmland, differing degrees of forest cover and open area, has led to a contrast in the dominant tree species found in each region. These species are *Markhamia lutea*, *Eucalyptus* spp. and *Acacia mearnsii* in the lower, middle and upper Yala regions respectively (Dietz and Kuyah, 2011).

2.2.2 Field Sampling

Three blocks of 10x10 km size were established along the altitudinal gradient of the Yala Basin in Western Kenya. Each block was randomly assigned 160 sample points, which were then randomly sub-sampled from (15% of the points in lower block, 30% of the points in the middle block, and 15% of the points in the upper block). On each of the sub-sample points, a 30x30 m sampling plot was randomly chosen and all trees within that plot were sampled. All trees in the plot with a diameter at breast height (dbh) greater than 2.5 cm were destructively sampled. Of the trees chosen for destructive sampling, a stem disc was taken at breast height (1.3 m). If the disc was between 30 and 60 cm, only a half stem disc, which included the pith was kept. If the disc was > 60 cm, only a quarter stem disc, which included the pith was kept. These discs were later used for dendrochronological analysis.

In total, 20 species were collected, in which 90 trees were sampled. However, 18 of the trees were not used in the development of the allometric equation. For the development of the allometric equation, 18 trees were sampled in the lower block, 36 were sampled in the middle block and 18 were sampled in the upper block. The trees were randomly selected within 6 predetermined dbh classes. Thus, 12 trees of each class were harvested. The dbh classes were as follows: 2.5 – 10; 10.1 – 20; 20.1 – 30; 30.1 – 40; 40.1 – 60 and > 60 cm. 66 of the 72 trees sampled were used for the development of the allometric biomass equation (Dietz and Kuyah, 2011). The remaining 6 trees (one from each diameter class) were used as a validation set for the equation. A subset of the 90 total trees destructively sampled was used for the dendrochronological analysis. This subset consisted of 67 trees spanning 14 species (*A. mearnsii, B. micrantha, C. molle, C. macrostachyus, C. lusitanica, E. camaldulensis, E. grandis, E. saligna, G. robusta, M. indica, M. lutea, P. americana, T. madagascariensis,* and *S. cuminii*). Dendrochronological potential for all 14 species was determined and then good candidates with a sample size of 3 or more trees were further analyzed to characterize annual patterns in diameter and biomass growth (Maingi, 2006). A summary of major botanical characteristics as well as the number of trees sampled per species is listed to aid in the explanation of each species dendrochronological potential (Table 2.2).In addition, each of the following species fell into one of the general shade tolerance categories: tolerant, moderately tolerant, and intolerant. The tolerant species included *B. micrantha, C. macrostachyus*, and *P. americana*. The moderately tolerant species included *A. mearnsii, C. molle*, and *C. lusitanica*. Lastly, the intolerant species included the *Eucalyptus* spp., *M. indica*, and *S. cuminii* (Plant Resources of Tropical Africa, 2012). Information on the shade tolerance of *G. robusta*, *M. lutea*, and *T. madagascariensis* is scarce.

2.2.3 Laboratory analysis

Wood samples were first sanded with progressively finer grits of sandpaper (up to 1200 grit), which is standard practice among dendrochronology studies in the tropics. The dendrochronological potential was then determined for each sample based on the rating system developed by Maingi (2006). The four categories used to determine the tree’s potential are distinctness of rings, circuit uniformity of rings, wedging out of rings, and variability of ring widths. After determining the quality of the sample in each of the categories, an overall potential for dendrochronology was assessed. Results of all samples within each species were averaged to obtain an overall species usefulness. The final ratings given were: 1) useful, 2) problematic, or 3) poor.

A total of 7 species (*Acacia mearnsii, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Mangifera indica and Markhamia lutea*) were elected as good candidates with a great enough sample size (i.e., 3 or more trees) for further analysis consideration. Each sample was visually cross-dated along 4 radii, either macroscopically or microscopically under a binocular microscope, to identify missing and/or false rings. During this process it was determined whether each species produced a single annual growth ring or a sub-annual ring, based on visual pattern of the ring widths. Each ring boundary was verified circumferentially between the other three radii of the disc. The number of successfully cross-dated samples within each species is shown in Table 2.2. Following verification of cross-dating, annual or sub-annual ring widths were measured using a stage micrometer coupled with a binocular microscope to the nearest 0.001 mm (Velmex: Bloomfield, New York). Disc samples were measured along 4 radii (or as many as were successfully crossdated) from the outmost growth ring inward toward the pith.

2.2.4 Dendrochronological measurements

For cross-sectional discs in which fewer than 4 radii were successfully cross-dated, a data correction procedure was applied to the ring width measurements in order to prevent over- or under-estimation of tree diameter estimates derived from ring width measurements (Gebrekirstos et al., 2008):

Correction Factor = $D_{IB,R} / D_{IB,A}$ (Eq. 2.1)

Where $D_{IB,A}$ is the actual diameter inside bark of the cross-sectional disk determined with a measurement tape and $D_{IB,R}$ is the maximum diameter inside bark determined from the cumulative ring width measurements. The ring width measurements were all divided by this correction factor. In cases where 4 radii were successfully cross-dated for a disc, this correction factor was not applied. It was assumed that when the measurements of the 4 radii were averaged, error in diameter estimation would be corrected for. At the end of each growth period, the corrected (or non-corrected) ring width measurements for each radius were converted to cumulative measures of diameter inside bark (D_{IB}). Cumulative in this sense is relative to the annual measures of diameter increment.

Bark thickness measurements were calculated by subtracting the measured diameter inside bark from the measured diameter outside bark. The bark ratio (BR) could then be determined using the bark thickness and the following equation (Bush and Brand, 2008):

BR = D_{IB} / D_{OB} (Eq. 2.2)

Where D_{IB} is the diameter inside bark and D_{OB} is the diameter outside bark. It was essential that cumulative D_{OB} values be obtained by dividing D_{IB} by BR because allometric biomass equations require D_{OB} as the input variable. Cumulative DOB values were input into a composite allometric equation developed for trees in the Yala Basin region relating total above ground tree biomass (AGB) to dbh (Dietz and Kuyah, 2011):

$\ln(AGB) = -2.403 + 2.471*\ln(dbh)$ (Eq. 2.3)

Annual diameter increment (cm year^{-1}) and annual stem biomass (kg year^{-1}) were calculated by subtracting cumulative growth in the previous year (t-1) from the current year (t). Annual stem diameter (cm year-1) and annual stem biomass (kg year-1) increment values calculated for radii of the same disc were averaged together (Table 2.3 and Table 2.4). Annual above ground carbon (AGC) increments were calculated by multiplying AGB by a carbon fraction of 0.5. The AGC increments for each species can be found in Table 2.5.

2.3 Results

2.3.1 Dendrochronological potential

The assessed dendrochronological potential of all 14 species can be found in Table 2.2. The majority of the species were found to be at least somewhat useful. The best species included *C. lusitanica*, the *Eucalyptus* spp. and *M. indica*. Although the ring boundaries of *M. lutea* were demarcated by marginal parenchyma, the species was very troublesome as many instances of ring wedging occurred. The species with the least amount of potential was *G. robusta*. The ring boundaries of this species were almost indistinguishable.

2.3.2 Tree-ring formation patterns

During the visual inspection of the wood anatomy of all studied species, structures were similar to that of other tropical species, but different than temperate and boreal species. The variation in ring boundary distinctiveness among the species is displayed in Figure 2.2. Several species exhibited ring boundaries denoted by a thin band of marginal parenchyma: *C. macrostachyus, M. indica, M. lutea* (Figure 2.2d, f, g). Narrow bands of fiber tissue (darker colored xylem tissue) separated by wide bands of parenchyma (light colored xylem tissue) was characteristic of *A. mearnsii, B. micrantha, P. americana, C. lusitanica, E. camaldulensis, E.*

grandis, and *E. saligna* (Figure 2.2a, b, h, k, l, m, n). Note that *C. lusitanica, E. camaldulensis, E. grandis*, and *E. saligna* all exhibit a bimodal ring structure and thus growth rings alternate between wide and narrow widths (Figure 2.2k, l, m, n). Tree ring boundaries in *S. cuminii* were expressed as alternating light and dark bands of xylem tissue in conjuncture with a condensing of the large vessels near the end of the growing season (Figure 2.2i). The *G. robusta* samples displayed only a slight alternating color pattern between darker and lighter parenchyma cells, with the color becoming lighter towards the end of the growing season (Figure 2.2e). The ring boundaries of *C. molle* were characterized by a zone relatively free of vessels (Figure 2.2c). Lastly, the ring boundaries of *T. madagascariensis* were characterized by zone relatively free of banded, confluent parenchyma, giving the appearance of a dark band.

2.3.3 Mean annual growth increments

By calculating annual growth parameters, quick comparisons can be made between the different species based on their rate of productivity (Table 2.3 and Table 2.4). Only seven of the original 14 study species (*A. mearnsii, C. lusitanica, E. camaldulensis, E. grandis, E. saligna, M. indica, M. lutea*) could be analyzed due to insufficient sample size of the other species. In addition, of the species analyzed, only sufficient samples from the same block (lower Yala, middle Yala, upper Yala) were included. For instance, in the case of *M. lutea*, 4 samples were from the middle Yala block and 1 sample was from the lower Yala block, yet only the 4 samples from the middle Yala block were used for the analysis. The three fastest growing species in the study, based on annual diameter increment, were *E. camaldulensis*, *E. grandis*, and *A. mearnsii* (Table 2.3).

In terms of annual biomass production, the three species that grew most rapidly were *E. camaldulensis*, *M. indica*, and *A. mearnsii* (Table 2.4). However, where *M. indica* is concerned, when only the first ten years of growth are taken into account (age 1-10), the annual aboveground biomass increment drastically drops and is no longer one of the fastest growing species. In contrast, *M. lutea* is a consistently slow growing species.

2.3.4 Cumulative growth trajectories

The cumulative diameter growth trajectories were divided into two groups of species. The first group contained the species most commonly grown in plantations (Figure 2.3a, *C. lusitanica, E. camaldulensis, E. grandis, E. saligna*), while the second group contained the species commonly found in a natural forest setting (Figure 2.3b, *A. mearnsii, M. indica, M. lutea*). The cumulative diameter growth trajectory of the plantation species showed all the *Eucalyptus* spp. growing faster within the first 5 years than *C. lusitanica,* with *E. grandis* being slightly higher than the other 2 *Eucalyptus* spp. Due to the short length of the *E. grandis* and *E. saligna* chronologies, it is impossible to determine their cumulative diameter growth rates beyond 5-10 years of age. Among the non-plantation species, *A. mearnsii* was clearly the fastest growing species from an early age. *M. indica*, however, surpassed *A. mearnsii* around the age of 25. *M. lutea* was well below the other two species in cumulative diameter growth.

Cumulative above ground biomass trajectories (Figure 2.4a, b) showed similar patterns to that of cumulative diameter growth trajectories (cf. Figure 2.3a, b). Over the entire period (age 1-End) of the plantation species, *E. camaldulensis* had the highest total biomass accumulation by a large margin. However, it is unknown whether or not *E. grandis* or *E. saligna* would have achieved a higher biomass accumulation than either *C. lusitanica* or *Eucalyptus camaldulensis*, had their life spans been longer. Once again, among the non-plantation species, *A. mearnsii* was the quickest to put on biomass, only to be passed by *M. indica* around the age of 26. *M. lutea* had an extremely low biomass accumulation over the course of its lifespan, relative to the other two species. Similarly, *E. grandis* accumulated the most biomass within the first 5 years of age.

2.4 Discussion

2.4.1 Dendrochronological potential

A certain degree of difficulty was present in detecting the growth-ring boundaries of several of the study species. It has been noted that ring boundaries tend to be clearer and more distinct in regions that exhibit a unimodal rainfall distribution (Worbes, 1995). The single annual rainy season allows for a more pronounced dry period in which the ring boundary can be formed. Western Kenya, unlike much of Africa, has a bimodal rainfall distribution, which may attribute to the reduction in clarity of the ring boundaries. The source of the bimodal rainfall distribution pattern is the intertropical convergence zone (ITCZ), defined by circulating systems of air colliding, rising, and releasing moisture (Shorrock, 2007). The ITCZ shifts throughout the year, resulting in dry and wet periods. A bimodal rainfall pattern creates the potential for some trees to form two ring boundaries in the same calendar year. However, even if the region of study experiences a bimodal rain pattern, certain tree species may still only produce one annual ring (Verheyden et al., 2004). All of the studied species displayed a unimodal ring structure, with the exceptions of *C. lusitanica* and the three *Eucalyptus* spp. The ring boundaries in each of these species were denoted by a dark band of fiber tissue, which can be linked to the size of the cell diameters decreasing in an attempt to mitigate water stress (Kozlowski et al., 1991). Since these species are plantation species and non-indigenous to the region, the bimodal ring pattern of these species could imply poor adaptation to the local climate (Kozlowski et al., 1991). The findings of this study support this suggestion in that many of the study species produced only one annual growth ring, despite growing in a region with a bimodal rainfall distribution.

Previous studies have developed a system of rating species, based on their dendrochronological potential. Tarhule and Hughes (2002) assigned species to three categories in terms of their usefulness: 1) potentially useful, 2) problematic, and 3) poor. Each species was placed into one of these categories based on the following criteria: 1) distinctiveness of annual ring boundaries, 2) ability to be crossdated, 3) ring circuit uniformity, 4) ring wedging, 5) and ring width variability (sensitivity). This same rating systems was later adopted by Maingi (2006), however, the "ability to crossdate" criterion was not included. This study also utilized this rating system as a way of determining dendrochronological potential. Unfortunately, neither study included any species that were examined in this study, so comparisons between results cannot be made.

The most frequent problems related to ring boundary identification were ring wedging, indistinct boundaries, and/or occasionally fire scars. Despite difficulties, several of the species showed high potential for dendrochronology. These species include *M. Indica, C. Lusitanica, E. camaldulensis, E. grandis*, and *E. saligna. M. indica*, the species with the highest dendrochronological potential, produced a distinct band of marginal parenchyma denoting the ring boundary. Another tree-ring study in Kenya, conducted by Maingi (2006), found that the species with the most distinct ring boundaries were those that produced marginal parenchyma. *C. lusitanica* and all three *Eucalyptus* species did not have a distinct line of marginal parenchyma marking the ring boundary, but rather a dark band of fiber tissue, with lighter colored parenchyma cells in between the boundaries. In the state of Rio de Janeiro, Brazil, de Oliveira et al. (2011) were able to successfully identify the tree-ring boundaries of *E. grandis* trees using X-ray densitometry techniques, the same methodology used by Delgado-Matas and Pukkala (2011) in Angola on *E. camaldulensis, E. grandis*, and *E. saligna* trees. Of the remaining potentially useful study species, few dendrochronological studies exist in which potential and growth productivity are examined, making comparisons difficult.

The species in this study determined to be either problematic or poor include: *A. mearnsii, B. micrantha, C. molle, C. macrostachyus, G. robusta, M. lutea, P. americana, S. cuminii,* and *T. madagascariensis.* The species that displayed the highest frequency of ring wedging was *M. lutea.* Its slow growing nature (Akyeampong et al., 2005), similar to that of an understory tree, may explain the high frequency of ring wedging found in the species (Couralet et al., 2010). Although *G. robusta* was not successfully crossdated in this study and no growth rates could be determined, Nath et al. (2011) found that *G. robusta* has a relatively fast growth rate in India in comparison to native shade trees. Growth rates were calculated using steel dendrometer bands. Although several of these species, such as *A. mearnsii* were listed as problematic and displayed varying difficulty of crossdating among samples, they were not completely useless for dendrochronological purposes. Few dendrochronological studies have been conducted on the remaining poor candidate species and so meaningful comparisons could not be made.

The samples used in this study were all stem discs. The majority of discs were complete, but a few were either half discs or quarter discs due the large circumference of the tree and difficulty of transportation. Previous studies (e.g. Maingi, 2006) included increment core samples as well, but determined that they were insufficient for accurate ring detection, based on the common occurrence of wedged and/or false rings. True ring boundaries in tropical trees typically span the entire circumference of the tree (Worbes, 2002). Therefore, using full stem discs helps in determining which ring boundaries are real and which are false. The *Eucalyptus* spp. examined in this study are good examples of false ring producers. Many times faint dark bands are present that at first appear to be boundaries. If only increment cores were used, these bands may be easily mistaken for actual ring boundaries. While full stem discs have been proven as better means for tropical dendrochronology, destructive sampling is required to obtain them.

Aside from the physical characteristics of the wood, several other issues can make tropical dendrochronology difficult. One of these issues is asynchrony of leaf senescence and bud break (Worbes, 2002). Some tree species hold onto their leaves for a longer period of time after the end of the rainy season and begin to develop their new leaves before the onset of the next rainy season. De Bie at al. (1998) describes the trigger for pre-mature leaf development as being an increase in air humidity. Photosynthesis is dependent on leaf presence and thus, the species that maintain their leaves for longer periods of time throughout the year have an advantage in biomass production. For this reason, climate-growth analysis, when comparing different species, should take phenology into account. *C. lusitanica,* an evergreen species considered in this study, surprisingly had very distinct ring boundaries. It would be expected that the presence of leaves year-round would decrease the distinctiveness of the boundaries, yet this was not the case. *C. lusitanica* is a conifer species native to wet forests in the mountainous regions of Mexico and Central America (Maundu and Tengnäs, 2005). The distinctiveness of its rings could be explained by its sensitivity to climate, edaphic conditions, and light exposure (Miller and Knowles, 1990; Cros et al., 1999; Nicholas, 2007; Watt et al., 2009). A majority of the species in the current study were in fact evergreen, with the exception of only *G. robusta* and *C. molle*. Deciduous species did not appear to have a clear advantage in ring distinctiveness, as *G. robusta* had one of the lowest potentials for dendrochronology.

2.4.2 Annual growth rates and cumulative growth trajectories

Surprisingly, the growth pattern of many of the studied species contradicts common ecological theories related to growth in temperate and boreal trees. The general growth pattern of a tree is characterized by an exponential growth phase as a youth (Silvertown and Charlesworth, 2001), followed by a decline in growth as the tree ages, reaches the canopy, and is forced to compete with neighboring trees for resources. Many of the trees in this study showed an increase in growth over time, suggesting that in dryer savanna ecosystems, trees require a longer establishment period in which root systems can reach the water table. However, further analysis on external and edaphic controls on radial growth are required to accurately explain this phenomenon (Schongart et al., 1996). In addition, the young age of many of the study species limits the context in which a true growth trajectory can be assessed.

Growth rates among the well-replicated species in the study varied greatly, with *E. grandis* being the fastest growing species during early years and *M. lutea* being the slowest growing species. Delgado-Matas and Pukkala (2011) successfully determined the growth rates of six *Eucalyptus* species in Angola through the use of X-ray densitometry, however, the mean diameter growths of *E. camaldulensis*, *E. grandis*, and *E. saligna* after 5 years were 5 cm, 4 cm, and 6cm, respectively, which were all below those of the current study. This discrepancy could be due to the significantly colder temperatures experienced during the winter months in Angola or the lack of thinning in the Angola study site. The early biomass production rates of *A. mearnsii* in Ethiopia were found to be very similar to the rates calculated in this study (Mekkonen et al., 2006). After 64 months, the total above ground biomass of their study trees had reached an average of 44.05 kg tree^{-1}, with the biomass of the trees in this study reaching just above 40 kg tree^{-1}. The relatively close proximity of study sites and climate patterns could explain the similar growth rates. In a mixed species plantation study in Australia, Forrester et al. (2004) found mean cumulative diameter growth in *A. mearnsii* to range from 10 to 16 cm at 11 years of age, with mean cumulative diameter of trees in this study falling within that range at 15 cm. In concurrence with this study, Akyeampong et al. (1995) also found in the highlands of Burundi that *M. lutea* was a very slow growing species, obtaining a diameter at breast height (dbh) of only 3.1 cm, three and a half years after planting. The diameter growth rates of *C. lusitanica* in this study are lower than previously reported rates of 14.6 cm at age 7 by Luoga et al. (1994) in Tanzania. These findings are surprising as Tanzania exhibits a precipitation pattern much like that of Kenya. Few wood productivity studies have been conducted on *M. indica*, as most studies focus on the fruit and reproductive aspects of the tree.

2.5 Conclusion

The findings of this study further provide evidence that tropical trees have dendrochronological value. Although not all of the study species were successfully crossdated, many of them were and demonstrated that they could be of use in further such studies. The problems encountered during this study were very similar to issues brought up by other researchers, but the exploration of novel techniques (wood staining, x-ray densitometry) is making tropical dendrochronology study more feasible. Growth rates were successfully determined for all of the well replicated species and compared relatively well with values reported in previous literature.

In general, half of a tree’s biomass is made up of carbon, which allows for the easy conversion of biomass to carbon mass. Therefore, dendrochronology studies such as this one can greatly benefit the implication of carbon offset programs. Developing countries, with limited resources can utilize allometric equations in combination with dendrochonological analyses in tropical trees to determine historical annual patterns of carbon content of a tree. Currently, these programs only account for carbon on a 5-year basis and require significant funding to obtain the necessary data for the calculations (Mbow et al., N.d.). Thus, projects are not able to receive any tradable income until the 5-year lag period is over. With the reduction in time and money created by equations from dendrochronological studies, annual carbon offset estimates could be obtained.

APPENDICES

Table 2.1 Average total annual precipitation and average mean annual temperature for each of the three study blocks

	Lower Yala	Middle Yala	Upper Yala
Total Annual Precipitation (cm)	187.4	197.7	104.3
Mean Annual Temperature (^{o}C)	23.4	20.8	17.2

Table 2.2 Dendrochronological Potential of all studied species

Species	**Region**	**Habit**	**Origin**	**Total Number of Trees Sampled**	**Number (Percentage) of Trees Successfully Crossdated**	**Mean Age (Minimum and Maximum Age Range)**	**Rating**
Acacia mearnsii	Upper Yala	Evergreen shrub/tree, 2-15 m	South-eastern Australia	6	6 (100)	17.8 (7, 27)	Problematic
Bridelia micrantha	Middle Yala	Evergreen tree, up to 13m	Indigenous	2	2 (100)	14.5 (11, 18)	Problematic
Combretum molle	Lower Yala	Small deciduous tree, 5-7m	Indigenous	1	1 (100)	31 (31, 31)	Problematic
Croton macrostachyus	Middle Yala	Deciduous tree, 3-25m	Indigenous	2	2 (100)	14 (18, 20)	Problematic
Cupressus lusitanica	Middle Yala	Evergreen tree, up to 35 m	Mexico, Guatemala	4	4 (100)	16.3 (12.5, 20.5)*	Useful
Eucalyptus camaldulensis	Middle Yala	Evergreen tree, up to 30 m	Eastern Australia	21	20 (95)	12.4 (5, 21)*	Useful
Eucalyptus grandis	Middle Yala	Evergreen tree, 40-50m	Coastal Eastern Australia	6	6 (100)	6.5 (5, 11)*	Useful
	Upper Yala			1	1 (100)	8 (8, 8)*	
	All			7	7 (100)	6.7 (5, 11)*	
Eucalyptus saligna	Middle Yala	Evergreen tree, 40-50m	Coastal Eastern Australia	6	4 (67)	5.5 (5, 6)*	Useful
Grevillea robusta	Lower Yala	Semi-deciduous tree, 20+ m	Eastern Australia	1	0 (0)	-	Poor

Table 2.2 (Cont'd)

Species	Region	Habit	Origin	Total Number of Trees Sampled	Number (Percentage) of Trees Successfully Crossdated	Mean Age (Minimum and Maximum Age Range)	Rating
Mangifera indica	Lower Yala	Evergreen tree,10-15m	Northern India, Burma	6	6 (100)	34.3 (22, 47)	Useful
	Middle Yala			1	1 (100)	25 (25, 25)	
	All			7	7 (100)	33 (22, 47)	
Markhamia lutea	Lower Yala	Evergreen tree,10-15m	Indigenous	1	1 (100)	39 (39, 39)	Poor
	Middle Yala			4	4 (100)	26.5 (20, 33)	
	All			5	5 (100)	29 (20, 39)	
Persea americana	Middle Yala	Evergreen tree, ≥10m	Central America	2	2 (100)	11 (8, 14)	Problematic
Syzygium cuminii	Lower Yala	Evergreen tree, up to 30m	India, Tropical Asia	1	1 (100)	29 (29, 29)	Problematic
	Middle Yala			1	1 (100)	16 (16, 16)	
	All			2	2 (100)	22.5 (16, 29)	
Trilepisium madagascariensis	Middle Yala	Evergreen tree, up to 40m	Madagascar, Seychelles	1	1 (100)	59 (59, 59)	Problematic

Table 2.3 Descriptive statistics of mean annual diameter increment summarized by tree species for which there was sufficient sample replication (n ≥ 3).

				Age Period: 1-End *	**Age Period: 1-10 ****
Species	**Region**	**Growing Season**	**Mean End Age**	**Mean, kg (n)**	**Mean, kg (n)**
Acacia mearnsii	Upper Yala	Unimodal	17.8	1.60 (6)	1.29 (5)
Cupressus lusitanica	Middle Yala	Long Rainy	16.3	1.24 (4)	0.84 (4)
		Short Rainy		0.19 (4)	0.13 (4)
		Combined Rainy		1.43 (4)	0.97 (4)
Eucalyptus camaldulensis	Middle Yala	Long Rainy	12.4	1.40 (19)	1.55 (15)
		Short Rainy		0.44 (19)	0.48 (14)
		Combined Rainy		1.88 (19)	2.03 (14)
Eucalyptus grandis	Middle Yala	Long Rainy	6.5	1.31 (6)	-
		Short Rainy		0.29 (6)	-
		Combined Rainy		1.60 (6)	-
Eucalyptus saligna	Middle Yala	Long Rainy	5.5	1.08 (4)	-
		Short Rainy		0.29 (4)	-
		Combined Rainy		1.37 (4)	-
Mangifera indica	Lower Yala	Unimodal	34.3	1.01 (6)	0.68 (6)
Markhamia lutea	Middle Yala	Unimodal	26.5	0.60 (4)	0.26 (4)

Note: * Age Period: 1-End refers to the time period from age one up to the entire period of averaged growth. ** Age Period: 1-10 refers to the time period from age one up to age 10 of averaged growth.

Table 2.4 Descriptive statistics of mean annual biomass increments summarized by tree species for which there was sufficient sample replication (n ≥ 2). Biomass was determined from a composite allometric equation relating tree biomass as a function of tree diameter.

				Age Period: 1-End *	**Age Period: 1-10 ****
Species	**Region**	**Growing Season**	**Mean End Age**	**Mean, kg (n)**	**Mean, kg (n)**
Acacia mearnsii	Upper Yala	Unimodal	17.8	20.49 (6)	9.56 (5)
Cupressus lusitanica	Middle Yala	Long Rainy	16.3	12.58 (4)	7.18 (4)
		Short Rainy		1.70 (4)	0.56 (4)
		Combined Rainy		14.28 (4)	7.74 (4)
Eucalyptus camaldulensis	Middle Yala	Long Rainy	12.4	22.14 (19)	18.74 (14)
		Short Rainy		6.04 (19)	4.98 (14)
		Combined Rainy		28.18 (19)	23.72 (14)
Eucalyptus grandis	Middle Yala	Long Rainy	6.5	8.98 (6)	-
		Short Rainy		0.99 (6)	-
		Combined Rainy		9.97 (6)	-
Eucalyptus saligna	Middle Yala	Long Rainy	5.5	5.48 (4)	-
		Short Rainy		0.61 (4)	-
		Combined Rainy		6.09 (4)	-
Mangifera indica	Lower Yala	Unimodal	34.3	25.81 (6)	2.46 (6)
Markhamia lutea	Middle Yala	Unimodal	26.5	4.13 (4)	0.68 (4)

Note: * Age Period: 1-End refers to the time period from age one up to the entire period of averaged growth. ** Age Period: 1-10 refers to the time period from age one up to age 10 of averaged growth.

Table 2.5 Descriptive statistics of mean annual carbon increments summarized by tree species for which there was sufficient sample replication (n ≥ 2). Carbon was determined by multiplying the mean annual biomass increment by a carbon fraction of 0.5

				Age Period: 1-End *	**Age Period: 1-10 ****
Species	**Region**	**Growing Season**	**Mean End Age**	**Mean, kg (n)**	**Mean, kg (n)**
Acacia mearnsii	Upper Yala	-	17.8	10.25 (6)	4.78 (5)
Cupressus lusitanica	Middle Yala	Long Rainy	16.3	6.29 (4)	3.59 (4)
		Short Rainy		0.85 (4)	0.28 (4)
		Combined Rainy		7.14 (4)	3.87 (4)
Eucalyptus camaldulensis	Middle Yala	Long Rainy	12.4	11.07 (19)	9.37 (14)
		Short Rainy		3.02 (19)	2.49 (14)
		Combined Rainy		14.09 (19)	11.86 (14)
Eucalyptus grandis	Middle Yala	Long Rainy	6.5	4.49 (6)	-
		Short Rainy		0.495 (6)	-
		Combined Rainy		4.985 (6)	-
Eucalyptus saligna	Middle Yala	Long Rainy	5.5	2.74 (4)	-
		Short Rainy		0.305 (4)	-
		Combined Rainy		3.045 (4)	-
Mangifera indica	Lower Yala	-	34.3	12.91 (6)	1.23 (6)
Markhamia lutea	Middle Yala	-	26.5	2.07 (4)	0.34 (4)

Note: * Age Period: 1-End refers to the time period from age one up to the entire period of averaged growth. ** Age Period: 1-10 refers to the time period from age one up to age 10 of averaged growth.

Table 2.6 Descriptive tree size and dry biomass statistics summarized by tree species. The mean ± 1 standard deviation are reported

Species	**Height (m)**	**Crown Diameter (m)**	**Trunk Biomass (kg)**	**Branch Biomass (kg)**	**Leaf Biomass (kg)**	**Total AGB (kg)**	**Total BGB (kg)**	**Root:Shoot Ratio**
Acacia mearnsii	12.3 ± 5.3	6.4 ± 2	253.9 ± 226.2	118.9 ± 128.2	32.6 ± 15.4	405.5 ± 358.4	101.2 ± 82.9	0.17 ± 0.02
Bridelia micrantha	8.5 ± 0.5	5.4 ± 3.2	57.9 ± 47.9	75.9 ± 93.2	9.2 ± 7.8	143 ± 148.8	39.7 ± 17.5	0.47 ± 0.36
Combretum molle	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Croton macrostachyus	N/A	4.3 ± 0.6	13.5 ± 8.1	6.7 ± 4.3	2.5 ± 1.7	22.7 ± 14.1	5.7 ± 2.8	0.26 ± 0.04
Cupressus lusitanica	13.1 ± 3	6.4 ± 0.1	107.8 ± 34.6	36.9 ± 4.6	43.2 ± 15.9	187.9 ± 38.6	34 ± 18.8	0.18 ± 0.08
Eucalyptus camaldulensis	21.2 ± 8.3	5.7 ± 2.9	362.9 ± 371.7	84.6 ± 98.2	23.5 ± 20.2	471 ± 475.6	125.3±127.4	0.26 ± 0.14
Eucalyptus grandis	13.1 ± 4.9	3.4 ± 1.1	37.7 ± 42.8	9.1 ± 9.8	6.3 ± 6.7	53.2 ± 58.8	8.5 ± 7.7	0.19 ± 0.05
Eucalyptus saligna	14.6 ± 7.9	3.9 ± 2	122.8 ± 153.2	32.5 ± 38.6	14 ± 17.5	169.3 ± 208.5	47 ± 63.2	0.22 ± 0.06
*Grevillea robusta**	15.4	8.7	332.5	279.6	52	664.1	220.3	0.33
Mangifera indica	8.7 ± 3.4	8.6 ± 3.6	357.4 ± 399	733.7 ± 800.2	123.9 ± 114.1	1214.9 ± 1311	315 ± 313	0.3 ± 0.05
Markhamia lutea	9.4 ± 3	3.9 ± 1.3	53.6 ± 64.3	30.9 ± 36	3.7 ± 1.4	88.2 ± 100.8	35.8 ± 24.4	0.59 ± 0.37
*Persea americana**	9.6	5.4	66.3	36.1	13.2	115.6	32.1	0.28
Syzygium cuminii	13 ± 1.3	7.2 ± 0.5	317.5 ± 150.1	188 ± 30.2	53.2 ± 19.1	558.7 ± 199.3	251.3±194.2	0.42 ± 0.2
Trilepisium madagascariensis	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

AGB: above ground biomass; BGB: below ground biomass
N/A: Data not available
*: only one sample of this species was available

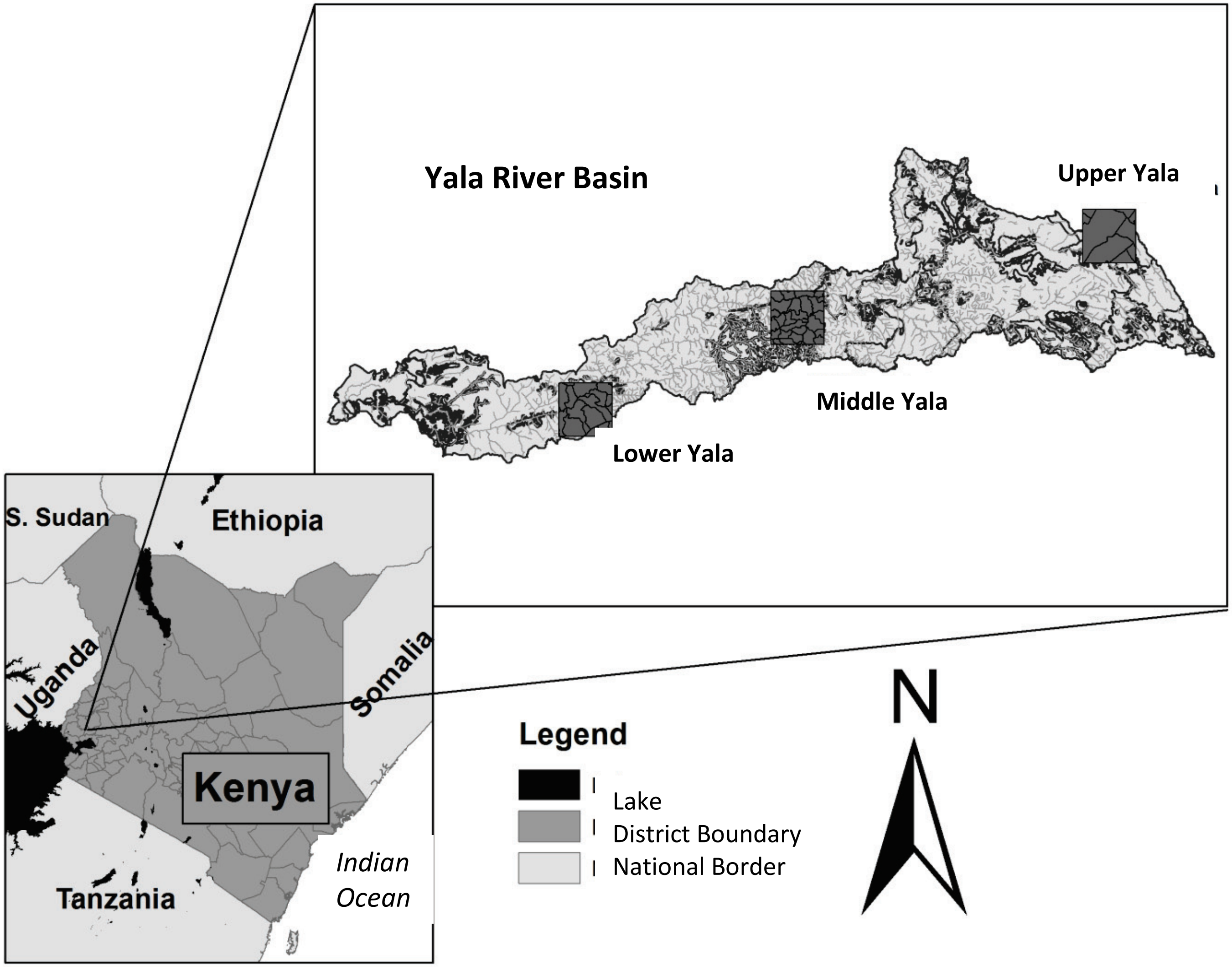


Figure 2.1 Locations of sample blocks in River Yala Basin of Western Kenya. The three blocks included lower Yala, middle Yala, and upper Yala

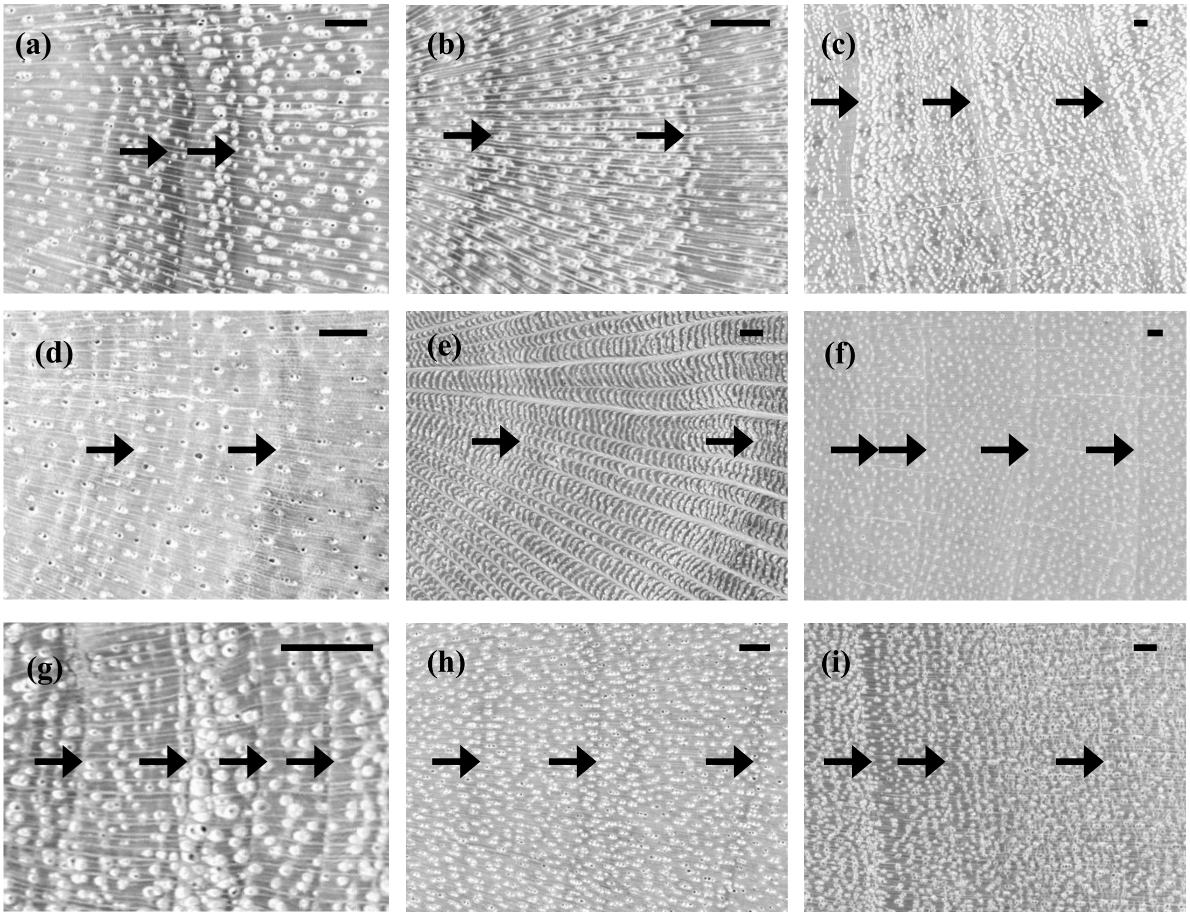


Figure 2.2 Images of the transverse surface of wood samples of 10 savanna tree species showing annual tree rings produced under a bimodal precipitation regime: *Acacia mearnsii* (a), *Bridelia micrantha* (b), *Combretum molle* (c), *Croton macrostachyus* (d), *Grevillea robusta* (e), *Mangifera indica* (f), *Markhamia lutea* (g), *Persea americana* (h), *Syzygium cuminii* (i) and *Trilepisium madagascariensis* (j) and four savanna tree species showing bi-annual tree rings produced under a bimodal precipitation regime: *Cupressus lusitannica* (k)*, Eucalyptus camaldulensis* (l)*, Eucalyptus grandis* (m)*, and Eucalyptus saligna* (n). The boundaries for one year of growth in the unimodal species and for a partial year's growth in the bimodal species are indicated by the tip of the black arrows. The direction of the arrows indicates the direction of growth from the start to the end of a growing season. The scale bar in the top-right corner of each sub-figure is equivalent to a length of 1 mm.

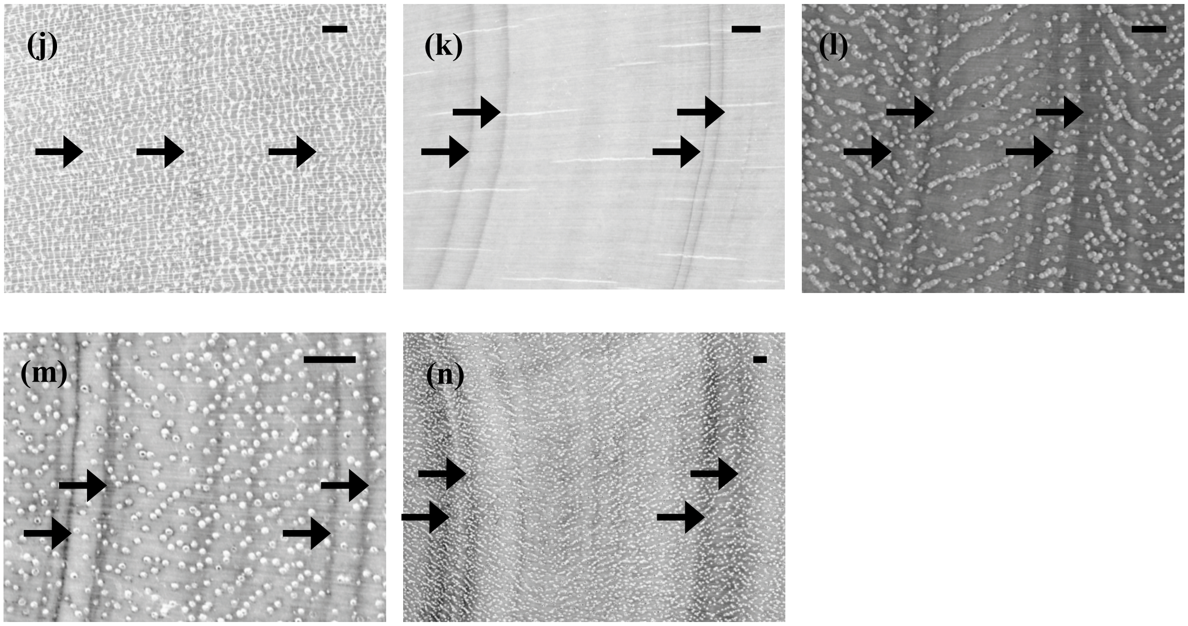


Figure 2.2 (cont’d)

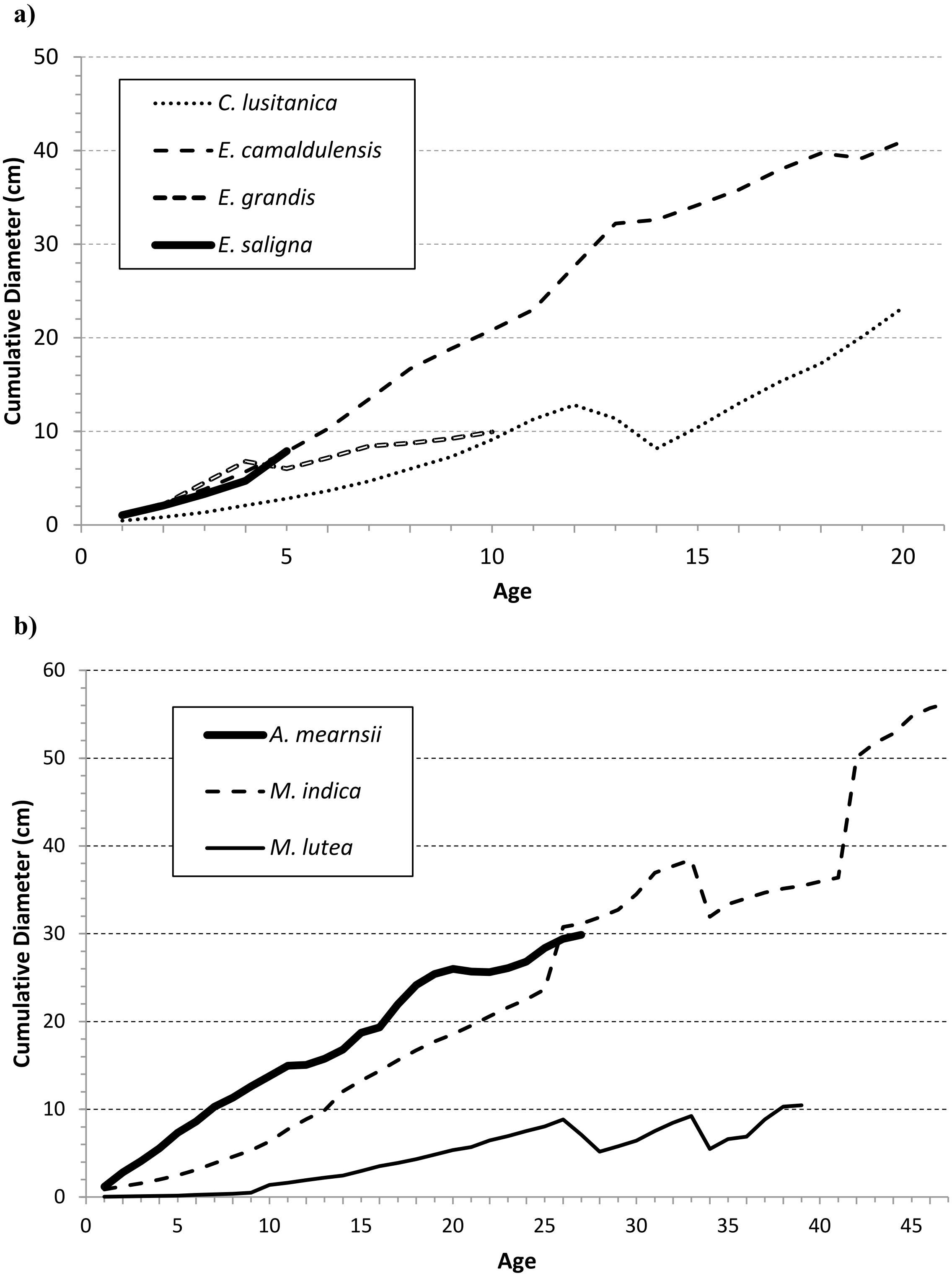


Figure 2.3 Cumulative patterns in diameter outside bark summarized by common plantation tree species (a) and non-plantation species (b).

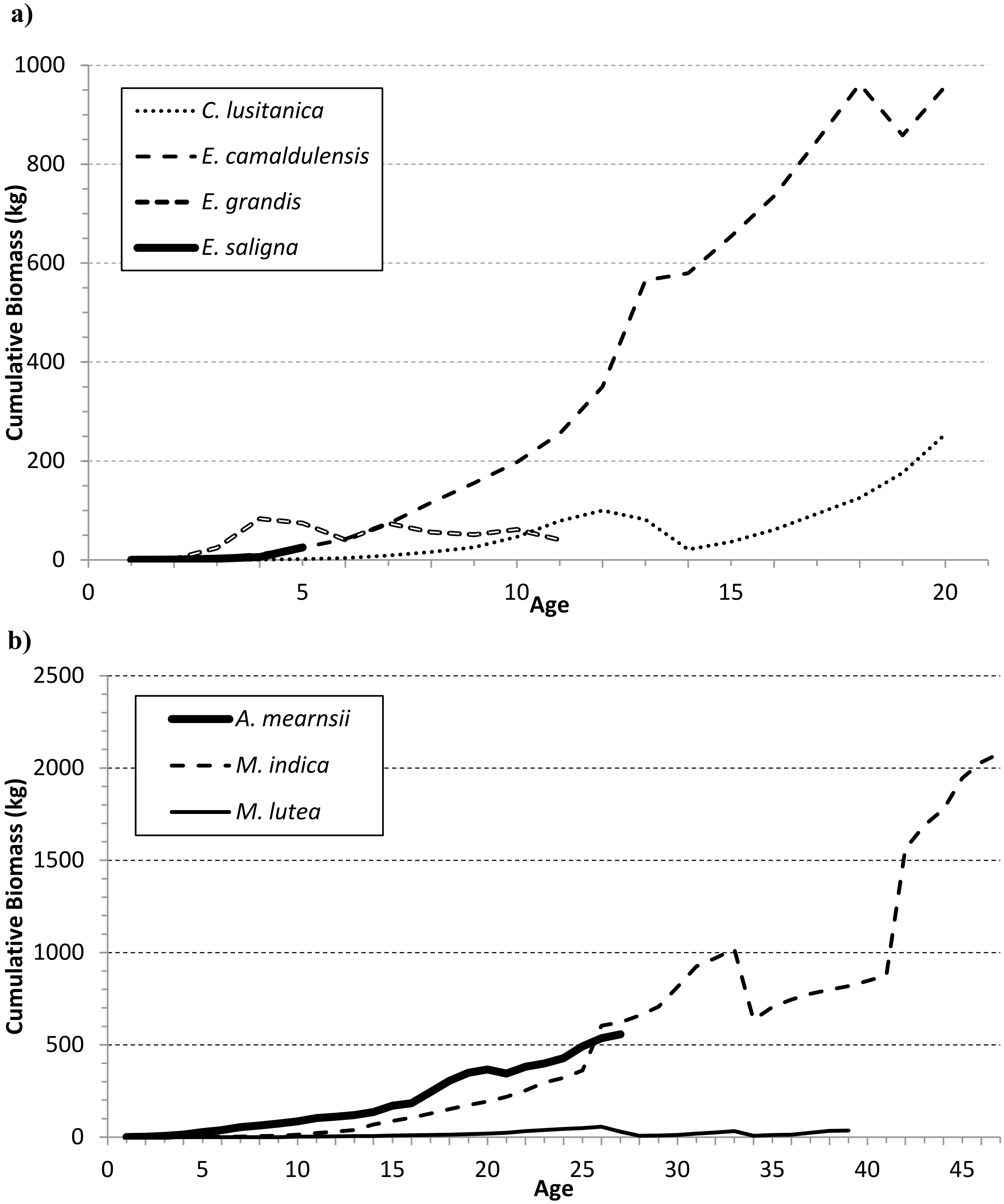


Figure 2.4 Cumulative patterns in biomass summarized by common plantation species (a) and non-plantation species (b).

REFERENCES

REFERENCES

Akyeampong, E., Hitimana, L., Franzel, S., Munyemana, P.C., 1995. The agronomic and economic performance of banana, bean and tree intercropping in the highlands of Burundi: an interim assessment. Agroforestry Systems 31, 199-210.

Bie, S.D., Ketner, P., Paasse, M., Geerling, C., 1998. Woody plant phenology in the West Africa savanna. Journal of Biogeography 25, 883-900.

Bush, R.R., and Brand, G. 2008. Lake States (LS) variant overview: Forest Vegetation Simulator. USDA For. Serv., Forest Management Service Center, Fort Collins, CO.

Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson (eds) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

CIFOR, 2009. Simply REDD: CIFOR's guide to forests, climate change and REDD. Center for I nternational Forestry Research, www.cifor.cgiar.org.

Couralet, C., Sass-Klaasen, U., Sterck, F., Bekele, T., Zuidema, P.A., 2005. Combining dendrochronology and matrix modeling in demographic studies: An evaluation for *Juniperus procera* in Ethiopia. Forest Ecology and Management 216, 317-330.

Couralet, C., Sterck, F.J., Sass-Klaassen, U., Van Acker, J., Beeckman, H., 2010. Species-Specific Growth Responses to Climate Variations in Understory Trees of a Central African Rain Forest. Biotropica 42, 503-511.

Cros, D.T.E., Ducrey, M., Barthelemy, D., Pichot, C., Giannini, R., Raddi, P., Roques, A., Salesluis, A., Thibaut, B., 1999. Cypress: A Practical Handbook. Studio Leonardo, Florence, Italy, 139 pp.

de Oliveira, B.R.U., Latorraca, J.V.D., Tomazello, M., Garcia, R.A., de Carvalho, A.M., 2011. Dendroclimatology correlations OF Eucalyptus grandis Hill ex Maiden of Rio Claro, RJ state - Brazil. Ciencia Florestal 21, 499-508.

Delgado-Matas, C., Pukkala, T., 2011. Comparison of the growth of six *Eucalyptus* species in Angola. Int. J. For. Res. Volume 2011, ID#980259.

Dietz, J., Kuyah, S., 2011. Guidlenines for establishing regional allometric equations for biomass estimation through destructive sampling, World Agroforestry Centre, Nairobi.

Forrester, D.I., Bauhus, J., Khanna, P.K., 2004. Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For. Eco. and Man. 193, 81-95.

Gebrekirstos, A., Mitlohner, R., 2008. Climate-growth relationships of the dominant tree species from semi-arid savanna woodlands in Ethiopia. Trees 22, 631-641.

Hudson, D.A. and R.G. Jones, 2002. Regional climate model simulations of present day and future climates of Southern Africa. Technical Note 39, Hadley Centre, Bracknell, 42 pp.

IPCC, 2007. Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F.

IPCC (Editor), 2008. Bilan 2007 des changements climatiques. Contribution des Groupes de travail I, II et III au Quatrieme Rapport d'Evaluation du Groupe d'Experts Intergouvernmental sur l'evolution du climat. Intergouvernmental Panel on Climate Change, 103 p.

Jaetzold, R., Schmidt, H., 1982. Farm management handbook of Kenya. Volume 2: Natural conditions and farm management information. Ministry of Agriculture, Kenya. 137-370.

Jenkins, G.S., G. Adamou and S. Fongang, 2002. The challenges of modelling climate variability and change in West Africa. *Climatic Change*, **52**, 263-286.

Kozlowski, T. T., Karmer, P. J., Pallardy, S. G., 1991. The Physiological Ecology of Woody Plants. Academic Press, ISBN: 0124241603.

Luoga, E.J., Chamshama, S.A.O., Iddi, S., 1994. Survival, growth, yield, and wood quality of a species and provenance trial of *Cupressus lusitanica*, *Cupressus lindleyi* and *Cupressus benthamii* at Hambalawei, Lushoto, Tanzania. Silvae Genetica 43, 190-195.

Maingi, J. K., 2006. Growth rings in tree species from the Tana River floodplain. J. East African Natural History. 95, 181-211.

Martin, D.M., Moss, J.M.S., 1997. Age determination of Acacia tortilis (Forsk.) Hayne from northern Kenya. African Journal of Ecology 35, 266-277.

Maundu, P., Tengnäs, B., 2005. Useful Trees and Shrubs for Kenya, World Agroforestry Centre, Nairobi.

Mbow, C., Chhin, S., Sambou, B., Skole, D. Potential of dendrochronology to assess annual rates of biomass productivity in savanna trees of West Africa. Manuscript submitted for publication.

Mekonnen, K., Yohannes, T., Glatzel, G., Amha, Y., 2006. Performance of eight tree species in the highland Vertisols of central Ethiopia: growth, foliage nutrient concentration, and effect on soil chemical properties. New Forests 32, 285-298.

Miller, J.T., Knowles, F.B., 1990. Introduced forest trees in New Zealand: recognition, role, and seed source. The Cypresses, Cupressus spp., Chamaecyparis spp. Forest Research Institute Bulletin No. 124, 33 pp.

Nath, C.D., Pelissier, R., Ramesh, B.R., Garcia, C., 2011. Promoting native trees in shade coffee plantations of southern India: comparison of growth rates with the exotic Grevillea robusta. Agroforestry Systems 83, 107-119.

Nicholas, I., 2007. Best Practice with Farm Forestry Timber Species, No. 1: Cypresses—NZFFA Electronic Handbook Series No. 1. www.nzffa.org,nz.

Plant Resources of Tropical Africa, Wageningen University. http://www.prota.co.ke/en/home. Accessed July 12, 2012.

Rozendaal, D.M.A., Zuidema, P.A., 2010. Dendroecology in the tropics: a review. Trees 25, 3-16.

Schongart, J., Orthmann, B., Hennenberg, K.J., Porembski, S., Worbes, M., 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Global Change Biology 12, 1139-1150.

Shorrocks, Bryan, 2007. The Biology of African Savannahs, New York.

Silvertown, J., Charlesworth, D., 2001. Introduction to plant population biology. 4th Edition. Blackwell Science, Oxford, UK.

Stahle D.W., 1999. Useful strategies for the development of tropical tree-ring chronologies. IAWA Journal 20, 249-253.

Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. Forest Ecology and Management 124, 217-229.

Swart, R., J. Mitchell, T. Morita and S. Raper, 2002. Stabilization scenarios for climate impacts assessment. *Global Environ. Chang.*,**12**, 155-165.

Tarhule, A., Hughes, M., 2002. Tree-ring research in semi-arid West Africa: need and potential. Tree-ring Research 58, 31-46.

Therrell, M.D., Stahle, D.W., Mukelabai, M.M., Shugart, H.H., 2007. Age and Radial growth dynamics of *Pterocarpus angolensis* in southern Africa. Forest Ecology and Management 244, 24-31.

Trouet, V., Esper, J., Beeckman, H., 2010. Climate/growth relationships of Brachystegia spiciformis from the miombo woodland in south central Africa. Dendrochronologia 28, 161-171.

Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2004. Growth rings, growth ring formation and age determination in the mangrove Rhizophora mucronata. Annals of Botany 94, 59-66.

Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytologist 167, 425-435.

Watt, M., Palmer, D., Dungey, H., Kimberly, M., 2009. Predicting the spatial distribution of *Cupressus lusitanica* productivity in New Zealand. Forest Ecology and Management 258, 217-223.

Worbes, M., 1995. How to meaure growth dynamics in tropical trees. A review. IAWA Journal 16, 337-351.

Worbes, M., Junk, W.J., 1999. How old are tropical trees? The persistence of a myth. IAWA Journal20, 255-260.

Worbes, M, 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. Dendrochronologia. 20: 217-231

Zomer, R.J., Trabucco, A., Coe, R., Place, F., 2009. Trees on farm: Analysis of global extent and geographical patterns of agroforestry, World Agroforestry Centre Working Paper no. 89. World Agroforestry Centre, Nairobi.

CHAPTER 3

GROWTH-CLIMATE RELATIONSHIPS OF TROPICAL TREE SPECIES IN WESTERN KENYA

3.1 Introduction

Growth rings in tropical trees have long been thought not to exist. However, research throughout the past several decades has revealed that in fact tropical trees can produce distinct ring boundaries, due to a number of possible environmental stressors (Rozendaal and Zuidema, 2010). Two of the key catalysts for ring boundary formation have been described as distinct dry seasons (Worbes and Junk, 1999), and seasonal flooding in floodplain regions (Schongart et al., 2002). Seasonality due to flooding and/or drought have been shown to produce either a single growth ring per year, non-annual rings in the case of complex rainfall distributions (Dunisch et al., 2003; Wils et al. 2009), two rings per year in regions exhibiting a bimodal rainfall distribution (Jacoby, 1989; Wayant and Reid, 1992; Gourlay, 1995) or fewer than one ring per year when extreme moisture conditions are present (Eshete and Stahl, 1999). With the knowledge that many tropical tree species produce growth ring boundaries, once the periodic nature of the rings for a tree is determined, tree-ring analysis can be used to provide understanding of climate-growth relationships of the tree (Rozendaal and Zuidema, 2010).

It is essential that we better understand the relationships that occur between trees growing in tropical zones and climatic variables for numerous reasons. The development of long-term diameter increments of tropical species and their response to climate will greatly aid in the development of sustainable silvicultural systems in developing countries (Worbes and Junk, 1999). In addition, climate-growth relationships can be used as a proxy to reconstruct historical climate (Gebrekirstos et al., 2008; Rozendaal and Zuidema, 2010) and even project future growth response to climate. Furthermore, better understanding of how tropical tree growth is affected by climate can help us estimate future annual carbon sequestration rates in these forests. With the growing interest in the global carbon cycle, these estimates become very valuable (Rozendaal and Zuidema, 2010). To be able to determine the annual carbon increment for tropical trees allows countries interested in implementing a carbon benefits project to begin earning tradable income immediately (Mbow et al., 2011). Several studies in Africa have looked at the direct relationships between tree growth increments and climate variables in an attempt to better understand the ecology of the various species studied, determine ring periodicity, and reconstruct historical climate conditions (Stahle et al., 1999; Eshete and Stahle, 1999; Worbes et al., 2003; Fichtler et al., 2004; Schongart et al., 2006; Therell et al., 2006). Many of the mentioned studies have shown that significant correlations exist between tree growth and climate parameters. However, very few such studies have been conducted in Kenya and thus, little is known about how the savannah and agroforestry systems in the western part of the country are responding and will respond to changes in climatic conditions.

Hence, this study aims to explore the climate-growth relationships of several commonly found tree species growing in the Yala River Basin of Western Kenya, namely: *Acacia mearnsii, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Mangifera indica*, and *Markhamia lutea*. The objectives of this study are to evaluate the climate-growth relationships of these species in terms of the growth response to a) precipitation, b) temperature, and c) climate moisture index. These insights should provide a better understanding of the key climatic drivers of growth dynamics of these trees.

3.2 Material and methods

3.2.1 Study area

This study was conducted at three 100 km^2 blocks of land located in the Yala River Basin of Western Kenya. These three designated areas were labeled as the Lower, Middle and Upper Yala regions with the Lower Yala region starting near Lake Victoria. The Yala River catchment, covering an area of 3351 km^2, drains into the Winam Gulf in Lake Victoria (Figure 3.1). The elevation, beginning in the Lower Yala region, ranges from 1,200 m above sea level to 2,200 m above sea level in the Upper Yala region. The average annual rainfall for the entire Yala Basin is 1487 mm and follows a bimodal distribution. Although the rainfall patterns of the region are highly variable, the approximate time period of the long rainy season is from March-May and the short rainy season is from October-November (Maingi, 2006).The climate patterns of the three study blocks differ slightly from one another (Figure 3.2a, b, c). The Lower Yala block experiences the greatest amount of precipitation, while the Upper Yala block experiences the least amount of precipitation (Figure 3.2a, c). The Lower Yala region also experiences the most well defined bimodal rainfall distribution pattern, with decreasing clarity in the middle and upper blocks. Temperature remains fairly constant throughout the year, but the coolest months of the year are from June to August and the warmer months from September to May. Average annual temperature is highest in the lower region and lowest in the upper region. Climate moisture index (CMI) closely relates to precipitation in that the most water availability occurs during the rainiest months. There are several major soil types present along the Yala Basin, including: acrisols, ferralsols and nitrosols (Jaetzold and Schmidt, 1982). These soil types exhibit the characteristics of good physical structure, well drained, deep to very deep and variable fertility.

The variety of soil and climatic conditions along the altitudinal gradient of the basin in conjuncture with a highly heterogeneous landscape which includes a mosaic of farmland, differing degrees of forest cover and open area, has led to a contrast in the dominant tree species found in each region. These species are *Markhamia lutea*, *Eucalyptus* spp. and *Acacia mearnsii* in the lower, middle and upper Yala regions respectively (Dietz and Kuyah, 2011).

3.2.2 Field Sampling

Three blocks of 10x10 km size were established along the altitudinal gradient of the Yala Basin in Western Kenya. Each block was randomly assigned 160 sample points, which were then randomly sub-sampled from (15% of the points in lower block, 30% of the points in the middle block, and 15% of the points in the upper block). On the plots selected, a 30x30 m sampling plot was randomly chosen and all trees within that plot were sampled. All trees in the plot with a diameter at breast height (dbh) (greater than 2.5 cm were destructively sampled. Of the trees chosen for destructive sampling, a stem disc was taken at breast height (1.3 m). If the disc was between 30 and 60 cm, only a half stem disc, which included the pith was kept. If the disc was > 60 cm, only a quarter stem disc, which included the pith was kept. These discs were later used for dendrochronological analysis.

In total, 20 species were collected, in which 90 trees were sampled. However, 18 of the trees were not used in the development of the allometric equation. For the development of the allometric equation, 18 trees were sampled in the lower block, 36 were sampled in the middle block and 18 were sampled in the upper block. The trees were randomly selected within 6 pre-determined dbh classes. Thus, 12 trees of each class were harvested. The dbh classes were as follows: 2.5 – 10; 10.1 – 20; 20.1 – 30; 30.1 – 40; 40.1 – 60 and > 60 cm. 66 of the 72 trees sampled were used for the development of the allometric biomass equation (Dietz and Kuyah, 2011). Six of the remaining trees (one chosen randomly from each diameter class) were used as a validation set for the equation. A subset of the 90 total trees destructively sampled was used for the dendrochronological analysis to assess growth-climate relationships. This subset consisted of 50 trees spanning 7 species (*Acacia mearnsii, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Mangifera indica,* and *Markhamia lutea*). The basis for species selection of the subset was sufficient sample size. Only species with a sample size greater than or equal to three were included.

3.2.4 Sample Processing

Wood samples were first sanded with progressively finer grits of sandpaper (up to 1200 grit), which is standard practice among dendrochronology studies in the tropics. Each sample was visually cross-dated along 4 radii, either macroscopically or microscopically under a binocular microscope, to identify missing and/or false rings. Each ring boundary was verified circumferentially between the other three radii of the disc. Following verification of cross-dating, annual or sub-annual ring widths were measured using a stage micrometer coupled with a binocular microscope to the nearest 0.001 mm (Velmex: Bloomfield, New York). Disc samples were measured along 4 radii (or as many as were successfully crossdated).

3.2.5 Dendrochronological measurements

For cross-sectional discs in which fewer than 4 radii were successfully cross-dated, a data correction procedure was applied to the ring width measurements in order to prevent over- or under-estimation of tree diameter estimates derived from ring width measurements (Gebrekirstos et al., 2008):

Correction Factor = $D_{IB,R} / D_{IB,A}$ (Eq. 3.1)

Where $D_{IB,A}$ is the actual diameter inside bark of the cross-sectional disk determined with a measurement tape and $D_{IB,R}$ is the maximum diameter inside bark determined from the cumulative ring width measurements. The ring width measurements were all divided by this correction factor. In the case where 4 radii were successfully cross-dated for a disc, this correction factor was not applied. It was assumed that when the measurements of the 4 radii were averaged, error in diameter estimation would be corrected for. At the end of each growth period, the corrected (or non-corrected) ring width measurements for each radius were converted to cumulative measures of diameter inside bark (D_{IB}).

Bark thickness measurements were calculated by subtracting the measured diameter inside bark from the measured diameter outside bark. The bark ratio (BR) could then be determined using the bark thickness and the following equation (Bush and Brand, 2008):

$$BR = D_{IB} / D_{OB} \qquad \text{(Eq. 3.2)}$$

Where D_{IB} is the diameter inside bark and D_{OB} is the diameter outside bark. Cumulative DOB values were used to calculate cumulative basal area. Annual basal area increment (cm^2 $year^{-1}$) was calculated by subtracting cumulative growth in the previous year (t-1) from the current year (t). Essentially, the formula for the area of a circle was used to calculate the current (t) and previous (t-1) years' area growth and the difference between these two areas is a representation of annual basal area increment. However, even when considering basal area, age related trends exist and standardization was used to eliminate those trends.

3.2.6 Chronology development

Each basal area increment series were detrended using a locally weighted regression with a neighborhood span equivalent to 10 years using the function *loess* (package STATS) in the program R (the open source version of program S) (Venables and Ripley, 2002; Chhin et al., 2008). Following detrending, indices were standardized by dividing the observed values by the predicted values. Standardization works to amplify the climatic signal (high frequency or interannual variation) and remove the effect of non-climatic factors (low frequency or long-term variation) (Fritts, 1976; Chhin et al. 2004). This standardization process generally promotes a stronger correlation between growth and yearly climate fluctuations. Standardization is justifiable because as a tree ages, the amount of cross-sectional area that the tree adds each year increases. Therefore, standardization works to eliminate this trend and amplify the climatic signal. Annual standardized stem basal area indices calculated for radii of the same disc were averaged together. The basal area index (BAI) of each species can be found in Figure 3.3. A BAI greater than one signifies above average growth for that year. A BAI below one signifies below average growth for that year.

3.2.7 Growth-climate Relationships

Climate data was obtained from the Kenya Meteorological Department in Nairobi, Kenya (Kenya Meteorological Department, http://www.meteo.go.ke/). The types of data included minimum and maximum monthly temperature and total monthly precipitation . The primary climate stations from which data was used were the Kisumu Meterological Station (ID#9034025; 0^{O}6’ S, 34^{O}45’ E) and Yala Tree Nursery (ID#8934189; 0^{O}8’ N, 34^{O}32’ E) for the Lower Yala, the Kakamega Meteorological Station (ID#8934096; 0^{O}16’ N, 34^{O}45’ E) and Kaimosi Farmer’s Training Center (ID#8934078; 0^{O}13’ N, 34^{O}57’ E) for the Middle Yala, and the Kakamega

Meteorological Station (ID#8934096; $0^{o}16'$ N, $34^{o}45'$ E) and Eldoret Meteorological Station (ID#8935181; $0^{o}32'$ N, $35^{o}17'$ E) for the Upper Yala (Kenya Meteorological Department, http://www.meteo.go.ke/). Three separate climate data sets were compiled for growth-climate analysis of each Yala block. Precipitation data for the lower block spanned from 1962-2003 and the temperature data spanned from 1967-2009. Precipitation and temperature data for the middle block both spanned from 1979-2009. Precipitation data for the upper block spanned from 1972-2009 and temperate data spanned from 1979-2009. Missing values in the data were estimated from neighboring stations. Climate moisture indices (CMI's) were calculated by subtracting monthly values of potential evapotranspiration (PET) from monthly precipitation (P) values. PET values were determined as a function of minimum and maximum temperature (Hogg, 1997). The following equations were used to calculate PET:

$$\text{When } T_{mean} > 10° \text{ C:} \quad PET = 93 * D * \text{Exp}(A / 9300) \qquad (3.3a)$$

$$\text{When } 10° \text{ C} > T_{mean} > -5° \text{ C:} \quad PET = (6.2 * T_{mean} + 31) D * \text{Exp}(A / 9300) \qquad (3.3b)$$

$$\text{When } T_{mean} < -5° \text{ C:} \quad PET = 0 \qquad (3.3c)$$

Where
T_{mean} = mean temperature (° C)
PET = potential evapotranspiration (mm)
D = vapor pressure deficit (kPa)
Exp = exponential function
A = altitude of climate station (m)

The vapor pressure deficit (D) was calculated as (Hogg, 1997):

$$D = 0.5\,(eT_{max} - eT_{min}) - eT_{dew} \qquad (2.5)$$

Where
D = vapor pressure deficit (kPa)
eT_{max} = saturation vapor pressure at maximum temperature
eT_{min} = saturation vapor pressure at minimum temperature
eT_{dew} = saturation vapor pressure at mean dewpoint temperature

CMI data spanned the period of time in which the temperature and precipitation data for each block overlapped.

Growth-climate relationships were examined between basal area indices (BAI's) of each species and climate variable (i.e. total monthly precipitation, average monthly temperature, and climate moisture index) from January of the previous year (t-1) to December of the current year (t). For species in which the BAI chronology was great than or equal to 15 years, dendroclimatic analysis was conducted using Pearson correlation analysis. For species in which the BAI chronology was shorter than 15 years, dendroclimatic analysis was run using Spearman rank correlation analysis. With such a short chronology length, it is unjustified to use a standard Pearson correlation analysis. All correlation analysis was done using the program SYSTAT (Chicago, Illinois, 2002) for the time periods listed above, depending on which block the samples were taken from. In addition, correlation analysis was conducted between BAI's and seasonalized climate data. Seasonal precipitation and CMI data were calculated as the summation of 3 month periods, beginning with January, February, and March of the previous year (t-1) and ending with October, November, and December of the current year (t). Seasonal temperature data was calculated as the average of 3-month periods beginning with January, February, and March of the previous year (t-1) and ending with October, November, and December of the current year (t). The last two months of each previous 3-month period overlap the first two months of the current 3-month period.

3.3 Results

3.3.1 Growth chronology

Several notable years stand out as periods of suppressed growth for all of the plantation species (Figure 3.3a). These years include 2002, 2005, and 2006. During these years, all basal area index chronologies are below one. In contrast, all plantation species showed a good year of growth in 2009. Of the non-plantation species, the chronologies matched up fairly well, with one of the species deviating from the other two at times (Figure 3.3b). 1993 was a below average growth year for *A. mearnsii* and *M. lutea*, but an above average year for *M. indica*. This pattern repeats itself many times throughout the chronology, but with the deviating species changing. Common years of suppressed growth include 2000 and 2002.

3.3.2 Response to precipitation

Many of the species showed a significant correlation to monthly precipitation with the exception of *A. mearnsii* and *M. lutea* (Figure 3.4a). *M. indica* was positively correlated with precipitation during January and November of the previous year (t-1). The *full* ring width chronology of *C. lusitannica* showed both negative and positive correlations with respect to precipitation, with the negative correlations coming in the dry period of the previous year and current years of growth and the positive correlations coming during the long rainy season of the previous year. The only *Eucalyptus* species to not display a significant correlation for the *full* ring width chronology was *E. camaldulensis*. A majority of the positive correlations were associated with the rainy seasons, while the negative correlations were more frequently associated with the dry seasons.

When considering seasonal precipitation, all species showed significant correlation, except for *M. indica*, *M. lutea, and E. camaldulensis* (Figure 3.4b). A majority of the correlations were positive correlations and coincided with rainy seasons. However, *E. grandis* and *E. saligna* both showed some negative correlations associated with the long rainy season of the current year.

3.3.3 Response to Temperature

The only species to show no significant correlation to monthly temperature data for the full ring width were *A. mearnsii* and *C. lusitanica* (Figure 3.5a). Both negative and positive correlations with monthly temperature existed among the other species. However, there appears to be no clear pattern relating negative or positive relationships to warmer or cooler months of the year. April of the previous year positively correlated with growth of *M. lutea*, yet correlated negatively with *E. saligna* of the same month. One interesting observation is that a majority of the negative temperature correlations for *E. saligna* and *E. grandis* were found in the previous year, while the positive correlations were found in the current year. The only significant correlations associated with *M. indica* and *E. camaldulensis* were negative correlations during dry periods of the current year.

Seasonal temperature showed more consistent correlations among species. *A. mearnsii* and *E. camaldulensis* were the only species to not show any significant correlations with seasonal temperature data (Figure 3.5b). *E. grandis* displayed negative correlations with seasonal temperature during the early hot months (JFM, FMA) of the previous year, as well as the cooler months (MJJ) late in the long rainy season. *M. lutea* and *M. indica* both showed significant correlations during the hotter months toward the end of the previous year and the start of the current year. However, *M. indica* showed negative correlations, while *M. lutea* showed positive correlations.

3.3.4 Response to climate moisture index

Monthly correlations to climate moisture index (CMI) were very reflective of precipitation correlations (Figure 3.6a). However, *A. mearnsii* was negatively correlated with CMI in February of the current year, while *M. lutea* and *E. camaldulensis* were the only two species without any significant correlations to CMI. June of the current year presented no significant correlations between precipitation and growth for *M. indica* and *E. grandis,* but it did present a significant correlation between CMI and growth. Most of the correlations present for CMI that were not present for precipitation were negative for *E. grandis*.

Again for seasonal CMI, correlations were similar to that of seasonal precipitation (Figure 3.6b). The most notable differences were in *A. mearnsii*. It showed negative correlations for a large part of the long rainy season of the previous year, where for precipitation no correlations were present. In addition, a positive correlation present during the dry season of the current year, no longer existed. Several other negative correlations became apparent during the short rainy season of the current year in *E. saligna*.

3.3.5 Bimodal response to climate variables

Every bimodal species showed at least one significant correlation between either the long or short rainy season ring growth and one of the climatic variables. The only two species to show significant correlations between the short and long ring growths and the *full* ring growth were *C. lusitanica* and *E. grandis*. C. lusitanica displayed this pattern for the precipitation and climate moisture index correlations (Figure 3.4a, b; Figure 3.6a, b) and *E. grandis* displayed this pattern for the temperature correlations (Figure 3.5a, b). The remaining species showed no clear pattern between correlations of the long and short rainy season growth and the *full* ring growth with climate variables.

3.4 Discussion

3.4.1 Bimodal responses to climate variables

The ring boundaries between the long and short rainy seasons of the bimodal species were at times unreliable, especially when describing the *Eucalyptus* species, and thus the correlations should be viewed with caution. Consequently, the focus of subsequent response sections will be on the *full* ring width correlations. Few dendroclimatic studies have been conducted in regions with a bimodal rainfall distribution. Gourlay (1995) describes a bimodal ring structure for some of the *Acacia* species that he studied, yet the boundaries were also inconsistent and short and long rainy season growth rings were not compared to climate data. Okullo et al. (2004) and Broadhead et al. (2003), describe some of the phenological characteristics of their respective study species in regions that exhibit bimodal rainfall distributions. Okullo et al. (2004) found that despite a bimodal rainfall pattern, leafing, fruiting, and flowering of *Vitellaria paradoxa* in Uganda was unimodal. Broadhead et al. (2003) found that native Kenya species (*Melia volkensii*) shed its leaves twice a year, while the exotic species (*Senna spectabilis* and *Gliricidia sepium*) shed their leaves only once a year during the long dry season. This would suggest that exotic species are less likely to exhibit a bimodal ring structure, yet in the case of this study, only exotic species showed a bimodal ring structure.

Positive correlations between precipitation and growth for the long and short rainy season rings are closely linked with the *full* ring width correlations of *C. lusitanica* during the previous growing season. This would suggest that rainfall during the long rainy season of the previous year is important for growth during both the long and short rainy seasons of the current year. Strong rains the previous year would provide a higher water table for the following year and greater water availability for the current year (Kozlowski et al., 1991). The only other species to show a similar strength in correlation patterns is *E. grandis*, when comparing growth to temperature. Interestingly, all of the negative correlations fall within the previous year, while the positive correlations fall within the current year (Figure 3.5a, b). The negative correlations can simply be explained by increased water stress as temperature rises, leading to a net loss in assimilated carbon (Fitter and Hay, 1981; Kozlowski et al., 1991). As *E. grandis* is an introduced species, outside of its native range, the positive correlations can be explained by the species growing outside of its optimum temperature range with growth decreasing as temperature falls below the optimum range (Kozlowski et al., 1991). The remaining *long* and *short* rainy season growth ring correlations for *E. camaldulensis* and *E. saligna* were primarily unrelated to the *full* ring width correlations with no clear pattern.

3.4.2 Species response to precipitation

Several species (*C. lusitanica, E. grandis, M. indica*) showed positive correlations with monthly precipitation during periods of the rainy seasons. Interestingly, all of these correlations were found in the previous year. Precipitation of the previous year has a significant impact on foliage formation and carbohydrate reserve storage of a tree (Kozlowski et al., 1991). Thus, the lack of sufficient precipitation during the previous growing season can have negative impacts on growth of the current year. Several other studies, conducted in Brazil, obtained similar results, in which annual wood increment growth of *E. grandis* plantation trees correlated positively with precipitation (Sette, et al., 2010; de Oliveira et al., 2011). It is commonly understood that moisture availability greatly impacts radial growth tropical species in many regions (Rozendaal and Zuidema, 2010). *A. mearnsii* displayed a strong positive correlation with seasonal precipitation during the dry season of the current year. This could suggest drought sensitivity within the species (Gebrekirstos et al., 2008). Significant drought could have major negative impacts on growth of this species.

Negative correlations, existing during the dry months for *C. lusitanica* and *E. grandis* could signify an excess of cloud cover (Buckley at al., 2007; Soliz-Gamboa et al. 2010; Rozendaal and Zuidema, 2010) or flooded soils leading to anaerobic conditions (Kozlowski et al., 1991). In addition, excess cloud cover tends to insinuate possible large storm events, which create high wind and lightning conditions, causing damage to tree crowns and stem breakage (Munishi and Chamshama, 1994). Tree crown repair takes priority in carbon allocation over radial growth; therefore, large storm events can have negative impacts on radial growth the following year (Kozlowski et al., 1991). A negative correlation found for *E. saligna* during the long rainy season of the current year, again suggests that too much precipitation insinuates increased cloud cover or possible large storm events, causing breakage of the crown (Munishi and Chamshama, 1994). In addition, a negative correlation was observed for *E. grandis* during the transitional period into the long rainy season. Here, transitional periods are defined as a grouping of months containing both rainy season and dry season months. Several theories for explaining positive relationships during the transition from a dry to a rainy period include: 1) transitional rains inducing bud-break and extending the growing period (Wright and Cornejo, 1990; Borchert, 1994; Borchert, 1999; Priya and Bhat, 1999), 2) an increase in soil water reserves over the course of the rainy season, nulling the impacts of short drought periods later in the rainy season (Brienen and Zuidema, 2005), and 3) the majority of ring growth occurring early in the rainy season (Priya and Bhat, 1999) as opposed to minor amount of ring growth later in the rainy season (Worbes and Junk, 1999). Although these theories provide viable explanations for positive correlations between precipitation and growth during the transitional period, negative correlations have yet to be explained. We speculate that excessive precipitation may favor growth of competitor tree species and grasses that are better able to take advantage of the increase in precipitation (Moustakas et al., 2009).

The high positive correlations with precipitation are said to be a reliable indicator of the annual nature of tree rings (Gebrekirstos et al., 2008). Thus, all the discussed species with positive precipitation correlations can be said to form annual ring boundaries. Worbes and Junk (1999) also discovered that positive correlations between tree-ring width chronologies and precipitation variable could be used as evidence for the annual nature of tree rings. The positive relationships between precipitation and radial growth during the rainy season found in this study coincide with the findings of several other tropical studies (e.g. Pumijumnong et al., 1995; Worbes and Junk, 1999; Enquist and Leffler, 2001; Dunisch et al., 2003; Fichtler et al., 2004; Brienen and Zuidema, 2005; Schongart et al., 2006; Trouet et al., 2006; Gebrekirstos at al., 2008; Sass-Klaassen et al., 2008; Brienen et al., 2010). However, these studies have no mention of negative relationships between growth and precipitation variables, suggesting that it is rare. Buckley et al. (2007) reported negative correlations between growth and precipitation among *Pinus merkusii* trees near Vientiane, with the explanation that factors other than moisture, such as low light levels, could be limiting growth. Although these studies all address the direct impacts of climate variables (precipitation, temperature, climate moisture index) on the growth of tropical tree species, they do not include any of the species covered in the current study. Studies examining the direct impacts of climate variables on growth of the studied species are limited, making species specific comparisons difficult.

3.4.3 Species response to temperature

Although few tropical dendroecology studies have reported correlations between temperature and growth, due to relatively limited interannual variation (Rozendaal and Zuidema, 2010), some researchers believe that even in tropical zones, temperature can play a role in growth dynamics. This study revealed several correlations between monthly and seasonal temperature data and growth, which is contrary to several studies that found no correlations (Sass-Klaassen et al., 2008; Brienen et al., 2010). Positive correlations, found during rainy season months of the previous year suggest that warmer temperatures may lead to increased relative air humidity, which in turn can lead to higher probability of precipitation and thus more growth (Kozlowski et al., 1991). *M. lutea* was the only species to exhibit such a response for the full ring width. In contrast, positive correlations were present during months of the dry season for both *M. lutea* and *E. grandis*. Significant positive correlations between temperature and growth of *E. grandis* trees coincide with the finding of Sette et al. (2010) in the state of São Paulo, Brazil. *M. lutea* and *E. grandis*, displayed some positive correlations between full annual growth and the transitional periods between the dry and rainy seasons. One possible explanation could be that the tree species are growing outside of their temperature optimum and thus if the region is relatively too cold compared to its native geographical range, growth will be negatively impacted (Kozlowski et al., 1991).

Negative correlations were present during months of the dry season for *M. indica*. The negative correlations agree with the findings of Trouet et al. (2001), Clark et al. (2003), and Fichtler et al. (2004), which all discovered negative correlations between growth and temperature during the dry season. This effect is caused by increasing respiration of the tree as temperature increases and/or greater evapotranspiration rates leading to increased moisture stress, ultimately resulting in a greater loss of assimilated carbon (Fitter and Hay, 1981; Kozlowski et al., 1991).

A majority of the seasonal correlations were also negative correlations during the dry seasons.

3.4.4 Species response to climate moisture index

Although many studies have examined the effects of precipitation and temperature on growth as separate analyses, few studies have considered both climate variables simultaneously. Interannual tree growth is directly affected by the amount of available water. The net amount of available water accounts for both precipitation and the evapotranspiration from the plant. Temperature plays a large role in the amount of evapotranspiration that occurs and thus, a ‘moisture index,’ which accounts for water loss due to higher temperatures, is actually a better predictor of tree growth (Lopez and Villalba, 2010). Brienen et al. (2010) agree that the importance of combining temperature and precipitation into a single measure of moisture availability, is accentuated by the significant correlations that cease to exist when the climate parameters are examined individually. One example in which this study agreed with this statement is during the seasonal period of July-August-September of the current year when *A. mearnsii* showed a positive correlation when only precipitation was considered, yet no correlation existed when precipitation and temperature were considered simultaneously (Figure 3.4b; Figure 3.6b). However, many examples existed in which new correlations appeared when considering CMI that previously did not exist when considering either precipitation or temperature alone.

The correlations found between climate moisture index and growth for both monthly and seasonal data are similar to that of precipitation data and can be explained in much the same way. One species in particular, *A. mearnsii*, shows negative correlations for climate moisture index during the transitional period from dry to rainy season of the previous year. This correlation could be the result of heavy storm rains early in the growing season causing crown breakage and forcing the tree to allocate more resources to repairs the following year (Munishi and Chamshama, 1994).

3.4.5 Conclusions

Significant correlations between growth and climate parameters existed for each study species. However, correlations among species did not present a clear pattern. Bimodal responses to climate variables appeared to be sporadic, with a few exceptions (*C. lusitanica* – precipitation, CMI; *E. grandis* – precipitation, temperature, CMI). *C. lusitanica, E. grandis,* and *M. indica* showed positive correlations with precipitation during periods of the rainy seasons and *A. mearnsii* during the rainy season months. Negative correlations existed during the dry months for *C. lusitanica* and *E. grandis*, the rainy season months for *E. saligna*, and the transitional period for *E. grandis*. Positive correlations with temperature existed for *M. lutea* during the rainy season and *M. lutea* and *E. grandis* during the dry season and transitional periods. Negative temperature correlations existed during the dry season for *M. indica*. For the majority of cases, climate moisture index correlations reflected what was seen for precipitation. The results of this study further support that tropical tree species can be effectively studied through dendrochronology and climate-growth relationships can be established.

APPENDICES

Table 3.1 List of studied species with summary of their habit

Species	Habit	Region	Plots	N	Range in ages and time span	dbh (cm)
Acacia mearnsii	Evergreen shrub/tree, 2-15 m	Upper Yala	3	6 (6)	7-27 (1984-2010)	12.8-29.0
Mangifera indica	Evergreen tree, 10-15m	Lower Yala	2	6 (6)	22-47 (1964-2010)	20.5-58.9
Markhamia lutea	Evergreen tree, 10-15m	Middle Yala	1	4 (4)	20-33 (1978-2010)	10.4-26.1
Cupressus lusitanica	Evergreen tree, up to 35 m	Middle Yala	2	4 (4)	12.5-20.5 (1990-2010)	29.7-35.7
Eucalyptus camaldulensis	Evergreen tree, up to 30 m	Middle Yala	6	21 (20)	5-21 (1990-2010)	3.9-48.5
Eucalyptus grandis	Evergreen tree, 40-50 m	Middle Yala	2	6 (6)	5-11 (2000-2010)	6.7-29.3
Eucalyptus saligna	Evergreen tree, 40-50 m	Middle Yala	2	6 (4)	5-6 (2005-2010)	4.8-17.7

N = number of stem discs investigated with successfully cross-dated trees in parenthesis; age range in years and time span in parenthesis; diameter at breast height (dbh) range of stem discs (dbh)

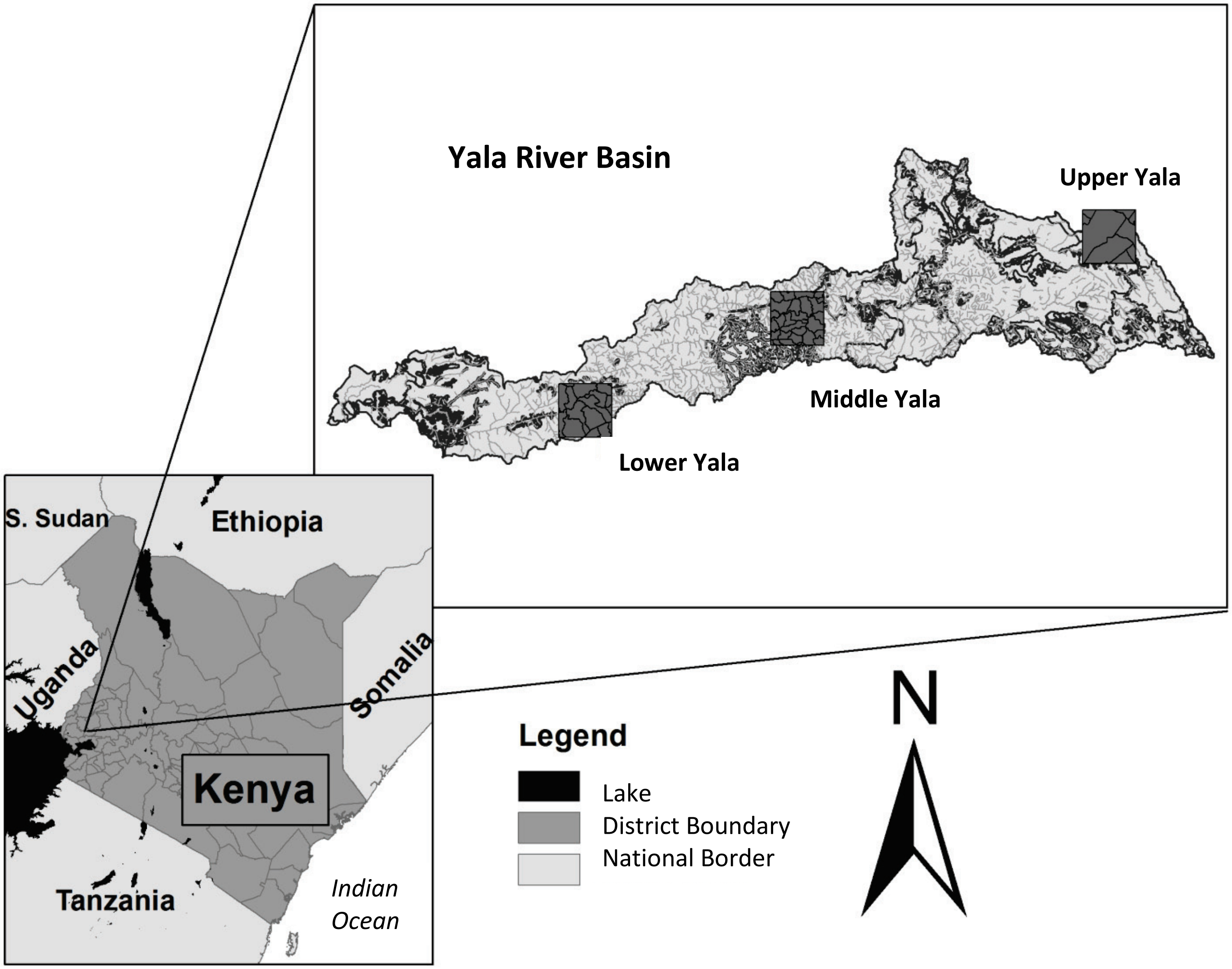


Figure 3.1 Locations of sample blocks in River Yala Basin of Western Kenya. The three blocks included lower Yala, middle Yala, and upper Yala.

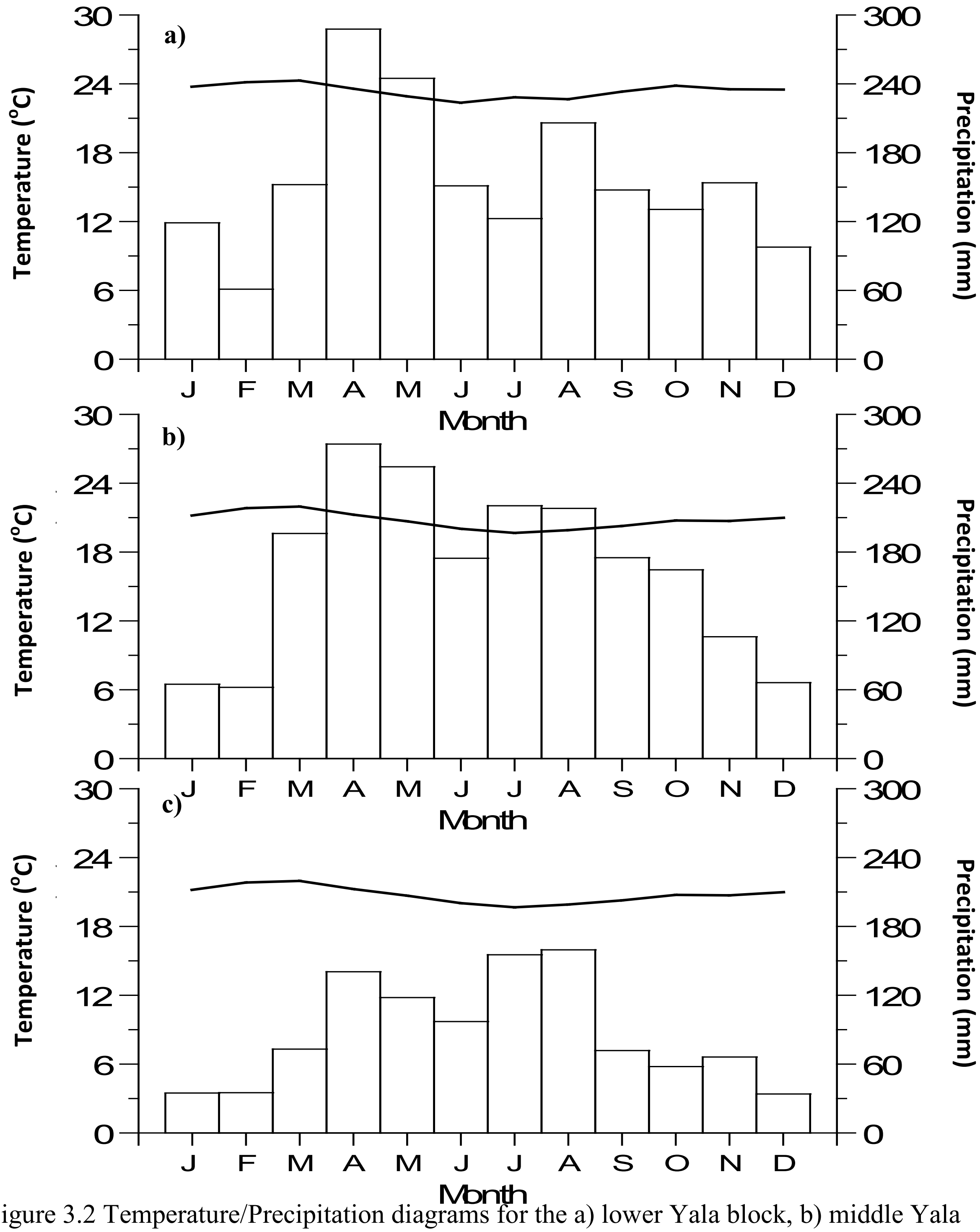


Figure 3.2 Temperature/Precipitation diagrams for the a) lower Yala block, b) middle Yala block, and c) upper Yala block and Climate Moisture Index (CMI) diagrams for the d) Lower Yala, e) Middle Yala, and f) Upper Yala blocks. Average monthly temperature (^{o}C) is represented by a solid line and total monthly precipitation (mm) is represented by vertical bars. Data for the lower block was averaged from 1962-2009. Data from the middle block was averaged from 1979-2009. Data from the upper block was averaged from 1972-2009.

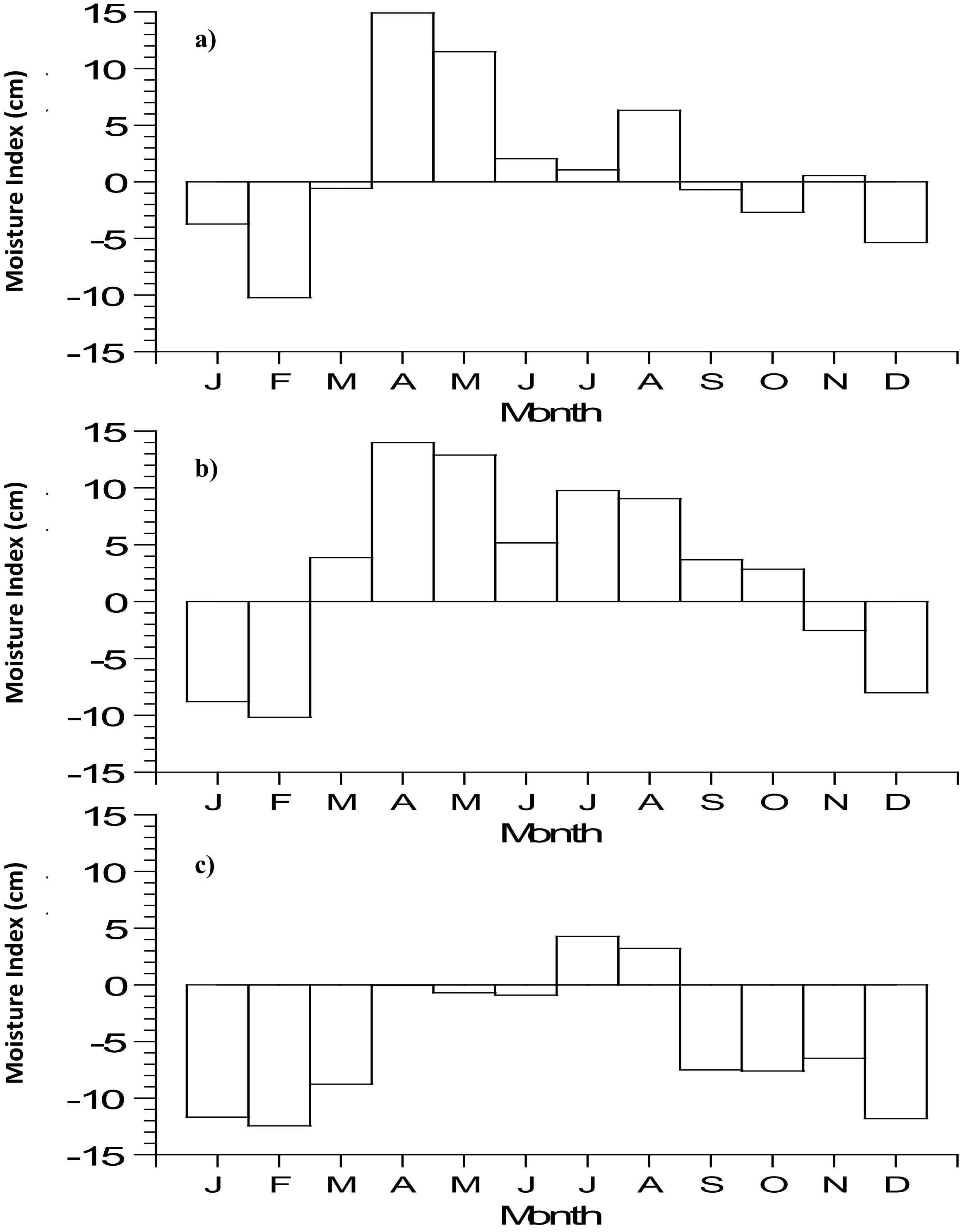


Figure 3.2 (Cont’d)

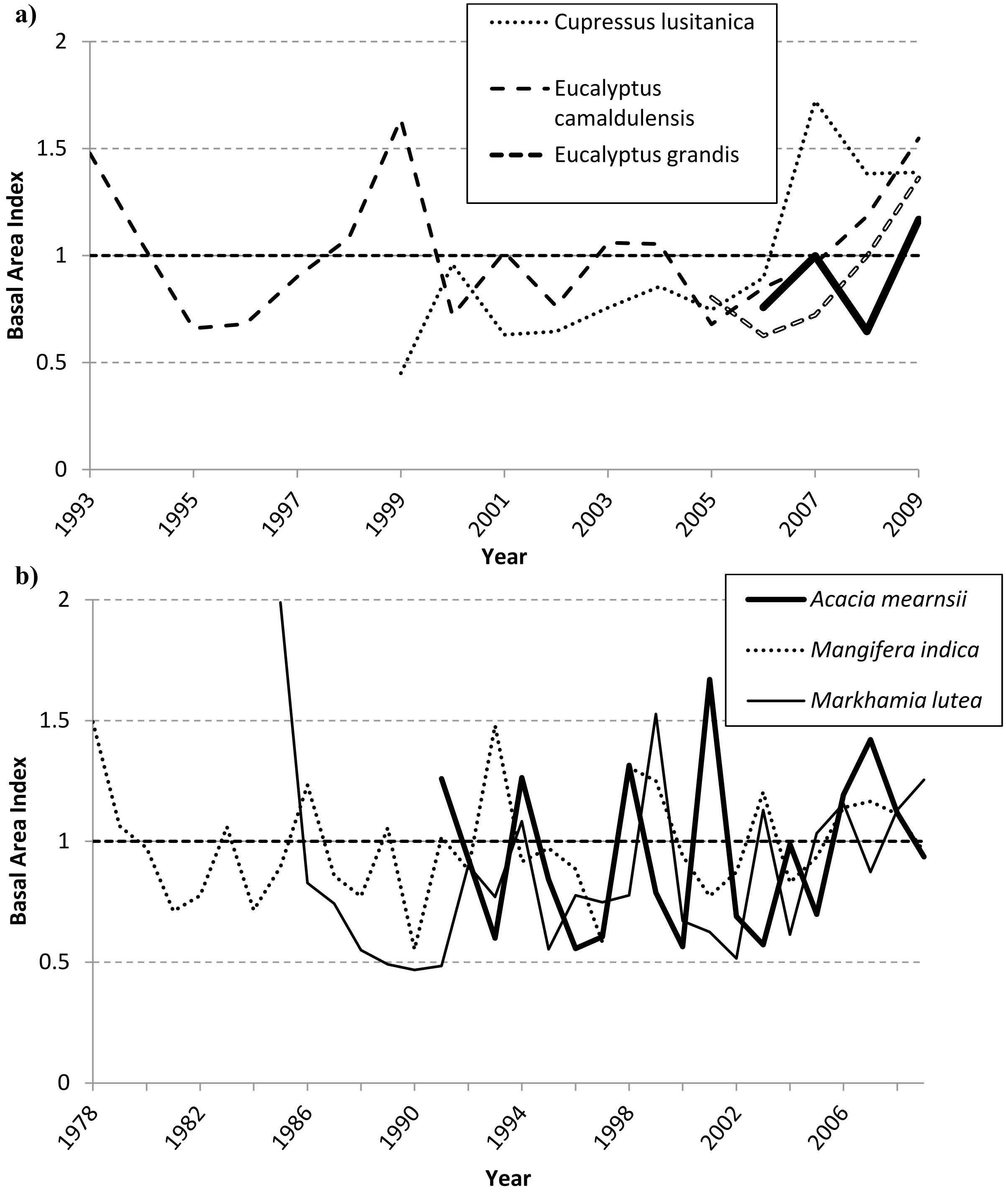


Figure 3.3 Basal area index (BAI) patterns summarized by common plantation species (a) and non-plantation species (b).

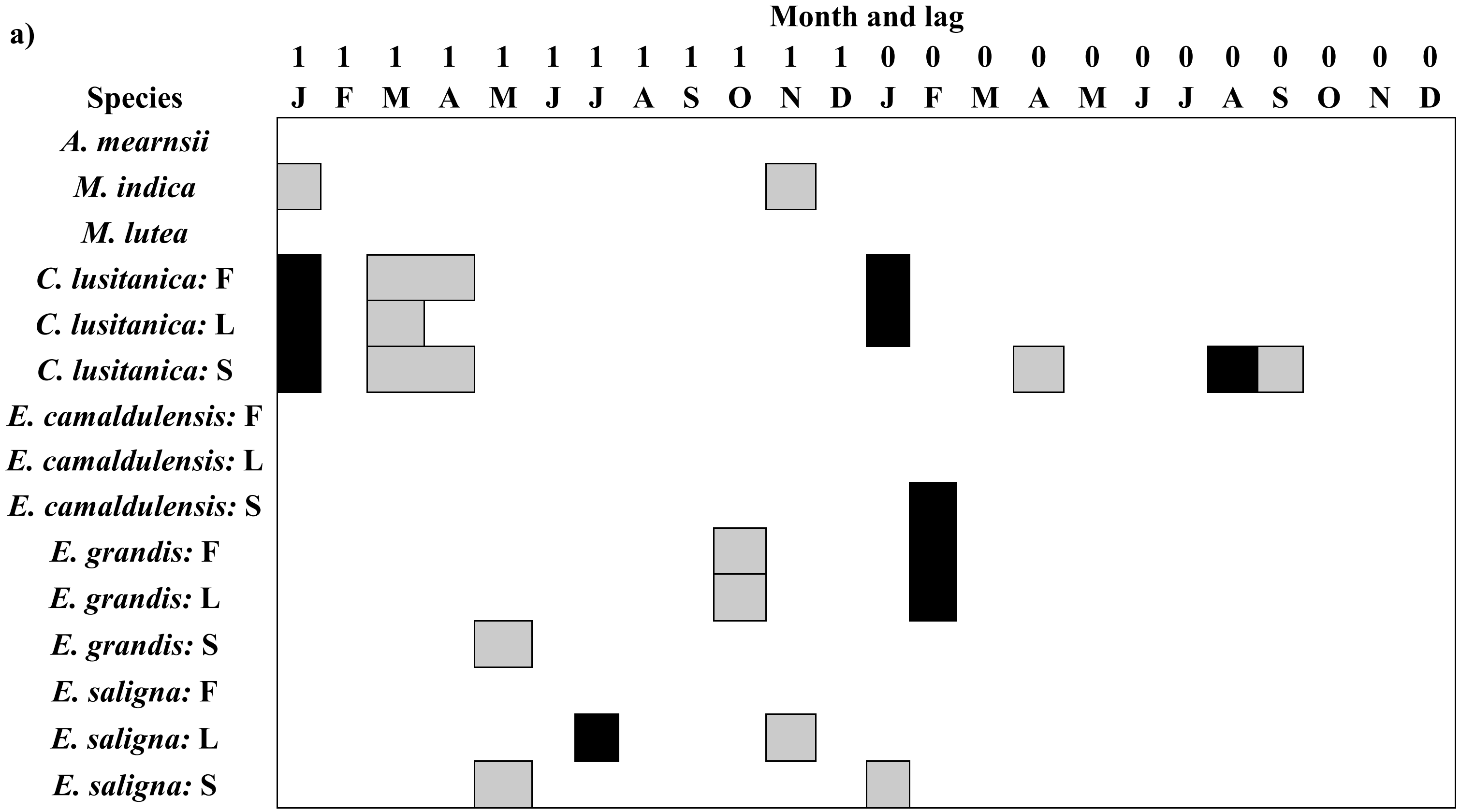
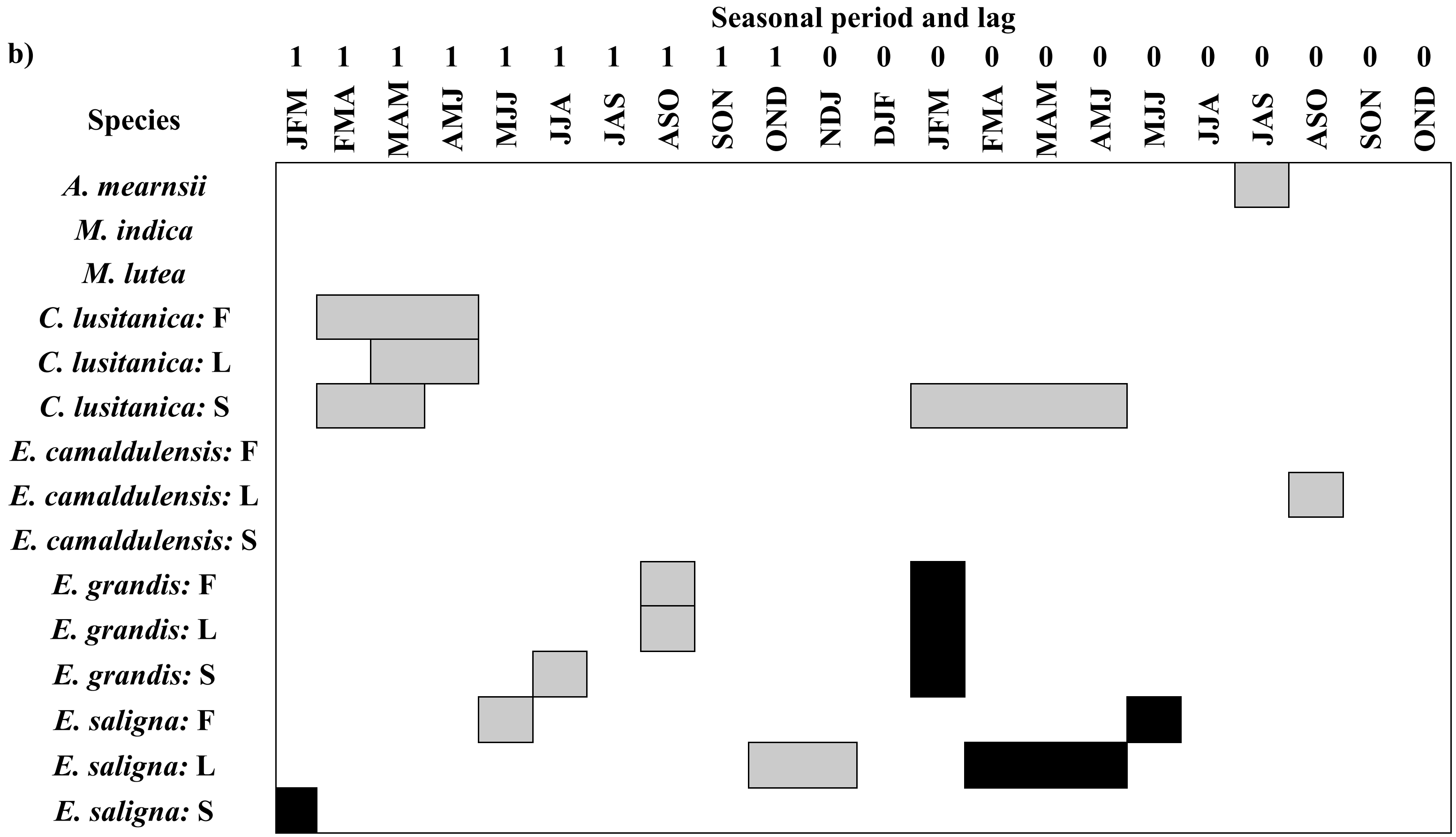


Figure 3.4 Correlation diagrams of all studied species for a) Monthly Precipitation and b) Seasonal Precipitation spanning from January of the previous year (lag 1) to December of the current year (lag 0). ‘F’ represents the full annual ring, ‘L’ represents the ring formed during the long rainy season, and ‘S’ represents the ring formed during the short rainy season. Significant positive correlations ($p < 0.05$) are denoted by grey boxes and significant negative correlations ($p < 0.05$) are denoted by block boxes. *A. mearnsii, E. camaldulensis, M. indica*, and *M. lutea* were all analyzed using a Pearson correlation test, while *C. lusitanica, E. grandis*, and *E. saligna* were analyzed using a Spearman Rank test.

b)

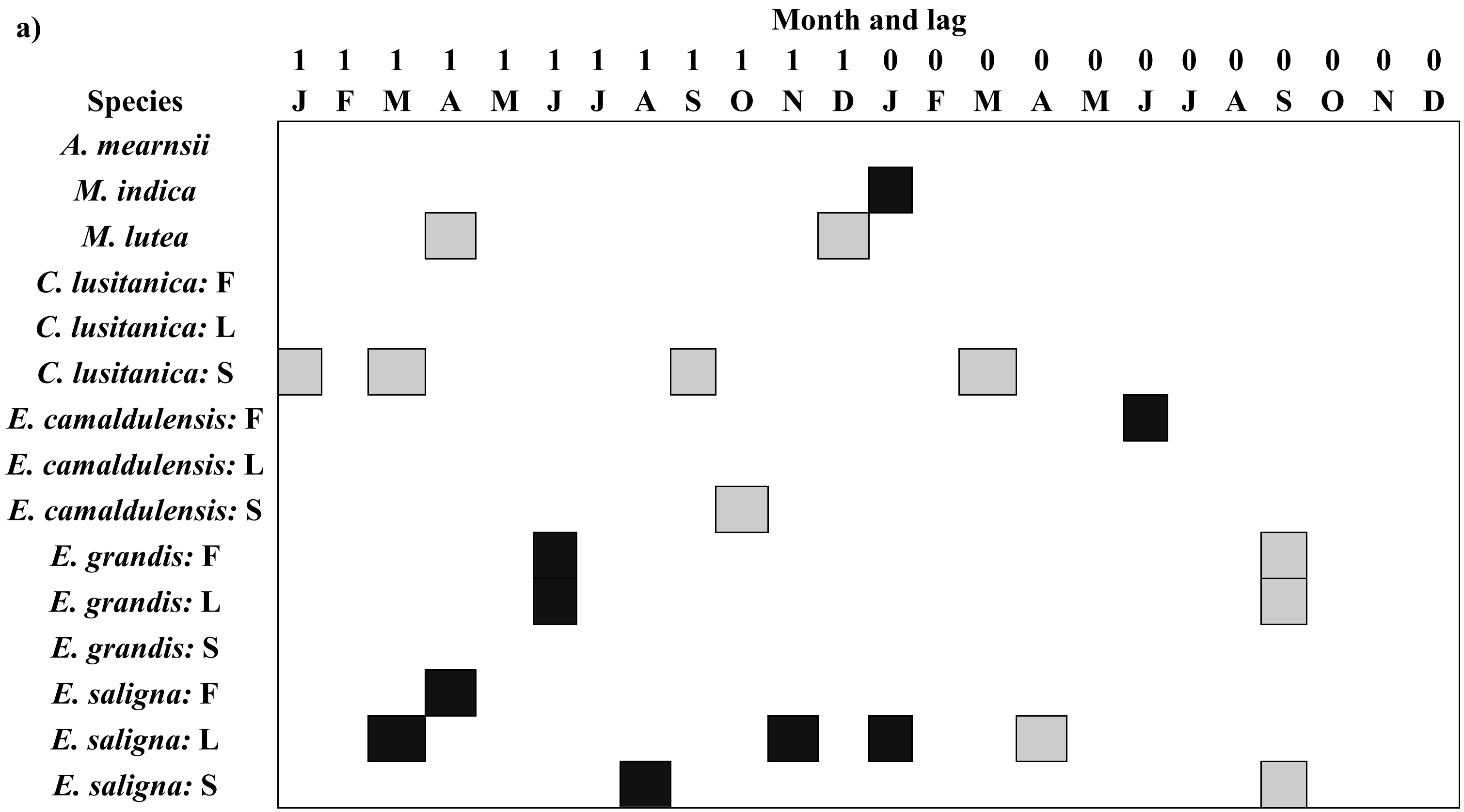


Seasonal period and lag

	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Species	**JFM**	**FMA**	**MAM**	**AMJ**	**MJJ**	**JJA**	**JAS**	**ASO**	**SON**	**OND**	**NDJ**	**DJF**	**JFM**	**FMA**	**MAM**	**AMJ**	**MJJ**	**JJA**	**JAS**	**ASO**	**SON**	**OND**
A. mearnsii																			▨			
M. indica																						
M. lutea																						
***C. lusitanica:* F**		▨	▨	▨																		
***C. lusitanica:* L**			▨	▨																		
***C. lusitanica:* S**		▨	▨										▨	▨	▨	▨						
***E. camaldulensis:* F**																						
***E. camaldulensis:* L**																				▨		
***E. camaldulensis:* S**																						
***E. grandis:* F**								▨					■									
***E. grandis:* L**								▨					■									
***E. grandis:* S**						▨							■									
***E. saligna:* F**					▨												■					
***E. saligna:* L**										▨	▨			■	■	■						
***E. saligna:* S**	■																					

Figure 3.4 (cont'd)

a)

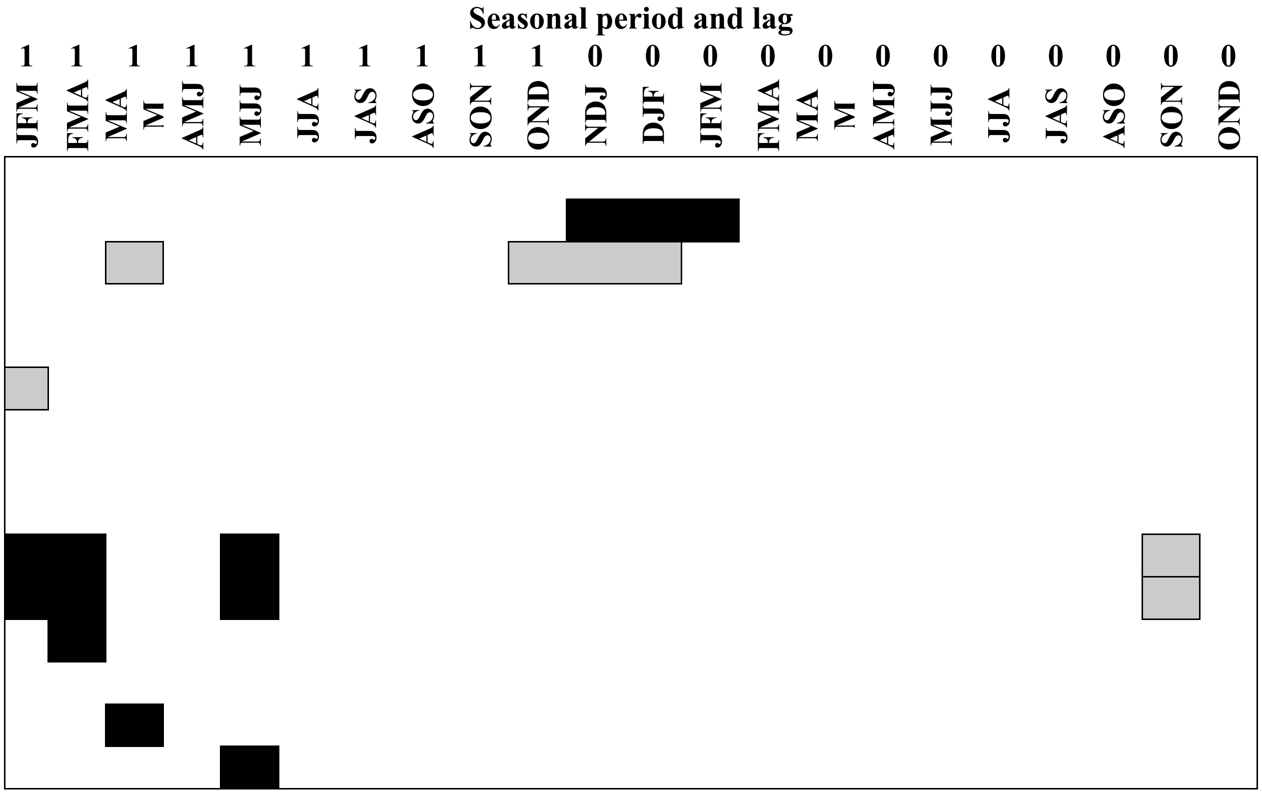


Month and lag

	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Species	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
A. mearnsii																								
M. indica													■											
M. lutea				▨								▨												
***C. lusitanica:* F**																								
***C. lusitanica:* L**																								
***C. lusitanica:* S**	▨		▨						▨						▨									
***E. camaldulensis:* F**																		■						
***E. camaldulensis:* L**																								
***E. camaldulensis:* S**										▨														
***E. grandis:* F**						■															▨			
***E. grandis:* L**						■															▨			
***E. grandis:* S**																								
***E. saligna:* F**				■																				
***E. saligna:* L**			■								■		■			▨								
***E. saligna:* S**								■													▨			

Figure 3.5 Correlation diagrams of all studied species for a) Monthly Temperature and b) Seasonal Temperature spanning from January of the previous year (lag 1) to December of the current year (lag 0). 'F' represents the full annual ring, 'L' represents the ring formed during the long rainy season, and 'S' represents the ring formed during the short rainy season. Significant positive correlations ($p < 0.05$) are denoted by grey boxes and significant negative correlations ($p < 0.05$) are denoted by block boxes. *A. mearnsii, E. camaldulensis, M. indica*, and *M. lutea* were all analyzed using a Pearson correlation test, while *C. lusitanica, E. grandis*, and *E. saligna* were analyzed using a Spearman Rank test.

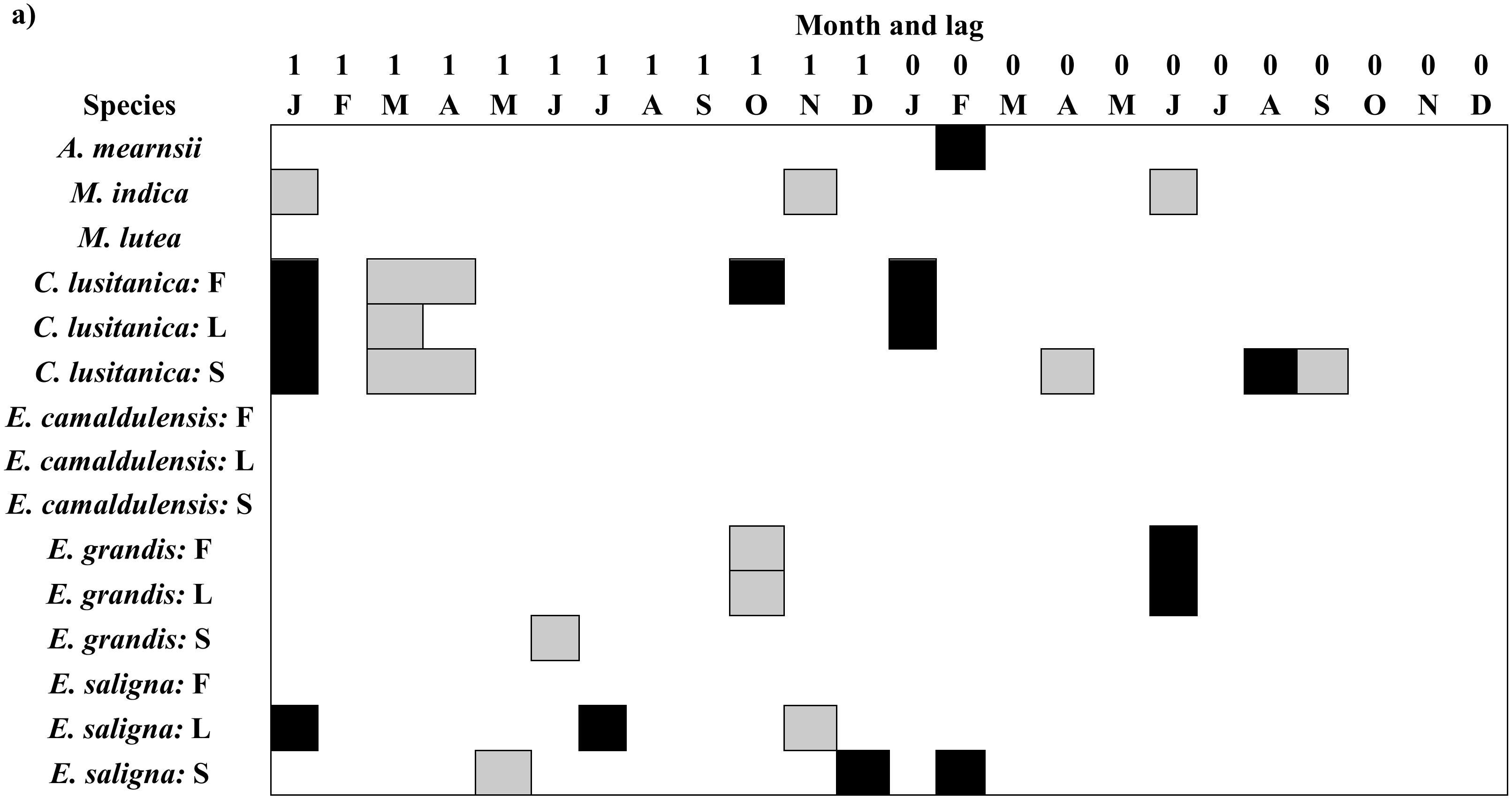
b)



Species	1 JFM	1 FMA	1 MAM	1 AMJ	1 MJJ	1 JJA	1 JAS	1 ASO	1 SON	1 OND	0 NDJ	0 DJF	0 JFM	0 FMA	0 MAM	0 AMJ	0 MJJ	0 JJA	0 JAS	0 ASO	0 SON	0 OND
A. mearnsii																						
M. indica											■	■	■									
M. lutea			▨							▨	▨	▨										
C. lusitanica: F																						
C. lusitanica: L																						
C. lusitanica: S	▨																					
E. camaldulensis: F																						
E. camaldulensis: L																						
E. camaldulensis: S																						
E. grandis: F	■	■			■																▨	
E. grandis: L	■	■			■																▨	
E. grandis: S		■																				
E. saligna: F																						
E. saligna: L			■																			
E. saligna: S					■																	

Figure 3.5 (cont'd)

a)

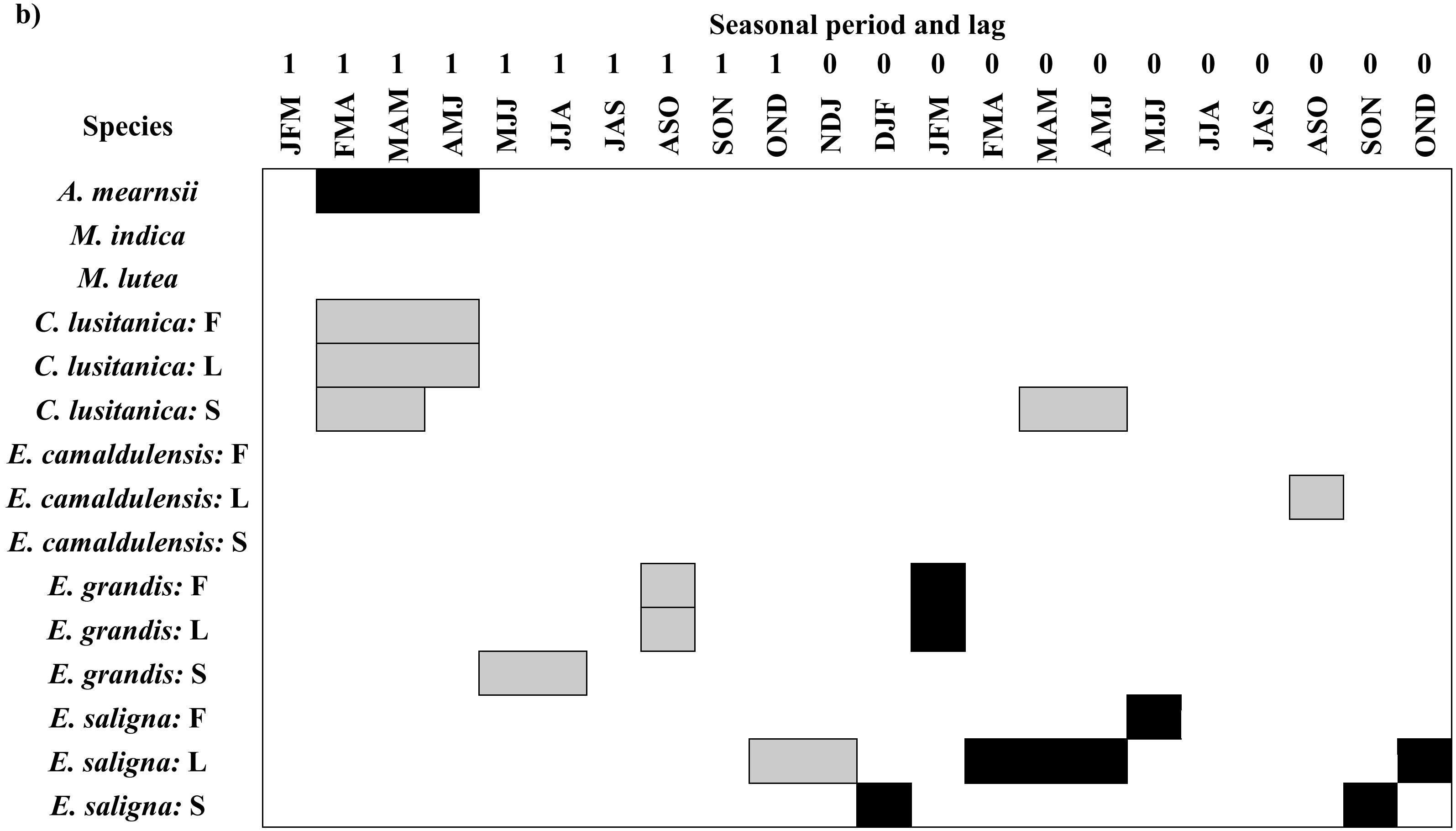


Month and lag

	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Species	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
A. mearnsii														■										
M. indica	▨										▨							▨						
M. lutea																								
***C. lusitanica:* F**	■		▨	▨						■			■											
***C. lusitanica:* L**	■		▨										■											
***C. lusitanica:* S**	■		▨	▨												▨				■	▨			
***E. camaldulensis:* F**																								
***E. camaldulensis:* L**																								
***E. camaldulensis:* S**																								
***E. grandis:* F**										▨								■						
***E. grandis:* L**										▨								■						
***E. grandis:* S**						▨																		
***E. saligna:* F**																								
***E. saligna:* L**	■						■				▨													
***E. saligna:* S**					▨							■		■										

Figure 3.6 Correlation diagrams of all studied species for a) Monthly Climate Moisture Index (CMI) and b) Seasonal Climate Moisture Index (CMI) spanning from January of the previous year (lag 1) to December of the current year (lag 0). ‘F’ represents the full annual ring, ‘L’ represents the ring formed during the long rainy season, and ‘S’ represents the ring formed during the short rainy season. Significant positive correlations ($p < 0.05$) are denoted by grey boxes and significant negative correlations ($p < 0.05$) are denoted by block boxes. *A. mearnsii, E. camaldulensis, M. indica*, and *M. lutea* were all analyzed using a Pearson correlation test, while *C. lusitanica, E. grandis*, and *E. saligna* were analyzed using a Spearman Rank test.

b)



Seasonal period and lag

	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Species	**JFM**	**FMA**	**MAM**	**AMJ**	**MJJ**	**JJA**	**JAS**	**ASO**	**SON**	**OND**	**NDJ**	**DJF**	**JFM**	**FMA**	**MAM**	**AMJ**	**MJJ**	**JJA**	**JAS**	**ASO**	**SON**	**OND**
A. mearnsii		■	■	■																		
M. indica																						
M. lutea																						
C. lusitanica: **F**		▨	▨	▨																		
C. lusitanica: **L**		▨	▨	▨																		
C. lusitanica: **S**		▨	▨												▨	▨						
E. camaldulensis: **F**																						
E. camaldulensis: **L**																				▨		
E. camaldulensis: **S**																						
E. grandis: **F**								▨					■									
E. grandis: **L**								▨					■									
E. grandis: **S**					▨	▨																
E. saligna: **F**																	■					
E. saligna: **L**										▨	▨			■	■	■						■
E. saligna: **S**												■									■	

Figure 3.6 (Cont’d)

REFERENCES

REFERENCES

Borchert, R., 1994. Water status and development of tropical trees during seasonal drought. Trees Struct Funct 8, 115–125.

Borchert, R., 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. IAWA J 20, 239–247.

Braüning, A., Volland-Voigt, F., Burchardt, I., Ganzhi, O., Nauss, T., Peters, T., 2009. Climatic control of radial growth of *Cedrela montana* in a humid mountain rainforest in southern Ecuador. Erdkunde 63, 337–345.

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146, 1–12.

Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martınez-Ramos, M., 2010, Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. Glob Change Biol 16, 2001–2012.

Broadhead, J.S., Ong, C.K., Black, C.R., 2003. Tree phenology and water availability in semi-arid agroforestry systems. For. Ecol. and Man. 180, 61-73.

Buckley, B.M., Duangsathaporn, K., Palakit, K., Butler, S., Syhapanya, V., Xaybouangeun, N., 2007. Analyses of growth rings of *Pinus merkusii* from Lao PDR. For Ecol Manage 253, 120–127.

Bush, R.R., and Brand, G. 2008. Lake States (LS) variant overview: Forest Vegetation Simulator. USDA For. Serv., Forest Management Service Center, Fort Collins, CO.

Chhin, S., Wang, G.G., Tardif, J., 2004. Dendroclimatic analysis of white spruce at its southern limit of distribution in the Spruce Woods Provinvial Park, Manitoba, Canada. Tree-Ring Research 60, 31-43.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany 86, 167–178.

Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rainforest growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc Natl Acad Sci USA 100, 5852–5857.

de Oliveira, B.R.U., Latorraca, J.V.D., Tomazello, M., Garcia, R.A., de Carvalho, A.M., 2011. Dendroclimatology correlations OF Eucalyptus grandis Hill ex Maiden of Rio Claro, RJ state - Brazil. Ciencia Florestal 21, 499-508.

Dietz, J., Kuyah, S., 2011. Guidlenines for establishing regional allometric equations for biomass estimation through destructive sampling, World Agroforestry Centre, Nairobi.

Dunisch, O., Montoia, V.R., Bauch, J., (2003). Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L.(Meliaceae) in the central Amazon. Trees-Struct Funct 17, 244–250.

Enquist, B.J., Leffler, A.J., 2001. Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. J Trop Ecol 17, 41–60.

Eshete, G., Stahl, E., 1999. Tree rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. Forest Ecol Manage 116,107–117.

Fichtler, E., Trouet, V., Beeckman, H., Coppin, P., Worbes, M., 2004. Climatic signals in tree rings of *Burkea Africana* and *Pterocarpus angolensis* from semi-arid forests in Namibia. Trees 18,442–451.

Fitter, A.H., Hay, R.K.M., 1981. Environmental physiology of plants. Academic, London.

Fritts, H. C., 1976. Tree Rings and Climate. Academic Press, Inc., London, UK.

Gebrekirstos, A., Mitlohner, R., 2008. Climate-growth relationships of the dominant tree species from semi-arid savanna woodlands in Ethiopia. Trees 22, 631-641.

Gourlay, I.D., 1995. Growth ring characteristics of some African acacia species. Journal of Tropical Ecology 11, 121-140.

Hogg, E.H., 1997.Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology 84, 115–122.

Jacoby, G. C., 1989. Overview of tree-ring analysis in tropical regions. IAWA Bulletin. 10: 99-108.

Kozlowski, T. T., Karmer, P. J., Pallardy, S. G., 1991. The Physiological Ecology of Woody Plants. Academic Press, ISBN: 0124241603.

Krepkowski, J., Braüning, A., Gebrekirstos, A., Strobl, S., 2010. Seasonal growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. Trees-Struct Funct. doi:10.1007/s00468-010-460-7.

Lisi, C.S., Tomazello, M., Botosso, P.C., Roig, F.A., Maria, V.R.B., Ferreira-Fedele, L., Voigt, A.R.A., 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. IAWA J 29, 189–207.

Lopez, L., Villalba, R., 2011. Climate influences on the radial growth of *Centrolobium microchaete*, a valuable timber species from the tropical try forests in Bolivia. Biotropica 43, 41-49.

Maingi, J. K., 2006. Growth rings in tree species from the Tana River floodplain. J. East African Natural History. 95, 181-211.

Mbow, C., Chhin, S., Sambou, B., Skole, D., 2011. Potential of dendrochronology to assess annual rates of biomass productivity in savanna trees of West Africa. Manuscript submitted for publication.

Moustakas, A., Sakkos, K., Wiegand, K., Ward, D., Meyer, K., Eisinger, D., 2009. Are savannas patch-dynamic systems? A landscape model. Ecological Modelling 220, 3576-3588.

Munishi, P.K.T., Chamshama, S.A.O., 1994. A study of wind damage on *Pinus patula* stands in Southern Tanzania. For. Ecol. and Man. 63, 13-21.

Okullo, J.B.L., Hall, J.B., Obua, J., 2004. Leafing, flowering and fruiting of *Vitellaria paradoxa* subsp. *nilotica* in savanna parklands in Uganda. Agroforestry Systems 60, 77-91.

Priya, P.B., Bhat, K.M., 1999, Influence of rainfall, irrigation and age on the growth periodicity and wood structure in teak (*Tectona grandis*). IAWA J 20, 181–192.

Pumijumnong, N., Eckstein, D., Sass, U., 1995. Tree-ring research on *Tectona grandis* on northern Thailand. IAWA J 16, 385–392.

Rodrıguez, R., Mabres, A., Luckman, B., Evans, M., Masiokas, M., Ektvedt, T.M., 2005. ‘‘El Nino’’ events recorded in dry-forest species of the lowlands of northwest Peru. Dendrochronologia 22, 181–186.

Rozendaal, D.M.A., Zuidema, P.A., 2010. Dendroecology in the tropics: a review. Trees 25, 3-16.

Sass-Klaassen, U., Couralet, C., Sahle, Y., Sterck, F.J., 2008. Juniper from Ethiopia contains a large-scale precipitation signal. International Journal of Plant Sciences 169, 1057-1065.

Schongart, J., Piedade, M.T.F., Ludwigshausen, S., Worbes M., (2002). Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. J Trop Ecol 18, 1–17.

Schongart, J., Junk, W.J., Piedade, M.T.F., Ayres, J.M., Huttermann, A., Worbes, M., 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Nin ˜o-Southern Oscillation effect. Glob Change Biol 10, 683–692.

Schöngart, J., Orthmann, B., Hannenberg, K.J., Porembski, S., Worbes, M., 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Global Change Biology. 12, 1139-1150.

Sette, C.R., Filho, M.T., dos Santos Dias, C.T., Laclau, J.P., 2010. Growth in diameter of *Eucalyptus grandis* W. Hill ex Maiden trees and relationship with climatic variables and mineral fertilization. Revista Árvore 34, 979-990.

Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. Forest Ecology and Management 124, 217-229.

Soliz-Gamboa, C.C., Rozendaal, D.M.A., Ceccantini, G., Angyalossy, V., van der Borg, K., Zuidema, P.A., 2010. Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees. Trees-Struct Funct. doi:10.1007/s00468-010-0468-z.

SYSTAT, 2002. SYSTAT for Windows, Version 10.2. SYSTAT Software Inc., Chicago, Illinois.

Therrell, M.D., Stahle, D.W., Mukelabai, M.M., Shugart, H.H., 2007. Age and Radial growth dynamics of *Pterocarpus angolensis* in southern Africa. Forest Ecology and Management 244, 24-31.

Trouet, V., Haneca, K., Coppin, P., Beeckman, H., 2001. Tree ring analysis of *Brachystegia spiciformis* and *Isoberlinia tomentosa*: evaluation of the enso-signal in the miombo woodland of eastern Africa. IAWA J 22, 385–399.

Trouet, V., Coppin, P., Beeckman, H., 2006. Annual growth ring patterns in Brachystegia spiciformis reveal influence of precipitation on tree growth. Biotropica 38, 375-382.

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S. 4th ed. Springer, New York, N.Y.

Volland-Voigt, F., Braüning, A., Ganzhi, O., Peters, T., Maza, H., 2010. Radial stem variations of *Tabebuia chrysantha* (Bignoniaceae) in different tropical forest ecosystems of southern Ecuador. Trees-Struct Funct. doi:10.1007/s00468-010-0461-6.

Wayant, J.G., Reid, R.S., 1992. Determining the age of *Acacia tortilis* with ring counts for South Turkana, Kenya: a preliminary assessment. Afr J Ecol 30,176–180.

Wils, T.H.G., Robertson, I., Eshetu, Z., Sass-Klaassen, U.G.W., Koprowski, M., (2009). Periodicity of growth rings in Juniperus procera from Ethiopia inferred from crossdating and radiocarbon dating. Dendrochronologia 27, 45–58.

Worbes, M., Junk, W.J., 1999. How old are tropical trees? The persistence of a myth. IAWA Journal 20, 255-260.

Worbes, M., Staschel, R., Roloff, A., Junk, W.J., 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. For Ecol Manage 173,105–123.

Wright, S.J., Cornejo, F.H., 1990. Seasonal drought and leaf fall in a tropical forest. Ecology 71, 1165–1175.

CHAPTER 4

CONCLUSIONS AND FUTURE RESEARCH

In Chapter 2, all of the studied species (*Acacia mearnsii, Bridelia micrantha, Combretum molle, Croton macrostachyus, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Grevillea robusta, Mangifera indica, Markhamia lutea, Persea americana, Trilepisium madagascariensis, and Syzygium cuminii*), were successfully crossdated, with the exception of *Grevillea robusta*. Biomass increments for all of the well-replicated species (*Acacia mearnsii, Cupressus lusitanica, Eucalyptus camaldulensis, Eucalyptus grandis, Eucalyptus saligna, Mangifera indica, Markhamia lutea*) were successfully calculated.

Climate-growth correlation analysis in Chapter 3 revealed significant relationships between basal area indices and precipitation, temperature, and climate moisture index. Although these relationships help in understanding the ecology of these species, due to small sample sizes and short chronologies lengths, few statements can be made regarding historical climate patterns. Understanding of these growth-climate relationships can greatly benefit the implication of carbon offset programs. Growth-climate relationships can be expressed as regression equations, where growth is a function of climate variables. Future climate data can then be input into these equations in order to project growth under future climate change scenarios. Currently, these programs only account for carbon on a 5-year basis and require significant funding to obtain the necessary data for the calculations. Thus, projects are not able to receive any tradable income until the 5-year lag period is over. With the reduction in time and money resulting from the application of equations from dendrochronological studies, annual carbon offset estimates could be obtained.

The outcomes of this study further solidify the connection between annual tree growth and climate variables. However, future studies on these economically important species should incorporate trees of known age, with a greater sample size and longer chronology. Analysis of short chronologies could be affected by juvenile growth patterns. Furthermore, in tropical regions, where growth ring boundaries can be very difficult to detect, working with samples of a known age can aid in verifying the validity of ring boundaries, as well as their periodic nature. If trees of known age are not available, methods such as cambial wounding (Lisi et al., 2008) or using dendrometers to monitor periodicity in tree growth (Brauning et al., 2009; Krepkowski et al., 2010; Volland-Voigt et al., 2010) are viable ways of determining ring periodicity. In addition, future studies should evaluate the impacts of ENSO events on these various species growing in Western Kenya, as these events have been found to have a significant impact on species in other similar studies (Schongart et al., 2004; Rodriguez et al., 2005; Therrell et al., 2006; Gebrekirstos et al., 2008). Insights into past climate patterns can also be determined from further growth-climate analysis of these species. Further, understanding the ecology of these trees can aid in management and utilization of these trees for carbon sequestration and timber resources in Kenya and other developing countries.

In addition, new dendrochronology techniques should be employed, such as X-ray densitometry (Delgado-Matas and Pukkala, 2011) and vessel feature analysis (Verheyden et al., 2005) to aid the in the detection of periodic growth increments. Furthermore, methods of a more quantitative nature should be established for the categorization of dendrochronological usefulness of tropical species. A more standardized categorization approach will ensure that all researchers come to similar results when analyzing samples of the same species.

REFERENCES

REFERENCES

Braüning, A., Volland-Voigt, F., Burchardt, I., Ganzhi, O., Nauss, T., Peters, T., 2009. Climatic control of radial growth of *Cedrela montana* in a humid mountain rainforest in Southern Ecuador. Erdkunde 63, 337–345.

Delgado-Matas, C., Pukkala, T., 2011. Comparison of the growth of six *Eucalyptus* species in Angola. Int. J. For. Res. Volume 2011, ID#980259.

Gebrekirstos, A., Mitlohner, R., 2008. Climate-growth relationships of the dominant tree species from semi-arid savanna woodlands in Ethiopia. Trees 22, 631-641.

Krepkowski, J., Braüning, A., Gebrekirstos, A., Strobl, S., 2010. Seasonal growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. Trees-Struct Funct. doi:10.1007/s00468-010-460-7.

Lisi, C.S., Tomazello, M., Botosso, P.C., Roig, F.A., Maria, V.R.B., Ferreira-Fedele, L., Voigt, A.R.A., 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in Southeast Brazil. IAWA J 29, 189–207.

Rodrıguez, R., Mabres, A., Luckman, B., Evans, M., Masiokas, M., Ektvedt, T.M., 2005. ‘‘El Nino’’ events recorded in dry-forest species of the lowlands of northwest Peru. Dendrochronologia 22, 181–186.

Schongart, J., Junk, W.J., Piedade, M.T.F., Ayres, J.M., Huttermann, A., Worbes, M., 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Nin ˜o-Southern Oscillation effect. Glob Change Biol 10, 683–692.

Therrell, M.D., Stahle, D.W., Mukelabai, M.M., Shugart, H.H., 2007. Age and Radial growth dynamics of *Pterocarpus angolensis* in southern Africa. Forest Ecology and Management 244, 24-31.

Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytologist 167, 425-435.

Volland-Voigt, F., Braüning, A., Ganzhi, O., Peters, T., Maza, H., 2010. Radial stem variations of *Tabebuia chrysantha* (Bignoniaceae) in different tropical forest ecosystems of Southern Ecuador. Trees-Struct Funct. doi:10.1007/s00468-010-0461-6.