Wood formation in six Kenyan mangrove tree species:

Relationship with the environment and dendrochronological potential

By

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Acknowledgement

Dedication

I dedicate my work to my mom Wilfrida Akinyi and late Father Peter Okello who helped me make the first steps in life and to my brothers and sister who supported my education after the death of my father. Last but not least, to my loving husband Eric, daughter Daisy and son Joe, your love and assurance that you are and will always be there for me gave me the comfort and the courage to work with confidence despite the distance barrier between us during my study.

Abstract

Though assumed for a long time to be absent in tropical trees, several studies unveiled growth rings in these trees and for the first time in mangroves by Verheyden *et al*., (2004) the presence and annual nature of rings in *Rhizophora mucronata* was noted. Furthermore, understanding the dynamics behind wood production and its interaction with the environment would provide important information for setting up management plans for silvicultural practices. The main aim of this study therefore was to explore wood formation in six Kenyan mangrove species and to gain insight in its relationship with the environment.

Cambial marking (pinning) was done in six mangrove tree species (*Sonneratia alba*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Lumnitzera racemosa*, *Heritiera littoralis* and *Xylocarpus granatum*) in May 2005 and February 2006 in Gazi bay, Kenya. These were later cut down in June 2006 dried and brought to Xylarium of the Royal Museum for Central Africa, Tervuren, Belgium as part of the wood collection. In the laboratory, they were sawed into transverse sectioned discs, sanded then viewed both macroscopically and microscopically for counting and determination of clarity of rings, anatomy of the growth ring borders as well as radial increment measurement.

X. granatum and *L. racemosa* had very clear rings with well defined borders. While merging unclear rings was a common phenomenon in *S. alba* and *B. gymnorrhiza*, *H. littoralis* had exceptionally thick bark and as a result the cambial marking was too shallow to create a proper reaction leading to imprecision in ring count and radial growth measurement. *C. tagal* had clear rings but periodicity could not be defined due to lack of ring formation during the study period (slow growth). Radial increment was found to be non uniform over the study period and varying in the different study sites. Further, the negative effect of *Salagenia discata* pest on radial growth of *S. alba* was shown to display a threshold level below which the attack was not reflected on wood production. The study thus concluded that *X. granatum* and *L. racemosa* both have potential for use in dendrochronology and that many factors including precipitation, salinity and phenology all play an integral role in manipulating radial growth to various degrees in the different species.

Key words: mangroves, growth rings, dendrochronology, radial increment.

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1. Introduction and literature review

1.1 Mangroves ecology and distribution

1.1.1 Biogeography

Mangrove forests are one of the primary features of the coastlines throughout the tropics and subtropics of the world (Tomlinson, 1986). The term "mangrove" refers to both an ecological group of halophytic fauna as well as to a variety of a complex plant community found along sheltered shores of the tropical coastlines (Upadhyay *et al.*, 2002). In this study, the term has been applied to the tree component of the mangrove ecosystem. Generally, mangroves are found in 117 countries but there is lack of exact statistics on the global and regional extent of the mangrove area in several countries (Upadhyay, *et al.*, 2002). According to Blasco *et al.* (1996); Saenger *et al.* (1983) and Spalding *et al.* (1997), the total world mangrove cover is estimated as between 180-200,000km^2.

Mangroves can be divided into 'New World' and 'Old World' groups (Banerjee and Ghosh, 1998). The Old World mangroves are confined to the Persian Gulf, Madagascar, East Africa south of the Persian gulf, Australian and Indo-Malaysian regions. The New World group includes North, Central and Southern America, and Western Africa (Banerjee and Ghosh, 1998). While East Africa and the Middle East hold the least mangrove area (Figure 1), South and South East Asia have substantial areas of mangrove forests (Islam and Wahab, 2005).

Globally, mangroves are estimated to include 16–24 families (Mangrove Action Project, 2002) which sum up to about 60–70 mangrove species throughout the world (Tomlinson, 1986). The occurrence of mangroves with floristic divergence between the Old and New World groups can only be explained by historical processes (Saenger, 1998; Ellison *et al.*, 1999). Being water dispersed, mangrove trees' propagules could only be spread where suitable passages of water existed between continents (Barth, 1982). Several interpretations have been offered to connect world mangrove distribution to past continental movements (Chapman, 1976; Van Steenis, 1962) but none has been universally accepted (Tomlinson, 1986). The earliest mangrove species appear to have originated in the Indo-Malayan region and spread with the help of their floating fruits, seeds and seedlings, both westward and eastward, occupying relatively sheltered lagoons and estuaries (Banerjee and Gosh, 1998).

However, the present distribution reflects the contribution of some more modern processes such as waves (Tomlinson, 1986).
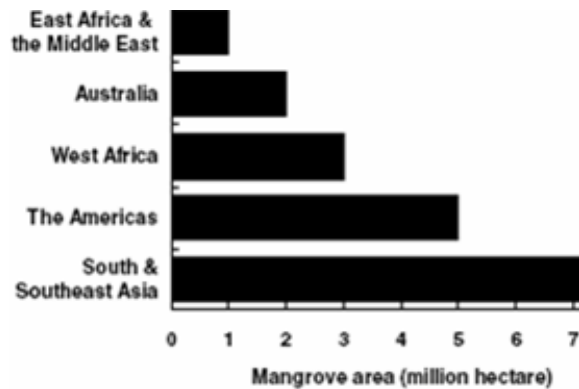
Figure 1. Relative proportions of mangrove global coverage adapted from Kathiresan and Bingham (2001).

1.1.2 Adaptations to the mangrove environment

For proper development, mangroves require mid to generally very fine-grained, muddy substrata in the zone between mid and high spring tide levels (Archibold, 1995), although the hardier species such as *Pemphis acidula* and *Heritiera littoralis* can grow on rocky areas (Karim *et al.,*1984). Mangrove habitats are thus characterized by a combination of periodic fluctuations with brackish or salty water and extremes in physico-chemical parameters such as salinity (Archibold, 1995). Despite the variability, the mangrove flora has successfully colonized this environment apparently aided by the morphological, physiological and reproductive adaptations (Clough*, et al.*, 1982; Hutchings and Saenger, 1987; Saenger, 1982; Tomlinson, 1986). These adaptations have been inferred by comparing the features of mangroves versus non-mangrove species (Saenger, 2002).

Mangroves occur in water logged soils that are oxygen deficient and unstable and to curb this, they possess special roots that aid in aeration and anchorage (Tomlinson, 1986). These roots can take various forms ranging from prop roots, over pencil and peg roots to knee roots. Furthermore, proper anchorage ensures protection against the high extent of wave and tidal actions (Wolanski *et al.*, 1992). Being able to cope with extreme conditions has thus enabled mangroves reduce competition with other offshore marine biotopes.

To deal with the excess salts, mangrove species have adopted different mechanisms, which enable them to grow sometimes even better in the presence of some salts (Khan and Aziz, 2001). The mechanisms include salt exclusion in the roots (Saenger, 2002) and extrusion through salt glands as seen in *Avicennia* leaves (Fitzgerald, *et al.*, 1992) and via cork warts in *Rhizophora* leaves (Tomlinson, 1986). In addition, *Rhizophora, Avicennia, Xylocarpus, Lumnitzera, Sonneratia,* and *Bruguiera* store excess salts as deposits in older leaves and in the bark (Clough *et al*., 1982). The findings of Werner and Stelzer (1990) on *Rhizophora mucronata* and *Ceriops tagal* from Gazi bay, Kenya supported this as senescing leaves were found to be enriched with chloride ions at the expense of nitrogen. Succulence in leaves as an extra mechanism has been interpreted by (Choong, *et al.*, 1992) as a xeromorphic feature to aid not only in conserving desalinated water and nutrients but also protection against herbivory.

Another adaptation mechanism which aids in increasing the chances of survival of young mangrove trees in the salty and dynamic environment of the intertidal zone is vivipary (Tomlinson, 1986). This is a condition found in some seed plants in which the sexually produced embryo of the seeds, while still attached to the parent plant, continues its development without dormancy. Vivipary can be divided into two major different forms, known as ''true vivipary'' and ''cryptovivipary,'' representing the two situations in which the embryo grows to break through the fruit wall, and the seed coat, respectively (Tomlison and Cox, 2000). Although true vivipary occurs occasionally in some seagrasses, such as Amphibolis, it is most developed in mangroves (Elmqvist and Cox, 1996; Tomlison, 1986).

1.1.3 Mangrove zonation

Mangrove forests tend to show a zonation profile along the intertidal zone (Tomlison, 1986). Tidal flats' profile diagrams show that zonation is a regular series of vegetation bands parallel to the coastline. However, depending on the strength and the distribution of the driving force influencing zonation mangrove forests can also develop in a mosaic pattern (Dahdouh-Guebas, 2004).

Different theories have been put forward in a bid to explain this unique arrangement of the various mangrove species. On one hand, Watson (1928) postulated that the response of mangroves to gradients in physiologically important factors such as salinity

or frequency of tidal inundation, determine where a given species occurs within the swamp. On the other hand, Rabinowitz (1974) put forward the hypothesis of optimal adaptation stating that a species will exhibit superior growth in its "home" swamp as it is optimally adapted to the sites in which it is ordinarily found. This was later confirmed by the geo-morphological control hypothesis by Beeckman *et al.* (1990), which explains regular zonation as being modified by local topography that determines tidal and fresh water run-off, and by sediment composition. In 1992, Robertson and Alongi instead stated under the theory of inter-specific competition that competitive interactions between species is the key to mangrove zonation.

1.2 Kenyan Mangroves

Kenya lies astride the equator and exhibits considerable climatic and physical variation due to changes in altitude and the strong continental influence inland and the marine influence to the east of the country. These together produce a hot and humid climate at the coast (UNEP, 1998). The Kenyan coastline is about 600 kilometres in length with distinctive features such as an almost continuous fringing coral reef. Other features include mangrove forests, rivers, bays, islands, harbours and ports. The mangrove forests form big to small patches along the coast relative to availability of suitable conditions required for their proper development. The total mangrove cover is 54,000 ha (UNEP, 2001) with the most extensive patch found in Lamu and Tana river districts, containing more than 70% of the total mangrove forest area to the North of Mombasa along the coastline (Gang and Agatsiva, 1992). Other smaller and isolated patches are found in Kilifi, Mida and Mtwapa creeks, Gazi bay, Funzi-Shirazi and around Vanga. Gazi bay has a mangrove cover of about 710 ha (UNEP, 2001)

There are nine mangrove species found in Kenya which follow a typical zonation pattern, as is evident in Gazi bay. *Sonneratia alba* grows closest to the low water line, followed mainly by *Rhizophora mucronata* found in inundation class 2 (Watson, 1928) then comes *Bruguiera gymnorrhiza, Ceriops tagal, Avicennia marina, Lumnitzera racemosa* and *Heritiera litoralis* respectively (Kairo, 1995). Although monospecificity is emphasised in mangrove zonation along the intertidal slope, surveys have revealed mixed mangrove stands as well (Speybroeck, 1992). In Gazi bay for instance, there is a major overlap in distribution pattern between *R. mucronata* and *B. gymnorrhiza*, between *C. tagal* and *A. marina* and between *Lumnitzera*

racemosa and *Xylocarpus granatum*. Furthermore, *A. marina* trees which are known to be found in the landward zone, are found mixed with *R. mucronata* in Gazi bay (Dahdouh-Guebas, 2004) while *X. granatum* occur in patches within the forest stand.

1.3 Need for Sustainable Management

1.3.1 Mangrove goods and services

The importance of mangrove forests can not be overlooked particularly after the horrifying tsunami ordeal (Dahdouh-Guebas, 2005). These forests provide goods and services to the people with values ranging from economic over ecological to environmental. Mangroves are valuable for their wood and non-wood products: timber, building poles, firewood, charcoal, fishing stakes, local medicines, animal fodder and vegetables (FAO, 2003). Environmentally, mangroves offer coastal protection against erosion and other damages caused by storm. They prevent siltation of adjacent sea grass beds and consequently protect coral reefs against turbid waters, which hinder maximised phytoplankton production and hence reduce fishery gains (FAO, 1994; Dahdouh-Guebas, 2005).

Mangroves' ecological values stem from their high energy production capacity (Christien, 1983), to the tune of 350– 500 g C m^{-2} yr^{-1} (Tomlinson, 1986; Ellison, 2000) and, from the role they play as nursery for fish and from their function as wildlife habitat (Tomlinson, 1986). Due to the high productivity, mangrove forests offer an enormous contribution to the food chain that supports the coastal fisheries (Tomlison, 1986). In addition, it gives them the capacity to store and to some extent process huge amounts of organic matter and dissolved nutrients, pesticides and other pollutants that are dumped in the environment from various anthropogenic activities and find their way in to the mangroves through rivers and continental drainage (Upadhyay *et al.*, 2002). As such, mangrove forests have been used for sewage disposal in most coastal cities in developing countries where there are no proper sewage systems (Barnette, 2000).

1.3.2 Mangrove Degradation

Lack of compatibility among the economic uses against environmental and ecological applications has led to serious degradation of mangrove forests. In Bangladesh for

example, vast areas of mangrove forest have been cleared and converted to areas for salt production and shrimp cultivation in various parts of the Sundarbans over the last two decades (Islam, 2005). Mahmood, (1986) stated that for sustainability to be achieved, for every hectare of semi-intensive shrimp culture, 38 hectares of mangrove forest are required for the ponds and an extra 189 hectares are needed per year to assimilate the wastes from the ponds. Modern shrimp farming is thus considered to be highly unsustainable in ecological terms because its operational requirements vastly exceed the carrying capacity of the surrounding mangrove ecosystem (Mahmood, 1986). The need for farming land due to the continuously increasing population in coastal villages has also led to encroachment into mangrove forests for agricultural purposes (Islam, 2005).

In Kenya, losses of mangroves have affected local economy as witnessed by shortages of firewood and building poles, reduction in fish catches and increased coastal erosion (Abuodha and Kairo, 2001). Studies conducted in Ungwana bay indicated that mangroves had suffered loss of species diversity due to preferential extraction of certain species and of trees of given specification (Bundotich thesis, unpublished). The Kenyan market is biased towards its timber demands and as such, a forest may appear healthy but consisting of relatively poor quality wood. Worse still, effective jurisdiction to adequately cover mangroves has not been put in place in Kenya (UNEP, 1998). Bans are put in place but ones lifted, serious cutting down of the trees follows due to lack of alternative sources of income. Poverty and ignorance among the local coastal dwellers have been outlined as the main contributing factors towards overexploitation of mangrove forests (Islam, 2005). In the Kenyan mangroves overexploitation of wood resources, conversion for other land uses and oil pollution are the main threats to this ecosystem (Abuodha and Kairo, 2001).

The dark part of it is that overexploitation of mangrove forests may lead to certain ecological changes in the ecosystem which are irreversible as the system may never acquire its original status again (Bosire *et al*., 2004). Erosion then becomes a common problem along the shorelines of East Africa, damaging or threatening tourism and communication infrastructure (Ogada, 1995). Other impacts include pollution of adjacent sea grass beds and coral reefs and consequently bleaching.

1.3.3 Replantation Efforts

Mangroves have the ability to regenerate naturally from natural seedlings only if given proper protection. However, if the habitat is completely destroyed, recovery becomes difficult due to changed environmental conditions such as soil salinity, tidal pattern, altered land use, enhanced biotic pressure, etc (Upadhyay *et al.*, 2002; Bosire *et al.*, 2004). In such cases, intensive human assistance is needed. Furthermore, natural regeneration is a relatively slow process, thus replantation is encouraged. Efforts should be made at all levels beginning with the local people to create awareness on the values of mangrove forests, and the negative results of their mismanagement (Upadhyay *et al.*, 2002). Involving the local people in plantation establishment and management as cited by Abuodha and Kairo (2001), results into a sense of belongingness and appreciation towards the resource by the people.

1.4 Tree Phenology

Phenology involves the study of the periodicity or timing of recurring biological events in a given species (Gentry, 1974). It looks at the causes of their timing with regard to biotic and abiotic forces, and how this timing affects the interrelation among the different phenological phases of the same or different species. Phenological events or phases in plants involve flowering, fruiting, leaf flushing and germination (Lieth, 1974). The schedule of these events has important effects on survival or reproductive success. It is not only abiotic environmental conditions such as temperature and humidity, but also biotic factors including intraspecific and interspecific competition for various resources and interactions with other organisms such as herbivores, pollinators, and seed dispersers, can be selective agents for plant phenology. To increase chances of seedlings' survival (Tevis, 1958), of high seed production (Augspurger, 1981), and of low predation rate (Aide, 1992), trees germinate, flower, and produce leaves during the peak season most favourable for the event in question.

One principal characteristic of phenology in tropical forests unlike temperate zones may be high variation of phenological patterns, partly because of the weaker physical constraints on schedules of biological activities (Gentry, 1974) leading to a significant reproductive success. The proportion of species with synchronized phenology in tropical forests is proportional to the strength of environmental cues, basically rainfall. Seasonally dry forests are often dominated by seasonally deciduous species,

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whereas in continually moist forests, deciduous species become less common (Reich 1995). Within the mangroves, a general unimodal and bimodal peaks in leaf production have been associated with mangrove forests growing in higher and low intertidal areas respectively due fluctuations in ground water salinity (Wium and Christensen, 1978). Also studies by Coupland (2005) on *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littoralis* and *Avicennia marina* species revealed a unimodal leaf growth pattern for trees growing in the highest intertidal area.

Seasonal stem diameter increment and leaf turnover are quite common phenomena of temperate and seasonally dry forests (Brien *et al*., 2008). Stem diameter increment with respect to phenological responses also occur in weak-seasonal biomes such as wet tropical forests. These two activities in plants together can be controlled by endogenous or exogenous factors. The degree of synchrony in wood production with respect to phenological responses in plants can indicate the control source: asynchronous responses are likely governed endogenously, whereas concerted responses are initiated by climatic, light, or other external stimuli such as floods (Ashton *et al.* 1988; Schöngart *et al*., 2002). On the same note studies have suggested the dependence of diameter increment on various phenological events. Chowdhury and Tandon (1950) noted that radial increment in stems close to tips forming buds increased highly during bud break. However, this is only the case with twigs as in most trees during reproduction (budding, flowering and fruiting) leads to significant reduction in girth increment (Chowdhury and Tandon 1950). It is noted that as much as photosynthesis is important as well for formation of wood involving, stem elongation, stem thickening and root growth, during reproduction, more photosynthates are used towards reproductive success at the expense of wood production (Baker, 1950; Kozlowski, 1962; Carlquist, 2001).

1.5 Growth rings

1.5.1 Formation of growth rings
Historically, the recognition of the presence of growth layers is dated back to 372-287 B.C. when it was noted that silver fir bark has many layers like an onion and that clear rings were present in conifers (Wimmer, 2002). Plants which do not form stems hence showing no secondary growth like ferns and most monocotyledons do not form rings

(Schweingruber, 1996). On one hand Primary growth occurs at the tips of roots and stems and results in their growing taller or longer. On the other hand, Secondary growth takes place in the vascular cambium and the cork cambium and results in an increase in the diameter of the stem or trunk of the tree (http://www.museum.state.il.us/muslink/forest/htmls/popups/how_tr_form.html). It is the interaction between secondary growth and variety of factors that create rings from the activities of the vascular cambium.

It is generally indicated that the vascular cambium is regulated by environmental (external) and genetic (internal) factors and as such the anatomy of the xylem will vary from one plant to the other depending on the two factors (Wimmer, 2002; Telewski and Lynch, 1991). Each time depending on environmental conditions and hormonal balance, the cambia will be initiated to form different kinds of a given cell say wide or narrow vessels and it is these differences that form the rings (Worbes and Junk, 1999). In a more simple way in the temperate regions, temperatures being the limiting factor (Schweingruber, 1992; Iqbal, 1995), rings form annually due to an alternation between cambium activity and complete dormancy (Koriba, 1958). In the tropics (except for mountainous areas) temperature and photoperiod are relatively constant throughout the year. Seasonally occurring stress factors here can be sporadic events such as drought and flooding (Worbes 1995) shoot growth flushes (Larson, 1994) or tree injury (Kramer and Kozlowski, 1979). These stress factors can as well induce cambial dormancy in tropical trees and consequently growth zones in the wood.

According to Cook, (1985), the wood anatomy of tree rings could be a function of the following factors:

- Tree age due to normal physiological aging processes
- Climate
- Disturbance within the forest stand such as wind blows, defoliating pests and anthropogenic activities
- Random processes (which he termed *error*) not accounted for by other processes

1.5.2 Growth ring boundaries

The process of differentiating between growth increments is dependent upon the visual differences within each growth ring and uniqueness of the terminal boundary between them (Coder, 1999). The terminal ring boundary in some species can be composed of high concentrations of axial parenchyma or thick-walled fibers. Many species have "squashed" elliptical-shaped (radially flattened) cells composing the last row of cells in a growth ring. Still other species generate thicker than normal cell walls. The interconnections between cells are also altered at the growth ring boundary both because of increasing fibre concentrations through the growth ring, and through pit-field locations and number changes (Coder, 1999).

The boundary between growth increments may not be visible without significant magnification. For ring delineation, within-growth-ring anatomy can provide information to the unaided eye or under low magnification (Coder, 1999). When under higher magnification microscope, a stem disc may have indistinct boundaries yet appear distinct when observed macroscopically. The distinctness of the ring boundary as observed under a microscope is thus the first over-riding consideration (Wheeler and Gasson, 1989). Distinct growth rings have an abrupt structural change at their boundaries. This is the case in most temperate tree species and includes a change in fibre thickness and/or fibre radial diameter. As seen in most tropical species, indistinct growth rings have poorly defined boundaries as they are marked by gradual structural changes (Wheeler and Gasson, 1989). For example in *Rhizophora mucronata* growth rings are formed by a gradual change in vessel density (Verheyden *et al*., 2004) while in *Avicennia* rings are formed by phloem. However, the difference between 'distinct' and 'indistinct' growth rings is sometimes arbitrary as there are always intermediates.

1.6 Dendrochronology

Dendrochronology is derived from two Greek terms (dendro and chronology) which were coined by Webb in 1983. *Dendro* refers to the Greek root word meaning tree and *chronology* to the study of time. Thus dendrochronology includes all branches of science involved in drawing some type of environmental information from tree ring sequences (Schweingruber, 1996). It is based on the technique of "cross-dating', a

procedure that uses variability of ring characteristics to determine the exact year in which each ring was formed (Fritts and Swetnam, 1989). In this way, the annual character of tree rings particularly in the temperate regions and general periodicity in tropics can be proven. When applying the principle of dendrochronology, it says that the variations in conditions present today must have been present in the past. However, the conditions may not be exactly the same but that similar kinds of influences affected the similar processes in the past. Any anatomical feature measured in tree rings can then be attributed to an exact time scale in case of annual ring development (Wimmer, 2002).

The major basis a dendrochronological study is that it requires the presence of periodically formed growth rings, which as indicated in studies by Détienne, (1989); Sass *et al*. (1995); Stahle (1999) are commonly absent in many tropical tree species. Furthermore, these studies seldom succeed in regions where conditions are continuously wet (precipitation in all months of the year exceeding 60-80 mm) (Wrobel, 1977; Worbes, 1989). However, Most parts of the tropics have seasonal climates with at least two arid months (Worbes, 1995) giving strong possibilities for such studies to be undertaken in the tropics by applying methods designed for use in temperate regions (Schweingruber, 1988).

In line with this many studies had hinted the presence of rings in tropical trees without demonstrating whether they were annual or not (Alvim, 1964; Chowdhury 1939, 1940). For example, the rings of many tree species growing in the tropics, may be indistinct, or bear no relationship with an annual growth cycle, or if they do, there are no visible patterns common between trees that can be used for crossdating (Eckstein *et al.,* 1981; Ogden, 1981). Certain authors however succeeded in explaining the periodicity in wood formation in the tropics (e.g. Brienen and Zuidema 2005; Roig *et al*. 2005; Verheyden *et al*. 2005; Schöngart *et al*. 2006) and linking physiology and ring anatomy (Fahn 1958; de Fay 1986). Existence and annual nature of rings were noted in *Rhizophora mucronata* from Kenya (Verheyden *et al*., 2004) composed of a zone of low vessel density and a zone of high vessel density, which are produced during, respectively, the rainy season (early-wood) and dry season (latewood). The author further therefore suggests that wood anatomical features in *R. mucronata* could be a potential proxy for past environmental conditions.

1.6.1 Techniques used in dendrochronology

A very simplified form of dendrochronology is ring counting and associating the results with rainfall and the physiology of trees (Kira *et al.*, 1977). However, this is an oversimplification as many other factors are considered in dendrochronology as tree growth can be affected by slope gradient, wind, soil properties, temperature and snow accumulation. The more a tree's rate of growth has been limited by such environmental factors, the more variation in ring width will be present. This method of ring counting is thus limited to trees of which accurate information about the date of planting is available such as trees from plantations, botanical gardens or, on rarer occasions, from the natural forest, if locals can provide reliable information (Gourlay, 1995; Worbes, 1995).

More recent studies than ring counting are based on repeated diameter measurements over short periods of time (Kira, *et al.*, 1967) as it is not easy to follow up for a long period. This provides information on short term growth and can thus not be precisely projected to give a precise picture of the factors that have shaped the tree

Another method is the cambial marking which is used in determining the periodic nature of tree rings by creating a 'timer' into the wood formation process to precisely date the onset and end of cambium activity as well as the transition from early- to latewood during the growing season (Jeong-Wook *et al.*, 2007). Cambial marking has been successfully applied to a number of species of the genus *Rhizophora*, including *R. mucronata* and *R. mangle* (Verheyden *et al.*, 2004: Shiokura, 1989; Menezes *et al.*, 2003) and to *Avicennia marina* (Schmitz *et al.*, 2006). Cambial marking may be done by, pinning or inducing changes in structure of growth rings by mimicking natural causes such as frost (Glock, 1955), removal of bark patches (Mariaux, 1967; Détienne, 1989) or even artificially induced drought (Carlquist, 2001; Kennedy and Farrar, 1965). All these have been tried with different degrees of success.

In pinning, a mechanical injury is inflicted to the cambium by inserting an epidermal needle, causing a wound response in the tree (Wolter, 1968). When a tree is wounded, a barrier zone is created by the cambium in form of a protective tissue to seal off internal tissues from the invasion of pathogens (Iqbal M, 1925.). The reaction may spread further the extent of which depends on traumatic signals generated when a plant is injured. The distance to which these signals can be propagated vary from minimal to quite high (Warren, 1978). After a given time the tree is harvested and the

generated callus tissue and other changes in anatomical feature in the wood around the wound remains as a dateable scar. This time marker then allows the study of growth formations in the wood around it by using it as a reference point to examine the origin of the cambium (Sass *et al.*, 1995; Worbes, 1995).

1.6.2 Dendrochronology Applications

Tree rings' examination has been applied for various purposes especially in ecological studies (Fritts and Swetnam, 1989). As the existing climatological or hydrological records are too short to detect long-term variability and changes (Fritts, 1989), tree ring analysis may provide information about the relationship between growth and environmental variables (including climate) and allows the detection of past changes in environmental conditions. As such dendrochronology can be used to reconstruct records of past climatic changes (Schulman, 1956; Fritts, 1976), which may aid in understanding forest dynamics and in resolving the ecological problems at hand. The tree-ring information on climate from the oldest trees is calibrated and compared with the existing records of climate (Fritts, 1976).

Another area where dendrochronology has been applied is the use of he dated rings to determine tree age (Worbes and Junk, 1999). In the temperate forests, a high correlation is noted between ring width variability and climate, supporting the periodic nature of the rings and in this way offering the possibility to determine tree age (Ogden, 1981). In tropical forests as well, climatically sensitive rings have been found for instance in bald cypress *(Taxodium distichum* L. Rich) growing in swamps (Stahle, 1999) and in Rhizophora mucronata (Verheyden *et al.*, 2004) that are cross-dateable and have provided useful chronologies for age determination (Ogden, 1982; Villalba *et aI.,* 1985). In connection to this, yearly tree-ring width sequences have been used to date structures, such as archaeological ruins, historic buildings and early Dutch paintings (BaiIlie, 1982; Douglass, 1935).

Dendrochronology has been applied in studying past forest disturbance such as pest and fire attacks. Unusual ring features or evidence of injury are dated by their association with rings formed in a particular growing season (Baillie, 1982). Dendrochronology has a high precision and can allow dating of fire scars in standing dead trees, logs or stumps (Ahlstran 1980; Dieterich 1980, 1984). Other disturbances

may not leave scars but affect the ring width, by influencing the tree's productivity and growth (Fritts 1989). These can be exploited by using dendrochronological dating of the annual rings to study the effects of say insect defoliation on tree growth by comparing the differences in ring growth of host trees and non-host trees (Fritts, 1989; Brubaker and Greene; 1979). It is further indicated that accurate dating is especially important in studies of insect defoliation and related studies as many rings can be locally absent or missing in severely defoliated or suppressed trees (Fritts, 1989).

1.7 Objectives

1.7.1 Rationale of the study

The coastal and marine environments of Kenya are very rich in resources. Yet they are the least studied of the Kenyan natural environments and thus a number of significant gaps exist in the data and information base (UNEP, 1998). Within the past few decades, mangrove ecosystem's complexities and importance to man have begun to be slowly appreciated (Upadhyay *et al*., 2002). However, these ecosystems remain largely less understood and hence usually not well managed leading to habitat loss and changes in species composition (Upadhyay *et al*., 2002). This calls for the establishment of management plans integrating reforestation and sustainable wood production (Kairo *et al*., 2001). To achieve the goal of sustainable production one has to clearly understand tree growth dynamics and project this knowledge to future management plans.

Trees being organisms that live for many years, following their development throughout their life span is not easy if not impossible. Dendrochronology has provided a useful tool to solve this problem by using growth rings to extract information about past environmental conditions and their effect on tree growth. In contrast to temperate tree species, the presence of growth rings in tropical trees has been shown to be less evident regardless of a seasonal climate (Détienne,1989; Sass *et al*., 1995; Stahle, 1999). However, several studies already unveiled tree rings in tropical trees (e.g Brienen and Zuidema 2005; Roig *et al.* 2005; Schöngart *et al.* 2006) indicating the possibility dendrochronological in these areas. Furthermore, the annual nature of tree growth rings has been investigated and verified for a large number of tropical trees ranging from dry zones (Gourlay 1995) to humid zones (Fichtler *et al.* 2004). Among the mangrove tree species presence and periodic nature of growth-

rings were discovered in Kenyan *Rhizophora mucronata* (Verheyden *et al*., 2004), Bangladeshi *Sonneratia apetala* and *Heritiera fomes* (Chowdhury *et al*., in press).

The present study ventured into growth ring and wood formation of six Kenyan mangrove species *Sonneratia alba, Bruguiera gymnorrhiza, Ceriops tagal, Lumnitzera racemosa, Heritiera litoralis* and *Xylocarpus granatum*. Next to environmental effects on tree growth, including climate, the possible influence of phenology on stem diameter increment was addressed as the relationship between phenology and secondary tree growth is largely unexplored in tropical trees (Brien *et al*., 2008). Besides, the extent of the effect on wood production of the insect pest *Salagenia discata*, currently threatening *Sonneratia alba* in Kenya, was studied. All these information would be important in bridging the gap in the already existing similar studies and to provide information useful in silvicultural practises.

1.7.2 Major study objective

The major aim of this study was to explore wood formation in six Kenyan mangrove species and to gain insight in its relationship with the environment.

1.7.3 Specific Objectives

To achieve the main objective, the following specific objectives were set:

1. To determine which, if any, of the mangrove species show clear growth rings.
2. To determine if these growth rings are annual.
3. To determine the rate of wood production in the study species.
4. To investigate the variation of tree radial growth with respect to, salinity levels and climatic conditions.
5. To investigate the relationship between phenology and wood production in *S. alba.*
6. To investigate pest attack effects on wood production in *S. alba.*

2. Materials and Methods

2.1 Study site

The study site is located in the mangrove forest of Gazi bay (4° 25′S and 39° 50′E), 55 km south of Mombasa, Kenya. The bay supports a fringing coral reef, sea grass beds and a mangrove forest with all nine species reported in Kenya represented. Two species, *Rhizophora mucronata* (local name Mkoko) and *Ceriops tagal* (Mkandaa), which are the dominant ones, make up 70% of the mangrove formation while the other form the remaining 30%. The total mangrove forest of Gazi covers about 710 ha (UNEP, 2001). It has two seasonal rivers, the Mkurumuji and the Kidogoweni which during wet season are an important freshwater source for the mangrove trees (Kitheka, 1997).

The five sampling sites (Figure 2; Kidogoweni KD, Begin Transect BT, Old Fisherman OF, Upstream US and New Fisherman NF) are located around Kidogoweni creek. The different mangrove species occur in a zonation pattern with certain species found together in one zone. *Sonneratia alba*, occurs in the littoral zone opening to the sea followed by *Rhizophora mucronata*. These are then followed by *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Avicennia marina*, *Lumnitzera racemosa* and *Heritiera littoralis* in that order (Kairo, 1995). However, major overlaps exist in the case of *R. mucronata* and *B. gymnorrhiza* as well as *C. tagal* and *A. marina*. *Xylocarpus granatum* is found in patches both sea-ward and land-ward. *A. marina* shows a double zonation where the species not only occurs in the landward zone but large trees are found as well in the *R. mucronata* zone (Dahdouh-Guebas, 2004).

The *S. alba* trees at NF site were pest infested (Figure 2; Figure 3) while those at the OF were unaffected (Table 1; Figure 2). This attack was first noted by a survey of Kenyan coast mangroves which revealed a serious decline due to an attack by an insect pest (Fergusson, 1993). *Salagena discata* as it came to be identified by Dr. Hollaway and Kenya National museums was found to be causing die-back and eventually death of *S. alba* trees (http://www.easternarc.org/html/NewPestK.html, Mwangi, 2001; Figure 3). This is an insect pest belonging to the order Lepidoptera (Integrated Taxonomic Systems- ITIS). The first damage was noticed in Kiunga, Lamu in early 1993 and a recent attack has been reported in Gazi bay and Tudor. *S. discata*'s larvae notches away the bark and burrow into the wood. The frass generated

from burrowing is used to cover the burrows making which is seen as a muddy substance on an affected tree Mwangi (2001).
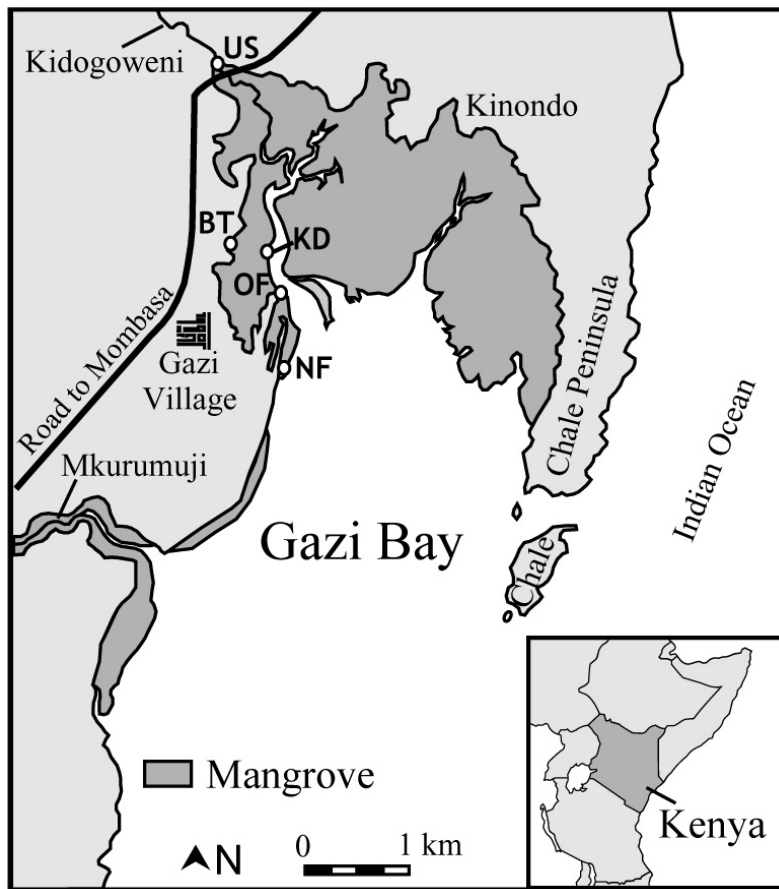
Figure 2. Map of study area showing the sampling sites (see also Table 1): adapted from Dahdouh-Guebas *et al.* (2002).

Figure 3. *Sonneratia alba* stem at the New Fisherman site in the mangrove forest of Gazi Bay infested by *Salagena discata* pest.

Table 1. Location of studied tree species in the five sites in the mangrove forest of Gazi Bay.

Species	Site	Inundation class
S. alba	New Fisherman-NF (infested)	1
	Kidogoweni-KD (not infested)	1
H. littoralis	Beginning Transect-BT	3
	Upstream-US	4
C. tagal	Beginning Transect-BT	3
B. gymnorrhiza	Kidogoweni-KD	1
	Old Fisherman-OF	1
X. granatum	Old Fisherman-OF	1
	Upstream-US	4
L. racemosa	Beginning transect-BT	3

2.1.1 Climate description

The climate along the Kenyan coast is characterized by a bimodal distribution of the precipitation. A distinct dry season (December–March) is followed by a long (April–July) and a short rainy season (October–November) (Figure 4). The monthly average temperature ranges from 23.3 to 29.9 °C with a mean annual temperature of 26.4 °C between 1931 and 1990 (Lieth *et al.*, 1999). The annual average of the minimum and maximum relative humidity is 65 and 81%, respectively for the period 1972–2001 (data obtained from the Kenyan Meteorological Department, Mombasa, Kenya).
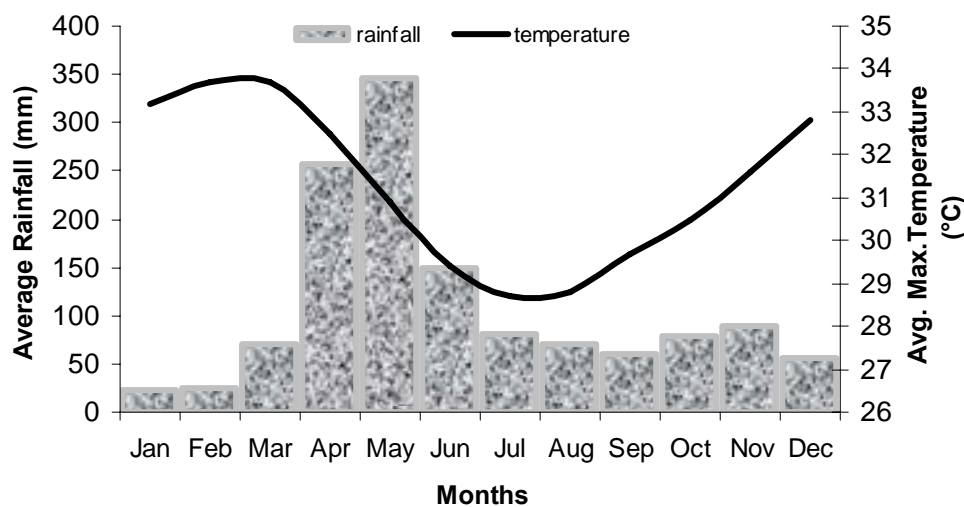
Figure 4. Average climatic conditions of Gazi, Kenya: calculated for monthly averages over 35 years (Kenya Soil Survey).

2.2 Base data

Data of different environmental characteristics, describing site conditions, were collected to help in analysing variation in wood anatomy and wood production. Soil salinity was determined from soil water collected at approximately 25 cm depth with a punctured plastic tube connected to a vacuum pump. At each site, 3 salinity measurements were carried out with a hand-held refractometer (ATAGO, Tokyo, Japan) from which the average salinity was calculated. To determine the inundation classes, the height above datum was calculated with the help of and tracing papers large tracing paper tied on to trees' stems at each site before high tide at positions estimated by use of tide tables. After the next high tide, the level reached by the water could be measured from the ground to the mark on the paper (Figure 5). Together with the high tide level mentioned on the tide table, height above datum could be calculated and classified according to Tomlinson (1986), where inundation classes one, two, three and four correspond to areas being inundated by 100–76, 75–51, 50–26 and 25–5 % of the high tides, respectively.

Calculation
Height above datum =X-Y
Where:
X is high tide level as from tide table
Y is the height measured on the tracing paper.

High water level

Figure 5. Tracing paper wrapped round a tree showing the level attained by water during the previous high tide.

2.3 Cambial Marking

Trees of the different study species were chosen randomly from the given sites (Table 1). However, care was taken as well to avoid extremely wide girthed trees which would be difficult to handle. Tree heights were measured trigonometrically using clinometer and lasermeter (Leica Disto^{TM} A5). Girth of the trees at breast height was

measured with a measuring tape from which diameter was calculated. This is conventionally done at 130 cm height from the ground level (D130cm). The cambial marking was performed by Nele Schmitz using a hypodermic needle of 18G; 1.2 mm diameter (Figure 6a), a first time towards end of May 2005 and again in February 2006 (Figure 6b). The second mark was made at two positions, about 2 cm above and at the right from the first one in February 2006 (Figure 6b). Paint was applied around each of the pinning marks and on the stem to ensure easier relocation of the tree samples during felling. All the trees were felled with a handsaw in June 2006, cut into convenient small sized 'logs' which each contained the three cambial marks (Sample collection by Nele Schmitz). As for *C. tagal*, only two samples were pinned and collected by Schmitz while the other four were pinned by Anouk Verheyden in October 1999 and cut at the same time as the other samples.

First mark

Second marks
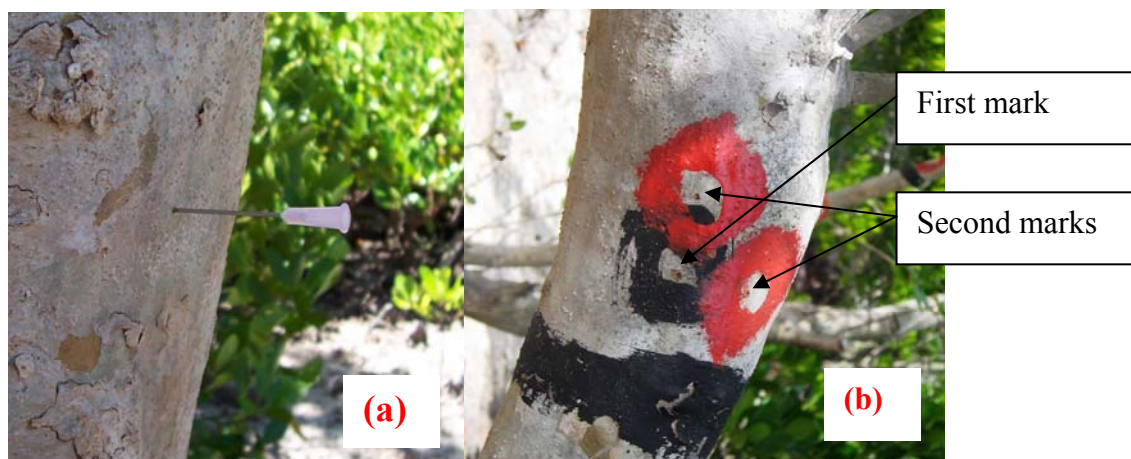
Figure 6. (a). An hypodermic needle pinned through the bark of a tree **(b).** Position of the successive pinning performed on the tree (pictures by Nele Schmitz).

2.4 Sample preparation and wood analysis

Wood samples were air-dried and are now part of the wood collection of the Xylarium of the Royal Museum for Central Africa, Tervuren, Belgium (see Table 6 for specimen number). On a working table, the wood samples were cut using a hand saw into disks, about 1.5cm thick. One disk contained the cambial mark of May 2005 and a second disc the cambial mark of February 2006. However, when both marks were perfectly in the same transverse plane (Figure 7a), the disc of the May mark could also be used to analyse the February mark. Sanding was then done using a series of

sandpaper from 50 to 1200 grit to expose the wound on a transversal face of the disk (Figure 7a).
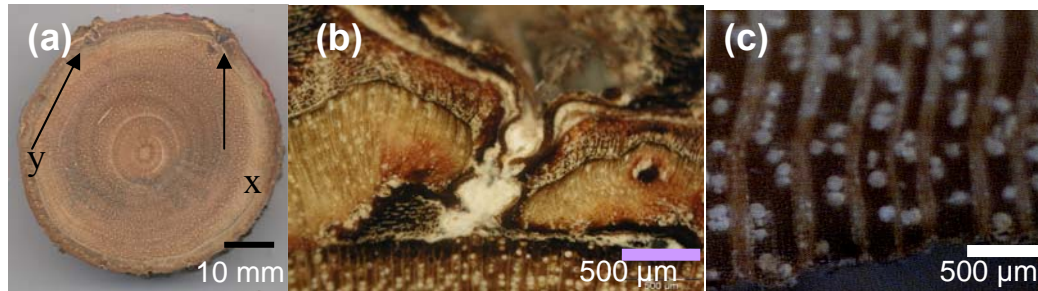
Figure 7. (a) A sanded disk of *H. littoralis* showing a cambial mark left after puncturing the tree stem in May 2005 (x) and February 2006 (y), **(b)** May wound zoomed at 4x magnification and **(c)** an example of a marker line in *B. gymnorrhiza* formed by bending rays.

First, wood discs were analysed both macro- and microscopically (Olympus SZ) for tree rings and their wood anatomical nature noted. The wound tissue was then carefully examined under the microscope (Olympus BX60) to locate the position of the cambial initials at the time of pinning indicated by the wound and a change in wood anatomy (marker line; Figure 7c). The number of growth layers formed since pinning was counted taking the marker line as a reference. In addition, the radial increment during the experimental period was measured with the image analysis software AnalySIS Pro 3.2 via a camera connected to the microscope. Measurement was done at both sides of the wound beginning from the marker line, whose anatomical nature differed from one species to the other (see Table 4). The increment was measured at about 2 mm distance from the wound, which in some cases was the furthest position showing the marker line. The distance was set to minimize the influence of the wounding on diameter increment, which is considered as 'abnormal growth' (Iqbal M, 1925).

2.5 Analysis

Based on the distribution of rainfall over the year in Gazi bay, the study period was divided into two. Period 1 was May 2005 – Feb. 2006 while period 2 was Feb. 2006 – June 2006. This was done to allow study of the association between climate

conditions and ring and wood formation. For the case of *C. tagal*, difference in monthly increment over the two periods was compare using only the two samples while Verheyden's samples were included in the analyses involving annual increment. Phenological data obtained from a study by Wang'ondu in 2005-2006 were used to check for relationship between radial increment and phenological events in *S. alba*.

2.5.1 Statistical analysis

A dependent t-test was used to test for significant differences between growth to the left and to the right of the wound. For subsequent analyses, the mean of the two measurements was used to get a general picture of the radial increment.

An analysis was done to compare the annual radial increment and monthly radial increment within each period among the species holding site factor constant. In all the above cases, data were tested for homogeneity of variance using Levene's test. If the variance was uniform then one-way ANOVA was used and if otherwise, data were transformed. If it still failed the Levene's test then a non-parametric test (Kruskal-Wallis) was used. In case a significant difference was noted in the groups being tested then a post hoc HSD was used for parametric tests. Within species differences were tested using independent t-tests for data with homogenous variance or Mann-Whitney U tests in case the data variances were not homogenous. Effect of salinity was as well tested by making use of the species that were found to be present at more than one salinity range and maximum salinity associated with the sites.

After determining normality of data using Shapiro-Wilk and Kolmogorov-Smirnov test, correlations were performed using product-moment coefficients to analyze the relationship between:

- Number of growth layers and stem or branch diameters (all samples included in the analysis)
- Radial increment and tree growth parameters (height and diameter at breast height)

For data that were not normally distributed, log transformation was used and the transformed data were tested for normality. If they still failed the test, Spearman Rank correlation was applied.

All statistics were executed in STATISTICA 8.0 (Stat Soft Inc., Tulsa, USA). Data were presented in graphs and tables produced from Excel.

3. Results

3.1 Site conditions

As shown in table 2, the position at the Upstream site where *X. granatum* trees were sampled had the lowest minimum as well as maximum salinity. The position where *H. littoralis* trees were sampled, at the other side of the river (see also Figure 2) and more land inward, had much higher salinity values. The Begin Transect site where *H. littoralis*, *L. racemosa* and *C. tagal* trees were sampled showed the largest variation in salinity with a low minimum and a high maximum salinity. The sites were calculated to belong to inundation classes 1, 3 or 4. The table also shows the heights of trees selected for pinning ranging from 2 to 7m and diameters at breast height (D130) of not more than 7 cm.

Table 2. Description of the environmental conditions of the study sites, the sampled tree heights and D130. (Nomenclature according to Tomlinson, 1986)

Family	Species	Site*	Soil water salinity (‰)			Inundation class	Av. Tree ht (m)	Av. D130§ (cm)
			Min.	Max.	Range			
Sonneratiaceae	*S. alba*	KD	21	46	25	1	6.0±1	4.7±0.7
		NF	25	36	11	1	6.0±2	6.0±2
Sterculiaceae	*H. littoralis*	BT	10	90	80	4	4.5±0.6	6.0±1
		US	5	68	63	3	5.0±4	5.0±3
Rhizophoraceae	*C. tagal*	BT	10	90	80	4	2.6±0.4	4.0±1
Rhizophoraceae	*B. gymnorrhiza*	KD	21	46	25	1	3.4±0.5	3.0±1
		OF	25	36	11	1	3.8±0.7	4.4±0.6
Meliaceae	*X. granatum*	OF	25	36	11	1	3.9±0.6	5.0±0.8
		US	0	11	11	3	7.0±1	4.1±0.7
Combretaceae	*L. racemosa*	BT	10	90	80	4	3.0±1	4.0±1

* - see Figure 2 and Table 1 in Methodology section
§ - stem diameter measured at 130cm from the ground
Av- Average
Ht – height

3.2 Trees' anatomical description

3.2.1 Macroscopic appearance of the growth rings

Table 3, second column shows the macroscopic appearance of the rings in the different tree species of this study. While all species showed some kind of growth rings when viewed at low magnification under the microscope, the ring borders were not always clearly demarcated. The shape and size of the disc played a role in the frequency of merged rings, particularly in *H. littoralis* as these were more common in asymmetric and larger discs than in symmetric and small ones.

Growth rings in *Sonneratia alba* were formed by an alternation between dark brown and light brown growth layers. This demarcation became however quite unclear further away from the pith. In most of the discs only the 2-3 innermost rings were clearly separated from each other with those towards the bark side merging into each other thus hindering ring counting. *B. gymnorrhiza* showed more concentric rings in the smaller/medium diameter branches and less in larger ones with the clarity of demarcation between rings faded away from the pith as seen in also in *S. alba*. Although there were merging rings towards the bark in this species too, it was noted to be to a less extent than in *S. alba*. In *H. littoralis*, even more rings appeared quite concentric with clear borders towards the pith than in the already mentioned two species. However, merging rings were as well common here as you move away from the pith especially in asymmetric discs. In *C. tagal* no merging rings were observed and as such the rings appeared quite concentric all over the sectioned discs. Besides, the discs seemed to have even clearer separation between one ring and the other than in both *H. littoralis* and *B. gymnorrhiza*. *X. granatum* had 10 out of 12 of the sanded discs with very clear rings running all around the stem circumference with only few merging rings. *L. racemosa* has rings which appear clearly separated from each other throughout each disc. These rings are marked by very clear alternating grey and light brown layers all over the disc.

3.2.2 Microscopic description of the ring borders

The borders in most of the tree species studied were much vaguer when observed under higher magnification (4x) with an Olympus BX60 microscope. Under most instances the borders were indistinct and marked by gradual changes in anatomical features (Table 3 second column).

S. alba's indistinct borders were characterised by an irregular combination of change in vessel density and gradual increase in fibre cell wall thickness. The borders were present under very few instances as in most cases the vessels appeared in more or less uniform distribution across the disc. *B. gymnorrhiza* had indistinct ring borders which were marked by a gradual change in vessel density. The ring borders of *C. tagal* were frequently characterised by gradual changes in vessel density and occasionally by narrow axial parenchyma bands of 2-3 cells wide. Here too just like in *S. alba*, the

parenchyma and vessel density changes were found in an irregular combination with no specific pattern (Table 3c).

Both *H. littoralis* and *X. granatum* had distinct ring borders marked by thin axial parenchyma bands of 2-4 cells thick in the former and of 1-5 cells in the latter. In the case of *X. granatum*, further from the pith, the bands appeared close to each other with relatively thick-walled fibre cells between them. *L. racemosa* ring borders were marked by a more or less regular combination of narrow parenchyma bands of 1-3 cells thickness, a change in vessel density and in fibre cell wall thickness. Note that in this species the vessels in the higher density zone were slightly smaller in size than those in the less dense zone (wood ring-porous) (Table 3f).

Table 3: Ring appearances in the different species at macro and microscopic levels in (a) *S. alba*, (b) *B. gymnorrhiza*, (c) *C. tagal*, (d) *H. littoralis*, (e) *X. granatum*, and (f) *L. racemosa*.

Macroscopic view of the discs	Microscopic view of part of the discs
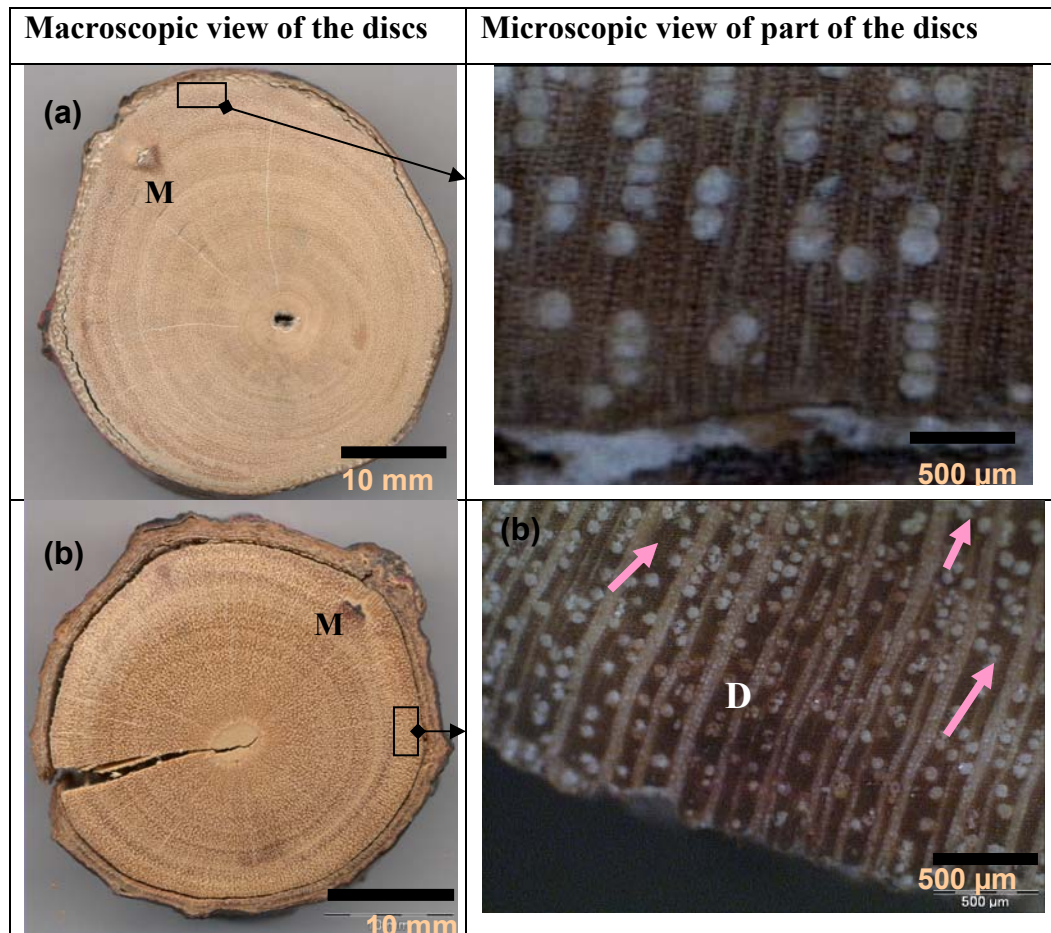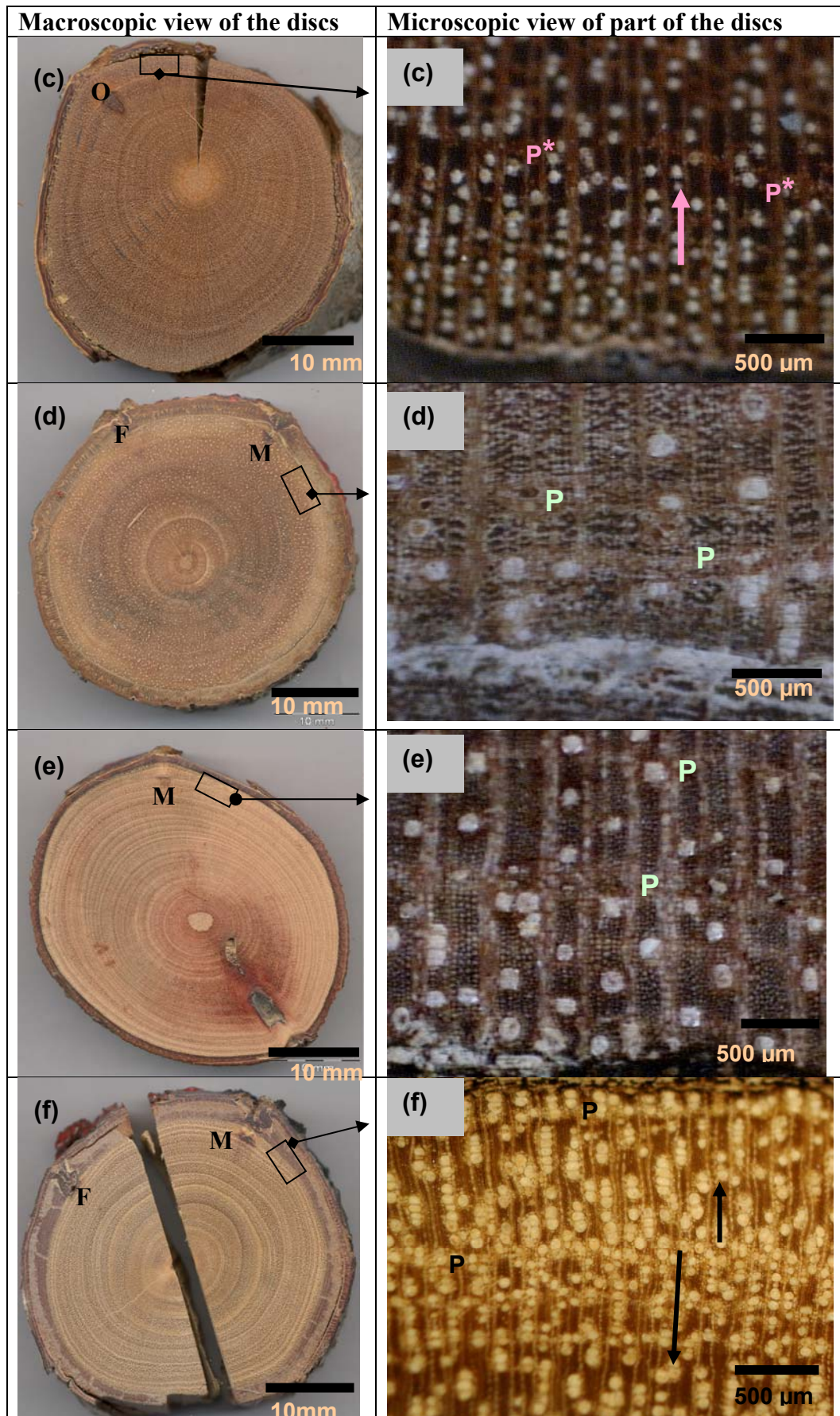
M; may 2005 wound, **F**; Feb. 2006 wound, **O**; Oct. 1999 wound; **P***; parenchyma band,
P; parenchyma band diffuse throughout the ring border, **D**; deposits in the vessels due
to wounding, **U**; absent border,↑ or↓; direction towards decreasing vessel density.

3.2.3 Cambial mark

In addition to the paint marks on the trees, the location of the cambial wounding was facilitated by a well defined reaction of the tree, resulting in a lenticel-like structure visible on the outer bark. The wounds inflicted in May 2005 had healed completely while in most of the studied tree species those in February 2006 were still open or only partly closed with very little new wood formed (see Table 3 macroscopic view). At the position where the needle was inserted, the canal remained visible as an empty cone (Figure 8), as a result of crushing and compressing xylem cells with the needle. The marker line (see Methodology section) from which radial increment measurements were made towards the bark was anatomically different among the species but not always clear (Table 4). Furthermore, *H. littoralis* had an exceptionally thick bark and in most disks pinning was not deep enough to create a visible reaction. In such cases where no proper reaction was seen, presence of callus tissue provided a good time mark. In the other cases it was as well a good alternative to the anatomical changes of the wood made after wounding (Table 4).
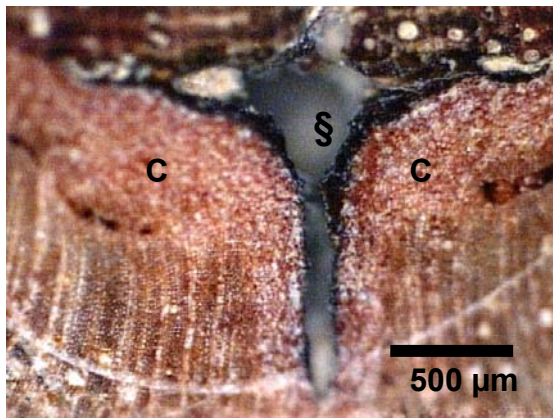
Figure 8. Picture of a section of a sanded disc showing; §-Canal created by the May 2005 pinning on a *X. granatum* and C- callus tissue produced due to wounding.

Table 4. Description of the marker lines caused by cambial wounding in the tree species studied.

Tree species	Type of marker line
S. alba	** callus tissue. * flattened fibre cells with a zone of relatively more tiny vessels above.
H. littoralis	**presence of a red line. **(Ψ)** *callus tissue. *arrangement of vessels in tangential bands next to the wound.
C. tagal	**tangential band made of dense aggregation of tiny vessels. *callus tissue. **bending of ray parenchyma away from the wound.
B. gymnorrhiza	**bending of ray parenchyma away from the wound. *tangential band made of dense aggregation of tiny vessels.
X. granatum	*parenchyma band formed in line with callus tissue. **dark line running within a parenchyma band (traumatic canals).
L. racemosa	*black line (thick walled fibre cells). **tangential band made of dense aggregation of tiny vessels.

*less frequent, ** more frequent

(Ψ) Red line represents a parenchyma band with cells filled with gums and other deposits, which separates the reaction zone to the inside of the wound where xylem cells are filled from the wood formed after wounding that is free from deposits.

3.3 Annual wood production

3.3.1 Growth ring counts

Counting of the growth rings formed after wounding of the cambium was best done macroscopically since demarcation of the rings was less clear at the microscopic scale. The highest number of growth layers formed during the study period was noted in *X. granatum*. In certain cases mostly *S. alba*, the counting of growth layers was hindered by unclear borders (Table 4; Figure 9). Considering the various species irrespective of the sites from which they were sampled, *X. granatum* and *L. racemosa* had the highest percentage of discs with clear rings (Table 5). A further effect of site was noted as the percentage number of disks with a given number of clear or unclear rings differed greatly (Figure 9). Generally, the percentage number of discs per species with a given number of rings was in the following order; X. *granatum* > L.

racemosa > *B. gymnorrhiza* while the rest of the species had a considerable percentage of discs with either no rings or unclear ring formation (Figure 9).

Table 5. Clarity of the rings formed during a period of one year in the species studied irrespective of the sampling site.

Species studied	Percent number of discs		
	Unclear rings	No rings formed	Clear rings
S. alba	50	0	50
H. littoralis	20*	40*	40*
C. tagal	0	100	0
B. gymnorrhiza	33.33	16.67	50
X. granatum	0	0	100
L. racemosa	0	0	100

* The percentage can be biased due to shallow pinning (see discussion)
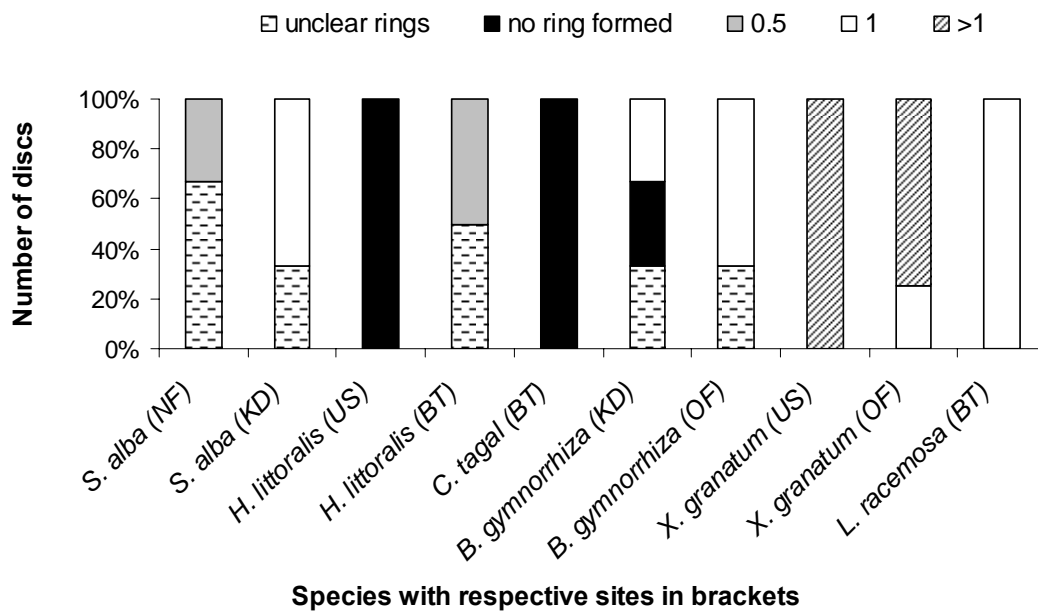
Figure 9. Number of discs with varying ring number expressed as percentage of total discs sampled (discs with May, 2005 pinning wound).

3.3.2 Radial increment

The radial increment measurements done to the left and right of the discs' wound were significantly different from each other (p=0.02446; df=60; t=-2.30799). The difference between the studied species' annual radial increment was highly significant (p=0.0013; df=5; F=5.91084) with *S. alba* at Kidogoweni site recording the highest increment (Table 6). Moreover, *X. granatum* recorded high annual radial increment irrespective of site. A Post hoc test supported the exceptional high radial increment of *X. granatum* in both the sites sampled (Table 7).

Table 6: Annual radial increment of the six mangrove tree species in the period between May 2005 and June 2006.

Tree species	Sites*	Specimen No.§	Annual radial increment mm / yr
S. alba	KD	Tw58983, 85 & 86	2.6±2
	NF	Tw58981, 82 & 85	1.8±0.5
H. littoralis	BT	Tw58978, 79 & 80	0.8±0.3
	US	Tw58976 & 77	0.3±0.4
C. tagal	BT	Tw58998 & 99	0.28±0.09
B. gymnorrhiza	KD	Tw58971, 74 & 75	0.2±0.1
	OF	Tw58970, 72 & 73	0.9±0.5
X. granatum	OF	Tw58965 - 68	2.5±1
	US	Tw58963 & 64	2.3±1
L. racemosa	BT	Tw58995 - 97	0.81±0.08

* See figure 2 and table 1.
§ Referring to the wood collection of the Royal Museum for Central Africa, Tervuren.

Table 7. Results of a Tukey HSD test (bold and italicised values are significant at p<0.05) for the log transformed annual increment.

	species	{1}	{2}	{3}	{4}	{5}	{6}
1	*S. alba*		0.076806	0.073899	***0.027136***	0.990578	0.39706
2	*H. littoralis*	0.076806		0.972792	0.999393	***0.023222***	0.994996
3	*C. tagal*	0.073899	0.972792		0.994754	***0.030648***	0.875305
4	*B. gymnorrhiza*	***0.027136***	0.999393	0.994754		***0.007167***	0.960597
5	*X. granatum*	0.990578	***0.023222***	***0.030648***	***0.007167***		0.185999
6	*L. racemosa*	0.39706	0.994996	0.875305	0.960597	0.185999	

While considering the monthly radial increment, all the tree species except for *X. granatum* had lower values in the period Feb. 2006 - June 2006, period 2 relative to

May 2005- Feb. 2006, period 1 (Figure 10). Further, the different tree species showed varying monthly radial increment rates in each of the periods analysed. These differences between species were statistically significant at p<0.05 within period 1 (p=0.02855; N=28; H=12.50690 Kruskal-Wallis) as well as in period 2 (p =0.0125; N=28; H=14.53949 Kruskal-Wallis).

Site variations were as well noticed as most of the species showed differences in monthly increment from one site to the other (Figure 10). A remarkable difference was noticed in *S. alba* where in period 1 the increment in Kidogoweni and New Fisherman sites were more or less the same while in period 2 the discs from the latter site showed a great reduction in monthly increment (Figure 10). The difference in monthly increment between the two periods within a given site was only statistically significant in *S. alba*, *B. gymnorrhiza* and *L. racemosa* (Table 8). Even within the same period and site, a given species showed lots of variation in radial growth as seen in the large standard deviations in most cases (Figure 10).
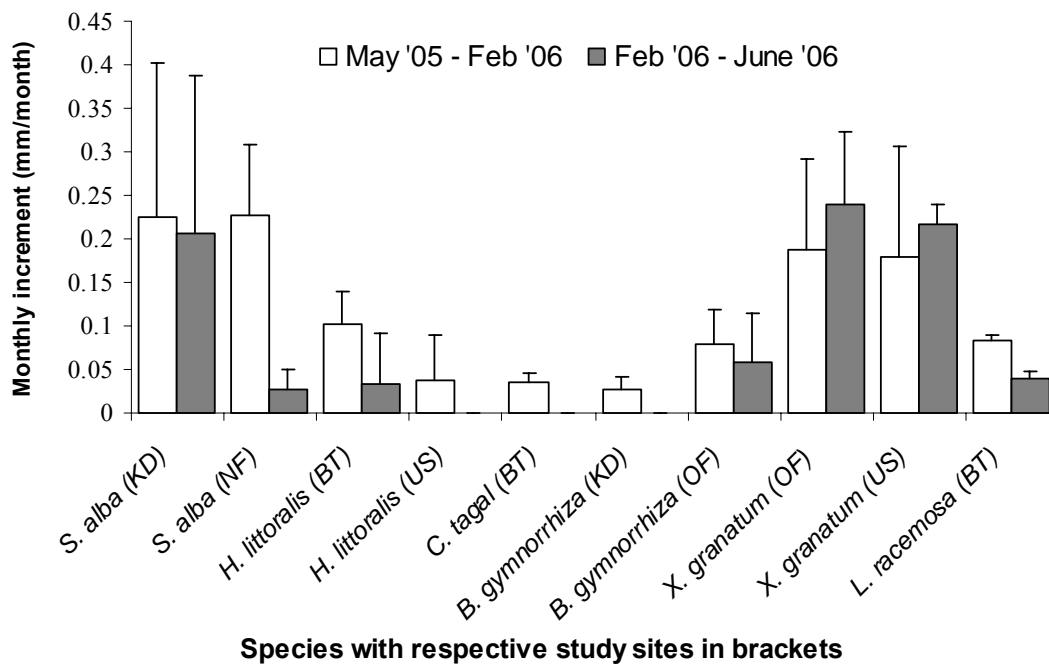
Figure 10. Monthly radial increment in the different study species, categorized by site (between brackets), within the two study periods.

Table 8. Results of **(a)** t-tests and **(b)** Mann-Whitney U tests to compare monthly radial increment between period 1 and 2 in the different tree species at their respective sites. (Bold and italicised p values indicate significance at p<0.05)

	Species	Site	p	df	t
(a)	*S. alba*	NF	***0.0138***	4	4.1865
		KD	0.9021	4	0.1310
	H. littoralis	BT	0.4227	2	1.0000
	B. gymnorrhiza	OF	0.6461	4	0.4900
	X. granatum	OF	0.4552	6	-0.8041
	L. racemosa	BT	***0.0029***	4	6.4919

	Species	Site	p	U	Z
(b)	*H. littoralis*	US	0.4386	1	0.7746
	C. tagal	BT	0.1214	0	1.5492
	B. gymnorrhiza	KD	***0.0370***	0	1.9634
	X. granatum	US	1.0000	2	0.0000

3.3.3 Radial increment and Tree parameters

In most of the species, there was a positive correlation between increment and tree parameters (Table 9). However, the correlations were not statistically significant in any one of them. Furthermore the plots relating annual radial growth with either diameter at breast height (D130cm) (Figure 11) or tree height (Figure 12) showed no proper trend except for *L. racemosa*. In this tree species, high annual radial increment coincided with larger stem diameter and height.

Table 9: Spearman Rank and product-moment (*) correlation test results between annual radial increment and height and stem diameter.

Species	Factor tested against Annual increment	R	p	N
S. alba	Log D130cm*	-0.4585	0.3600	6
	Height*	0.3989	0.4330	6
H. littoralis	D130cm	-0.2000	0.7471	5
	Height	-0.1000	0.8729	5
C. tagal	Disc diameter	0.2000	0.8000	4
	Height§	–	–	–
B. gymnorrhiza	D130cm	0.2571	0.6228	6
	Height	0.0286	0.9572	6
X. granatum	D130cm	0.7714	0.0724	6
	Height	0.2571	0.6228	6
L. racemosa	D130cm	0.8660	0.3333	3
	Height*	0.9946	0.0660	3

R is correlation coefficient and N is sample size

§ Height data available for only two samples therefore test not carried out.
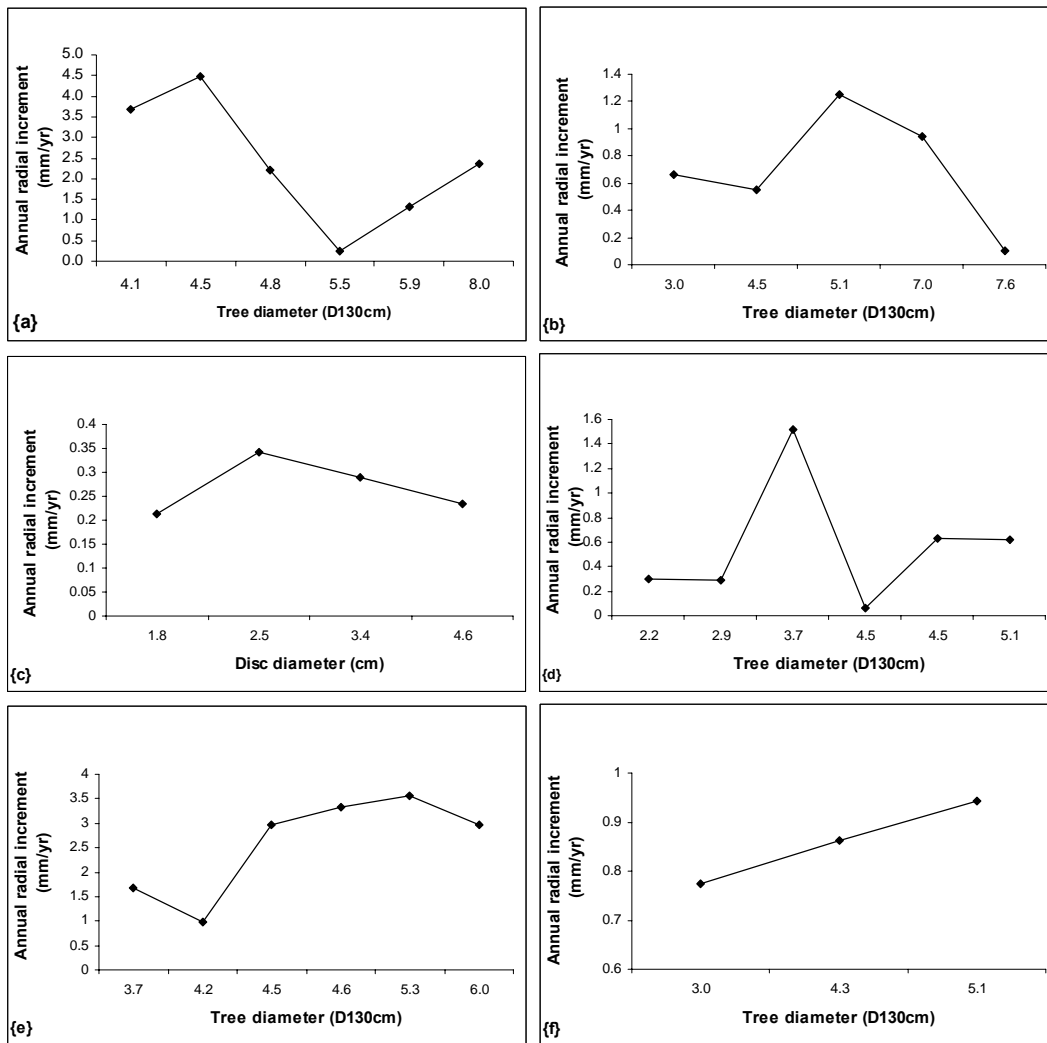
Figure 11. {a-f} Annual radial increment and tree diameter at breast height relations in (a) *S. alba*, (b) *H. littoralis*, (c) *C. tagal*, (d) *B. gymnorrhiza*, (e) *X. granatum*, and (f) *L. racemosa*. (For *C. tagal*, data on tree diameter were unavailable therefore disc diameter was used).
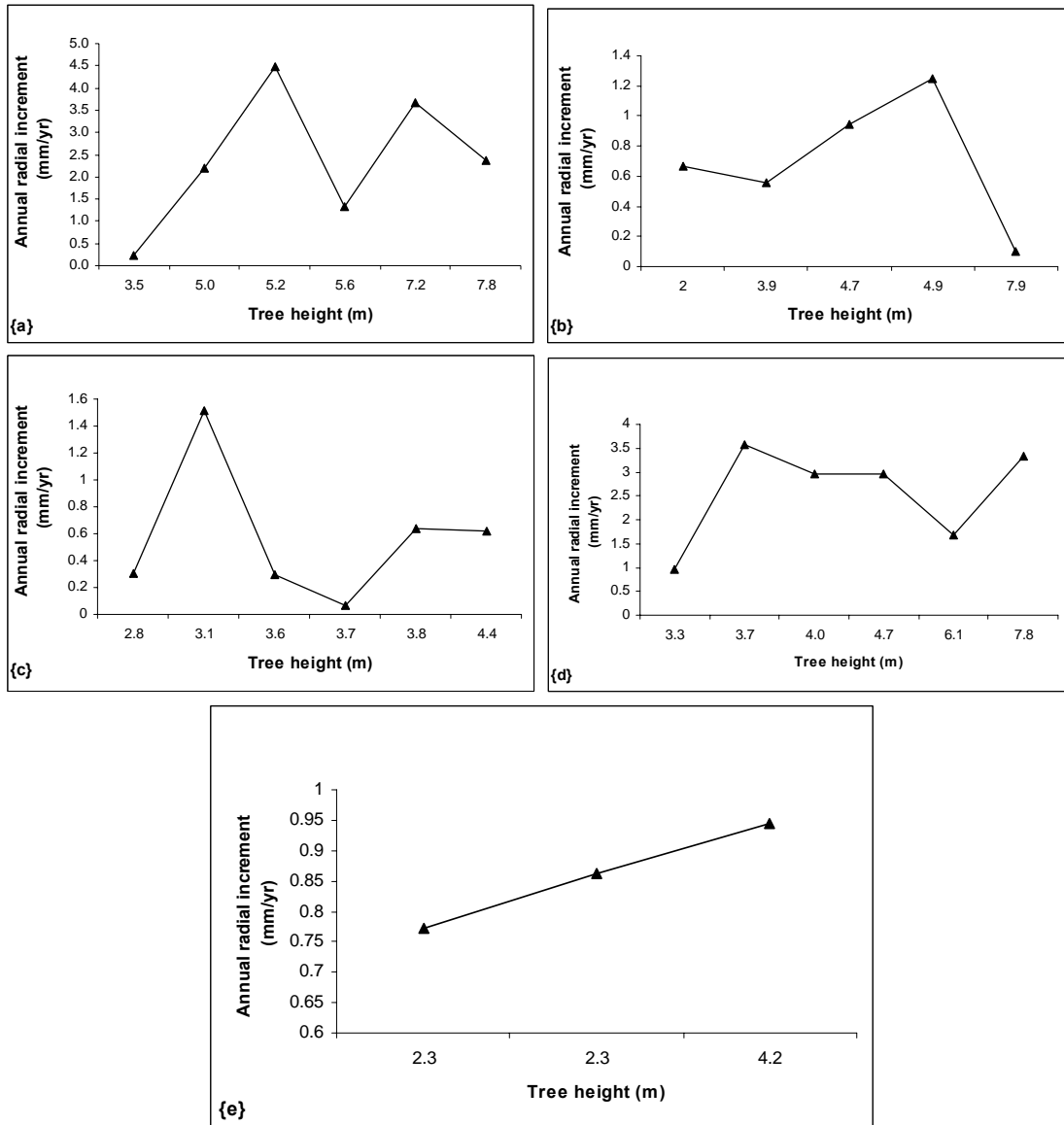
Figure 12. {a-e}: Annual radial increment and height relations in (a) *S. alba*, (b) *H. littoralis*, (c) *B. gymnorrhiza*,(d) *X. granatum* and (e) *L. racemosa*.
(Height data were only available for two *C. tagal* trees therefore this species was not included here).

3.3.3 Radial increment and salinity

Except for *S. alba*, a general higher radial increment was registered by trees growing in sites which have lower maximum values (Figure 13A) and experience less variation in salinity (narrow salinity range) (Figure 13B) as compared to those with higher max. and wider ranges. Mann-Whitney U test however showed no significant difference at $p<0.05$ in radial growth for the specific species found at different max. salinity and salinity ranges associated with the sites; *S. alba* (p=0.126, U=1; Z= -1.528), *B. gymnorrhiza* (p=0.05; U=0; Z=1.964), *H. littoralis* (p=0.2248; U=1; Z=-1.155) and X.

granatum (p=0.165; U=1; Z=1.389). Note that similar values were obtained in both tests involving salinity ranges and maximum salinity associated with sites from which the samples were collected and also that test was not performed trees species only present in one salinity range.
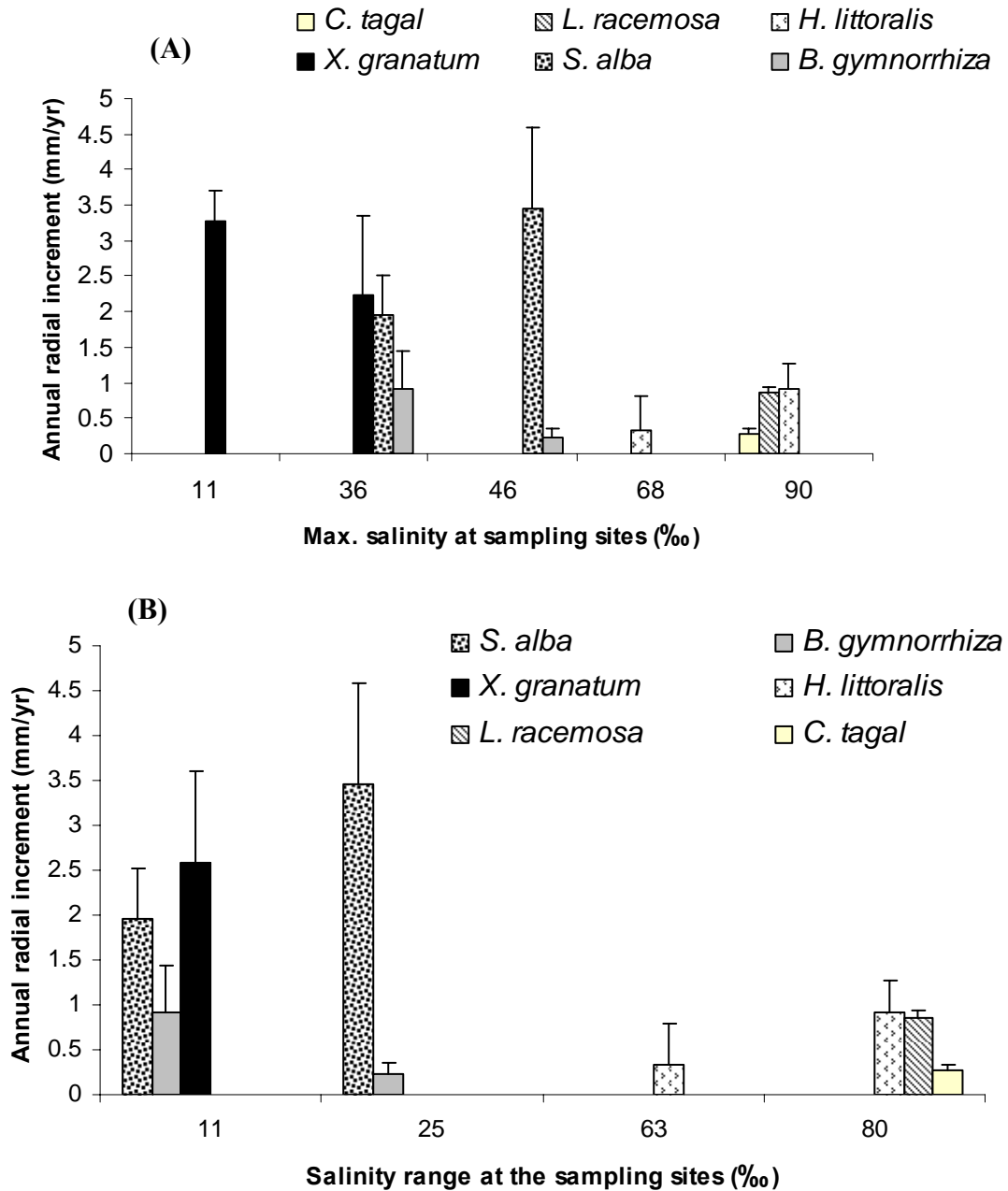
Figure 13. Annual increment in the studied species grouped by (A) maximum salinity attained at a given site and (B) salinity range.

3.3.4 Phenology and wood production

The relationships between wood production and phenology in *S. alba* are inferred using studies conducted between Jan. 2005 and Nov. 2006 in Gazi bay in the NF site by Virginia Wang'ondu (Figure 14 and 15). In May 2005-Feb. 2006 (period 1) there was a higher increment than in Feb. 2006-June 2006 (period 2), the latter coinciding with a long period of leaf loss with very little new leaves formed (Figure 10; Figure 15). During this period the trees also experienced fruit production and fruit fall (Figure 14). In period 2, no reproductive event was experienced (Figure 14) and it coincided with decreased leaf loss coupled with a higher gain in new leaves than in the previous period (Figure 15).
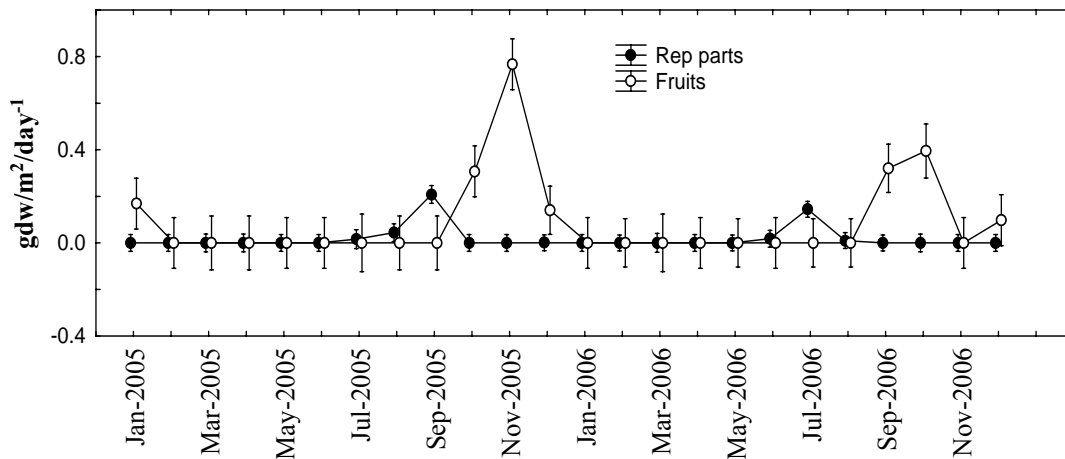
Figure 14. Fruit fall and dropping of other reproductive parts in *S. alba* during the study period from Jan. 2005-Dec. 2006 (data obtained from a phenological study by Virginia Wang'ondu).
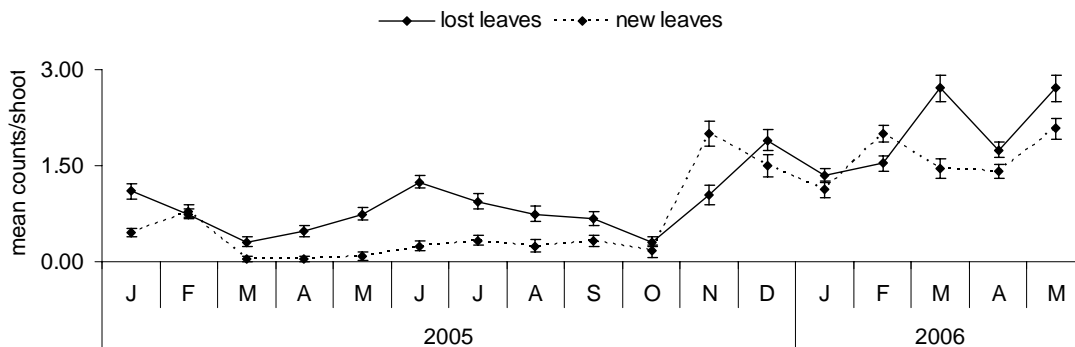
Figure 15. Vegetative phenograms showing mean monthly counts of leaf gain and fall for *S. alba* (data obtained from phenological study by Virginia Wang'ondu).

4. Discussion

4.1 Growth Ring anatomy in the six mangrove species

4.1.1 Clarity of growth rings in mangroves

Mangrove trees can show some form of ring structure but it is not always clear in all the species as noted in this study. The high frequency of unclear rings in *S. alba* as noted could be due to lack of a stressing condition in the environment which as explained by Worbes (1995) and Trouet *et al.* (2006) is necessary for ring border formation. *S. alb*a grows in the zone open to the sea (inundation class 1) and thus remains exposed for quite a short time during the low tides (Watson, 1928). Furthermore, the difference in soil water salinity between dry and wet season in this zone is negligible due to the high frequency of inundation and the great dilution effect. It thus follows that the environmental conditions here are more or less uniform throughout the year resulting in the absence of rings due to lack of stressing factors.

The more clear rings in mangrove tree species *C. tagal, L. racemosa* and *H. littoralis* could thus be due to the fact that they occur further in the tidal flat (Inundation class 3 and 4) which are known to suffer great fluctuations in soil water salinity due to lower frequency of inundation (Watson, 1928). Under such conditions, presence and absence of rainfall could play a role in manipulating salinity which in turn acts as a stressing factor to determine vessel density resulting in creation of ring borders as noted as well in *R. mucronata* (Schmitz *et al.,* 2006). A high salinity creates an osmotic stress subjecting the xylem vessels to the risk of cavitation and subsequent embolism (Sperry and Tyree, 1988; Tyree and Sperry, 1989; Hacke *et al*., 2001). The associated increase in vessel density has been interpreted as a strategy to ensure maximum conduction of water even with cavitation of certain vessels.

B. gymnorrhiza though being found in inundation class 1, it occurs further from the open sea and is thus exposed for relatively longer periods than *S. alba* enhancing the chances of environmental factors such as salinity to play a role in formation of the clearer rings. Ability of temporal changes in soil salinity to be recorded in wood anatomical changes has been reported in *R. mucronata* by Verheyden *et al.* (2005). Moreover, Verheyden *et al.* (2005) and Schmitz *et al.* (2006) noted a minor influence of precipitation on the yearly fluctuating vessel density of *R. mucronata* which also

mark the ring borders in both the tree species an indication that salinity could be the major driving factor. In addition to salinity, the indistinct ring border marked by a gradual change in vessel density in *B. gymnorrhiza* species could also related to genetic factors as the same has been noted in *C. tagal* and by Verheyden *et al.* (2005) in Kenyan *R. mucronata* all of which belong to the family Rhizophoraceae.

Despite the patchy distribution (no zonation) of *X. granatum* within the tidal flats, this tree species seems to be restricted to a given salinity range just like the other species. The extremely clear rings formed could thus be attributed to morphological differences among species which Cook (1985) refers to us to as genetic contribution to ring formation. Moreover, a possible influence of drought-rainfall transition on ring border formation in this species has been noted (see further, § 4.2). Other factors which could not be proved in this study such as tree phenology (Slim *et al.*, 1996; Drew, 1998) and nutrients (February and Manders, 1999) could have also played a role in ring border formation in *X. granatum* and the other tree species as they have been found to do so in *Cyrilla racemiflora* trees and fynbos shrubs respectively.

Though it is not always the case that clear rings observed macroscopically are distinct microscopically (Wheeler and Gasson, 1989), in *L. racemosa* and *X. granatum* the clear rings as seen with the naked eye translated to distinct ring borders at the cellular level. Similar results were noted by Détienne (1989) and Worbes (1995) in *Tectona grandis* and trees from the family Fabacae, which had ring porous wood with growth ring borders marked by a gradual change in vessel density and terminal parenchyma bands respectively. These features (axial parenchyma and ring porous wood) are as well observed in *X. granatum* and *L. racemosa* in that order in this study.

4.1.2 Merging rings

Merging rings which were found to be quite common in *S. alba*, *H. littoralis* and *B. gymnorrhiza* are also referred to as wedging or locally absent rings (Tarhule and Hughes, 2002). The presence of locally absent rings could be in response to non uniform growth over the discs as it has been noted in this study that radial increment recorded to the left of the cambial wound was significantly different from the growth at the right side of the wound. In these particular three mangrove species, mergence of rings was more common towards the outer part of the disc, similar to findings by

Trouet *et al.* (2006) who noted the same in *Brachystegia spiciformis*. It has also been stated that radial growth rates are much lower towards the bark (Tarhule & Hughes, 2002) and this might have contributed to the higher frequency of merging rings at these points of the discs. Though size of discs does not directly translate to age, merging rings were as well found in this study to be a common phenomenon in larger discs. This could be inline with the findings by Trouet *et al.* (2006) who noted a direct relationship between age of *B. spiciformis* trees and number of merging rings. The bigger discs could be from much older trees and hence the relationship.

4.2 Wounding response in mangroves

The marker lines formed as a result of wounding responses were of various magnitude and anatomy in the tree species studied. This is in agreement with tree wounding response studies which indicate that the reaction could extend from just around the wound to some distance away and may vary from one tree to the other (Wodzicki and Zajaczkowski, 1970; Shigo and Dudzik, 1985). As further stated by Warren (1978) the extent of spread depends on the nature of the traumatic signals produced as a result of injury and the distance to which the signals are propagated which varies between species. In *S. alba* for instance, most of the discs had only reaction around the wound characterised by callus formation. This was as well noted in *C. tagal* and *H. littoralis* but to a less extent.

This study has revealed formation of traumatic canals close to the pinning wound in *X. granatum* a species belonging to the family Meliaceae. The same feature has been found to form in other tree species such as *Capara procera* belonging to the same family as reaction to an injury (Wheeler, 1989). The canals were present as well at certain points away from the pinning wound an indication that *X. granatum* could be forming these canals during any form of stress. The bending of ray parenchyma in *B. gymnorrhiza* and *C. tagal* could be taken as a general occurrence in the family as the two tree species belong to the same family Rhizophoraceae. Filling of wood tissues with gums and other deposits (Wheeler, 1989) is a phenomenon which is known to aid in preventing pathogens from entering further in to the wood. In this study, *H. littoralis* produces red deposits spreading away from the wound.

4.3 Dendrochronological potential of the study species

The almost absent borders and lots of merging rings as seen in *S. alba* makes it difficult to separate false rings that form due to irregular environmental events (Fritts, 1976) from periodic rings hence disqualifying this species as a candidate for dendrochronology. *B. gymnorrhiza* had fewer discs with unclear ring formation over the study period than *S. alba*. However, the merging rings also reduce its potential for such studies.

Although all *C. tagal* trees and the *H. littoralis* trees from Upstream did not even form one ring during the study period, this does however not immediately rule out the possibility of using these tree species for dendrochronological applications. For instance, though *C. tagal* is generally a slow growing species, requiring more than a year to at least form a ring it did not form merging rings. *H. littoralis* showed rather distinct borders but also had a very thick bark and as such this meant that in most cases the cambium was not punctured. It thus follows that there probably was new growth during the experimental period which was however not detected due to failure of the cambial markings and could not be quantified at all or only to a less extent in some discs leading to imprecision in ring count. It is worth noting that site differences might have caused the differences in bark thickness between trees of the Upstream site and trees of the Begin Transect site with the former having much thicker barks. Thick bark is one of the xerophitic features in plants (Burkart, 1976) and *H. littoralis* growing much to the landward zone generally require water conserving mechanism to survive the constantly dry conditions. It could therefore be said that Upstream had harsher (drier sediment) conditions than Begin Transect site.

In Gazi bay, there are two rainy seasons, one very dry and a moderate season (Figure 4); on one hand, it would thus be expected that the trees form at least 2 rings in a year to coincide with either number of wet or dry seasons or the transitions. On the other hand, a tree would be expected to form only one ring if the extreme dry season is the trigger (Figure 4). That is because these conditions could cause changes in trees' wood anatomy (Worbes, 1995). For instance Verheyden *et al.* (2005) found out that *R. mucronata* formed many vessels to transport water during the dry season and less during the wet season resulting in annual rings. This was not the case in all species that formed rings except for *X. granatum* which formed more than one ring and all *L. racemosa* discs. As a result, this also reduces the ease with which seasonality of ring

formation can be determined in the other four tree species by relating to climate and consequently their use in dendrochronology to reflect past climatic events.

For a tree to qualify for use in dendrochronology the rings have to be periodic and thus be dateable. In this study, the marker lines did not coincide with the ring borders apart from *X. granatum* and *L. racemosa*. It could thus be that ring borders in these species form in May which is a transition from rainy to dry season. However, in *X. granatum* more than one ring was formed in a year. Rings are thus not annual but could still be periodic. The time of ring border formation in the other species can not be determined easily in this study as the borders lie slightly above and below the marker line.

Table 10. Summary of tree species' dendrochronological potential

Tree species	Rings present	Merging rings	Rings periodic	Use in dendrochronology
S. alba	×	√	×	×
B. gymnorrhiza	√	√	×	×
H. littoralis	√	×	–	–
C. tagal	√	×	–	–
X. granatum	√	×	√	√
L. racemosa	√	×	√	√

(√Yes, × No, ─ Not confirmed in this study)

4.4 Wood production in mangroves

4.4.1 Site effect on wood production

In this study, a clear difference was noted in wood production rate for the different species between the different sites which could be linked to salinity. It is an obvious fact that different species have different growth rates with notably *C. tagal* cited as a slow grower (Shiokura, 1989). However, in this study it is quite remarkable that different species growing in sites which have lower maximum salinity values and do not experience great fluctuations show relatively higher rate of radial increment than species growing in sites with higher salinity values. This is in agreement with experiments by Hasegawa *et al*. (2000) on cellular and molecular responses of selected terrestrial plants to high salinity which showed that stress induced by salinity leads to decreased growth and reduction in yield. Moreover, it has been stated by

Marschner (1995) and Zhu (2001) that increased accumulation of salts around the roots due to high salinity causes the development of an osmotic stress that disrupts cell ion homeostasis by inducing inhibition in the uptake of essential nutrients like potassium and calcium. Potassium for instance plays an important role in regulating water balance, promoting normal cell division, opening and closing of stomata and transport of amino acids to protein synthesising sites among other roles. This means that any factor that interferes with K uptake has a potential to deter plant development. Even in salt tolerant tree species such as *Tamarindus indica* and olive, studies by Gebauer *et al.* (2004) and Chartzoulakis (2005) respectively have shown that there exist a salinity threshold above which such trees experience reduced growth and fruit production.

It is worth noting however that *H. littoralis* and *S. alba* did not express an effect of increased salinity on their growth giving the probability that factors other than salinity played a role. In the case of *S. alba* this strengthens the argument that pest attack played a big role in manipulating growth (see further, § 4.3.4) while for *H. littoralis*, the anomalies could be attributed to the failure of the cambial markings.

4.4.2 Wood production in relation to tree growth parameters

Apart from *H. littoralis* and *S. alba,* the four other tree species showed a positive relationship between radial increment and both tree diameter and height. This is contrary to expectations that for a given species, bigger trees tend to show a decrease in radial increment (Schweingruber, 1996). Furthermore it is stated by Lässig (1991) that the trees' growth potential usually increases from bottom of the tree where the tree diameter is wide towards the smaller part of the stem and branches. It should however be noted that though the correlation tests gave correlation coefficient values considerably away from zero, the valid N (sample size) was too small and hence statistical significance was lacking. Furthermore, there graphical presentations showed no proper trend in wood production and either height or tree diameter. This is similar to findings by Shiokura (1989) who found no relationship between radial increment and diameter at breast height in *S. apiculata*, *B. gymnorrhiza* and *Avicennia officinalis*.

4.4.3 Seasonality of wood production?

A general non uniform rate of wood production has been noted in this study over a year. This finding is in agreement with Koriba (1958) who found out from a study in Malaysia that even in the tropics, in conditions which he referred to as ideal for uniform growth; only 15% of the tree species reflected this. He noticed that at one point the growth seemed to cease or become very slow. While considering the two periods of which study was divided, it is only in *X. granatum* that the high rainfall during period 2 (see climate diagram, figure 4) translated directly to increased diameter increment while drought during period 1 hindered radial growth as expected. This is in line with studies by Voegeli and Reinhart (1956) who noted that drought hinders the increase in radial diameter. Détienne (1989) also found out that cambial activity either comes to a halt or slows down a lot during the dry season. However, the reversed situation in the other five species could be attributed to carry over effects where we find that radial increment during period 2 seemed to have been influenced by the dry months in period 1. Similar findings were noted by Zweifel *et al.* (2006) in oak and pine woodland where a relatively dry year led to reduced radial growth in the following wetter year. Next to carry over effects, Shiokura (1989) also found similar results but which he attributed to production of more cells with greater diameter during the dry season to transport more water. Phenological activities which trees carry out during a given period may contribute towards reduction or increase in radial increment despite the climatic conditions. For instance, reproductive processes in trees may lead to slowed down radial increment (Kozlowski, 1962). Though not studied for all the species, this reverse relationship was seen in *S. alba* as explained here below.

4.4.4 Phenology and wood production in *S. alba*

During period 2 (Feb. 2006-June 2006), *S. alba* gained many new leaves as the old ones were lost. This might have translated to higher photosynthetic rates thus we expect an increase in diameter growth during this period. Furthermore, studies by Freeland (1952) showed that though older leaves of evergreen trees may make a distinct contribution to the photosynthetic capacity of a tree, the younger (new season's) leaves are the most important. However, in this study we noticed a reduced radial growth during period 2 when trees have plenty of young leaves while during

period 1 when there was a relatively low production of new leaves coupled by lower loss of the old ones there was a higher increase in girth. This could probably be due to the fact that the contribution of young leaves to tree growth is more directed to apical growth than to radial increment (Larson, 1964).

Further explanation could be found in the distribution of photosynthates as most studies reveal that there exists prioritisation. Kozlowski (1962) noted that less than 45% of the photosynthates go towards stem elongation, thickening and root elongation while the rest is used in production of new leaves and reproduction. It would therefore mean that during fruiting and high production of new leaves as in period 2 the tree would probably show decreased radial increment. In this study the production of abundant new leaves in period 2 might have contributed largely to the decreased radial increment. In period 1 the tree experiences a whole cycle of reproductive events ranging from, budding over flowering to fruiting but coupled with lower leaf production. It could therefore mean that in this case, the low leaf production acted to counteract the fruiting or that during the time when the trees were not in fruits, the trees experienced high radial growth that masked the slow increment when they had the reproductive parts on.

4.4.3 Pest effect on *S. alba*

S. alba trees at the New Fisherman site reflected the *Salagena discata* (insect pest, order Lepidoptera) attack in a slowed down rate of annual wood production. This could be attributed to the fact that injuries inflicted by pests may locally kill the cambium as indicated by Robin *et al.* (1992) who noted that certain pathogens are capable of killing the cambium at the point of invasion and as such slowing down its activities as it takes time to heal. However, we noticed that a significantly lower radial increment is only experienced in period 2 while both pest attacked and unattacked *S. alba* trees showed a more or less similar radial growth during the first period of the experiment. This could be associated with the presence of a threshold level in the affected proportion of a tree before the pest attack is manifested in a reduced growth.

Even though the pest attack had been noticed some time back before the onset of the experiment, the intensity of the attack was probably still mild during period 1. It is only in period 2 that a critical level of infestation might have been reached that it is

directly reflected in a slowed wood production. A similar delayed effect was found before in a field experiment mimicking attack by green spruce aphids (*Elatobium abietinum*) on 3-year old spruce trees (*Picea sitchensis*) (Straw *et al.,* 2002). They found out that the total number of new needles produced by defoliated and undefoliated trees in the first and second year of infestation was similar, but that defoliated trees produced 10% fewer needles two years later. This is a clear indication that there exists a level below which an attack on trees by a pest is not reflected on its physiological activities.

5. Conclusion

- Among the six mangrove tree species studied, *X. granatum* and *L. racemosa* had well defined ring borders with possibilities of annual and general periodicity (ring borders forming during the transition from wet to dry season) in ring formation in the two respectively thus are promising for use in dendrochronological studies.

- Furthermore, the number of rings formed in *X. granatum* and *L. racemosa* can be used in age determination. In the latter, simple ring counting would directly translate to age while in the former, the number of drought-rain transitions that exist in a year can be extrapolated to the past by counting the rings in an entire disc and relating with the transitions. The growth rings' periodicity could also be used to infer past climatic conditions by looking for missing rings or 'abnormal' anatomic feature laid down in a ring in the past.

- It has also been noted that *X. granatum* forms traumatic canals not only around the pinning wound but also at other points. This is an indication that the canals could be used to infer timing of past forest disturbances.

- Radial increment in the mangrove tree species studied is not uniform over the study period and has no proper relationship with either tree height or diameter at breast height.

- As much as precipitation could be important in growth, the study gives possibility of an integrated role played by other factors such as salinity, phenology and pest attack in the manipulation of radial increment. The negative effect of *Salagenia discata* pest on radial growth has been demonstrated to display a threshold level below which the attack is not reflected on wood production.

6. Recommendations

- As confirmed in this study, *C. tagal* is a slow growing tree species explaining the lack of ring formation during the one year study period. Cambial marking experiments involving this tree species should therefore be run over a longer period of time to gauge the timing of ring border formation.

- The problem of an extremely thick bark in *H. littoralis* trees requires that deeper wounds are inflicted to ascertain that the cambium is injured during pinning.

- Possibility of annual ring formation has been noted in *L. racemosa* requiring further study on more trees and for more than one year to affirm this strongly.

- Monthly pinning on *X. granatum* are necessary to find out the exact timing of border formation as more than 1 border was formed in a year.

- Though in natural forests, there are several forms of defects on tree forms which could limit the kind of trees from which samples can be collected; future studies should involve a larger sample size to mask the differences in biological replicates. This would increase chances of differences existing between samples to be recognised statistically thus giving a stronger argument in the interpretations.

- Field data on trees neighbouring the sampled ones can be useful for a better understanding and interpretation of wood reactions while in the laboratory (Stoffel *et al*., 2005); a more detailed description and the documentation of state and form of other trees in the field is necessary for such studies in the future to look for possible influence of trees growing close to the sampled ones.

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