Tree Growth and Tree Regeneration in Two East African Rain Forests as related to the Abiotic Environment after Human Disturbance

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Acronyms

% circ:	Relative growth
abs.:	Absolute growth
ACE:	Species estimator
acetate:	Ammonium acetate extracted
acid:	Nitric acid extracted
a.s.l.:	Above sea level
B:	Biso (part of Budongo Forest)
BA:	Basal Area
BCFS:	Budongo Conservation Field Station
BCI:	Barro Colorado Island Forest
BDO:	Biodiversity Observatory
BF:	Budongo Forest
BIOTA:	Biodiversity Monitoring Transect Analysis
BU:	Buyangu Hill (part of Kakamega Forest)
C:	Carbon
Ca:	Calcium
CA:	Campforest (part of Kakamega Forest)
CDI:	Commercial Disturbance Index
CE:	Crown exposure
CEC:	Cation Exchange Capacity
Chao 1:	Species estimator
Chao 2:	Species estimator
circ.:	Circumferential
Cmol:	Coulomb per mole
CO:	Colobus (part of Kakamega Forest)
DBH:	Diameter at Breast Height
DBH max:	Maximum DBH
DBH min:	Minimum DBH
EA:	East African herbarium in Nairboi, Kenya
EC:	Electrical Conductivity
e.g.:	exempli gratia
EM:	Ectomycorrhiza
FD:	Forest Department, Kenya
Fisher’s alpha:	Diversity Index
FTEA:	Flora of Tropical East Africa
ha:	Hectare
Height max:	Maximum height
Height min:	Minimum height

HOH:	Herbarium of the University of Hohenheim
IDH:	Intermediate disturbance hypothesis
IM:	Intermediate
indiv.:	Individuals
IPav:	Monthly Incident Precipitation
IP2:	Summed two-monthly Incident Precipitation
IP3:	Summed three-monthly Incident Precipitation
IK:	Ikhuywa (part of Kakamega Forest)
IS:	Isecheno (part of Kakamega Forest)
IT:	Shade-Intolerant
ITCZ:	Inter Tropical Convergence Zone
Jackknife 1:	species estimator
Jackknife 2:	species estimator
K:	Potassium
KA:	Kaimosi (part of Kakamega Forest)
KI:	Kisere (part of Kakamega Forest)
km^2 :	Square kilometer
KF:	Kakamega Forest
KP11:	Kaniyo-Pabidi 11th compartment (part of Budongo Forest)
KWS:	Kenyan Wildlife Service
LAI:	Leaf Area Index
LDI:	Local Disturbance Index
MA:	Malava (part of Kakamega Forest)
MANOVA:	Analysis of variance
MFNP:	Murchison Falls National Park
Mg:	Magnesium
MH:	Maximum height
MHU:	Herbarium of the Makerere University, Uganda
Mn:	Manganese
mNN:	Meter über Normalnull
N:	Nitrogen
N3:	Nyakafunjo 3rd compartment (part of Budongo Forest)
N4:	Nyakafunjo 4th compartment (part of Budongo Forest)
N15:	Nyakafunjo 15th compartment (part of Budongo Forest)
n.d.:	Not determined
NFA:	National Forestry Authority, Uganda
NESS:	Normalized Expected Species Shared
NMDS:	Non-metrical dimensional scaling
No.:	Number
ODI:	Overall Disturbance Index

p:	Probability
P:	Phosphorus
PG:	Physiological Group
pH:	Power of hydrogen
precip.:	Precipitation
RD:	Number of rainy days
RDM:	Repeated diameter measurements
rel.:	Relative
SAI:	Salazar I (part of Kakamega Forest)
SAII:	Salazar II (part of Kakamega Forest)
SD:	Standard Deviation
Shannon H’:	Shannon-Wiener-H’ Diversity Index
Simpson:	Simpson Diversity Index
ST:	Shade-Tolerant
T:	Temperature
TFav:	Sum of monthly throughfall
TF2:	Sum of two-monthly throughfall
TF3:	Sum of three-monthly throughfall
Ti:	Titanium
UWA:	Ugandan Wildlife Authority
VAM:	Vesicular-arbuscular mycorrhiza
W21:	Waibira 21st compartment (part of Budongo Forest)
W22:	Waibira 22nd compartment (part of Budongo Forest)
W36:	Waibira 36th compartment (part of Budongo Forest)
water:	Water extracted
YA:	Yala (part of Kakamega Forest)
yr:	Year

Summary

This study deals with the stem growth and seedling regeneration of different native tree species in two East African rainforests influenced by human disturbance in Kenya (Kakamega Forest) and Uganda (Budongo Forest), also considering spatially and temporally variable environmental influences. In the lower montane rainforest (1500 to 1700 m a.s.l.) Kakamega Forest (KF) surveys were conducted on trees ≥ 5 cm diameter at breast height (DBH) on an overall area of 2.08 ha (1 ha plot and 27 plots x 400 m^2, 2007 individuals, equalling 965 ha^{-1}), 3 inventories in 7 years). At the same time 91 tree species from 39 families were identified. In addition, in subplots within the permanent plots, 8441 saplings and seedlings ≤ 5m DBH distributed among 59 tree species from 29 families were recorded (on 432 m^2, over 6 years). In the lowland rainforest (1000 to 1100 m a.s.l.) Budongo Forest (BF) a total of 1010 trees (1403 ha^{-1}), distributed among 91 tree species from 30 families, were recorded in surveys on an overall area of 0.72 ha (18 plots à 400 m^2, 2 inventories in 5 years). During the observation period saplings and seedlings (on 72 m^2, 708 individuals, in 3 years) belonging to 38 tree species from 18 families were recorded. The study areas were situated in forest areas characterised by different successional stages. These stages have emerged as a result of differing degrees of human disturbance for commercial purposes in the recent past. As this research was part of a joint project, highly resolved data on factors such as soil values, climate values, canopy characteristics and disturbance indices e.g. the Commercial Disturbance Index (CDI) was also available for a few permanent plots.

It was established that the level of species richness and species diversity is low in areas with either no or very high levels of past commercial human disturbance (e.g. after clear-cutting), whereas areas with intermediate disturbance were seen to be richer or more diverse in species. The distribution of β-diversity also indicated a disturbance gradient. The degree of human disturbance was as well reflected in the successional stages within the structure of the forest areas. The mean stem volume of trees in BF increased as the disturbance index decreased, in KF however the highest stem volume occurred in areas with intermediate CDI. The tree populations in areas with a low level of disturbance in BF were characterised by high volumes together with lower stem numbers per plot and were more stable, as manifested in the lower turnover. The openness of the canopy varied in the differently disturbed areas and had a positive effect on seedling density in BF, which in turn underlines the importance of light for the regeneration of seedlings.

In order to test the regeneration capacity of individual tree species for the most part in the intermediate stages of succession in both forests, the stem increment of 1198 trees (≥ 10 cm DBH) was measured monthly using dendrometer bands. At the same time the phenology of leaves, flowers and fruits of these trees was monitored over a period of three (in BF) and five years (in KF). In addition regeneration and establishment dynamics were analysed by counting, identifying and measuring seedlings (≤ 100 cm high) in the subplots every three months. The tree species could then be classified and allotted to their position along the pioneer-climax continuum. The early successional pioneer species were characterised by rapid growth and higher mortality rates, had no to few seedlings in the understorey and were shade intolerant. The late successional climax species however grew more slowly, had a low mortality rate, were well-established as seedlings in the understorey and shade tolerant. Most species possessed either characteristics somewhere in between these extremes or both characteristics of early and late successional species and were thus classified as intermediate. The annual stem increment varied considerably between tree species ranging from 0.6 to 2.5 mm in BF and from 0.6 to 4.4 mm in KF, and the relative diameter growth ranged from 0.3 to 1% in BF and from 0.25 to 1.58% in KF. The variability in the growth rates within tree species was even higher than that between species. Moreover the annual variability in growth within a species was higher in thinner than in thicker individuals. Individual trees however grew at a relatively constant rate.

Beside the inherent growth potential, monthly changes in the climatic conditions also had an influence on the growth pattern of many of the tree species in KF and on all of the species in the more strongly seasonal BF. During the warm dry season the growth rate decreased and then increased again when the rainy season set in. This was confirmed by positive correlations between monthly growth rates and the sum of rainfall over two or three months respectively and also by strongly negative correlations between monthly growth and maximum temperature. The intensity of these relations varied according to species. The phenological features of most species were also dependent on the climate, e.g. leaf shedding or flowering in the dry season and fruiting in the rainy season. Seedling dynamics showed a tendency towards an increase in the populations in the rainy season and a decrease in the dry season depending on the species. The distribution of the tree parameters was not as clearly related to the spatial distribution of soil parameters. There were a few correlations between tree diversity and soil parameters in KF, positive correlations with acid-extracted Ca, C and N and negative with electrical conductivity. Furthermore significant correlations were established in KF between tree growth and Ca, C and N, as well as negative ones with Mn and Mg in the soil, whereby the intensity of the relationship was species specific. Seedling diversity also correlated positively with Ca, C and N, as well as negatively with Mn. The distribution and density of the seedlings was however more highly dependent on recurring pulses of newly recruited individuals at irregular intervals than on the abiotic environment.

The study provides a first, precise insight into ecological regeneration processes of tree species populations and forest communities after human disturbance that have for the most part not yet been the subject of investigation, and can serve as a basis for forest management and forest models.

Zusammenfassung

Thema dieser Studie ist das Stammwachstum und die Regeneration verschiedener einheimischer Baumarten auch in Bezugnahme auf räumlich und zeitlich variable Umwelteinflüsse in zwei durch menschliche Eingriffe beeinflusste ostafrikanische Regenwälder in Kenia (Kakamega Forest) und Uganda (Budongo Forest). Im unteren-montanen Regenwald (1500 bis 1700 mNN) Kakamega Forest (KF) wurden daher Bestandsaufnahmen von Bäumen ≥ 5 cm Brusthöhendurchmesser (BHD) auf insgesamt 2,08 ha (1 ha Fläche und 27 Flächen à 400 m^2, 2007 Individuen, was 965 ha^{-1} entspricht, 3 Bestandsaufnahmen in 7 Jahren) durchgeführt. Dabei wurden 91 Baumarten aus 39 Pflanzenfamilien identifiziert. In Subplots innerhalb der Dauerflächen wurden außerdem 8441 kleine Bäume und Keimlinge ≤ 5 cm BHD (auf 432 m^2, in 6 Jahren) aufgenommen, die sich auf 59 Baumarten aus 29 Pflanzenfamilien verteilten. Im Tieflandregenwald (1000 bis 1100 mNN) Budongo Forest (BF) wurden auf insgesamt 0,72 ha Bestandsaufnahmen von (18 Flächen à 400 m^2, 2 Inventuren in 5 Jahren) 1010 Individuen, was 1403 ha^{-1} entspricht, durchgeführt, die sich auf 91 Arten aus 30 Pflanzenfamilien verteilten. Während des Observationszeitraums wurden in Subplots kleine Bäume und Keimlinge (auf 72 m^2, 708 Individuen, in 3 Jahren) zu 38 Baumarten aus 18 Pflanzenfamilien zugehörig, erfasst. Die Untersuchungsflächen lagen in Waldgebieten, die sich in verschiedenen Sukzessionsstadien befanden. Diese Stadien haben ihre Ursache in unterschiedlich starken Störungseinflüssen in Form von menschlichen Eingriffen mit kommerziellem Interesse in der jüngeren Vergangenheit. Da diese Arbeit im Kontext eines Projektverbundes steht, standen für einige der Dauerflächen kleinräumig erhobene Faktoren wie Bodenwerte, Klimawerte, Kronencharakteristik und Störungsindizes, z.B. der Commercial Disturbance Index (CDI), zur Verfügung.

Es wurde festgestellt, dass Artenreichtum und -diversität niedrig in Gebieten mit keiner und sehr hoher vorangegangener kommerzieller menschlicher Störung (z.B. Kahlschlag) waren, während Gebiete mit mittlerer Störung als artenreicher bzw. diverser identifiziert wurden. Auch die Verteilung der β-Diversität spiegelte einen Störungsgradienten wieder. Die Nachwirkungen, in den durch menschliche Störung entstandenen Sukzessionsstadien sind auch in der Struktur der Waldgebiete ersichtlich. Das mittlere Stammvolumen der Bäume in BF nahm mit abnehmendem Störungsindex zu, wohingegen in KF das höchste Stammvolumen in Gebieten mit mittlerem CDI auftrat. Die Baumpopulationen in Gebieten mit geringer Störung in BF zeichneten sich durch hohe Volumen bei geringerer Stammzahl pro Fläche und waren stabiler, was auch durch ihren geringen Turnover gezeigt wurde. Auch die Öffnung des Kronendachs war verschieden in den unterschiedlichen stark gestörten Gebieten und hatte einen positiven Einfluss auf die Keimlingsdichte in BF, welche wiederum die Bedeutung des Lichts für die Regeneration der Keimlinge aufzeigte.

Um die Regenerationsfähigkeit von einzelnen Baumarten zu testen, wurde hauptsächlich in den intermediären Sukzessionsstadien der beiden Wälder an 1198 Bäumen (≥ 10 cm BHD) monatlich der Stammzuwachs mit Dendrometerbändern gemessen. Zusätzlich wurde die Phänologie der Blätter, Blüten und Früchte der Bäume über einen Zeitraum von drei (in BF) bzw. fünf Jahren (in

KF) erhoben. Außerdem wurde die Regenerations- und Etablierungsdynamik analysiert, indem Keimlinge (≤ 100 cm Höhe) in den Subplots vierteljährlich gezählt, identifiziert und deren Höhe gemessen wurden. Die Baumarten konnten je nach gefundenen Charakteristiken in das Pionier-Klimax Kontinuum eingeordnet werden. Die früh-sukzessionellen Pionierarten wuchsen eher schnell, besaßen hohe Mortalität, hatten keine bis wenige Keimlinge im Unterwuchs und waren schattenintolerant. Die spät-sukzessionellen Klimaxarten hingegen zeigten langsameres Wachstum, wenig Mortalität, waren als Keimlinge im Unterwuchs gut etabliert und schattentolerant. Zwischen diesen Extremen lagen die meisten Arten, die entweder dazwischenliegende Charakteristiken oder sowohl Charakteristiken von früh- als auch von spät-sukzessionellen Arten aufwiesen und daher als intermediär klassifiziert wurden. Der jährliche Stammzuwachs zwischen den Baumarten war sehr variabel von 0,6 bis 2,5 mm in BF und von 0,6 bis 4,4 mm in KF und bei relativem Durchmesserwachstum zwischen 0,3 und 1 % in BF und zwischen 0,25 und 1,58 % in KF. Die Variabilität der Wachstumsraten innerhalb der Baumarten war noch größer als zwischen den Baumarten. Außerdem war die jährliche Variabilität des Wachstums innerhalb einer Art bei dünneren höher als bei dickeren Individuen. Einzelne Baumindividuen dagegen wuchsen relativ konstant.

Monatliche klimatischen Änderungen hatten Einfluss auf das monatliche Wachstum einiger Baumarten in KF und aller Arten im stärker saisonalen BF. In der warmen Trockenzeit war das Wachstum reduziert und nahm mit einkehrender Regenzeit wieder zu. Positive Korrelationen zwischen monatlichem Wachstum und dem über 2 bzw. 3 Monate aufsummierten Niederschlag bzw. stark negative Korrelationen mit der Maximaltemperatur bestätigten dies. Die Stärke dieser Beziehungen war artspezifisch verschieden. Auch die phänologischen Merkmale der meisten Arten waren abhängig vom Klima, wie z.B. Blattabwurf und Blühen in der Trockenzeit und Fruchtbildung in der Regenzeit. Die Dynamik der Keimlinge zeigte tendenziell eine Zunahme der Populationen in der Regenzeit und eine Abnahme in der Trockenzeit, je nach Art verschieden. Die Verteilung der Baumparameter zeigte weniger klare Zusammenhänge in Relation zu der räumlichen Verteilung der Bodenparameter. Es gab einige wenige Korrelationen zwischen Baumdiversität und Bodenparametern in KF, positive Korrelationen mit säureextrahiertem Ca, C und N und negative zur elektrischer Leitfähigkeit. Weiterhin wurden signifikante Korrelationen in KF zwischen Baumwachstum und Ca, C und N, sowie negative zu Mn und Mg im Boden festgestellt, wobei die Intensität dieser Beziehung artspezifisch war. Die Diversität der Keimlinge korrelierte ebenfalls positiv mit Ca, C und N, sowie negativ mit Mn. Die Verteilung und Dichte der Keimlinge hingegen wurde eher von unregelmäßig wiederkehrenden Schüben von neu gekeimten Individuen bestimmt als durch abiotische Umweltfaktoren.

Die Studie liefert einen Einblick in die ökologischen Regenerationsvorgänge der Baumgesellschaften von Baumarten und Waldgesellschaften nach menschlichen Eingriffen und kann als Grundlage für Forstwirtschaft und Waldmodelle dienen.

1 Introduction

This study attempts to provide a comprehensive picture of successional processes, examining both growth and regeneration after past human disturbance in the light of highly resolved abiotic factors in two tropical East African forests, Kakamega Forest (KF), Kenya and Budongo Forest (BF), Uganda.

The first section of the introduction (Section 1.1) provides an overview of the general characteristics of tropical forests and considers the important role they play in maintaining the global carbon balance and also the threats that they are facing. Section 1.2 then describes the mechanisms of successional stages created by disturbance and how they influence levels of tree diversity. In forests which have been left undisturbed succession often results in climax stages with monodominant species, while highest levels of diversity are commonly found at the intermediately disturbed forest sites. Subsection 1.2.1 deals with the process of tree seedling regeneration as the starting point of succession along the pioneer to climax continuum in tropical forests emphasizing the effects of the small-scale climate, light and edaphic factors. The next subsection of the introduction (Subsection 1.2.2) reviews tree growth plays a a major role in successional dynamics and its relations to abiotic factors. Section 1.3 is devoted to the aim of the study and the hypotheses upon which it is based.

Chapter 2 then describes the study sites and Chapter 3 concentrates on the materials and methods used in this study. The results for KF and BF respectively are contained in Chapters 4 and 5, and a comparison of the main results in the two forests is the subject of Chapter 6. Finally the discussion and the conclusion are presented in Chapter 7.

This study was part of the BIOTA (BIODIVERSITY MONITORING TRANSECT ANALYSIS) East project E03 entitled: “Regeneration of tropical upland trees spatio-temporal dynamics of feedback processes”. The main study hypothesis was that if both the characteristics and the composition of tree species vary, this has a strong influence on the canopy structure, which affects the spatial heterogeneity of abiotic factors, such as light, canopy throughfall and soil parameters. This influence is brought about through the process of nutrient uptake, through the interception and redistribution of precipitation by tree canopies and through the incorporation of nutrients into the biomass and their release on the soil surface e.g. as litter. The spatial distribution of abiotic factors influences the micro-environment for seedling establishment as well as tree competition through growth and thus also influences tree diversity. There is therefore a positive feedback mechanism between tropical trees species and abiotic factors, which plays a role in generating and maintaining the high tree diversity in tropical rain forests (DALITZ ET AL. 2004, MUSILA ET AL. 2005). The examination of this positive feedback mechanism forms an important part of this study.

1.1 Characteristics of tropical rain forests

Tropical rain forests are „evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianas and in woody as well as herbaceous epiphytes“ (Schimper 1898). They are among the most species rich and most complex ecosystems in the world (Whitmore 1993) containing between one half and two thirds of the world's species (Lewis 2006). They are characterized by a high number of plant species and are particularly rich in tree species (Richards 1996), throughout the tropics (Connell & Lowman 1989). Even though the diversity especially of trees is not evenly distributed in the neotropics and the paleotropics.

The highest tree diversity in the world is found in the equatorial tropical lowland forests of South America where there are up to 300 species (DBH ≥ 10cm) ha^{-1} (Yanamono, Peru) (Gentry 1988). The highest values for Asian forests reach 200 to 220 species ha^{-1} (Condit et al. 1996, Richards 1996). The lowest number of tree species in the equatorial tropics is found on the African continent with maximum numbers reaching 100 to 150 species ha^{-1} (Richards 1996). The African tree flora is “poor” compared to tropical forests of the Amazon and south-east Asia. This is attributed largely to past climate influences (O'Brien 1998, Field et al. 2005). As a result of the paleoclimatic history of the continent, African plant species are better adapted to relatively cool and dry conditions. Thus, if areas with similarly cool and dry conditions are compared, then diversity in Africa is similar to or even higher than in the Amazon (Parmentier et al. 2007). However, the low diversity may also be explained by the assumptions that natural extinction processes in Africa were possibly stronger in the past because the African forests covered a smaller area (Parmentier et al. 2007), this in turn may also have been as a result of stronger anthropogenic impacts (Richards 1996).

Besides their important role of supporting high levels of diversity, tropical rain forests are also important modulators of climate, so that any change in their cover can have a strong influence on the rate of climate change (Lewis 2006) as they have a high carbon storage capacity (Keeling & Phillips 2007) and could act as further carbon sinks (Clark 2004b). Thus deforestation can have alarming consequences, as in the process of deforestation carbon is released in the atmosphere (Ramankutty et al. 2007) and can produce positive feedbacks on global warming for example as a result of increases in albedo, higher surface temperatures and lower evapotranspiration rates (Foley et al. 2003).

In recent decades there has been a drastic change in the proportion of existing forest area in relation to potential forest area, because vast areas of rain forest have been cleared (Richards 1996). Human beings have contributed most strongly to the loss of a great part of ”wild nature” since the emergence and spread of agriculture (Richards 1996). Official estimations are that we have cleared around 50 % of all natural habitats with a current annual loss of 0.5-1.5% (UNEP 2002 Global Environmental Outlook 3, cited in (Balmford et al. 2003)). Africa lost more than 9% of its forest area from 1990 to 2005 (FAO 2007). Recent studies estimate a total global loss of 35 - 50 % of the originally closed (canopy) tropical forest (UNEP 2005, Wright & Muller-Landau 2006). Unlike forest areas in temperate regions, which nowadays remain fairly constant, most tropical countries are still rapidly losing forest area due mainly to anthropogenic activities in connection with increasing population densities and land use pressures (such as cultivation of land and agriculture, legal and illegal logging, or extensive cattle grazing) (LAURANCE & WILLIAMSON 2001, FAO 2007, UNEP 2005) and the rate of forest loss is accelerating BALMFORD & BOND 2005). In an attempt to compensate for this development new large nature reserves have been established in Africa (FAO 2007). But a recent interdisciplinary study is curbing optimism by questioning whether a single governance arrangement will be able to prevent overharvesting at all locations (OSTROM & NAGENDRA 2006). The study reinforces the proposals put forward by other scientists (e.g. TERBORGH) who maintain that it is imperative to engage "users" (local communities) to support forest management strategies (OSTROM & NAGENDRA 2006). Forest management plans that take all these aspects into account can only be developed if there is adequate background knowledge on small-scale forest ecology in the present (e.g. DALITZ ET AL. 2004, OESKER 2008).

1.2 Tree succession and disturbance

Disturbance shapes the distribution and dynamics of ecosystems by creating different stages of succession (SOUSA 1984). In periods without major disturbances a climax stage of e.g. a forest is formed, characterized by a high level of energy, stability and showing low dynamics (HORN 1974). Man-made or natural disturbances depending on their intensity, severity, shape, size, location, the heterogeneity of the environment and the time the disturbance was created, alter these stable systems (SOUSA 1984). As it is improbable that a population can persist indefinitely in the climax stage, tree dynamics are always undergoing change and successional processes, starting anew after disturbance. The disturbances cause a patchiness in the forest ecosystem, e.g. resulting in the patchiness of the available environmental factors and further influencing the efficiency of recruitment and establishment of different types of species (BAZZAZ & PICKETT 1980). High or intermediate intensities of disturbance give rise to earlier stages of succession in the forest (SOUSA 1984), which are characterised by greater productivity, faster growth rates and higher tree densities than are observed in mature-type ecosystems (ODUM 1969) with the aim of reconstructing the original, undisturbed community (HORN 1974).

Large clearings, e.g. after clearcuts in forests, are colonized by early-successional species that possess widely dispersed propagules (SOUSA 1984). On the other hand small clearings, e.g. due to the death of a single canopy tree, quickly fill up with the offspring from adjacent surviving trees (SOUSA 1984). Many clearings are a result of intermediate disturbances e.g. by selective logging, windthrow or fires often resulting in a mixture of remaining surviving trees and new colonizing species (SOUSA 1984). The colonizers are pioneers (fast-growing, short lifespan, light-demanding, small seeds, low wood density) and thus need gaps to regenerate, while the surviving trees are shade-tolerant species (slow growth rates, long-living, shade-tolerant, large seeds, high wood density) and their seedlings are able to survive in the forest understorey until a gap opens up and the tree is released to reach upper layers (e.g. RICHARDS 1996, SWAINE & WHITMORE 1988, GOURLET-FLEURY & HOULLIER 2000). However, the majority of species lie somewhere in between these extremes and some tree species even switch their adaptation strategies as they grow and become older (BARALOTO ET AL. 2005B). Gaps caused by disturbance can therefore be important sites for the recruitment of a wide range of species, favouring early successional species more than late climax species (TURNER 2001). If disturbance favours early successional species then these are more abundant at more severely disturbed sites. A relevant hypothesis describing this process is the intermediate disturbance hypothesis, which focuses on the successional stages that occur after disturbance and claims that highest diversity is found in the areas with intermediate levels of disturbance resulting in intermediate stages of succession (CONNELL 1978).

Indeed a number of tropical African forests reach a climax stage resulting in the monodominance of tree species especially from the Caesalpiniaceae[1], examples are *Cynometra alexandri* in Budongo Forest in Uganda, *Gilbertiodendron dewevrei* in Ituri Forest in Congo (GROSS ET AL. 2000) and *Microberlinia bisulcata* in Korup forest in Cameroon (GREEN & NEWBERRY 2001, CHUYONG ET AL. 2004b). Several theories have emerged which try to explain this monodominance of the Caesalpiniaceae in African primary forests. One theory is that their robustness resulting from their high wood density better equips them to survive disturbance occurring in the form of damage by elephants (SHEIL 2001, LAWES & CHAPMAN 2008), thus making them better competitors. Their competitiveness is further enhanced by their symbiosis with nitrogen-fixing bacteria, although not all dominant species are nodulated by these bacteria. Another theory emerged claiming that these tree species contain mycorrhizas of the ectomycorrhizal type (EM), which are more effective in acquiring nutrients than the vesicular arbuscular mycorrhiza (VAM) more commonly associated with tree species (CONNELL & LOWMAN 1989). Soils with low phosphorus, as is the case in many tropical forests (VITOUSEK 1984), are therefore commonly occupied by species with ectomycorrhizal fungi (GARTLAN ET AL. 1986). But this possible advantage was also ruled out by a study in Ituri Forest, Congo, which showed that some of the analysed monodominant species including *Cynometra alexandri* did not form EM (TORTI & COLEY 1999). Another theory is that reduced herbivory of the young seedlings acts as a mechanism leading to tree monodominance (GROSS ET AL. 2000). However, the monodominance of tree species of the Caesalpiniaceae probably cannot simply be explained by one mechanism alone, but is rather the result of a mixture of different advantageous plant characteristics.

Apart from different successional stages of the vegetation, disturbance also creates patchiness of the abiotic environment, which forms the background to the environmental variability hypothesis (PALMER 1994). The patchiness of environmental conditions in particular the light regime, canopy throughfall and the soil factors have been shown to influence the level of tree diversity. For instance, in some studies a positive effect of soil factors on plant diversity has been established on landscape scale ($<10^2$-10^4 km^2) (TUOMISTO ET AL. 2002, TUOMISTO ET AL. 2003, PHILLIPS ET AL. 2003) and on regional

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[1] According to APG III the Caesalpiniaceae are now the Caesalpinoidae being part of the Fabaceae.

scales (1-10^2 km^2) (Clark et al. 1998, Clark et al. 1999). Also on a regional scale other important abiotic factors influencing tree diversity positively are the amount of rain, dry season length, solar radiation and temperature (rainfall: Clinebell et al. 1995, climate seasonality: Davidar et al. 2007, Ter Steege et al. 2003, temperature: Punyasena et al. 2008). On a local scale (< 1 km^2) it was shown that 36 - 51 % of tree species were strongly associated with soil nutrient distributions (John et al. 2007). However, in other studies in tropical forests soil nutrients only showed minor effects on tree diversity by comparison with climatic factors especially rainfall and temperature (Clinebell et al. 1995, Slik et al. 2009) and low-fertile soils in the tropics often contain highly diverse forests, which is interrelated with the amount of rainfall in a region (Huston 1980). Further, relations between the variability of abiotic factors and the distribution of tree diversity have been established (Oesker et al. 2008, Oesker et al. in press). Human disturbance also alters other biotic factors relevant for tree regeneration such as the density of frugivore populations, which are more common in more disturbed parts and affect seedling distribution, establishment (Kirika 2007), and recruitment (Babweteera & Brown 2010), and thus tree distribution and consequently tree diversity in those forest parts. Another factor to be taken into consideration is the vegetation history encompassing both the paleoclimatic history and recent past human impact. The present degree of diversity is a result of the combination of all these influences in one locality.

Apart from the changes in the floristic composition changes, the forest structural parameters also change along disturbance gradients. Tree heights may decrease, mean diameter at breast height (DBH) decreases (Fashing et al. 2004), tree basal area decreases, gaps increase (Plumptre 1996) and liana density increases (Schnitzer & Carson 2001, Swaine & Grace 2007) as a result of higher disturbance.

1.2.1 Seedling regeneration

The different patches that are created by succession and thus lead to a patchy vegetation also influencing seedling regeneration, which is the beginning of the succession process of tree populations stands. Species regenerate according to their inherent species characteristics and the abiotic and biotic environment. Seedling establishment therefore depends on the position of a species in the pioneer-climax continuum.

A pre-condition of tree regeneration is seed production, which depends on the reproductive phenological patterns of trees. Internal rhythms of phenological activities are affected by changes in abiotic factors (van Schaik et al. 1993, Borchert 1998), especially rainfall (Opler et al. 1976, Tweheyo & Babweteera 2007) and are important in terms of natural regeneration of indigenous tree species (Bendix et al. 2006).

The dispersal of seeds determines spatial patterns of short-term seedling establishment. It is influenced by the trade-off between dispersability and establishment (Kitajima 2007) depending on a species, life strategy in the pioneer-climax continuum. Seeds of most pioneer species are tiny, have a high dormancy and a long life span in contrast to late successional forest species (Bazzaz & Pickett 1980) The dispersal limitation of seeds, together with the post-dispersal establishment success is an important factor, in creating seedling distribution patterns in gaps (Dalling & Hubbell 2002). Climax species produce large seeds that produce seedlings, which perform better in early stages of succession than seedlings from smaller seeds, because they have more reserves, called the reserve effect (Green & Juniper 2004). This effect allows the seed to invest in early root growth to pass the layer of litter and to access water in the soil (Silvertown 1987). At later stages large-seeded species grow in height at a relatively slower rate than species with smaller seeds (Kitajima 1994, Poorter & Rose 2005). The seedlings of large-seeded species possess storage cotyledons that serve as energy reservoirs in stress periods, while small seeds produce seedlings with photosynthetic cotyledons, which do not store such energy (Zanne et al. 2005). Light-demanding species invest more in fast-growth and leaf area, resulting in seedlings that are weaker than those belonging to shade-tolerant species, which normally invest more in stability e.g. denser wood, thicker leaves (Kitajima 2007). There is therefore a trade-off between survival and growth for the seedlings that differs according to the functional group (light-demanding to shade-tolerant) (e.g. Kitajima 2007, Poorter & Kitajima 2007). Lower survival rates amongst tropical forest seedlings are commonly found in early - rather than late-successional species (e.g. Kitajima 2002, Condit et al. 1999, Odhiambo et al. 2004), which is reflected in the species inherent morphology and C allocation pattern (e.g. Blundell & Peart 2001, Poorter & Kitajima 2007).

As seedlings grow they become independent of seed reservoirs at an earlier or later stage depending on their strategy. Seedling populations are regulated by mortality and fecundity, which are altered by density-dependent effects like self-thinning and density-independent effects like the abiotic environment (Silvertown 1987). Seedlings need to cope with a wide range of biotic and abiotic stresses including e.g. pathogens, herbivory, drought and litterfall (e.g. Augspurger 1984 a,b; Clark & Clark 1989, Kitajima & Augspurger 1989, Engelbrecht et al. 2005) and the distribution of arbuscular mycorrhizal fungi (Silvertown 2004). Physical defences such as leaf tissue density and leaf toughness (Alvarez-Clare 2005, Alvarez-Clare & Kitajima 2008) as well as wood density, deciduousness (Poorter & Markesteijn 2008), energy reservoirs in the form of nonstructural carbohydrates (Poorter & Kitajima 2007, Myers & Kitajima 2006), the ability to resprout or allocate reserves of lost tissue from roots to above ground parts (Barberis & Dalling 2008) and also chance (Hubbell et al. 1999) enhance seedling survival at such times.

After the establishment spatial heterogeneity in abiotic factors and interactions with the local neighbourhood then affect seedling distribution (Metz et al. 2008, Dalitz et al. 2004, Oesker 2008).Light availability influences the density of seedlings per area and also the diversity of recruits (Hubbell et al. 1999, Norden et al. 2007). In many experiments the influence of light on seedling survival and performance was tested. Seedlings grow at a fast rate in medium rather than in low light environments found in the understorey and the magnitude of the response is species-specific (Popma & Bongers 1988, Davidson et al. 2002, Montgomery & Chazdon 2002, Bunker & Carson 2005). Seedlings that grow at a fast relative rate in low light also grow at a fast rate in high light environments, which is determined by differences in seedling morphology e.g. the leaf area ratio (Kitajima 1994, Poorter 1999, Bloor & Grubb 2003, Dalling et al. 2004, Baraloto et al. 2005a). Maximum growth rates of species ranging along the pioneer-climax continuum are often found at intermediate light levels (Agyeman et al. 1999), even if plants have been irrigated continuously (Poorter 1999). Further, physiological adaptations are characteristic of a plants life strategy. Pioneer species possess multi-layers of leaves with few branching patterns, as this enhances productivity in high light environments (Horn 1974). It is therefore not the amount of available assimilates that determines competitive success alone, but also the differences in morphology and carbon allocation that compensate for differences in photosynthetic production, by better utilization in particular plant architectural or growth forms (Küppers 1989).

Efficiency is an important factor in the survival strategies of shade-tolerant species, as even small changes in the light availability can have large consequences on the seedling carbon balance (Montgomery & Chazdon 2002). In general, in order to survive trees need a positive net C-balance (Myers & Kitajima 2006, Poorter & Kitajima 2007), which is equal to the net carbon balance minus loss caused by herbivores (Bryant et al. 1983), disease and physical disturbance (Kitajima 1996). This is particularly difficult to maintain in the forest understorey, where the seedlings are likely to experience a wide range of biotic and abiotic stresses (e.g. Augspurger 1984 a, b; Clark & Clark 1989, Kitajima & Augspurger 1989, Engelbrecht et al. 2005, Alvarez-Clare & Kitajima 2008). One major tactic used assisting the survival of shade-tolerant species under such conditions is the storage of carbohydrates in stems and roots (Myers & Kitajima 2006). In this way they therefore perform better in terms of survival, which is reflected in the fact that a lower proportion of seedlings from shade-tolerant species than from shade-intolerant species die in both shade and gaps (Augspurger 1984a, Kobe 1999). The ability to survive in the forest understorey is not achieved by faster growth in shade but by tolerating the inevitable tissue loss or decrease due to the various hazards (Kitajima 2007). This is due to the efficient use of carbon, in growth and morphology (Küppers 1989).

Soil fertility can also have a positive influence on seedling growth and survival in both experimental and natural environments (e.g. Gunatilleke et al. 1997, Hall et al. 2003, Yavitt & Wright 2008). This can influence seedling establishment positively (Norden et al. 2009a), with the response to soil fertility being species-specific (Veenendaal et al. 1996).

Water availability, and thus the available soil water can also influence seedling density (Engelbrecht et al. 2007) spatially. The canopy throughfall (TF) is distributed in a highly spatial heterogeneity on the forest floor creating different soil moisture niches (Oesker 2008, Todt personal communication). But there are hardly any studies on the amount and distribution of TF in relation to seedling parameters. However, no strong relation between seedling density and rainfall could be established over a period of 32 years in respect of one tree species (Connell & Green 2000). Differences in dry season length and thus soil water storage can relate to differences in mortality rates at different sites (Comita & Engelbrecht 2009), because the root system of seedlings is only able to access superficial sources of water (Paz 2003). This was confirmed by a study in BCI, Panama with the highest mortality rates of seedlings occurring in the harsh dry seasons (Condit et al. 2004). Seedling survival rates especially in strong seasonal forests with a pronounced dry season, depend on the species-specific survival strategy (Engelbrecht et al. 2007). In such forests species can be divided into three functional groups: the drought avoiders (deciduous), drought resisters (evergreen with tough leaves) and light-demanders (extensive below ground foraging) (Poorter & Markesteijn 2008). The drought-resisters are largely composed of species with typical attributes like high wood density, high root:shoot ratio, tough leaves that are designed to tolerate drought events (Engelbrecht et al. 2002). The response to different levels of water availability is therefore characteristic of the plant functional type (Bongers et al. 1999, Slot & Poorter 2007). Species can be grouped according to drought sensitivity and can thus be assigned to soil moisture gradients (Engelbrecht et al. 2007).

The traits in seedlings are connected to the traits in mature trees in different ways. For instance shade-tolerance traits of young seedlings are related to wood density, growth rates and thus many parameters of mature trees (Augspurger 1983), so that in the case of many tree species, traits found in seedlings are also present in mature trees. The regeneration of tree species is expected to vary with successional status and thus the environment of the respective forest type.

1.2.2 Stem growth

Knowledge of the growth of trees is an important pre-condition for an understanding of the dynamics of tropical forests (e.g. Clark & Clark 1999, Homeier 2004) and has been in the focus of many studies worldwide including African tropical forests in the past decades (e.g. Richards 1939, Njoku 1963, Hopkins 1970, Lieberman 1982, Swaine et al. 1990, Newberry et al. 2002). Maximum tree growth rates can be observed in the respective species under artificial conditions, such as are found in tree plantations without competition (Bauch & Dünisch 2000). The diameter growth rates in that study frequently reach > 10 mm per year and even increments > 20 mm have been reported (Ng & Tang 1974). In a recent compilation of different studies on tree growth it was generally established that African forests are carbon sinks, probably due to the availability of resources that cause increased growth, like the level of carbon dioxide (Lewis et al. 2009), but positive above-ground primary productivity can also mean succession is taking place after past unknown disturbances (Muller- Landau 2009). Interrelations between abiotic factors and tree growth have often been established and some examples are given below. Tree growth rates depend on the successional stage to which a species belong. Pioneers, as they are highly productive, have high growth rates, which is associated with rapid accumulation of nutrients (Bazzaz & Pickett 1980). In early successional forest stands daytime net production exceeds nighttime respiration so that biomass is accumulated

(Odum 1969). With the aging of tree populations a decline in production has been observed (Horn 1974), as the forest slowly reaches a steady state comparable to its untouched stage (Odum 1969). The selection pressure favours the shade-tolerant species with lower growth potential, as they possess better capabilities for competitive survival (Odum 1969). Apart from the characteristics inherent in the species, environmental factors influence tree growth.

Firstly, forest growth is limited by temperature, with a mean of ~ 28 °C up to which closed-canopy forests can be maintained (Wright et al. 2009). Optimum temperature for growth of plant parts lies at around 25 °C (Went 1953) which was also established under artificial conditions for *Eucalyptus grandis* (Thomas et al. 2007). The negative effect on growth at temperatures above 25 °C is explained by reductions in stomatal conductance (Lloyd & Farquhar 2008). But according to the model of Lloyd & Farquhar (2008) there is no evidence to suggest that tropical forests are dangerously close to their optimum temperature range. Increasing temperature in particular in extremely warm years (e.g. El Niño years) may explain an inverse relation of tree growth to mean annual minimum temperatures (Clark et al. 2003). It has been argued that a decrease in growth at elevated temperatures is caused by an increase in day and night-time respiration in relation to the rate of photosynthesis resulting in a reduction in net carbon assimilation (Clark et al. 2003, Clark 2004, Malhi & Wright 2004, Feeley et al. 2007, Clark et al. 2009). Furthermore, under natural conditions an increase in air temperature results in an increase in soil temperatures, thus leading to an increase in soil mineralization rates and ultimately to nutrient availability (Lewis et al. 2004a), which again affects tree growth.

In addition different levels of soil moisture also influence tree growth (Baker et al. 2003). In most of the terrestrial tropics the annually recurrent intervals of low soil water content is the factor which limits tree growth most (Bullock 1997, Worbes 1999), also in other tropical forests in Africa (Hopkins 1970, Schöngart et al. 2006). In general, growth rates of tropical trees have been negatively correlated to reduced water availability (e.g. da Silva et al. 2002, Vieira et al. 2004, Feeley et al. 2007). Radial tree growth is influenced by climate, particular by rainfall (Clark & Clark 1994, Roderick & Berry 2001), and physiological processes such as photosynthesis and nutrient transfer are reduced as the stores of water available to the plant decrease (Porporato et al. 2001). Tree growth therefore is more frequently limited by a lack of water than by other factors (Nepstad et al. 2002, Brando et al. 2008). Droughts caused by El Niño and Southern Oscillation events show strong impacts on tree growth in the Amazon basin. Firstly the warmer and more cloud-free weather during droughts increases photosynthetic active radiation and thus growth, without creating soil moisture deficits large enough to inhibit photosynthesis (Valladares et al. 1997, Brando et al. 2008). Once the soils dry out, net primary productivity of plants decreases - with stem growth expected to be the most sensitive component to drought, as it is low on the carbon allocation hierarchy behind the allocation of C to leaves and roots (Chapin et al. 1990). Such effects are observed in natural ecosystems for instance in a rain forest in Venezuela receiving up to 1,700 mm of rainfall annually (Worbes 1999). Too much rainfall however can also affect tree growth negatively by creating anaerobic conditions for the roots and coinciding with greater cloud cover, both resulting in decreasing rates of photosynthesis and thus growth rates (Vieira et al. 2004, Schuur 2003).

Moreover soil factors are important variables influencing tree growth, for example in some tropical lowland forests available phosphorus (P) was found to be limiting tree growth (Vitousek 1984), also nitrogen (N) limits tropical tree growth in montane environments (Tanner et al. 1990, Tanner et al. 1992). Other studies in tropical forests in Costa Rica and Borneo did not find any strong relations between growth and investigated soil parameters (Clark et al. 1998, Ashton & Hall 1992) and if present at all quite often no or only a few relations between soil nutrients and tree growth (Clark et al. 1998). Although nutrient limitation might be expected, it does not occur frequently as there is often a virtually a closed cycling system, where nutrients are stored in tree biomass and move from fallen leaves back to the biomass extremely quickly via a host of adaptations (Jordan 1985). N-fertilization is taking place world-wide as a result of anthropogenic activities, so that this will alter the nutrient balance, as for instance more biomass can be then produced, if enough water is available (Asner et al. 2001).

1.3 Aim of this study

This study sets out to analyse the successional stages created by past human disturbance and then to examine the highly temporally and spatially resolved regeneration and succession of trees in relation to small-scale and temporal heterogeneity of environmental factors in two East African forests. These forests have been subject to a large number of past and present human interferences, so that a mosaic of forest successional stages has emerged along disturbance gradients. The aim is first to describe the tree populations as well as forest structure and tree diversity. Following on from that the successional tree dynamics are considered on a large scale (forest), on a site scale (successional forest type), on a tree species scale and on a seedling scale, as no single mechanism explains the patterns on all scales (Levin 1992).

On a forest scale the analysis encompasses tree diversity, forest structure and from a temporal viewpoint the turnover rate, which includes productivity, survival and mortality. On site-scale in addition to the influence of disturbance gradients an attempt is made to provide a spatio-temporal insight into species distribution, diversity and tree structure in relation to data on the abiotic environment (light, soil, climate within and outside the forest). Moreover a high temporal resolution of seedlings dynamics and tree growth together with the abiotic data, partly collected at the same time (canopy throughfall and temperature), enables a detailed description of seasonality at plot and species specific level, which is unique in this form over such a long period of time in African forests.

It is hoped that this study will contribute towards a better understanding of the mechanisms that underlie tree succession after human disturbance and will provide new insights into the ecology of the tree species in the target region and the population dynamics that occur in connection with succession. The results provided by this study can then be put to practical use in forest models or in forest management plans, where this specific knowledge is required.

The main research hypotheses are listed below:

1) Different levels of past human disturbance have created different stages of succession, resulting in the patchiness of the forest environment and thus in the patchy occurrence of tree species and in patchy forest structure.

2) In the intermediately disturbed sites, where there is a wide variety of species from the pioneer-climax continuum, differing life strategies determine the competition potentials of the different tree species.

3) Spatio-temporally distributed environmental factors produce a species-specific response of trees, thus altering the competitive abilities of the respective species.

2 Study Sites

The study took place in two East African rain forest remnants in Kakamega Forest, Kenya and Budongo Forest, Uganda, which will be described below. They are part of the equatorial, humid Zonobiome I (WALTER & BRECKLE 2004) that stretches along the Equator.

In East Africa (Uganda, Kenya and Tanzania) the area of continuous forest coming from the Congo basin reaches Bwamba in Western Uganda (HAMILTON 1974). East of the Albertine Rift Valley continuous forest is absent except for outliers of various sizes e.g. Budongo and Mabira Forest in Uganda, a relic near Kakamega in Western Kenya amongst other small areas (HAMILTON 1974) (Figure 2-1). East Africa thus does not have large expanses of forest, containing only 0.7 % of the world's moist forest. These forest areas possess endemic species (0.45/ 1000 km^2), serve in the mostly dry countries as important watersheds and contain vital resources (CHAPMAN & CHAPMAN 1996). Most of the forests occur where a rise of elevation results in a local increase in rainfall (CHAPMAN & CHAPMAN 1996). During the glacial periods forest islands emerged, which then increased in size and connected again about 12,000 years ago during the post-glacial period (HAMILTON 1974, LIVINGSTONE 1975). Lowland forests covered the then existing grassland in Mid-Uganda as far as Lake Victoria, probably up to Kakamega Forest, which was converted back to grassland after human deforestation 2000 to 5000 years ago (HAMILTON 1974). So the forests that are left today are only remnants of much

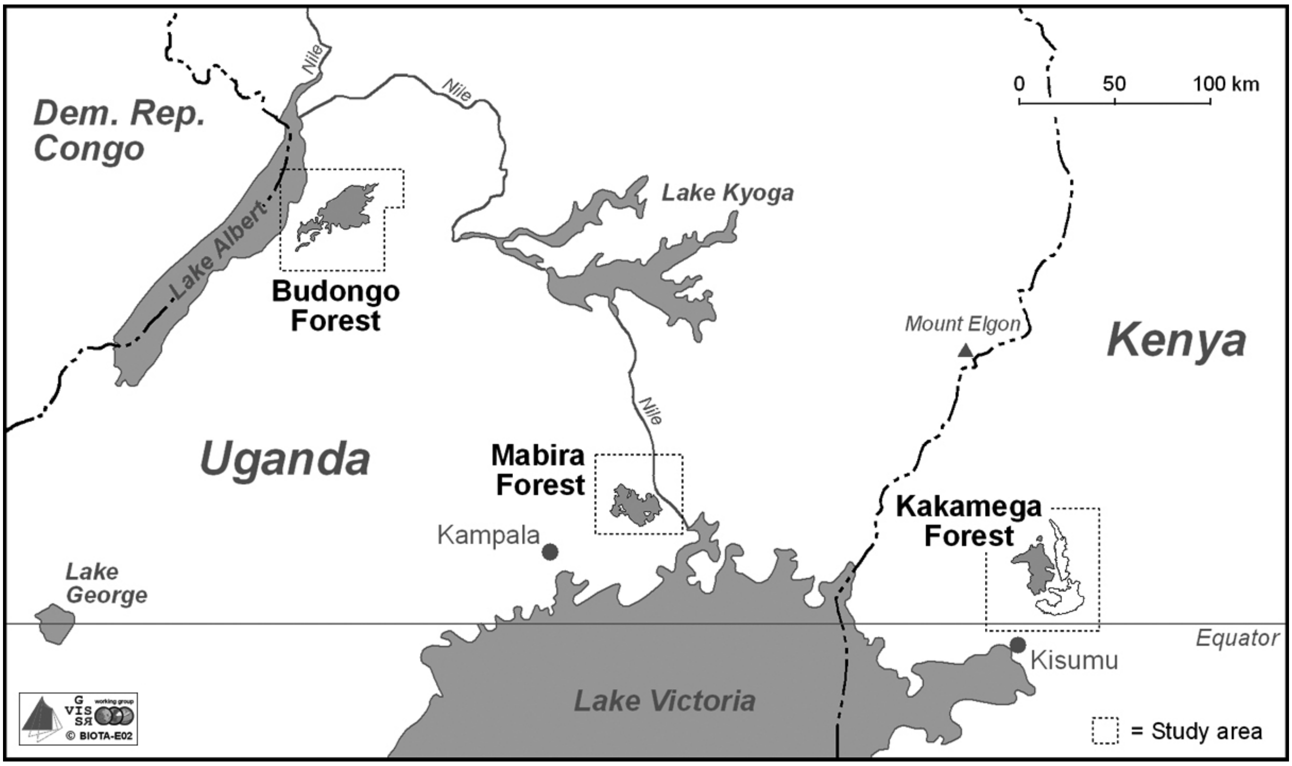

Figure 2-1: Map of the part of East Africa that includes the two study forests Budongo (Uganda) and Kakamega (Kenya). (Map by courtesy of SCHAAB, BIOTA E02)

more extensive formerly connected forest blocks. The diversity of the remnants decreases the further east the location and the higher the altitude (Mitchell & Schaab 2008).

Kenya and Uganda each contain between 5,000-6,500 plant species, which is a relatively small number compared to mega diverse countries like Ecuador or Indonesia. Generally the neotropics are more rich in species per area than the paleotropics (Table 2-1).

Table 2-1: The diversity of vascular plants, birds and mammals in both study countries (Kenya and Uganda) is shown and compared to some mega diverse countries. The numbers of species are given as absolute numbers (http://earthtrends.wri.org/).

Country	Area [km^2]	Vascular Plants	Birds	Mammals
Kenya	582,646	6,506	1,103	407
Uganda	241,040	4,900	1,015	360
Madagascar	587,041	9,505	262	165
Ecuador	256,730	19,362	1,515	341
Indonesia	1,919,270	29,375	1,604	667

The total area of forest in East Africa covers 76,000 hectares, which decreased at a rate of up to 1.5 % per year between 2000 and 2005 (FAO 2007). An increase in population as a result of high birth rates and the arrival of refugees in recent years has led to an increased demand for living space and for large amounts of fuel wood of up to 250 million m^3 in 2005 alone (FAO 2007). The loss of these forests can lead to an increase in drought effects, as important water catchment areas are then under threat as illustrated by the recent debate over Mau forest in Kenya (Nkako et al. 2005).

2.1 Kakamega Forest in Kenya

2.1.1 Geography

Kenya is the easternmost country along the equator in Africa covering an area of 582,646 km^2. From the coast on the Indian Ocean the low plains rise to central highlands (Livingstone 1975). The highlands are bisected by the Great Rift Valley, a fertile plateau in the east. The highlands contain peaks of up to 5,200 meters (Mount Kenya) and continue West until the Mt. Elgon area. Kenya’s vegetation is influenced by four main regions: the coastal region, the savannahs, montane regions and the forests (Livingstone 1975).

Kakamega Forest (KF) (0°10´N-0°21´N, 34°48´-34°58´E) lies in Kenya’s Western Province 50 km north-east of Kisumu and Lake Victoria, and 80 km to the west of the Ugandan border near the town of Kakamega (Glenday 2006). It is part of the Nyanza deep plateau (Haupt 2000) and lies at an altitude of between 1,500 and 1,700 m above sea level (a.s.l.) (Lung 2004) and is thus transitional being categorized between lowland and montane forest (Lebrun 1935 cited in Richards 1996). The forest used to be connected to the neighbouring North- and South Nandi forests, which once formed a combined area of 74,718 ha (Mitchell et al. 2006). This area has now decreased to 26,467 ha as a result of a loss in forest cover of around 65 % from 1913 to 2001 in this region (Mitchell et al. 2006). This drastic loss was mainly caused by heavy human disturbance (Tsingalia 1990, Bleher et al. 2006), which resulted in the creation of KF in its present state together with its adjacent fragments. The three largest fragments Kakamega (the main forest block), Yala (YA) and Ikuywa (IK) cover around 12,288 ha and form KF together with smaller fragments namely, Kisere (KI), Malava (MA) in the northern part and Kaimosi (KA) in the south (Figure 2-2), as well as Bunyala (not shown on the

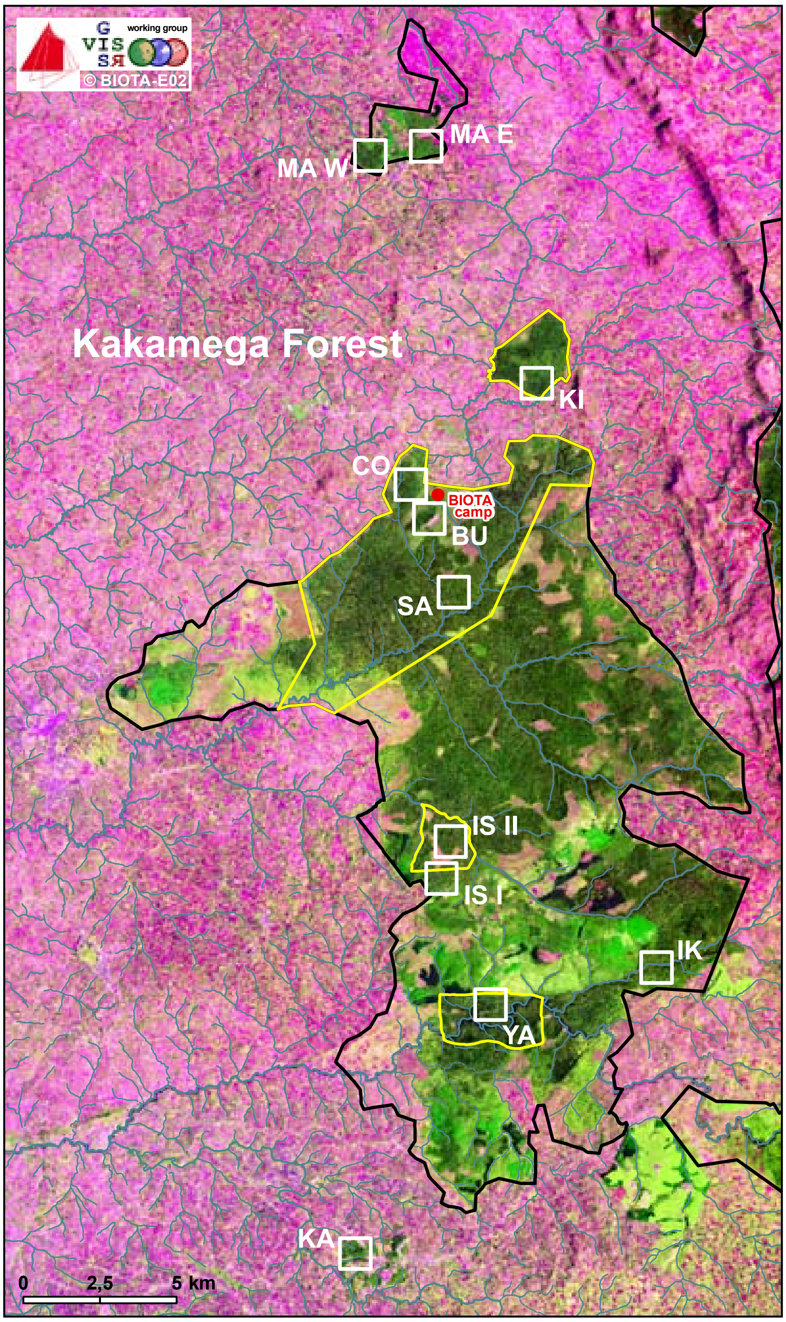

Figure 2-2: Satellite map of Kakamega Forest and its fragments (black boundary marks forest). The white squares show the location of the BIOTA-Biodiversity Observatories (BDO‘s). Dark green indicates primary forest, light green indicates secondary forest with various shades in between. BU: Buyangu; CO: Colobus; IK: Ikuywa; IS I and II: Isecheno I and II; KA: Kaimosi; KI: Kisere; MA: Malava; SA: Salazar; YA: Yala. (Map by courtesy of Prof. Dr. Schaab, BIOTA E02).

map) (Lung & Schaab 2004). The area of the main forest block (Kakamega, Yala and Ikuywa) and the fragments Kisere, Malava and Kaimosi stretches across around 20,000 ha (Lung & Schaab 2004). The topography is fairly flat with a few hills in between.

2.1.2 Geology and Soils

The underlying rocks were formed in the Lower Precambrian period and are locally covered by recent alluvium (White 1983). Geologically, Kakamega forest is characterised by the Nyanzian and Kavirondian rock formations, the oldest rocks in Kenya (Musila 2007). The Nyanzian rock formation is comprised of acid to basic volcanic lavas, with minor tuff, agglomerate bands and gold-bearing quartz veins (Musila 2007). The Kavirondian rock formations are predominantly conglomerates, grits and mudstones and three quarters of the forest is made up of this type of rock formation (Musila 2007). The northern and eastern edge of the forest consists of small strips of granitic rock types (Musila 2007).

Four soil classes, namely Ferralsols, Lixisols, Cambisols and Phaeozems were identified by a recent detailed soil survey (Musila 2007). The dominant soil class is ferralsols. Morphologically, Kakamega soils are deep having diffuse horizons and a shallow, brownish black A horizon. The subsurface horizons vary from brown, bright brown, reddish brown to red indicating that these horizons are rich in iron oxides. The soils have deep profiles almost uniform (even in colour), are porous and permeable and contain many roots (Musila 2007).

Soil pH ranges from 4.5 to 6.5. The soils have moderate (1.0 - 2.0 % C) to adequate organic C content (2.0 - 4.0 % C). Availability of the alkaline cations declines in the sequence Ca > Mg > K. Cation exchange capacity (CEC) ranges from 5 to 15 Cmol kg^{-1} in the topsoils (0-10cm). Soils are highly deficient in phosphorus and potassium. The clay mineralogy of Kakamega soils is comprised of kaolinite, mica and quartz goethite, kaolinite being the most dominant. High kaolinite content is consistent with the intense weathering conditions experienced by these soils and implies that the mineral fraction contributes little to the CEC and causes pH dependent charged soils. Thus, the ability of Kakamega soils to hold and exchange nutrient cations is primarily dependent upon their organic matter. This makes the soils susceptible to nutrient losses. So we can say that Kakamega soils are old, strongly weathered, acidic and have a low nutrient content e.g. of Ca, Mg, K and P (Musila 2007).

2.1.3 Climate

Interacting with weather conditions the topography of eastern Africa produces many local rain shadows. This may be affected by divergent flows of air from the Indian Ocean and probably the tropical jet stream, but the general pattern is one of remarkably low equatorial rainfall (Livingstone 1975). The climate in Kakamega is influenced by these rain shadows and can be classified as semi to sub-humid. It is also affected on the one hand by the Inter Tropic Convergence Zone (ITCZ) and on the other hand by the proximity to Lake Victoria (Lung 2004). On account of the equatorial position the ITCZ crosses the Kakamega area twice per year and creates two rainy seasons, one in April/May the other in August/September (Lung 2004).

The driest period occurs on average from December to February (Figure 2-3), but the annual amount of precipitation and the beginning and end of the dry and wet seasons vary considerably. The distinction between the two rainy seasons is not therefore clearly evident on the mean annual diagram. Lake Victoria and its air mass system has a stronger influence on the local day to day climate. Trade and ocean winds meet above the lake. This causes humid air to rise, which is then blown northwards and leads to heavy thunderstorms that occur every day in the area of Kakamega during the afternoon or evening (Haupt 2000). The mean annual rainfall is around 1,915 mm for the period of 1990 to 2006 and the mean annual temperature is 18.7 °C (Figure 2-4). This is less than the reported 2,147 mm for the period from 1959-1985 (Tsingalia 1988) and shows that rainfall amounts have decreased in the region over the past decades.

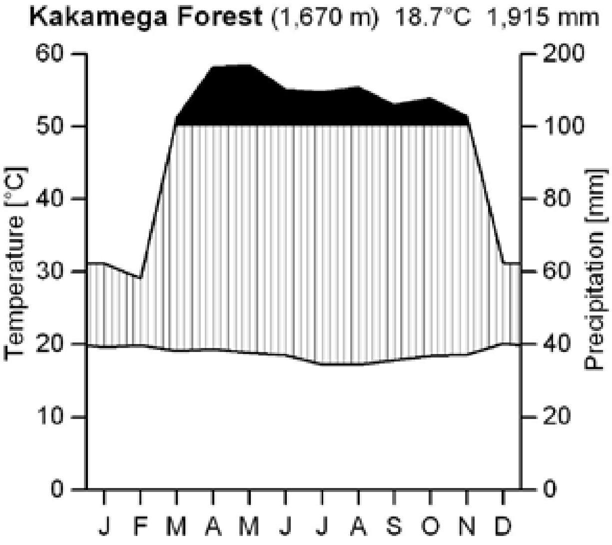

Figure 2-3: Climate diagram of Kakamega Forest. The values are means for rainfall 1990 to 2006 and for temperature from 2002 and 2007 (by Todt; data by courtesy of Kenyan Meteorological Service (KMS) and BIOTA E02 (Steinbrecher)).

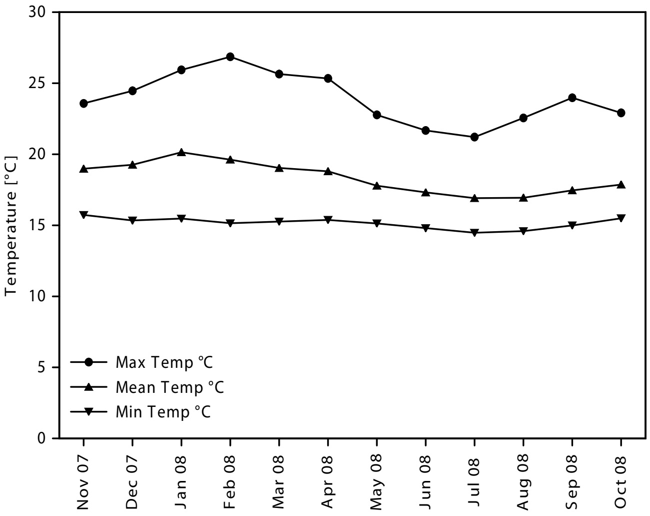

Figure 2-4: Monthly mean, maximum and minimum in situ temperature in the BDO Buyangu Hill between November 2007 and October 2008 measured with a Hobo data logger.

In some of the plots temperature was logged every 15 minutes using a HOBO data logger. Figure 2-5 shows the maximum, mean and minimum temperatures of the site Buyangu Hill. The mean temperature for the period from November 2007 until October 2008 shows little fluctuation between 17 °C in June, July and August and a warmer period with around 20 °C in January and February, which represents the dry season. The minimum temperature is more or less constant per month at around 15 °C, whereas the maximum temperature varies between 21 °C (in July) and 27 °C (in February).

2.1.4 Vegetation

Apart from being categorized as transition forest (Lebrun 1935 cited in Richards 1996), Kakamega Forest has been characterized as a mid-altitudinal tropical rain forest (Farwig et al. 2008) strongly influenced by elements of the guineo-congolian and the afromontane flora (Schultka 1975), being the easternmost relic of the equatorial forests that stretch across Africa from the Congo basin (Hamilton 1974, Blackett 1994). It has the highest species richness in Kenya with a large number of rare animals and some endemic plant species (Blackett 1994). It lies in the floral region K5 of the Flora of Tropical East Africa (FTEA). The climax vegetation is unknown, due to the disappearance of many climax species caused by logging activities (Althof 2005), but the current vegetation suggests that the final stage is mixed forest (Fashing et al. 2004).

Today most of the forest is medium-aged secondary forest, surrounded by young secondary forest (Althof 2005). Differences in species composition occur as a result of differences in logging history and management regimes, rather than as a result of differences in edaphic or climatic conditions (Fashing et al. 2004, Althof 2005). The disturbance of KF resulted in 17 patches of different vegetation units (Althof 2005). If management and protection efforts do not improve, the prognosis for Kakamega Forest is bleak, as certain species are no longer able to regenerate in habitats, where they formerly occurred (Kiama & Kiyiapi 2000, Fashing et al. 2004).

A total of 400 vascular plant taxa have been recorded in the forest, consisting of 112 tree species, 62 shrubs, 58 climbers and 114 herbs (Althof 2005), additionally 137 species of folicolous lichens have also been found (Kumelachev 2008). Of the 212 recorded woody species, 41 % were of guineo-congolian origin, 33 % were related to the Afromontane system and 26 % were transitional species (Althof 2005). According to latest information there are now 873 vascular plant species (Prof. E. Fischer, University of Koblenz, unpublished data).

2.1.5 Human impact

Commercial logging in KF started in the 1930's and continued until 1975, which caused heavy disturbance, clear-felling and the establishment of fast-growing exotic tree and softwood plantations (Mitchell 2004). The plantations were set up mainly in the southern part of the forest and started in 1934 and are estimated to occupy 1,700 to 2,400 ha. The continuous human pressure has resulted in land cover changes (e.g. fragmentation) and a reduction of the forest area (Mitchell 2004).

KF is surrounded by the highest population density ~ 600 people per km^2 in Kenya (Tsingalia 1990, Blackett 1994). This has led to considerable long-term human influence on the forest. Human settlement was common until the forest was gazetted, and partly followed by the introduction of the shamba system, a form of agroforestry where farmers are encouraged to cultivate primary crops on previously clear cut public forest land on the condition that they replant trees (Oduol 1986), were which put additional pressure on the forest, together with the herding of cattle to the natural interior grasslands (Mitchell 2004). The forest served as a source of gold, charcoal, fuel wood, medicinal plants, timber and construction materials as well as for hunting purposes (Mitchell 2004, Kokwaro 1988). A high degree of human impact was found, with illegal pitsawying and logging being most widespread depending also on the different types of forest management (Bleher et al. 2006). The northern part, managed by the Kenyan Wildlife Service (KWS) since the 1980s, is less disturbed than the southern part, managed by the Kenyan Forestry Service (KFS former Forest Department) (Bleher et al. 2006; Mitchell & Schaab 2008). Much of the disturbance occurs in the form of illegal logging, firewood collection (Tsingalia 1990) and cattle grazing (Fashing et al. 2004). Further information on the disturbance history of Kakamega Forest is discussed in Tsingalia (1990) and Mitchell (2004).

2.2 Budongo Forest of Uganda

2.2.1 Geography

The country of Uganda lies between Congo and Kenya and covers an area of approximately 241,040 km^2. It can be divided climatically into the semi-arid north-eastern part and the more humid southern part affected by its proximity to Lake Victoria. Uganda is characterized by a number of large lakes resulting from the Albertine Rift, which runs through the country, and also by the white Nile, savannahs, rain forests and alpine regions such as the Rwenzori mountains.

Budongo Forest (BF) (Figure 2-5) (1°35'-1°55'N and 31°18'-31°46'E) is situated in western Uganda just east of the escarpment of the Albertine Rift Valley and Lake Albert (Sheil 1996) (Figure 2-5). The forest lies in the Bunyoro and Hoima districts, larger towns nearby are Hoima and Masindi. It consists of a cluster of reserves namely Siba, Budongo and Kaniyo-Pabidi, which run from southwest and to northeast (Sheil 1996). The combined area of the BF reserve is approximately 81,661 ha (Lung & Schaab 2008), making it Uganda's largest forest reserve (Hamilton 1974), of which 44,340 ha have been recorded as forest (Karani et al. 1997 cited by Mitchell & Schaab 2008). The reserves are contiguous with three protected areas: the Murchison National Park (MFNP), the Bugunga Game Reserve and the Karuma Game Reserve which overlap with Siba in the north, and together add up to 6,000 km^2 (Sheil 1996). There is a slight slope north east towards the escarpment. Altitude is generally between 1,000 and 1,100 m a.s.l., with a few hills reaching 1,200 meters and the shallowest point being at 750 m (Sheil 1996) and thus it can be classified as lowland tropical forest (Richards 1996). Budongo Forest is a catchment area for four small rivers which flow north-west through the forest, over the escarpment and into Lake Albert (Eggeling 1947). These rivers from east to west are the Waisoke, the Sonso, the Kamirambwa and the Siba (Reynolds 2005).

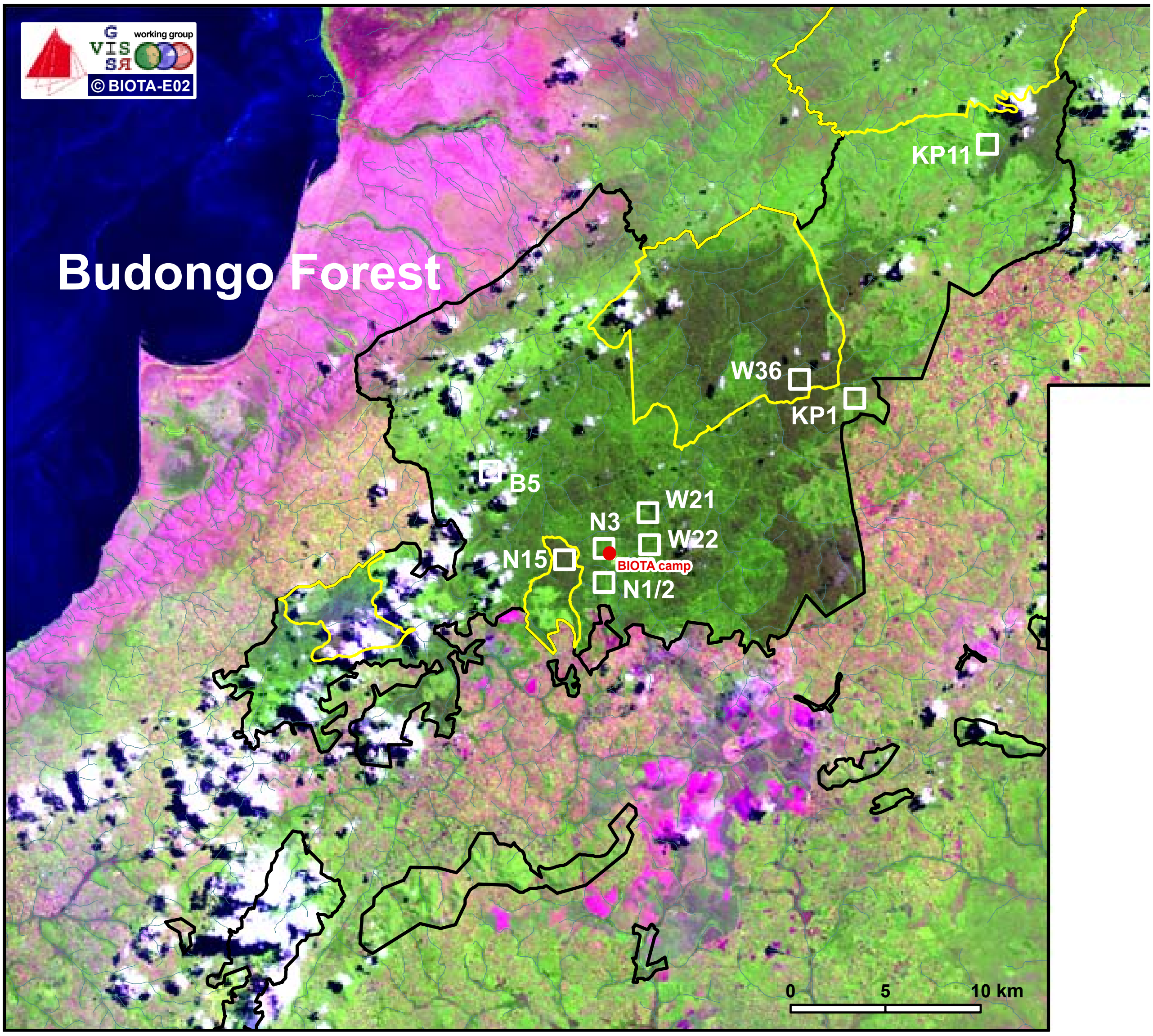

Figure 2-5: Satellite map of Budongo Forest and its fragments (black line is the boundary). The white squares indicate the location of the BIOTA-BDO's. Dark green indicates primary forest, light green indicates secondary forest with various shades in between. Blue depicts part of the nearby Lake Albert. Letters and numbers indicate different forest compartments according to the Ugandan National Forest Authority (NFA), which were used as BIOTA study sites. The compartments are B: Biso, KP: Kaniyo-Pabidi, N: Nyakafunjo and W: Waibira. The red dot marks the location of the BIOTA Camp (Map by courtesy of Prof. Dr. Schaab, BIOTA E02).

2.2.2 Geology and Soils

The underlying geology of the region is Pre-cambrian, pre-dating the formation of the Albertine Rift Valley, which began in the late Tertiary (Sheil 1996). It forms a heavily weathered basement complex of gneisses, granulites and schists.

The soils are very ancient sandy loamy clay of volcanic origin (Langdale-Brown 1960). They are fertile ferrisols, lithosols and histosols and are associated with the more recent landforms along the western rift (Howard 1991). The soils are classified as lateritic or ferralitic types (Richter & Babbar 1991). The pH ranges between 5.5 and 7.0, depending on the disturbance that has occurred, but evidently logging has increased the acidity of the soils (Bahati 2005, Musila, unpublished data).

Similarly the levels of C and N content were also found to be dependent on the disturbance history of the site, with lower levels in the more recently logged sites (Bahati 2005). The same pattern has been found for the base cations (K, Na and Mg), which appear in higher concentrations in the top soil of the undisturbed sites, while calcium was highest in the recently logged parts (Bahati 2005). Silt proportions are highest in the less disturbed sites and lowest in the recently disturbed areas (Bahati 2005).

2.2.3 Climate

The pattern of precipitation is bimodal as the ITCZ crosses twice a year. The peaks in rainfall occur from March to May and in September but with a pronounced dry season from January to March with rainfall less than 50 mm per month (Sheil 1996). Mean temperatures outside the forest lie around 22.2 °C, mean annual precipitation reaches 1,638 mm (Figure 2-6). At the forest station in Sonso the mean monthly temperature was around 20 °C in the drier part of the year 2006 (January and February) (Figure 2-7). In this part mean monthly maximum temperatures reached around 29 °C, while minimum temperature reached around 16-18 °C. In the northeastern part Kaniyo-Pabidi (KP11) climate was also measured for one year with a microclimate station between October 2005 and January 2007. This part appeared to be much drier with approximately 700 mm less rainfall in the same observation period compared to the Sonso climate station.

Further, solar radiation was measured from November 2005 until November 2006. Mean monthly radiation was 190 W m^{-2}, the maximum value measured in the driest (least cloudiest) month February was 216 W per m^2, while the lowest monthly values were measured in July at 162 W m^{-2} using a pyranometer (see Section 3.2).

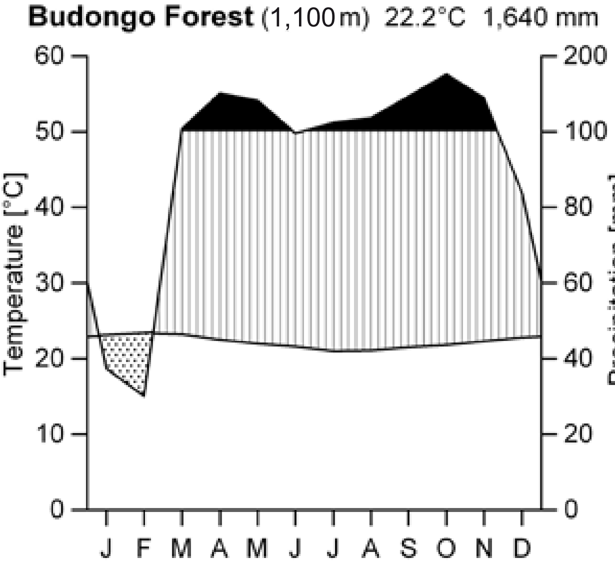

Figure 2-6: Climate diagram of Budongo Forest with data for rainfall and temperature recorded between 1993 and 2009 (diagram by Todt, data by courtesy of Budongo Conservation Field Station (BCFS)).

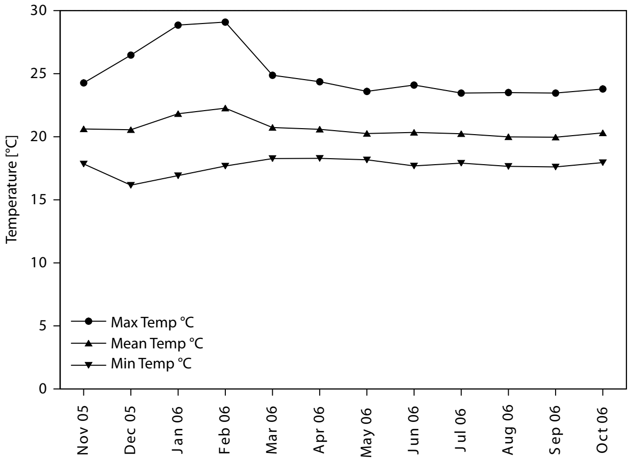

Figure 2-7: Monthly mean, minimum and maximum temperatures in Nyakafunjo 4 between November 2005 and October 2006 measured using a HOBO datalogger.

2.2.4 Vegetation

BF has been classified as a medium altitude moist semi-deciduous forest (Babweetera et al. 2000) or as lowland rain forest (Eggeling 1947), although the amount of rainfall is close to the minimum limit for a rainforest (Whitmore 1993).

The *Cynometra* zone is present in BF, which is one of Uganda's four types of medium-altitude vegetation (Hamilton 1974). Eggeling 1947 identified four main forest types for BF: Colonizing forest (6 %) with the dominant species being *Maesopsis eminii*, mixed forest (60 %) with a mixture of frugivorous species such as *Celtis spp*. and ironwood forest (32 %) which is to a large degree dominated by *Cynometra alexandri*, which forms up to 75 % of the forest canopy and is at the climax stage. The remaining forest is comprised of grasslands and swampy forests (2%), which is also regarded as climax forest. The forest would normally reach a climax stage, in this case ironwood or swampy forest, where a small number of species dominate. More recently four forest community types have been identified: *Pseudospondias microcarpa* Swamp forest, *Funtumia elastica - Pouteria altissima* Forest, *Lasiodiscus mildbraedii - Khaya anthotheca* Forest and *Cynometra alexandri - Rinorea ilicifolia* Forest (Mwavu 2007).

BF is one of the west Ugandan forests, that are situated within the floral area U2 of the FTEA (various authors 1952 et seq: Hamilton 1974). It is ranked third amongst all forests in Uganda both for general species richness and for overall biodiversity importance (Howard 1991).

2.2.5 Human Impact

Since the 1930s BF has had the world's longest forest management history in the tropics (Plumptre 1996) and the forest, the way Eggeling (1947) and others once observed it, has changed a lot since commercial logging was introduced. Budongo has experienced a number of human impacts.

In the 19th century, anthropogenic fires were used to control the spread of BF into surrounding savanna. Fires were lit to clear away dry growth from the previous year and to produce fresh grass for cattle (Paterson 1991). The number of fires was reduced with the arrival of the Europeans in the early 20th century (Nangendo et al. 2006). Commercial logging started in 1917, up until then only small amounts had been removed from the forest (Eggeling 1947). Timber cutting increased with the start of the first sawmill in 1926 (Eggeling 1947). From then onwards the exploitation was considerable. Of the 68 compartments established by the sawmills, 60 were logged. Of the 8 unlogged compartments one is in Nyakafunjo block (N15), 3 in the Kaniyo-Pabidi block (KP11, KP12 and KP13) and four in the Waibira block (W17, W30, W31 and W36) (Plumptre 1996).

The forest was the prime source of the most valuable timber, the African mahoganies (*Khaya spp*. and *Entandrophragma spp*. of the Meliaceae), and the dominant iron wood (**Cynometra alexandri**) in

Uganda (Plumptre 1996). Today *Khaya anthotheca* is the most dominant remaining African mahogany species (in contrast to the *Entandrophragma spp*.) due to its ability to regenerate well at different light levels (Bahati 2005). In total 872,627 m^3 of timber were extracted in 60 years (Plumptre 1996), leading to timber exploitation in most areas of the reserve (Plumptre & Reynolds 1994).

Apart from the logging impact, management decisions like the use of arboricides to remove non-marketable tree species (like **Cynometra alexandri**) to encourage the regeneration of the African mahogany species (*Entandrophragma spp, Khaya spp*.) changed the vegetation and species composition. This poisoning treatment was used in 34 blocks until 1970 (Plumptre 2001). Logging stopped in the mid 1990s and at present mechanized logging is not taking place as the sawmills are no longer operating. Instead illegal logging particularly in the former unlogged nature reserves has become a threat to the remaining mahogany trees (Reynolds 2005). The illegal activities are increasing also due to an increase in the population density over the past decades (Muhereza 2003). Thus in particular the above-mentioned African mahogany species are vulnerable or endangered, but also species like *Cordia millenii* and *Alstonia boonei* are highly sought after for their timber, which has affected their regeneration (Mwavu & Witkowski 2009b). The commercial selective logging activities have altered the forest structure by increasing the proportion of successional mixed forest while reducing the dominance of the climax *Cynometra alexandri* forest (Plumptre 1996).

2.3 Main differences between the two forests

BF lies at a lower altitude compared to KF, therefore the annual mean temperature is higher in BF than in KF. Also the annual sums of rainfall differ from each other. KF is wetter and cooler, further the dry season is not as severe as in BF (Table 2-2). The soils in KF are on average more acidic than the more alkaline soils of BF indicating that more disturbance occurred in KF. C and N content are on average higher in KF than in BF (Table 2-2).

Table 2-2: Comparison of abiotic factors of the two study forest. Climatic data are in KF by courtesy of BIOTA E02 and H. Todt in BF by courtesy of the Budongo Conservation Field Station. Soil data are by courtesy of Musila (2007) for KF and by Musila (personal communication) for BF

Comparison of forests	KF	BF
Altitude [m]	1,600	1,000
Mean annual temperature [°C]	18.7	22.2
Annual Rainfall [mm]	1,915	1,638
Number of months < 100 mm rainfall	3 to 4	4 to 5
Number of months < 50 mm rainfall	0 to 1	2 to 3
Range of soil pH	4.5 - 6.5	5.5 - 7.0
Soil C [%]	6.1	3.38
Soil N [%]	0.6	0.36

Recent local disturbance is by far greater in KF than in BF (MITCHELL & SCHAAB 2008). Also logging in BF, where management plans have existed since the 1930s (PLUMPTRE 1996), was carried out more systematically and professionally than in KF. Also the larger total area of BF, which is not exposed to as much pressure from human settlements, may explain why BF was used more sustainably and moreover left to recover from past disturbances.

3 Material and Methods

The study was part of the BIOTA (Biodiversity Monitoring Transect Analysis) AFRICA project. It was jointly founded by African and German researchers aiming at the establishment of research supporting sustainable use and conservation of biodiversity in Africa (www.biota-africa.org). By encompassing a variety of disciplines the BIOTA project has tried to increase the pool of knowledge on how African ecosystems function. This study was part of the BIOTA East Africa, which links a set of thematically and geographically strictly co-ordinated analyses of biodiversity changes in the East African rain forests of Budongo and Mabira in Uganda and Kakamega in Kenya. The study sites were set up in two of the forests along degradation/disturbance gradients in areas of 1 km^2 each, defined as Biodiversity Observatories (BDO‘s).

The data was collected from 2004 until 2009, during a number of field trips to BF and KF. The field-station in BF is run by the Budongo Conservation Forest Station (BCFS), while in KF the field-station is Udo’s Campsite under the Kenyan Wildlife Service (KWS). The vegetation data for trees and seedlings that were recorded prior to August 2004 were collected by Dana Uster for the BIOTA-project E03 and will also be published by her in more detail including other aspects in a separate dissertation.

3.1 Study plots

Study plots of 400 m^2 each are used, so that apart from the tree vegetation structure and diversity, small scale heterogeneity of a certain region in regard to environmental factors can be assessed. For comparison a 1 ha plot was established at one site. The plot size of 400 m^2 used here has already been chosen in a number of other studies to examine the species composition in comparable inventory areas (Liebermann et al. 1985, Wattenberg & Breckle 1995, Homeier 2004) and within gradients (Kessler 2000, 2001). The installation of such a permanent plot from the first identification and measurement of the trees (≥ 5 cm DBH) and seedlings onwards can be accomplished by two well-trained people within a week. According to the definition three plots of 400 m^2 represent a site (= 3* 400 m^2), that has similar tree structure and tree species composition. This plot design in each forest part guarantees relatively similar stand conditions, which is a necessary pre-condition for the analysis of the relation between a site and its vegetation (see Clark & Clark 1999, Paulsch 2002). Further it enables the investigation of the relation between spatially varying conditions and vegetation within a forest site.

In KF 27 plots were established in 2001 at nine sites by members of the BIOTA subproject E03, of which 21 lie in 7 of the BIOTA BDO’s. In BF the 18 plots were set up in October 2004 at six sites, of which 12 plots lie in the BIOTA BDO’s (see Figure 2-5), which cover a successional as well as a south-west/north-east gradient. Additional plots were set up in two nature reserves to create a geographical gradient. In each forest type three plots per site were set up.

The study sites were chosen according to the following criteria:

- the study sites should be able to represent the different vegetation types in both study forests as well as possible.
- the areas were supposed to possess a closed canopy without gaps and without evidence of anthropogenic activities
- the structure and species composition of the plots were supposed to be representative of the surrounding forest type and its topography.
- the selection according to these criteria was done randomly.

All plots were demarcated with plastic tubes and strings, which divided the plot into 4 equally large parts. In each of the study plots, four subplots for tree seedling and sapling surveys were also demarcated using tubes and string (Figure 3-1).

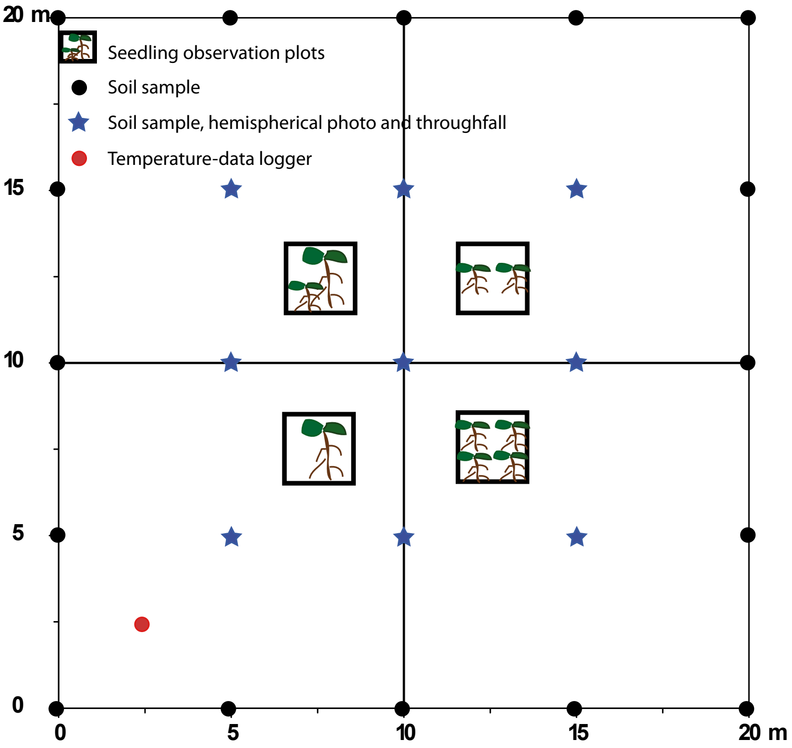

Figure 3-1: Scheme of the 20 x 20 m plot design and the points, at which measurements were done.

In addition for the abiotic data in 12 plots both in Kakamega and Budongo 25 soil samples were taken in a 5 m grid system and analysed (Musila 2007). In nine plots throughfall was collected at 9 positions in the centre of this 5 m grid system and analysed for chemical composition (H. Todt forthcoming) in Kakamega. Further hemispherical photographs were taken above each rain collector and seedling subplot. The geographical positions and altitudes of each plot (Table 3-1 & Table 3-2) were measured with the use of a GPS-receiver (Garmin GPS 12) using UTM (Universal Transverse Mercator) with the map datum Arc 1960, Kenya, where possible at the centre of the respective study plot.

The nine sites in KF lie at altitudes from 1,566 to 1,677 m a.s.l. (Table 3-1). Three of the sites are situated in fragments (MA, KI and YA), the other sites are part of the main Kakamega forest block (BU, CA, CO, IS, SAI and SAII) (see figure 2-2). The site names were chosen according to the local names of the respective forest parts (Table 3-1). The six sites in Budongo lie at altitudes from 980 to 1,100 m a.s.l. (Table 3-2). Three of the sites are situated in Nature Reserves (KP11, W36 and N15) and the other three (N4, W21 and W22) in sites that experienced commercial logging in the recent past (Table 3-3). The site names in Budongo were chosen according to the names of the forest compartments classified by the local forest authority (Table 3-2).

Table 3-1: The altitude and UTM coordinates are shown for the sites and plots in Kakamega Forest, Kenya. All plots are exposed to the North. Grid system 36N.

Site	Plot-No.	Altitude [m]	UTM N	UTM E
Buyangu Hill (BU)	BU1	1612	707355	38663
	BU2	1622	707234	38540
	BU3	1609	707508	38729
Colobus (CO)	CO1	1614	706815	39555
	CO2	1600	706695	39568
	CO3	1600	706706	39420
	CO* (1 ha)	1615	706498	40152
Camp (CA)	CA1	1616	707775	39284
	CA2	1601	707872	39112
	CA3	1600	707914	39064
Isecheno (IS)	IS1	1629	707752	27917
	IS2	1640	707776	28113
	IS3	1640	707798	28170
Kisere (KI)	KI1	1610	711078	42842
	KI2	1600	711007	42798
	KI3	1610	710951	42734
Malava (MA)	MA1	1670	706911	50283
	MA2	1677	707017	50208
	MA3	1670	707007	50327
Salazar1 (SAI)	SAI1	1586	708885	37051
	SAI2	1566	708998	36980
	SAI3	1579	709079	36820
Salazar2 (SAII)	SAII1	1592	707955	36018
	SAII2	1603	708049	35962
	SAII3	1600	708174	36145
Yala (YA)	YA1	1571	709312	22463
	YA2	1571	709383	22233
	YA3	1573	709318	22225

Table 3-2: The altitude and UTM coordinates are shown for the sites and plots in Budongo Forest, Uganda. All plots are exposed to the North. Grid system 36N.

Site	Plot-No.	Altitude [m]	UTM N	UTM E
Kaniyo-Pabidi 11 (KP11)	KP11A	997	357625	212299
	KP11B	987	357850	212313
	KP11C	992	357864	212506
Nyakafunjo 15 (N15)	N15A	1055	335947	191227
	N15B	1036	335714	191240
	N15C	1034	335472	191132
Nyakafunjo 4 (N4)	N4A	1076	336898	191119
	N4B	1078	336761	191233
	N4C	1076	336803	190828
Waibira 21 (W21)	W21A	1072	339558	193293
	W21B	1077	339610	193190
	W21C	1081	339821	193173
Waibira 22 (W22)	W22A	1089	339741	191494
	W22B	1092	339719	191814
	W22C	1088	339715	191907
Waibira 36 (W36)	W36A	1050	348234	199925
	W36B	1060	348152	199919
	W36C	1047	348488	199683

3.1.1 Disturbance classification

The two East African forests have been heavily influenced by different types of disturbance (see also Sections 2.1.5 and 2.2.5). The human demands on ecosystem services from the forest and particularly the recent logging history up to the 1970s has had a strong impact on forest structure and tree species composition. The impact of past human disturbance thus deserves special attention and plays an important role in the following analyses. The disturbance indices introduced to describe the two study forests by Mitchell & Schaab 2008 best quantify the disturbance in all BDOs. In their analysis they combined several studies on the two forests (e.g. for KF: Bleher et al. 2006, Mutangah 1996, Lung & Schaab 2006; for BF: Plumptre 1996), with observations on land cover changes, forestry records and also oral evidence enabling them to develop reliable indices. Disturbance is quantified by a commercial disturbance index (CDI) (e.g. logging, planting etc.), a local disturbance index (LDI) (e.g. firewood collection) and a forest cover change index (Mitchell & Schaab 2008), which all add up to an overall disturbance index (Table 3-3). The index most relevant to this study, the CDI, was derived from forestry maps and records, as well as oral evidence from foresters and locals (Mitchell & Schaab 2008). For example a CDI with a medium value was allocated to forest sites that had only been selectively logged once in the last 50 years (Mitchell & Schaab 2008). If selective logging occurred again within a short time or if for instance improvement planting was carried out, then this would lead to a higher CDI value (Mitchell & Schaab 2008). For the sites that were not located within the BDOs (CA and SAII) assessments of the local and commercial disturbance indices were based on personal observations, communication and interviews with people living locally. As the evaluation of the CDI, on a scale ranging from 1 to 10, was derived from many different sources this seemed to be a good measure of past human disturbance.

Table 3-3: Disturbance index and managing authority for the studied forest sites in both forests, that lie in the BIOTA Biodiversity observatories (BDO's) are presented. The higher the disturbance value, the more disturbed the site on a scale from 1 to 10 for commercial, local disturbance and forest cover change index, while the overall disturbance index shows the sum of the three indices (after Mitchell & Schaab 2008). Abbreviations of managing authorities are explained in the Acronyms. Sites marked with * were included and categorized for commercial and local disturbance according to personal observations.

BDO	**Managing Authority**	**Commercial disturbance index (e.g. logging, planting, etc.)**	**Local disturbance index (i.e. forest use by local population/ researchers etc.)**	**Forest cover change index (since early 20th century)**	**Overall Disturbance Index**
Kakamega					
MA	FD	8	7	4	19
KI	KWS	2	5	-2	5
CO	KWS	6	3	-3	6
BU	KWS	7	2	-3	6
SAI	KWS	6	1	-1	6
IS	FD	6	6	-2	10
Y	FD	0	2	5	7
CA*	KWS	10	5	-	-
SAII*	KWS	4	1	-	-
Budongo					
W22	NFA	6	2	0	8
W21	NFA	7	1	0	8
N3	NFA	6	2	1	9
N4*	NFA	6	2	-	-
N15	NFA	0	2	0	2
W36*	NFA	2	2	-	-
KP11*	UWA/NFA	0	0	-	-

3.1.2 Recording of forest stand structure and tree diversity

The recording of data in permanent sample plots is well described by Condit (1998). This work forms the basis for the methods used in the present study. In the plots all tree-like plants DBH ≥ 5 cm were tagged with aluminium tags. The plants defined in this way are called "trees" throughout this study. For all trees the positions in the plot, height and DBH were recorded. For the measurement of the **positions of the trees** a flexible metal measuring tape and laser distometer (Leica type) were used to measure the distance from the tree centre to the closest plot boundary with an accuracy of < 10 cm. With the help of the positions, plot maps were created to simplify locating the trees for example for re-identification.

Tree heights ≤ 5 m were measured with a measuring tape, trees > 5 m were measured by using a clinometer (Suunto PM-5/360PC). Then the height was calculated trigonometrically. Another way of measuring tree heights was by using the laser distometer (Leica type) horizontally aiming at the top of the tree and thus obtaining a direct height value. The tallest point of a tree was defined as the highest bud. **Tree diameters** were measured directly using a digital caliper for trees ≤ 10 cm DBH. For larger trees the DBH was calculated via the circumference, which was measured using a measuring tape. Before measurement, trees were cleared of lianas, climbers and mosses. **Tree volume** was calculated using the approximation of a cone with the ground diameter and height of a tree. **Slenderness ratio** represents the proportion of tree height to tree diameter.

All trees ≥ 10 cm DBH were equipped with dendrometer bands in the plots BU 1-3, CO 1-3, SAI 1-3 and SAII 1-3 in Kenya and in the plots N15 A-C, N4 A-C, W21 A-C and W22 A-C in Uganda to test for the spatial variability of tree growth. The dendrometers were read monthly, at the same time phenological observations for each tree were recorded (also see Section 3.2).

The number of **tree seedlings** (≤ 1 m height) and saplings was also recorded once every three months in the four subplots (see Section 3.3) in all of the respective plots. **Seedling heights** were measured using a measuring tape or the laser distometer. At the beginning in 2001 seedlings were tagged, measured and identified by DANA USTER. From 2004 onwards I continued the data collection in the same subplots. New seedling recruitments were tagged, measured and identified. If seedlings or saplings were no longer found in the subplots and only their tag was left over, they were recorded as being dead. This was done in 4 x 4 m^2 subplots within every plot (see Figure 3-1) in KF and in 4 x 1 m^2 subplots in BF.

3.1.2.1 Hemispherical photography

In all 9 sites in KF above the position of the seedling subplots and the throughfall collectors and in 6 sites in BF above the position of the throughfall collectors, hemispherical photos were taken with a digital camera and the respective system (HemiView-complete system from Delta-T) for calculating the canopy openness and understorey radiation. The photos in BF were incomplete so that sets of photos are only complete for 4 sites, 15 plots and 60 subplots. The photos were taken by DANA USTER, HENNING TODT in 2002 at the sites in KF and by DR. MATHIAS OESKER and myself at the sites BF in 2009. The calculations were performed with the HemiView software 2.1 (DELTA-T DEVICES). Hemispherical photos are an indirect, but fast, practical and reliable way of describing the crown structure (OESKER 2008). The resulting value of the visible Sky (VisSky) is used as canopy openness [%], while the ratio of direct radiation below canopy (DirBe) and direct radiation above canopy (DirAb) is used as understorey radiation [%] in analyses.

3.1.2.2 Canopy parameters and light measurements

The description of the tree canopy helps to characterize the light availability and exposure of an individual tree. The distance from the bole to the crown edge was measured at each of eight compass points on each tree, with each point determined from directly below the crown edge, which was used to draw maps of the crown shapes (see Young & Hubbell 1991, Muth & Bazzaz 2002). Another factor recorded was crown exposure (CE), which was classified according to Dawkins (1956). He classified light regimes for the trees as follows (Table 3-4):

Table 3-4: The crown exposure categories after Dawkins (1956).

Crown exposure description	Value
Crown not exposed to any sunlight	1
Crown exposed to lateral sunlight	2
Crown exposed to lateral and direct sunlight	3
90 % of the crown exposed to direct sunlight	4
Crown fully exposed to direct sunlight	5

3.1.2.3 Species identification and collected material

All recorded tree individuals ≥ 5cm DBH in the plots were as far as possible identified to species-level. For each tree individual a herbarium specimen was collected with a branch-cutting machine for trees ≤ 10 m. Trees ≥ 10 m were sampled by a tree climbing assistant, who managed to climb even tall trees and collect a plant sample with the help of a branch-cutting machine. Further, misidentification was ruled out by collaborating with the botany BIOTA subproject E04, by providing additional verification based on analyses of wood density as well as by conducting macroscopical examinations of the wood anatomy for almost all large trees (≥ 30 cm DBH) (Braun 2010) and by using my own field experience, so that the species determination in this study should be very reliable. The collected plant material was pressed and dried in self-made drying ovens or directly in the sun. Collected specimens are stored in the herbaria of the east African herbarium in Nairobi, Kenya (EA) and of the Makerere University MHU, Uganda, as well as of the University of Hohenheim (HOH), Germany. Literature used for identification was mainly:

Beentje (1994), Hamilton (1991), Agnew & Agnew (1994), Coates Palgrave (2002), Maundu & Tengnäs (2005) and the web site www.visualplants.de. Accepted names were used according to the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/). Additionally to the collected material, photos were taken of most of the plants and included in the Visual Plants database (Dalitz 2002, Dalitz & Homeier 2004). For all trees species that were identified in both forests during the research period a list of the species is given in the appendix table 10-11. It also states whether a herbarium specimen was collected. The other classification used in this study of late/early climax/pioneer species was adopted from a list produced by Althof (2005).

3.1.3 Additional data on the abiotic environment

The analysis in such depth of the interrelationship between highly resolved data on abiotic site factors was enabled by the research results made available by the BIOTA E03 project, by MUSILA (2007) for soil parameters in KF and in BF by WINFRED MUSILA (unpublished data), by HENNING TODT (unpublished data) for incident precipitation and throughfall, by DANA USTER (unpublished data) partly for hemispherical photos and vegetation assessments of trees and seedlings in KF and by MATHIAS OESKER (unpublished data) for hemispherical photos in BF. The large amounts of data and the frequency of their collection is a special feature of this study. Data on abiotic factors has rarely been collected on such a large scale in other studies. Data on further factors, which might have contributed useful information and have been seen to have an influence on growth in other studies, such as air mass carbon dioxide content (LEWIS 2006), soil moisture, herbivory, genetically inherent differences or mycorrhizal fungi (HUSBAND ET AL. 2002) were not available or could not be taken into account within this study.

As well as the history of climate and phytogeographical factors, present edaphic and climatic factors can also influence a site and the composition of plant communities (GENTRY 1988). The following parameters were taken into consideration to analyse spatial heterogeneity between the studied plots

In KF **rainfall** data used for this study was measured daily from 2001 until 2008 both in and outside the forest (H. TODT, unpublished data) using rain collectors (OESKER 2008). The term for rainfall in the forest is **throughfall (TF)**, for rainfall outside the forest **incident precipitation (IP)**. Figure 3-1 shows the sampling design including TF in the permanent study plots. In total, 81 collectors were set up in 9 plots at the sites of BU, CO and SAI. The IP was collected at three sites with three rain collectors per site in an open area adjacent to the respective plots. Further rain data was made available by the Kenya Meteorological Service from IS and MA, as well as for YA by the Rondo Retreat Centre in Kakamega. For the Ugandan forest, only IP data that had been collected daily in a single rainfall collector directly at the forest station was used for analyses. The data used for the analyses are by courtesy of the BCFS. The correlation between rainfall and growth was calculated using the rainfall of the months of growth measurement and in addition rainfall data (both IP and TF) summed for 2 and 3 months prior to measurement and the monthly number of rainy days were used to perform the analyses.

In KF in 12 plots, in the sites BU, CO, SAI and IS, **soil samples** were taken at 25 points at different depths (0-150 cm) (MUSILA 2007), as well as in BF at the sites N15, N4, W21 and W22. In this study only the upper layers will be considered (0-10 cm). This soil depth was chosen, because it contains most of the roots (MUSILA 2007) and therefore has a strong influence on growth.

The following chemical parameters were measured: pH, EC, %C, %N, the C:N ratio and the cation contents of K, Mg, Ca and Mn for the nitric acid and acetate extractable fraction of the soil samples in Kakamega and for the distilled water extractable fractions of the respective cations of the soils collected in BF (for a detailed description of the methodology see Musila 2007). Additionally for KF on site scale (BU, CO, IS, KI, MA, SAI and YA) physical soil parameters were analysed by Musila (2007), of which penetration resistance, bulk density, % Sand, % Silt, % Clay and the Silt:Clay ratio were used to conduct the analyses. The location of the sampling and the data in each site and plot is summarized in table 3-5.

Table 3-5: The distribution of available abiotic data for the two forests in the respective study sites is presented. An x marks the presence of the data while - means this data was not recorded. Small-scale indicates that the abiotic factor was sampled on plot and subplot scale. SD: soil data; TFD: throughfall data; IPD: Incident precipitation data; HPD: hemispherical photo data; MCD: in situ micro-climatic data.

Forest	**Site**	**SD**	**TFD**	**IPD**	**HPD**	**MCD**	**Small-scale SD**	**Small-scale TFD**	**Small-scale HPD**
Kakamega	Temperature and solar radiation data outside the forest not available								
	BU	x	x	x	x	-	x	x	x
	CO	x	x	x	x	-	x	x	x
	CA	x	-	x	x	-	-	-	x
	IS	x	-	x	x	-	x	-	x
	KI	x	-	-	x	-	-	-	x
	MA	x	-	x	x	-	-	-	x
	SAI	x	x	x	x	-	x	x	x
	SAII	-	-	-	x	-	-	-	x
	YA	x	-	-	x	-	-	-	x
Budongo	Temperature and solar radiation data outside the forest available								
	KP11	-	-	-	-	x	-	-	x
	N15	x	-	-	-	x	x	-	x
	N4	x	-	-	-	x	x	-	x
	W21	x	-	-	x	x	x	-	x
	W22	x	-	-	x	x	x	-	x
	W36	-	-	-	x	x	-	-	x

The mean values in the analyses were calculated on **site scale** for all 75 sample points in the respective plot triplet, on **plot scale** for all 25 samples and on **subplot scale** for the mean of the four samples taken around the respective subplot. Further in KF weighted means were calculated on **tree scale**. As the positions of the trees were measured per plot and the soil samples were taken in the grid system (Figure 3-1), it was possible to weight the four soil samples taken from points surrounding each tree. The weighting was performed by measuring the distance from the centre of each tree to the four surrounding soil sample points using Pythagoras' theorem. The four distances calculated in this way were then transformed into a percentage value for each soil parameter.

Temperature values for KF outside the forest could only be recorded for a period of 7 months and are not presented in the analyses. Temperature values from BF outside the forest were measured by members of the BCSF, also monthly minimum and maximum temperature was measured and used in the analysis. Solar radiation was measured from November 2005 until November 2006 in BF. The data was measured with a pyranometer (S-LIB-M003; 300-1100 nm; Onset) and logged by a HoBo®H8 industrial logger (Onset).

The microclimate in the forest was measured using data loggers that recorded temperature and humidity with the help of sensors (HOBO H8 Pro Series H08-032-08 from the Onset company) in some of the study plots in Uganda from October 2005 and in Kenya starting from April 2006. The collected data was saved according to the preset measuring intervals. The loggers were installed at the measuring site and due to the large storage capacity were left to log data for up to one year. They were fixed on tree stems at 2 m height and were covered with a plastic cover to protect them from falling debris and direct water. The measuring interval was set at 15 minutes, the values were then processed to mean monthly values and used as such in the analyses.

3.2 Stem growth measurements

Tree stem growth is regarded as one of the major structure parameters of forest ecosystems, the basis for the understanding of the demography and the dynamic of tree populations (CLARK & CLARK 1999; PELISSIER & PASCAL 2000, TERBORGH ET AL. 1997). For the tree growth analysis 817 trees in Kenya and 381 trees in Uganda were equipped with self-constructed dendrometers.

In recent decades there have been many studies on tree growth worldwide including the African tropical forests (Table 3-2). A lot of publications on tree growth focus on West African forests. But data has also been published on tree growth in BF using repeated diameter measurements (RDM) (SHEIL 1997), while growth data for KF are as good as non-existent in the literature. The majority of studies on tree growth in tropical Africa were carried out in lowland forests (HOPKINS 1970, LIEBERMAN 1982, BAKER ET AL. 2003) and not many have focused on lower montane forests (SHEIL 1997). Relatively few studies using monthly dendrometer band measurements have been published on tree growth in African rain forests and in those studies the number of individuals was low or the study time period short (LIEBERMAN 1982, SWAINE ET AL. 1990, BAKER ET AL. 2003), whereas many more such studies have been carried out in the neotropics (e.g. VIEIRA ET AL. 2004, HOMEIER ET AL. 2002, CLARK & CLARK 1999, FELFILI 1995, DA SILVA ET AL. 2002).

Data from tree ring analyses and dendrochronologies on growth rates and on age are present in studies from West African forests that experience a distinct dry season each year (MARIAUX 1969, SCHÖNGART ET AL. 2006, WORBES ET AL. 2003) or in dry forests like the miombo woodlands and savannas (SHACKLETON 2002). Even in wet tropical rainforests like La Selva in Costa Rica with a dry period of only 10 to 21 days, tree rings formed in the wood so that their analysis was possible (FICHTLER ET AL. 2003). But so far not many growth ring analyses have been performed on tropical trees especially in Africa (WORBES 2002). Another direct way of determining tree ages and growth rates is the method of ^{14}C dating (Worbes 1995, Martinez-Ramos & Alvarez-Buyalla 1998, Worbes 1999), as in the case of ironwood trees in Borneo that were dated to around 1000 years (Kurokawa et al. 2003). For a more detailed discussion on the method of ^{14}C dating see Martinez-Ramos & Alvarez-Buyalla (1998) and Worbes (1999).

3.2.1 Dendrometer bands

With the help of the workstation of the University of Bielefeld a cheap and strong dendrometer band type for the field was developed (see Homeier 2004). The material for the dendrometer band is 1.5 cm wide and consists of 1 meter long strips of aluminium (Al-MG3 F23, 0.5 mm thick). As the length of the dendrometer bands depends on the tree circumference, the dendrometer bands were constructed for each tree individually. For trees with a circumference ≥ 70 cm two strips had to be connected. At one end of the strip a loop of the same material was fixed, through which the overlapping end was pushed. The fixing of the dendrometer to the tree was achieved by piercing small holes in the strips to provide a connection for the main spring (Figure 3-2).

Figure 3-2: Example of a dendrometer mounted on a tree.

Each dendrometer was mounted stably on the previously cleaned stem surface at breast height (1.30 m). In the case of trees with buttresses they were fixed 50 cm above the beginning of the buttress with the help of self-constructed ladders. The point of measurement was then marked by piercing a mark on the dendrometer and finally the overlapping end of the main spring was fixed. The springs used are rustless (Quality: X12CrNi177, Number: 1.4310, extent of the spring: 0.5 mm x 5.5 mm x 1000 mm) and are a length of around 6 cm long, when they are not expanded.

The spring has the function of keeping the overlapping end of the metal strip close to the stem. The loop, in which the free strip end passes, is pressed together using pliers, until the end of the strip is not movable and only moves if the stem grows and thus pushes the strip further through the loop. Care has to be taken not to squeeze the loop together too strongly with the pliers. This would lead to the stem overgrowing the dendrometer band and make it useless.

Owing to the limited elasticity of the dendrometer material, the circumference of a tree should not be ≤ 30 cm. The number of the tree stem was written on the dendrometer band with waterproof permanent markers. Furthermore the structure of the respective tree bark had to be considered. A rough bark will not allow the dendrometer to lie exactly on the stem, which means the dendrometer will need longer to adjust to the growth of the tree. Generally all data for the analysis of growth rates were first considered three months after the dendrometer had been attached to the tree. Earlier measurements can lead to lower growth rates, because the dendrometer bands may not have been connected to the tree properly (SHEIL 2003, KEELAND & SHARITZ 1993).

Changes in tree diameter are the result of a combination of two factors: increase in dry matter from cambial cell division and short-term fluctuations caused by changes in tree water status (SHEIL 1995). These short- term fluctuations occur both diurnally and seasonally particularly in the seasonal tropics (REICH & BORCHERT 1984, LIEBERMAN 1982, SWAINE ET AL. 1990) and can only be measured using high-precision dendrometers. These were not used here as they are costly and need regular maintenance and as they are not necessary to ensure the measurement of long-term tree growth developments.

3.2.2 Selected species

In both study forests abundant tree species were selected for tree growth measurements (Table 3-6 and Table 3-7: 19 species in Kenya and 7 species in Uganda). For each species between 15 to 77 tree individuals were identified and equipped with dendrometer bands. The selected species grew throughout the study sites and were distributed over several DBH classes. The species were chosen according to their successional status to represent the whole continuum of life strategies in the forests e.g. climax species (*Lasiodiscus mildbraedii* and *Diospyros abyssinica*) and those that primarily occur in more open spaces (*Polyscias fulva*, *Funtumia africana* and *Ficus exasperata*) (Tables 3-6 & 3-7). Species like *Celtis gomphophylla* occur in both early and late successional stages of the forest. *Rinorea angustifolia ssp. ardisiiflora* will be referred to as *Rinorea angustifolia*. The species names are accepted according to the African Plants Database from 4th April 2010. All tree individuals were at least ≥ 9cm in their DBH. They were only chosen, if they made a vital impression, which means having no signs of damage at their stems and/or crowns.

In general, the mean diameter increment of a forest stand says little about the influence of abiotic site factors, as long as the successional stage of the stand is not taken into consideration. In young pioneer stands with a high percentage of fast-growing, light-demanding trees with low wood density, wood increment rates are generally higher than in old multi-storied forests. The bias of extreme successional stands was compensated by measuring the growth of identified species mainly in plots

Table 3-6: Selected tree species for growth measurement and their categorization in ecological groups regarding their occurrence (S secondary forest, P primary forest, S-P secondary to primary forest) in Kakamega Forest, Kenya. n: number of replicates.

Species	Family	Ecological Group	n
Antiaris toxicaria Lesch.	Moraceae	S-P	77
Englerophytum (syn. Bequaertiodendron) oblanceolatum (S.Moore) Heine & J.H.Hemsl.	Sapotaceae	P	15
Blighia unijugata Baker	Sapindaceae	P	26
Celtis africana Burm.f.	Ulmaceae	S-P	31
Celtis gomphophylla Baker	Ulmaceae	S-P	52
Celtis mildbraedii Engl.	Ulmaceae	P	31
Croton megalocarpus Hutch.	Euphorbiaceae	S	28
Diospyros abyssinica (Hiern) F.White	Ebenaceae	P	24
Ficus exasperata Vahl	Moraceae	S	20
Ficus sur Forssk.	Moraceae	S-P	25
Funtumia africana (Benth.) Stapf	Apocynaceae	S-P	70
Heinsenia diervilleoides K.Schum.	Rubiaceae	P	22
Markhamia lutea (Benth.) K.Schum.	Bignoniaceae	S-P	31
Morus mesozygia Stapf	Moraceae	P	22
Polyscias fulva (Hiern) Harms	Araliaceae	P	65
Strychnos usambarensis Gilg	Strychnaceae	P	54
Trichilia emetica Vahl	Meliaceae	P	18
Trilepisium madagascariense DC.	Moraceae	S-P	29
Vepris nobilis (Delile) Mziray (syn. *Teclea nobilis*)	Rutaceae	P	29

of the commonly intermediate successional forest types with CDIs of 6 & 7. In KF these are the sites: BU, CO, SAI and SAII and in BF the sites N15, N4, W21 and W22. Additionally single trees outside the plots were equipped with dendrometers in Nyakafunjo3 (N3) in Budongo, a site similar to N4 and in BU and CO in Kakamega.

Table 3-7: Selected tree species for growth measurement and their categorization in ecological groups regarding their occurrence (S secondary forest, P primary forest, S-P secondary to primary forest) in Budongo Forest, Uganda. n: number of replicates.

Species	Family	Ecological Group	n
Celtis gomphophylla Baker	Ulmaceae	S-P	17
Celtis mildbraedii Engl.	Ulmaceae	P	42
Cynometra alexandri C.H.Wight	Caesalpinaceae	P	36
Funtumia elastica (Benth.) Stapf	Apocynaceae	S-P	49
Khaya anthotheca (Welw.) DC.	Meliaceae	S-P	35
Lasiodiscus mildbraedii Engl.	Rhamnaceae	P	36
Rinorea angustifolia ssp. ardisiiflora (Oliv.) Grey-Wilson	Violaceae	P	36

3.2.3 Tree stem growth measurement

The dendrometer bands were read monthly in Kenya from June 2003 to December 2007 and in Uganda from January 2005 to December 2007 with a digital caliper by field assistants. The collection of tree growth and phenological data for the BIOTA-project E03 was originally started by DANA USTER from June 2003 to July 2004 and I took over the collection of growth data from August 2004. A series of 13 measurements represent one year of growth measurement. The number of days between consecutive measurements varied between 23 to 39 days due to logistic circumstances. The dendrometer accuracy was higher than the measuring accuracy so negative incremental growth could be measured for slow growing trees. The dendrometer band material and its construction does not however enable the measurement of „negative growth“, which can occur due to stem shrinkage during dry periods (DAUBENMIRE 1972). The advantage of the type of dendrometer bands used here, is that only true growth is measured, disregarding the seasonal shrinkage in the dry season and the re-swelling. Trees possess a reservoir of water in their stems and transpiration induces stem constriction through reduction in xylem pressure (KOZLOWSKI ET AL. 1991). Because, as other studies show, monthly increases in stem size can be as large as > 0.3 mm in diameter, this can mean that they are often underestimated if classical band dendrometers are used (SHEIL 2003). After the measurement the functioning of the dendrometers was tested and possibly interfering climbers and/or mosses were removed.

Missing values arose due to temporary outage caused by destruction of the dendrometer band. Trees with missing values were disregarded for this analysis. The quality of data was crosschecked by comparing the dendrometer data of following months. Obviously wrong values (extremely fast growth or negative values) were corrected e.g. low negative values were equalled to zero growth, if possible. If this was not possible, values were discarded (see CLARK & CLARK 1999, HOMEIER 2004, VIEIRA ET AL. 2004).

3.2.4 Stem growth rates

As the number of days between two consecutive measurements varied, a growth rate for each day was calculated. The daily growth rate calculated in this way was then summed for each month.

Growth rates were calculated in two different ways:

1) **Absolute circumferential growth**: the monthly increment directly measured on the dendrometer bands, as mentioned above.

2) **Relative circumferential growth**: the respective absolute circumferential increment as measured on the dendrometer band as a proportion of the respective initial tree circumference for each month.

In the literature the use of absolute growth rates is common. There is surprisingly little data on relative growth, although this appears to explain certain ecological contexts, like the prediction of mortality rates, better than absolute growth (Chao et al. 2008), as it is a more precise measure of tree vigour (Bigler et al. 2004).

3.2.5 Tree phenology surveys

Tree phenology was observed monthly, during the same time period as the dendrometer band reading took place. The categories for flowering and fruiting behaviour of the tree individuals were: few young, few old, many old, many young or a mixture of old and young flowers or fruits. The state of the foliage was categorized as either having only young, only old, a mixture of many young and a few young, a few old and many young leaves or no leaves at all.

3.2.6 Tree age calculation

A method of estimating tree age is to calculate the number of years required for trees to pass from one size class to the next. Five size classes were therefore used starting from a DBH of 10 cm to 20cm, then followed by 20 cm to 30 cm, 30 cm to 40 cm, 40 cm to 50 cm and > 50 cm DBH. The size-related increment rates were calculated by adding the mean values and the standard deviation, because it is more realistic to weight the mean growth in favour of the fastest-growing trees, as they are the ones most likely to survive subsequent size-classes (Swaine et al. 1987b). According to these increment rates the years were calculated for a tree to reach its next size class. For each species the calculated age values to reach from 10 cm to the maximum DBH of a species were then summed to gain a tree age estimation.

The ages can only be estimations because the relatively short study period could only cover the growth rates of a small part of the lifespan of a tree. This means that the growth conditions observed at the time of the study may be the result of a change in climate so that they provide better or worse conditions for growth than in the past, and this may have distorted the age estimations to some extent (Worbes et al. 2003). For instance rainfall patterns have changed in KF with a decline in rainfall in the last 20 years (data from Kenya Meteorological Service provided by H. Todt). As rainfall correlates positively with growth, trees in former times with more rainfall might have been able to grow faster than today. Also the age before trees reach a DBH of ≥ 10 cm is not considered in the calculations and probably some larger trees from the species that have reached larger DBH_{max} are not fully included.

In addition the data on year-to-year variations in growth in relation to differences in climatic conditions enables approximations of growth rates for the past, where long-term climate records are available (Schreck & Semazzi 2004) and is a good indication of the likely reaction of tree growth to expected climatic changes.

3.3 Seedling surveys

The four subplots in each plot were used for the observation of tree seedlings and saplings with a DBH ≤ 5 cm. Throughout this study all the young trees ≤ 100 cm are called "seedlings". In Kenya all 432 m^2 of subplots were monitored every three months, while in Budongo Forest due to logistical circumstances only 4 sites (48 m^2) were monitored every three months. Seedlings at the other two sites KP11 and W36 were surveyed every six months. The spatio-temporal heterogeneity in plant distribution is particularly important in the earlier stages of tree development and determine the regeneration of forest trees and thus in the long term the forest tree composition (Norden et al. 2007, Connell & Green 2000).

At the start all woody seedlings in the seedling plots, including self-supporting lianas, if not identified as such, were tagged with a unique number and their height was measured. Individual seedlings were identified to morpho-species. Collected seedling samples were matched to specimens in the EA, Kenya and the MHU, Uganda and use was also made of the extensive knowledge of B.Dumbo, N.Sajita, J.Sajita, G. Mwale and A. Afeku who have long-term experience of identifying plants in the forests of East Africa. If specimens could still not be identified reliably, they were given morpho-species names until the trees grew taller and were easier to identify. Subsequent censuses took place every three months (in 2006 monthly). During each census, new seedlings, the **seedling recruits**, were tagged and measured, and missing seedlings were recorded as „dead". At the same time all other seedlings were measured.

The influence of soil, TF and light was tested by using existing data sets from the measuring points in the plots and averaged for the four points around each subplot. In contrast to other studies ecological tree measurements (monthly for tree growth and phenology; quarterly for seedlings) were collected at relatively short intervals thus enabling a very high resolution of data. An even more frequent recording of measurements was not feasible because of the limited logistical capacities, so that possible fluctuations within the interval between recordings (monthly for tree growth and phenology; quarterly for seedlings) could not be considered in this study.

3.4 Data handling and statistics

The recorded data were archived in Microsoft Excel sheets and in self-developed relational databases (4th Dimension) with the help of the Dipl. Inform. Jörg Waltemathe. The statistical analysis was performed using the software programs EstimateS 8.2.0 (Colwell 2006), Programs for Ecological Methodology (Krebs 1999), Statistica 8, R 2.9.1 and Xact 8.0. The graphical displays were produced using Xact 8.0, Adobe Illustrator CS3 and Adobe Photoshop CS3. The writing was done with Adobe InDesign CS3. In the following the statistical procedures are described.

3.4.1 General Statistics

The use of parametrical statistical tests requires normally distributed and variance homogeneous data. The normal distribution was tested using the Kolmogorov-Smirnov-test for single samples. The growth data were partly not normally distributed. The statistical tests therefore had also to be conducted using non-parametric statistical analysis in the form of the Mann-Whitney U test for two groups or the Kruskal-Wallis test for multiple groups. Correlations were analysed using Spearman's R.

Differences at different sites or between different experimental approaches were examined using an analysis of variance as these data were normally distributed (Statistica : Module ANOVA/MANOVA). Correlations for normally distributed data were calculated using Pearson's r. The post-hoc test of significance was the Tukeys HSD-test for unequal n (Bortz 1993). The following levels of significance were used in this study:

n.s.	$= p > 0.05$	not significant
*	$= p \leq 0.05$	significant
**	$= p \leq 0.01$	highly significant
***	$= p \leq 0.001$	very highly significant

3.4.2 Estimates of the actual species richness

It is almost impossible to find all occurring species, when studying species rich tropical ecosystems. Although the African tropics are not as rich in biodiversity as the neotropics, there will always be species that are not found or remain unidentified. The use of different extrapolation methods allows estimations of the expected species number in a given habitat, which can then be used to reach conclusions on the rate of coverage of the species found in the study plots (= sample). Five estimation methods were calculated with the programme EstimateS 8.2.0 (Colwell 2006), to find the potentially given species number in the studied habitats of both forests: Jackknife 1, Jackknife 2, Chao 1, Chao 2 and ACE (Abundance-based Coverage Estimator). In Jackknife 1 only the number of singletons (Species appearing with one individual) is used to estimate the number of unseen species, whereas Jackknife 2 calculates the unseen species based on singletons and doubletons (species that occur with 2 individuals) (Chao et al. 2005). Chao 1 is based on the number of species represented by a single individual and those represented by exactly two individuals (abundance-based estimator) while Chao 2 relies on the number of species found in only one plot and those found in exactly two plots (regardless of the number of individuals; incidence-based estimator) (Chao et al. 2005). The ACE-procedure calculates the species number out of the abundances of rare species (≤ 10 individuals) (Chao et al. 2005). The options for the calculation with EstimateS 8.2.0 were set in such a way that the sequence of the plots was changed randomly fifty times. In these diversity statistics only individuals were considered which could be allocated to the respective taxa. Additionally a sample-based rarefaction method (MaoTau) was applied. Rarefaction curves estimate species richness for a sub-sample of the pooled total species richness, based on all species actually discovered (Colwell et al. 2004).

3.4.3 α-diversity

The α-diversity describes the species richness within a habitat. As numbers of individuals fluctuate within the recorded samples (study plots), a direct comparison of species numbers is not always possible. A common procedure is the Shannon-Wiener-Index (see Krebs 1999). This index rates the abundance of rare species in comparison to other indices more strongly and is thus well-suited to the studies (relatively small samples with a high species diversity) performed in diverse tropical rain forests. Parameter N1 used in this study, is based on the number of equally frequently occurring species, which a sample should possess, to receive the value for the Shannon-Wiener-Diversity (H'). It is simply the information entropy of the distribution, treating species as symbols and their relative population sizes as the probability. Simpson's Index measures the probability that two individuals randomly selected from a sample will belong to the same species (or some category other than species). It takes into account the number of species present, as well as the relative abundance of each species. Further Fisher's alpha was calculated (Fisher et al. 1943). However, these indices are all very closely related (Hill 1973), and there is no reason to disregard one in favour of others. In particular, the exponent of the Shannon Index is linearly related to inverse Simpson (Hill 1973) although the former may be more sensitive to rare species. The calculations are based on formulas by Krebs (1999) and were assessed with R 2.9.1.

3.4.4 β-diversity

The NESS (= Normalized Expected Species Shared)-Index (Grassle & Smith 1976) was used to describe beta-diversity. It is similar to the Morisita-Index, but it weights in comparison the rare species more strongly. The NESS-Index gives for a sample size m the number of expected shared species in the compared samples. For m=1 the NESS-Index equals the Morisita-Index. With an increase of m rare species are weighted more strongly. In the present study the maximum possible value for m (mmax) was used for the calculation, which is optimal for analyses of ordination (Brehm 2002). After the NESS-Index had been calculated a non-metrical dimensional scaling (NMDS) was applied.

4 Results: Kakamega Forest

In all nine plot triplets (see Section 3.1) inventories of trees (≥ 5cm diameter at breast height (DBH)) and quarter annual seedling surveys were carried out from 2002 until 2008. In the three marked Biodiversity observatories (BDO's) Colobus, Buyangu Hill and Salazar (Table 3-1) monthly tree growth was recorded from June 2003 until the end of 2007.

4.1 Tree diversity

4.1.1 α-diversity

In the 27 plots (400 m^2 each) and one hectare plot in Kakamega Forest (KF) a total of 2007 tree individuals with a DBH ≥ 5 cm were recorded (see Subsection 3.1.1). The woody spermatophytes were represented by 91 species from 39 families, of which 71 species from 33 families reached DBH ≥ 10 cm.

Of the taxa 84 (92.3 %) were identified to species-level, 4 (4.4 %) up to genus level and 3 (3.3 %) remained unidentified. Table 10-11 in the appendix shows their occurrence in the forest including their availability in the Hohenheim herbarium (HOH). The most important tree families in the investigated area were Moraceae and Euphorbiaceae with 11 species each, then followed by Rubiaceae and Ulmaceae with 5 species each. In addition 14 families occurred, which were each represented by only one species throughout the study site. The three species richest genera were *Ficus* (6 species, Moraceae), *Croton* (3 species, Euphorbiaceae) and *Celtis* (3 species, Ulmaceae). The five most abundant species were *Heinsenia diervilleoides* (77 individuals, Rubiaceae), *Funtumia africana* (66, Apocynaceae), *Rinorea brachypetala* (62, Violaceae), *Antiaris toxicaria* (58, Moraceae) and *Blighia unijugata* (54, Sapindaceae).

During the whole study period a total of around 105 species from 42 families were identified (Appendix, table 10-11) in and outside the study plots. Table 4-1 shows the estimated total species number for the forest area. The trees identified in the 27 study plots represent 76.5 to 85.8 % of the potential species number.

Table 4-1: Estimates of the potential tree species number for the habitats studied in Kakamega Forest using different extrapolation methods and the percental coverage of the species found in the study plots.

Method	Jackknife 1	Jackknife 2	Chao 1	Chao 2	ACE
Estimated species number	111	119	115	106	108
Percent. of found species	82.0	76.5	79.1	85.8	84.2

4.1.1.1 α-diversity as related to environmental factors

The tree species abundances found in the plots set against the commercial disturbance index (CDI), which was established by Mitchell & Schaab (2008) for the respective study sites (see Subsection 3.1.1) is shown in figure 4-1. The highest species numbers occur at intermediate CDIs between 5 and 8 (Figure 4-1a). Lower species numbers were identified in the least and most disturbed sites. This relation was also strong for trees with a DBH ≥ 10 cm, but there the peak occurs as early as a CDI of 4. This was demonstrated by using a gauss fit, assuming that the species number is highest at intermediate disturbances levels.

The alpha diversity expressed by the Shannon-Wiener H’ index increased to a CDI between 5 and 7 and then decreased with a higher level of disturbance (Figure 4-1 b). This was in line with the values determined in respect of the species number.

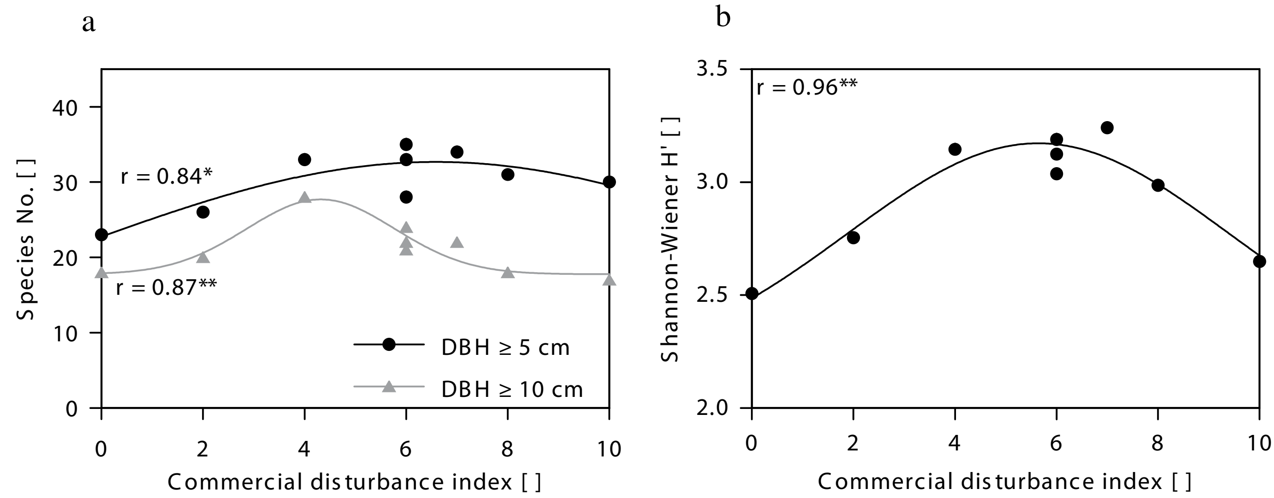

Figure 4-1: a) Species number [ ] and b) Shannon-Wiener H’ [ ] diversity in the nine study sites in relation to the commercial disturbance index (CDI). The gauss fit was calculated using $f(x)=a+b\times\exp\left(-\left(\frac{(x-c)}{d}\right)^2\right)$. The correlation coefficient r is given together with asterisks, which indicate the level of significance: * $p \leq 0.05$; ** $p \leq 0.01$. n = 9.

In another approach three species diversity indices Fisher’s alpha, Simpson and Shannon-Wiener were tested linearly against factors other than the CDI (Appendix table 10-2). Positive correlations were found with the incident precipitation, but these were not significant. Negative correlations were found with the soil physical parameters Silt:Clay ratio and the electrical conductivity (EC), in the case of Fisher’s alpha this relation is significant for both parameters (-0.79 for Silt:Clay and -0.72 for EC respectively). Significantly positive correlations were established between the alpha diversity and the acid extractable Ca for two of the indices. Further strong significant relations were established between Fisher’s alpha and the C and N content of the soil.

4.1.2 Effect of disturbance on β-diversity

The analysis of β-diversity was performed using the NESS-Index explained in Subsection 3.4.4. The results were plotted using non-metrical multidimensional scaling (NMDS) and presented two-dimensionally. The sites were now scattered on the two ordinates in respect of their species similarity (Figure 4-2). The grouping of the sites was based on the NESS-Index with the maximum parameter m (m = 46). The stress-value was strong (x= 0.0000068) so that the NESS-Index can be accepted.

Dimension 1 correlated with the CDI (r = 0.62 *), the light parameters both canopy openness (r = 0.70 *) and understorey radiation (r = 0.69 *) and the soil parameters both silt:clay ratio (r = 0.90 **) and bulk density (r = -0.87 *). All the correlated parameters result from the disturbance and thus the dimension 1 represents a degree of disturbance. In the following, analyses were therefore performed by using the CDI as a grouping category for the sites.

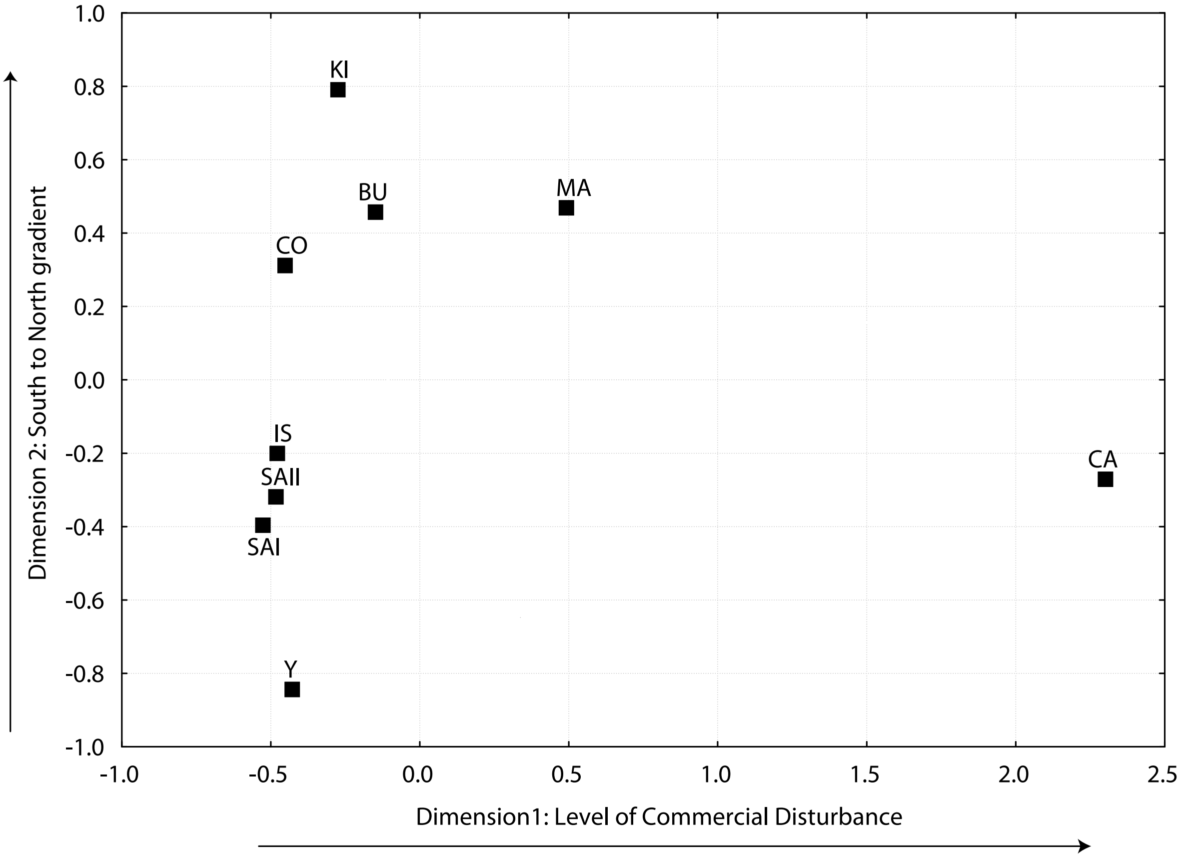

Figure 4-2: Two-dimensional scatterplot of the distance matrices from a NMDS after calculation of the NESS-Index with m_{max} (m = 46). The letters are abbreviations for the study sites described in table 3-1. The arrows along the axes are interpretations of the distribution of the β-diversity.

The values of dimension 2 correlated best with the acetate extractable soil potassium values measured within the first 10 cm of soil (r = 0.7472 *). According to the geographical position of the sites the second dimension can best be explained by a floristic north-south gradient. The full correlation matrix is shown in the appendix table 10-4.

4.2 Tree dynamics

4.2.1 Stem growth of all study trees

Growth values presented in this section were calculated by using dendrometer bands in the study period from 2003 to 2007 (see Section 3.2) and are recorded for plot trees only. As the plots were chosen randomly and all trees ≥ 10 cm DBH were included, the growth rates presented in this section are representative of the forest and the respective study sites. The plots contained 230 trees that were part of the dendrometer experiment in the most common forest types with CDIs of 4, 6 and 7.

On average the absolute diameter of tree stems increased at around 2.1 mm per year absolute in diameter, which was equivalent to around 1.5 % relative diameter growth per year. The mean values were temporally stable, but the maximum increments declined from 2004 to 2007. As these values were calculated on the basis of dendrometer data recorded in complete years, only the years from 2004 to 2007 were taken into consideration. A comparison between the sets of data on diameter increment collected in each of the four study years did not reveal a statistically significant difference (Figure 4-3).

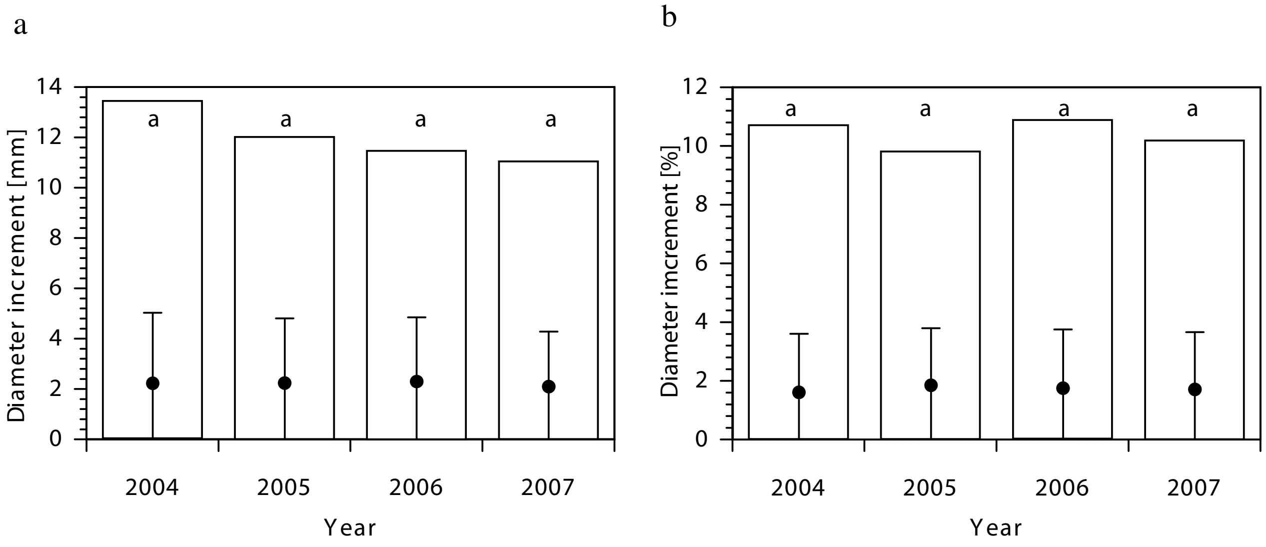

Figure 4-3: Absolute (a) and relative (b) mean annual diameter increment distribution for 4 years using dendrometer band measurements of plot trees in Kakamega Forest. The bars represent the range, the mean and the SD. The letters indicate significant ($p \leq 0.05$) differences according to the Kruskal - Wallis test. n = 230.

4.2.2 Stem growth of selected tree species

Apart from the 230 trees in plots 587 dendrometer bands were also installed on single trees in transects. The data, collected from 622 of the total 817 trees fitted with bands, were used for the following analyses. The measurement data for the remaining trees had to be discarded due to measurement errors or because they had died during the study period or because the number of individuals belonging to the respective species was fewer than 17. The five species with most dendrometer bands were *Antiaris toxicaria* (73 individuals, 8.9 % of dendrometer trees), *Funtumia africana* (72 individuals, 8.8 %), *Strychnos usambarensis* (52 individuals, 6.4 %), *Polyscias fulva* (52 individuals, 6.4 %) and *Celtis gomphophylla* (50 individuals, 6.1 %). The 622 trees represent a total of 18 species including at least 17 individuals each (Table 3-4).

The **mean annual circumferential absolute and relative growth rates** per species for the period between 2003 and 2007 is shown in figure 4-4. The **absolute circumferential growth** ranged from slow-growing understorey species such as *Blighia unijugata, Heinsenia diervilleoides* and *Vepris nobilis* with rates between 0.20 to 0.27 cm yr^{-1} to the fast-growing canopy species *Trilepisium madagascariense*, *Croton megalocarpus* and *Funtumia africana* with rates between 0.94 to 1.4 cm growth yr^{-1} (Figure 4-4a) Further there appear to be significant differences in the **relative circumferential growth** between the examined species. Understorey species like *Heinsenia diervilleoides* and *Vepris nobilis*, as well as shade-tolerant climax species such as *Diospyros abyssinica* and *Strychnos usambarensis* have little relative increment with 0.25 to 0.57 % yr^{-1} compared to more light-demanding early climax canopy species such as *Funtumia africana*, *Trilepisium madagascariense* and *Croton megalocarpus* with high **relative circumferential growth rates** between 1.5 and 1.8 % yr^{-1} (Figure 4-4b & Appendix table 10-12)

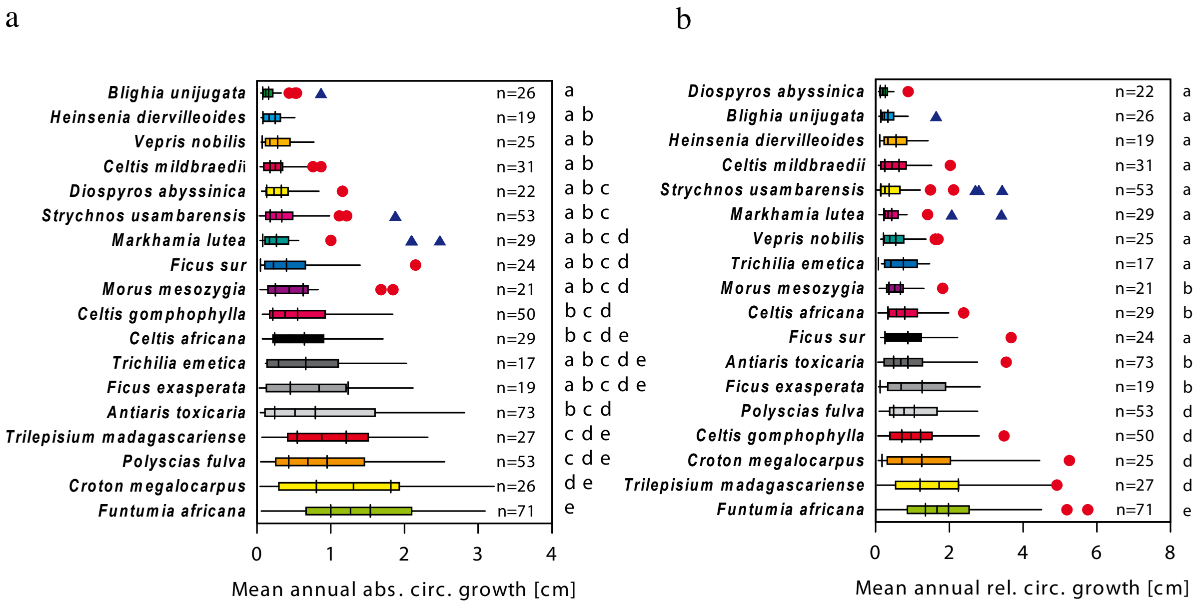

Figure 4-4: Mean annual absolute (abs.) (a) and relative (rel.) (b) circumferential (circ.) growth rates are presented. The boxes represent the lower to the upper quartile with the median, the whiskers the range. Red dots are outliers, blue triangles extreme outliers. The letters at the box and whisker plots denote significant ($p \leq 0.01$) different groups according to the Kruskal-Wallis-Test.

4.2.3 Temporal constancy of stem growth

With regard to the constancy of **absolute annual circumferential growth rates** on a temporal scale figure 4-5 indicates that increments of single trees in successive years possess a high autocorrelation. The strength of the correlation decreases with time. This means that increment rates of trees were fairly constant over a long period of time. It is appropriate, therefore, to use annual mean growth rates for the 5-year study period to describe the performance of individual trees.

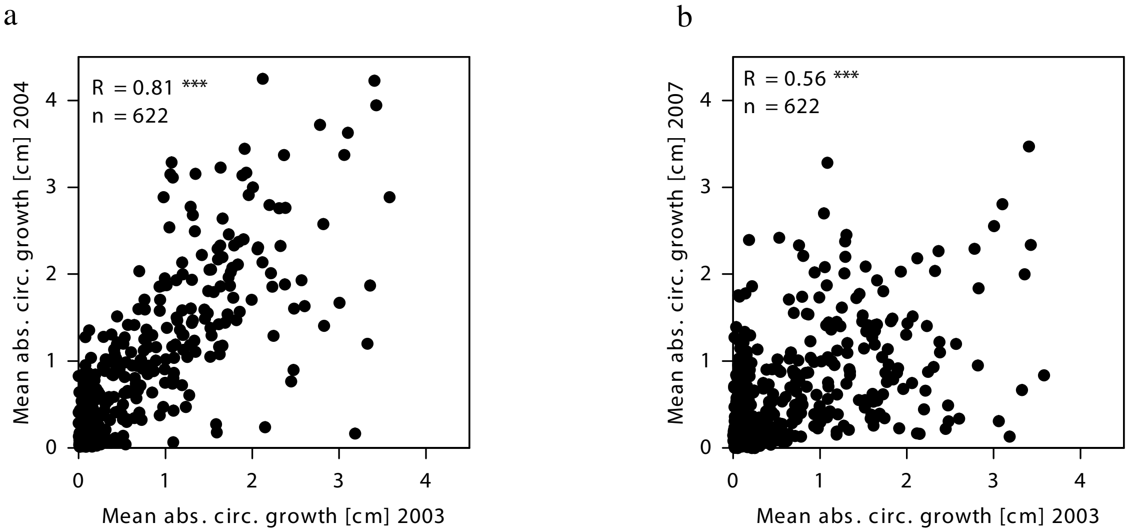

Figure 4-5: Correlation between successive absolute circumferential growth rates for individual trees of all species. (a) 2nd year (2004) growth depending on the 1st year (2003) (b) 5th year (2007) growth depending on 1st year (2003). Spearman's R is given together with asterisks, which indicate the level of significance (*** $p \leq 0.001$). n = 622.

The correlation between successive **absolute and relative growth rate** for individual trees persisted for several years and was still highly significant after 5 years, but became constantly weaker (Table 4-2). The apparent dependence of growth on past performance was evident in most cases for trees showing faster absolute and relative growth. The correlation remained strong over a longer period of time, shown by the comparison of the growth rate of the second and fifth year in relation to the growth rate of the first year.

Table 4-2: The four different growth rates of 2003 for all trees correlated with the respective growth rates of the following years. The numbers represent Spearman's R with the asterisks giving the significance: *** $p \leq 0.001$. n = 622.

Growth rate	2004	2005	2006	2007
Absolute circumferential growth 2003	**0.81*** **	**0.70*** **	**0.67*** **	**0.56*** **
Relative circumferential growth 2003	**0.74*** **	**0.68*** **	**0.62*** **	**0.51*** **

4.2.4 Stem growth as related to phenological dynamics

The influence of monthly phenological patterns on monthly absolute and relative stem girth growth and performance is shown in table 4-3. Both absolute and relative circumferential growth rates of trees were negatively related to flowering, fruiting and leaf shedding of the individual trees, in some instances significantly. The more trees invested in reproduction, the less they increased in girth. Further, there was a significant positive correlation between flowering and the monthly percentage of fruiting and leaf shedding tree individuals. Flowering was related to the shedding of leaves (Table 4-3), which often took place in the dry season (January to March) in some species. In total 11 species were observed that shed leaves completely. This was most evident in connection with tree species of the Moraceae and Ulmaceae.

Table 4-3: Correlation between the monthly tree phenology and the two monthly tree absolute and relative circumferential (circ.) growth rates during the period between 2004 and 2007. Pearson's r is shown together with the level of significance (without p > 0.05; * p ≤ 0.05; *** p ≤ 0.001).

Factor	Absolute circ.	Relative circ.	Trees flowering	Trees fruiting
Trees without foliage	**-0.27***	-0.26	**0.27***	-0.17
Trees flowering	**-0.34***	**-0.33***	-	**0.68*****
Trees fruiting	-0.26	**-0.28***	-	-

The diagram of the phenological dynamics (flowers, fruits and foliage) in relation to growth for the mean of all species is shown in figure 4-6. During the drier months (December to February) flowering increased, more individuals shed their leaves, followed by fruiting peaks in the early rainy season (March to May). This again is reflected in the wavelike character of the mean absolute circumferential

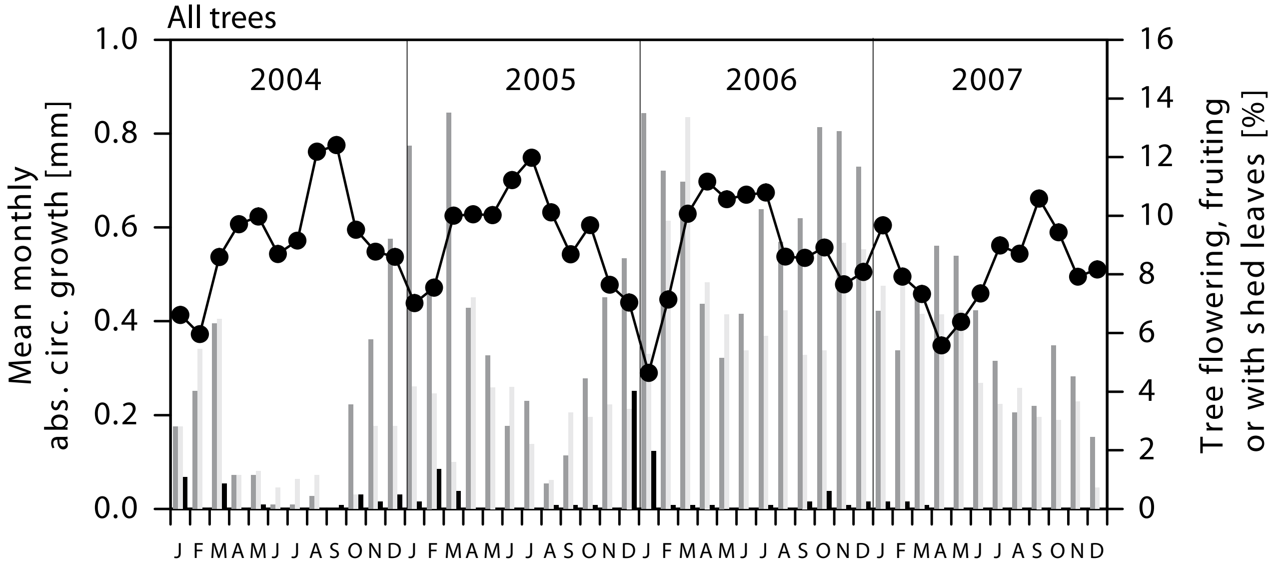

Figure 4-6: Monthly phenological dynamics and absolute circumferential (abs. circ.) growth during 2004-2007 for all trees (n = 622) ≥ 10cm DBH. The colours represent absolute circumferential tree growth —●—, % trees flowering ▨ % trees fruiting □ and trees with shed foliage ■

growth of all species. A total of 12 species from 5 families was found to be deciduous.

The **absolute circumferential growth** curves in relation to phenology for two exemplary species are shown in Figures 4-7a and 4-7b, the same relation for the other 16 species is shown in the appendix (Figure 10-2). The two species shown display different growth characteristics. While *Celtis gomphophylla* clearly showed a wavelike curve with the low growth peaks coinciding with the drier months January to March and a high peaks in flowering and fruiting activities, such a clear trend was not observed in the tree individuals of *Funtumia africana*, for which the growth rates were relatively constant without clear seasonal rhythms.

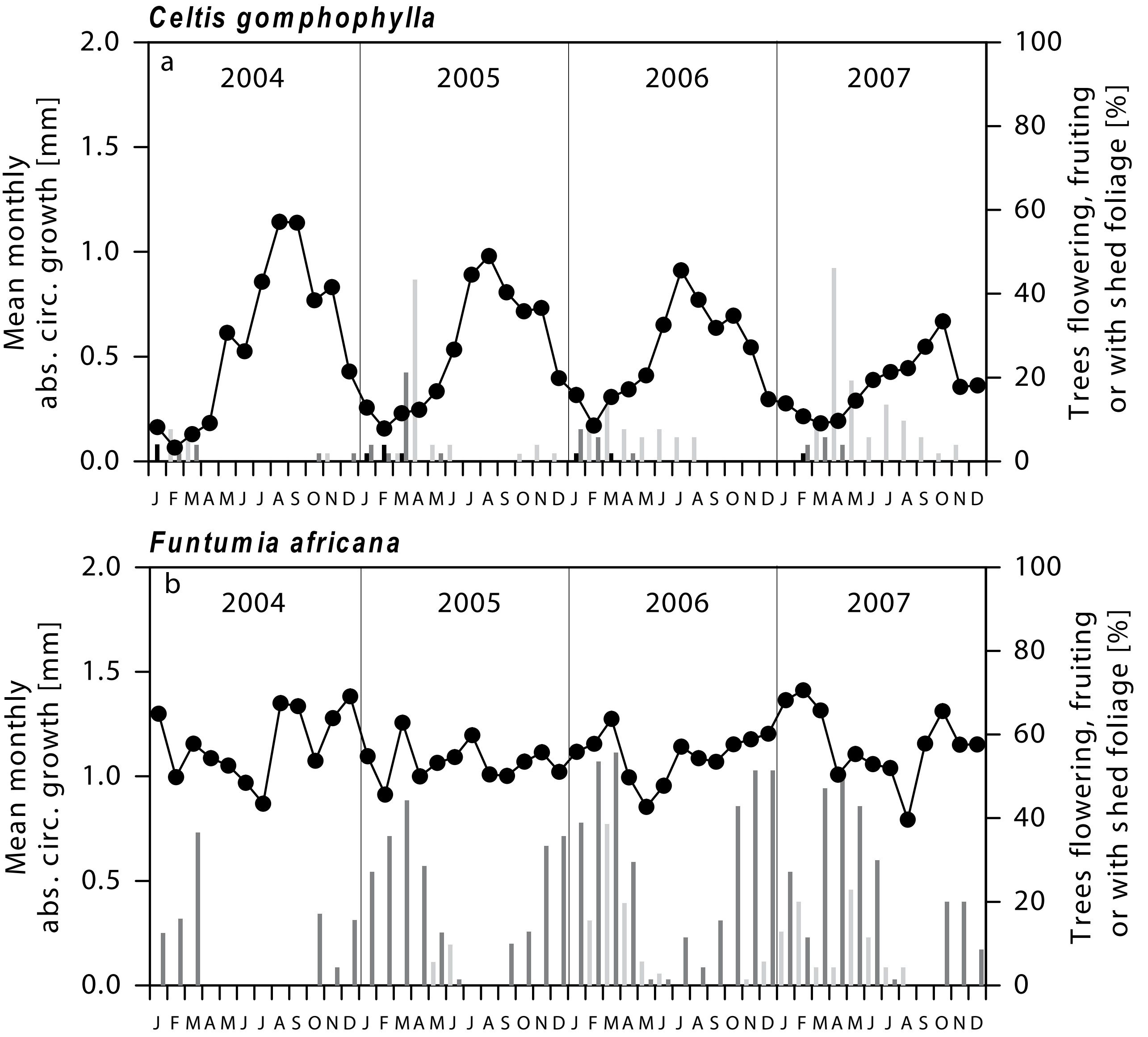

Figure 4-7: Monthly phenological dynamics and absolute circumferential (abs. circ.) growth during 2004-2007 for trees of (a) *Celtis gomphophylla* (n = 50) and (b) *Funtumia africana* (n = 70) ≥ 10cm DBH. The colours represent absolute circumferential tree growth—●—, % trees flowering ▨ % trees fruiting ░ and trees with shed foliage ■

4.2.5 Tree turnover

4.2.5.1 Tree age

An estimated age calculation for the examined species in the time period between 2003 and 2007 is presented in table 4-4. Fast-growing species like *Trilepisium madagascariense*, *Funtumia africana*, *Croton megalocarpus* and *Polyscias fulva* would need between 78 and 167 years to reach their maximum size from a starting point of 10 cm DBH. They grew up to 4 times faster than slow-growing species like *Strychnos usambarensis*, *Diospyros abyssinica* and *Trichilia emetica*, which would need approximately more than 300 years or more to grow up to their maximum diameter. The understorey species *Heinsenia diervilleoides* and *Vepris nobilis* had the slowest growth rates, but would not have a life expectancy of more than a 100 years.

Table 4-4: Mean annual DBH increment rates and the extrapolated time period, that is needed for the tree species to reach their maximum DBH (DBH_{max}), which equals the largest stem in the whole study area for the respective species, starting from a DBH of 10 cm. For the calculation the mean, adding the value of the SD, was assumed to be the increment in the different DBH classes.

Tree species (No. of individuals)	**Mean DBH-increment [mm year^{-1}]**	**DBH_{max} [cm]**	**Time period for reaching DBH_{max} [years]**
Antiaris toxicaria (72)	3.21	119.94	197
Blighia unijugata (25)	0.63	36.64	193
Celtis africana (25)	1.97	82.57	183
Celtis gomphophylla (50)	1.93	76.43	218
Celtis mildbraedii (31)	0.87	79.55	241
Croton megalocarpus (26)	4.23	86.39	167
Diospyros abyssinica (23)	1.06	65.35	356
Ficus exasperata (19)	3.33	172.21	274
Ficus sur (25)	1.41	93.33	164
Funtumia africana (70)	4.35	64.9	78
Heinsenia diervilleoides (20)	0.65	21.2	106
Markhamia lutea (29)	1.38	68.47	224
Morus mesozygia (21)	1.72	79.13	213
Polyscias fulva (54)	3.36	76.41	130
Strychnos usambarensis (53)	1.22	76.46	301
Trichilia emetica (17)	1.90	120.89	319
Trilepisium madagascariense (29)	2.99	116.66	166
Vepris nobilis (26)	0.86	26.58	108

4.2.5.2 Self-thinning and tree mortality

It was tested whether mortality depended on self-thinning of the tree population in the different sites. The relation between mean volume per tree and the tree density of the tree (DBH ≥ 5 cm) populations in the nine forest sites is presented in figure 4-8a. Highest volume and lowest density is found at IS (CDI 6), while highest tree density with a lowest mean tree volume is found at CA (CDI 10). The least disturbed site YA (CDI 0) has intermediate tree volume, density values and the lowest mortality rate. Apart from BU and CA the other plots are not close to the self-thinning line, which is a line with slope -3/2. As long as mean plant volume is below that line the tree populations increase in volume. The growth study mainly took place at CO, with some additional trees in BU, SAI and SAII. There is still capacity for an increase of volume in most of the sites, so that the net-BA increment was found to be positive and mortality is not density dependent (Table 4-5).

Mean annual mortality rates ranged from 0.7 % in the least disturbed site to 6.9 % per year in the most disturbed site (Figure 4-8b). The species (n ≥ 20) with highest mortality rates most often occurred at the most severely disturbed sites, for example the early pioneer species *Combretum molle* (6.5 % annual mortality rate) and *Harungana madagascariensis* (4.4 %) and do not have a large BA. At the other sites high mortality rates were recorded for the late pioneer species *Polyscias fulva* (5.4 %), *Ficus sur* (3.7 %) and for the understorey species *Vepris nobilis* (3.4 %). This effect along the disturbance gradient could be interpreted as self-thinning of the tree populations.

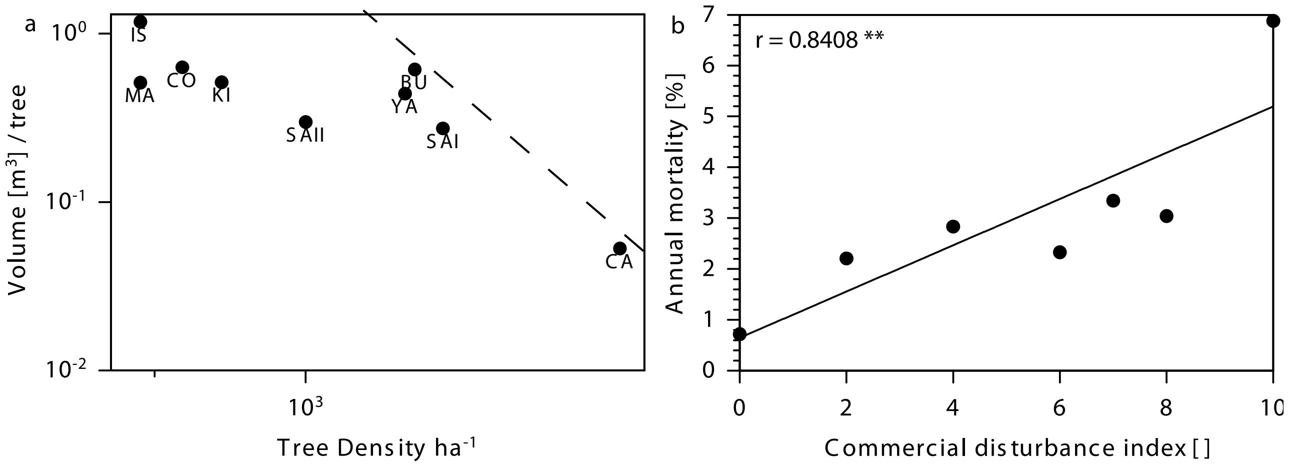

Figure 4-8: The tree populations a) mean volume in relation to its tree density with the site abbreviations (n = 9), the dashed line indicates, at which point self-thinning of the tree populations may take place. and b) the mean annual mortality rate for the period from 2002 to 2009 for trees ≥ 5 cm DBH in relation to the CDI is presented (n = 7). Pearson's r is given together with asterisks, which indicate the significance (** p ≤ 0.01).

4.2.5.3 Balance of tree turnover

The basal area and its annual increment in the study sites is shown in table 4-5. The sites differed strongly in their increment rates with a tendency towards more stand basal area with an intermediate level of commercial disturbance (CDI 6 and 7). The largest basal area increment was measured in the most disturbed plots, that also had lowest tree basal area. On average the basal area loss through mortality reaches 1.48 % per year for trees with a DBH ≥ 10 cm. In the study period no tree ≥ 10 cm DBH died in the least disturbed site. The most disturbed site CA had the lowest stand basal area, but the highest relative BA increment. All sites showed an annual net-BA increment.

Table 4-5: Growth and mortality in sites of 3 * 400 m^2 for trees ≥ 10 cm DBH. Sum of BA increment was calculated using dendrometer band data and for the remaining plot trees inventory data from 2002 and 2009 was used. BA: Basal area; CDI: commercial disturbance index. Site abbreviations are explained in table 3-1.

Site	**YA**	**KI**	**SA II**	**CO**	**IS**	**SA I**	**BU**	**MA**	**CA**
CDI	0	2	4	6	6	6	7	8	10
BA [m^2 1200 m^{-2}] of all stems in 2002	6.33	6.04	6.62	6.34	9.84	5.24	9.01	5.48	2.22
Sum of BA-increment [cm^2 1200 m^{-2}] (7 years)	605	470	891	1103	728	971	1077	976	756
Mean annual BA increment [% yr^{-1}]	0.95	0.78	1.35	1.74	0.74	1.85	1.2	1.78	3.4
Mean mortality (BA-loss) [% yr^{-1}]	0	4.49	1.59	2.66	0.04	1.71	1.02	1.02	0.76
Mean annual net BA-increment [m^2 ha^{-1}]	0.50	0.39	0.74	0.92	0.61	0.81	0.90	0.81	0.63

4.2.6 Stem growth as related to structural tree parameters

The correlation between structural parameters and the two tree growth rates explained in Subsection 3.2.4 is shown in table 4-6. There were very strong significantly positive relations between **absolute circumferential growth rates** and the four structural parameters described. The **relative circumferential growth rate** is more independent of size and crown exposure. Relative growth rates will therefore be analysed in the following and, as absolute growth rates are very often used in literature, absolute growth rates will also be presented. The correlation between the factors DBH, height and crown area is shown in the appendix, table 10-3.

Table 4-6: Correlation between the absolute (abs) and relative (rel) circumferential (circ) growth of all dendrometer trees and tree structural parameters. The numbers represent Spearman's R with the asterisks giving the significance: without: no significance, *** p ≤ 0.001. As the data were not normally distributed Spearman's rank correlation were applied. n = 622.

Factor	**Abs circ growth**	**Rel circ growth**
DBH	**0.49** ***	0.06
Height	**0.53** ***	**0.18** ***
Crown exposure	**0.53** ***	**0.24** ***
Crown area	**0.44** ***	**0.15** ***

4.2.6.1 Between species stem growth by DBH categories

The mean **absolute annual circumferential stem girth increments** for 3 of the 18 analysed tree species are shown exemplarily in Figure 4-9 (the other species are shown in the appendix Figure 10-1). Within the same species a high variability was established. The variability was seen in the case of fast-growing species like *Polyscias fulva* and *Croton megalocarpus*. For these species **absolute mean annual girth increments** varied between 0.1 and 3.3 cm yr^{-1}. For slow-growing species like *Blighia unijugata*, *Vepris nobilis* and *Heinsenia diervilleoides* increments ranged between 0.1 and 0.8 cm yr^{-1}

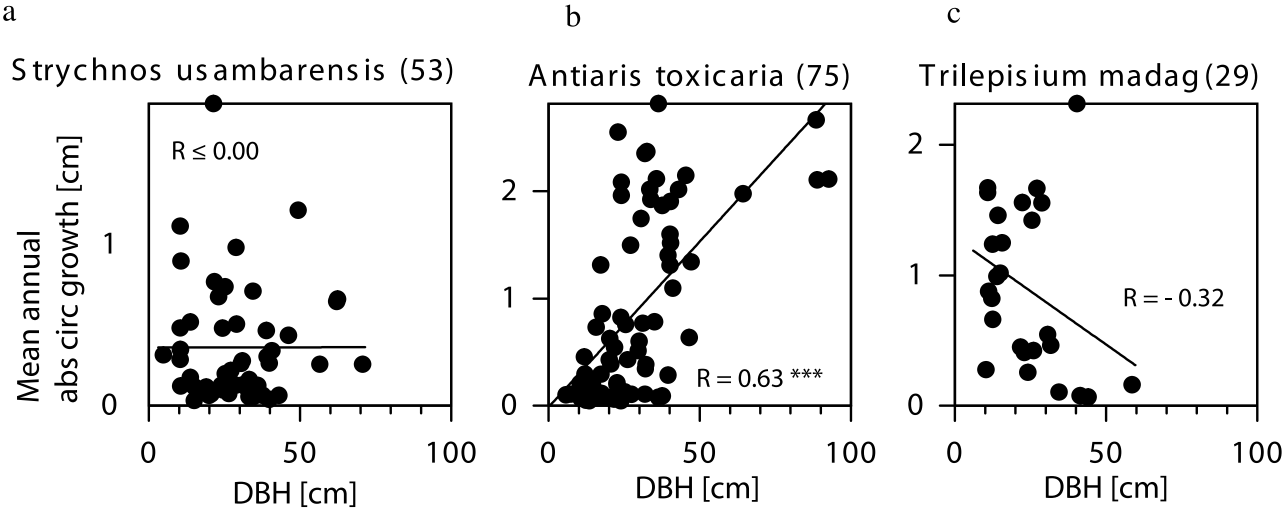

Figure 4-9: Mean annual absolute circumferential growth rates in relation to the initial diameter for a) *Strychnos usambarensis*, b) *Antiaris toxicaria* and c) *Trilepisium madagascariense*. The number in brackets refers to the individuals examined per species. The different scaling of the ordinates has to be considered. Spearman's R is given for the regression line. The asterisks mean different significances (*** p ≤ 0.001).

also showing high intra-specific variability. It was evident that **absolute circumferential growth rates** were highly variable when different species were compared. Some species showed a strong tendency towards more growth, the larger the tree individuals were. This trend was highlighted in the case of the fast-growing canopy species like *Antiaris toxicaria* (Figure 4-9 b) and pioneer species like *Polyscias fulva*. Other species possessed no relation between their growth and diameter. This was particularly evident in the case of slow growing shade-tolerant and understorey species like *Heinsenia diervilleoides, Strychnos usambarensis* (Figure 4-9 a) and *Vepris nobilis*. These shade-tolerant understorey/subcanopy species grew at a constant rate in all size categories. Some species reached the maximum growth rates for the stems in the lower diameter size categories. A few tree species showed a trend towards decreasing annual growth with increasing DBH size, as observed for *Croton megalocarpus* and *Trilepisium madagascariense* (Figure 4-9 c). Some species had a growth

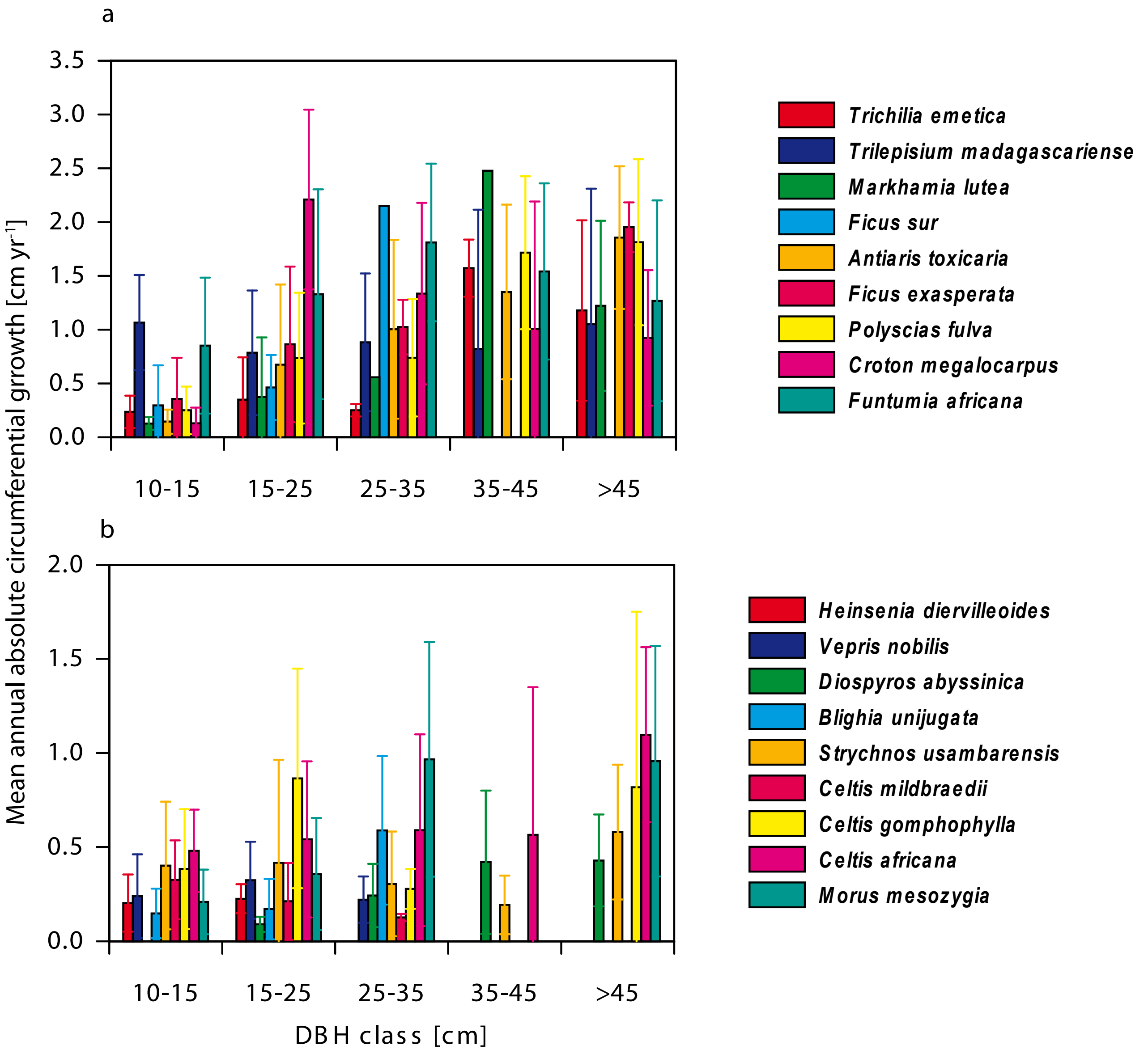

Figure 4-10: Mean annual absolute circumferential increments in five diameter size classes and the SD for the 18 species that were examined are shown. a) shows the results for the faster growing and the b) the results for the slower growing species. The different scaling of the ordinate has to be considered. Values are given, if at least two individuals were present in the respective size class.

peak in medium DBH categories, especially true of the fast-growing canopy species. Due to the high inter-specific variability, growth rates for any size category of trees must be approached with caution.

Figure 4-10 shows the DBH size category division and the **mean absolute circumferential girth increments** in five categories for the studied tree species. The main reason for the choice of size category division was to gain an even distribution of the individuals of all species in the different categories. Most of the species increased their annual growth rate with increasing diameter. Most species therefore reached their maximum increment rates for the stems in higher diameter categories. A trend towards decreasing growth is only revealed in a few species e.g. *Croton megalocarpus*, which had highest increment rates (2.2 cm) in the category between 15 and 25 cm of DBH. For some of

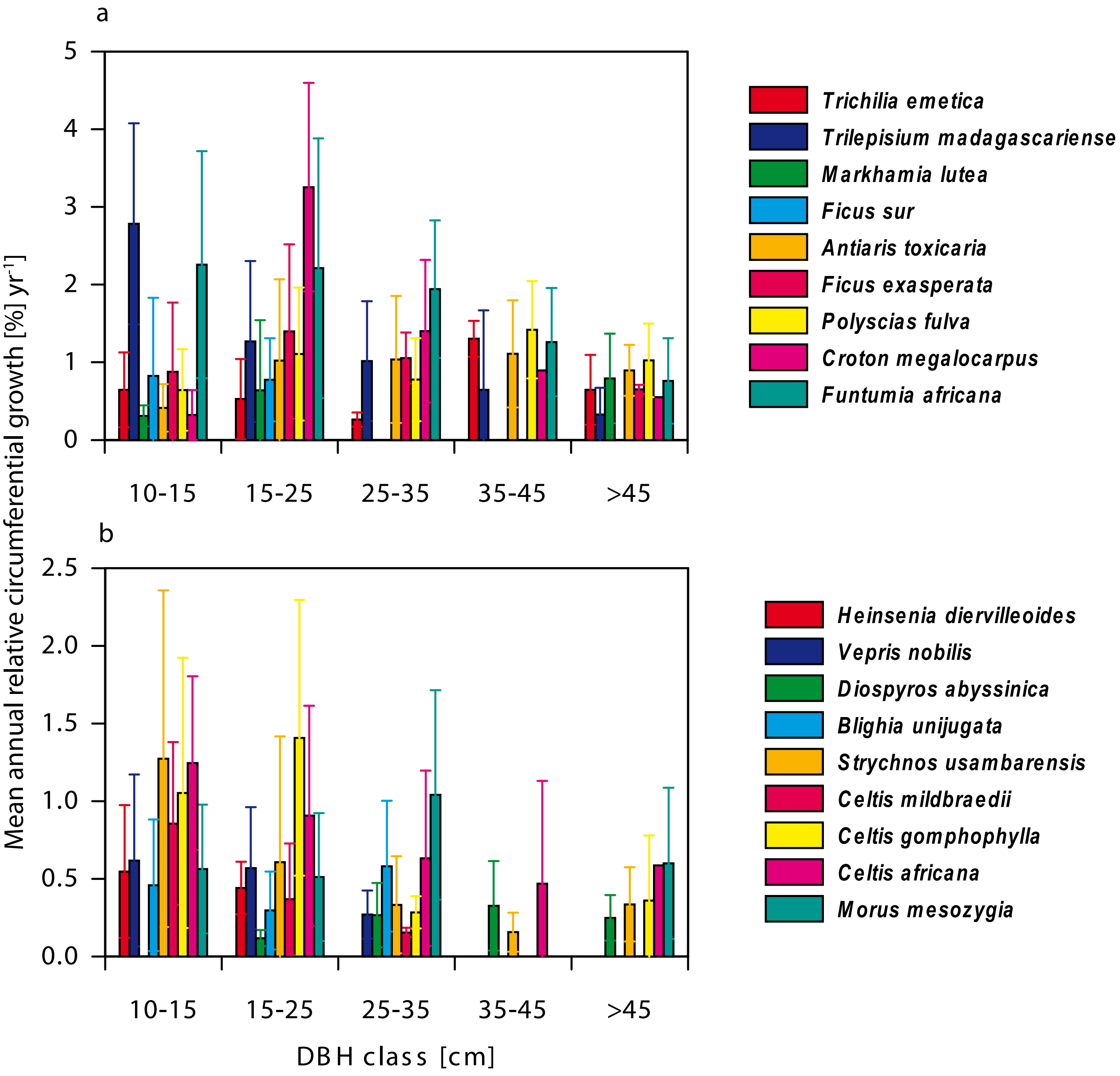

Figure 4-11: Mean annual relative circumferential stem increments in five diameter size classes and the SD for the 18 species are shown. (a) shows the results for the faster growing and (b) the results for the slower growing species. The different scaling of the ordinates has to be considered. Values are given, if at least two individuals were present in the respective size class.

the slow-growing understorey species like *Heinsenia diervilleoides* and *Vepris nobilis*, no trees were found in size categories ≥ 25 cm DBH.

The **mean annual relative circumferential stem girth increment** in the different DBH sizes categories (Figure 4-11), displayed a slight trend towards more growth in the smaller size categories with some exceptions such as *Morus mesozygia*. But more species had their highest relative growth performance in the lower DBH categories (between 10 and 25 cm).

4.2.6.2 Between species stem growth by height categories

The between species growth in different height categories is shown in the following diagrams (Figures 4-12 & 4-13). A height category of ≤ 20 m included all the understorey trees and some of the shaded subcanopy trees, while the height class > 20 m included both upper subcanopy and canopy trees that were exposed to more light. Figure 4-12 presents the two height categories in relation to the **mean absolute circumferential growth** of the different tree species. Trees of *Funtumia africana*, the pioneer species *Polyscias fulva* and early climax trees of *Trilepisium madagascariense* were the fastest growing in the ≤ 20 m category (Figure 4-12 a), while the shade-tolerant understorey trees like *Heinsenia diervilleoides*, *Vepris nobilis, Englerophytum oblanceolatum,* the shade-tolerant subcanopy species *Blighia unijugata* and *Morus mesozygia* and canopy species *Celtis mildbraedii* as well as the early climax trees *Antiaris toxicaria* and *Markhamia lutea* showed the slowest growth rate. An intermediate group was formed by tree individuals of *Celtis africana* and *gomphophylla*, as well as by the *Ficus* species *exasperata* and *F. sur*, further *Strychnos usambarensis* and *Trichilia emetica* were included.

In the height category of > 20 m (Figure 4-12 b) a different picture emerges. Most of understorey species did not have enough individuals to be included in the diagram. *Funtumia africana* formed the significantly fastest growth group, followed by a group consisting of early climax canopy trees, *Antiaris toxicaria, Croton megalocarpus* and the pioneer species *Polyscias fulva.* In both height categories the shade-tolerant canopy trees *Morus mesozygia, Trilepisium madagascariense* and *Celtis africana* grew at constant slow to intermediate rates and in addition in the height category > 20 m. The late-climax shade-tolerant species *Diospyros abyssinica* and *Strychnos usambarensis* formed the group growing at the slowest rate.

A comparison of growth rates in the lower and upper height categories (Figure 4-12) showed that *Antiaris toxicaria* switched from slow to fast growth, *Celtis africana, Morus mesozygia* and *Strychnos usambarensis* remained in the intermediate group, *Funtumia africana* and *Polyscias fulva* grew at a fast rate in both categories and *Trilepisium madagascariensis* switched from the group of fastest growing to intermediately growing tree species with increasing height. In general, most species grew faster in the height category > 20 m than in the height category ≤ 20 m. The mean relative circumferential growth rates in figure 4-13 a and b showed growth patterns roughly similar to those based on absolute growth. The understorey and shade-tolerant species form the slowest-growing group for trees ≤ 20 m. *Funtumia africana* and *Trilepisium madagascariense* grew at the fastest rate. But *Polyscias fulva* here only grew at intermediate rates in contrast to the absolute growth rates, while *Celtis gomphophylla* was part of the intermediate group and was found in the slow-growing group in respect of absolute

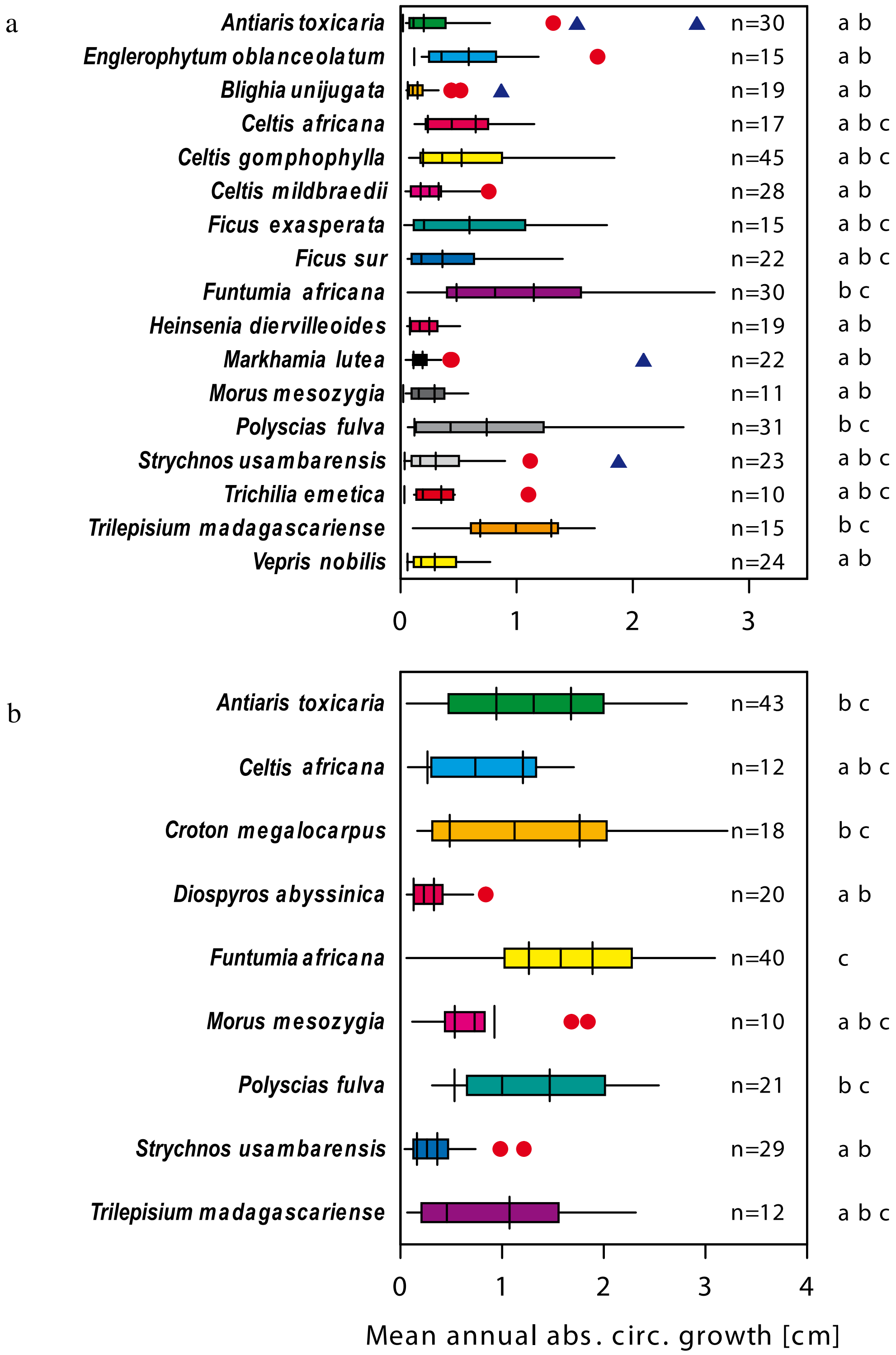

Figure 4-12: Mean annual absolute circumferential growth in two height classes (a) trees ≤ 20 m and (b) trees > 20 m. The boxes represent the lower to the upper quartile the whiskers the range, additionally the median is shown. Red dots stand for outlier values, blue triangles for extreme outliers. The letters at the box and whisker plots denote significantly ($p \leq 0.01$) different groups according to the Kruskal-Wallis-Test.

growth. For trees > 20 m Figure 4-13 b is similar to Figure 4-12 b with the exception that *Diospyros abyssinica* forms the slowest-growing group here on its own and the fastest growing group consists of *Funtumia africana* and *Polyscias fulva*.

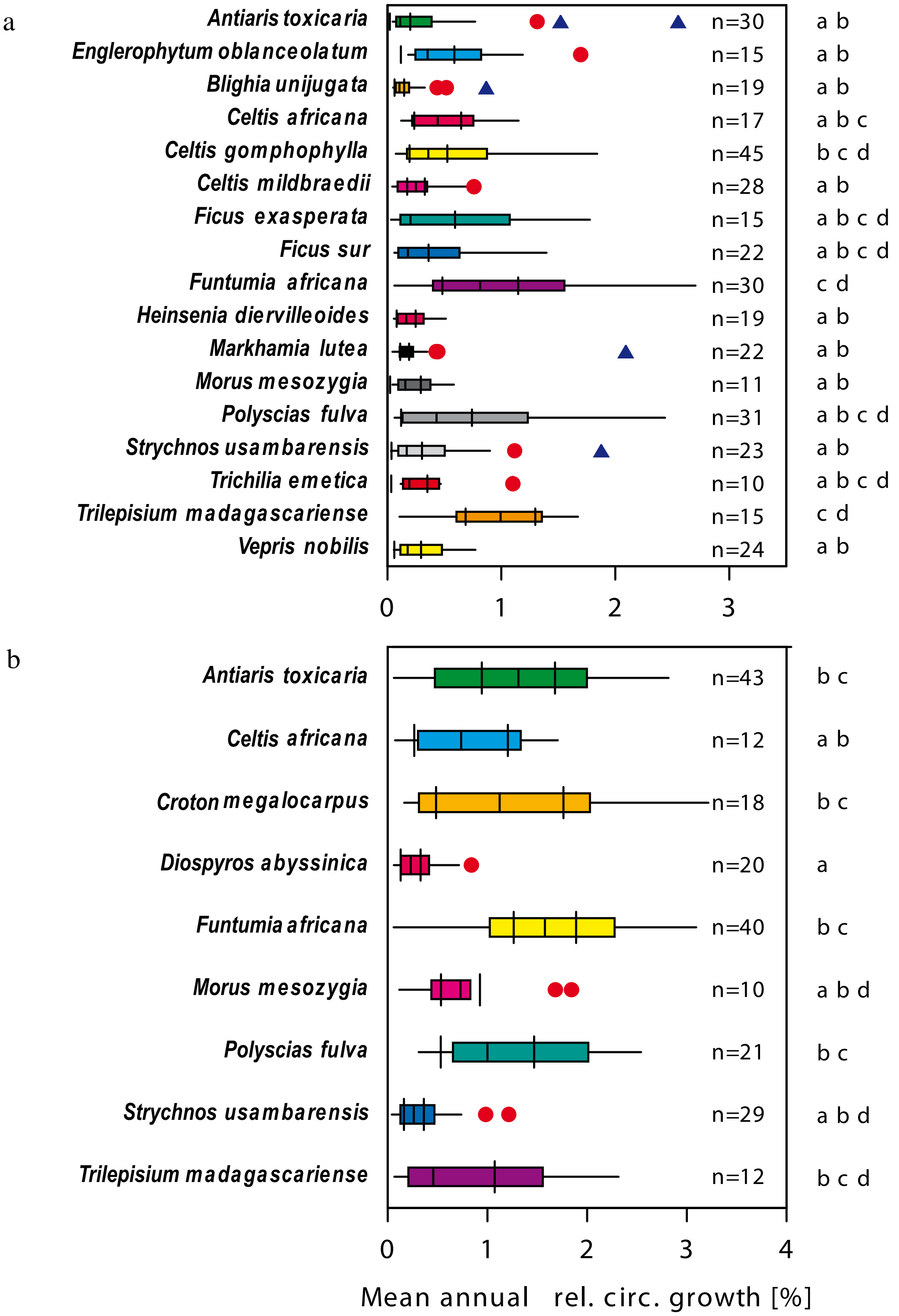

Figure 4-13: Mean annual relative circumferential growth in two height classes a) trees ≤ 20 m and b) trees > 20 m. The boxes represent the lower to the upper quartile the whiskers the range, additionally the median is shown. Red dots stand for outlier values, blue triangles for extreme outliers. The letters at the box and whisker plots denote significantly ($p \leq 0.01$) different groups according to the Kruskal-Wallis-Test.

4.3 Forest structure as related to human disturbance

In this section effects of structural parameters in relation to the commercial disturbance index (CDI) are presented, as disturbance has had a major influence on the structural distribution of the trees. Note that in Kakamega Forest sites with CDI values of 1, 3, 5 and 9 were not part of this study.

Various parameters for the trees in the respective study sites are listed in table 4-7 (plot scale in appendix table 10-1). The number of individuals per site ranged from 74 to 132 individuals per 1200 m^2, with tree densities of up to 68 trees per site with a DBH ≥ 10 cm and up to 61 trees per site in the size class of DBH ≥ 5 ≤ 10 cm.

Table 4-7: Characteristics of trees ≥ 5 cm DBH in the study sites (1200 m^2 each) are presented. The numbers after the ± represent the standard deviation. Values per hectare have been extrapolated for the sites. Additionally results for the hectare plot (CO*) are shown. BA: Basal area; CDI: Commercial disturbance index, Site abbreviations explained in table 3-1. n = 3.

Site	Indiv. [No. ha^{-1}]	DBH [cm]	Height [m]	BA [m^2 ha^{-1}]	Volume [m^3 ha^{-1}]	Species [No.]	CDI [ ]
BU	925	18.9 ± 22.0	14.2 ± 9.0	73.3 ± 32.5	648.4 ± 85.7	34	7
CA	825	10.9 ± 7.6	8.1 ± 4.0	21.6 ± 4.5	101.4 ± 10.1	33	10
CO	825	20.7 ± 20.1	15.1 ± 9.5	53.5 ± 11.0	475.9 ± 62.5	30	6
IS	683	23.1 ± 28.7	15.2 ± 10.0	86.2 ± 22.0	888.2 ± 109.4	33	6
KI	750	17.5 ± 21.1	12.7 ± 8.6	32.4 ± 6.0	248.9 ± 54.0	35	2
MA	617	18.5 ± 20.6	11.4 ± 7.9	48.4 ± 33.0	462.6 ± 47.6	28	8
SA I	925	15.9 ± 15.0	12.1 ± 6.1	43.6 ± 20.9	321.9 ± 39.9	31	6
SA II	800	17.8 ± 14.6	13.7 ± 8.7	51.4 ± 26.2	417.4 ± 35.6	26	4
YA	1100	16.4 ± 18.4	12.1 ± 8.0	56.3 ± 18.1	531.8 ± 60.7	23	0
CO*	751	18.0 ± 21.9	11.2 ± 8.2	47.4	419.5	69	6

The mean extrapolated tree number per hectare taking all plots into consideration was 828 trees with a DBH ≥ 5 cm and 562 trees with DBH ≥ 10 cm. The average height reached by the trees in the study plots for trees with DBH ≥ 10 cm was 12.4 m in the CA plots and around 20 m in the CO and IS sites. The tallest tree in all sites was an *Olea capensis* with a height of 38.4 m. The tree with the largest DBH of 156 cm was a *Zanthoxyllum gilletii* in SAII. The basal areas (BA) of trees per plot with a DBH ≥ 5 cm and ≤ 10 cm ranged from 0.75 m^2 in the highly disturbed sites of MA 2 and in the least disturbed plot YA 3 to 15.1 m^2. On average, trees in the plots contained a BA of 6.4 m^2. In the case of larger trees the Isecheno site showed a trend towards the largest BA and the lowest was found in the site CA. The extrapolated BA for all trees ≥ 5 cm DBH lay between 18.73 $m^2 * ha^{-1}$ in the CA 2 and 109.95 $m^2 * ha^{-1}$ in the BU Plot 3. The mean BA for all plots reached 51.2 $m^2 * ha^{-1}$. There was a trend towards larger BA with decreasing CDI.

The hectare plot (CO*) fits well to the range of the other site values. Numbers of tree individuals were a bit lower than average. Further the species number is much higher in the hectare plot. In Figure 4-14 forest types were grouped according to their CDI value, as it is a good way of describing the species similarity (see Figure 4-2) and explaining structural parameters. The tree structure with regard to DBH and height distribution appeared to be more or less uniformly distributed with the exception of the extremely disturbed site CA. The volume of wood ranged from 12.2 m^3 to 106.6 m^3 per site (1200 m^2). The lowest volume was found in the most disturbed site of CA with a CDI of 10, the highest volume in the intermediately disturbed site of BU, which had a CDI of 7. The relation of BA and slenderness ratio to the CDI is shown in Figure 4-15 a and b. There was a highly significant negative correlation between slenderness ratio and CDI. The correlation between all structural parameters and the disturbance indices is presented in the appendix (Table 10-5).

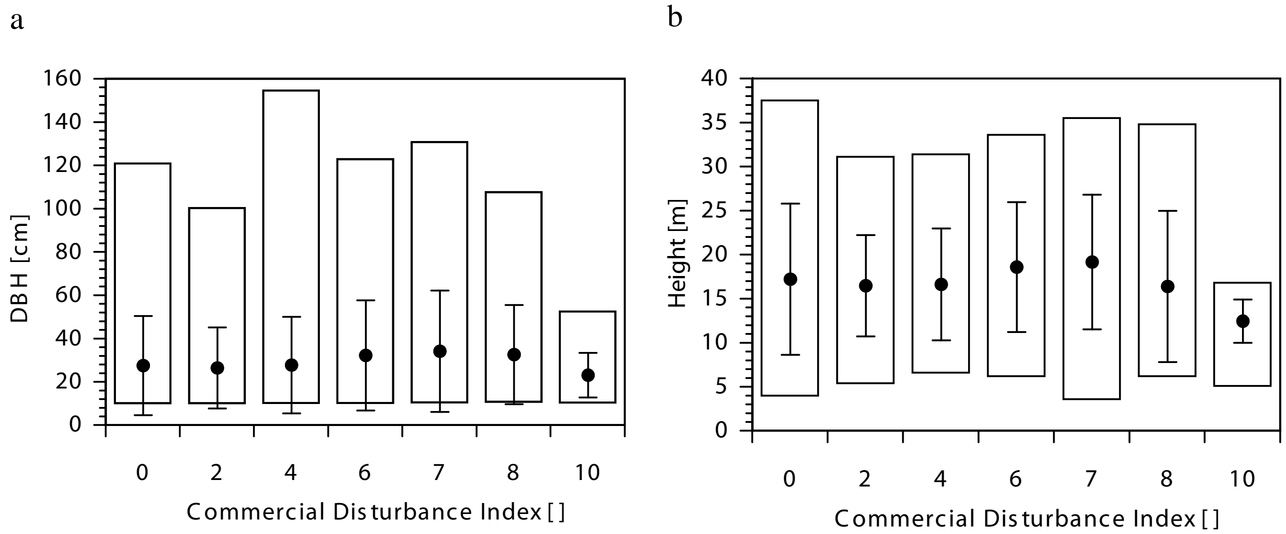

Figure 4-14: Diameter distribution of trees with DBH ≥ 10 cm (a) and height distribution of trees ≥ 10 cm DBH (b) in the differently disturbed forest types. The bars represent the range, the dots the mean with standard deviation (SD). The different scaling needs to be considered.

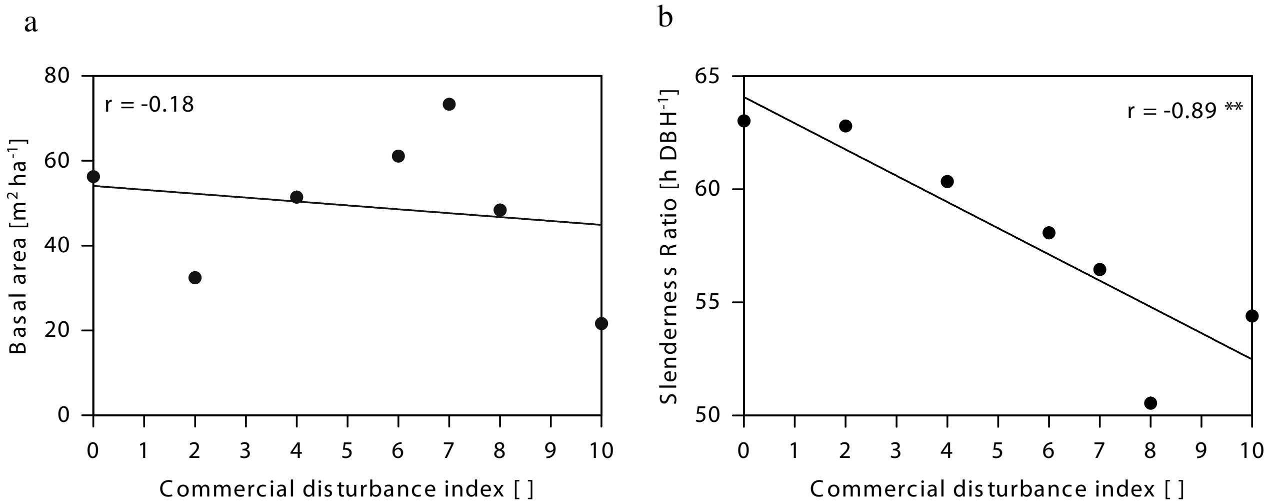

Figure 4-15: Correlation between (a) basal area and (b) mean slenderness ratio (relation of tree height to tree diameter) of the trees in the study sites and the commercial disturbance index. Pearson's r is given together with asterisks, which indicate the level of significance: without $p > 0.05$; ** $p \leq 0.01$. n = 7.

4.3.1 Effect of plot size

The plot size of a site (1200 m^2) was compared to the size of 1 ha at the site CO (CDI: 6) considering both structure and diversity. DBH, BA and volume did not differ in the two plot sizes, but trees were on average significantly taller in the smaller area (Figure 4-16). Further the hectare-plot covered a wider range of values and had fewer wide quartiles. Diversity indices were comparable with Shannon-Wiener H' indices of 3.124, 3.447 and Fisher's alpha values of 18.000 and 17.592 in the 1200 m^2 and the one hectare plot respectively. Species numbers were higher in the hectare plot with 69 species (Table 4-7 see above).

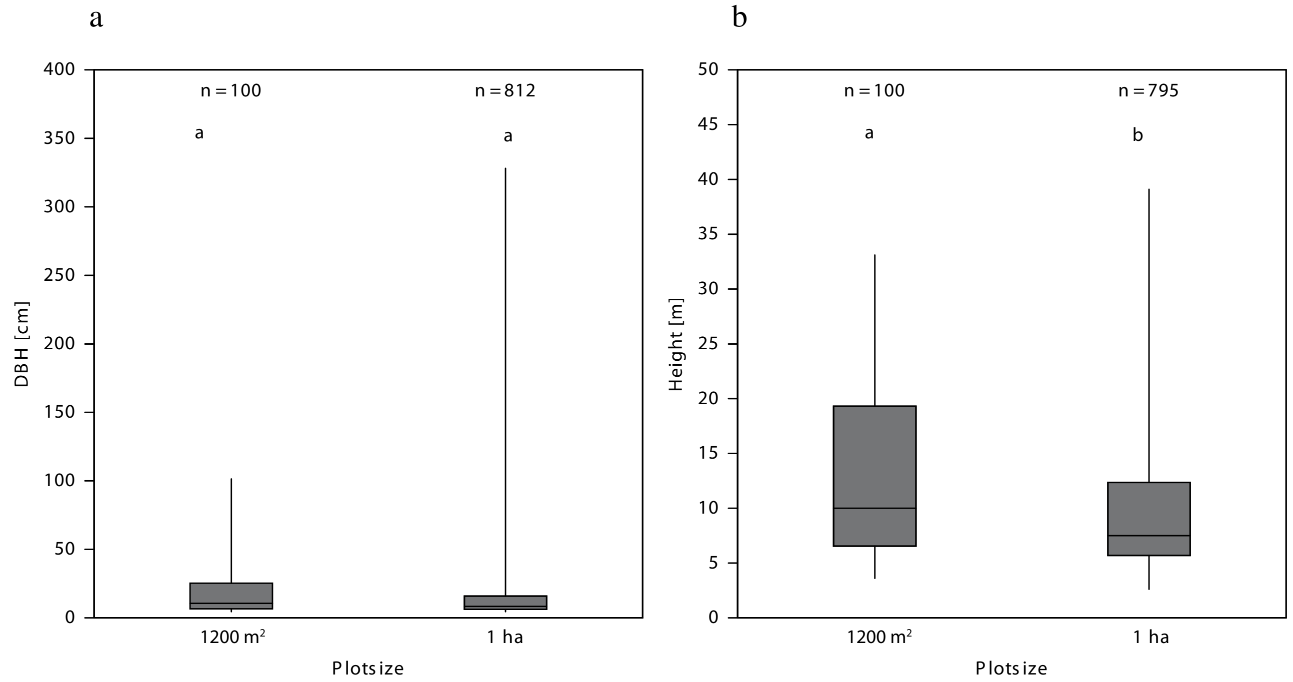

Figure 4-16: Tree structural (≥ 5 cm DBH) comparison of (a) DBH and (b) height in two plot sizes. The boxes contain the median, the lower and the upper quartile, the whiskers represent the range. n is shown. The letters in the graph denote significant differences between the sites (MANOVA, Tukeys HSD-test for unequal n, $p \leq 0.05$)

4.3.2 Canopy parameters

Another characteristic related to different levels of commercial disturbance was the varying light regime at the sites. The light environment in the different forest types was analysed using hemispherical photographs. The percentage of radiation reaching the forest floor varied between 3 and 19 % radiation of the above canopy radiation. Figure 4-17a shows that the plots with a CDI ≥ 8 received significantly more understorey radiation than plots with a lower level of disturbance. The site with the least disturbance had the smallest range and standard deviation for this parameter, which means that the crown structure was even and thicker than that at other sites, in particular than at sites with CDIs of 6 and 7 that appear to have more canopy gaps. The data on canopy openness (Figure 4-17b) shows a clearer trend.

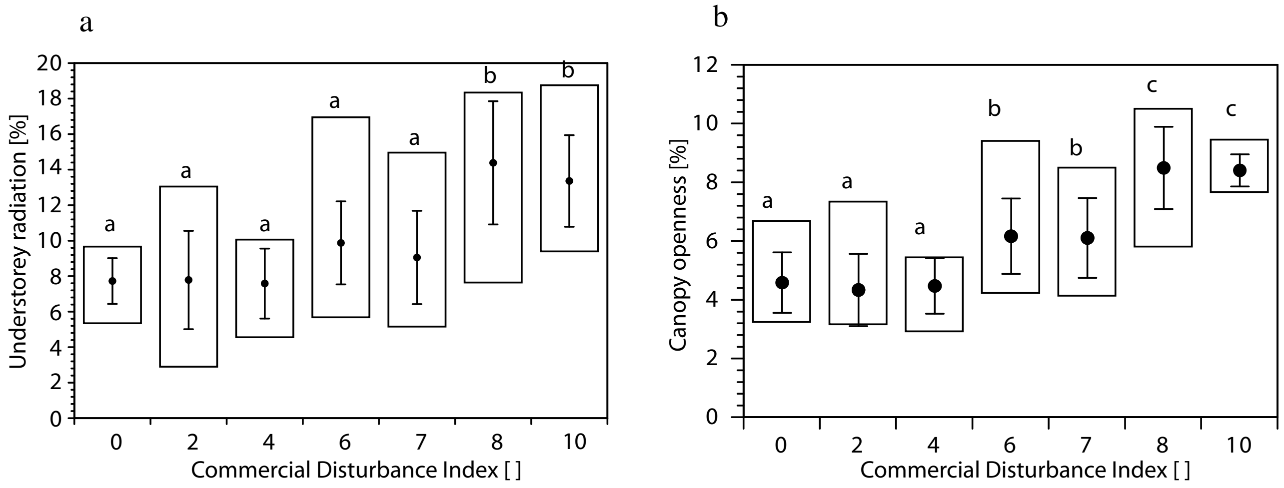

Figure 4-17: (a) The percentage of understorey radiation and (b) the percentage of canopy openness (calculated using hemispherical photos) in the differently disturbed sites is shown. The bars represent the range, the dots the mean value, SD is given. The letters in the graph denote significant differences between the sites (MANOVA, Tukeys HSD-test for unequal n, $p \leq 0.05$).

The distribution of the crown area in the five crown exposure (CE) classes is shown in figure 4-18. Trees that are less exposed to light (CE 1 and 2) have less crown area than trees with CE 3 to 5. Canopy structure influences the abiotic environment, throughfall and soil parameters.

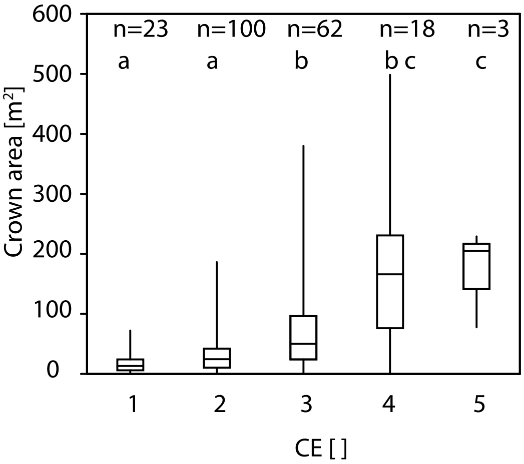

Figure 4-18: Crown area [m^2] in the five different crown exposure (CE) categories is shown. The letters in the graph denote significant differences according to the Kruskal-Wallis test ($p \leq 0.05$) and replication number is given (n).

4.4 Effects of climatic factors on tree dynamics

The effect of disturbance was more or less equal for all trees that were part of the growth study, as this examination was performed in forest areas with comparable levels of past human disturbance (CDI 6 & 7). The environmental factors are defined by the forest structure, especially the canopy.

4.4.1 Effect of incident precipitation and canopy throughfall on stem growth

Summaries of both **absolute and relative circumferential growth rate** of the 18 species in relation to precipitation are given in tables 4-8 and 4-9, both inside the forest (throughfall: TF) and outside the forest (incident precipitation: IP). In addition summed IP and TF for two and three months prior to the dendrometer measurements and the monthly number of rainy days (RD) per month were correlated with growth.

The **absolute circumferential growth rates** of the focal tree species in Kakamega mostly showed weak relations, but in some cases significantly positive relations (Table 4-8). Such significant relations were found for 7 of the 18 species with some of the seven rainfall parameters. Particularly

Table 4-8: The correlation between the mean monthly absolute circumferential growth and the monthly throughfall (TF av), the summed throughfall for 2 months (TF 2) and 3 months (TF 3), the monthly incident precipitation (IP av), the summed IP for 2 months (IP 2) and 3 months (IP 3) and rainy days (RD) for 54 months is shown. The values represent Pearson’s r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01. n = 54

Species	**TFav**	**TF 2**	**TF 3**	**IPav**	**IP 2**	**IP 3**	**RD**
Antiaris toxicaria	**0.30***	**0.31***	0.23	**0.37****	**0.37****	**0.28***	0.24
Blighia unijugata	0.12	0.17	0.08	0.11	0.12	0.01	0.05
Celtis africana	0.25	**0.31***	**0.32***	0.25	**0.32***	**0.37****	**0.27***
Celtis gomphophylla	0.11	0.20	**0.32***	0.14	0.21	**0.31***	0.17
Celtis mildbraedii	0.05	-0.10	-0.22	0.06	-0.02	-0.10	-0.12
Croton megalocarpus	0.17	0.17	0.26	0.17	0.16	0.21	0.10
Diospyros abyssinica	0.17	0.15	0.23	0.02	0.03	0.16	0.11
Ficus exasperata	0.20	0.26	**0.29***	0.25	**0.30***	**0.31***	0.23
Ficus sur	-0.08	-0.13	-0.20	-0.16	-0.17	-0.20	-0.15
Funtumia africana	-0.04	-0.17	-0.25	-0.09	-0.14	-0.15	-0.11
Heinsenia diervilleoides	0.07	0.18	**0.28***	-0.02	0.09	0.14	0.05
Markhamia lutea	0.12	0.06	0.05	0.13	0.08	0.10	0.04
Morus mesozygia	0.22	0.16	0.12	0.20	0.11	0.06	0.07
Polyscias fulva	0.20	0.15	0.18	0.22	0.16	0.16	0.11
Strychnos usambarensis	0.18	0.19	0.22	0.18	0.22	**0.28***	**0.28***
Trichilia emetica	**0.37****	0.16	0.13	**0.32***	0.11	0.04	0.12
Trilepisium madagascariense	0.03	-0.05	-0.04	0.05	-0.03	-0.03	-0.05
Vepris nobilis	0.23	0.25	0.25	0.19	0.20	0.21	0.19
Mean all trees	**0.28***	0.25	0.27	0.27	0.23	0.25	0.19

absolute circumferential growth rates of *Antiaris toxicaria* (Figure 4-19b), *Celtis africana* and *Ficus exasperata* related positively, in some cases significantly and even highly significantly, to all the analysed rainfall parameters. But also the growth rates for *Celtis gomphophylla, Heinsenia diervilleoides, Strychnos usambarensis* and *Trichilia emetica* showed a positively significant relation to at least one of the rainfall parameters. The mean absolute circumferential growth rate averaged for all measured trees, related positively to all rainfall parameters, but significantly only to the TF measured in the same months as the growth measurement (Figure 4-19a).

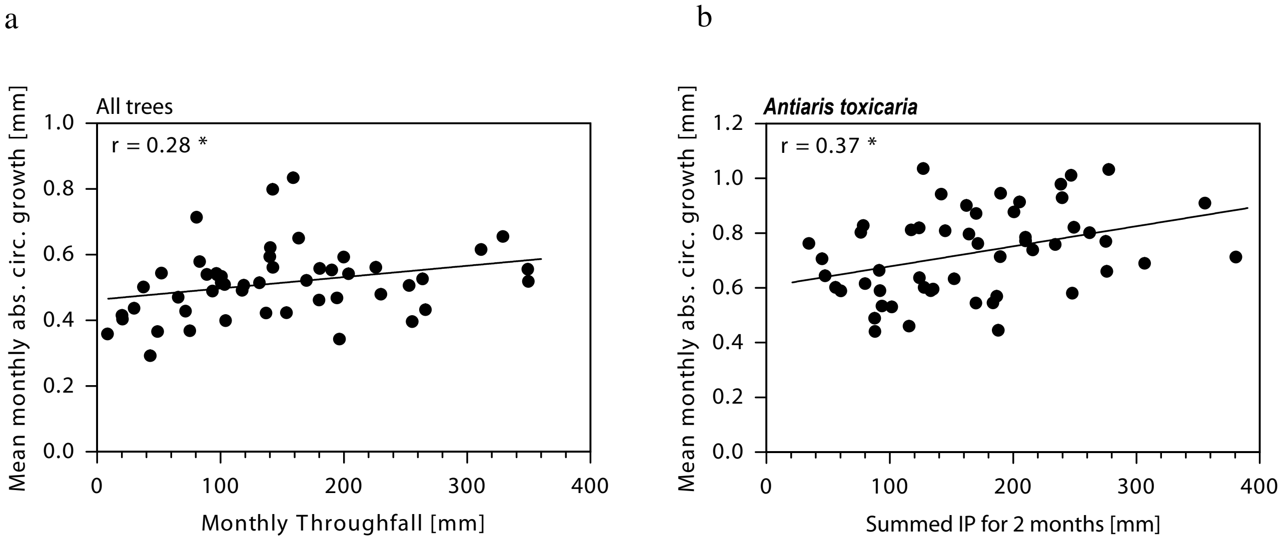

Figure 4-19: Mean monthly absolute circumferential (abs. circ.) growth of (a) all measured trees in relation to the monthly throughfall and of (b) trees of *Antiaris toxicaria* in relation to the mean incident precipitation (IP) for the two months prior to growth measurements. The different scaling of the ordinates has to be considered. The values represent Pearson's r with the asterisks giving the significance: * $p \leq 0.05$; n = 54

Most correlations between **relative circumferential growth** and rainfall parameters were positive (Table 4-9), some significantly to very highly significantly positive for 6 of the investigated species namely *Antiaris toxicaria* (Figure 4-20a), *Celtis africana, Celtis gomphophylla, Ficus exasperata, Strychnos usambarensis* and *Trichilia emetica* (Figure 4-20b). The species **relative circumferential growth** correlated most often to the TF and IP summed for three months prior to the dendrometer reading. The relative growth rates of *Antiaris toxicaria, Celtis africana* and further *Ficus exasperata* related positively to almost all the rainfall parameters.

Some tendencies were observed: the mean TF and IP values summed for more than one month prior to the dendrometer growth correlated more strongly with growth rates than rainfall parameters for the same month. Also there were some weakly significant positive correlations between the RD and the relative growth rates of some species.

Table 4-9: The correlation between the mean monthly relative circumferential growth and the monthly throughfall (TF av), the summed throughfall for 2 months (TF 2) and 3 months (TF 3), the monthly incident precipitation (IP av), the summed IP for 2 months (IP 2) and 3 months (IP 3) and rainy days (RD) for 54 months is shown. The values represent Pearson's r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001. n = 54

Species	**TF**	**TF 2**	**TF 3**	**IP**	**IP 2**	**IP 3**	**RD**
Antiaris toxicaria	**0.43****	**0.44****	**0.35***	**0.47*****	**0.48*****	**0.37****	**0.33***
Blighia unijugata	0.13	0.19	0.12	0.11	0.16	0.08	0.09
Celtis africana	0.25	**0.30***	**0.32***	0.25	**0.31***	**0.37****	**0.27***
Celtis gomphophylla	0.11	0.19	**0.31***	0.13	0.19	**0.29***	0.15
Celtis mildbraedii	0.07	-0.10	-0.21	0.08	-0.02	-0.09	-0.09
Croton megalocarpus	0.14	0.14	0.21	0.15	0.13	0.16	0.06
Diospyros abyssinica	0.17	0.14	0.22	0.00	-0.01	0.10	0.07
Ficus exasperata	**0.29***	**0.42****	**0.46****	**0.34***	**0.44****	**0.45****	**0.29***
Ficus sur	-0.04	-0.09	-0.17	-0.11	-0.13	-0.17	-0.12
Funtumia africana	-0.01	-0.09	-0.17	-0.06	-0.08	-0.11	-0.11
Heinsenia diervilleoides	0.08	0.18	0.27	0.00	0.10	0.14	0.06
Markhamia lutea	0.06	0.03	0.02	0.01	-0.04	-0.04	-0.08
Morus mesozygia	0.11	0.02	-0.07	0.10	0.01	-0.09	-0.03
Polyscias fulva	0.23	0.19	0.22	0.24	0.19	0.18	0.11
Strychnos usambarensis	0.22	0.25	0.27	0.21	0.26	**0.31***	**0.31***
Trichilia emetica	**0.40****	0.18	0.19	**0.31***	0.13	0.12	0.12
Trilepisium madagascariense	0.02	-0.07	-0.03	0.04	-0.06	-0.05	-0.07
Vepris nobilis	0.25	0.28	0.27	0.21	0.23	0.22	0.20
Mean all trees	0.26	0.24	0.26	0.25	0.22	0.24	0.17

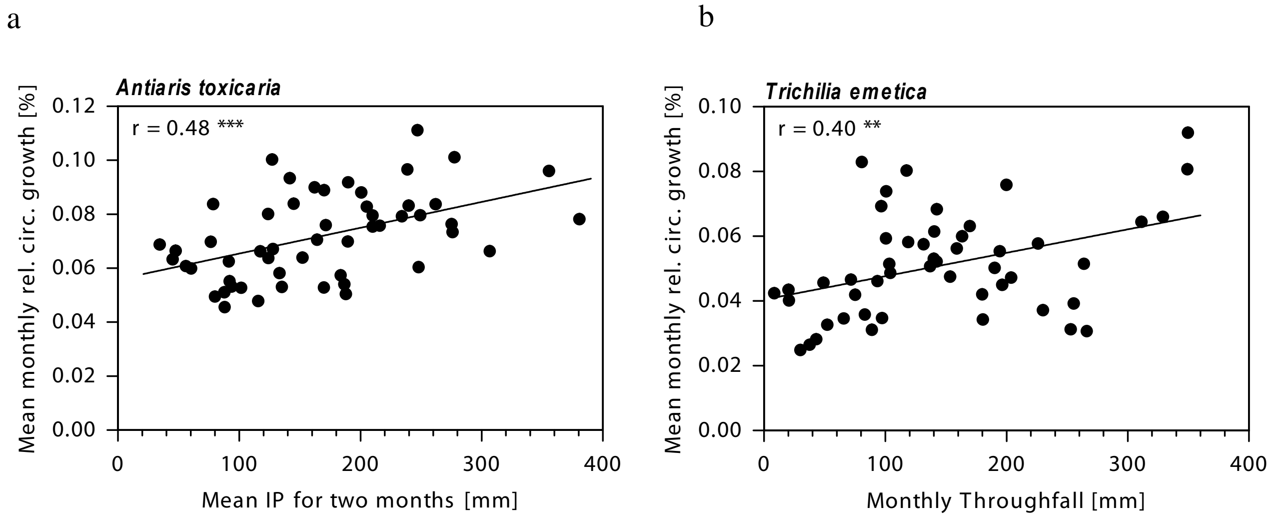

Figure 4-20: Mean monthly relative circumferential (rel. circ.) growth of (a) trees of *Antiaris toxicaria* in relation to the mean IP for the two months prior to growth measurements and of (b) trees of *Trichilia emetica* in relation to the mean throughfall in the month of growth measurements. The different scaling of the ordinates has to be considered. The values represent Pearson's r with the asterisks giving the significance: ** p ≤ 0.01; *** p ≤ 0.001. n = 54.

4.4.2 Effect of temperature on stem growth

The correlation between the **monthly absolute and relative circumferential growth rate** and the temperature measured inside the forest over a period of 16 months is shown in table 4-10. Mean temperatures did not correlate strongly with **monthly absolute circumferential growth** with the exception of *Croton megalocarpus*, which showed a significantly negative relation. The relation between the absolute growth of all tree individuals and the mean monthly temperature displayed a slightly negative trend. Maximum temperature related negatively to absolute circumferential growth rates for all species, for three species this relation was significant, namely *Celtis gomphophylla, Markhamia lutea* and *Trilepisium madagascariense*. The relation to the mean absolute circumferential growth of all tree individuals was significantly negative (Figure 4-21a). Minimum temperatures showed both negative and positive correlations, being significant in the case of three species *Antiaris toxicaria, Celtis africana* and *Diospyros abyssinica*. The trend for all species was weakly positive.

Monthly relative circumferential growth rates in relation to the monthly logged temperature values in the forest are presented in table 4-10. Relative growth related weakly negatively to the mean

Table 4-10: The correlation between the mean monthly absolute and relative circumferential (circ.) growth and the monthly mean (T_{mean}), minimum (T_{min}) and maximum (T_{max}) temperature [°C] in situ for 16 months from April 2006 until December 2007 is shown. The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$. n = 16

	Absolute circ. growth			**Relative circ. growth**		
Species	T_{Mean}	T_{Max}	T_{Min}	T_{Mean}	T_{Max}	T_{Min}
Antiaris toxicaria	0.27	-0.20	**0.63***	0.31	-0.21	**0.71****
Blighia unijugata	0.29	0.31	0.31	0.33	0.33	0.29
Celtis africana	0.28	-0.30	**0.58***	0.27	-0.28	0.47
Celtis gomphophylla	-0.48	**-0.57***	-0.12	**-0.51***	**-0.58***	-0.16
Celtis mildbraedii	-0.25	-0.43	-0.13	-0.28	-0.44	-0.13
Croton megalocarpus	**-0.61***	-0.46	-0.39	**-0.61***	-0.45	-0.36
Diospyros abyssinica	-0.28	-0.32	-0.09	-0.26	-0.20	-0.24
Ficus exasperata	-0.02	-0.22	0.34	-0.09	-0.13	0.15
Ficus sur	0.29	0.35	-0.01	0.42	0.42	0.10
Funtumia africana	-0.15	-0.27	0.13	-0.17	-0.32	0.16
Heinsenia diervilleoides	-0.35	-0.10	**-0.66****	-0.33	-0.06	**-0.69****
Markhamia lutea	-0.24	**-0.59***	0.24	-0.31	-0.47	0.02
Morus mesozygia	-0.01	-0.29	0.06	0.05	-0.30	0.12
Polyscias fulva	-0.17	-0.11	-0.23	-0.19	-0.14	-0.25
Strychnos usambarensis	-0.28	**-0.57***	0.10	-0.14	**-0.50***	0.32
Trichilia emetica	-0.31	-0.39	-0.34	-0.37	-0.45	-0.27
Trilepisium madagascariense	-0.06	**-0.52***	0.44	-0.14	**-0.56***	0.30
Vepris nobilis	-0.06	-0.10	-0.12	-0.01	-0.03	-0.15
Mean all trees	-0.22	**-0.53***	0.13	-0.26	**-0.54***	0.07

temperature, if all tree individuals were considered. Two species *Celtis gomphophylla* and *Croton megalocarpus* had significantly negative relations to the mean monthly temperature. There was a significantly negative relation between the maximum temperatures and mean growth rates of all trees and also of the three species *Celtis gomphophylla* (Figure 4-21b), *Strychnos usambarensis* and *Trilepisium madagascariense*. The relation between relative growth and minimum temperature was slightly positive for all trees, for one species *Antiaris toxicaria* there was a highly significant positive relation and in the case of another species *Heinsenia diervilleoides* the relation was significantly negative.

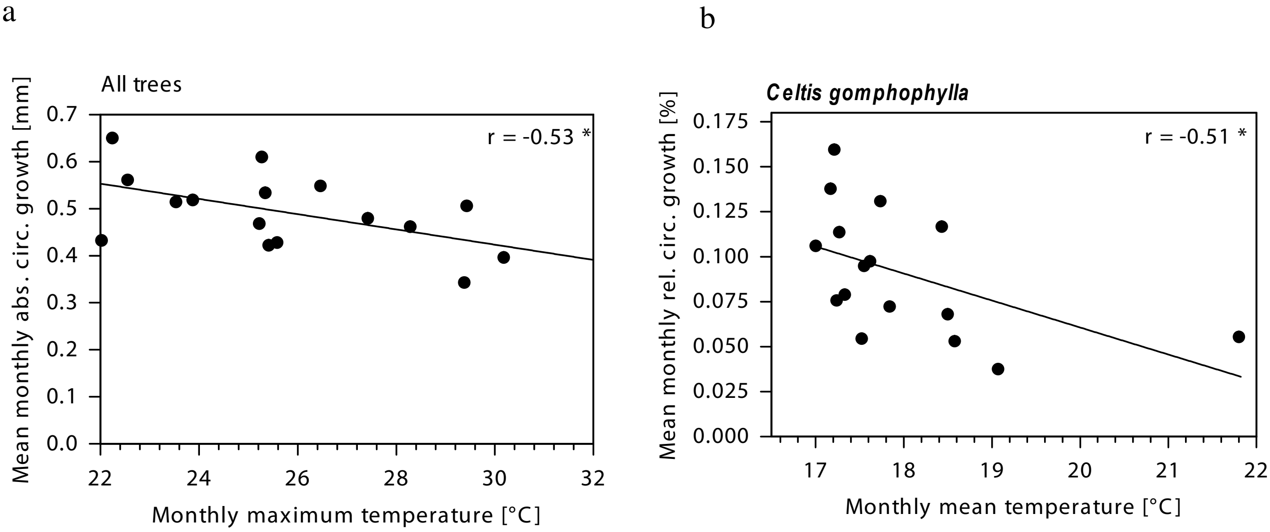

Figure 4-21: (a) Mean monthly absolute circumferential (abs. circ.) growth of all tree individuals in relation to the monthly maximum temperature [°C] and (b) mean monthly relative circumferential (rel. circ.) growth of *Celtis gomphophylla* trees in relation to the monthly mean temperature [°C]. The values represent Pearson's r with the asterisks giving the significance: * $p \leq 0.05$; ** $p \leq 0.01$, n = 16.

The strongest relation between growth rates and temperature was a negative relation between both absolute and relative growth and maximum temperatures. There was a more variable relation between mean and minimum temperature and monthly growth rates. The different species showed specific responses to temperature.

Many species such as *Morus mesozygia*, *Polyscias fulva* and *Celtis gomphophylla* showed seasonal growth trends during the study period reflected in the wavelike growth curves of the respective tree species. This characteristic was more evident for fast than slow-growing species. The high peaks occur in many cases in April to June, the growth curves do not show such a steep slope in January to March (Figure 4-22).

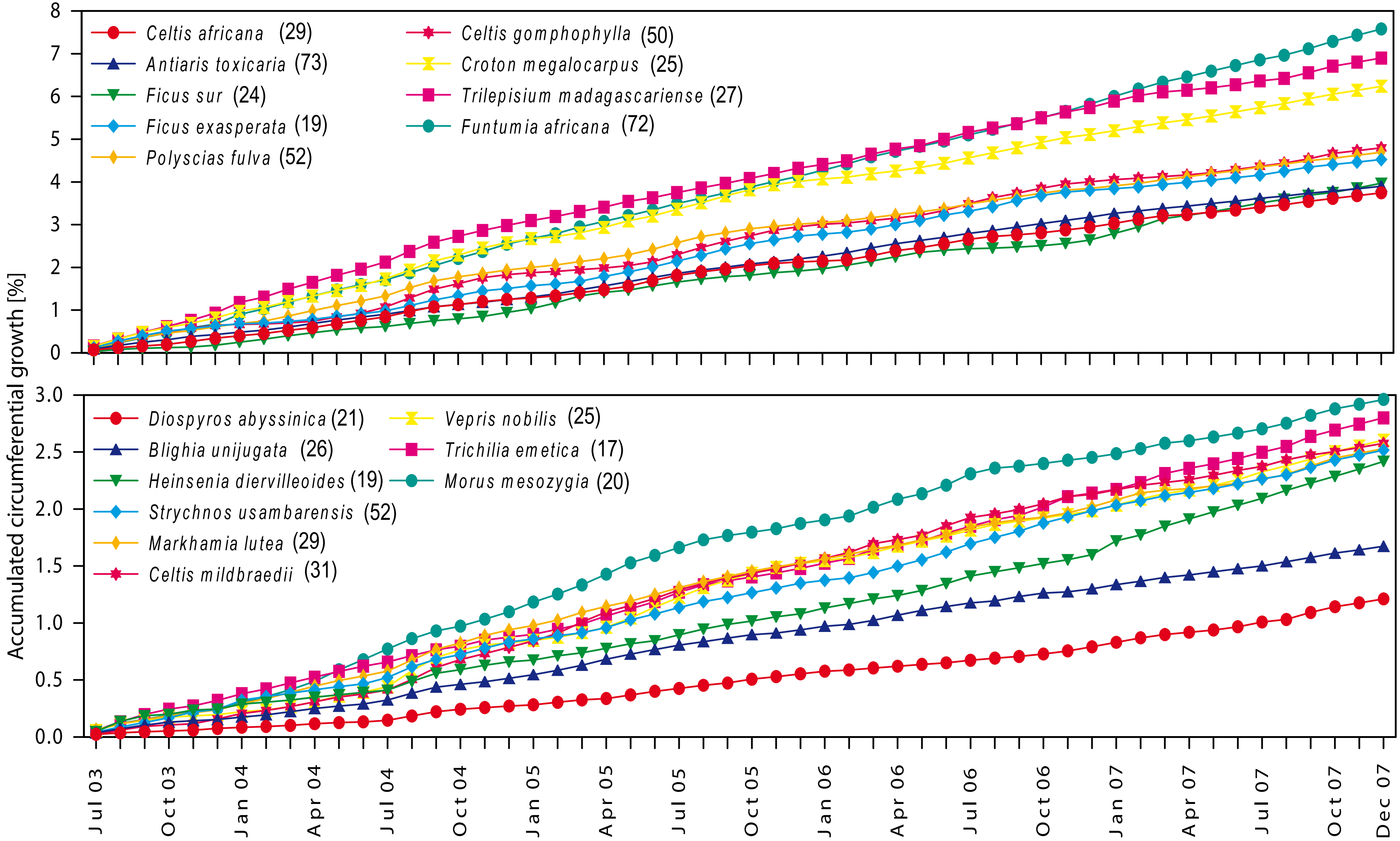

Figure 4-22: Summed mean relative circumferential increment for 18 examined species in Kakamega Forest during a period of 54 months from July 2003 until December 2007. The upper diagram shows the nine fastest growing species, in the diagram below are the curves of the slower growing species. The number of replicates per tree species is given in brackets. The different scaling of the y-axis must be taken into consideration.

4.4.3 Effect of climatic factors on tree phenology

The correlation between the phenological parameters of all dendrometer trees and the abiotic factors rainfall, both in the forest (TF) and outside the forest (IP), and temperature inside the forest during the study period of 54 months is shown in table 4-11. The monthly percentage of individuals flowering did not correlate significantly with any of the climatic factors. The monthly observed percentage of individuals fruiting correlated positively with all rain parameters, highly significantly with the number of rainy days (RD). The minimum temperature also correlated significantly with the mean monthly percentage of individuals fruiting. The monthly percentage of individuals that had shed foliage correlated negatively with all rain parameters, highly significantly with the mean IP and the TF of the preceding two and three months.

Table 4-11: Correlation between monthly phenological parameters and monthly abiotic factors between July 2003 and December 2007. The numbers represent Pearson‘s r with the asterisks giving the level of significance: without $p > 0.05$; * $p \le 0.05$; ** $p \le 0.01$. $n = 54$ for precipitation and $n = 16$ for temperature parameters.

Abiotic parameter	Trees flowering	Trees fruiting	Trees without foliage
Incident precipitation of same month	0.18	**0.35****	-0.20
Incident precipitation of last two month	0.18	**0.42****	-0.31
Incident precipitation of last three month	0.08	**0.41****	**-0.39****
Rainy days of same month	0.23	**0.47****	-0.21
Throughfall of same month	0.15	**0.32***	-0.23
Throughfall of last two month	0.08	**0.32***	**-0.38***
Throughfall of last three month	-0.05	0.25	**-0.47****
Mean monthly temperature in forest	-0.01	0.34	0.08
Max. monthly temperature in forest	-0.24	-0.02	-0.16
Min. monthly temperature in forest	0.30	**0.56***	0.36

4.4.4 Effect of soil parameters on tree growth

4.4.4.1 Plot scale

The correlation between the two growth rates and soil conditions in each plot is shown in table 4-12. Soil samples were collected in plots, so that the correlation was analysed at plot scale. The overall growth rates averaged for 2003 to 2007 did not show a strong relation to the soil parameters, in contrast to the growth rates of 2003. The relative growth rate had more and stronger correlations with the soil parameters than the absolute growth rates per plot.

Significantly positive correlations between the mean relative growth performance and the proportion of N and C in the soil, the acid extractable soil Ca content and the pH values were also evident. There were also two significantly negative correlations with acid extractable Mg (Figure 4-23a) and Mn both the acid and acetate extracted. The mean annual growth rates averaged for 2003 to 2007 did not correlate significantly with the soil parameters with the exception of the C content in the soil, which showed a significantly positive correlation with the relative growth rate (Figure 4-23b).

Table 4-12: The correlation between the mean annual absolute and relative circumferential growth for 2003 and a mean from 2003 to 2007 with the soil parameters, mean acid and acetate extractable Ca, K, Mg and Mn, as well as pH, electrical conductivity (EC), the N and C content evaluated for 9 plots is shown. The values represent Pearson's r with the asterisks giving the significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01 n = 9.

	Mean growth 2003		Mean growth 2003-2007	
Soil parameter	**Absolute growth**	**Relative growth**	**Absolute growth**	**Relative growth**
K acid	0.19	0.28	0.03	-0.03
Mg acid	**-0.69***	**-0.71***	-0.48	-0.58
Ca acid	**0.69***	**0.86****	0.50	0.57
Mn acid	-0.63	**-0.75***	-0.60	-0.63
K acetate	**-0.73***	-0.61	-0.55	-0.59
Mg acetate	-0.07	0.18	-0.46	-0.01
Ca acetate	0.55	0.68	-0.41	0.55
Mn acetate	**-0.68***	**-0.85****	-0.09	-0.57
pH	0.66	**0.72***	0.27	0.35
EC	0.55	0.60	0.35	0.50
N	**0.69***	**0.70***	0.52	0.63
C	**0.72***	**0.88****	0.63	**0.78***
C:N ratio	0.12	0.47	0.28	0.38

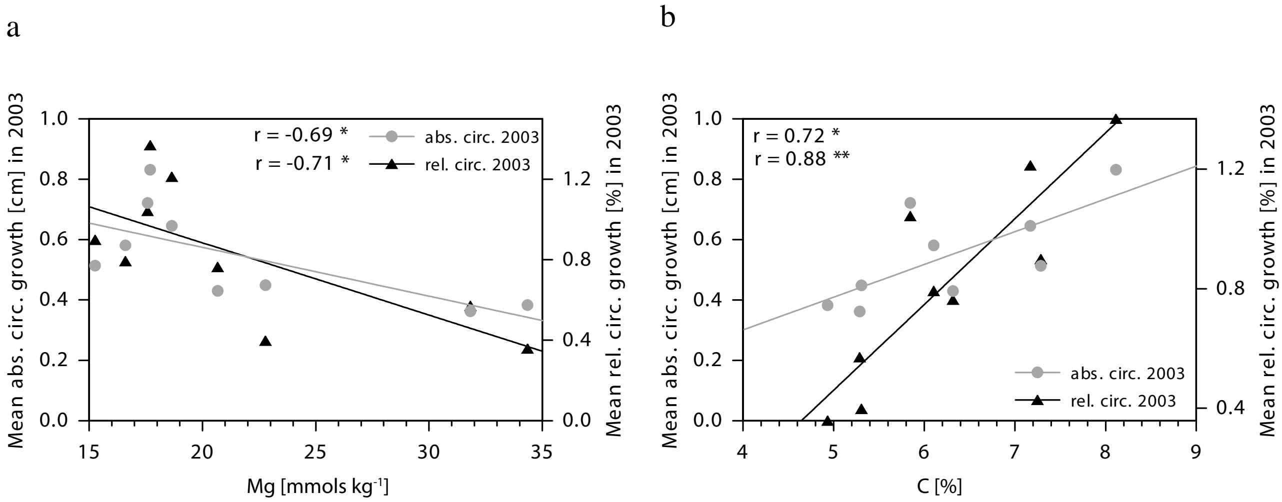

Figure 4-23: Mean annual relative (rel. circ.) and absolute (abs. circ.) circumferential growth rates for the trees (DBH ≥ 10 cm) of nine plots in relation to a) the acid extractable Mg soil content and to b) the percentage of C in the soil of the respective plots. The values represent Pearson's r with the asterisks giving the level of significance: * p ≤ 0.05; ** p ≤ 0.01. n = 9.

4.4.4.2 Tree individual scale

At three of the sites (BU, CO and SA I) the positions of the trees were determined and soil samples were also taken from points within a 5 m grid system (Figure 3-1). The four soil samples taken from points surrounding each dendrometer tree were weighted according to the distance to the centre of each tree. The correlation between the weighted soil values and the absolute circumferential growth of the plot trees in the year 2003 is shown in table 4-13. Significantly positive correlations were found for the growth rate of *Funtumia africana* and *Strychnos usambarensis* and the acid extractable K as well as for the growth of trees > 15 m and the acetate extractable Ca. Significantly negative correlations were established between the growth rate of trees > 15 m and the acid extractable K, and the growth rate of trees ≤ 15 m and the acid extractable Mn. *Antiaris toxicaria* did not show any significant relations to the weighted soil parameters.

Table 4-13: The correlation between the mean annual absolute circumferential growth rate for 2003 with the soil parameters, mean acid and acetate extractable Ca, K, Mg and Mn, as well as pH and electrical conductivity (EC) for 9 plots and 3 species (n ≥ 13) is shown. The values represent Pearson's r with the asterisks giving the significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01.

	Absolute circumferential growth rate 2003				
Parameter	*Funtumia africana*	*Strychnos usambarensis*	*Antiaris toxicaria*	> 15m	≤ 15m
n	15	13	17	77	50
pH	0.20	-0.09	0.11	0.08	-0.09
EC	-0.20	-0.23	0.18	0.11	-0.20
Ca acetate	0.02	-0.17	0.43	**0.28****	-0.05
K acetate	-0.21	-0.38	-0.21	-0.19	0.03
Mg acetate	-0.13	-0.05	-0.09	0.08	-0.04
Mn acetate	-0.42	-0.23	-0.16	-0.09	-0.15
Ca acid	0.27	0.05	0.22	0.19	-0.02
K acid	**0.60***	**0.59***	0.00	**-0.24***	0.19
Mg acid	-0.23	-0.42	-0.24	0.18	-0.22
Mn acid	-0.23	-0.47	-0.28	-0.08	**-0.33****

The relation of the relative growth rates from 2003 and the soil parameters from 2002 is shown in table 4-14. Significantly negative correlations were found between the growth of *Funtumia africana* and the acetate and acid extractable Mn and the acid extractable Mg. The relative growth rate of *Strychnos usambarensis* was not significantly related to any of the weighted soil values, while there was a significantly negative correlation between trees of Antiaris toxicaria and acid extractable Mg and Mn. The growth rates of taller trees > 15 m showed a significantly negative relation to K, while the growth rates of smaller trees ≤ 15 m showed a significantly negative relation to the EC, the acid extractable Mg and Mn and significantly positive relation to the acid extractable K.

Table 4-14: The correlation between the mean annual relative circumferential growth rate for 2003 with the soil parameters, mean acid and acetate extractable Ca, K, Mg and Mn, as well as pH and electrical conductivity (EC) for 9 plots and 3 species (n ≥ 13) is shown. The values represent Pearson's r with the asterisks giving the significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01.

	Relative circumferential growth rate 2003				
Parameter	*Funtumia africana*	*Strychnos usambarensis*	*Antiaris toxicaria*	> 15m	≤ 15m
n	15	13	17	77	50
pH	0.25	-0.08	0.06	0.04	-0.09
EC	-0.16	-0.20	0.13	0.12	**-0.33***
Ca acetate	-0.05	-0.13	0.32	0.23	-0.13
K acetate	-0.37	-0.43	-0.19	**-0.30****	-0.05
Mg acetate	-0.36	-0.01	-0.41	-0.00	-0.16
Mn acetate	**-0.58***	-0.20	-0.41	-0.22*	-0.25
Ca acid	0.20	0.12	0.28	0.18	-0.04
K acid	0.50	0.53	0.34	-0.17	**0.31***
Mg acid	**-0.60***	-0.41	**-0.53***	0.17	**-0.38****
Mn acid	**-0.52***	-0.45	**-0.55***	-0.18	**-0.47****

4.5 Tree seedling establishment

4.5.1 Tree seedling α-diversity

A total of 8441 seedlings (here defined as ≤ 100 cm height) and saplings (≤ 500 cm height) were recorded in the study period between February 2002 and December 2007 in the 108 four m^2 subplots located within the main study plots (Figure 3-1). The spermatophytes belonged to 59 species from 29 families, of which the seedlings (≤ 100 cm) consisted of 8142 individuals belonging to 57 species from 29 families, the saplings (≥ 100 cm) belonged to 42 species from 22 families. The most important families for both height classes were Euphorbiaceae (7 species each), Sapotaceae (6), Flacourtiaceae, Moraceae and Rubiaceae (4) and 15 families representing one species. The most species rich genera were *Celtis* (3 species) and *Albizia* (2), all other 52 species each belonged to a single genus. The three most abundant species recorded in the plots in one seedling survey were *Trilepisium madagascariense* (2037 individuals), *Prunus africana* (1654) and *Diospyros abyssinica* (1280). Two early pioneer species only occurred in the plots as seedlings but not as trees, namely *Erythrina abyssinica* and *Peddieae fischeri*.

Mean seedling densities were 23 seedlings m^{-2} with densities ranging between 4 to 115 seedlings m^{-2}. Simpson's Diversity Index values ranged from 0.024 to 0.809 in the subplots with a mean index value of 0.284. No strong relationship was found between seedling diversity and spatio-temporal distribution and the commercial disturbance index.

4.5.1.1 Tree seedling diversity as related to abiotic factors

The seedling diversity in the **subplots** was described by using three diversity indices, Fisher's alpha, the Simpson and the Shannon-Wiener H' index. The distribution of the seedling diversity did not relate strongly to the seedling density in each seedling subplot (Table 4-15). TF measured around each seedling subplot in the year 2002 was related negatively to the diversity indices, significantly with the Simpson index. Of the soil parameters the C:N ratio showed a significantly positive correlation with the diversity indices. The pH correlated positively with diversity, weakly significantly with Fisher's alpha. There was a relation between two other soil parameters and the diversity indices: The acid extractable Ca related positively to all indices with two relations being highly significant, and acid extractable Mn displayed a significant relation to all three indices.

In Figure 4-24 consideration of the correlation of the Shannon-Wiener Indexes of three different years shows that the diversity of most subplots remained relatively constant, but that the diversity in some subplots changed considerably.

Table 4-15: Correlation between the three diversity indices and the subplot parameters in the year 2002 is shown. The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$. n is given for each parameter set. acid: soil cations extracted by nitric acid; acetate: soil cations extracted by ammonium acetate.

Parameter for subplots	**Fisher's alpha**	**Simpson**	**Shannon-Wiener H'**
Density parameters (n = 102)			
Seedling density 2002	-0.00	0.14	0.12
Light (n = 98)			
Canopy openness	-0.11	-0.09	-0.10
Understorey radiation	-0.18	-0.17	-0.19
Rainfall (n = 36)			
Throughfall 2002	-0.17	**-0.34***	-0.30
Soil (n = 48)			
N	-0.03	-0.32	-0.23
C	0.15	-0.12	-0.03
C:N ratio	**0.45****	**0.40****	**0.43****
pH	**0.32***	0.10	0.19
EC	0.04	-0.16	-0.08
K acid	0.04	0.03	0.04
Mg acid	-0.03	0.13	0.07
Ca acid	**0.46****	0.27	**0.37****
Mn acid	**-0.37***	**-0.29***	**-0.33***
K acetate	0.27	**0.35***	**0.35***
Mg acetate	0.28	0.12	-0.11
Ca acetate	0.14	-0.08	0.11
Mn acetate	**-0.36***	-0.11	-0.20

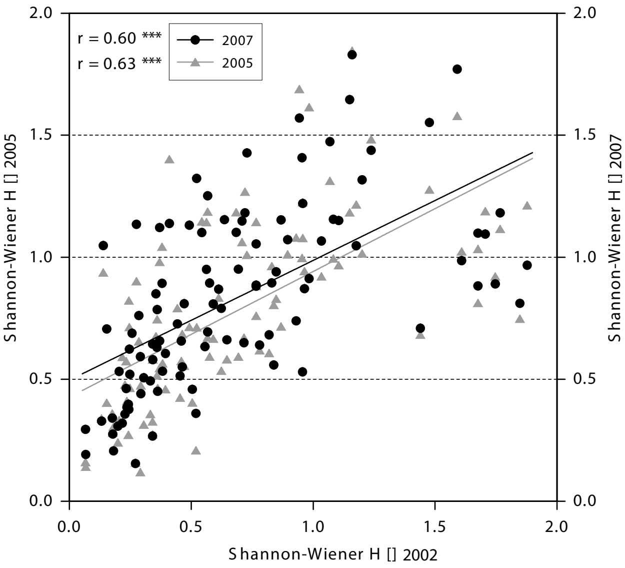

Figure 4-24: Shannon-Wiener H' Index for seedling diversity in each subplot from the year 2002 set against the Shannon-Wiener Indexes of 2005 and 2007 in the same subplots. The values represent Pearson's r with the asterisks giving the level of significance: *** p ≤ 0.001.n = 108.

4.5.2 Dynamics of seedlings in space and time

4.5.2.1 Seedling recruitment

Seedling recruitment (≤ 30 cm) distribution for most of the common species varied to a great extent not only spatially, but also temporally (Table 4-16).

The **temporal heterogeneity** is illustrated by the example of *Antiaris toxicaria* recruits. In 2005 the highest number of recruitments were recorded, which was 8-10 times more seedlings than monitored in the other study years. Also *Prunus africana* varied in the amount of seedlings recruited annually. Years with high recruitment were followed by years of up to five times fewer seedling recruitments. *Croton megalocarpus* recruits were found only in 2003 in high numbers, but never again in the following years. Recruitments of *Diospyros abyssinica* were very abundant in BU with mast years occurring in 2002 and 2004 to 2006. Seedling recruitments of *Funtumia africana* peaked in 2002 and 2003 and decreased in the following years with only one other peak in 2006 in IS. The young recruitments of *Rinorea brachypetala* did not occur in large numbers but were constant particularly at the sites SA I, SA II and YA. Another observation based on table 4-16 was that hardly any recruits were found in 2007 at all sites for all species.

Further, some species provide a good example of **spatial heterogeneous** distribution in the plots. Most of the tree seedling species occur in only a few of the sites. Others like *Diospyros abyssinica* had mast seedling recruitment events at one site in BU, but were present in fewer numbers at all other sites. *Trilepisium madagascariense* occurred with highest numbers in the CO site, while *Prunus africana* not only had mast seedling recruitment in IS, but also in SA II, however in the year 2006. Only three species, namely *Diospyros abyssinica*, *Funtumia africana* and *Antiaris toxicaria* were

Table 4-16: Species, sample sizes and population densities of seedlings of each species present in the study plots in 2002, and at the census 2003, 2004, 2005, 2006 and 2007. Sites are explained in table 3-1. Species were chosen according to the highest abundances of recruitments (R.).

Kakamega	**Year**	**R. n**	**Population density [seedlings ≤ 30 cm per m²] by site**								
Species			BU	CA	CO	IS	KI	MA	SA I	SA II	YA
Antiaris toxicaria	2002	82	0.0583	0.0250	0.0167	0.4833	0.0333	0.0083	0	0	0.0833
	2003	26	0.0833	0	0	0.1083	0.0083	0	0	0	0.0167
	2004	23	0.0833	0.0083	0.0167	0.0500	0.0083	0.0083	0.0083	0	0.0083
	2005	237	1.4583	0	0.0083	0.4250	0.0417	0	0.0083	0.0083	0.0250
	2006	64	0.1917	0.0083	0	0.2583	0.0417	0	0	0.0167	0.0167
	2007	0	0	0	0	0	0	0	0	0	0
Croton megalocarpus	2002	28	0	0	0	0.2250	0	0	0.0083	0	0
	2003	26	0.1083	0	0	0	0	0.0917	0	0	0.0167
	2004	0	0	0	0	0	0	0	0	0	0
	2005	4	0	0	0	0	0	0	0.0167	0	0.0167
	2006	0	0	0	0	0	0	0	0	0	0
	2007	0	0	0	0	0	0	0	0	0	0
Diospyros abyssinica	2002	308	2.1083	0	0.0250	0.0417	0.1250	0.0500	0.1083	0.0333	0.0750
	2003	26	0.1083	0	0	0	0.0333	0.0083	0.0250	0.0417	0
	2004	192	1.4500	0	0.0250	0.0250	0	0.1000	0	0	0
	2005	579	4.5333	0.0083	0.0333	0.0083	0.0417	0.0500	0.0917	0.0333	0.0250
	2006	133	1.0417	0	0.0083	0.0083	0.0083	0.0083	0.0333	0	0
	2007	1	0.0083	0	0	0	0	0	0	0	0
Funtumia africana	2002	205	0.4583	0.0500	0	0.9000	0	0.0167	0.2250	0.0083	0.0500
	2003	247	0.1167	0.0583	0.0167	0.6667	0	0	0.7667	0.3833	0.0500
	2004	20	0.0083	0.0083	0	0.0167	0.0083	0	0.0750	0.0167	0.0333
	2005	5	0	0.0167	0	0	0	0	0.0167	0.0083	0
	2006	23	0.1750	0	0	0.6000	0	0	0	0.0083	0.0083
	2007	0	0	0	0	0	0	0	0	0	0
Prunus africana	2002	218	0.0083	0	0.0250	1.7833	0	0	0	0	0
	2003	572	0.1583	0.0083	0	4.6000	0	0	0	0	0
	2004	95	0	0	0	0.7417	0	0	0.0167	0.0333	0
	2005	199	0.0167	0.0083	0.0083	1.4000	0.1667	0	0.0333	0.0250	0
	2006	497	0.0583	0.0167	0	0.6250	0.1417	0	0.1417	3.1583	0
	2007	72	0	0	0	0	0	0	0	0	0
Rinorea brachypetala	2002	70	0.0083	0	0.0083	0.0167	0	0	0.1167	0.1417	0.3417
	2003	61	0	0	0.0083	0.0250	0.0083	0	0.0333	0.0500	0.3917
	2004	29	0	0	0	0.0167	0	0	0.0167	0.0250	0.1833
	2005	50	0	0	0	0	0.0083	0	0.3417	0.0083	0.0583
	2006	15	0	0	0	0	0	0	0.0333	0.0083	0.0833
	2007	0	0	0	0	0	0	0	0	0	0
Trilepisium madagascariense	2002	510	0.0583	0	4.1333	0.0750	0.0083	0	0	0	0
	2003	57	0.0083	0	0.3750	0.0833	0	0	0	0.0083	0
	2004	436	0.0083	0	3.5000	0.1083	0	0	0.0167	0	0
	2005	152	0.0333	0	1.1917	0.0250	0	0	0.0167	0	0
	2006	618	0.2083	0	4.7917	0.0750	0	0	0	0.0750	0
	2007	248	0	0	2.0667	0	0	0	0	0	0

recorded at least once at all sites with *Diospyros abyssinica* occuring at all sites at the most constant rate over the six years. Seedling recruitments of the observed species, which are early to late climax species, were recorded most frequently at the sites such as BU, CO, IS and SA II, with intermediate levels of disturbance (CDI: 4, 6 & 7) rather than at sites with higher levels of disturbance like MA and CA (CDI 8 & 10 respectively).

The seedling survival of newly recruited seedlings in 2003 with known age is shown in table 4-17. The sites (3 x 4 x 4 m^2 seedling plots each) contained different levels of seedling densities ranging from 21 up to 671 seedlings m^{-2}. The survival rates of the seedling recruitments also differed between the sites ranging from 3 to 43 % for the 6 years of monitoring. Most seedlings, but also those with the lowest survival rate, occurred in IS where a mast-recruitment event of *Prunus africana* had taken place. Highest survival rates were recorded at the two least disturbed sites KI and YA, as well as at the most highly disturbed site CA. Lowest numbers of seedlings were found in the two forest fragments KI and MA. Mean growth rates between the sites varied from 1.50 cm in YA to 3.50 cm in MA per year.

Table 4-17: Seedling performance over 6 years as shown by proportion surviving [%], and mean and maximum annual growth rates [cm yr^{-1}] for seedlings that were newly recorded in 2003 in 432 m^2 for sites and selected species. n for growth rates was only included for seedlings surveyed for ≥ 1 yr with positive height change. Site abbreviation are described in table 3-1.

Tree seedling recruitments in 2003	**Survival 2003-2008**		**Growth rate [cm yr^{-1}]**		
	n	[%]	n	Mean	Max
Sites					
Total	1212	10	266	2.13	23.50
BU	80	4	3	2.58	18.45
CA	41	34	14	3.44	23.50
CO	49	8	36	1.83	7.23
IS	671	3	60	1.93	14.62
KI	21	43	17	1.57	10.18
MA	21	24	9	3.50	20.00
SA I	184	15	54	2.27	14.36
SA II	85	13	35	2.05	13.22
YA	60	37	38	1.50	12.10
Species					
Total	1015	14	224	2.68	9.36
Antiaris toxicaria	26	12	25	1.50	6.08
Croton megalocarpus	26	0	5	7.78	9.84
Diospyros abyssinica	26	27	20	1.82	5.00
Funtumia africana	247	10	92	2.20	14.62
Prunus africana	572	1	20	2.33	10.64
Rinorea brachypetala	61	33	37	1.26	12.09
Trilepisium madagascariense	57	16	43	1.90	7.23

For the species-specific analyses of all individuals throughout all sites only species with ≥ 25 individuals were considered. They showed a high variation in recruitment density, mortality rates and growth rates. Species like *Prunus africana* and *Croton megalocarpus* had hardly any surviving seedlings over 6 years, while understorey and shade-tolerant species like *Diospyros abyssinica* and *Rinorea brachypetala* had higher chances of survival. The survival rates of seedlings with known age tended to be lower than for individuals that were recorded in the first seedling survey (Table 4-21) e.g. *Antiaris toxicaria, Funtumia africana* and *Rinorea brachypetala*.

On average, species increased in height growth by 2.13 cm yr^{-1} ranging from 1.3 cm yr^{-1} for the understorey species *Rinorea brachypetala* to 7.78 cm yr^{-1} for the fast-growing species *Croton megalocarpus*. The mean growth rate of *Croton megalocarpus* was much higher compared to that of other species and could be part of their life strategy in particular the growth-survival trade-off.

4.5.2.2 Dynamics of seedlings as related to canopy throughfall

The correlation between the TF parameters and the seedling dynamics for all species during the study period from 2002 to 2007 on subplot scale is shown in table 4-18. Each seedling parameter recorded quarterly was related to the quarterly mean respective TF parameter for each subplot. Density showed a slightly positive and significant relation to TF measured one and two months before the seedling survey. The mean number of recruits also related weakly positively to the TF parameters, very highly significantly with the TF measured one month before seedling survey and highly significantly with the sum of TF 2 months prior to the seedling survey. The mean quarterly mortality rate did not show clear trends in its correlation with any of the TF parameters.

Table 4-18: Correlation between the mean quarterly seedling density, recruitments and mortality and the quarterly throughfall (TF) summed for one (TF1), two (TF2) and three (TF3) months at subplot level from 2002-2007. The values represent Pearson’s r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; *** p ≤ 0.001. n = 792.

Parameter	TF 1	TF 2	TF 3
Seedling density	**0.08***	**0.09***	0.03
Seedling recruitments	**0.12******	**0.10***	0.06
Seedling mortality rate	0.02	0.07	0.02

Figure 4-25a shows the relation between the quarterly recorded recruitments and the TF measured in each subplot one month prior to the seedling survey, exemplified by one subplot (4 x 4 m^2) over the 6 years. A highly significantly positive relation was observed. A similar, but weaker relation was observed between all recruitments in all subplots and the TF summed for the two months prior to the seedling survey (Figure 4-25b).

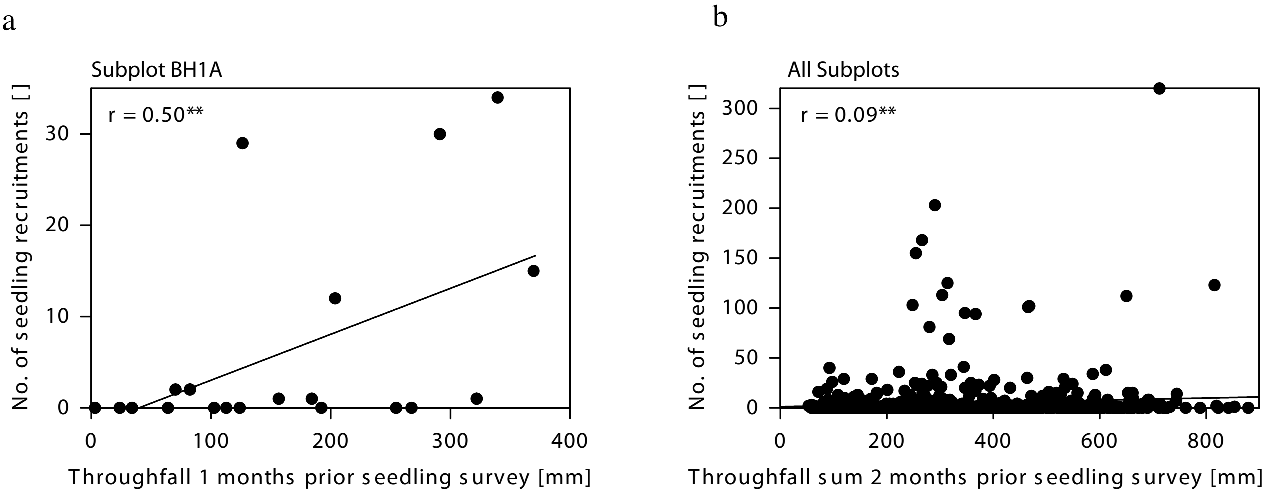

Figure 4-25: Quarterly seedling recruitments in relation to the throughfall measured a) in the month of the seedling survey in subplot BU1A (n = 20) and b) summed for two months for all subplots prior the seedling survey (n = 792). The values represent Pearson's r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001.

4.5.2.3 Seedling dynamics and incident precipitation

The correlation between quarterly seedling dynamics (density, recruitment and mortalities) for each of the species observed (in 19 surveys between 2002 and 2008) and IP and RD is presented in table 4-19. Seedling **density** (Table 4-19a) did not show any significant relations to the rainfall parameters. Only the quarterly density of one species (*Blighia unijugata*) related positively to the RD per 3 months. The total mean quarterly density related slightly positively to the rainfall, most strongly to the RD, but not significantly. The number of seedling **recruitments** (Table 4-19b) per three months shows few significantly positive correlations for three species (*Croton megalocarpus, Diospyros abyssinica* and *Strychnos usambarensis*) with all three rainfall parameters. The trend for all recruitments in relation to rainfall was positive, strongest for RD and IP in the month of measurement. The number of seedling **mortalities** (Table 4-19c) per three months shows one significantly negative relation for *Vepris nobilis*. The other correlations were not significant. There was a slight negative trend for the relation between seedling mortality and the IP for the month of the survey, no relation to the IP summed for the three months prior to the survey and a weak positive relation to the RD.

The quarterly fluctuations of seedling density in KF is shown in figure 4-26. Recruitment peaks commonly occurred in the 2nd and/or 3rd quarter, while some mortality peaks were also seen in the 3rd quarter of a year. The recruitment was highly variable with inter-seasonal and inter-annual fluctuations in the density. The same trend was observed for the seedling mortality, which fluctuated both inter-annually and inter-seasonally. The density in each year decreased in the 1st quarter of a year, which represents the dry season and peaks in the 2nd or 3rd quarter, which represents the rainy season. The species-specific seedling dynamics during the 6-year study period is highlighted in figure 4-27. Seedling species like *Trilepisium madagascariense* had the highest numbers of seedlings with mast recruitment occurring periodically in the 2nd and 3rd quarter and mortalities in almost every

Table 4-19: Correlation between the mean quarter annual a) seedling density, b) seedling recruitments and the c) seedling mortalities and the monthly rainfall parameters for each tree species from 2002-2008 (19 surveys). The values represent Pearson's r with the asterisks giving the level of significance: * p ≤ 0.05. IP: incident precipitation of the month of seedling survey; IP3: incident precipitation summed for the three months prior seedling survey; RD: number of rainy days in the month of seedling survey. n = 19.

	a) Density			**b) Recruitment**			**c) Mortality**		
Species	IP	IP 3	RD	IP	IP 3	RD	IP	IP 3	RD
Albizia grandibracteata	0.25	0.22	0.33	0.39	0.08	-0.03	0.09	0.16	0.18
Antiaris toxicaria	0.19	0.19	0.36	0.38	0.05	0.08	0.16	0.17	0.19
Blighia unijugata	0.24	0.40	**0.56***	0.25	-0.17	0.14	-0.16	0.15	0.02
Croton megalocarpus	0.21	0.29	0.03	0.44	**0.50***	0.27	-0.07	0.20	0.11
Diospyros abyssinica	0.11	0.23	0.47	**0.47***	-0.05	0.10	-0.12	0.08	0.22
Funtumia africana	-0.16	0.07	-0.12	0.03	0.19	0.06	-0.39	-0.23	-0.43
Khaya anthotheca	0.14	0.35	0.46	0.13	0.26	0.37	-0.11	0.06	0.13
Prunus africana	0.08	0.30	0.26	0.17	0.03	0.18	-0.25	-0.07	0.02
Rinorea brachypetala	0.02	0.12	0.21	0.31	0.25	-0.04	-0.29	-0.19	-0.08
Strychnos usambarensis	0.32	0.43	0.43	0.19	-0.07	**0.47***	-0.06	0.06	0.29
Trichilia emetica	-0.05	-0.44	0.14	0.35	-0.11	-0.05	-0.29	-0.22	-0.22
Trilepisium madagascariense	-0.03	0.09	0.19	-0.01	0.05	0.28	-0.04	0.09	0.32
Vepris nobilis	-0.04	-0.10	-0.04	0.20	-0.18	-0.04	**-0.54***	-0.36	-0.38
Total density	0.08	0.25	0.41	0.33	0.07	0.33	-0.22	0.00	0.15

1st quarter of a year. *Prunus africana* had high recruitment peaks, which occurred periodically but decreased in number after one or two quarters of a year. Other species like *Diospyros abyssinica, Antiaris toxicaria* and *Funtumia africana* experienced one peak in their seedling density during the six years. The understorey species *Rinorea brachypetala* had a low number of seedlings, but these remained at a constant density throughout the study.

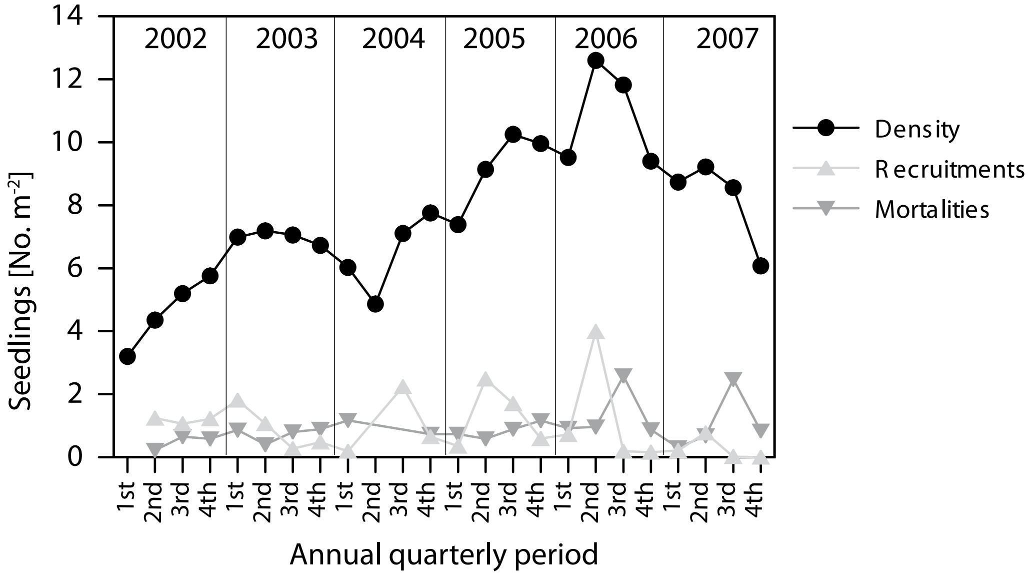

Figure 4-26: Quarterly inter-seasonal variation in seedling density (2002-2007). (Quarters: 1st: January-March; 2nd: April- June; 3rd: July-September; 4th: October-December).

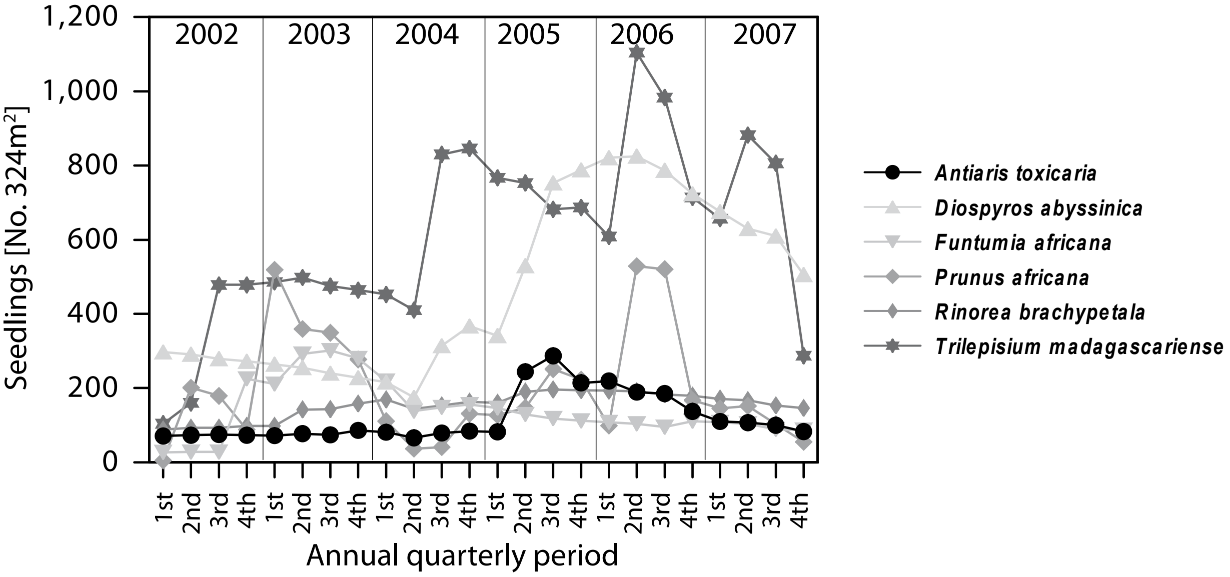

Figure 4-27: Quarterly species-specific inter-seasonal variation in seedling density (2002-2007) in 432 m². (Quarters: 1st: January-March; 2nd: April-June; 3rd: July-September; 4th: October-December).

4.5.2.4 Distribution of tree seedlings as related to soil parameters

The correlation between the seedling distribution on subplot, plot and site scale and the abiotic factors measured in 2001 and 2002 is shown in table 4-20. Most parameters did not correlate strongly with the distribution of the seedling density in the study plots. The only trends were observed for soil EC on plot and site scale and the K on site scale. The EC of the soil solution correlated negatively on all scales with seedling density, highly significantly on plot scale and significantly on site scale.

4.5.2.5 Survival of tree seedlings from initial census

The survival of seedling individuals (≤ 100 cm) with at least 28 individuals over a period from 2002 until 2007 is shown in table 4-21. The number of established seedlings varied between 28 to 520 seedling individuals per species throughout the whole forest. Most species with a high number of individuals in 2002 had low survival rates after 6 years. But a low survival rate did not necessarily mean that the absolute number of surviving seedlings was also low, (but see *Prunus africana*). Species with lowest survival rates belonged to the early climax species e.g. *Croton megalocarpus, Prunus africana, Albizia grandibracteata, Trilepisium madagascariense* and *Funtumia africana*. The species with the highest survival rates were late-climax species mostly from the understorey e.g. *Uvariopsis congensis, Vepris nobilis* and *Rinorea brachypetala*. The species with the highest survival rate was the mahogany *Khaya anthotheca* reaching almost 70 %. The survival rate of seedling individuals of all species for the seven-year period was 37.2 %. The so established species in turn determine the diversity and structure of the mature forests of the future.

Table 4-20: Correlation between the mean seedling density 2002 and for the mean density between 2002 and 2007 and the mean soil parameters on subplot, plot and site scale recorded. The values represent Pearson's r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001. acid: extracted by nitric acid; acetate: extracted by ammonium acetate. n is given in the table.

Parameter for Subplots	**Subplot 2002**	**Plot 2002**	**Site 2002**	**Subplot 02-07**	**Plot 02-07**	**Site 02-07**
Commercial disturbance	-	-0.17	0.06	-	-0.03	0.05
Light	n = 104	n = 26	n = 9	n = 104	n = 26	n = 9
Canopy openness	-0.04	0.02	0.02	-0.02	-0.03	-0.18
Understorey radiation	-0.02	0.03	0.09	-0.07	-0.12	-0.26
Soil	n = 48	n = 12	n = 4	n = 48	n = 12	n = 4
N	-0.07	-0.29	-0.18	-0.26	-0.38	-0.86
C	-0.01	-0.21	-0.01	-0.17	-0.20	-0.63
C:N ratio	0.10	0.04	0.11	0.15	0.26	0.50
pH	0.07	-0.13	-0.26	0.05	0.10	0.02
EC	-0.16	**-0.40****	**-0.34***	-0.25	-0.35	-0.48
K acid	-0.01	0.13	**0.55*****	-0.12	-0.15	-0.31
Mg acid	-0.09	0.25	-0.09	**0.34***	0.56	0.75
Ca acid	0.17	-0.07	-0.06	0.15	0.10	-0.08
Mn acid	-0.24	0.00	0.11	-0.15	-0.24	-0.31
K acetate	0.10	0.03	0.32	-0.10	-0.23	-0.37
Mg acetate	0.14	0.44	0.02	0.11	0.10	0.80
Ca acetate	-0.14	-0.21	-0.02	-0.32	-0.01	-0.42
Mn acetate	0.06	0.24	-0.44	0.05	0.14	0.20

Table 4-21: Survival pattern of all tree seedlings (≤ 100 cm) from each species (minimum 28 individuals) that were at least 6 yr old in 2008 in a total of 324 m^2 of subplots sorted by survival rate. n: Number of individuals.

Species (≤ 100 cm)	**n 2002**	**n dead 2008**	**n survived 2008**	**Survival rate [%]**
Croton megalocarpus	28	28	0	0
Prunus africana	218	217	1	0.5
Albizia grandibracteata	79	74	5	6.3
Trilepisium madagascariense	520	456	64	12.3
Funtumia africana	226	192	34	15.0
Strychnos usambarensis	46	36	10	21.7
Diospyros abyssinica	323	243	80	24.8
Antiaris toxicaria	85	49	36	42.4
Vepris nobilis	80	44	36	45.0
Blighia unijugata	31	13	18	58.1
Uvariopsis congensis	103	38	65	63.1
Rinorea brachypetala	98	34	64	65.3
Khaya anthotheca	41	14	27	65.9

5 Results: Budongo Forest

In all 6 plot triplets (see Section 3.1) inventories of trees (≥ 5cm diameter at breast height (DBH)) and seedlings (≤ 100 cm height) were carried out from 2004 until 2008. In the four marked BDOs N15, N4, W21 and W22 monthly tree growth and quarterly seedling dynamics were recorded from June 2003 until the end of 2008.

5.1 Tree diversity

5.1.1 α-diversity

In the 18 study plots a total of 1010 tree individuals with a DBH ≥ 5 cm were recorded. The trees belonged to 91 species from 30 families, of which 56 species from 25 families reached a DBH ≥ 10 cm.

Of the taxa 79 (86.8 %) were identified to species level, 8 (8.8 %) to genus level and 4 (4.4 %) remained unidentified. The species abundances in the respective plots are shown in the appendix (Table 10-11) including their collection number as assigned by the HOH.

In the investigated area in Budongo Forest (BF) the most important tree families were Euphorbiaceae with 12 species, followed by Meliaceae and Moraceae each possessing 7 species and Ulmaceae with 6 species. In addition 21 families occurred, which were each represented by only one species throughout the study area. The genera containing most species were *Celtis* (4 species, Ulmaceae), *Chrysophyllum* (4 species, Sapotaceae) and *Ficus* (4 species, Moraceae). The five most abundant species in the study area were *Lasiodiscus mildbraedii* (131 individuals, Rhamnaceae), *Rinorea angustifolia* (123 individuals, Violaceae), *Celtis mildbraedii* (103 individuals, Ulmaceae), *Funtumia elastica* (103 individuals, Apocynaceae) and *Uvariopsis congensis* (67 individuals, Annonaceae).

The estimated species numbers are listed in table 5-1. Depending on the choice of calculation method, from those explained in Subsection 3.4.2, the species coverage for the study area of the 18 study plots ranged from 58 to 68.4 %. Up to now during all research periods in the forest 118 species from 33 families have been identified in and outside the study sites.

Table 5-1: Estimates of the potential tree species number for the studied habitats in Budongo Forest using different extrapolation methods and the percentage coverage of the species found in the study plots.

Method	**Jackknife 1**	**Jackknife 2**	**Chao 1**	**Chao 2**	**ACE**
Estimated species number [ ]	133	157	151	147	141
Found species [%]	68.4	58.0	60.3	61.9	64.5

5.1.1.1 α-diversity as related to environmental factors

The species composition has been influenced by the logging history of the forest. The commercial disturbance index (CDI) describes this disturbance and is used in the following graphs to categorize the differently composed parts of the forest.

The relation between the total species number of a site (= one plot triplet) and the CDI determined by using a gauss fit to check for a humpbacked curve is shown in Figure 5-1a. The humpbacked curve peaked at CDI values of 6. The relation of trees ≥ 5 cm DBH to the CDI determined using the gauss fit was strong and highly significant, for trees ≥ 10 cm DBH it was significant. A similar pattern emerged in the relation between the Shannon-Wiener Diversity Index (H') and the CDI (Figure 5-1 b) using a gauss fit. It produced a very highly significant positive gauss fit correlation.

Furthermore three indices, namely Fisher's alpha, Simpson's and the Shannon-Wiener H', were used to test diversity against other factors (Appendix table 10-7). Negative trends between diversity and the light parameters and the three above mentioned soil parameters were evident, but no significant relations were found.

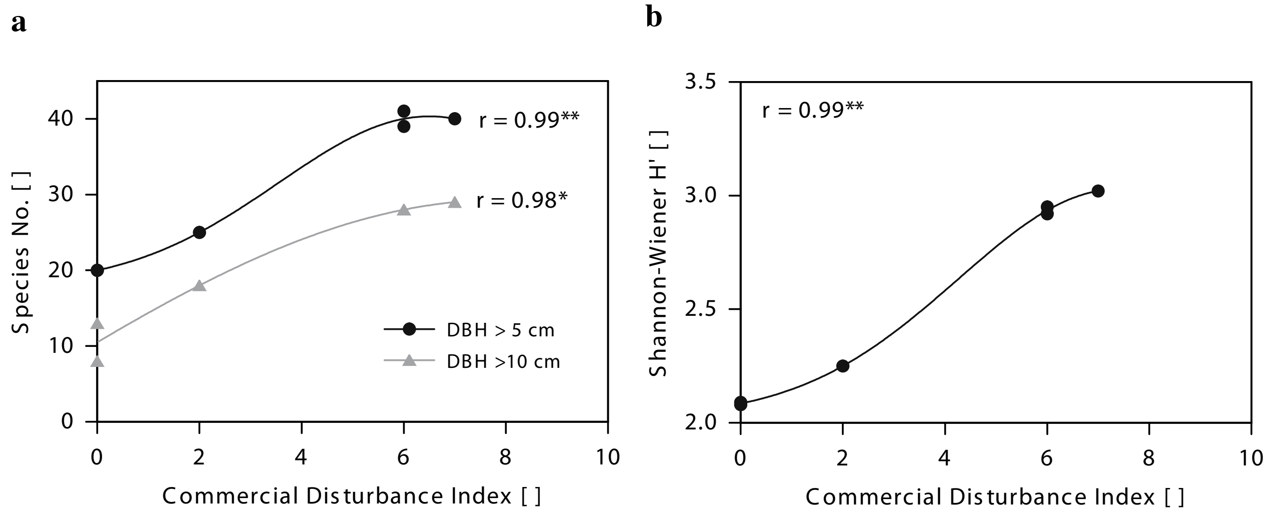

Figure 5-1: a) Species number [ ] for trees with a DBH ≥ 5cm and for trees with DBH ≥ 10 cm and b) Shannon-Wiener H' [ ] diversity for trees ≥ 5cm in the six study sites in relation to the commercial disturbance index (CDI). The gauss fit was calculated using $f(x) = a + b \times \exp\left(-\left(\frac{(x-c)}{d}\right)^2\right)$.The correlation coefficient r is given together with asterisks, which indicate the level of significance: * p ≤ 0.05; ** p ≤ 0.01.

5.1.2 β-diversity

The analysis of β-diversity was performed using the NESS-Index mentioned in Subsection 3.4.4. The results were plotted using multidimensional scaling and presented two-dimensionally. The sites were then scattered on the two ordinates in respect of their species similarity (Figure 5-2). The grouping of the sites was based on the NESS-Index with the maximum parameter m (m = 66). The stress-value was strong (0.000042) so that the NESS-Index could be accepted.

The values of the first dimension were best explained by the soil magnesium content (water extractable) (r = 0.9713 *). The values of the second dimension were related to soil pH (r = - 0.9519 *). There is a weakly significant relation between the CDI and the values of dimension two (r = 0.76; p = 0.079). Dimension 2 is therefore interpreted as influenced by the level of disturbance, while dimension1 is interpreted as a geographical south-east to north-western gradient of β-diversity.

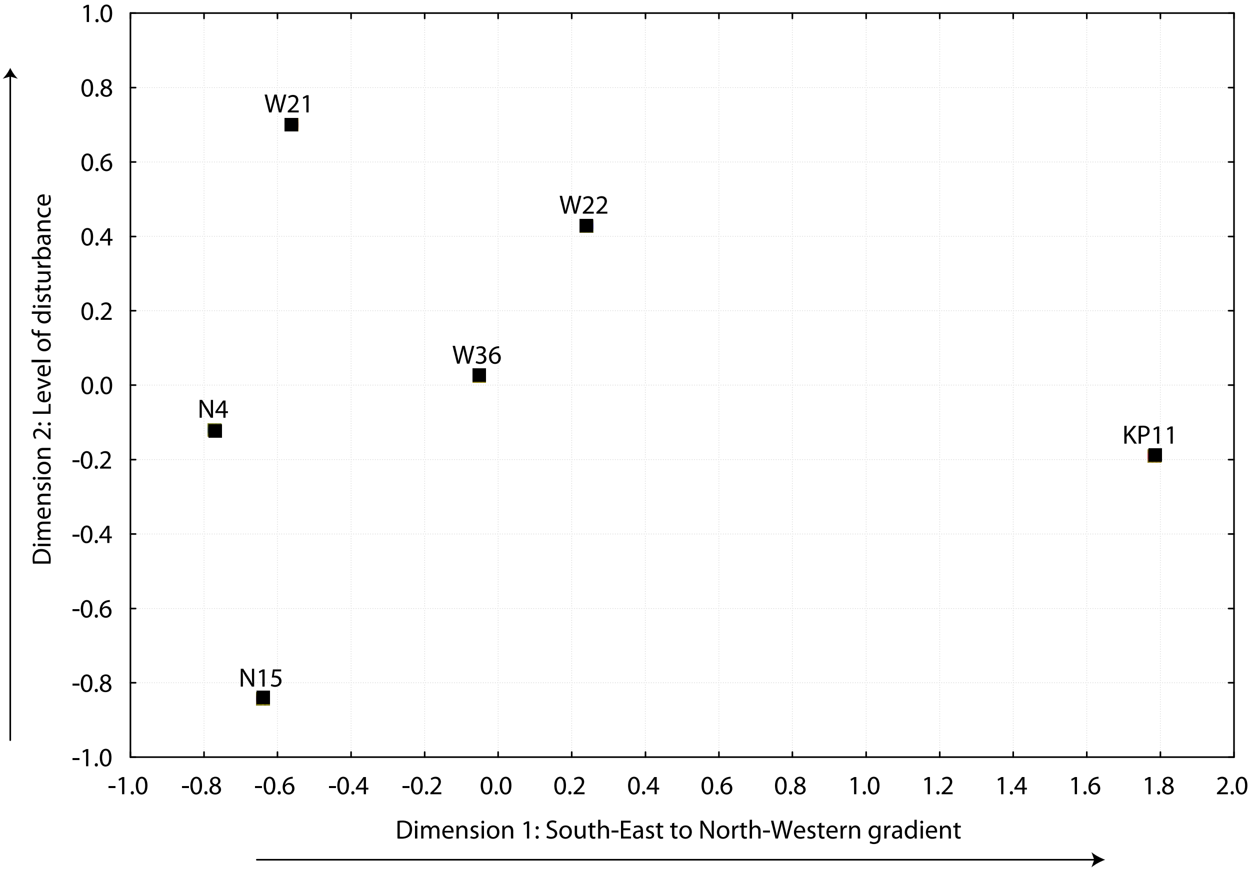

Figure 5-2: Two-dimensional scatter plot of the distance matrices from a non-metrical multidimensional scaling after calculation of the NESS-Index with m_{max} (m = 66). The letters are abbreviations for the study sites explained in table 3-2. The arrows along the axes are interpretations of the distribution of the β-diversity.

5.2 Tree dynamics

5.2.1 Stem growth of all study trees

The growth values presented in this section were calculated using dendrometer bands during the study period from 2004 to 2007 (see Section 3.2). The dendrometer experiment was set in 12 plots with CDIs of 0, 6 and 7 using 325 of the trees with dendrometers. The following graphs and tables contain both absolute and relative growth rates and display results for the mean of all trees and the growth at different sites. The average **absolute diameter growth** for trees reaches around 1.1 mm yr^{-1} (Figure 5-3a), the relative girth increment reached up to 1.3 % yr^{-1} (Figure 5-3b). The values were fairly stable, but the maximum values declined slightly from 2005 to 2007. Only the years 2005 to 2007 were included in the analysis as these were the years with a complete set of dendrometer data. A comparison of the three study years did not reveal a significant difference in diameter increment (Figure 5-3).

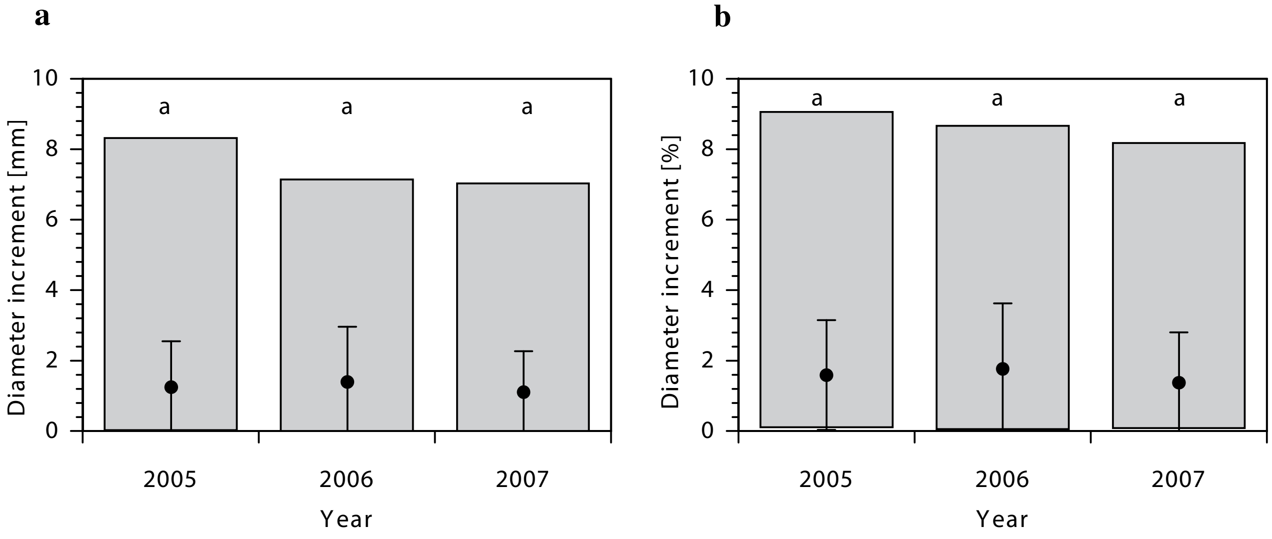

Figure 5-3: Absolute (a) and relative (b) mean annual diameter increment distribution for 3 years using dendrometer band measurements in Budongo Forest. The bars represent the range (coloured rectangle), the mean and the SD. Only years with complete data are shown. The letters indicate significant ($p \leq 0.05$) differences according to the Kruskal - Wallis test.

5.2.2 Stem growth of selected tree species

A total of 325 dendrometer bands were installed on trees within the plots and on 56 additional single trees outside the plots. The trees were located in four of the six sites and the randomly chosen trees in the compartment N3 covered all the occuring four disturbance classes. From the 381 trees 364 were used for the following analyses, the measurements of the other trees were discarded due to measurement errors, because they died during the study period or because the number of individuals was not high enough.

The 364 trees belonged to 7 species from 6 families with at least 12 individuals or more. They were chosen either according to their abundance in the study plots - *Celtis gomphophylla* (4 %) and *Celtis mildbraedii* (9.3%), *Funtumia elastica* (12.7 %), *Lasiodiscus mildbraedii* (9.8 %), *Rinorea angustifolia* (12.2 %), their ecological value - *Cynometra alexandri* (4.4 %) or according to their economic value - *Khaya anthotheca* (1.6 %). Most of the dendrometer bands were installed in October 2004. The single trees were added in October 2005. The readings started in January 2005.

Figure 5-4 (also appendix table 10-12) shows that species' absolute and relative growth rates differed. In respect of the **absolute circumferential growth** (Figure 5-4a) the understorey tree *Rinorea angustifolia* grew at the slowest rate reaching on average 0.2 cm yr^{-1}. The species with the fastest absolute growth rate was *Cynometra alexandri* with annual growth rates reaching on average around 0.8 cm. In respect of **relative circumferential growth** (Figure 5-4b) *Celtis gomphophylla* grew at the slowest rate of 0.3 % yr^{-1} and again *Cynometra alexandri* displayed the fastest growth rate with an increment of more than 1.7 % yr^{-1}. Trees of *Cynometra alexandri* and *Khaya anthotheca* form a statistical group, which contained significantly higher values both for absolute and relative growth rates than the other five species.

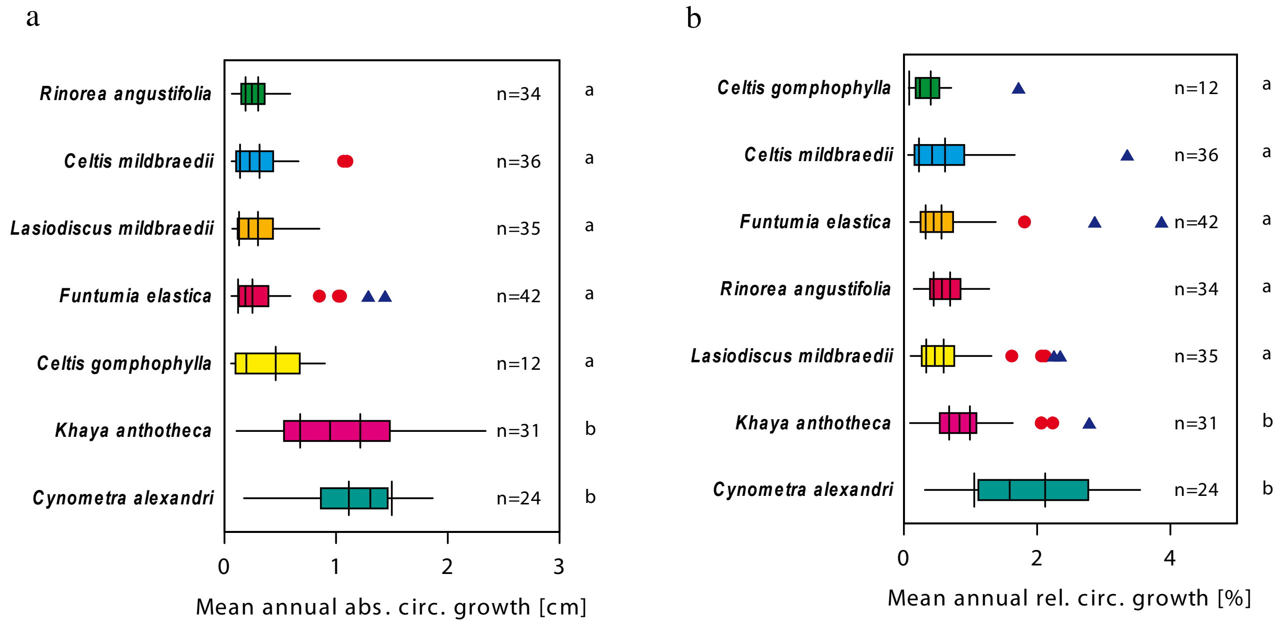

Figure 5-4: Mean annual absolute (abs.) (a) and relative (rel.) (b) circumferential (circ.) growth from beginning of 2005 until end of 2007. The boxes represent the lower to the upper quartile the whiskers the range, additionally the median is shown. Red dots stand for outlier values, blue triangles for far outliers. The letters at the box and whisker plots denote significant ($p \leq 0.01$) differences according to the Kruskal-Wallis analysis. n shown for each species.

5.2.3 Temporal constancy in stem growth

There was a high autocorrelation in absolute and relative annual growth rates during following years (Table 5-2 & figure 5-5). Mean annual growth rates were therefore used in the following analyses that were calculated for the three study years. The correlation between successive absolute and relative growth rates for individual trees persisted for 3 years. The apparent dependence of growth on past performance favours trees growing at a faster rate.

Table 5-2: The growth rates of 2005 for all trees correlated with the respective growth rates of the following years. The numbers represent Spearman's R with the asterisks giving the level of significance *** $p \leq 0.001$, n = 364.

Growth rate	**2006**	**2007**
Absolute circumferential growth 2005	0.66***	0.49***
Relative circumferential growth 2005	0.66***	0.50***

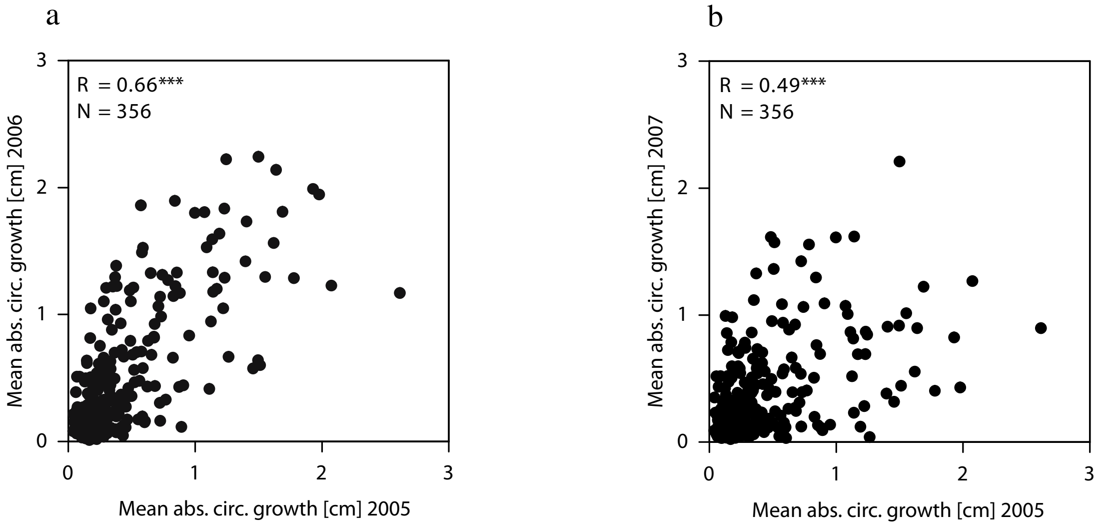

Figure 5-5: Correlation between successive absolute circumferential (abs. circ.) growth rates for individual trees of all species. (a) 2nd year growth rate (2006) depending on the 1st year (2005) (b) 3rd year (2007) growth rate depending on 1st year (2005). Spearman‘s R is given together with asterisks, which indicate the levels of significance (*** $p \leq 0.001$). n = 364.

5.2.4 Stem growth as related to phenological dynamics

The correlation between monthly phenological tree characteristics and monthly growth rates is presented in table 5-3 and figure 5-6. The flowering and fruiting habits of the study trees did not seem to influence growth rates. On the other hand there was a significantly negative correlation between monthly growth rates and deciduous trees. The phenological characteristics also related to each other. Flowering correlated positively and highly significantly with leaf shedding. Flowering was triggered by the shedding of leaves. In total 11 species were observed that shed leaves completely during the dry season. This was most evident in the case of species of the Moraceae and Ulmaceae.

Table 5-3: Correlation between the tree phenology with the tree growth rates for the period between 2005 and 2007 (n = 36 months). Pearson’s r is shown together with asterisks (no asterisks $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). abs circ: absolute circumferential growth [mm|, abs BA: absolute basal area growth [m^2]; % circ: relative circumferential growth; % BA: relative basal area growth.

Factor	Abs circ	Abs BA	% circ	%BA	Trees fruiting	Trees without foliage
Tees flowering	0.09	0.07	0.04	0.05	0.02	**0.69*** **
Trees fruiting	0.22	0.22	0.15	0.11	-	-0.08
Trees without foliage	**-0.41***	**-0.43****	**-0.43***	**-0.39***	-	-

Figure 5-6a shows the phenological dynamics (flowers, fruits, foliage) in relation to growth for all species. In the dry months (December to February) flowering activities increased, followed by fruiting peaks in the rainy season (March to April and June to August). The phenological dynamics and growth of single species (Figure 5-6 b and c) showed that some species were subject to growth seasonality like *Celtis gomphophylla* and a seasonality in phenological activity, while others like *Funtumia elastica* did not seem to follow such trends. The relation between growth and phenology relation for the other species is presented in the appendix (Figure 10-3).

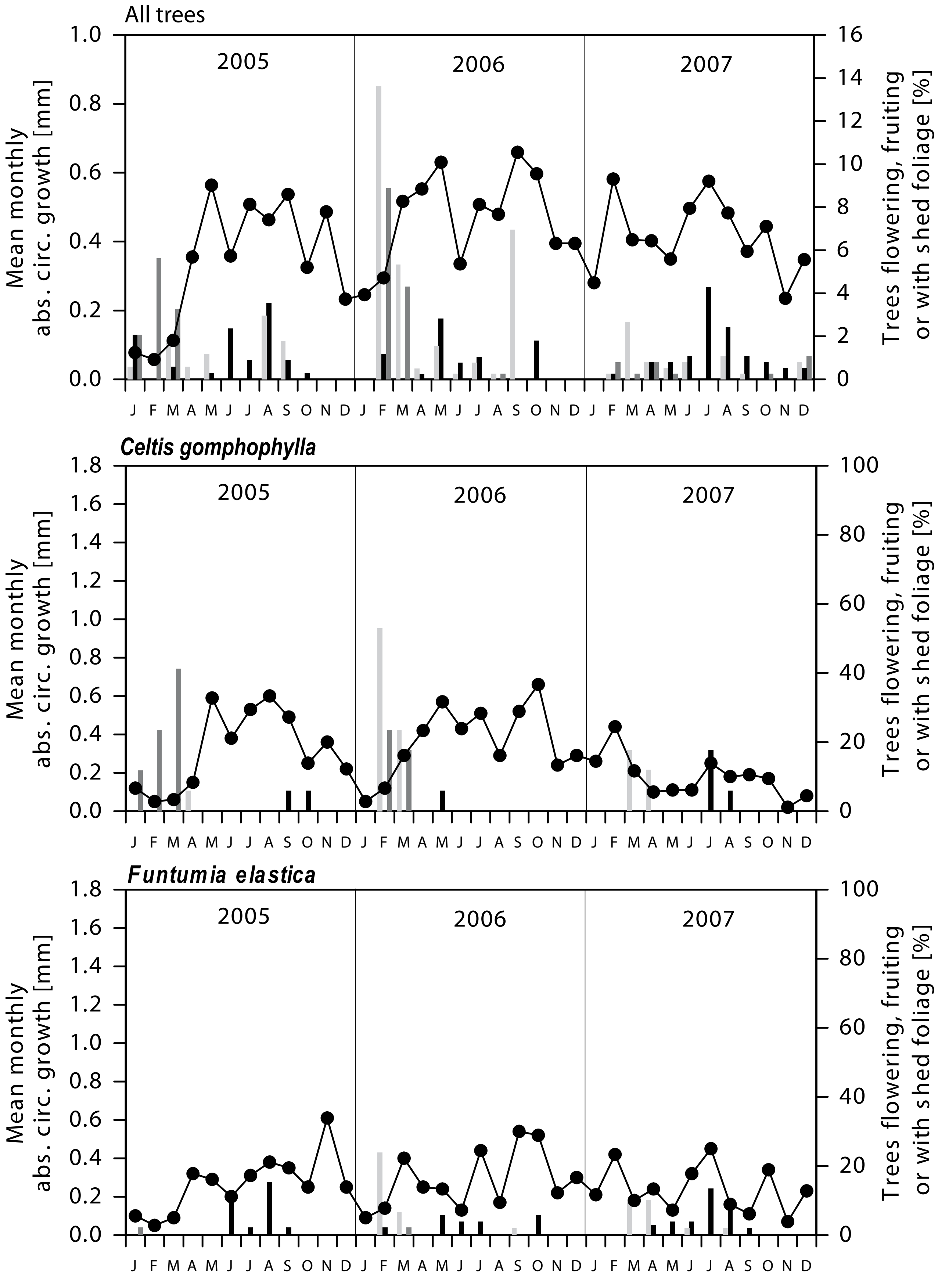

Figure 5-6: Monthly phenological dynamics and absolute circumferential (abs. circ.) growth during 2004-2007 for trees (a) all trees (n = 364), (b) *Celtis gomphophylla* (n = 13) and (c) *Funtumia elastica* (n = 43) ≥ 10cm DBH. The colours represent absolute circumferential tree growth ─●─, % trees flowering ▨ % trees fruiting ░ and trees with shed foliage ■

5.2.5 Tree turnover

5.2.5.1 Tree age

Using the **mean absolute circumferential increment rates** in the different diameter size classes, the time duration required for a tree with an original DBH ≥ 10 cm to grow to its maximum diameter was calculated for each species (see Section 3.2.5). The estimated age for each species based on the time period from 2005 to 2007 is presented in table 5-4. Based on the mean absolute circumferential growth rates in the different diameter size classes an estimate was made of the length of time required by each species, for a tree with a starting DBH ≥ 10 cm, to grow to the maximum diameter recorded in the study site for that species.

A common method is to calculate the number of years required for trees to pass from one size class to the next. The annual increment rates necessary to reach each of the five different size classes were then summed. The trees reaching their DBH_{max} fastest were two understorey species *Lasiodiscus mildbraedii* and *Rinorea angustifolia*, as well as the timber species *Khaya anthotheca*, which needed around 170-194 years. The oldest tree individuals appear to be *Celtis mildbraedii* reaching extrapolated ages of almost 700 years.

Table 5-4: Mean annual DBH increment rates and extrapolated time period that is needed for the tree species to reach the maximum DBH (DBH_{max}), which equals the largest stem in the whole study area for the respective species, starting from a DBH ≥ 10 cm. For the calculation the mean inclusive standard deviation was assumed to be the increment in the different DBH classes (Subsection 3.2.5).

Tree species (No. of individuals)	Mean DBH-increment [mm $year^{-1}$]	DBH_{max} [cm]	Time needed to reach DBH_{max} [years]
Celtis gomphophylla (13)	1.23	53.38	251
Celtis mildbraedii (41)	1.00	88.39	678
Cynometra alexandri (35)	3.00	109.82	301
Funtumia elastica (43)	1.02	41.06	221
Khaya anthotheca (34)	3.01	83.02	167
Lasiodiscus mildbraedii (35)	0.98	25.59	194
Rinorea angustifolia (34)	0.86	27.44	171

5.2.5.2 Self-thinning and tree mortality

The relation between mean volume per tree and the tree density of the tree (DBH ≥ 5 cm) populations in forest sites with different levels of disturbance is presented in figure 5-7a. It is used to estimate at which point in the different tree populations in the study sites, self-thinning of the population may have been reached. The plots in the nature reserve N15 have a high mean tree volume, low tree density and a low tree mortality (Figure 5-7b). Plots in the most disturbed part in BF (CDI: 7), were characterised by high tree densities and low volume, and mortality rates were higher than in the less disturbed parts. Mortality in N15 and W36 could be caused by density-dependence.

The correlation between the mean annual mortality rate (from 2004 to 2009) of trees with a ≥ 5 cm DBH and the CDI was weakly significant (Figure 5-7b). Mortality rates ranged from 1.1 % in the least disturbed sites (N15 & KP11) to 2.1 % per year in the more disturbed sites (W21).

The species with highest mortality rates calculated only for trees with more than 20 individuals i.e. for the early successional understorey species *Rinorea dentata* (4.6 % annual mortality rate) and *Acalypha neptunica* (3.1 %), occurred in the most disturbed site. In the case of canopy trees (height ≥ 25 m) high mortality rates were calculated for the late pioneer species *Celtis gomphophylla* (3.5 %) and *Funtumia elastica* (2.3 %). Not one single death of a tree from the dominant species *Cynometra alexandri* was recorded during the study period.

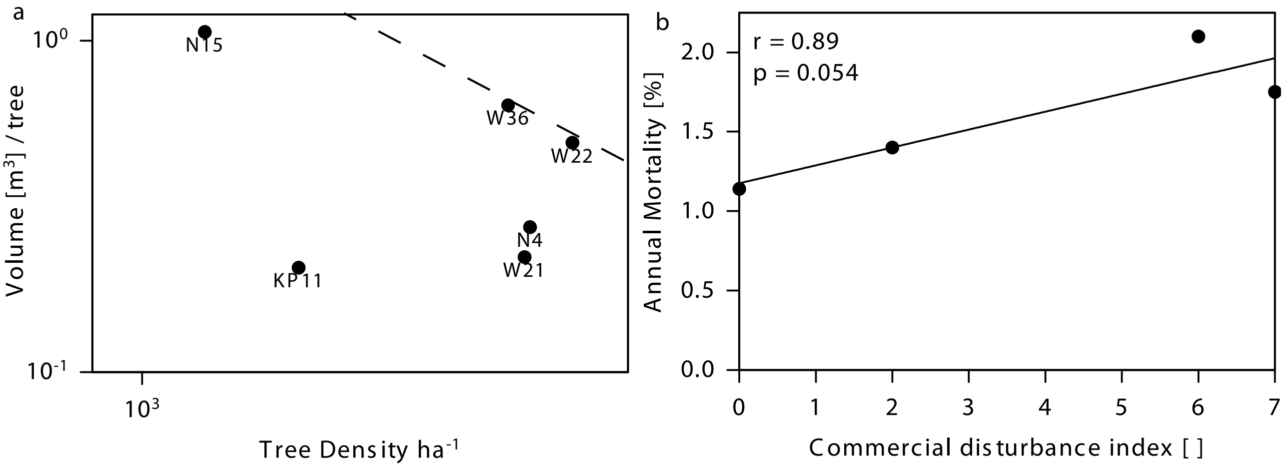

Figure 5-7: The tree populations a) mean volume in relation to its tree density with the numbers representing the CDI values, the dashed line indicates, at which point self-thinning of the tree populations may take place and b) the mean annual mortality rate for the period from 2004 to 2009 for trees ≥ 5 cm DBH in relation to the CDI is presented. Pearson's r is shown.

5.2.5.3 Balance of tree turnover

The BA and its annual increment in the study sites is shown in table 5-5. The plots differed in their BA, with most BA in the least disturbed sites N15 (CDI: 0) and W36 (CDI: 2). By contrast KP11 (CDI: 0) had almost the lowest BA. The intermediately disturbed sites (CDI: 6 & 7) had BA between 4.2 and 8.4 m^2 per $1200m^2$. The highest BA increment was measured in the sites N4, W21 and W 22 (CDI: 6 & 7). But at the same time, losses due to tree deaths were more common in the respective sites, which caused a net BA decrease for the three sites. Recently W22 suffered high basal area losses due to the natural tree fall of a large canopy tree that buried other plot trees beneath it. The net-BA increment is not strongly positive at all sites and in fact a loss of net-BA increment was observed at three sites.

Table 5-5: Growth and mortality in sites of 3 * 400 m^2 for trees ≥ 10 cm DBH. Sum of BA increment was calculated using dendrometer band data and for the remaining plot trees inventory data from 2004 and 2009. BA: Basal area; CDI: commercial disturbance index. Site abbreviations are explained in table 3-2.

Site	**KP11**	**N15**	**N4**	**W21**	**W22**	**W36**
CDI	0	0	6	7	6	2
BA [m^2 1200m^{-2}] of all stems in 2005	4.32	12.36	5.86	4.21	8.43	9.60
sum of BA-increment [cm^2 1200 m^2] in 4 years	231	456	593	260	740	422
mean annual increment [% yr^{-1}]	0.53	0.39	1.29	0.65	1.07	0.59
mean mortality (BA-loss) [% yr^{-1}]	0.45	0.05	2.35	0.41	2.92	0.87
net annual BA-increment [m^2 ha^{-1}]	0.03	0.33	-0.40	0.08	-1.07	-0.17

5.2.6 Stem growth as related to structural parameters

Different structural parameters generally have an influence on tree growth. Especially factors connected with size and thus light availability have major influences reflected in very highly significant positive correlations with absolute growth rates (Table 5-6), whereas the relative growth rates were more independent of the factors describing light availability and size. In Budongo there was instead rather a negative relation between the factors and the relative growth rates. The correlation between DBH, height and crown area is shown in the appendix table 10-8.

Table 5-6: Correlations for the absolute (abs) and relative (rel) circumferential (circ) growth of all dendrometer trees. The numbers represent Spearman's R with the asterisks giving the level of significance: without: no significance, * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. As the data were not normally distributed Spearman's rank correlation were applied. n = 364

Factor	**Abs circ growth**	**Rel circ growth**
DBH	**0.28 *** **	**-0.13 ** **
Height	**0.28 *** **	**-0.25 *** **
Crown exposure	**0.31 *** **	-0.10
Crown area	**0.26 *** **	**-0.13 * **

5.2.6.1 Between species growth by DBH categories

The mean annual **absolute circumferential growth rates** for the 7 analysed tree species is shown in Figure 5-8. It appears that growth rates were highly variable in the DBH categories between trees of the same species. The variability was particularly high for the fast-growing species like *Khaya anthotheca* and *Cynometra alexandri*. For these species mean annual girth increments varied between 0.1 and 2.0 cm yr^{-1}, for slow growing species like *Lasiodiscus mildbraedii* and *Rinorea angustifolia ssp. ardisiiflora* between 0 and 0.8 cm yr^{-1}.

Some species showed a strong correlation between the rate of growth and the size of the tree, whereby the larger the tree individuals were, the faster was the growth rate. This trend was clearly shown by the fast-growing canopy species *Khaya anthotheca*. Other species possessed no relation between their growth and diameter. This was especially evident in the case of slow-growing species. Species like *Cynometra alexandri* and *Celtis mildbraedii* showed a negative relation between absolute annual growth rate and DBH size category.

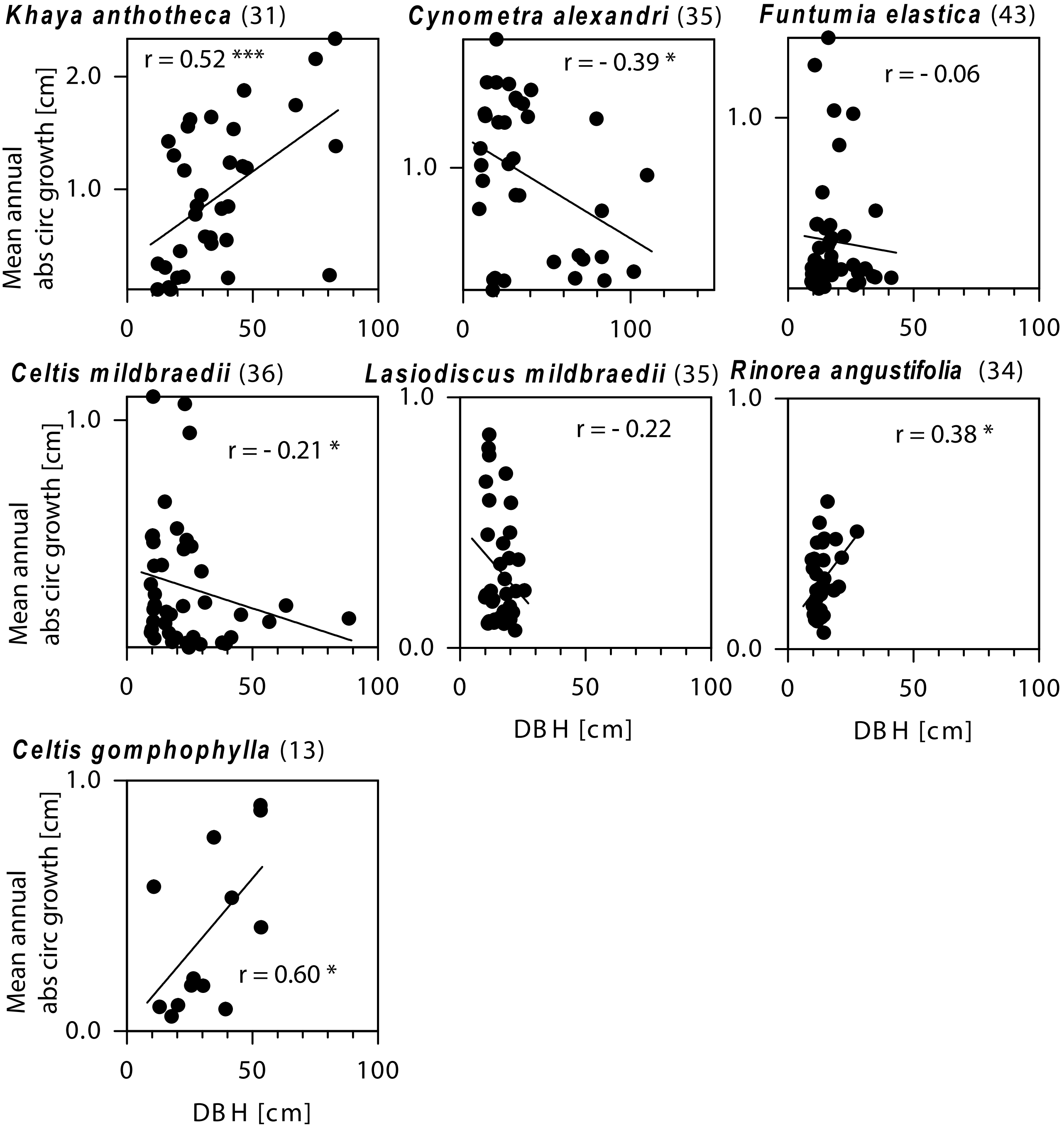

Figure 5-8: Mean annual absolute circumferential (abs. circ.) growth in relation to the starting diameter for the seven tree species measured. The number in brackets are the measured individuals per species. The different scaling of the ordinates has to be considered. Pearson's r is given for the regression line. The asterisks indicate different levels of significance: without $p > 0.05$, * $p \leq 0.05$, *** $p \leq 0.001$.

Figure 5-9 gives the size category division and the mean absolute girth increments in five DBH categories for the tree species subject to examination. The criterium for the chosen size category division was that the individuals of all species were evenly distributed between the different categories. *Khaya anthotheca* and *Celtis gomphophylla* increased their annual growth rate with increasing diameter. These species therefore reached their maximum absolute growth rates in larger diameter categories. The growth rate of *Cynometra alexandri* increased with size until the trees possessed a DBH of around 45 cm, from which point onwards a decrease in growth was observed. The understorey trees *Rinorea angustifolia* and *Lasiodiscus mildbraedii* appeared in the first two size categories up to a DBH of 25 cm, as larger individuals were not present at the study sites. The **relative circumferential growth rates** in different DBH size categories show a different trend (Figure 5-9 b), high relative circumferential growth for some species like *Cynometra alexandri* and *Khaya anthotheca* was reached in the smallest category and a slight decrease was observed in larger categories.

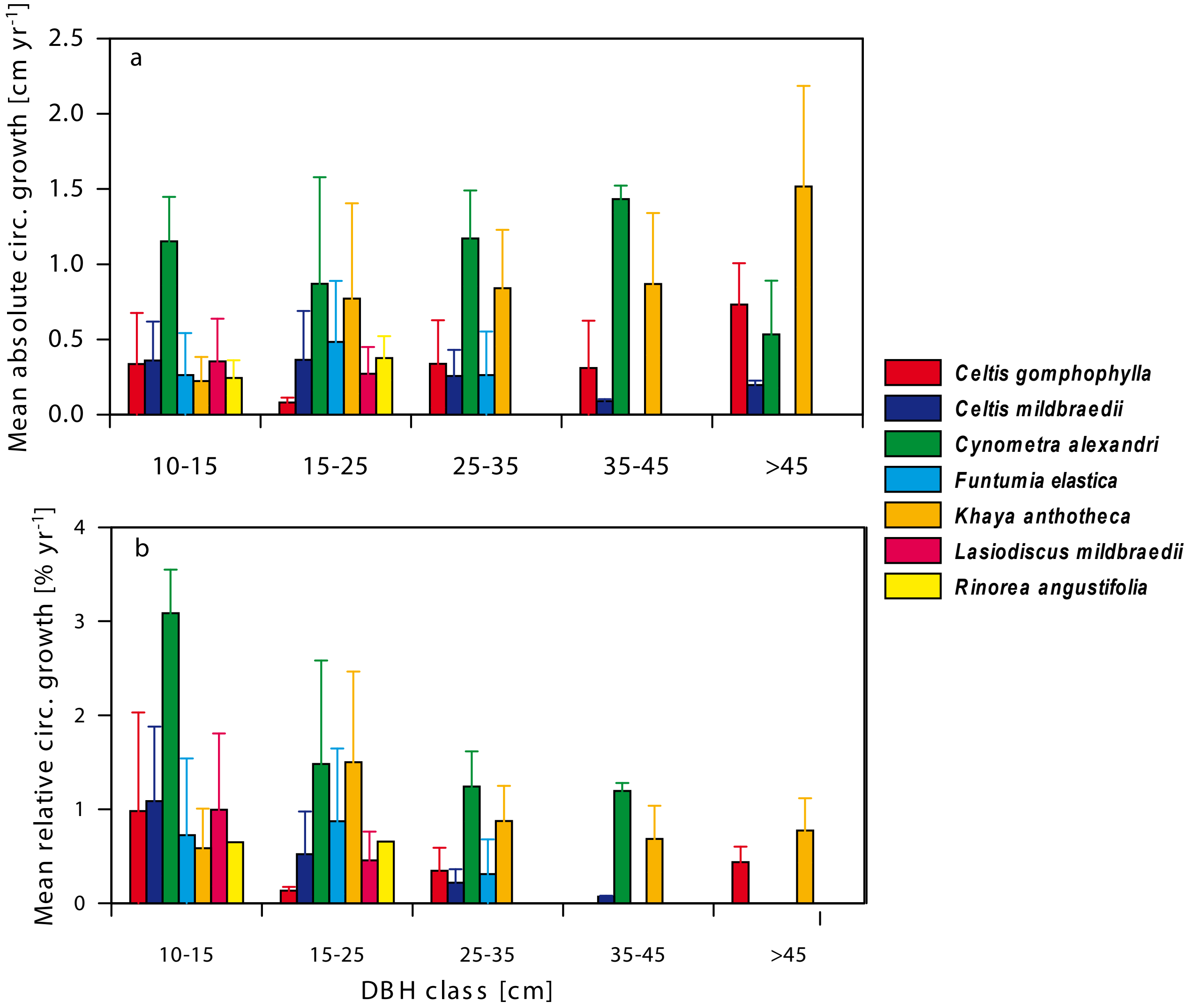

Figure 5-9: Mean annual (a) absolute (abs.) and (b) relative (rel.) circumferential (circ.) growth in five diameter size classes and the standard deviation for the 7 species that were examined in Budongo Forest are presented. The different scaling of the ordinates has to be considered. Values are given, if at least two individuals were present in the respective size class.

5.2.6.2 Between species growth by height categories

As tree growth rates in different height categories were found to vary for all tree individuals, a similar analysis was performed at species level (Figures 5-10 and 5-11). But it was not possible to use the same height categories as there were not enough tree individuals to represent most of the species. Consequently only two categories were formed: trees that were ≤ 18 m, representing the understorey and parts of the subcanopy in the forest, and trees > 18 m, representing subcanopy and canopy trees in the forest. Thus the number of individuals per species was ≥ 8. In respect of the absolute circumferential

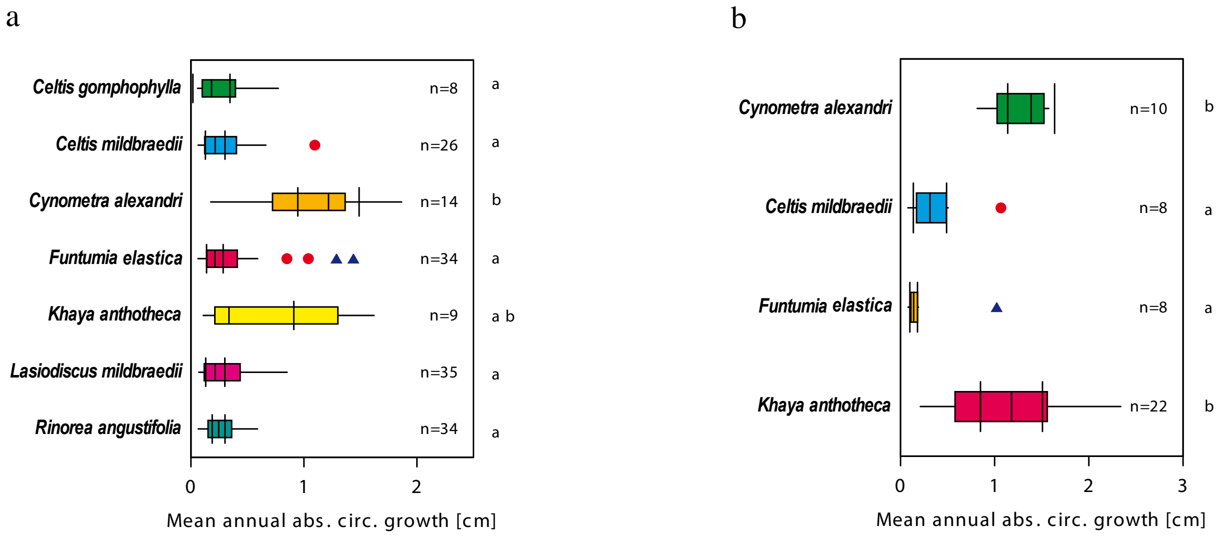

Figure 5-10: Mean annual absolute circumferential growth in two height classes (a) trees ≤ 18 m and (b) trees > 18 m. The boxes represent the lower to the upper quartile, the whiskers the range, additionally the median is shown. Red dots stand for outlier values, blue triangles for far outliers. The letters at the box and whisker plots denote significant (p ≤ 0.01) different groups according to the Kruskal-Wallis analysis. n shown for each species.

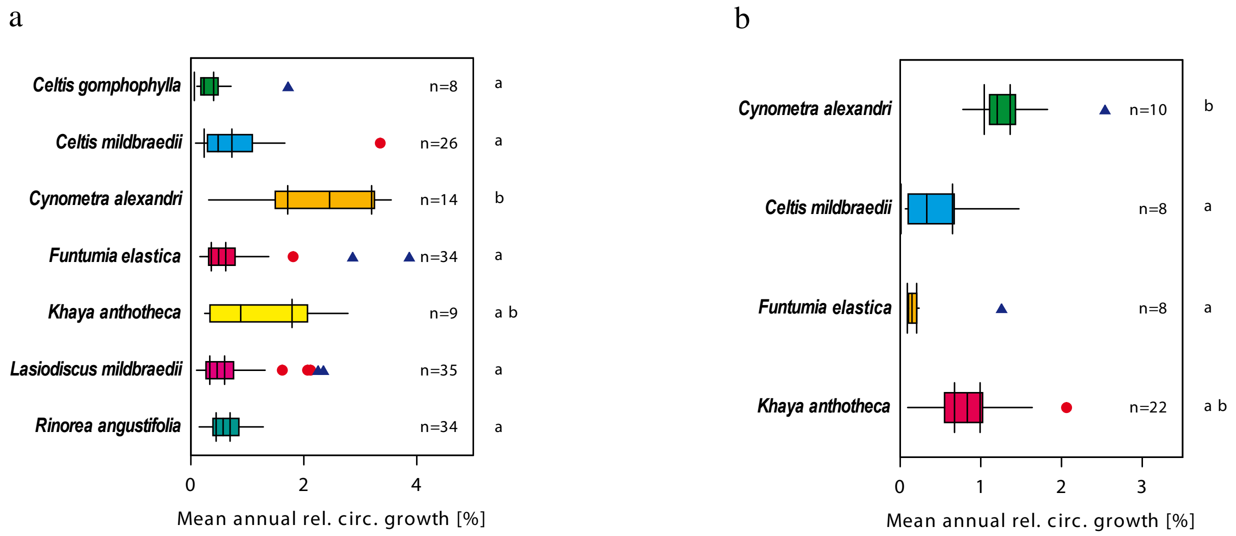

Figure 5-11: Mean annual relative circumferential growth in two height classes (a) trees ≤ 18 m and (b) trees > 18 m. The boxes represent the lower to the upper quartile, the whiskers the range, additionally the median is shown. Red dots stand for outlier values, blue triangles for far outliers. The letters at the box and whisker plots denote significant (p ≤ 0.01) different groups according to the Kruskal-Wallis analysis. n shown for each species

growth two statistically independent categories were distinguished. *Cynometra alexandri* grew statistically faster in both ≤ 18 m and > 18 m height groups. Growth rates of tree individuals of *Khaya anthotheca* were as fast as those of *Cynometra* trees ≤ 18 m and they therefore belonged to the same statistical group for trees > 18 m (Figures 5-10 a and b). This trend was also observed with regard to the relative circumferential growth in both height categories (Figures 5-11 a and b).

5.3 Forest structure as related to human disturbance

In this section effects of structural site parameters on the CDI are shown, as the CDI also had a major influence on the diversity and structural distribution of trees. Table 5-7 lists parameters (see appendix table 10-6 for plot scale) for the trees in BF in the respective study sites.

The number of individuals (≥ 5 cm DBH) ranged from 127 in N15 to 186 in W22 (per 1200 m^2). The number of trees ≥ 10 cm DBH ranged from 54 in KP11 to 85 in W36. Mean extrapolated tree numbers ha^{-1} throughout all plots were 1357 trees ≥ 5cm DBH and 611 ≥ 10 cm DBH.

The mean tree heights in the sites ranged from 10.3 m in W21 to 13.8 meters in N15. The tallest tree throughout all the sites was a *Cynometra alexandri* with a measured height of 45.6 m. The tree with the largest DBH was an individual of *Alstonia boonei* with 224.4 cm. Both recorded trees occurred in the nature reserve N15. Basal areas (BA) per plot (400 m^2) ranged from 0.61 m^2 in KP11B to 6.19 m^2 in N15B. The sites contained 46.57 m^2 basal area on average.

The diameter distribution across the differently disturbed sites (Figure 5-12) did not differ significantly between sites. The most disturbed site (CDI 7) had the lowest maximum DBH (Figure 5-12 a). Figure 5-12 b highlights tree heights along the disturbance gradient using the CDI. The heights were evenly distributed in both size classes for small and larger trees. The correlation between BA and the CDI did not produce a clear trend (Figure 5-13 a). For the relation between slenderness ratio and CDI a slight negative trend was established (Figure 5-13 b). The relation of different structural parameters to the disturbance indices is shown in the appendix, table 10-9.

Table 5-7: Characteristics of trees ≥ 5 cm DBH in the study sites (1200 m^2 each) are presented. The numbers after the ± represent the SD. Values per hectare are extrapolated from the sites. BA: Basal area; CDI: Commercial disturbance index. Site abbreviations are explained in table 3-2.

Site	Indiv. [No.ha^{-1}]	DBH [cm]	Height [m]	BA [m^2 ha^{-1}]	Volume [m^3 ha^{-1}]	Species [No.]	CDI [ ]
KP11	1125	15.0 ± 11.9	11.6 ± 7.3	29.9 ±3.6	242.9 ± 28.9	21	0
N15	1058	21.2 ± 25.8	13.9 ± 9.6	85.6 ± 10.2	1133.2 ± 135.1	20	0
N4	1492	13.9 ± 14.9	11.0 ± 5.8	51.4 ± 6.1	408.5 ± 48.8	43	6
W21	1467	13.6 ± 12.5	10.1 ± 7.1	38.6 ± 4.6	330.0 ± 39.4	40	7
W22	1550	15.9 ± 18.5	11.1 ± 7.8	68.1 ± 8.1	767.4 ± 91.7	38	6
W36	1450	15.7 ± 21.7	12.1 ± 8.7	82.9 ± 9.9	931.7 ± 111.2	26	2

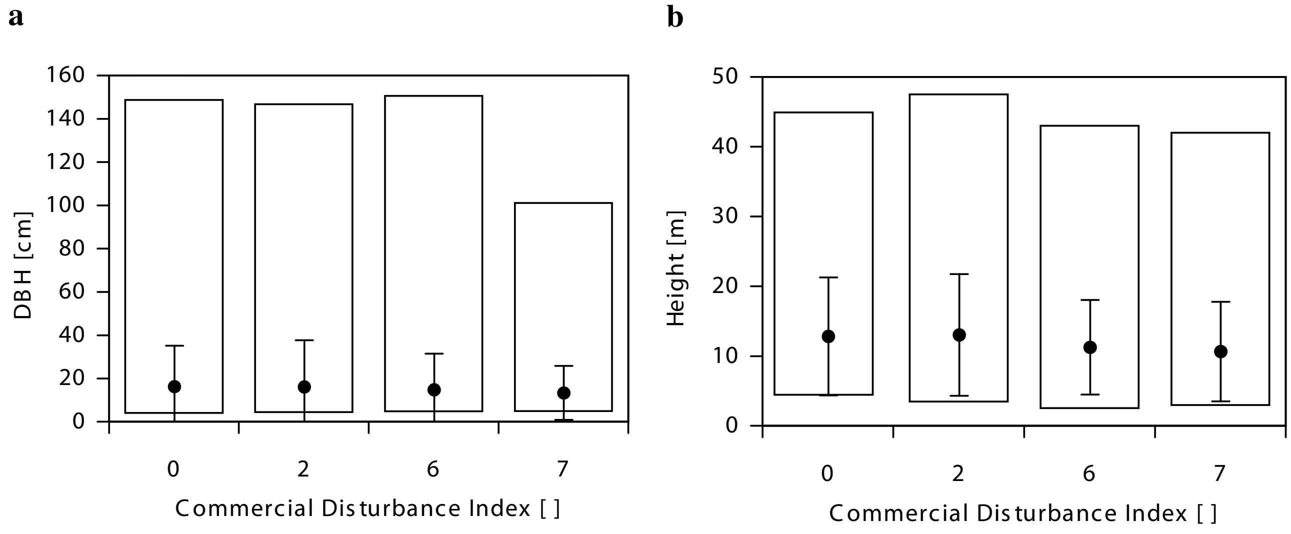

Figure 5-12: a) Diameter and b) height distribution of trees with DBH ≥ 10 cm in the forests according to the commercial disturbance index. The bars represent the range, the dots the mean, the SD is given. The different scaling needs to be considered.

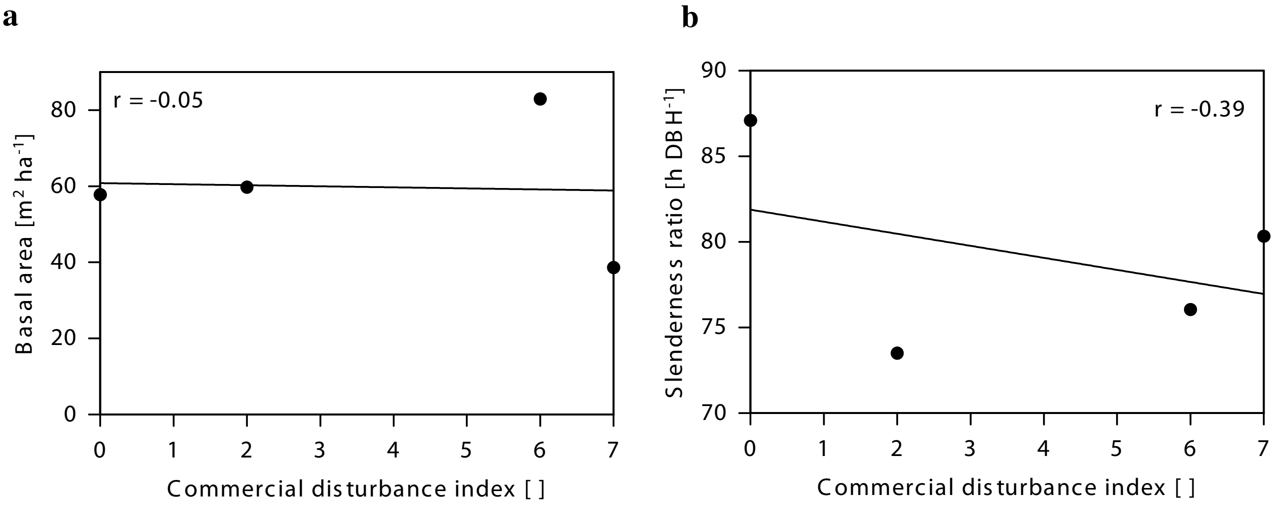

Figure 5-13: Correlation between (a) basal area and (b) mean slenderness ratio (relation of tree height to tree diameter) of the trees in the study sites depending on the commercial disturbance index. Pearson's r is given ($p > 0.05$).

5.3.1 Canopy parameters

The distribution of two light parameters calculated using hemispherical photographs along the CDI is demonstrated in figure 5-14. The understorey radiation was statistically similar in the most and least disturbed site and significantly higher than that in the intermediately disturbed sites. The mean values ranged from 9 to 12 % radiation of the above-canopy radiation, the minimum and maximum values ranged from 6 to around 19 %. The percentage of canopy openness was significantly higher in the least disturbed sites but comparable in the more disturbed sites. The mean values ranged from 5 to 7

% canopy openness, the minimum and maximum values ranged from 3 to around 9 %. The factors describing tree crown area and crown exposure (CE) were recorded for dendrometer trees. They interrelated, so that trees with a large crown area in most cases had a high CE value (Figure 5-15).

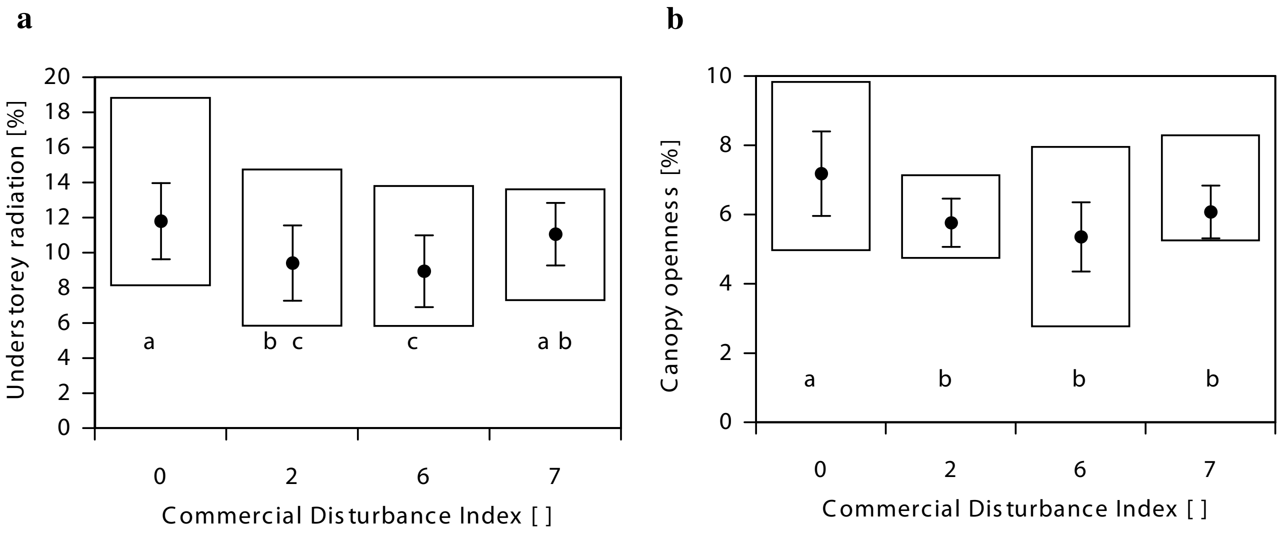

Figure 5-14: The graph shows (a) the percentage of understorey radiation and (b) the percentage of canopy openness (calculated using hemispherical photographs) in the differently disturbed sites. The bars represent the range, the dots the mean, the SD is given. The letters in the graph denote significant different groups (MANOVA, Tukeys HSD-test for unequal N, p < 0.05).

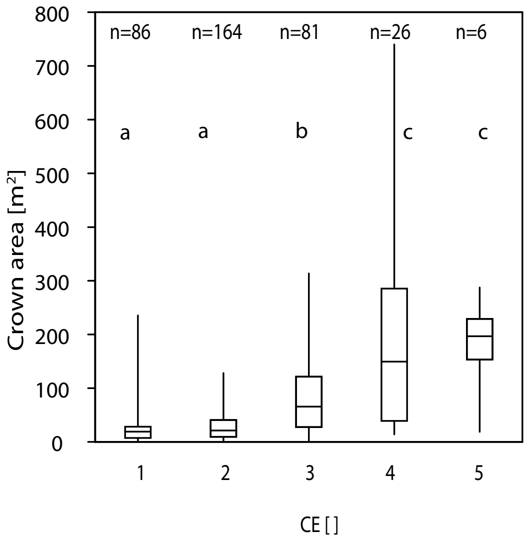

Figure 5-15: Crown area [m²] in the five different crown exposure (CE) categories is shown. The letters in the graph denote significant differences according to the Kruskal-Wallis test ($p \leq 0.05$). n shown in the graph.

5.4 Effect of climatic factors on tree dynamics

5.4.1 Effect of incident precipitation on stem growth

A summary of the monthly **absolute circumferential growth** in relation to the monthly IP is given in table 5-8. In contrast to KF no throughfall data were available for the study period. In addition the sum of the IP for 2 and 3 months and the monthly sum of the number of rainy days were correlated with growth. The **absolute circumferential growth** rates of all trees in BF showed a clear trend towards an increase with higher rainfall. This relation was evident for all precipitation parameters. Particularly the mean rainfall for the three months and the number of rainy days for the month prior to growth measurement showed most and significant correlations to the absolute growth rates (Figure 5-16). This trend was observed for all species, with strongest correlations for *Cynometra alexandri* and weakest for *Funtumia elastica* with regard to species level.

Table 5-8: The correlation between the mean monthly absolute circumferential growth, the incident precipitation (IPav), the summed IP for 2 months (IP 2) and 3 months (IP 3) [mm], as well as the number of days with rainfall per month. The numbers represent Pearson's r with the asterisks giving the level of significance: without: $p > 0.05$, * $p \leq 0.05$, ** $p \leq 0.01$. n = 36

Species	IPav	IP 2	IP 3	Rainy days
Celtis gomphophylla	0.25	**0.38 ***	**0.45 ****	**0.39 ***
Celtis mildbraedii	0.20	**0.38 ***	**0.37 ***	0.30
Cynometra alexandri	**0.35 ***	**0.45 ****	**0.45 ****	**0.50 ****
Funtumia elastica	0.16	0.30	0.31	0.29
Khaya anthotheca	0.30	**0.40 ***	0.29	**0.44 ****
Lasiodiscus mildbraedii	0.33	**0.39 ***	**0.42 ***	**0.44 ****
Rinorea angustifolia	0.22	0.27	0.32	**0.35 ***
Mean all trees	**0.38 ***	**0.51 ****	**0.51 ****	**0.55 ****

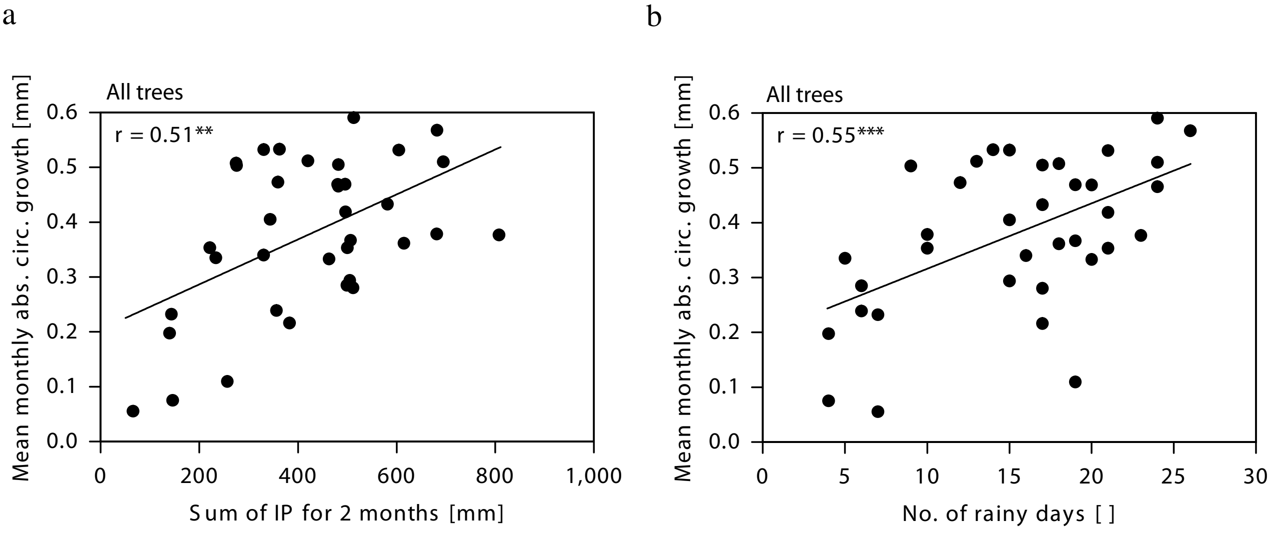

Figure 5-16: Mean monthly absolute circumferential (abs. circ.) growth [mm] of all measured trees (a) in relation to the sum of IP for 2 months [mm] and (b) in relation to the monthly numbers of rainy days. The values represent Pearson's r with the asterisks giving the level of significance: ** $p \leq 0.01$; *** $p \leq 0.001$. n = 36.

The correlation matrices for monthly **relative circumferential growth** in relation to IP showed a similar trend (Table 5-9 and Figure 5-17). Overall there were significant positive correlations, the strongest and most frequent again with the number of rainy days per month. The relative growth rates of *Celtis mildbraedii* and *Funtumia elastica* showed no significant relation to the rainfall parameters, while *Cynometra alexandri* possessed strongest relations.

Table 5-9: The correlation between the mean monthly relative circumferential growth, the incident precipitation (IPav), the summed IP for 2 months (IP 2) and 3 months (IP 3) [mm], as well as the number of days with rainfall per month is shown. The numbers represent Pearson's r with the asterisks giving the level of significance: without: p > 0.05, * p ≤ 0.05, ** p ≤ 0.01. n = 36

Species	IPav	IP 2	IP 3	Rainy days
Celtis gomphophylla	0.28	**0.38***	**0.45***	**0.39***
Celtis mildbraedii	0.11	0.30	0.30	0.22
Cynometra alexandri	**0.35***	**0.48****	**0.48****	**0.46****
Funtumia elastica	0.16	0.29	0.30	0.30
Khaya anthotheca	0.25	**0.42***	0.31	**0.44****
Lasiodiscus mildbraedii	0.33	**0.42***	**0.46****	**0.46****
Rinorea angustifolia	0.21	0.26	0.30	**0.34***
Mean all trees	**0.35***	**0.48****	**0.50****	**0.51****

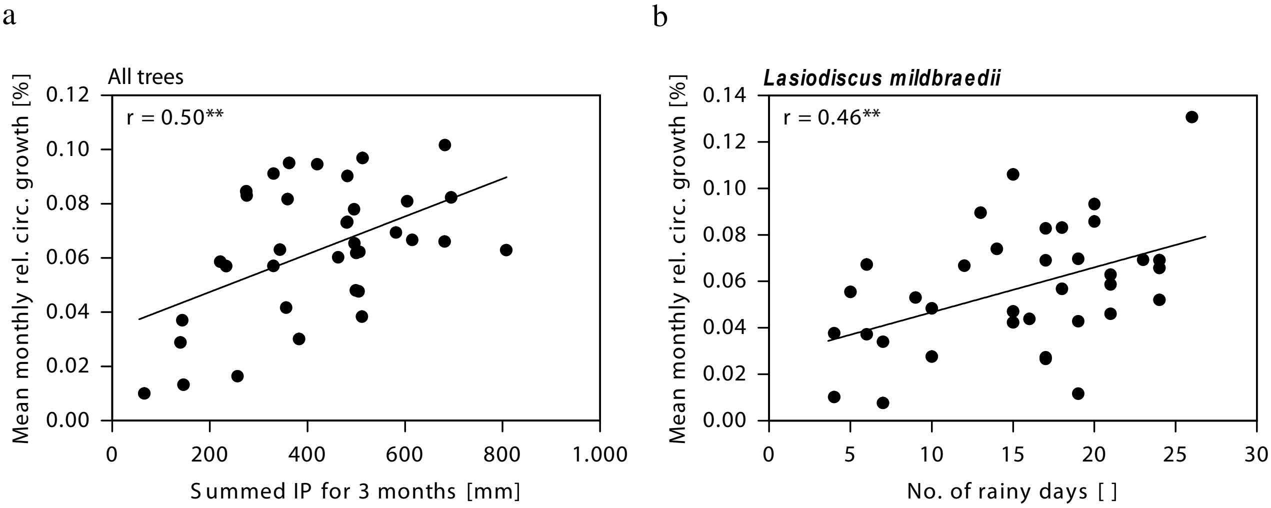

Figure 5-17: Mean monthly relative circumferential (rel. circ.) growth [%] of (a) all trees in relation to the sum of IP for 3 months [mm] and of (b) *Lasiodiscus mildbraedii* in relation to the monthly numbers of rainy days. The values represent Pearson's r with the asterisks giving the level of significance: ** p ≤ 0.01. n = 36.

5.4.2 Effect of temperature on stem growth

The correlations between the **monthly absolute circumferential growth** and both the mean monthly temperatures measured inside and outside the forest and the mean monthly solar radiation are shown in table 5-10. There were clear partially significant trends towards less growth with higher maximum temperatures and more growth with higher minimum temperatures. In particular there were strong, in most cases very highly significant, correlations between the maximum temperatures and absolute circumferential growth. The mean temperatures did not correlate significantly with absolute growth, with the exception of *Cynometra alexandri*, which exhibited a significantly negative correlation with temperature within the forest. Solar radiation correlated in all cases negatively with absolute growth, for *Cynometra alexandri* and *Rinorea angustifolia* this was significant. Figure 5-18 shows that the trend for the absolute circumferential growth of all trees relates positively to minimum and negatively to maximum temperature measured outside the forest.

The correlation between the monthly **relative circumferential growth** and the mean monthly temperature and solar radiation parameters is presented in table 5-11. A similar trend in relation to the absolute growth rates (Table 5-10) was evident. Mean temperatures did not correlate significantly in most cases with relative growth, apart from *Cynometra alexandri*. Maximum temperatures showed a significant negative correlation with mean relative growth in most cases highly significant except

Table 5-10: The correlation between the mean monthly absolute circumferential growth and mean monthly solar radiation [W m^{-2}], monthly mean (T_{mean}), minimum (T_{min}) and maximum temperatures (T_{max}) [°C] outside for 36 months and inside the forest for 25 months is shown. The values represent Pearson's r with the asterisks giving the level of significance: without: p > 0.05, * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001. n shown in table.

	Outside forest (n = 36)			Inside forest (n = 25)		
Species	**T_{Max}**	**T_{Min}**	Solar radiation	**T_{Mean}**	**T_{Max}**	**T_{Min}**
Celtis gomphophylla	**-0.56*** **	0.15	-0.30	-0.21	-0.31	0.13
Celtis mildbraedii	**-0.49** **	0.31	-0.38	-0.03	-0.04	0.22
Cynometra alexandri	**-0.63*** **	0.25	**-0.57***	**-0.42***	-0.31	0.17
Funtumia elastica	**-0.42** **	0.18	-0.25	-0.18	-0.29	0.19
Khaya anthotheca	-0.29	**0.39***	-0.02	0.09	0.06	0.24
Lasiodiscus mildbraedii	**-0.54** **	0.26	-0.34	-0.21	**-0.45***	**0.41***
Rinorea angustifolia	**-0.58*** **	0.24	**-0.64***	-0.33	**-0.41***	0.28
Mean all trees	**-0.71*** **	**0.34***	-0.50	-0.31	**-0.40***	**0.43***

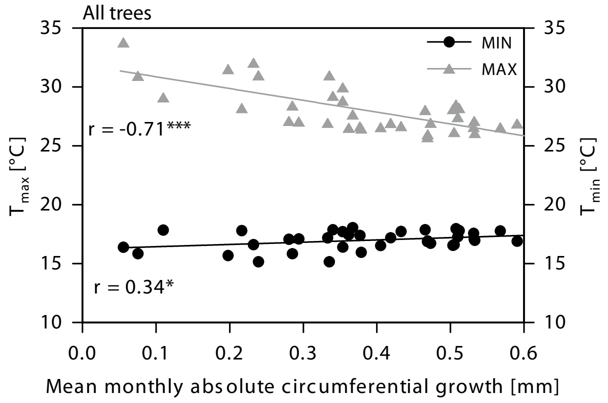

Figure 5-18: Mean monthly absolute circumferential growth of all tree individuals in relation to the monthly maximum and minimum temperature [°C]. The values represent Pearson's r with the asterisks giving the level of significance: * p ≤ 0.05; *** p ≤ 0.001. n = 36.

for *Khaya anthotheca* (Figure 5-19b). Minimum temperatures correlated positively with relative growth rates, some correlations being significant including one highly significant correlation for *Khaya anthotheca*. Solar radiation correlated negatively with the relative growth rates, in the case of *Lasiodiscus mildbraedii* even significantly. Inside forest temperatures did not correlate as well as the outside temperatures, but overall significant trends for the inside maximum and minimum temperatures were found (Figure 5-19a). The mean of the annual sum of **relative growth** over the investigated species for a study period of 36 months is presented in figure 5-20. There were evident differences in the seasonal relative growth. *Cynometra alexandri* grew fastest with an increase of more than 4 % of its initial circumference. *Khaya anthotheca* followed reaching nearly 3 % of relative basal area growth. After that came the other species with a lower increase in increment, *Celtis gomphophylla,* growing at the slowest rate with an increase in basal area of around 1.0 % in three years. A wavelike growth pattern emerged especially in respect of *Cynometra alexandri*.

Table 5-11: The correlation between the mean monthly relative circumferential growth and monthly mean solar radiation [W m^{-2}], monthly mean (T_{mean}), minimum (T_{min}) and maximum temperatures (T_{max}) [°C] outside for 36 months and inside the forest for 25 months. The values represent Pearson's r with the asterisks giving the level of significance: without: p > 0.05, * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001. n shown in table.

	Outside forest (n = 36)			Inside forest (n = 25)		
Species	**T_{Max}**	**T_{Min}**	**Solar radiation**	**T_{Mean}**	**T_{Max}**	**T_{Min}**
Celtis gomphophylla	**-0.58*** **	0.13	-0.36	-0.26	-0.36	0.18
Celtis mildbraedii	**-0.42** **	0.27	-0.29	0.03	0.02	0.18
Cynometra alexandri	**-0.60*** **	0.23	-0.49	**-0.40***	-0.30	0.13
Funtumia elastica	**-0.41***	0.17	-0.23	-0.15	-0.28	0.19
Khaya anthotheca	-0.31	**0.45** **	-0.03	0.14	0.03	0.26
Lasiodiscus mildbraedii	**-0.59*** **	0.28	-0.38	-0.28	**-0.51** **	**0.42***
Rinorea angustifolia	**-0.57*** **	0.24	**-0.64***	-0.29	-0.38	0.28
Mean all trees	**-0.69*** **	0.32	-0.50	-0.27	**-0.40***	**0.41***

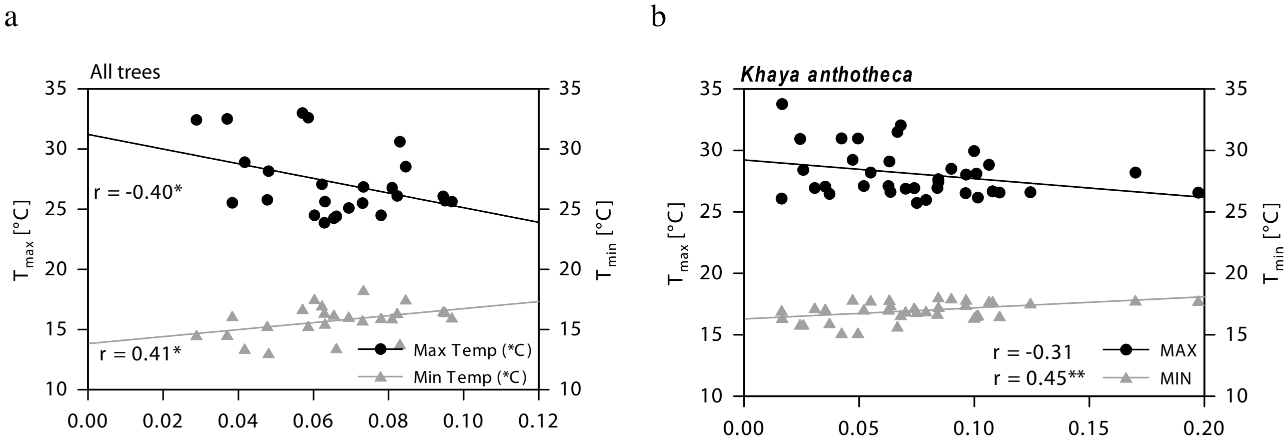

Figure 5-19: Mean monthly relative circumferential growth of (a) all tree individuals in relation to the monthly maximum and minimum temperature [°C] and of (b) *Khaya anthotheca* in relation to the monthly maximum and minimum temperature [°C] outside the forest. The values represent Pearson's r with the asterisks giving the level of significance: without p > 0.05; * p ≤ 0.05; ** p ≤ 0.01. n = 36.

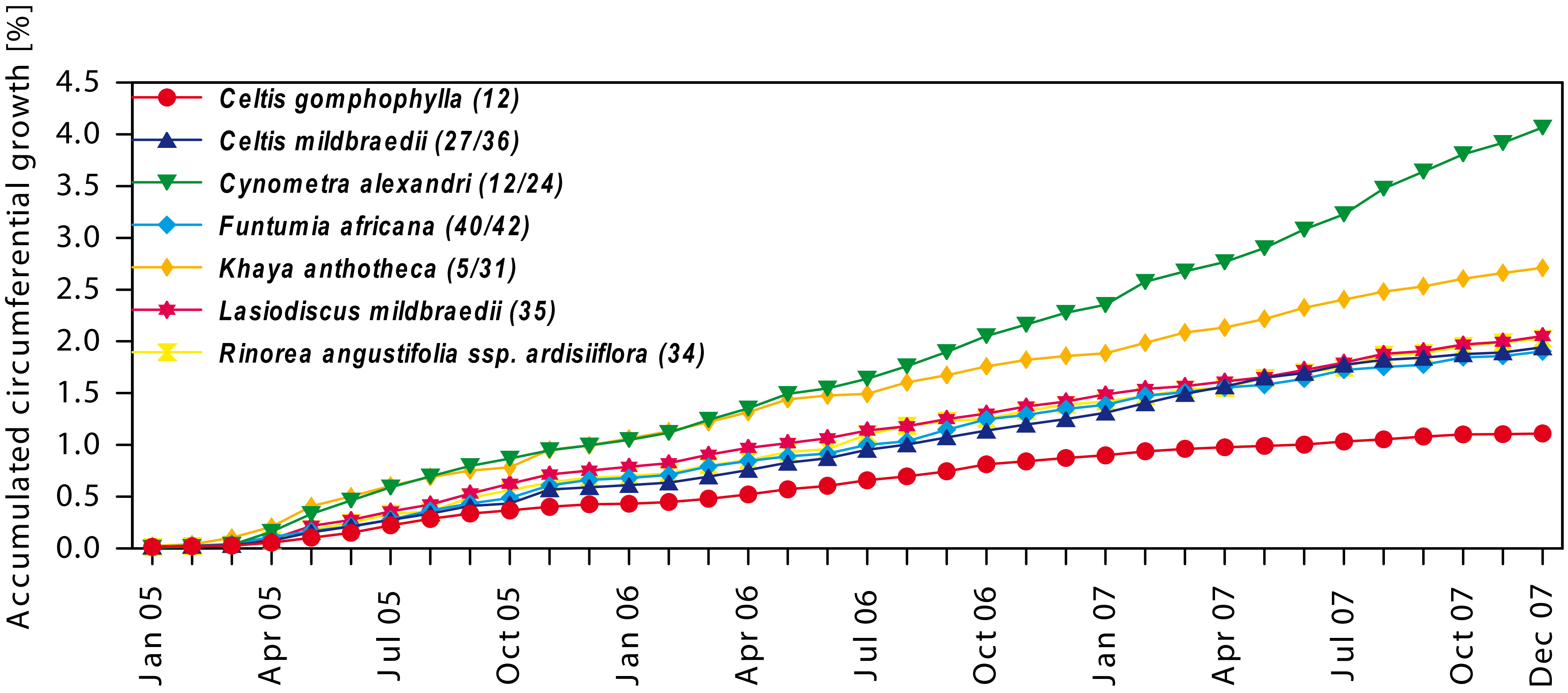

Figure 5-20: Summed mean monthly relative circumferential increment for 7 in Budongo Forest examined species during a period of 36 months from January 2005 until December 2007. The number of tree individuals is given in brackets, with the number of individuals followed by the number of individuals including added single trees.

5.4.3 Effect of climatic factors on tree phenology

The relation between the abiotic factors, incident precipitation (IP), rainy days, temperature parameters and solar radiation and the percentage of individuals flowering, fruiting and those that had shed foliage for the study period of 36 months is shown in table 5-12. There was a significant positive correlation between the percentage of individuals flowering and the mean temperature recorded in the forest. The proportion of fruiting individuals did not correlate significantly with the abiotic factors listed above. The percentage of individuals without foliage after shedding correlated most strongly with the climatic factors. The rainfall parameters showed a negative correlation, which in the case of the mean IP of the last 2 and 3 months was highly significant. The correlation between temperature and proportion of individuals without leaves after shedding was very highly significantly positive in respect of the outside maximum temperatures, highly significantly positive for the inside mean temperature and significantly positive in respect of the mean monthly maximum temperature. Most species shed their leaves during the dry season. Growth was also affected by lower rainfall and thus the drier season resulted in low seasonal growth activity from December until February.

Table 5-12: Correlation between monthly phenological parameters and monthly climatic factors for 36 months between January 2005 and December 2007. The numbers represent Pearson's r with the asterisks giving the level of significance: without: no significance, * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. IPav: Incident precipitation; IP2: IP sum of 2 months; IP3: IP sum of 3 months; T_{mean}: mean monthly temperature; T_{min}: mean monthly minimum temperature; T_{max}: mean monthly maximum temperature; out: measured outside the forest; in: measured inside the forest. n = 36.

Abiotic parameter	Trees flowering	Trees fruiting	Trees without foliage
IPav	-0.03	-0.00	-0.25
IP 2	-0.17	0.04	**-0.44 *****
IP 3	-0.30	0.14	**-0.58 *****
Rainy days	-0.07	0.14	-0.33
T_{max} out	0.25	-0.33	**0.63 *****
T_{min} out	0.02	0.08	-0.06
T_{mean} in	**0.44 ***	-0.34	**0.55 ****
T_{max} in	0.39	-0.23	**0.45 ***
T_{min} in	-0.03	0.15	-0.06
Solar radiation	0.00	-0.20	-0.00

5.4.4 Effect of soil parameters on stem growth

The correlations between the growth parameters and soil conditions for each plot are shown in table 5-13. The different growth rates for the first year 2005 and the mean for all years do not correlate significantly with any of the observed soil parameters that were measured in 2004. The pH value correlates negatively with all growth rates and only produces a trend which is not however significant.

Table 5-13: The correlation between the mean annual absolute and relative circumferential (circ) growth for 2005 and a mean from 2005 to 2007 with mean water extractable soil cations K, Mg, Ca and Mn, the pH evaluated, the C, N content and the C:N ratio for 12 plots in 2004 is shown. The values represent Pearson's r with the asterisks giving the level of significance: without: p > 0.05.

	mean growth 2005		mean growth 2005-2007	
Soil parameter	**Absolute circ**	**Relative circ**	**Absolute circ**	**Relative circ**
K water	0.03	0.13	0.11	0.26
Mg water	0.03	-0.02	0.15	0.12
Ca water	0.11	0.26	0.14	0.44
Mn water	0.15	0.22	0.10	0.10
pH	-0.47	-0.37	-0.32	-0.16
N	-0.01	0.03	0.11	0.06
C	-0.14	-0.06	0.02	0.15
C:N ratio	-0.15	0.13	-0.27	-0.19

5.5 Tree seedling establishment

5.5.1 Tree seedling α-diversity

A total of 708 seedlings and saplings (≤ 500 cm height) were recorded in the study period between May 2005 and December 2007 in the 72 x 1 m^2 subplots, that were located within the main study plots. The spermatophytes belonged to 38 species from 18 families, of which the seedlings (≤ 100 cm) consisted of 648 individuals belonging to 34 species from 17 families and the 61 saplings (≥ 100 cm) belonged to 17 species from 11 families. The most common families for both height classes were Sapotaceae and Meliaceae (5 species each), Sapindaceae (4), Violaceae (4) and 9 families representing one or two species. The most species rich genera were *Rinorea* (4 species), followed by *Celtis, Trichilia* and *Chrysophyllum* (3 species each) , all other 25 species each belong to a single genus. The three most abundant species recorded in the plots were *Rinorea angustifolia* (157 individuals), *Entandrophragma cylindricum* (103) and *Lasiodiscus mildbraedii* (89). Thirty-one of the species also occurred as trees ≥ 5 cm DBH in the plots, which represented 34 % of the species of the mature trees ≥ 5 cm DBH.

5.5.1.1 Seedling diversity as related to abiotic factors

Seedling densities averaged six seedlings per m^2 with densities ranging between 1 to 16 seedlings m^{-2}. The Simpson diversity index in the subplots ranged from 0.044 to 0.785 with a mean value of 0.343. The seedling diversity in the subplots was described by using three diversity indices, Fisher's alpha, the Simpson and the Shannon-Wiener-Index H'. The spatial distribution of seedling diversity showed a very highly significantly positive relation to the seedling density in each seedling subplot in respect of the three indices (Table 5-14 and Figure 5-21). The soil parameters for each subplot did not correlate strongly with any of the three diversity indices (Table 5-14). The canopy parameters, openness and understorey radiation, calculated using hemispherical photography for each subplot, exhibited a highly significantly positive relation with the seedling diversity indices. The relation of the Shannon-Wiener H' per subplot in 2005 to the seedling density shown in Figure 5-21b, indicates that with an increase in canopy openness more seedlings occur.

Table 5-14: The correlation between the diversity indices and abiotic subplot parameters for the year 2005 is shown. The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. Sites W36 and KP11 are not considered.

Parameter for subplots	**Fisher's alpha**	**Simpson**	**Shannon Wiener H'**
Density (n=44)			
Seedling density 2005	**0.65*** **	**0.67*** **	**0.69*** **
Light (n=28)			
Canopy openness	**0.52** **	**0.59** **	**0.57** **
Understorey radiation	**0.40* **	**0.53** **	**0.49** **
Soil (n=44)			
N	0.08	0.13	0.17
C	0.08	0.15	0.17
C:N ratio	0.09	0.13	0.11
pH	0.15	0.18	0.20

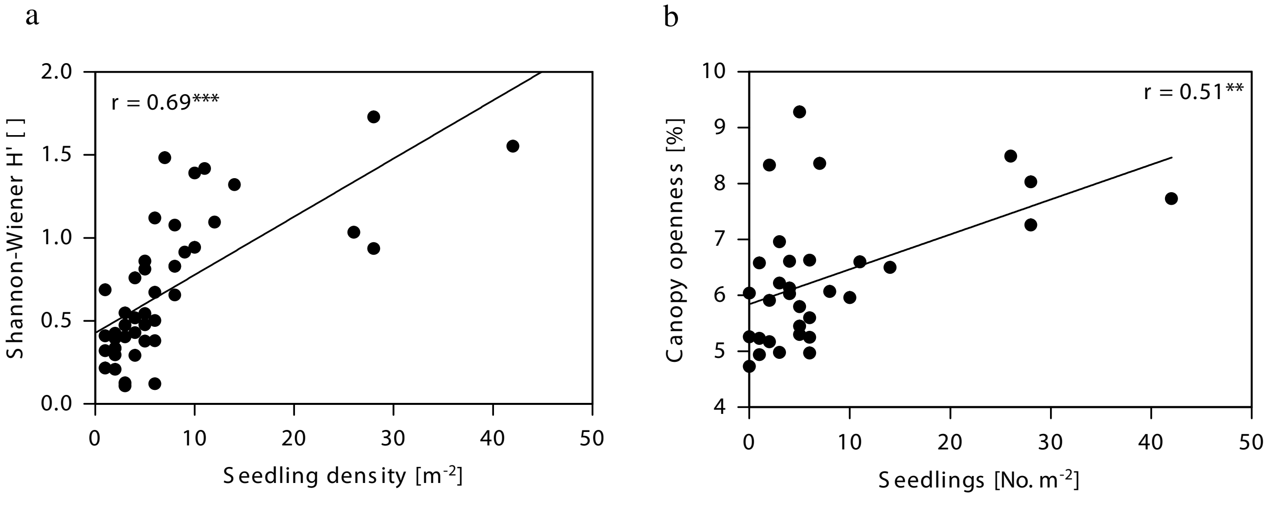

Figure 5-21: Mean seedling density in the year 2005 per subplot in relation (a) to the Shannon-Wiener H' ($n = 44$) and (b) to the canopy openness [%] for each subplot ($n = 28$). The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

5.5.2 Dynamics of seedlings in space and time

5.5.2.1 Seedling recruitment

The new seedling recruitment distribution for common species varied to a large extent not only spatially, but also temporally (Table 5-15). On a **temporal scale** most *Lasiodiscus mildbraedii* recruits were found in 2006, which was 4-5 times more seedlings than monitored in the other study years. Also the amount of *Entandrophragma cylindricum* seedlings recruited in each year varied greatly. Years with high recruitment in 2005 were followed by years with hardly any recruits. Seedling recruitments of *Celtis zenkeri* were quite constant in certain parts of the forest. *Rinorea angustifolia* recruitments were high in 2005 and 2006 and then decreased to six in 2007, while the recruitments of *Uvariopsis congensis* were only recorded in 2006.

On a **spatial scale** it was evident that seedlings of *Entandrophragma cylindricum* only occurred in one of the nature reserve sites. None of the observed species were recorded at all sites. *Rinorea angustifolia* and *Lasiodiscus mildbraedii* occurred at five of the six sites, while *Entandrophragma cylindricum* and *Uvariopsis congensis* were only recorded at a single site. The distribution of seedling recruitments of the selected species differs amongst the sites with the geographically more closely connected sites N15, N4, W21 and W22 having more uniform species occurrences than the sites KP11 and W36.

Table 5-15: Species, sample sizes and population densities of seedlings [No. m^{-2}] of each species present in 2005, and species and density of recruits of each species at the census in which they were initially tagged (2006, 2007). The abbreviations for the sites and the species are explained in table 3-1 and table 3-5 respectively.

Budongo	**Year**	**R. n**	**Population density [No. m^{-2}] by site**					
Species			KP11	N15	N4	W21	W22	W36
Celtis zenkeri	2005	8	0	0.0694	0	0.0278	0.0139	0
	2006	15	0	0.0833	0.0417	0.0556	0.0278	0
	2007	2	0	0	0.0139	0	0.0139	0
Entandrophragma cylindricum	2005	104	0	1.4444	0	0	0	0
	2006	1	0	0.0139	0	0	0	0
	2007	0	0	0	0	0	0	0
Lasiodiscus mildbraedii	2005	12	0	0.1111	0.0417	0	0.0139	0
	2006	40	0	0.0417	0	0.0139	0	0.5000
	2007	8	0	0	0.0694	0	0	0.0417
Rinorea angustifolia	2005	74	0	0.2917	0.2083	0.3194	0.2083	0
	2006	39	0.0556	0.0139	0	0.0139	0	0.4583
	2007	6	0	0	0.0139	0	0	0.0694
Uvariopsis congensis	2005	0	0	0	0	0	0	0
	2006	27	0.3750	0	0	0	0	0
	2007	0	0	0	0	0	0	0

The seedling survival of newly recruited seedlings from 2006 until 2008 is shown (Table 5-16) whereby the age of the seedlings is known. The sites (3 x 4 m^2 seedling subplots each) displayed differing patterns of seedling densities of newly established seedlings ranging from 5 to 22 per site. The survival rates also varied amongst the sites between 41% and 71% during the 2 years of monitoring. The survival rates were 54 % in all study sites. For the species-specific analyses for all individuals throughout all sites only species with ≥ 15 recruitment individuals were considered. The only species that could be included due to the number of individuals were the subcanopy species *Celtis zenkeri* and the understorey species *Lasiodiscus mildbraedii*. The *Celtis* seedlings had a survival rate of 27 % over the two years and a height increment of 2.5 cm yr^{-1}, while *Lasiodiscus* had a survival rate of 63 % and a growth rate of 1.4 cm yr^{-1}.

Table 5-16: Seedling performance of newly recruited seedlings over 1 yr as shown by proportion surviving [%], and mean and maximum annual growth rates [cm yr^{-1}] for seedlings that were newly recorded in 2006 in 72 m^2. n for growth rates was only included for seedlings surveyed for ≥ 1 yr with positive height change.

Recruits (2006 ≤ 30cm)	**Survival 2006-2007**		**Growth rate [cm yr^{-1}]**		
	n	[%]	n	Mean	Max
Site					
Total	88	54	28	2.0	9.0
KP11	5	40	-	-	-
N15	17	41	9	2.1	6.0
N4	14	71	1	2.0	6.2
W21	14	64	3	2.5	4.4
W22	15	47	2	2.6	3.3
W36	22	59	13	1.3	9.0
Species					
Total	31	45	14	2.0	6.1
Celtis zenkeri	15	27	6	2.5	6.2
Lasiodiscus mildbraedii	16	63	8	1.4	6.0

5.5.2.2 Dynamics of seedlings as related to climatic factors

The correlation between the climate parameters and the seedling dynamics for all species during the study period from 2005 to 2008 is shown in table 5-17. Each seedling parameter recorded quarterly was related to the quarterly mean respective rainfall parameter. Density related positively, but not significantly, to the rainfall parameters. The mean number of recruits related slightly positively to the rainfall parameters, the mean quarterly mortality rate negatively. Mean quarterly maximum temperature related negatively to density, and positively to mortality and recruitment. Mean quarterly minimum temperature related positively to density, negatively to mortality and positively to recruitment. Similar trends were found at species level with only seedling density and recruitment of *Celtis zenkeri* correlating significantly with the sum of rainfall for the 2 or 3 months prior to the seedling survey.

Seedling density of *Celtis zenkeri* was significantly positively related to IP3, the other rain parameters showing a positive trend. This positive trend was also evident for all species density. Maximum temperature values for all species showed a slightly negative relation to density, while minimum temperatures showed a positive relation. Quarterly mortality values did not show clear relation patterns at species level, but a slight trend was seen towards the mortality of all species increasing with higher maximum temperature and relating negatively to minimum temperature and RD. Quarterly recruitment dynamics related significantly with IP2 and IP3 for *Celtis zenkeri*, further *Cynometra alexandri* and *Rinorea dentata* showed a similar trend. Recruitment dynamics of *Lasiodiscus mildbraedii* and *Rinorea angustifolia* exhibited a slightly positive relation to mean quarterly maximum temperatures.

Table 5-17: Correlation between the mean quarterly (11 quarters) a) seedling density, b) seedling recruitment and c) seedling mortality dynamics and the quarterly rainfall and temperature parameters on species level from 2005-2008. The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$. n = 11. IPav: incident precipitation, IP 2: summed IP for 2 months, IP 3: summed IP 3 for 3 months, RD: rainy days, T_{max}: maximum temperature, T_{min}: minimum temperature

a) **Density** n = 11	IPav	IP 2	IP 3	RD	T_{max}	T_{min}
Celtis zenkeri	0.53	0.58	**0.62***	0.32	-0.30	0.06
Cynometra alexandri	0.17	0.15	0.09	0.10	0.08	0.06
Lasiodiscus mildbraedii	0.21	0.12	0.03	0.02	0.14	-0.11
Rinorea angustifolia	0.09	0.01	-0.08	-0.10	0.27	-0.13
Rinorea dentata	-0.26	-0.21	-0.19	-0.19	0.24	-0.20
Total density	0.45	0.50	0.47	0.48	-0.28	0.27

b) **Recruitment** n = 11	IPav	IP 2	IP 3	RD	T_{max}	T_{min}
Celtis zenkeri	0.58	**0.71***	**0.74****	0.50	-0.29	0.28
Cynometra alexandri	0.32	0.32	0.26	0.40	-0.07	0.41
Lasiodiscus mildbraedii	-0.21	-0.33	-0.46	-0.26	0.58	-0.03
Rinorea angustifolia	-0.16	-0.21	-0.32	-0.16	0.44	0.08
Rinorea dentata	0.19	0.25	0.26	0.41	-0.28	0.30
Total recruitments	0.10	0.07	-0.02	0.15	0.21	0.27

c) **Mortality** n = 11	IPav	IP 2	IP 3	RD	T_{max}	T_{min}
Celtis zenkeri	-0.24	-0.12	0.01	-0.24	0.08	-0.23
Cynometra alexandri	-0.03	0.03	0.08	-0.33	0.37	-0.32
Lasiodiscus mildbraedii	-0.18	-0.08	0.06	-0.41	0.14	-0.48
Rinorea angustifolia	-0.28	-0.20	-0.07	-0.51	0.23	0.16
Rinorea dentata	-0.11	-0.05	-0.07	0.09	0.23	0.16
Total mortalities	-0.18	-0.09	-0.01	-0.40	0.31	-0.35

Figure 5-22 shows the quarterly fluctuations of seedling density for the mean of all species in Budongo from 2005 to 2007. Recruitment peaks commonly occurred in the 2nd and/or 3rd quarter, while mortality peaks were found in the 1st quarter of a year, coinciding with the dry season. The recruitment was highly variable with inter-seasonal and inter-annual fluctuations in the density. The same trend was observed in respect of the seedling mortality, which fluctuated both inter-annually and inter-seasonally. There was a slight reduction in density during the study period. At species level (Figure 5-23) there was an evident variability in seedling densities. *Entandrophragma cylindricum* exhibited a recruitment peak with more than a hundred seedlings in existence in the 2nd quarter of 2005 from which one year later only one seedling remained. Seedlings of the understorey *Rinorea angustifolia* maintained a level of at least around 30 to 40 individuals with a peak in 2006. The other three species, two understorey *Lasiodiscus mildbraedii* and *Rinorea dentata*, as well as the late climax species *Cynometra alexandri,* showed little variation in seedling dynamics.

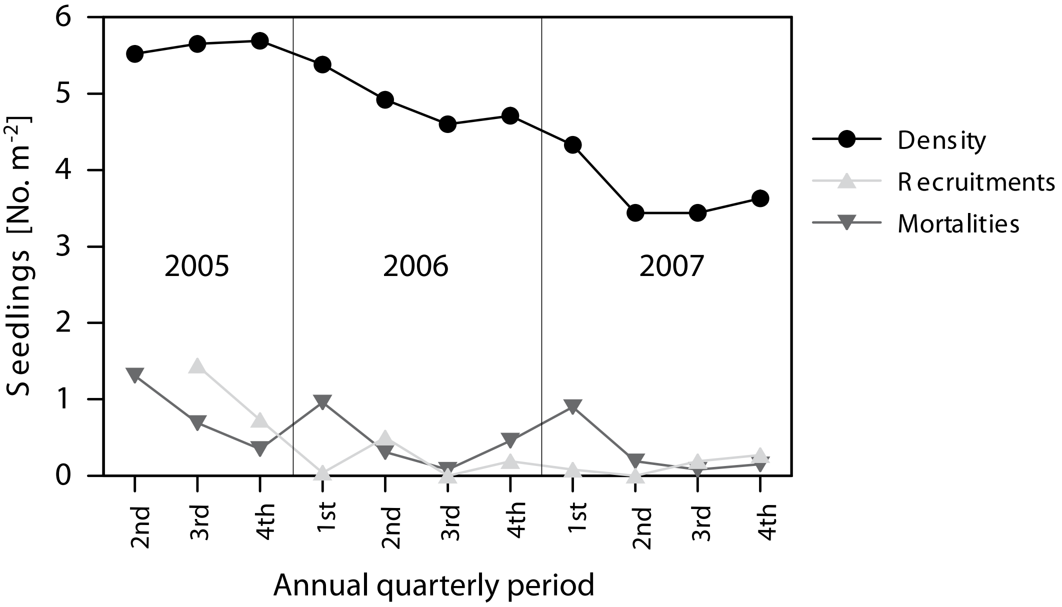

Figure 5-22: Quarterly inter-seasonal variation in seedling density on an area of 48 m^2 (2005-2007). (Quarters: 1st: January-March; 2nd: April- June; 3rd: July-September; 4th: October-December).

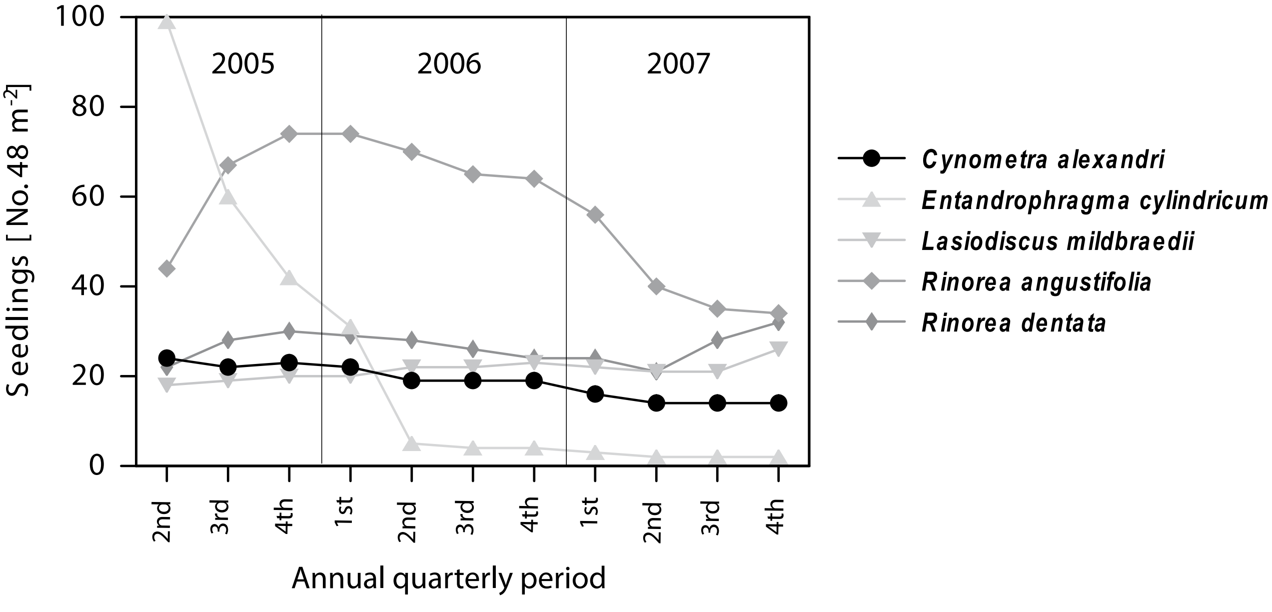

Figure 5-23: Quarterly inter-seasonal variation in seedling density (2005-2007) for 5 common tree species. (Quarters: 1st: January-March; 2nd: April- June; 3rd: July-September; 4th: October-December).

5.5.2.3 Distribution of seedlings as related to the abiotic environment

The correlation between the seedling distribution on subplot, plot and site scale and the abiotic factors measured for the respective area in 2005 is shown in table 5-18. A highly significant positive correlation was found between seedling densities in the subplot and the light parameters at subplot level (Figure 5-24), establishing a positive trend at plot and site level. Most parameters did not seem to correlate strongly with the distribution of the seedling density in the study area. The soil parameters did not appear to influence the distribution of seedling densities in the subplots.

Table 5-18: Correlation between the seedling density 2005 and the abiotic parameters on subplot, plot and site scale recorded in the year 2004 is shown. The values represent Pearson's r with the asterisks giving the level of significance: without $p > 0.05$; ** $p \leq 0.01$. The number of replicates varied for the canopy and soil parameters, as some hemispherical photos and soil samples were missing (see Subsection 3.1.2).

Parameter for Subplots	**Subplot**	**Plot**	**Site**
Light	n = 44	n = 12	n = 4
Canopy openness	**0.51****	0.17	0.47
Understorey radiation	0.28	0.05	0.56
Soil	n = 44	n = 12	n = 4
N	0.09	0.05	0.25
C	0.04	0.02	-0.06
C:N ratio	0.02	-0.04	-0.67
pH	0.12	0.09	0.11

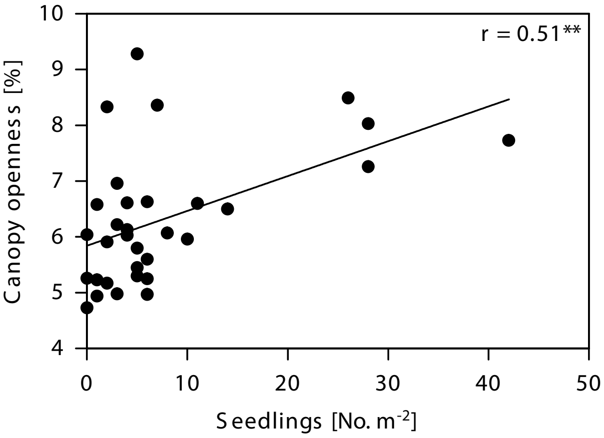

Figure 5-24: The seedling density m^{-2} in relation to the canopy openness per subplot is presented in 2005. The values represent Pearson's r with the asterisks giving the level of significance: ** $p \leq 0.01$. n = 44.

5.5.2.4 Survival of tree seedlings from initial census

The survival rates of individuals ($n \geq 22$) of seedlings (≤ 100 cm) from 2005 until 2008 is given in table 5-19. The number of established seedlings varies between 22 to 104 seedling individuals per species found in the whole forest. The mahogany light-demanding species *Entandrophragma cylindricum* had a low survival rate, while a more shade-tolerant understorey species like *Lasiodiscus mildbraedii* had a very high survival rate. The seedlings of the late climax species *Cynometra alexandri* had a 53.9 % survival rate over the three-year study period. The understorey species *Rinorea dentata* and *angustifolia* had intermediate survival rates of 52.8 and 37 % respectively.

Table 5-19: Survival pattern of all tree seedlings (≤ 100 cm) from species with ≥ 22 individuals that were at least 3 years old in 2008 in a total of 72 m^2 of subplots. n: Number of individuals.

Species (≤ 100 cm)	**n 2005**	**n dead 2008**	**n survived 2008**	**Survival rate [%]**
Lasiodiscus mildbraedii	22	4	18	81.8
Cynometra alexandri	26	12	14	53.9
Rinorea dentata	36	17	19	52.8
Rinorea angustifolia	81	51	30	37.0
Entandrophragma cylindricum	104	103	1	1.0

6 Forest Comparison

This chapter presents a summary of the results contained in chapters 4 and 5 enabling to make a direct comparison of the two study forests.

6.1 Tree diversity and forest structure

A comparison between diversity and structure in the two forests showed that the sites in KF were more diverse than in BF. This was confirmed by the rarefaction analysis (Figure 6-1). While the curve describing KF was almost satiated, the rarefaction curve for BF indicating that the satiation point of the curve was still on the ascent. The impact of disturbance on tree diversity based on the rarefaction estimator Mao Tau was still visible and peaked at intermediate levels (Figure 6-1b). The number of tree individuals extrapolated per hectare was higher in BF than in KF. Mean DBH and mean height of the study trees (≥ 5 cm DBH) are higher in KF than in BF. Mean basal area per site and tree volume per site were higher in BF than in KF (Table 6-1).

Table 6-1: Comparison of diversity and structure values of trees ≥ 5 cm DBH in the forest sites. The minimum (Min), mean and maximum (Max) values per site (1200 m^2).Values per hectare have been extrapolated.

Forest	**Kakamega**			**Budongo**		
Diversity and structure	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**
Shannon-Wiener H'	2.51	2.96	3.24	2.08	2.61	3.02
Individuals of DBH ≥ 5 cm [ha^{-1}]	617	820	1100	1058	1357	1550
DBH [cm]	10.9	17.8	23.1	13.9	15.9	21.2
Height [m]	8.1	12.6	15.2	10.1	11.6	13.9
Basal Area [m^2 ha^{-1}]	21.6	51.4	86.2	29.9	54.9	85.6
Volume [m^3 ha^{-1}]	101.4	451.6	888.2	242.9	635.6	1133.2

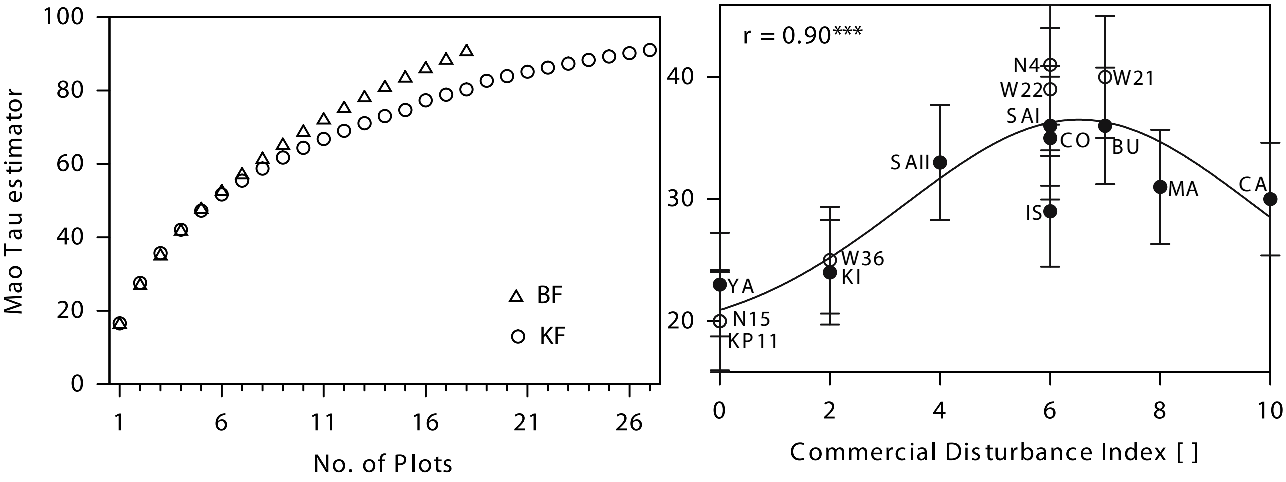

Figure 6-1: A) Sample-based rarefaction curves (Mao Tau = expected species accumulation curves) of the study plots in Budongo Forest (BF) and Kakamega Forest (KF). B) Expected species using the Mao Tau in the different study sites in the two forests. Open circles represent sites in Budongo Forest, while closed circles are the sites in Kakamega Forest, standard deviation of each site for three plots is given. A gauss-fit was performed with the asterisks presenting the level of probability being at $p < 0.0001$.

6.2 Stem growth

The relation between the mean and maximum (the value of the fastest-growing tree) annual absolute diameter growth rates is shown in Figure 6-2. The mean growth rates of most species range from 0.7 to 3 mm yr^{-1}, the maximum growth rates reach the two to fourfold of the mean growth rates.

The investigated tree species occur in the same range in both forests with the exception of the two fastest-growing species (*Croton megalocarpus* and *Funtumia africana*) are only found in KF. Four of the seven species in BF are in the group of slowest-growing trees.

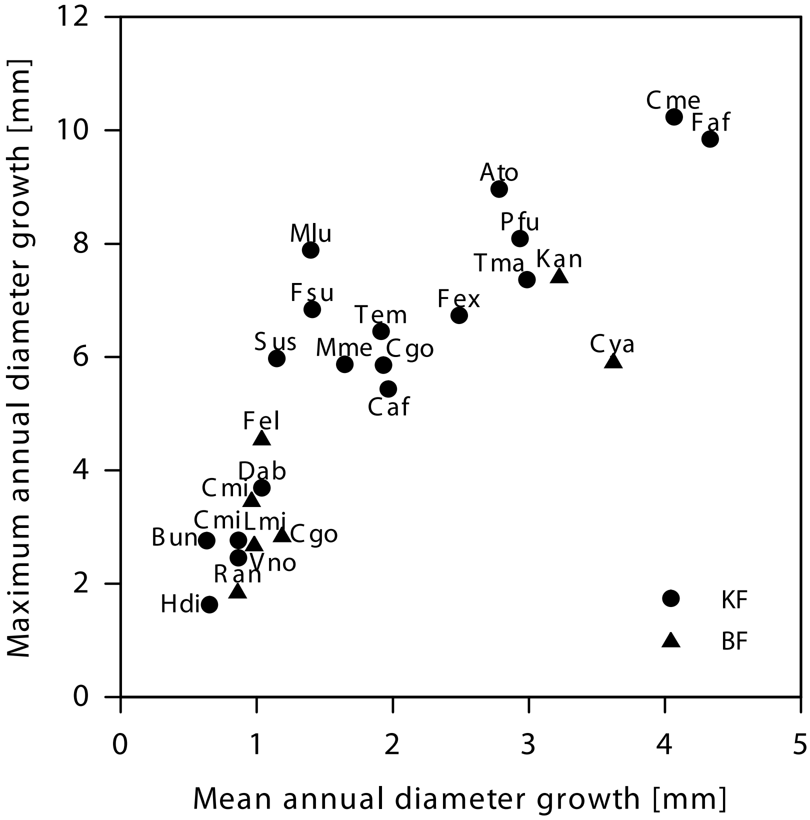

Figure 6-2: The relation between the maximum (the value of the fastest-growing tree) and mean annual diameter growth rates for the 25 studied tree species in **KF** Kakamega Forest (**Ato** *Antiaris toxicaria,* **Bun** *Blighia unijugata,* **Caf** *Celtis africana,* **Cgo** *Celtis gomphophylla,* **Cmi** *Celtis mildbraedii,* **Cme** *Croton megalocarpus,* **Dab** *Diospyros abyssinica,* **Fex** *Ficus exasperata,* **Fsu** *Ficus sur,* **Faf** *Funtumia africana,* **Hdi** *Heinsenia diervilleoides,* **Mme** *Morus mesozygia,* **Pfu** *Polyscias fulva,* **Sus** *Strychnos usambarensis,* **Tem** *Trichilia emetica,* **Tma** *Trilepisium madagascariense,* **Vno** *Vepris nobilis*) and **BF** Budongo Forest (**Cgo** *Celtis gomphophylla,* **Cmi** *Celtis mildbraedii,* **Cya** *Cynometra alexandri,* **Fel** *Funtumia elastica,* **Kan** *Khaya anthotheca,* **Lmi** *Lasiodiscus mildbraedii,* **Ran** *Rinorea angustifolia*).

6.2.1 Tree growth as related to abiotic factors

A general overview of the annual mean of the absolute and relative growth rates of all trees in relation to abiotic factors for the two study forests is shown in table 6-2. More frequent and more strongly significant correlations between growth and rainfall were found in BF than in KF. The same trend can be observed for correlations between temperature and growth. More frequent and more strongly significant relations were detected between soil parameters and growth in KF than in BF. Throughfall and many soil parameters were not available for BF.

Table 6-2: Comparison of the correlation between mean absolute (Abs) and relative (Rel) circumferential (circ) growth of all study trees and the abiotic factors, throughfall (TF, incident precipitation (IP), mean, maximum and minimum temperature (Tmean, Tmax and Tmin), solar radiation and soil parameters. acetate: soil cations extracted by using ammonium acetate. The values represent Pearson's r with the asterisks giving the level of significance: without: p > 0.05, * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001.

	Kakakmega		**Budongo**	
Abiotic factor	**Abs circ**	**Rel circ**	**Abs circ**	**Rel circ**
Climate				
TF	**0.28***	0.26	-	-
TF2	0.25	0.24	-	-
TF3	0.27	0.26	-	-
IP	0.27	0.25	**0.38***	**0.35***
IP2	0.23	0.22	**0.51****	**0.48****
IP3	0.25	0.24	**0.51****	**0.50****
RD	0.19	0.17	**0.55****	**0.51****
T_{mean}	-0.22	-0.26	-	-
T_{max}	**-0.53***	**-0.54***	**-0.71*****	**-0.69*****
T_{min}	0.13	0.07	**0.34***	0.32
Solar Radiation	-	-	-0.31	-0.5
Soil				
Ca acetate	0.55	0.68	-	-
K acetate	**-0.73***	-0.61	-	-
Mg acetate	-0.07	0.18	-	-
Mn acetate	**-0.68***	**-0.85****	-	-
pH	0.66	0.72*	-0.47	-0.37
EC	0.55	0.60	-	-
N	**0.69***	**0.70***	-0.01	0.03
C	**0.72***	**0.88****	-0.14	-0.06
C/N	0.12	0.47	-0.15	0.13

6.2.2 Species growth comparison

Two of the study species, *Celtis gomphophylla* and *Celtis mildbraedii* occur in both forests. A direct comparison between the mean annual circumferential growth rates was possible after selecting trees of similar DBH size. The trees selected from *Celtis gomphophylla* showed a significant difference in growth, growing at a faster rate in KF than in BF, while trees of *Celtis mildbraedii* did not differ significantly (Table 6-3).

Table 6-3: Direct comparison of mean annual absolute (Abs) circumferential (circ) growth and the DBH for selected trees with comparable DBH from the species *Celtis gomphophylla* in KF (27 individuals) and in BF (12) as well as for *Celtis mildbraedii* in KF (31) and BF (35). The numbers represent the p-values with the asterisks giving the level of significance: without: n.s., * $p \leq 0.05$.

Species	**DBH**	**Abs circ**
Celtis gomphpohylla	n.s. 0.1709	**0.0207***
Celtis mildbraedii	n.s. 0.9693	n.s. 0.5248

6.3 Seedling density as related to abiotic factors

The correlation between seedling density and the values for the abiotic factors is shown in Table 6-4. Throughfall correlates significantly with seedling density in KF. Apart from these no other significant relations were evident in KF. In BF a significant correlation was detected between seedling density and canopy openness.

Table 6-4: Comparison of the correlation between mean seedling density and the abiotic factors, throughfall (TF, incident precipitation (IP), mean, maximum and minimum temperature (Tmean, Tmax and Tmin), solar radiation, soil and site canopy parameters at subplot level. Acetate: soil cations extracted by using ammonium acetate. The values represent Pearson's r with the asterisks giving the level of significance: without: $p > 0.05$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Abiotic factors	**Kakamega**	**Budongo**
Temporal		
Climate		
TF	**0.08***	-
TF2	**0.09***	-
TF3	0.03	-
IP	0.08	0.45
IP3	0.25	0.47
RD	0.41	0.48
Tmax	-	-0.28
Tmin	-	0.27
Spatial		
Soil		
Ca acetate	-0.14	-
K acetate	0.10	-
Mg acetate	0.14	-
Mn acetate	0.06	-
pH	0.07	0.12
EC	-0.16	-
N	-0.07	0.09
C	-0.01	0.04
C/N	0.10	0.02
Canopy		
Canopy openness	-0.04	**0.51****
Understory radiation	-0.02	0.28

7 Discussion

The discussion is structured as follows: section 7.1 presents the influence of different levels of past human disturbance on forest scale (7.1.1) and on the different successional stages, which were created in the forests (7.1.2). In section 7.2 tree succession in the disturbed forest types with regard to the species that occur there along the pioneer-climax continuum (7.2.1), the role of the spatio-temporal climatic variability (7.2.2) and the role of the spatial variability of soil parameters (7.2.3) is discussed. The conclusion of the discussion is presented in section 7.3.

7.1 Influence of human disturbance on the two forests

7.1.1 Tree diversity and growth on forest scale

On a forest scale if the data from all the study sites are considered together, a comprehensive picture can be made of the tree diversity and growth in the two forests after human disturbance. Tree species richness is 91 species ≥ 5 cm DBH found in 0.72 ha in Budongo Forest (BF). This is comparable to the numbers of species found by EGGELING (1947) and SHEIL (2001), but higher than assessed by EILU ET AL. (2004) in the same forest (Table 7-1, p. 123). A list of tree species is given for the forest by SYNNOTT (1985), who provided a full plant species composition including 240 species of trees. The number of 91 tree species ≥ 5 cm DBH in 2.08 ha recorded for Kakamega Forest (KF) is also within the range of other studies on KF. FASHING & GATHUA (2004) found 81 species on nine ha in respect of trees ≥ 15 cm DBH in KF for the two sites BU and IS, while KIRIKA (2007) identified 74 species on six ha in forest types with both low and high levels of disturbance. The species numbers covered at least 80 % of the numbers calculated by using the species estimators in KF and 70 % in BF. The higher estimated numbers of tree species in BF than in KF projected by the respective extrapolation methods (Tables 4-1, p. 47 & 5-1, p. 87) can be explained by the presence of several trees in BF that only occur with one or two individuals, the singletons and doubletons, thus influencing the extrapolation results (CHAO ET AL. 2005). Further the rarefaction curves confirmed higher levels of tree diversity in BF than in KF (Figure 6-1, p. 117). Compared to the number of species found by other researchers, which lie at around 200 or more species (SYNNOTT 1985, MWAVU 2007) the species numbers calculated by the estimators in BF are low, for KF the estimators produced suitable results. The plot design seems well suited to the aim of covering the different types of forest in KF, while in BF some sites like swamp or early secondary parts could not be included. However, most dominant families were found in the plots showing that the plots were representative of the two forests.

The dominant tree families were Moraceae and Euphorbiaceae in KF, while in BF the vegetation in the study plots was dominated by Euphorbiaceae, Meliaceae and Moraceae. Also in another study in BF the most common plant families were the same, but in addition Fabaceae and Rubiaceae were identified as being dominant (MWAVU 2007). The high frequency in both forests of the Moraceae can be explained by the continuing high density of mammals that feed on the figs in particular, which in turn disperse the seeds (Mammides et al. 2008, Plumptre & Reynolds 1994, Kirika 2007). A comparison of the two study forests reveals that several genera and some species are common to both forests. These belong to the guineo-congolese species, an observation which supports the hypothesis that KF and BF were once connected to the forests of the Congo basin (Blackett 1994).

The species numbers and characteristics of both study forests are comparable with those of other lowland and lower montane African forests (Table 7-1, p. 123). In Uganda these are the Bwindi, Kasyoha, Kibale (Eilu et al. 2004) and Mpanga forests (Taylor et al. 2008), the latter being the most species rich per area and Kasyoha having least species per area. Other forests listed are in Nigeria the Omo forest (Okali & Ola-Adams 1987), in Tanzania the East Usambara Mountains (Huang et al. 2003), in Ghana the Kade forest (Swaine et al. 1987a), in Congo the Beni forest and the Okapi Wildlife Reserve (Makana & Thomas 2006), in Cameroon the Korup (Chuyong et al. 2004a) and Bibindi (Van Gemerden et al. 2003) forest and in Equatorial Guinea the Nsork forest (Senterre & Lejoly 2001), of which highest tree species numbers have been recorded in Bibindi on an area of 16 ha. The species numbers documented per area in the study forests were high compared to most African forests, probably owing to the study design, with many small plots scattered all over the forests thus including species from different successional stages, in contrast to most of the studies that use one large plot in an area with more uniform successional conditions.

Furthermore, in KF and BF a number of 57 and 34 tree seedling species respectively were identified, which were with two exceptions in KF offspring of tree species that had been identified in the plots. The species richness of seedlings is within the range of other studies carried out both in KF with 29 species on 540 m^2 (Farwig et al. 2009), 58 on 4 ha (Odhiambo et al. 2004), 64 on 810 m^2 (Kirika 2007) and in studies from BF with 47 species on 540 m^2 (Kirika 2007). This shows that a plot design with subplots scattered over the forest, can cover just as high a number of species as subplots within a few large plots that are set in just a few forest parts. However, if the study area is much larger more species are found, as shown in another study in BF covering 16 ha, in which around 200 tree species ≥ 2 cm DBH from 46 families respectively were recorded (Mwavu & Witkowski 2009a). The level of seedling diversity remained relatively constant during the study period in the subplots in KF (Figure 4-24 p. 79), showing that diversity fluctuation was low.

The mean forest values of BA per hectare in the two study forests are higher than those found in other African forests, even though they include parts with both high and low levels of disturbance (Table 7-1, p. 123). This may however also be connected with the choice of the study plots, which are healthy closed canopy plots without gaps and thus, when extrapolated, overestimate the mean state of the forest, - this is also known as the “majestic effect” (Sheil 1995, Sheil et al. 1995). It was partly possible to rule out this effect as the larger 1 ha plot and its structure were compared to three 400 m^2 plots at the same site. A comparison between the two plot sizes revealed no significant differences in the mean BA (Figure 4-16, p. 66). The tree density (≥ 10 cm DBH) values established in this study

Table 7-1: Comparison of tree diversity and structure of published data of some chosen African forests.

Author	Country	Vegetation	Altitude [m] a.s.l.	Area [ha]	Trees ≥ 10 cm [ha^{-1}]	Species ≥ 10 cm	BA ≥ 10 cm [m^2 ha^{-1}]
Huang et al. (2003)	Tanzania, Usambara Mountains	lowland mixed	1070-1500	0.1	880	33	
Okali & Ola-Adams (1987)	Nigeria, Omo	moist semi evergreen	150	4.05	563	63	
Eggeling (1947)	Uganda, Budongo	late successional lowland mixed (Pl.7)	1000-1100	1.48	472	49	
Sheil (2001)	Uganda, Budongo	late successional lowland mixed (Pl.7)	1000-1100	1.86	584	60	24
Eilu et al. (2004)	Uganda, Budongo	lowland mixed	1000-1100	1	522	32	
Eilu et al. (2004)	Uganda, Bwindi	mixed	1530	1	424	33	
Eilu et al. (2004)	Uganda, Kasyoha	mixed	975- 2100	1	460	28	
Eilu et al. (2004)	Uganda, Kibale	mixed	1100-1600	1	509	32	
Taylor et al. (2008)	Uganda, Mpanga	lowland mixed	1140-1200	0.64	519	47	42
Swaine et al. (1987a)	Ghana, Kade	moist semi-deciduous	180	2	552	45	30.9
Makana & Thomas (2006)	Congo, Beni	moist evergreen	750- 950	0.32	636	20	26.5
Makana & Thomas (2006)	Congo, Okapi Reserve	moist evergreen	750- 950	0.2	427	50	22.6
Chuyong et al. (2004a)	Cameroon, Korup Forest Plot	lowland evergreen	150	1	492	87	26.1
van Gemerden et al. (2003)	Cameroon, Bibindi	lowland evergreen	520	16	522	400	29.7-42.6
Senterre & Lejoly (2001)	Equatorial Guinea, Nsork	lowland evergreen	500-700	1.28	538	149	
Fashing & Gathua (2004)	Kenya, Kakamega	lower montane mixed	1600	1.79	414	64	
own data	Uganda, Budongo	lowland mixed along dist. gradient	1000-1100	0.72 (18 x 0.04 ha)	611	56	29.9-85.6 (mean 53.3)
own data	Kenya, Kakamega	lower montane mixed along dist. gradient	1500-1700	2.08 (27 x 0.04 ha+ 1ha)	388	91	21.2-86.2 (mean 48.9)

of 562 ha^{-1} for KF and 611 ha^{-1} for BF are close to the average of other African forests (Table 7-1, p. 123) where they range from 414 to 880 individuals ha^{-1}. It shows that the plot design, consisting of many scattered 400 m^2 plots, is just as well suited for extrapolating tree densities and partly for BA per hectare, as the methods used in other studies.

Even though disturbances altered the successional stages of the forest, mean annual absolute circumferential growth rates in the intermediate successional parts of the forests were within the range of other tree growth studies on African forests. However, tree growth in a study by LIEBERMAN (1982) reaches values of up to 17.3 mm yr^{-1}, which is highest, while slowest-growing trees were recorded in Ghana (SWAINE ET AL. 1990) and in Nigeria (HOPKINS 1970) (Table 7-2, p. 125). However, the values listed cannot easily be compared, as different types of methods were used and measurement durations and numbers of individuals/species varied. Mean annual relative circumferential growth rates have only been presented for one other African forest, in the study by SWAINE ET AL. 1990, who found slightly higher values compared to the values in this study (Table 7-2, p. 125). Species-specific annual circumferential growth rates ranged from 0.2 (*Blighia unijugata*) to 1.4 cm (*Funtumia africana*) in KF and from 0.2 (*Rinorea angustifolia*) to 1.2 cm (*Cynometra alexandri*) in BF, while relative circumferential growth rates ranged from 0.25 (*Diospyros abyssinica*) to 1.8 % (*Funtumia africana*) in KF and from 0.3 (*Celtis gomphophylla*) to 1.7 % (*Cynometra alexandri*) (Figures 4-4, p.51 & 5-4, p. 91). A comparison of the absolute circumferential growth of single tree individuals showed that intra-specific differences were high, even higher than mean inter-specific differences (Figures 4-9, p. 58 & 5-9 p. 98, Appendix, figure 10-1, p. 175), also confirmed by CLARK & CLARK (1994).

The analysis shows that even though the forest parameters were altered by past human disturbance, on forest scale using the plot design and the growth measurements of this study, the diversity values found are comparable to other studies using other methodologies in forests in Africa. The collection of dendrometer data and the study of seedlings over such a long period of time and and in such detail seems to be unique for African forests, and growth studies on forests at such an altitude on the African continent are generally rare.

7.1.2 Different successional stages

Different levels of past commercial disturbance have led to different stages of succession within the two forests. This secondary succession after commercial disturbances represents a new attempt, striving to regain the original state of the forest community (HORN 1974).

In KF the most severely disturbed site (Commercial disturbance index (CDI): 10) has been recolonized by young successional early pioneer tree species (e.g. *Acacia abyssinica, Harungana madagascariense, Psidium guajava*) after a clearcut around 30 years ago. The tree individuals there contained lowest mean tree stem volume, had highest tree density and highest mortality rates (Figure 4-8, p. 56). In

Table 7-2: Comparison of tree stem increment rates in chosen tropical African forests. DC = Dendrochronolies, RDM = Repeated diameter measurements, precip.=precipitation, individ.= individuals

Author	**Country**	**Method**	**DBH size class [cm]**	**Time period [years]**	**Altitude [m]**	**Precip. [mm yr^{-1}]**	**No. of species**	**No. of indiv.**	**Abs DBH increment [mm yr^{-1}]**	**Rel DBH increment [% yr^{-1}]**
Hopkins 1970	Nigeria	RDM	-	2	150	1232	11	33	0.2-2.29	-
Lowe & Walker 1977	Nigeria	RDM	≥ 5	24	-	-	2	56 / 165	5.3 / 5.7	-
Lieberman 1982	Ghana	dendrometer	≥ 10	1.2	250	1100	12	104	3.1-17.3	-
Swaine et al. 1990	Ghana	RDM/ dendrometer	3.2 / ≥ 10	8/1	290	900-1000	7	645/12	0.58-1.59	0.90-3.54
Sheil 1997	Uganda	RDM	≥ 10	> 60	1000	1640	37	> 2000	1.0-4.0	-
Newberry et al. 2002	Cameroon	RDM	≥ 10	5	150	> 5000	17	732	1.33-3.55	-
Baker et al. 2003	Ghana	dendrometer	≥ 20	2	300 / 250	1288 / 1993	2	20 / 10	1.5 / 5.0	-
Worbes et al. 2003	Cameroon	DC	≥ 10	41-220	600	1900	21	361	2.0-8.1	-
Schöngart et al. 2006	Benin	DC	≥ 10	70-232	120-600	1230	5	102	3.1-6.2	-
Schöngart et al. 2006	Ivory Coast	DC	≥ 10	102-230	300-500	1150	3	89	2.2-4.6	-
own data	Kenya	dendrometer	≥ 10	4.5	1500-1700	1915	18	622	0.6-4.4	0.25-1.58
own data	Uganda	dendrometer	≥ 10	3	1000-1100	1640	7	364	0.6-2.5	0.3-1

contrast the high mean tree volume and low tree density found at the second most disturbed site (CDI: 8) can be explained by the fact that this forest site was replanted some time ago, so that forestry influenced the tree population there. In KF the species with the highest mortality rates were the early pioneers *Harungana madagascariense* and *Combretum molle* in the most disturbed site, where self-thinning is still taking place at short intervals, as also the closeness of the site CA to the estimated self-thinning line proved (Figure 4-8, p. 56). The annual mortality rates of trees (DBH ≥ 5 cm) in KF ranged from 0.7 % to 7 % at the most disturbed site and in BF from 1.1 to 2.1 % (Figures 4-8, p. 56 & 5-7, p. 95). These are comparable to the annual mortality rates recorded in other studies in tropical forests, which lie at around 1 to 2 % (SWAINE ET AL. 1987b) e.g. 1.77 % in Kade, Ghana (SWAINE ET AL. 1987a) and 2 % in Barro Colorado Island Forest (BCI), Panama (CONDIT ET AL. 1995). In general, pioneer and early successional species have a short life span and low wood density, as well as rapid growth rates (e.g. CONDIT ET AL. 1995, MARTINEZ-RAMOS & ALVAREZ-BUYALLA 1998, TURNER 2001). Forest stability, defined as the absence, or inverse of species' turnovers and of population fluctuations, is low in early successional forest types (HORN 1974). Furthermore, highly disturbed parts had more open canopies due to the absence of subcanopy and understorey layers, for instance at the site CA regeneration after clearcuts has only just started (CDI: 10) (MITCHELL & SCHAAB 2008). High levels of disturbance caused by e.g. clearcuts or selective logging, result in open areas allowing the widely dispersed seeds of pioneers to colonize and establish (SOUSA 1984). The tree seedling populations in those forest sites consisted of early-successional species, with late successional species not occurring at all, which shows that it generally takes long for primary forest species to return (BAZZAZ & PICKETT 1980).

In the intermediately selectively logged sites in KF and BF (CDI 6 & 7 respectively, mixed young and old secondary forest) tree sample-based species richness was highest compared to other sites (Figures 4-1, p. 48 & 5-1, p. 88). The impact of disturbance leads to more light reaching the understorey resulting in higher liana (BABWETEERA ET AL. 2000) and pioneer tree abundance (SCHNITZER & CARSON 2001, WRIGHT 2002). However, a mixture was found consisting of invader pioneer and early secondary successional species (e.g. in KF *Polyscias fulva, Albizia gummifera, Funtumia africana*; in BF: e.g. *Alstonia boonei, Chrysophyllum spp.*) and regenerating remaining mid-successional and climax tree species (in KF e.g. *Diospyros abyssinica, Olea capensis, Strychnos usambarensis;* in BF: e.g. *Rinorea angustifolia, Lasiodiscus mildbraedii, Celtis mildbraedii, Cynometra alexandri*) and therefore showing a temporal mass effect of species richness (PALMER 1994), while other selectively logged species like e.g. *Entandrophragma spp.* in KF may have been almost completely removed up until the late 1970s. In BF, tree volume decreased in sites with increasing values of CDI (Figure 5-7, p. 95). Tree stem volume is higher in the intermediately disturbed than in the undisturbed forest parts in KF especially at the site IS (Figure 4-8, p. 56). As the particular site IS also had low species numbers, it could mean that past human disturbance may not have been as strong as would have been expected on the grounds of the CDI. In the other sites it could be due to higher productivity caused by the environmental patchiness at those sites (DAY ET AL. 2003). Also the occurrence of superabundant shrubs in the understorey such as *Dracaena fragrans* (Dracaenaceae) in BU and CO and *Brillantaisia nitens* (Acanthaceae) in IS could have played a role. It seems they invaded as an indirect result of commercial disturbance. In particular they have had a highly negative impact on tree seedling regeneration (personal observation, FASHING & GATHUA 2004, STRUHSAKER 1997). But if regeneration is hindered, then this prevents the emergence of the small trees that would normally have been expected so that the large trees are not exposed to as much competition for resources leading to higher stem volume of a site (e.g. IS). Mortality rates at forest sites that had experienced intermediate disturbance in both forests were quite high between 2 % and 3 % annually, and can be explained by the natural death of large trees at the respective sites and tree removal by illegal loggers and firewood collectors especially in KF, resulting in the reduction of BA-increment at some sites. Low mortality rates at other sites could also be attributable to the majestic effect, which means that in plots specifically chosen for their location in naturally gapless forest areas, trees are more healthy and not likely to have high mortality rates (CONDIT 1997, SHEIL & MAY 1996, LEWIS ET AL. 2004a). In the seedling populations in these stages of succession no early pioneers were found, instead mostly seedlings of the secondary and late climax type of species.

Commercially undisturbed parts (CDI: 0) in both forests had low species numbers (Tables 4-7, p. 64 & 5-7, p. 100), in N15 in BF even a monodominance of *Cynometra alexandri* was observed. In KF study plots contain late climax species like *Celtis mildbraedii* and *Trichilia emetica* and in BF ironwood (*Cynometra alexandri*) and mahogany species (*Entandrophragma spp., Khaya spp.*). Highest tree stem volume was found in the least disturbed site, the nature reserve N15 (CDI: 0) (Figure 5-7, p. 95), showing that the self-thinning of the tree populations had taken place (SILVERTOWN 1987) and confirming the assumption that maximum biomass culminates in the mature stages of a stabilized ecosystem (ODUM 1969). This is in line with another study from BF, in which the nature reserve N15 was found to have the highest BA values of all other forest compartments (PLUMPTRE 1996). Surprisingly other undisturbed parts in both forests did not display the highest stem volume, probably either due to unrecorded illegal logging activities which have taken place there, thus giving rise to the comparatively low tree volume and high tree density today in YA in KF and W36 in BF or to a drier environment as is the case in KP11 in BF. Also in the analysis of β-diversity KP11 differed very much from the other sites in BF (Figure 5-2, p. 89). In another source it was suggested that KP11 may have been colonized more recently and would thus be at a younger stage (NANGENDO ET AL. 2006) than the nature reserves N15 and W36, which would explain the lower tree stem volume found there today. The values for tree volume in the two nature reserves in BF, excluding KP11 were higher than values for volume and tree density in the undisturbed sites in KF (Table 6-1, p. 117). Only a few tree deaths were recorded over the study period in the least disturbed sites in the two forests, showing that the primary forests are relatively stable, as they are protected from perturbations (ODUM 1969). The tree mortality rates in the low disturbed KI (CDI: 2) can be explained by a recent increase in local disturbance e.g. tree cutting of small trees and fuel wood collection in the plots (personal observation). In BF the least disturbed sites (KP11 & N15) had significantly more open canopies than the other sites (Figure 5-14, p. 102), because there the understorey vegetation was not very dense. By contrast, the significantly lower canopy openness of the least disturbed parts in KF (YA & KI) can be explained by high dense layers of subcanopy and understorey vegetation, further supporting the assumption that these parts, although they have not been commercially logged, must at some time have experienced disturbance e.g. illegal logging or pitsawying that created gaps large enough to allow young primary species to regenerate.

Also a significantly positive relation between canopy openness and tree seedling density was found in BF at seedling subplot level (Table 5-18, p. 115), which was to be expected as more open areas and tree fall gaps generally contain more seedlings (HUBBELL ET AL. 1999), but not in KF (Table 4-20, p. 86). The higher stem densities in gaps generally also lead to an increase in sapling diversity, although on a per stem basis there is no difference between gap and non-gap areas (HUBBELL ET AL. 1999, BROKAW & BUSING 2000). There was a significantly positive correlation in all cases between seedling density and the three diversity indices (Tables 4-15, p. 78 & 5-14, p. 110), in KF this was significantly positive in respect of two of the indices, in BF the correlation with all three indices was highly positive. A positive density-dependence on seedling diversity is often observed, as was also found by HARMS ET AL. (2000), VOLKOV ET AL. (2005) and PAINE & HARMS (2009). In the undisturbed forest sites, seedling populations consisted of late-climax species with some invasive early climax species. Certain species like *Entandrophragma cylindricum* were only observed here as seedlings. This is attributable to the limited seed dispersal distances of the tree species and thus the dispersion of adult trees in the plots, which can result in a patchy seed distribution (HUBBELL ET AL. 1999, MULLER-LANDAU ET AL. 2002) and thus in a patchy seedling establishment, although it has also been shown that the habitat of a tree does not commonly coincide with the habitat requirements and occurrence of seedlings (COMITA ET AL. 2007).

The relation between tree diversity and the level of past commercial disturbance in KF and in BF described by the CDI resulted in a humpbacked distribution (Figures 4-1, p. 48 & 5-1, p. 88), as species diversity was lowest in the least as well as in the most commercially disturbed sites and highest in the sites rated with intermediate disturbance. Also the analyses of β-diversity indicates that the level of disturbance influences the distribution of diversity. As some soil and light factors and the CDI all correlated with the first dimension (Appendix, tables 10-4, p. 174 & 10-10, p. 180), this allows the interpretation that the environmental factors change according to the level of disturbance, as demonstrated by the example of the canopy parameters (Figure 4-17, p. 67). Further the analyses of β-diversity in both forests showed that differences in the NESS-Index at each site in both forests along the other dimension could be interpreted as the geographical distribution of species (Figures 4-2, p. 49 & 5-2, p. 89). This possible geographical diversity gradient can be attributed to local climatic gradients caused by the proximity to Lake Victoria in KF and to Lake Albert in BF.

Different intensities of past commercial disturbance gave rise to a variety of environmental and successional patches caused by human interference without allowing natural competitive exclusion. The findings gained from data collected in KF and partly from BF offer convincing evidence in support of one diversity hypothesis, the intermediate disturbance hypothesis (IDH) (CONNELL 1978), which states that the highest diversity of tropical rain forest trees should occur either at an intermediate stage in succession after a large disturbance or with smaller disturbances that are neither very frequent or infrequent; either represents an open non-equilibrium. However it has been hotly debated, with some researchers either claiming that local richness is a temporary successional property maintained by disturbance (CONNELL 1978) or that monodominance in tropical forests exists because large disturbances have not occurred for a long time (HART ET AL. 1989) resulting in a vegetation dominated by competitively dominant monopolists (HORN 1974), while others argue that s higher level of species richness of this kind is characteristic of late-successional equilibrium communities (PHILLIPS 1997).

The IDH is only one of several diversity theories and has its weaknesses (PALMER 1994, WRIGHT 2002), for instance a re-evaluation of Eggeling's plots after 54 years showed that plots that had originally been more severely disturbed maintained high diversity, but also that originally undisturbed plots increased in diversity (SHEIL 2001) and were not stable and thus not protected from species invasions (ODUM 1969). This implies that other environmental influences play a role in creating diversity. The IDH therefore has its limits, but it provides one good explanation for the species distribution and composition at the study sites. In a study on the north-eastern part of Budongo Forest, Uganda a successional gradient, in this case due to fire disturbance by humans, was analysed and a similar result emerged (NANGENDO ET AL. 2006). Areas with the lowest disturbance levels and those with the highest were here also found to contain the lowest number of species (NANGENDO ET AL. 2006), also higher past human disturbance led to higher diversity there (MWAVU 2007). The IDH has been successfully applied to other tropical forests that have been disturbed by human logging (MOLINO & SABATIER 2001, CANNON ET AL. 1998, SHEA ET AL. 2004)

The increase in the diversity at intermediate levels of disturbance does not however imply that human disturbance has in general resulted in positive effects. A comprehensive insight into all the effects of disturbance on vegetation, species richness and diversity cannot be gained unless other parameters such as the respective species composition and stand structure are taken into consideration. Human disturbance in tropical forests always has a degrading effect on highly evolved ecosystems. The loss of species, especially climax species, may occur under all human disturbance scenarios, even at low levels. In subsequent and continuative studies on the relation between disturbance and diversity intensity, duration and frequency of disturbance events should be considered as well, as also suggested by SHEA ET AL. (2004). The analysis of the quality of disturbance and the consequences for the ecosystem can provide important knowledge for forest management in terms of restoration and enrichment planting in the respectively differently disturbed forest parts.

7.2 Tree succession in disturbed forest sites

7.2.1 The pioneer-climax continuum

The species that were identified in the forest, especially in the intermediate stage of succession covered the whole range of the continuum from pioneer to climax species. The identified early-, mid- and late-successional tree species at the intermediate stages of succession have many contrasting attributes. Below some examples of the study tree species are given.

In KF the species *Polyscias fulva* is a typical pioneer or early successional species, which probably invaded the intermediately disturbed forest parts, when light gaps were available in the past. It grew fast as mature tree both absolutely and relatively, had a low wood density (Braun 2010) and did not reach a high age. But when adequately large gaps were no longer available, it suffered high adult mortality rates due to intense competition, and hardly any or no seedlings were found to be regenerating in the forest understorey. It also showed signs of seasonal growth (Appendix figure 10-2, p. 175), although no strong relations to climate were established. Further it grew faster the larger the tree was (Figures 4-10, p. 59 & 4-12, p. 62), indicating that the tree depends on light availability as it grows. It also minimizes its energy investment by a simple branching system (personal observation), which is characteristic of early successional species (Timm et al. 2004) The pioneer characteristic can also be confirmed by its production of many tiny seeds (Omondi et al. 2004). The high mortality rates of this species during the study period in the intermediately disturbed sites indicate that it cannot compete with other species unless light is available. Apart from *Polyscias fulva* other pioneers did not occur in this frequency at the study sites, as they have possibly already been displaced.

Other common species in the intermediately disturbed sites are late pioneers or early climax species. These are species like *Croton megalocarpus*, *Trilepisium madagascariense, Antiaris toxicaria, Funtumia africana*, *Morus mesozygia, Prunus africana* in KF and *Khaya anthotheca* in BF which grew as fast as the early pioneers (Figure 6-2, p. 118, Appendix figures 10-2, p. 175 & 10-3, p. 176), had a relatively short estimated life span and low seedling survival rate in the understorey. In the intermediately disturbed parts they grew slowly in the understorey and much faster in the subcanopy/canopy level, emphasising their light-demanding nature (Figures 4-12, p. 62, 4-13, p. 63, 5-10, p. 99 & 5-11, p. 99). This shows that the species are light-demanding, as they invest a large amount of energy in growth when light is available, as also supported by other studies (Worbes et al. 2003, King et al. 2005, King et al. 2006). They further however possess larger seeds (Omondi et al. 2004) than early pioneers, and seedlings of *Trilepisium madagascariense* were produced in such strong recurring cycles of recruitment (Table 4-16, p. 80) that some were still able to endure in the understorey despite the high mortality rates that were probably caused by predator satiation. For other species this was not the case e.g. for *Croton megalocarpus* and *Prunus africana*. The species *Antiaris toxicaria* was also fast-growing, but estimated tree age was higher than the above-mentioned species. Furthermore, seedling establishment and survival was high for this species (Tables 4-16, p. 80, 4-17, p. 81 & 4-21,

p. 86). This shows that some fast-growing trees displayed both the characteristics of light-demanding and shade-tolerant late successional species as they matured. These could be grouped as species that become established under the closed forest canopy but need a gap to mature.

Species that had intermediate growth rates and estimated life spans varying from around 160 to 320 years were *Markhamia lutea, Ficus sur, Morus mesozygia, Celtis gomphophylla, Celtis africana, Trichilia emetica* and *Ficus exasperata* in KF (Table 4-4, p. 55). Most of them grew faster with increasing tree size (Figures 4-12, p. 62 & 4-13, p. 63), but although their seedlings were found, they were not very common. They can be rated as mid-successional species, although it is difficult to allocate them to one distinct category as some of the species appeared to be moderately shade-tolerant whereas others were more shade-tolerant thus approaching the late climax species (Appendix, table, p. 182 10-13). In particular many of these species showed positive relations to the rainfall seasonality.

Late climax trees encompasses species such as *Blighia unijugata*, *Celtis mildbraedii, Diospyros abyssinica*, *Strychnos usambarensis* in KF and *Funtumia elastica* and *Celtis mildbraedii* in BF, which can be clearly categorized as shade-tolerant. They grew constantly at slow rates (Figures 4-12, p. 62, 4-13, p. 63, 5-10, p. 99 & 5-11, p. 99), reached ages of more than 300 years (Tables 4-4, p. 55 & 5-4, p. 94), suffered hardly any losses of mature trees during the study period and had relatively high wood density (BRAUN 2010). Further they produce large seeds (OMONDI ET AL. 2004) and most were well established as seedlings in the understorey (Table 4-16, p. 80). Although the survival rates of the seedlings were low, high densities of established seedlings still occurred. In particular, *Strychnos usambarensis* showed slight seasonal stem growth (Figure 6-2, p. 118, Appendix figures 10-2, p. 175 & 10-3, p. 176), a relation to climatic factors, but no strong relation to the tree size, showing that the trees do not need a lot of light. Also its seedling density was influenced by climate seasonality. The seedlings of some of these species showed density-dependent mortality, but were generally well established in the understorey (Tables 4-16, p. 80, 4-17, p. 81 & 4-21, p. 86).

Other late-climax species are the typical understorey species *Vepris nobilis* and *Heinsenia diervilleoides* in KF and *Lasiodiscus mildbraedii* and *Rinorea angustifolia* in BF, which grew fairly slowly (Figure 6-2, p. 118), had a high wood density (BRAUN 2010) and only reached an estimated age of around 100 years (Tables 4-4, p. 55 & 5-4, p. 94). Further the low seedling mortality of *Vepris nobilis* and the constant size of the seedling populations underlined their shade-tolerant characteristics (Tables 4-16, p. 80, 4-21, p.86, 5-15, p. 111 & 5-19, p. 116). No strong relations between growth and DBH size were established (Figures 4-10, p. 59 & 5-9, p. 98). In BF the strong climate seasonality influences the growth of understorey species (Tables 5-8, p. 103, 5-9, p. 104, 5-10, p.105 & 5-11, p. 106). Seedling survival was high, and the seedlings are also widely distributed within the forest as shown for the two species from BF (MWAVU 2007). The short life span and thus high mortality rate of understorey species could be ascribed to their low adult stature, as these trees have less access to light (POORTER ET AL. 2008). As the slowest-growing individuals of a species usually have the highest mortality rates (O'Brien et al. 1995, Swaine et al. 1987b, Swaine 1989) and tree growth possesses a strong autocorrelation, fast-growing trees are obviously at an advantage. Amongst the adult trees of a species there will therefore always be a large number of trees that have grown quickly with above-average increment rates and have thus reached maturity in a relatively short period of time.

Cynometra alexandri, the naturally monodominant late-successional species in BF, is also common and widespread in the intermediate stages of the succession in many parts of BF (Mwavu 2007). It grew constantly at fast rates (Figure 5-9, p. 98), but was shade-tolerant and has high wood density (Kityo & Plumptre 1997, Braun 2010). The estimated age was high at around 300 years (Table 5-4, p. 94). Further the growth rate of this species declined in larger trees probably as an effect of senescence (Table 5-9, p. 104). *Cynometra alexandri* had a well established constant population of seedlings in the forest understorey (Table 5-19, p. 116) and medium-sized seeds and is wide-spread as sapling in the forest (Mwavu 2007). Further the species does not shed its leaves during the dry season (Mwavu 2007). All these characteristics contribute to the monodominant position of this species in climax forest parts in BF.

The relative annual growth increment per DBH of each tree species showed that there were hardly any differences in the growth rates of the trees in the different size classes, but rather a decrease with increasing size class (Figures 4-10, p. 59, 4-11, p. 60 & 5-9, p. 98), which indicates that with increasing DBH and thus age, trees reduce their relative growth. The patterns in the DBH size classes show that the use of absolute growth rates alone can lead to misinterpretations of growth patterns, as a decrease in growth rate sometimes only becomes apparent if the relative growth rates are taken into account. There is surprisingly little data on relative growth, although this appears to explain some ecological processes better than absolute growth (Chao et al. 2008, Bigler et al. 2004).

Changes in the successional stage and thus the species composition can take a long time. It is estimated that short-lived pioneers remain for 10-30 years, succeeded by long-lived pioneers reaching ages between 75 and 150 years and then finally followed by the climax species (Finegan 1996). The age values calculated in this study for the different tree species lie between 78 for the long-lived pioneer *Funtumia africana* and 356 years for the late climax species *Diospyros abyssinica* in KF and between 167 for the long-lived pioneer *Khaya anthotheca* and 678 years for the early climax species *Celtis mildbraedii* in BF (Tables 4-4, p. 55 & 5-4, p. 94). This shows that the climax vegetation after destruction by disturbance will take centuries to recover. In other studies the mean projected life span assessed using repeated diameter measurements, was 230 years in La Selva in Costa Rica for all tree individuals (Clark & Clark 1992) or maximum tree ages of 442 years and 529 years for two species in Ecuador (Korning & Balslev 1994). Worbes & Junk (1999) and Martinez-Ramos & Alvarez-Buballa (1998) also found values between 400 to 600 years. Condit et al. (1995) used a hypothetical model based on mortality rates and calculated tree ages as old as 2000 years in the tropical rain forests. In a tree ring based study in Cameroon tree maximum ages ranged from 60 to 220 years with the age class representing most trees being between 41 and 60 years (Worbes et al. 2003). In another study in Benin and Ivory Coast the maximum ages of trees estimated by tree ring analysis ranged from 146 to 368 years (SCHÖNGART ET AL. 2006). The age calculated in this study can only be a rough estimation compared to tree ring analyses and radiocarbon dating, because the relatively short study period could only cover the growth rates of a small part of the life span of a trees. The advantage of such analysis is that it is non-destructive, easy to perform and gives first estimations.

7.2.2 Role of the temporal variability of climatic factors

The different types of successional tree species responded specifically to climatic factors in the two forests, thus influencing the successional balance and competition potential of the species. As most tree populations in the sites have not yet reached the estimated self-thinning lines in both forests, it shows that tree productivity is determined by other factors (Figure 4-8, p. 56, 5-7, p. 95). An attempt was therefore made to assess the temporal effect of climate variability on the growth rates of the tree species, as this variability changes the inherent competition potential of the different species. Many species showed seasonal growth (Figures 4-21, p. 72 & 5-20, p. 107) and positive relations to rainfall, showing that rainfall is limiting growth for many species, especially during the dry season, while for others these effects were weaker. In most cases the weak positive relations in KF (Tables 4-8, p. 69 & 4-9, p. 70) were found for species at the mid to late successional stages. In general, early successional species are better adapted to low soil water conditions (BAZZAZ 1979). In BF rainfall seasonality affected all the investigated species (Tables 5-8, p. 103 & 5-9, p. 104), including the early and late successional. Water availability is however higher in KF and the trees with lower water availability in BF are more affected by the rainfall seasonality. The water conditions that plants experience as drought can vary greatly and are species-specific (e.g. HOPKINS 1970, ENQUIST & LEFFLER 2001, FICHTLER ET AL. 2003, NATH ET AL. 2006), depending on temperature, humidity, and the availability of water in the soil, as well as on intrinsic factors such as the extent and depth of the root system of tree species (VAN SCHAIK ET AL. 1993, HUTYRA ET AL. 2007). Water availability depends on the level of the ground water table, which seems to be low in KF being as deep as 15 m (MUSILA 2007). In general, also tree mortality rates increases with the severity of dry periods (CHAZDON ET AL. 2005) at critical thresholds of plant-available soil water (LWANGA 2003, NEPSTAD ET AL. 2007).

The most and strongest correlations of the trees with rainfall parameters were found between growth and the number of rainy days in a month (RD) and the summed rainfall of both incident precipitation and canopy throughfall for 2 and 3 months. The availability of water for the trees, which is reflected in the soil water potential (BAKER ET AL. 2003) determines growth rates of trees in drier periods and decreases in periods of 2 and 3 months with low rainfall. This matches the usual length of the dry season in the two forests, defined as months with an average rainfall below 100 mm, and the relation found in this study may well be a response of tree growth to dry season length (see Sections 2.1.3 & 2.2.3). The parameter RD was a better predictor of growth than the sum of rainfall in a month showing that more small rain events rather than the total monthly amount of rain in few heavy events maintain a higher level of soil moisture over a longer period (Knapp et al. 2008). Also in a study carried out in La Selva, Costa Rica by Clark et al. (2009), rainfall in the dry season and the sum of two months of rainfall prior to the measurement was significantly related to tree growth.

Trees of two species were the subject of dendrometer analysis in both forests (Table 6-4, p. 120). The faster growth of *Celtis gomphophylla* in KF as compared to BF may be explained by the higher water availability in KF, as the species' growth showed positive correlations with rainfall. This relation was not so strong in trees of *Celtis mildbraedii* so that its growth rates did not differ significantly between the two forests, as its growth is not so much water limited. This indicates that competition potential can shift depending on the forest environment.

The throughfall distribution on subplot scale, which is highly variable in KF and BF (Todt unpublished data), affected the seedling distribution by creating niches and thus also affected the distribution of seedlings and the early stages of a tree's life. Further, in BF seedlings had highest mortality rates in the first annual quarter (Figure 5-22 & 5-23, p. 114), the dry season, which was also confirmed by Lieberman & Li (1992). In KF over the six-year study period seedling regeneration was shaped by recruitment pulses of only a few species (Figures 4-26, p. 84 & 4-27, p. 85), often occurring in the second quarter of the year and coinciding with the wet season. These recruitment pulses were a major cause of the variability in seedling densities and diversity across the forest understorey (Norden et al. 2007). They are most intense but also most variable in the wet season (Lieberman & Li 1992). A weakly positive trend was found between throughfall and seedling density. This is consistent with the finding that artificial irrigation during the dry season enhances seedling growth, survival, stem density and diversity of young seedlings (Paine et al. 2009), which has also been documented in seedling irrigation experiments (Bongers et al. 1999). The strength of the response of seedling parameters to rainfall was also species-specific with most and strongest significant relations found for the recruitment of late-successional species.

Moreover the strength of the reaction of trees to monthly temperature variation was species-specific and more variable than the relation to rainfall. For instance the correlation coefficient for mean temperature and growth ranged from $r = -0.6$ to approximately $r = 0.3$ in KF (Table 4-10, p. 71). But in this case the pattern could not be assigned to a specific functional group in KF, while in BF all species apart from *Khaya anthotheca* showed a negative response to maximum temperature (Table 5-10, p. 105 & 5-11, p. 106). This can mean that temperatures in BF are too high for all species, while in the cooler KF this is not the case. The significantly negative effect of the maximum temperature and solar radiation on tree growth interrelates to reduced water availability in the dry season. The negative effect on growth under the influence of maximum temperatures could be explained by a reduction in the photosynthetic rate at leaf temperatures above 30 °C (Clark 2004, Lloyd & Farquhar 2008) affecting the topmost and most productive leaf layer of canopy trees (Doughty & Goulden 2008). The negative effect on tree growth resulting from maximum temperatures was more exposed in BF than in KF, further indicating that in BF tree growth is more often negatively affected by the more severe dry season there. The slightly positive effect of the minimum temperature as well as the negative effects of the maximum temperature reflect the sensibility of trees to deviations from the growth optimum temperature.

Although growth variability is seasonal and variable both inter- and intra-specifically the majority of single tree individuals grew at a fairly constant rate over a long period of time, as shown by the high correlations between increments of following years (Tables 4-2, p. 52 & 5-2, p. 91). Such temporal autocorrelations of absolute growth rates have been described in several studies (CONDIT ET AL. 1995, SWAINE ET AL. 1987A, SWAINE 1989). The highest variations in annual increment between individuals of a species were found in lower DBH sizes (Figures 4-9, p. 58, 5-8, p. 97 & Appendix, figure 10-1, p. 175). This could be the result of a stronger reaction of younger trees to the availability of abiotic factors e.g. light and water. For trees from larger DBH classes the intra-specific variation in annual increment rates was not as high, because those trees probably already occupy a stable position in the canopy and their root area is well established so that they are thus more tolerant to stress (FELFILI 1995, PELISSIER & PASCAL 2000). It means that the respective individuals are provided with a more or less stable amount of the required resources and often remain in a similar competition situation lasting several years (BRIENEN ET AL. 2006).The presence of a larger root system and canopy improves the availability of the resources required by the tree and enhances tolerance towards stress situations, for instance by covering larger areas the roots extend across more spatial soil and water niches.

The seasonality of the climate was also reflected in the species-specific phenological characteristics of the trees in the two study forests (Figures 4-6, p. 53, 4-7, p. 54 & 5-6, p. 93 and Appendix 10-2, p. 176 & 10-3, p. 181). Again most of the fast-growing early successional tree species in KF had annual recurring seasonal phenology, with flowering activities in the dry and fruiting in the wet season. In BF such seasonal trends were not very obvious apart from *Celtis gomphophylla*. The leaflessness observed in some individuals in the dry season (Tables 4-11, p. 54 & 5-12, p. 108) in seasonal tropical forests is a mechanism of drought avoidance, as explained by the water-limitation hypothesis (BORCHERT 1991, FETCHER ET AL. 1994, VAN SCHAIK ET AL. 1993, WRIGHT & VAN SCHAIK 1994). In wet tropical forests the production of new leaves is also a way of maximizing light capture. Since new young leaves have greater photosynthetic assimilation rates than older leaves, photosynthesis is maximized during the sunny season, explained by the insolation-limitation hypothesis (VAN SCHAIK ET AL. 1993, WRIGHT & VAN SCHAIK 1994, O'BRIEN ET AL. 2008). As the two study forests are situated near the equator and seasonally water limited, it is assumed that for most of the tree species water availability and thus drought avoidance is the main factor influencing the leaf shedding.

The positive relation between fruiting and rainfall in KF (Table 4-11, p. 74) shows that in general tree species can be attributed to drought-sensitivity (e.g. FRANKIE ET AL. 1974, REICH & BORCHERT 1984, ZIMMERMAN ET AL. 2007), as the timing of seedfall and germination allows seedlings to become well-established (e.g. ENGELBRECHT ET AL. 2007, ZIMMERMAN ET AL. 2007) before the onset of the next dry season. However, few species showed fruiting during the dry season, which is characteristic of drought-tolerant species and can be explained by a deeper rooting system of the respective species (Wright & van Schaik 1994). Indirectly the positive correlation between fruiting and rainfall in KF (Tables 4-11, p. 74 & 5-12, p. 108) may also reflect an adaptation of tree species to the seasonality of seed dispersers (Lieberman 1982, van Schaik et al. 1993). The inter-annual variation in phenological characteristics was high amongst the studied tree species (Figures 4-6, p. 53, 4-7, p. 54 & 5-6, p. 93 and Appendix 10-2, p. 176 & 10-3, p. 181), also found by Tweheyo & Babweteera (2007). Long-term changes of phenological dynamics were found in a long-term study in Kibale, a Ugandan forest, and were attributed to climatic changes resulting in an increase in fruiting activity over the past 12 years (Chapman et al. 2005). Such changes in the phenology of trees have also been observed in another tropical rain forest over a period of 18 years in connection with an increase of El Niño events during the study period (Wright & Calderon 2006). The climatic variability affects not only growth species-specifically, but also other phenological tree activities that indirectly influence growth and thus the competition potential of the species.

7.2.3 Role of the spatial variability of soil parameters

Apart from the climatic factors the soil parameters can also create patches that may allow certain tree species to compete better than others as succession proceeds. The spatial effect of the soil parameters on the tree growth and the regeneration of the tree species was therefore assessed. The soil parameters did not show strong relations to tree growth on plot and site scale in BF and only few significant relations to growth in KF (Tables 4-12, p. 75 & 5-13, p. 109). On plot scale the relative growth rates correlated more often and more strongly with the soil parameters than did the mean absolute growth rates per plot (Tables 4-12, p. 75 & 5-13, p. 109). The positive correlations between tree growth and total acid and acetate extractable Ca of the soil can be explained by the low concentrations of Ca occurring in the soils of Kakamega (Musila 2007), which means that tree growth might be limited by Ca. However, the acetate-extractable Ca being more closely related to plant nutrient availability, showed a weaker correlation to tree growth, which cannot be explained. But the distribution of plant species can be better attributed to the acid than to the salt extractable fraction of the soil in some situations (Vitousek & Sanford 1986). There were also significantly negative correlations or trends between growth rates and nitric acid extractable Mg and Mn as well as the ammonium acetate extractable K and Mn on plot scale, which are also unexplainable. Also there were some significant relations between the weighted soil parameters and the growth rates of individual trees in KF (Tables 4-13, p. 76 & 4-14, p. 77). Even though the strength of the relations was species-specific and means that tree species adapt differently to soil nutrient availability, clear trends could not be ascertained.

Positive relations between growth and soil parameters mean that trees react to fertile soils with an increase in growth, because a soil component might be limiting their growth. The negative relations between growth and soil nutrients could imply that the nutrients for the respective trees are available in excess and may be toxic in too high concentrations. A positive relation between nitrogen (N) and growth in KF is consistent with the results of other studies. N limits tropical tree growth in montane environments (Tanner et al. 1990, Tanner et al. 1992), where the proportion of the total N in the soil is higher than that found in the above-ground biomass (Edwards & Grubb 1982) and N is limited by low rates of mineralization (Tanner 1977). N-deficiency has further been identified as limiting growth on soils of organic origin in Hawaii (Vitousek et al. 1993), but most tropical forests are not likely to be nitrogen-limited (Tanner et al. 1998), which also seems to be the case for BF. The strong relations between species diversity and the C and N content in the soil in KF may be due to the following reasons: low disturbance of a forest site can lead to an accumulation of C in forest soils (Zhou et al. 2006) which could explain why the sites with low diversity and high disturbance have low C content in their soil. However, in mathematical models higher biodiversity was shown to lead to higher nutrient retention in the ecosystem caused by reduced nutrient losses due to inter-specific differences in resource use (Tilman et al. 1997), which contradicts the findings that higher diversity occurs on soils containing higher levels of N.

The positive correlation between seedling diversity and acid-extracted soil Ca on subplot scale (Table 4-15, p. 78) could be explained by the assumed Ca limitation of the KF soils (Musila 2007, Gliniars 2004), suggesting that a higher Ca availability produces more favourable conditions in terms of niches for more species. Positive relation was identified in respect of soil fertility and diversity have also been found in another study (Norden et al. 2007). Contrarily, an extensive study in BF revealed that less fertile soils contained higher seedling diversity (Mwavu & Witkowski 2009a) in accordance with Huston's (1979) general hypothesis that species diversity is highest under conditions of low-nutrient availability. This could not however be confirmed by the correlations between soil parameters and the values of the three diversity indices in this study. Moreover in a study by Bahati (2005), who investigated the regeneration of seedlings of mahogany species (*Entandrophragma spp.* and *Khaya spp.*) in BF, a positive effect on regeneration was found in the more fertile and less disturbed sites. According to Mwavu (2007) the soil factor that best describes seedling distribution was titanium. In KF a significantly negative correlation between seedling distribution and the spatial distribution of the soil EC and a positive correlation with the acid extractable K were also established at plot and site level (Table 4-20, p. 86). EC is influenced by many chemical soil components and is also a function of some physical soil properties (Corwin et al. 2003), it is therefore not possible to come to a clear conclusion on which are the most decisive parameters for this relationship. The positive relation established with K can mean that seedling density and thus establishment can be enhanced by more K in the soil.

The finding that some tree seedling species were generally common throughout the forest, whereas others were by comparison restricted through specialisation to certain habitats (Tables 4-16, p. 80 & 5-15, p. 111) can be attributed to the distribution of the mature trees, but further it may imply that for instance the movement pattern of seed dispersers (e.g. mammals, insects and birds) contributes to the variability (Fragoso 1997), there may be temporal fluctuation in seed dispersal e.g. depending on the population dynamics of the dispersers (Kirika 2007), or other factors like the high temporal and spatial variability of arbuscular mycorrhizas can influence seedling recruitment in tropical forests (HUSBAND ET AL. 2002, HART ET AL. 2003) e.g. by altering soil niches (SILVERTOWN 2004). In many other studies seedling populations are found to undergo long-term changes in abundance in the course of time, mainly as a result of inter-annual fluctuations in recruitment rather than of high mortality rates (e.g. CONNELL & GREEN 2000, DELISSIO ET AL. 2002, NORDEN ET AL. 2007, METZ ET AL. 2008). Also seedlings of *Prunus africana, Funtumia africana* and *Uvariopsis congensis* in KF as well as of *Entandrophragma cylindricum* and *Uvariopsis congensi*s in BF were found clumped in high densities (Tables 4-16, p. 80 & 5-15, p. 111) often near conspecific mature trees (personal observation). The low survival rates can therefore mean that self-thinning by pest pressure caused by e.g. phytophagous insects on *Prunus africana* (ODHIAMBO ET AL. 2004), mammals or damping-off diseases near the parent trees might have had a strong effect on seedling survival. This pest pressure hypothesis has been examined in several studies and is one explanation for high tree diversity in the tropical forests (e.g. JANZEN 1970, CONNELL 1971, HARMS ET AL. 2000, VOLKOV ET AL. 2005). For the species that still had numerically high rates of survival in spite of having high mortality rates, the predator satiation hypothesis could be valid (KITAJIMA 2007), which implies that if enough seedlings are present in an area their predators will not be able to completely extinguish the population, as at some point the predator is satiated. Species-specific differences in population dynamics may be explained by spatial differences in seed production (AUGSPURGER 1983, DE STEVEN & WRIGHT 2002), as fruiting did not occur every year in all trees. Mast-fruiting events can lead to high recruitment events, as observed in other studies (HART 1995) and may well depend on climatic factors, but also on internal tree processes (NEWBERRY ET AL. 2006a).

Stem growth rates and seedling density of the year closest to the soil sampling date in KF related better to the soil parameters than growth rates of years with greater temporal distance or than mean annual growth values over a longer period (Table 4-12, p. 75 & 4-20, p. 86). This indicates that there is a temporal variability of soil parameters, which could be the subject of further investigation. Of course the quantity and quality of the relations depend on the scale of the investigation.

One reason why the soil parameters did not relate more strongly to tree growth and seedling parameters in BF can be attributed to the fact that the soil there is relatively fertile (HOWARD 1991) and thus not deficient. Furthermore, altogether the few and weak relations in both study forests can be explained on the one hand by the fact that the soil does not vary enough to reveal clear effects and on the other hand by the fact that the root system of trees may span a wide unknown area covering many different soil niches (WILSON 2000), so that a mean tree or plot value may not provide a satisfactory description of the soil parameters affecting a tree, especially in the case of trees that grow close to the plot boundary. Also temporal heterogeneity, the influence of microbes and mycorrhizas make the system soil very complex (FITTER ET AL. 2000) and therefore clear results can be expected. Further studies on species-specific root systems and their interactions to soil heterogeneity would lead to a deeper understanding of the root-soil relationship, and also temporal changes in soil conditions during different seasons should also be examined.

7.3 Conclusion

The influence of different levels of past human commercial disturbance (in some cases over 30 years ago) had and still has wide and long-reaching consequences on the two investigated East African rain forests. The disturbance altered the competition balance of the trees in the two forests giving rise to different stages of succession as reflected in tree diversity and forest structure. Undisturbed parts without human disturbance contain late climax vegetation and have high tree stem volume, as the succession took place naturally via self-thinning. Because the climax stage has been reached, turnover rates are low. Early successional vegetation is found in highly disturbed forest parts with low stem volume per tree, where self-thinning cycles are frequent because turnover rates are high. The stages of intermediate succession are found in the intermediately disturbed parts of the forests. They contain the highest numbers of species with high stem volume per tree individual. The intermediate disturbance hypothesis adequately describes both species richness and diversity along these gradients in the two forests. The loss of tree diversity through different intense levels of human disturbance however leads to a loss of the "quality of tree diversity", which has further implications e.g. a reduction in the biomass and carbon storage capacities of a forest and thus in its climate change mitigation potential. The different levels of disturbance and thus successional levels of forests therefore always need to be taken into consideration when planning tree enrichment planting and choosing conservation areas.

Most human commercial disturbance took place around 30 years ago, so that after different stages of succession were created by human interference, a process of natural succession is in progress today. In the patchy forest parts that were created in the intermediate stage of succession the whole continuum of pioneer to climax species occurs and competes for environmental resources. Fast-growing early successional tree species were light-demanding, had a short life span and as a rule low seedling establishment in the understorey with some exceptions. Late-successional canopy species grew at slower rates, had a longer life span and generally possessed a well-established seedling layer on the forest floor. The late-successional understorey species had shorter life-spans. In most species stem growth was periodical according to the climate seasonality. In the dry season there was a reduction in growth due to the lower amount of rainfall coinciding with high temperature and solar radiation values, while in the rainy season growth rates increased. At the same time the trees' phenological dynamics, are adapted by shedding of foliage during the dry season as a mechanism of drought avoidance. The strong influence on growth of the number of rainy days and the sum of rainfall and throughfall over the 2 and 3 months prior to the month of measurement, rather than rainfall amounts in the month of measurement, implies that stronger seasonality expected on account of present and projected climatic changes, will give rise to less productive forests thus also reducing the climate change mitigation potential of the forests. Further the species-specific responses to climatic variables imply that future climatic changes may lead to „winners and losers“ amongst the investigated tree species. This could lead to a change in species composition in favour of more drought-resistant species. In particular trees in BF showed more and stronger responses to the stronger climatic seasonality. Relations between soil parameters and growth rates on plot scale were also established producing a more complex picture with several single soil factors having significant correlations (few positive, few negative and most without any), especially in KF. In particular positive correlations to Ca, C and N, as well as negative relations to Mn and Mg are found when different parameters such as tree diversity, growth and seedling diversity are related to soil parameters. Tree growth in BF does not relate significantly to soil factors and does not seem to be limited by soil conditions.

Tree regeneration is shaped by the high recruitment events of a small number of species. Differences in distribution patterns are species-specific, with some species limited to just a few sites, while others occur in all forest parts. Survival rates of seedlings in the forest are highest for understorey and late climax species. Some species suffered from density-dependent thinning, while others seem to satiate their predators and despite high mortality rates still have a high number of surviving seedlings. As the connection between the environmental factors and seedling demography is only weak, this indicates that other factors apart from the abiotic environment, such as specific fruiting seasonality, predators or dispersability, have a stronger influence on the dynamics observed in these forests.

The two forests are still being utilised, partly sustainably, but often illegally, preventing natural regeneration processes and altering the successional stages. In addition predicted climatic changes (IPCC 2007) will also alter the species balance, as indicated by the species-specific response to the abiotic environment shown in this study. Against this background the forest management in the two forests is trying hard to sustain the forests with the resources they have at their disposal. But more attention should be given to the conservation of the remaining primary forest parts. They should have top priority as these are part of our invaluable cultural heritage and can convey to coming generations the beauty of forests that have developed themselves without human interference. Moreover the forest should be divided into well-defined zones that are strictly adhered to. This can only be successfully achieved if local communities are encouraged to work together not by coercion but because they have been persuaded by the transfer of knowledge that forests should be used sustainably. For only people who are themselves convinced that it is possible to lead a sustainable life will attempt to protect the forest resources. However, how this can be achieved is a matter for politics and finance. If these requirements are fulfilled, then the data on tree species obtained in this research project can be used to provide a reliable basis for recommendations in the context of silvicultural management e.g. plantations and reforestation. But forest projects of this kind can only be carried out successfully if species are selected on the basis of precise ecological data. One basic requirement for this is detailed knowledge of the species-specific "adaptation potential" of trees, especially their survival, growth and productivity strategies in relation to projected unfavourable environmental conditions. The data gathered can not only provide a reliable basis for management recommendations but also for modelling forest dynamics (e.g. FORMIND).

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Earth Trends:	http://earthtrends.wri.org/
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10 Appendix

10.1 Kakamega Forest

Table 10-1: Plot structural parameters for trees ≥ 5 cm DBH are presented for the year 2002. Further mean seedling dynamics, diversity and canopy parameters are shown. The tree stem volume was calculated using the approximate volume of a cylinder with the height and the diameter of the trees. The plot abbreviations are explained in table 3-1. Continued on next page.

	Plot	BU1	BU2	BU3	CO1	CO2	CO3	CA1	CA2	CA3	IS1	IS2	IS3
Trees ≥ 5 cm DBH	**Individuals**	60	41	40	42	33	25	35	67	89	25	38	31
	Basal area [m^2]	2.20	2.73	4.34	2.29	1.75	2.49	1.04	0.79	0.84	3.32	4.20	2.50
	Tree Volume [m^3]	18.6	29.7	38.0	20.9	15.8	26.4	4.4	3.0	2.8	39.3	44.9	26.3
	Mortality rate [% yr^{-1}]	4.76	2.79	1.79	1.36	2.16	2.29	5.71	7.46	6.90	2.86	1.50	1.38
	Species richness	21	20	22	20	19	14	14	16	13	15	18	15
	Fisher's alpha	11.0	9.86	13.5	11.1	9.33	7.48	3.23	6.46	2.56	9.06	11.0	5.40
	Shannon H'	2.46	2.36	2.31	2.35	2.24	2.07	1.62	2.04	1.33	2.02	2.28	1.87
	Simpson-Index	0.89	0.89	0.89	0.88	0.88	0.84	0.76	0.83	0.64	0.79	0.84	0.78
Trees < 5 cm DBH	**Density m^{-2}**	9.2	6.2	18.7	1.30	5.3	32.6	1.3	3.0	2.4	19.2	13.5	7.0
	Mortality m^{-2}	0.88	1.05	1.49	0.05	0.32	4.45	0.06	0.15	0.07	3.95	1.79	0.57
	Recruitment m^{-2}	1.11	1.23	2.34	0.10	0.44	4.81	0.11	0.26	0.17	4.27	2.18	0.81
	Species richness	7	5	15	5	10	11	4	5	4	15	10	10
	Fisher's alpha	1.45	1.66	5.17	3.22	8.54	3.09	1.62	5.16	4.93	7.88	2.82	7.48
	Shannon H'	0.31	0.82	2.13	1.47	2.06	0.87	0.94	1.85	1.86	1.99	1.30	1.90
	Simpson- Index	0.11	0.38	0.83	0.75	0.84	0.34	0.44	0.75	0.76	0.77	0.62	0.78
	Understorey radiation [%]	6.6	5.1	6.6	5.0	7.3	6.7	8.7	8.0	8.5	6.3	4.9	5.7
	Canopy openness [%]	9.8	8.1	9.2	9.3	10.7	10.2	14.3	12.3	13.4	11.9	9.2	9.4

Continued from previous page.

	Plot	**KI1**	**KI2**	**KI3**	**MA1**	**MA2**	**MA3**	**SAI1**	**SAI2**	**SAI3**
Trees ≥ 5 cm DBH	**Individuals**	25	38	43	33	24	37	57	49	41
	Basal area [m^2]	1.36	1.52	3.37	1.22	1.46	2.98	1.64	1.18	2.71
	Tree Volume [m^3]	12.8	11.8	29.8	7.6	11.5	29.1	12.6	7.1	20.5
	Mortality rate [% yr^{-1}]	3.43	1.13	2.66	3.46	4.17	1.93	3.51	3.79	2.09
	Species richness	13	13	12	17	10	17	23	18	19
	Fisher's alpha	5.95	5.29	6.97	4.88	3.36	3.36	8.14	4.71	7.88
	Shannon H'	1.67	1.95	1.89	1.73	1.57	1.51	2.21	1.87	2.02
	Simpson-Index	0.70	0.80	0.75	0.72	0.69	0.66	0.82	0.76	0.75
Trees < 5 cm DBH	**Density m^{-2}**	6.7	5.3	4.3	2.20	0.86	4.43	3.94	3.84	2.13
	Mortality m^{-2}	0.30	0.34	0.18	0.11	0.04	0.20	0.34	0.28	0.05
	Recruitment m^{-2}	0.52	0.51	0.36	0.20	0.09	0.42	0.48	0.41	0.14
	Species richness	10	12	13	8	8	9	12	5	10
	Fisher's alpha	2.87	3.92	5.63	3.36	4.35	4.00	6.61	1.56	4.42
	Shannon H'	1.09	1.96	2.18	1.66	1.39	1.63	1.85	1.35	1.72
	Simpson- Index	0.46	0.80	0.85	0.76	0.60	0.72	0.74	0.70	0.73
	Understorey radiation [%]	5.5	3.9	3.6	9.3	7.7	8.4	5.0	6.6	8.0
	Canopy openness [%]	8.9	5.5	9.0	15.5	14.4	13.3	7.3	9.1	11.5

	Plot	**SAII1**	**SAII2**	**SAII3**	**Y1**	**Y2**	**Y3**
Trees ≥ 5 cm DBH	**Individuals**	39	49	32	38	38	63
	Basal area [m^2]	1.86	1.34	1.78	2.84	1.36	2.43
	Tree Volume [m^3]	16.3	5.5	14.0	26.1	12.0	23.1
	Mortality rate [% yr^{-1}]	4.76	2.04	1.34	1.13	1.50	0.00
	Species richness	13	24	19	14	12	13
	Fisher's alpha	3.38	10.08	9.05	5.44	3.84	4.26
	Shannon H'	1.70	2.13	1.86	1.62	1.51	1.69
	Simpson-Index	0.72	0.76	0.68	0.65	0.66	0.70
Trees < 5 cm DBH	**Density m^{-2}**	1.96	4.19	1.59	2.99	4.16	5.56
	Mortality m^{-2}	0.10	1.09	0.11	0.07	0.09	0.19
	Recruitment m^{-2}	0.16	1.20	0.15	0.19	0.26	0.39
	Species richness	4	8	2	13	11	14
	Fisher's alpha	1.08	3.30	0.47	5.26	3.62	4.74
	Shannon H'	1.20	1.42	0.64	2.03	1.86	2.17
	Simpson- Index	0.67	0.62	0.45	0.80	0.79	0.84
	Understorey radiation [%]	3.9	5.0	n.d.	4.0	4.1	5.6
	Canopy openness [%]	6.8	8.4	n.d.	7.2	7.8	8.2

Table 10-2: The correlation between the tree diversity indices of the study sites and the site parameters is shown. The numbers represent Pearson's r with the asterisks giving the level of significance: without: no significance, * p ≤ 0.05. acid: soil cations extracted by nitric acid; acetate: soil cations extracted by ammonium acetate. n is shown in the table.

Parameter	Fisher's alpha	Simpson	Shannon-Wiener H'	n
Incident Precipitation	0.38	0.45	0.47	7
Light				
Canopy openness	-0.09	0.15	0.12	8
Understorey radiation	-0.21	0.01	0.01	9
Soil				
Sand	-0.08	0.25	0.10	7
Silt	-0.71	-0.59	-0.57	7
Clay	0.48	0.04	0.20	7
Silt:Clay ratio	**-0.79***	-0.40	-0.49	7
Bulk Density	0.40	0.21	0.22	7
Penetration Resistance	0.16	-0.14	-0.05	7
pH	0.38	0.65	0.59	8
EC	**-0.72***	-0.52	-0.66	8
K acetate	-0.02	0.03	0.12	8
Mg acetate	-0.28	-0.16	-0.15	8
Ca acetate	-0.02	0.08	0.06	8
K acid	-0.02	0.03	0.12	8
Mg acid	0.65	0.68	0.66	8
Ca acid	0.60	**0.74***	**0.75***	8
C	**0.96***	0.64	0.67	4
N	**0.98***	0.86	0.88	4
C:N ratio	0.07	0.49	0.48	4

Table 10-3: The table shows the correlation of tree structural (DBH ≥ 5 cm) parameters. The values represent Pearson's r with the asterisks giving the level of significance: *** p ≤ 0.001. n = 1310.

Structure parameter	Height [m]	CE	Crown Area [m^2]
DBH [cm]	**0.81 *** **	**0.67 *** **	**0.67 *** **
Height [m]	-	**0.70 *** **	**0.44 *** **
Crown exposure (CE)	-	-	**0.43 *** **

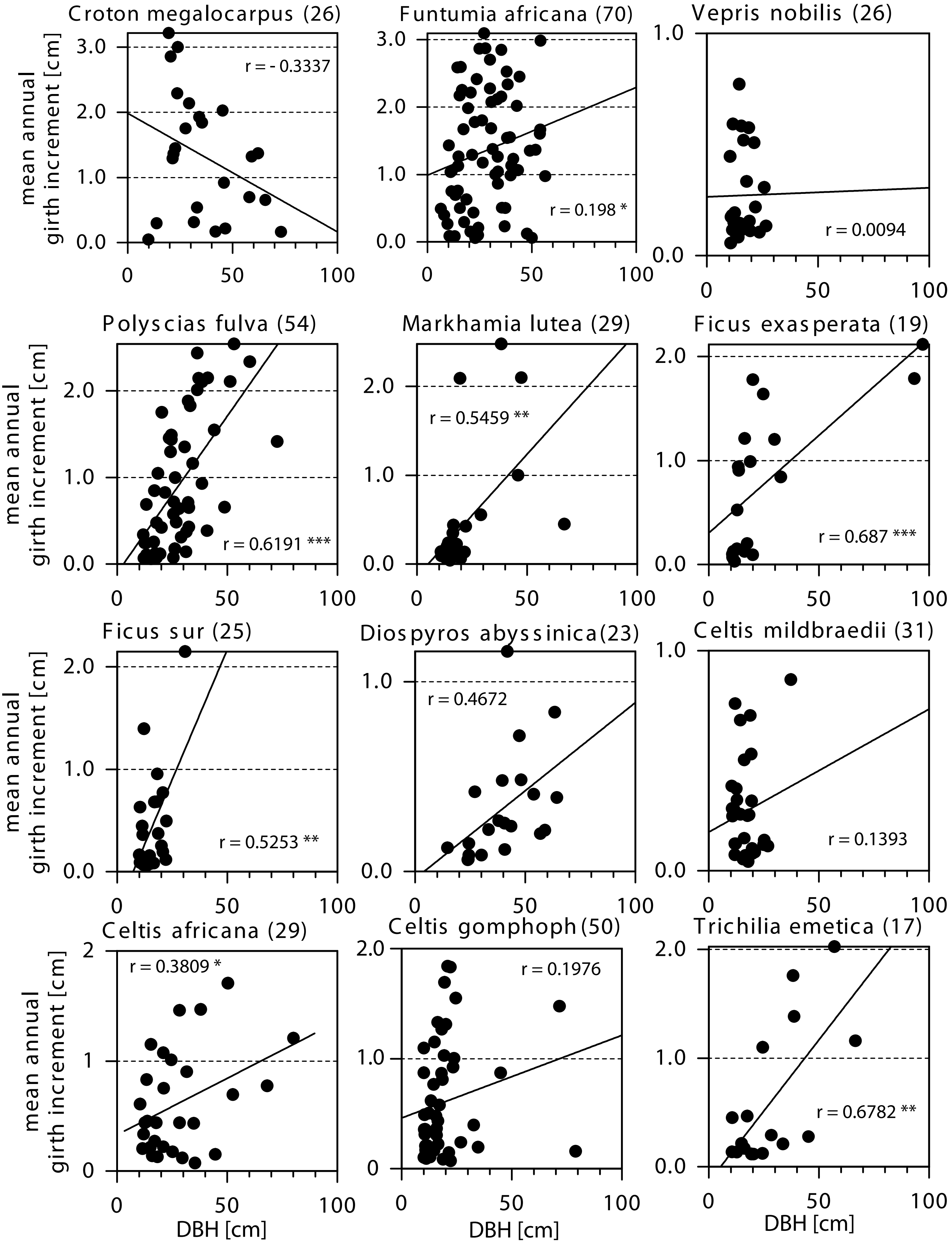
Table 10-4: The correlation between the two dimension of the NMDS of the NESS-Index and abiotic factors. The values represent Pearson‘s r with the asterisks giving the level of significance: without: no significance * p ≤ 0.05 ** p ≤ 0.01 *** p ≤ 0.001. acid: cations extracted by nitric acid, acetate: cations extracted by ammonium acetate.

Factor	**NESS-Index Dimension 1**	**NESS-Index Dimension 2**
Soil (N = 8)		
pH	-0.32	0.26
Sand	0.24	-0.19
Silt	0.63	0.33
Clay	-0.61	0.03
Silt:Clay Ratio	**0.90****	0.21
Bulk density	**-0.86***	-0.24
K acid	0.02	-0.13
Mg acid	-0.07	0.05
Ca acid	0.52	0.07
K acetate	0.03	0.74
Mg acetate	-0.00	0.29
Ca acetate	-0.05	0.20
Light & Disturbance (N = 9)		
Canopy openness	**0.70***	0.22
Understorey radiation	**0.69***	0.27
CDI	**0.63***	0.76

Table 10-5: Correlation between three of the disturbance indices and structural parameters. The values represent Pearson‘s r with the asterisks giving the level of significance: without: no significance. * p ≤ 0.05 ** p ≤ 0.01 *** p ≤ 0.001. CDI: commercial disturbance index N=4; LDI: Local disturbance index N=3; ODI: Overall disturbance index N=5. n.d.: not determined.

Structure parameter	CDI	LDI	ODI
Number at start	-0.51	-0.83	-0.38
Number died	0.73	-0.10	0.77
DBH [cm]	0.10	0.63	-0.29
Slenderness ratio	**-0.88** **	**-0.92** **	-0.74
Basal area [m^2]	-0.20	0.24	-0.55
Volume [m^3]	-0.23	0.38	-0.49
Height [m]	-0.38	0.21	-0.65
Height min [m]	-0.40	0.11	-0.39
Height max [m]	-0.57	0.35	-0.69
DBH min [cm]	-0.37	0.37	0.04
DBH max [cm]	-0.47	0.17	-0.67
Annual mortality rate [%]	**0.84** *	0.27	0.81
Crown exposure	0.25	n.d.	n.d.
Crown area [m^2]	0.31	n.d.	n.d.

Figure 10-1: The mean annual absolute circumferential growth rates in relation to the starting diameter the examined species except for *Strychnos usambarensis*, *Antiaris toxicaria* and *Trilepisium madagascariense,* which are shown in Figure 4-15. The number in bracets are the individuals examined per species. The different scaling of the ordinates has to be considered. Spearman's R is given for the regression line. The asterisks mean different levels of significance (* p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001).



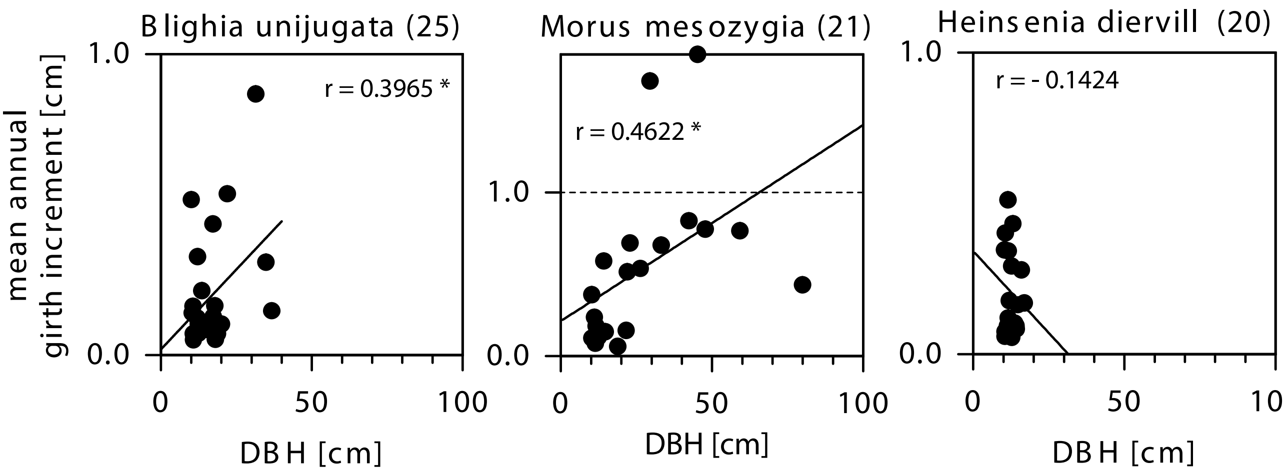
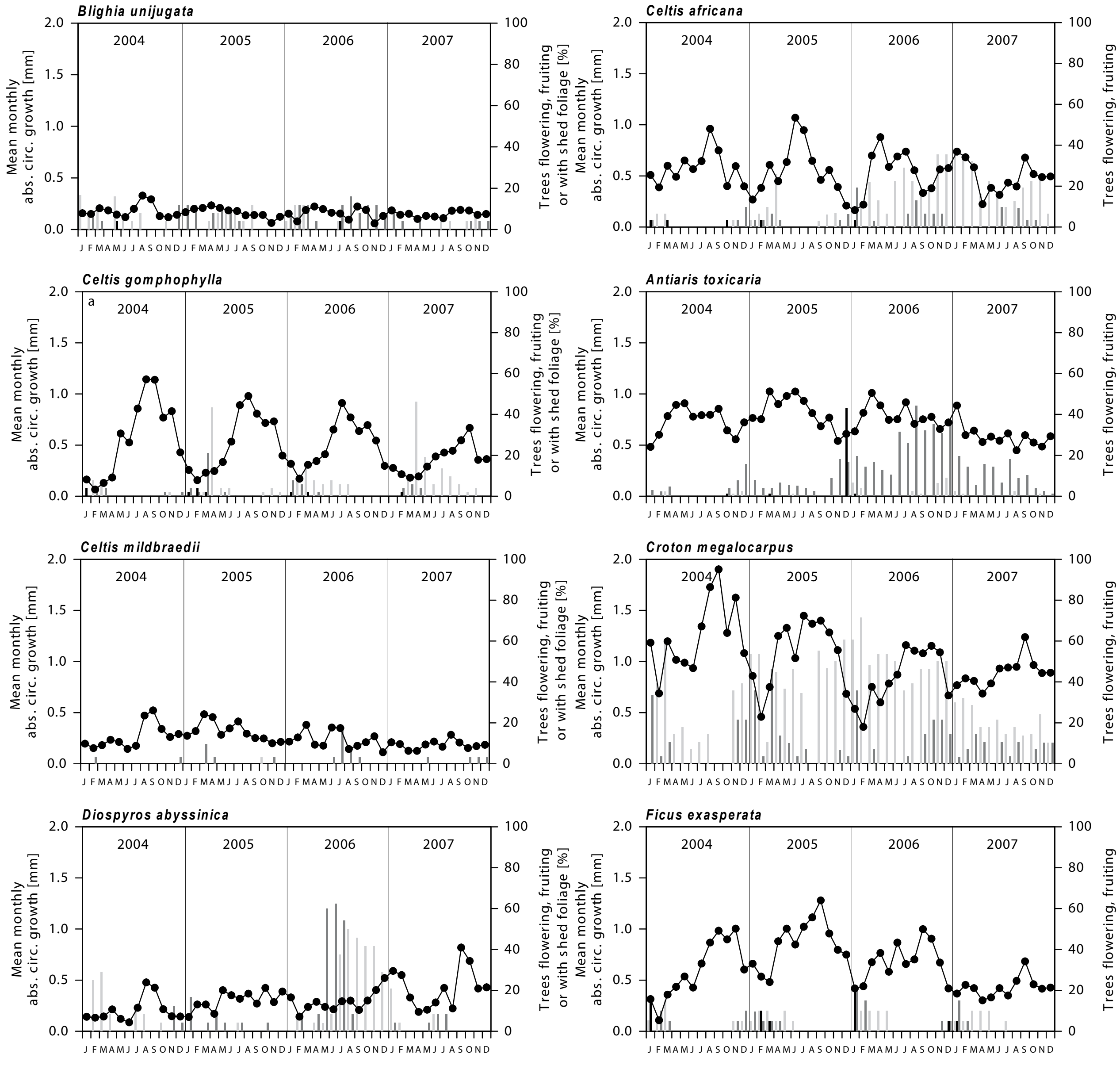
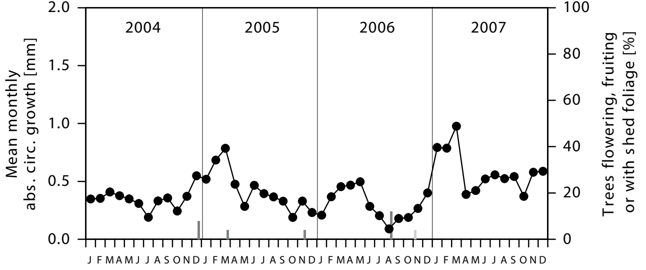


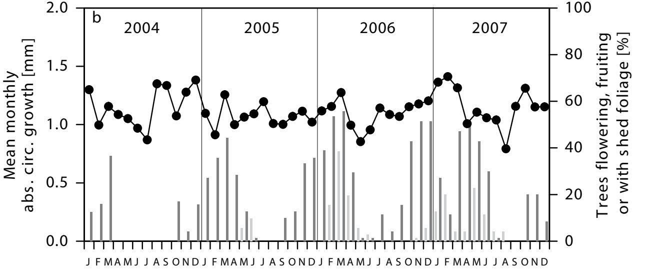
Figure 10-2: Monthly phenological dynamics and absolute circumferential growth during 2004-2007 for trees all tree species except for *Celtis gomphophylla* (N = 50) and *Funtumia africana* (N = 70) ≥ 10cm DBH, which are shown in Figure 4-20. The colours represent absolute circumferential tree growth—●—, % trees flowering ▩ % trees fruiting ░ and trees with shed foliage ■



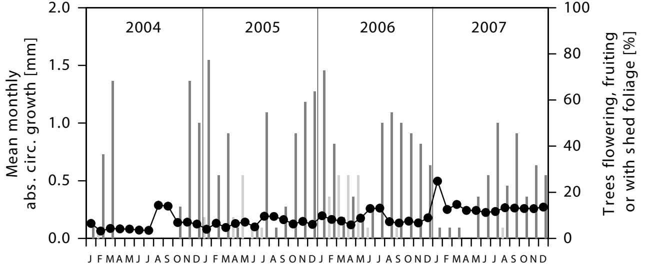
Ficus sur



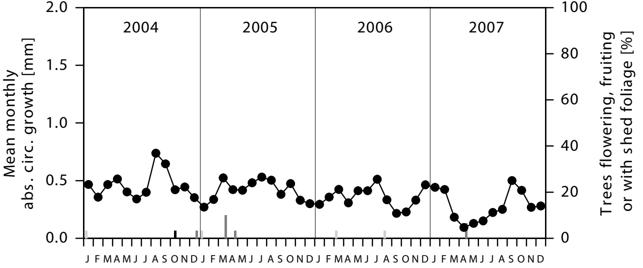
Funtumia africana



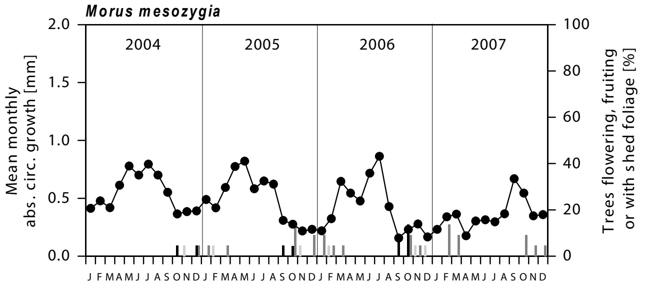
Heinsenia diervilleoides



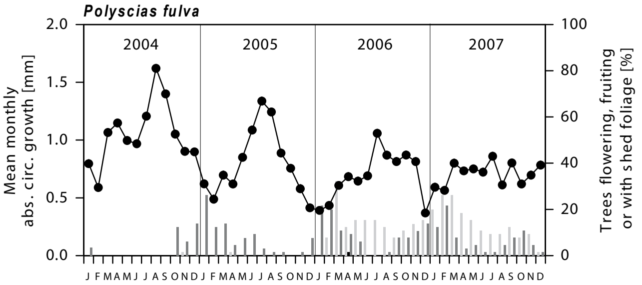
Markhamia lutea



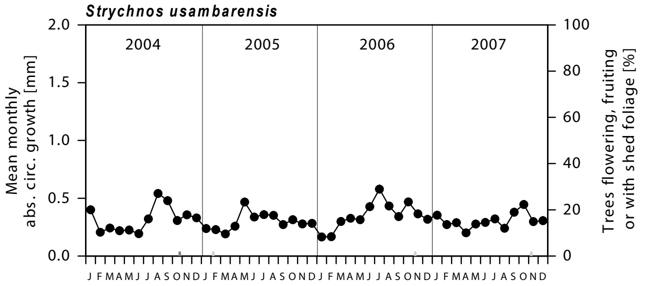
Morus mesozygia



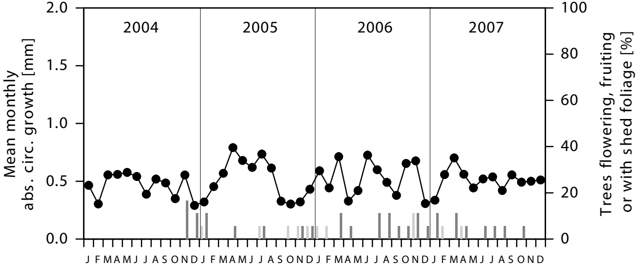
Polyscias fulva



Strychnos usambarensis



Trichilia emetica



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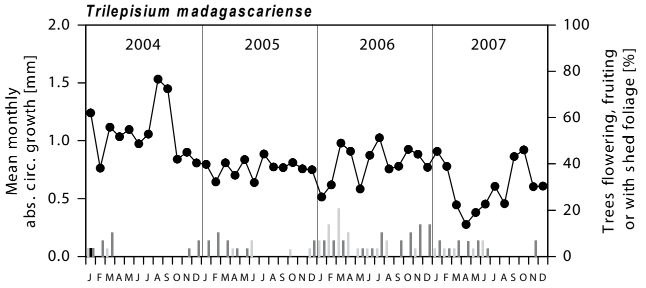

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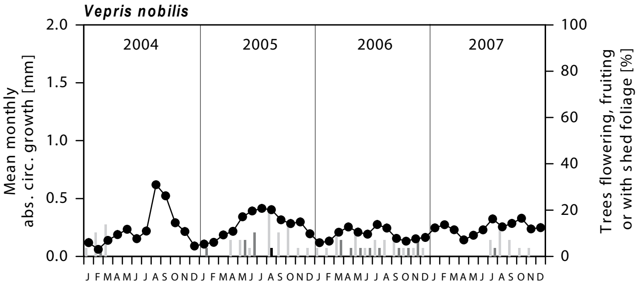

10.2 Budongo Forest

Table 10-6: Plot tree stand structural and diversity parameters (DBH ≥ 5 cm) are presented for Budongo Forest. The tree stem volume was calculated using the approximate volume of a cylinder with the height and the diameter of the trees. Further seedling structural and diversity parameters as well as canopy light parameters for each plot are shown. Plot abbreviations are explained in table 3-2. Continued on next page.

	Plot	**KP12A**	**KP12B**	**KP12C**	**N15A**	**N15B**	**N15C**
Trees ≥ 5 cm DBH	**Individuals**	58	43	40	39	46	43
	Basal area [m^2]	1.06	1.06	1.48	1.26	6.33	2.69
	Tree Volume [m^3]	8.6	9.0	11.6	11.1	89.9	35.0
	Mortality rate [%]	1.15	0.52	2.78	1.14	0.97	0.52
	Species richness	13	9	8	11	12	12
	Fisher's alpha	4.45	1.59	1.81	4.35	4.26	5.19
	Shannon H'	1.71	1.00	1.09	1.86	2.01	1.84
	Simpson-Index	0.78	0.52	0.55	0.82	0.84	0.75
Trees < 5 cm DBH	**Density m^{-2}**	3.1	4.1	9.0	10.1	7.3	4.5
	Mortality m^{-2}	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	Recruitment m^{-2}	n.d.	n.d.	n.d.	4.6	1.6	2.4
	Species richness	6	11	7	9	10	6
	Fisher's alpha	2.47	19.94	4.63	3.11	4.36	4.52
	Shannon H'	0.94	1.75	1.52	1.47	1.79	1.81
	Simpson- Index	0.48	0.82	0.77	0.63	0.78	0.81
	Understorey radiation [%]	8.65	6.82	7.95	7.17	6.37	6.47
	Canopy openness [%]	14.95	10.49	11.82	10.82	10.95	11.67

	Plot	**N4A**	**N4B**	**N4C**	**W21A**	**W21B**	**W21C**
Trees ≥ 5 cm DBH	**Individuals**	55	64	60	65	56	57
	Basal area [m^2]	1.75	1.63	2.79	1.49	1.15	1.99
	Tree Volume [m^3]	11.5	11.3	26.3	13.7	8.8	17.0
	Mortality rate [%]	1.21	1.39	0.37	1.71	1.59	1.95
	Species richness	26	24	21	20	18	22
	Fisher's alpha	8.42	16.29	9.65	9.83	7.13	11.79
	Shannon H'	2.32	2.64	2.42	2.23	2.20	2.35
	Simpson-Index	0.88	0.90	0.88	0.84	0.85	0.84
Trees < 5 cm DBH	**Density m^{-2}**	1.0	3.3	1.9	6.3	1.9	5.0
	Mortality m^{-2}	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	Recruitment m^{-2}	3.1	1.7	1.2	1.9	2.0	2.0
	Species richness	2	3	4	2	7	5
	Fisher's alpha	1.58	1.50	2.78	1.58	7.75	2.26
	Shannon H'	0.96	1.21	1.40	1.23	1.77	1.52
	Simpson- Index	0.59	0.66	0.71	0.63	0.74	0.74
	Understorey radiation [%]	4.91	5.24	6.53	n.d.	6.56	5.89
	Canopy openness [%]	8.63	8.86	9.91	n.d.	11.98	10.52

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	Plot	**W22A**	**W22B**	**W22C**	**W36A**	**W36B**	**W36C**
Trees ≥ 5 cm DBH	**Individuals**	67	46	74	64	60	51
	Basal area [m^2]	1.61	4.12	2.45	3.76	4.89	1.30
	Tree Volume [m^3]	13.0	56.6	22.5	46.0	54.6	11.2
	Mortality rate [%]	2.32	0.97	5.40	0.70	1.11	2.61
	Species richness	22	20	19	17	15	12
	Fisher's alpha	8.53	11.03	8.18	5.52	5.70	3.47
	Shannon H'	2.22	2.22	2.25	2.05	2.02	1.70
	Simpson-Index	0.84	0.81	0.84	0.81	0.81	0.75
Trees < 5 cm DBH	**Density m^{-2}**	4.3	7.2	4.8	10.3	11.6	3.9
	Mortality m^{-2}	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	Recruitment m^{-2}	0.7	1.3	2.4	n.d.	n.d.	n.d.
	Species richness	11	10	9	6	6	5
	Fisher's alpha	7.96	4.78	4.99	0.91	1.84	1.37
	Shannon H'	2.11	2.07	1.82	0.81	1.16	0.88
	Simpson- Index	0.82	0.84	0.78	0.52	0.60	0.49
	Understorey radiation [%]	5.12	n.d.	n.d.	6.13	5.80	5.52
	Canopy openness [%]	8.49	n.d.	n.d.	7.46	10.75	9.98

Table 10-7: The correlation between the diversity indices and the site parameters canopy openness, understorey radiation, pH, C and N is shown. The numbers represent Pearson's r. n is shown in the table.

Parameter	**Fisher's alpha**	**Simpson**	**Shannon-Wiener H'**	**N**
Light				
Canopy openness	-0.72	-0.67	-0.72	6
Understorey radiation	-0.56	-0.49	-0.56	6
Soil				
pH	-0.59	-0.88	-0.70	4
C	-0.22	-0.45	-0.29	4
N	-0.32	-0.37	-0.33	4

Table 10-8: The table shows the correlation of the tree structural parameters (DBH ≥ 5 cm). The values represent Pearson's r with the asterisks giving the level of significance: without: no significance * $p \leq 0.05$ ** $p \leq 0.01$ *** $p \leq 0.001$. n = 939.

Structure parameter	Height [m]	Crown exposure	Crown Area [m^2]
DBH [cm]	0.84 ***	0.70 ***	0.80 ***
Height [m]	-	**0.78 *****	**0.72 *****
Crown exposure	-	-	**0.55 *****

Table 10-9: Correlation between three of the disturbance indices and structural parameters. The values represent Pearson's r with the asterisks giving the level of significance: without: no significance * $p \leq 0.05$ ** $p \leq 0.01$. CDI: commercial disturbance index n = 4; LDI: Local disturbance index n = 3; ODI: Overall disturbance index n = 6. n.d.: not determined.

Structure parameter	CDI	LDI	ODI
Number at start	0.81	0.24	**0.82***
Number died	0.56	0.20	0.49
DBH [cm]	-0.53	0.52	-0.34
Slenderness Ratio	-0.29	-0.98	-0.50
Basal area [m^2]	-0.31	0.60	-0.11
AGTB [kg] (Chave 2005)	-0.40	0.54	-0.23
Volume [m^3]	-0.74	0.93	-0.21
Height [m]	**-0.82***	0.13	-0.04
Height min [m]	-0.20	0.49	0.01
Height max [m]	-0.16	0.45	-0.08
DBH min [cm]	0.58	**0.85***	0.72
DBH max [cm]	-0.17	0.73	-0.01
Annual Mortality rate [%]	0.48	0.13	0.40
Crown exposure	-0.15	n.d.	n.d.
Crown area [m^2]	**-0.75 ****	n.d.	n.d.

Table 10-10: Correlation between the two dimension of the NMDS of the NESS-Index and abiotic factors. The values represent Pearson's r with the asterisks giving the level of significance: without: no significance * $p \leq 0.05$ ** $p \leq 0.01$ *** $p \leq 0.001$. Cations extracted by distilled water.

Factor	**NESS-Index Dimension 1**	**NESS-Index Dimension 2**
Soil (n = 4)		
pH	-0.55	**-0.95***
C	0.13	-0.58
N	0.52	-0.44
Ca	0.93	0.12
K	-0.39	0.08
Mg	**0.96***	0.64
Mn	-0.22	-0.41
P	**0.97***	0.31
Light and Disturbance (n = 6)		
Canopy openness	0.63	-0.45
Understorey radiation	0.47	-0.31
CDI	-0.45	0.76
LDI	-0.76	-0.16
ODI	-0.60	0.62

Figure 10-3: Monthly phenological dynamics and absolute circumferential growth (abs. circ.) during 2005-2007 for trees all tree species except for *Celtis gomphophylla* and *Funtumia elastica* ≥ 10cm DBH, which are shown in Figure 4-20. The colours represent absolute circumferential tree growth —●—, % trees flowering ▨ % trees fruiting ☐ and trees with shed foliage ■.

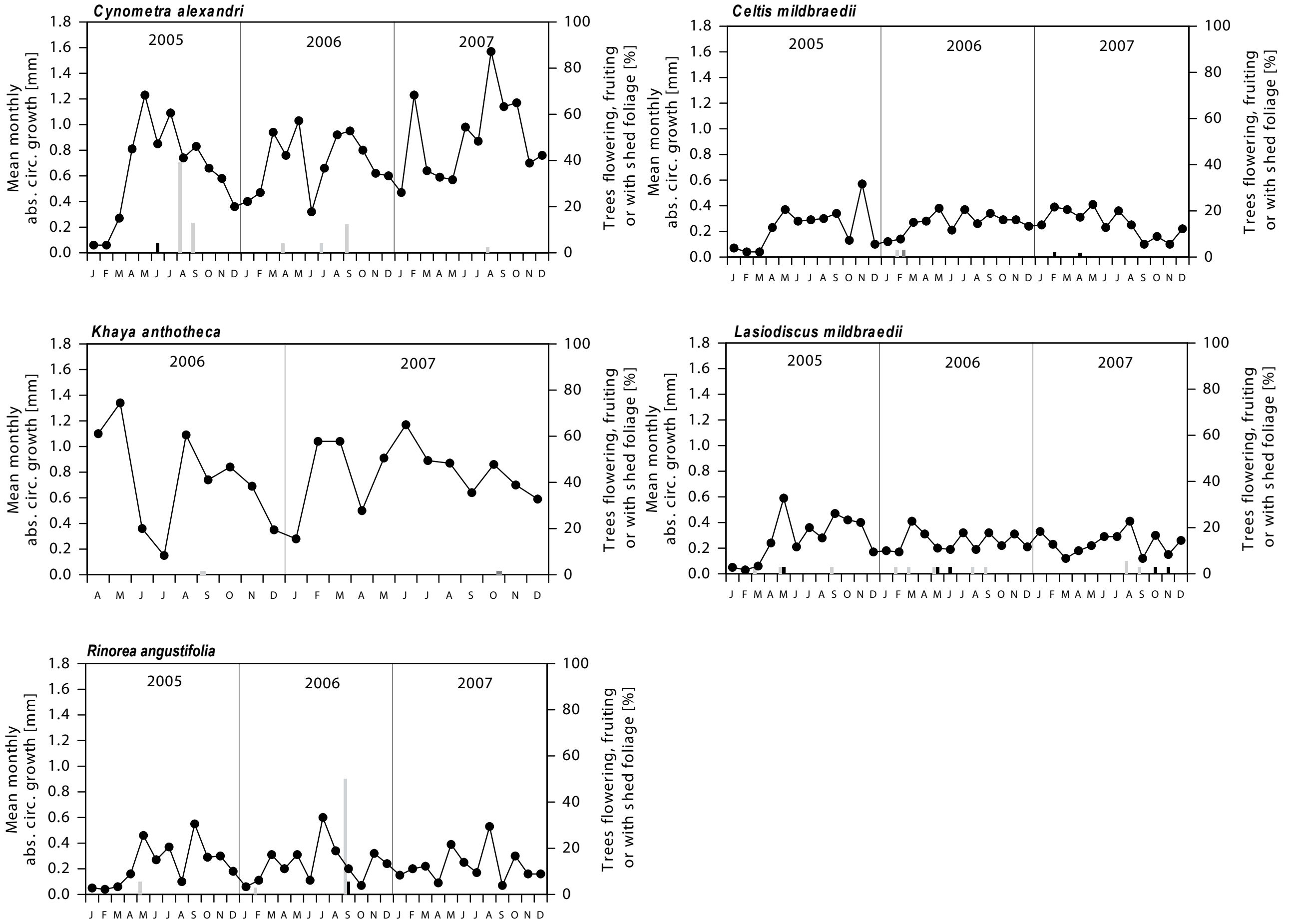

Table 10-11: List of the tree species ≥ 5cm dbh that were identified in the two East African forests.
In the table all trees in both study forests (KF=Kakamega Forest, BF=Budongo Forest) that were found during the study period in and outside the study plots. The most abundant species of the plots were categorized concerning their maximum height (MH [m]) with the help of literature (Hamilton 1991, Beentje 1994) and the collected personal data on trees. Accepted names were used according to the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/).The categorization was for the physiological group was done using tree growth, seedling mortality, habitat preference data and further confirmed by wood density values collected by S. Becker & D. Braun (unpublished data). IM: Intermediate; ST: Shade-tolerant; IT: Shade-Intolerant; MH [m]=Maximum height; PG=Physiological group; HOH=collected sample stored in the Hohenheim herbarium.

Family	**Genus**	**Species**	**MH [m]**	**PG**	**KF**	**BF**	**HOH**
Alangiaceae	*Alangium*	*chinense*	27	IM	x		x
Anacardiaceae	*Pseudospondias*	*microcarpa*		IM	x	x	x
Annonaceae	*Annona*	*senegalensis*				x	x
Annonaceae	*Cleistopholis*	*patens*				x	x
Annonaceae	*Monodora*	*myristica*	30	ST	x		x
Annonaceae	*Polyalthia*	*suaveolens*				x	x
Annonaceae	*Uvariopsis*	*congensis*	17	ST	x	x	x
Apocynaceae	*Alstonia*	*boonei*	50	IM		x	x
Apocynaceae	*Funtumia*	*africana*	38	IM	x	x	x
Apocynaceae	*Funtumia*	*elastica*	30	IM		x	x
Apocynaceae	*Rauvolfia*	*caffra*		IT	x		x
Apocynaceae	*Tabernaemontana*	*pachysiphon*				x	x
Apocynaceae	*Tabernaemontana*	*stapfiana*				x	
Araliaceae	*Polyscias*	*fulva*	27	IT	x		x
Asteraceae	*Vernonia*	*conferta*			x		x
Balanitaceae	*Balanites*	*wilsoniana*			x	x	x
Bignoniaceae	*Kigelia*	*spc.*	15	IM	x	x	x
Bignoniaceae	*Markhamia*	*lutea*	30	IM	x	x	x
Bignoniaceae	*Spathodea*	*campanulata*	20	IT	x		x
Bignoniaceae	*Stereospermum*	*kunthianum*			x	x	x
Boraginaceae	*Cordia*	*africana*	32	IT	x		x
Boraginaceae	*Cordia*	*millenii*	38	IM		x	x
Boraginaceae	*Ehretia*	*cymosa*		IT	x	x	x
Buddlejaceae	*Nuxia*	*congesta*	25	IM	x		
Burseraceae	*Canarium*	*schweinfurthii*				x	
Caesalpiniaceae	*Cynometra*	*alexandri*	50	ST		x	x
Caesalpiniaceae	*Erythrophleum*	*suaveolens*				x	x
Capparaceae	*Maerua*	*duchesnei*				x	x
Capparaceae	*Ritchiea*	*albersii*	15	ST	x	x	x
Cecropiaceae	*Myrianthus*	*holstii*				x	x
Celastraceae	*Maytenus*	*heterophylla*	6	IT	x		x
Chrysobalanaceae	*Parinari*	*excelsa*				x	x
Clusiaceae	*Harungana*	*madagascariensis*	18	IT	x	x	x
Clusiaceae	*Mammea*	*africana*				x	x
Combretaceae	*Combretum*	*collinum*		IT	x	x	x
Combretaceae	*Combretum*	*molle*		IT	x	x	
Combretaceae	*Terminalia*	*brownii*			x	x	x

Family	**Genus**	**Species**	**MH [m]**	**PG**	**KF**	**BF**	**HOH**
Connaraceae	*Cnestis*	*ugandensis*				x	x
Dichapetalaceae	*Tapura*	*fischeri*				x	x
Ebenaceae	*Diospyros*	*abyssinica*	30	ST	x	x	x
Euphorbiaceae	*Acalypha*	*neptunica*	6	ST	x	x	x
Euphorbiaceae	*Alchornea*	*laxiflora*	7	ST	x	x	x
Euphorbiaceae	*Antidesma*	*laciniatum*				x	x
Euphorbiaceae	*Bridelia*	*micrantha*		IT	x		x
Euphorbiaceae	*Croton*	*macrostachyus*		IM	x	x	x
Euphorbiaceae	*Croton*	*megalocarpus*	36	IM	x	x	x
Euphorbiaceae	*Croton*	*sylvaticus*	29	IM	x	x	x
Euphorbiaceae	*Discoclaoxylon*	*hexandrum*				x	x
Euphorbiaceae	*Drypetes*	*gerrardii*	32	IM	x		x
Euphorbiaceae	*Drypetes*	*ugandensis*				x	x
Euphorbiaceae	*Macaranga*	*monandra*				x	x
Euphorbiaceae	*Mallotus*	*oppositifolius*				x	x
Euphorbiaceae	*Margaritaria*	*discoidea*	24	IM	x	x	x
Euphorbiaceae	*Neoboutonia*	*macrocalyx*			x	x	x
Euphorbiaceae	*Ricinodendron*	*heudelotii*				x	x
Euphorbiaceae	*Sapium*	*ellipticum*	20	IT	x		x
Euphorbiaceae	*Suregada*	*procera*	18	ST	x		x
Fabaceae	*Craibia*	*brownii*	28	ST	x		x
Fabaceae	*Erythrina*	*abyssinica*		IT	x	x	x
Fabaceae	*Erythrina*	*excelsa*				x	x
Fabaceae	*Mildbraediodendron*	*excelsum*				x	x
Fabaceae	*Piliostigma*	*thonningii*				x	x
Flacourtiaceae	*Caloncoba*	*schweinfurthii*		IT		x	x
Flacourtiaceae	*Casearia*	*battiscombei*	40	IM	x		x
Flacourtiaceae	*Dasylepis*	*racemosa*				x	
Flacourtiaceae	*Dovyalis*	*macrocalyx*	8	IT	x		x
Flacourtiaceae	*Lindackeria*	*schweinfurthii*				x	x
Flacourtiaceae	*Oncoba*	*spinosa*	16	IT	x		x
Flacourtiaceae	*Rawsonia*	*lucida*	20	ST	x	x	x
Flacourtiaceae	*Trimeria*	*grandifolia*		IT	x		x
Icacinaceae	*Apodytes*	*dimidiata*		IT	x		
Meliaceae	*Ekebergia*	*capensis*	30	ST	x	x	x
Meliaceae	*Entandrophragma*	*angolense*				x	
Meliaceae	*Entandrophragma*	*cylindricum*				x	
Meliaceae	*Entandrophragma*	*excelsum*				x	
Meliaceae	*Entandrophragma*	*utile*				x	x
Meliaceae	*Khaya*	*anthotheca*	40	IM	x	x	x
Meliaceae	*Khaya*	*grandifoliola*				x	x
Meliaceae	*Lovoa*	*trichilioides*				x	
Meliaceae	*Trichilia*	*dregeana*				x	x
Meliaceae	*Trichilia*	*emetica*	35	ST	x	x	x
Meliaceae	*Trichilia*	*prieuriana*				x	x

Family	**Genus**	**Species**	**MH [m]**	**PG**	**KF**	**BF**	**HOH**
Meliaceae	*Trichilia*	*rubescens*				x	x
Meliaceae	*Turraea*	*holstii*		IM	x		x
Meliaceae	*Turraea*	*robusta*	19	IM	x		x
Melianthaceae	*Bersama*	*abyssinica*		IT	x		x
Mimosaceae	*Acacia*	*abyssinica*		IT	x		x
Mimosaceae	*Albizia*	*coriaria*		IM		x	
Mimosaceae	*Albizia*	*ferruginea*				x	
Mimosaceae	*Albizia*	*glaberrima*		IM		x	
Mimosaceae	*Albizia*	*grandibracteata*	25	IM	x		x
Mimosaceae	*Albizia*	*gummifera*	25	IM	x		x
Mimosaceae	*Tetrapleura*	*tetraptera*			x	x	x
Moraceae	*Antiaris*	*toxicaria*	45	IM	x	x	x
Moraceae	*Broussonetia*	*papyrifera*				x	x
Moraceae	*Ficus*	*bubu*	30	IM	x		x
Moraceae	*Ficus*	*cyathistipula*	15	IT	x		x
Moraceae	*Ficus*	*exasperata*	31	IM	x		x
Moraceae	*Ficus*	*lutea*	25	IT	x		x
Moraceae	*Ficus*	*mucuso*				x	x
Moraceae	*Ficus*	*natalensis*				x	x
Moraceae	*Ficus*	*ovata*				x	
Moraceae	*Ficus*	*sansibarica*				x	x
Moraceae	*Ficus*	*sp. 1*			x		
Moraceae	*Ficus*	*sur*	31	IM	x	x	x
Moraceae	*Ficus*	*thonningii*			x	x	x
Moraceae	*Ficus*	*vallis-choudae*			x	x	x
Moraceae	*Morus*	*mesozygia*	29	IM	x	x	x
Moraceae	*Trilepisium*	*madagascariense*	35	IM	x	x	x
Myristicaceae	*Pycnanthus*	*angolensis*				x	x
Myrsinaceae	*Maesa*	*lanceolata*		IT	x		x
Myrtaceae	*Psidium*	*guajava*		IT	x	x	x
Myrtaceae	*Syzygium*	*guineense*	18	IM	x		x
Ochnaceae	*Ochna*	*afzelii*				x	x
Ochnaceae	*Ochna*	*insculpta*	9	IM	x		x
Ochnaceae	*Ouratea*	*densiflora*				x	x
Olacaceae	*Strombosia*	*scheffleri*	30	ST	x		x
Oleaceae	*Chionanthus*	*mildbraedii*	14	IM	x	x	x
Oleaceae	*Olea*	*capensis*	40	ST	x		x
Oleaceae	*Schrebera*	*alata*			x		
Pittosporaceae	*Pittosporum*	*viridiflorum*		IT	x		x
Polygalaceae	*Carpolobia*	*alba*			x		x
Rhamnaceae	*Lasiodiscus*	*mildbraedii*	20	ST		x	x
Rhamnaceae	*Maesopsis*	*eminii*	45	IM	x	x	x
Rhizophoraceae	*Cassipourea*	*ruwensorensis*	14	ST	x		x
Rosaceae	*Prunus*	*africana*	33	IM	x		x
Rubiaceae	*Belonophora*	*hypoglauca*				x	x

Family	**Genus**	**Species**	**MH [m]**	**PG**	**KF**	**BF**	**HOH**
Rubiaceae	*Craterispermum*	*schweinfurthii*	15	ST	x		x
Rubiaceae	*Dictyandra*	*arborescens*				x	
Rubiaceae	*Heinsenia*	*diervilleoides*	12	ST	x	x	x
Rubiaceae	*Oxyanthus*	*speciosus*		IM		x	x
Rubiaceae	*Rothmannia*	*urcelliformis*		ST	x		x
Rubiaceae	*Tarenna*	*pavettoides*		IM	x		x
Rubiaceae	*Vangueria*	*apiculata*	9	IM	x		x
Rubiaceae	*Vangueria*	*infausta*		IM	x		x
Rutaceae	*Clausena*	*anisata*		IT	x		x
Rutaceae	*Fagaropsis*	*angolensis*		IM	x		x
Rutaceae	*Vepris*	*nobilis*	20		x	x	x
Rutaceae	*Zanthoxylum*	*gilletii*	30	ST	x		x
Sapindaceae	*Blighia*	*unijugata*	25	ST	x	x	x
Sapindaceae	*Blighia*	*welwitschii*				x	
Sapindaceae	*Deinbollia*	*kilimandscharica*	12	ST	x		x
Sapindaceae	*Glenniea*	*africana*				x	x
Sapindaceae	*Lecaniodiscus*	*spec.*				x	x
Sapindaceae	*Lepisanthes*	*senegalensis*	27	ST	x		x
Sapotaceae	*Afrosersalisia*	*cerasifera*	35	ST	x		x
Sapotaceae	*Chrysophyllum*	*albidum*	40	ST	x	x	x
Sapotaceae	*Chrysophyllum*	*gorungosanum*				x	
Sapotaceae	*Chrysophyllum*	*muerense*	30	IM		x	x
Sapotaceae	*Chrysophyllum*	*perpulchrum*	35	IM		x	x
Sapotaceae	*Chrysophyllum*	*viridifolium*	30	ST	x		x
Sapotaceae	*Englerophytum*	*oblanceolatum*	13	ST	x	x	x
Sapotaceae	*Lychnodiscus*	*cerospermus*				x	x
Sapotaceae	*Manilkara*	*butugi*			x		x
Sapotaceae	*Pouteria*	*altissima*	45	ST	x		x
Sterculiaceae	*Cola*	*gigantea*				x	x
Sterculiaceae	*Dombeya*	*rotundifolia*		IT	x		x
Sterculiaceae	*Pterygota*	*mildbraedii*				x	x
Sterculiaceae	*Sterculia*	*dawei*				x	x
Strychnaceae	*Strychnos*	*usambarensis*	29	ST	x		x
Thymelaeaceae	*Peddiea*	*fischeri*		IT	x		x
Tiliaceae	*Desplatsia*	*dewevrei*				x	x
Tiliaceae	*Glyphaea*	*brevis*				x	x
Tiliaceae	*Grewia*	*mildbraedii*				x	x
Ulmaceae	*Celtis*	*africana*	29	ST	x		x
Ulmaceae	*Celtis*	*gomphophylla*	25	ST	x	x	x
Ulmaceae	*Celtis*	*mildbraedii*	40	ST	x	x	x
Ulmaceae	*Celtis*	*phillippensis*	35	ST		x	x
Ulmaceae	*Celtis*	*zenkeri*	40	ST		x	x
Ulmaceae	*Chaetacme*	*aristata*	15	ST	x		x
Ulmaceae	*Holoptelea*	*grandis*				x	x
Ulmaceae	*Trema*	*orientalis*	15	IT	x	x	x

Family	**Genus**	**Species**	**MH [m]**	**PG**	**KF**	**BF**	**HOH**
Verbenaceae	*Premna*	*angolensis*		IM	x		x
Violaceae	*Rinorea*	*angustifolia ssp. ardisiiflora*	15	ST		x	x
Violaceae	*Rinorea*	*brachypetala*	9	ST	x	x	x
Violaceae	*Rinorea*	*dentata*	14	ST		x	x
Violaceae	*Rinorea*	*ilicifolia*		ST		x	x
Violaceae	*Rinorea*	*oblongifolia*		ST		x	x

Table 10-12: Characteristics of tree species that were analysed for stem increment. DBH: mean diameter at breast height, Height: mean height CE: mean crown exposure, abs DBH: mean absolute diameter increment, rel DBH: mean relative diameter increment, SD: standard deviation, KF: Kakamega, BF: Budongo.

Species	Forest	n	DBH [cm]	Height [m]	CE	abs DBH [cm yr^{-1}]	SD DBH [cm yr^{-1}]	rel DBH [% yr^{-1}]	Sd rel DBH [% yr^{-1}]
Antiaris toxicaria	KF	73	29.6	21.9	2.6	0.30	0.29	0.95	0.80
Blighia unijugata	KF	26	16.8	16.5	2.1	0.07	0.05	0.43	0.49
Celtis africana	KF	29	27.8	18.6	2.7	0.20	0.15	0.84	0.31
Celtis gomphophylla	KF	50	19.2	15.1	2.4	0.19	0.15	1.08	0.65
Celtis mildbraedii	KF	31	17.1	13.2	2.2	0.11	0.07	0.69	0.80
Croton megalocarpus	KF	21	35	25.5	3.5	0.41	0.27	1.39	0.55
Diospyros abyssinica	KF	19	40.5	24.9	2.7	0.15	0.11	0.37	1.15
Englerophytum oblanceolatum	KF	15	17.6	11.3	1.9	0.11	0.07	0.66	0.20
Ficus exasperata	KF	19	25.4	15.1	2.4	0.29	0.27	1.22	0.93
Ficus sur	KF	23	15.9	13.2	2	0.15	0.13	0.98	0.85
Funtumia africana	KF	71	28	21	2.9	0.44	0.28	1.77	1.25
Heinsenia diervilleoides	KF	19	12.6	9.2	1.9	0.08	0.05	0.62	0.38
Markhamia lutea	KF	25	20.8	16	2.2	0.13	0.18	0.55	0.61
Morus mesozygia	KF	20	27.2	20.8	2.4	0.17	0.15	0.68	0.41
Polyscias fulva	KF	47	28.7	19.7	2.5	0.29	0.22	0.95	0.60
Prunus africana	KF	14	58.2	24.1	3.2	0.44	0.28	0.93	0.68
Strychnos usambarensis	KF	51	28.9	19.5	2.3	0.13	0.10	0.56	0.61
Trichilia emetica	KF	16	28.1	18.7	2.6	0.20	0.20	0.64	0.40
Trilepisium madagascariense	KF	27	27	19.9	2.6	0.27	0.17	1.43	1.18
Vepris nobilis	KF	25	16.2	13.3	2	0.10	0.07	0.64	0.45
Celtis gomphophylla	BF	12	31.5	16.7	2.6	0.12	0.10	0.42	0.44
Celtis mildbraedii	BF	34	20.1	14.2	2.2	0.10	0.08	0.67	0.68
Cynometra alexandri	BF	18	22.9	17.9	2.8	0.35	0.15	2.03	1.10
Funtumia elastica	BF	42	18	15.7	2.3	0.10	0.10	0.66	0.73
Khaya anthotheca	BF	23	38.3	22.5	2.4	0.27	0.18	0.91	0.66
Lasiodiscus mildbraedii	BF	34	15.9	11.9	1.7	0.10	0.07	0.70	0.64
Rinorea angustifolia	BF	33	13.6	10.4	1.3	0.09	0.04	0.65	0.31