**Dissertationes Forestales 148**

# Restoration of degraded dry semideciduous forest ecosystems in Ghana: Effects of African mahogany species on soil chemistry, tree diversity and the application of leaf morphometrics for provisional seed zonation

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Academic dissertation

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# ABSTRACT

The dry semideciduous forest zone is one of the most fragile and highly threatened ecosystems in Ghana. Recurrent bushfires and other anthropogenic disturbances have degraded this forest zone and converted a large proportion to savannah woodland. Moreover, the invasion of weeds following disturbances has impeded natural regeneration. Hence, the likely solution to this problem is restoration through the use of native forest tree species to catalyse natural regeneration. The use of African mahogany species in this regard has been emphasised.

This study aims to (i) investigate the levels of phenotypic plasticity and ecogeographic and morphometric variation as well as similarity among populations of *Khaya anthotheca* and *Khaya ivorensis* with respect to leaf morphology as a basis for developing a preliminary framework for seed zonation for restoration; (ii) determine the effects of stand structure and native tree density on the recruitment of mahogany species in line-enrichment planting; and (iii) assess the effects of mahogany species on resident or native tree species diversity and soil chemical properties in restorations of degraded semi-deciduous forest ecosystems in Ghana.

The results of the study indicated a highly significant phenotypically plastic response of leaf morphology to precipitation, temperature, altitude and latitude in *Khaya ivorensis* populations. In addition, it was established that leaf size in *Khaya ivorensis* and *K. anthotheca* varies inversely with latitude, annual potential evapotranspiration and aridity index. However, leaf traits vary directly with a precipitation gradient among the respective species. The results suggested a south-north clinal relationship to leaf traits, with the southern populations of the two *Khaya* species having larger leaf sizes than the northern populations. Thus, seeds collected from higher latitudes could be planted in the same zone or moved to lower latitude with high amounts of rainfall. However, the results from Poisson regression modelling indicated that stand basal area, growing space and crown diameter were positively associated with recruitment. However, stand dominant height was negatively associated with recruitment. The results indicated that mixed mahogany species foster the recolonisation of a diversity of native tree species and accelerate the regeneration rate in the restoration of fire-degraded dry semi-deciduous forest ecosystems compared to natural regeneration. Moreover, relatively higher amounts of Ca, Mg, base saturation, CEC, organic C and organic matter and low amounts of Al were recorded in the soils beneath mixed mahogany plantation sites compared to natural regeneration sites.

**Keywords:** *Khaya* and *Entandrophragma* species, leaf morphological variation, phenotypic plasticity, restoration, seed zonation, environmental gradient, soil chemical properties

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Joensuu, August 2012

Jones Abrefa Danquah

# LIST OF ORIGINAL ARTICLES

This thesis is based on the following six articles, which will be referred to in the text as Roman numerals I-VI. Articles I-IV are reprinted with the kind permission of the publishers or with the right retained as author and articles V-VI are the author versions of the submitted manuscripts.

**I** Danquah, J.A. 2010. Phenotypic plasticity of leaf length to an environmental gradient in *Khaya ivorensis* (Meliaceae) populations in Ghana. African Journal of Environmental Science and Technology 4(12): 860-865.
doi:10.5897 /AJEST 10.227

**II** Danquah, J.A., Appiah, M., Pappinen, A. 2011. Eco-geographic variation in leaf morphology of African mahogany (*Khaya anthotheca and Khaya ivorensis*) provenances in Ghana. European Journal of Scientific Research 51(1): 18-28.
http://www.eurojournals.com/EJSR_51_1_02.pdf

**III** Danquah, J.A., Appiah, M., Pappinen, A. 2011. Leaf morphometric variation in two species of African mahoganies: *Khaya ivorensis* and *Khaya anthotheca* (Meliaceae). European Journal of Scientific Research 54(3): 325-338.
http://www.eurojournals.com/EJSR_54_3_01.pdf

**IV** Danquah, J.A., Appiah, M., Pappinen, A. 2011. Enrichment planting of African mahoganies in fire-degraded dry semi-deciduous forests in Ghana: The Effect of the stand structure and species numbers on recruitment. European Journal of Scientific Research 52(2): 213-225.
http://www.eurojournals.com/EJSR_52_2_09.pdf

**V** Danquah, J.A., Appiah, M., Pappinen, A. 2012. The Effect of African mahogany species on soil chemical properties in degraded dry semi-deciduous forest ecosystems in Ghana. International Journal of Agriculture and Biology 14: 321-328.
http://www.fspublishers.org/p_issuevol.jsp?&acc1=VOL_14_NO_3

**VI** Danquah, J.A., Appiah, M., Pappinen, A. 2011. Comparison of post-fire planted and natural dry semi-deciduous forest communities in Ghana. African Journal of Agricultural Research 6(23): 5266-5277.
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### The author's contribution

Jones Abrefa Danquah had primary responsibility for the collection of field data, its analysis and the writing of articles II, III, IV, V, and VI, whereas the co-authors participated in formulating the research task and commenting on the manuscripts. Article I was written by the author alone.

# TABLE OF CONTENTS

# ABBREVIATIONS

| | |
|---|---|
| AAI | Annual Aridity Index |
| ANOVA | Analysis of Variance |
| APET | Annual Potential Evapotranspiration |
| BA | Basal Area |
| $^{o}$C | Degree Celsius |
| $C_s$ | Sorensen's Index |
| C*d* | Crown diameter |
| CEC | Cation exchange capacity |
| cm | Centimetre |
| CSIR | Council for Scientific and Industrial Research – Ghana |
| D | Simpson's Index |
| D-1 | Simpson's Diversity Index |
| DBH | Diameter at Breast Height |
| DFA | Discriminant Function Analysis |
| ESPI | Environmental Standardized Plasticity Index |
| FAO | Food and Agriculture Organization of the United Nations |
| FIV | Family Importance Value Index |
| FORIG | Forestry Research Institute of Ghana |
| g | Gramme |
| GPS | Global Position System |
| H | Shannon-Wiener Diversity Index |
| IVI | Importance value Index |
| J | Pielou's Evenness Index |
| km | Kilometre |
| $km^2$ | Square Kilometre |
| mm | Millimetre |
| MAP | Mean Annual Precipitation |
| MTS | Modified Taungya System |
| NFPDP | National Forest Plantation Development Programme |
| UPGMA | Unweighted-Pair Group Method with Arithmetic Average Algorithm |
| PCA | Principal Component Analysis |
| PC1 | Principal Component One |
| S | Growing Space |
| SDI | Stand Density Index |
| TEB | Total Exchangeable Bases |

# ERRATA

**Study I**
The name Buzzaz should be written Bazzaz in the reference list.

**Studies II, III and IV**
The captions of the figures of studies II, III and IV are placed above the figures. This is the style of the journal (European Journal of Scientific Research). The normal practise is the captions should be placed below the figures.

# 1 INTRODUCTION

## 1.1 Background

The dry semi-deciduous forest zone or ecosystem covers an area of approximately 2,144,000 ha, comprising 8% of the total area of high forest, or approximately 8.2 million ha, in Ghana (FAO 2002). It lies between the savannah-forest transitional zone and moist semi-deciduous forest zone in the south and the guinea savannah in the north (Swaine 1992). Principally, it serves as a buffer between the high forest zone and the guinea savannah by virtue of its strategic location. It provides tremendous ecosystem services by safeguarding the basins of major river bodies that are sources of potable drinking water to urban centres and recharge the Volta Lake, a major hydroelectric supply as well as a sanctuary for diverse fauna in Ghana. However, overpopulation, agriculture expansion, recurrent bushfires and other anthropogenic disturbances have impacted the natural vegetation, converting a large proportion to high savannah woodland.

Moreover, natural regeneration is usually impaired after major anthropogenic disturbances due to weed invasion (Awanyo et al. 2011). Resolving this problem requires some kind of intervention through the restoration and reforestation of the area. However, the large-scale deployment of trees in the ecosystem through reforestation projects has been criticised as negatively impacting hydrological (Bellot et al. 2004, Maestre and Cortina 2004) and nutrient recycling dynamics as well as soil chemical reactions (Montagnini 2000). In addition, the planting of forest trees affects native floral diversity (van Wesenbeeck et al. 2003). Thus, the use of trees for restoration and reforestation purposes requires careful evaluation prior to implementation.

However, in Ghana, the intact forest cover that remains in the dry semi-deciduous forest zone is in the form of isolated patches along riverine courses, sacred groves and in the remaining 40 forest reserves located in this ecological zone. Moreover, most of these forest reserves are partly or completely degraded, notably the Pamu Berekum, Tain I and Tain II forest reserves (Hawthorne and Abu-Juan 1995). In general, deforestation in Ghana is estimated at an annual rate of 1.7% of the total forest area (FAO 2000). As a result, it has become a policy of the government of Ghana beginning in the 1990s to vigorously pursue restoration or rehabilitation activities to re-establish the ecological, social and economic values of degraded forest reserves in the country.

## 1.2 Provisional procedure for seed zonation of African mahogany populations in Ghana

Restoration activities require the use of seedlings or seeds from sources with the highest level of adaptation to the prevailing ecological conditions at the restoration location. Seed movement guidelines are usually not available for most tropical timber tree species for which restoration and reforestation activities are conducted, as in the case of African mahoganies. Thus, simple assessment tools that do not require extensive provenance tests or trials are a necessary prerequisite. The application of ecogeographic variation and phenotypic responses in plant populations along environmental gradients with respect to leaf morphology has been employed as a preliminary assessment tool to delineate ecological zones for seed collection and movement in some forest tree species (Uribe-Salas et al. 2008). However, other studies have focused on a common garden approach to assess genetic variation with respect to ecogeographic gradients and quantitative traits in plant populations (Saenz-Romero et al. 2006, Viveros-Viveros et al. 2009). These practical procedures emphasised the intimate inter-linkage between tree morphometric variations in particular leaf morphological characters, growth performance and environmental factors (Uribe-Salas et al. 2008, Viveros-Viveros et al. 2009, Hopkins et al. 2008). In general, variations in plant morphological traits across extensive ecogeographical areas follow clinal patterns of differentiation at both species and population levels (Endler 1986, Petru et al. 2006). Such variations in morphological traits occur in particular under conditions of environmental heterogeneity with respect to ecogeographical variables and environmental gradients (Endler 1986). These variations in morphological characters offer practical flexibility for matching appropriate phenotypes to specific environmental conditions without extensive provenance trials, based on the assumption that adaptive differentiation corresponds to environmental heterogeneity (Gonzalez-Rodriguez and Oyama 2005, Li and Yu 2009, Picotte et al. 2009). Thus, adaptations to local conditions are responsible for creating differences among plant populations with respect to clinal variations in ecological and geographical parameters. Ecogeographic variations in plants can be adaptive in nature, but may also be genetically controlled and/or due to phenotypically plastic responses to environmental gradients (Cordell et al. 1998, Hopkins et al. 2008, Hovenden and Vander Schoor 2003, Warren et al. 2005). However, the importance of phenotypically plastic responses in plants is to produce better variation in phenotype-environment matching under heterogeneous environmental conditions that will result in the highest degree of fitness (Gianoli and Gonzalez-Teuber 2005, Navas and Garnier 2002, Xu et al. 2008).

Variations in leaf morphology and morphometric relationships have been used to differentiate and discriminate among plant populations (Viscosi et al. 2009, Boratynski et al. 2008). Additionally, leaf morphometrics have been used to detect hybridisation and assess the level of introgression in some forest tree species (Kremer et al. 2002, Hodalova et al. 2008, Borazan and Babac 2003). Thus, these approaches offer suitable procedures or proxies to determine similarities and differences in leaf morphology with respect to ecological parameters among the populations or provenances of African mahoganies in the various forest reserves across different ecological zones in Ghana. In addition, this information provides provisional guidelines for delimiting the populations for the purposes of seed collection and movement.

## 1.3 Conceptual framework for the restoration of degraded dry semi-deciduous forest ecosystems

In the absence of natural or anthropogenic disturbances, degraded dry semideciduous forests are expected to regenerate and go through the normal succession pathway to a stable climax state (Figure 1). However, this process does not occur as predicted because of the slow pace of recovery and the low amount or virtual absence of seeds or propagules in the soil seed bank to facilitate natural regeneration. The major disturbances in dry semi-deciduous forest ecosystems are anthropogenically induced recurrent bushfires, which decimate the forest cover and allow the invasion of noxious grasses such as *Imperata cylindrica*, *Pennisetum purpureum,* and *Adropogon* species and the invasive broad weed *Chromolaena odorata*. These weeds suppress natural regeneration and further convert the original forest to a savannah-like ecosystem (Awanyo et al. 2011). Moreover, agricultural activities in the dry semi-deciduous forest zone involve traditional slash-and-burn methods. Traditional slash-and-burn under shifting cultivation leads to poor soil fertility and the abandonment of agriculture with subsequent weed invasion. The static nature of the environment and the presence of perturbation require some form of intervention to remove these limiting factors and initiate the process of natural regeneration. The appropriate approach involves restoration through the planting of indigenous tree species to catalyse the process of natural regeneration (Parrotta et al. 1997a) or the cessation of recurrent bushfires to allow the slow process of natural forest regeneration to take place. However, in the absence of anthropogenic disturbance, the perceived pathway to natural regeneration may deviate from the normal succession trajectory under a perfect, closed system due to the invasion of weeds.

In the case of the dry semi-deciduous forest zone in Ghana, succession could lead to a climax community of savannah woodland with low tree species diversity. This is because recurrent wildfires exert selection pressure for fire-resistant tree species to the detriment of non-fire-resistant tree species (see Hooper et al. 2004). A low tree diversity could also stem from a low density of seeds and propagules in the soil seed bank (e.g., see Aide and Cavelier 1994). The likely solution is a restoration effort involving a dual approach that integrates fire prevention and the use of indigenous tree plantations to foster natural regeneration and the establishment of tree diversity. In Ghana, the main primary techniques used in restoration efforts to mitigate the effects of degradation on forest ecosystems are natural regeneration, enrichment planting, mixed plantation, monoculture and land rehabilitation using agroforestry systems (Taungya) as well as fire prevention.

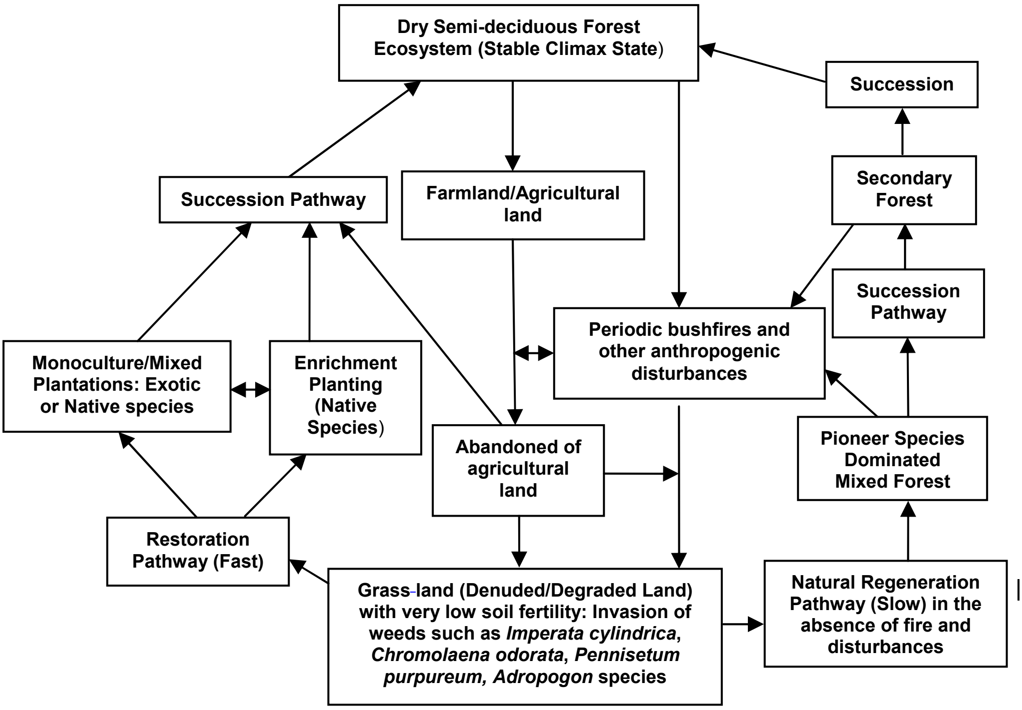

**Figure 1.** Schematic presentation of the use of fast-growing indigenous tree species plantation in the restoration of degraded dry semi-deciduous forest ecosystems in Ghana. The indigenous tree species plantations facilitate or catalyse the regeneration, recruitment and establishment of a greater diversity of native flora.

### 1.4 Effects of stand structure and tree species numbers on recruitment

Enrichment planting is normally employed to increase the economic value of overexploited secondary forest by increasing the density of high-value timber species. The planting procedure involves clearing strips in the existing vegetation that mimic natural gaps. However, other desirable tree species are usually left in the stand. The amount of light energy reaching the strips or gaps depends on the strips' width and orientation and the height of existing vegetation in the stand (Doucet et al. 2009). However, in enrichment planting, the stand's characteristics have tremendous effects on recruitment and tree establishment through their influence on resource availability, particularly light and nutrients. Stand-level characteristics such as basal area, dominant tree height, crown width and growing spaces are the key variables used in investigating or modelling the effects of stand characteristics on recruitment and tree establishment.

Basal area has been documented to be positively associated with recruitment (Pacala et al. 1993 cited in Schweiger and Sterba 1997). However, it has been shown that the basal areas of the surrounding canopy trees in the forest stand could be moderately negatively associated with recruitment (Noguchi and Yoshida 2009). Any incremental change in the basal area of a stand could lead to a decrease in the amount of light reaching the ground level. Moreover, photosynthetically active radiation has a negative exponential relationship with basal area (Espelta et al. 1995). The growing spaces and strips width in enrichment plantings mimic natural gaps, which define resource availability for understory tree species. Hence, recruitment success increases with increasing gap size and decreases with canopy closure.

The dominant height of the surrounding vegetation in the stand determines the amount of shade that the strips in line or gap enrichment plantings receive (Lamprecht 1989). Moreover, the recruitment of young saplings or seedlings has been demonstrated to vary with stand canopy height (Welden et al. 1991). Competition from other species also influences the success of the recruitment and establishment of young plants within the strips of line or gap enrichment plantings. The interactions among the tree species could be asymmetrical, with the dominant species outcompeting or excluding weak and inferior species from the available resources (Leathwick and Austin 2001, Luo and Chen 2011). Moreover, the degree of competition among plants increases with increasing density or population (Miller and Weiner 1989, Kochy and Wilson 2000). The presence of certain tree species in particular suppresses natural regeneration and the recruitment and establishment of young plants or seedlings (Chick and Kielbaso 1998).

### 1.5 Effects of mixed indigenous tree plantings on tree species composition and diversity and soil chemical properties

Mixed indigenous forest tree plantations general have an intrinsic capacity to hasten the recolonisation of degraded, formerly forested areas by providing a suitable substrate for the natural regeneration and recruitment of diverse forest tree species through the removal of any perturbation that may occur in the soil medium (Parrotta et al. 1997a, Parrotta et al. 1997b). This process enables the natural trajectory of the succession pathway to be initiated and self-sustained without further human intervention. Additionally, this promotes the restoration of degraded forest sites (Parrotta et al. 1997a). Moreover, forest tree plantations serve as a conduit for seed dispersal, attracting myriad dispersers that distribute diverse seeds across the degraded site (Wunderle Jr. 1997). This augments the limited number of seeds in the soil seed bank, which invariably increases tree species diversity. In fact, the effects of forest trees plantation in increasing tree diversity, particularly for native tree species in previously degraded forest sites, have been documented (Griscom and Ashton 2011, Stephens and Wagner 2007, Bremer and Farley 2010, Butler et al. 2008).

Forest tree plantations have been used extensively to maintain ecosystem function and to restore soil fertility in degraded zones (Singh et al. 2002, Singh et al. 2004). Forest tree plantations exert tremendous and significant influences on soil chemical reactions and nutrient accumulation and recycling (Nobel and Randall 1999). Forest tree species, through their influence on soil nutrient availability, tend to affect species interactions and successional processes. Forest tree plantations influence nutrient availability and recycling through the incorporation of organic matter and organic carbon from the soil matrix. Additionally, forest tree plantations are the primary sink for atmospheric carbon through the development of both above- and below-ground biomass (Sharrow and Ismail 2004, Ceuvas et al. 1991). There is a direct relationship between soil carbon and organic matter. High levels of soil organic carbon have been reported under mixed plantation after the restoration of a degraded pasture site (Jimenez et al. 2007). Forest tree plantations affect soil pH and chemistry. Changes in soil pH dynamics upon the establishment of forest plantation have been documented (Goma-Tchimbakala et al. 2008, Marcos et al. 2007, Rhoades and Binkley 1996). Moreover, CEC, which is an integral part of soil chemical reactions and a measure of soil fertility status, is greatly influenced by forest tree plantation and the types of tree species. Differential changes in specific cations have been observed following the restoration of a degraded site through forest tree plantations (Boley et al. 2009, Goma-Tchimbakala et al. 2008, Parrotta 1992, 1999). In general, in the tropical ecosystem, nitrogen and phosphorus are major limiting factors. However, forest tree plantings tend to improve soil nitrogen and phosphorus, especially at degraded sites (Marcos et al. 2007, Rhoades et al. 1998). The effect of tree plantings on soil nitrogen and phosphorus depends on the type of tree species planted (Cuevas and Lugo 1998). Nevertheless, high phosphorus availability under mixed native forest tree plantings has been reported (Montagnini et al. 1995). In general, nitrogen-fixing tree species incorporate a high amount of nitrogen into the soil compared to non-nitrogen-fixing species.

## 1.6 Aims of the study

The primary aims of this study were to develop a provisional and rapid framework for delimiting zones for seed production, collection and movement that is based on variations in leaf morphology in relation to environmental variables in African mahoganies, and to identify seed sources from populations with a high level of adaptedness to the prevailing environmental conditions that will facilitate the restoration of degraded forest reserves in dry semi-deciduous ecosystems through reforestation and enrichment planting. In addition, an understanding of the effects of African mahoganies on the species richness, diversity of native trees and nutrient recycling are of paramount concern. However, at the stand level there is limited information on the factors influencing the recruitment and establishment of African mahogany species in enrichment plantings. The specific aims of this research were as follows:

I To develop a provisional framework for seed zonation based on phenotypically plastic responses in quantitative leaf morphological traits along environmental gradients in *Khaya ivorensis* (**Paper I** )

II To evaluate the pattern of quantitative geographic variation in leaf morphology among populations of *Khaya anthotheca* and *Khaya ivorensis* in different ecological zones in Ghana (**Paper II**)

III To examine the inter- and intraspecific variation and evaluate the similarities or dissimilarities among the populations of *Khaya anthotheca* and *Khaya ivorensis* with respect to leaf morphology for purposes of seed zonation (**Paper III**)

IV To assess the impacts of stand structure and numbers of resident tree species on the recruitment of African mahoganies in line-enrichment plantings (**Paper IV**)

V To investigate the differences in soil chemical properties between mixed mahogany plantation and previously degraded, naturally regenerated secondary forest (**Paper V**) ,and

VI To evaluate the effect of mixed mahogany plantation on resident tree species diversity, structure and composition (**Paper VI**).

# 2 MATERIAL AND METHODS

## 2.1 Study areas

The present study was conducted in 12 forest reserves across four ecological zones defined by a precipitation gradient. However, the restoration and enrichment planting experiments involving mixed mahogany species were conducted solely in the Pamu-Berekum (7°30´N, 3°30´W) (Studies IV, V & VI) forest reserve in the dry semi-deciduous ecological zone. Leaf samples for morphometric analyses were obtained from the remaining 11 forest reserves or provenance sites. The leaf samples were collected in May 2008 during the peak of the rain season. In studies II and III, leaf samples from *Khaya anthotheca* populations were collected from five provenance sites located in the dry semi-deciduous ecological zone, namely the Afram Headwaters forest reserve (7°12´N, 1°41´W), Aparapa Shelterbelt forest reserve (7°49´N, 1°16´W), Boma forest reserve (7°11´N, 1° 16´W), Boabeng Fiema Monkey Sanctuary (7°42´N, 1°41´W) and Northern Scape East (6°21´N, 0°46´W). Leaf samples from *Khaya ivorensis* populations for studies I, II and III were obtained from the Bobiri Butterfly Sanctuary (6°42´N, 1°21´ W), Pra-Anum forest reserve (6°16´N, 1°10´W) and Kajeas (6°23´N, 0°59´W), all in the moist semideciduous ecological zone. Additional leaf samples of *Khaya ivorensis* were collected from the Tano Nimiri forest reserve (5°39´N, 2° 36´W) and Subiri forest reserve (5°09´N, 1°52´W) in the moist evergreen ecological zone and Ankasa Conservation (5°16´N, 2°28´W) in the wet evergreen ecological zone.

## 2.2 Leaf morphometrics and data generation (Papers I, II, III)

In paper I, the data were generated from six provenances of *K. ivorensis* in three ecological zones, whereas for papers II and III, the data came from six provenances of *K. ivorensis* and five of *K. anthotheca* in four major ecological zones. A total of 195 mature trees were sampled for the data set used in papers II and III. In paper I, the data set included samples from 120 mature trees. On average, a maximum of 20 populations and minimum of 9 populations were sampled on the basis of availability at the provenance sites. Fifty leaflets per mature tree were sampled at random from the major branches of the crown with the aid of a handheld GPS unit in compass mode facing west.

The sampling methods and design were the same for each provenance site. In total, data on 9750 leaflets from *K. ivorensis* and *K. anthotheca* were used in papers II and III. However, in paper I, a total of 2400 leaflets solely from *K. ivorensis* were used. Fourteen morphological traits were measured, four of which were synthetic or computed variables (Table 1). The synthetic variables, in most cases, constituted ratios that are normally employed to generate additional information with respect to the shape and behaviour of the variable under consideration (Frampton and Ward 1990, Wright and Ladiges 1997). The suitability of the morphological traits selected in the analyses (papers I, II & III) was based on information drawn from the existing published literature (e.g., Bruschi et al. 2003, Gonzalez-Rodriguez and Oyama 2005). The fresh leaf materials for papers I, II, and III were press dried to maintain their shape, preserve them and facilitate easy scanning (Blanco et al. 2006).

The leaves were scanned with an Epson Expression 1640 XL flat bed scanner connected to a personal computer that was configured with an image analysis program (WinFOLIA 4.0, Regent Instrument Inc., Canada) to automatically measure various morphological characters of the leaves for papers I, II and III (Figure 2). However, an interactive method (i.e., manual measurements taken with the cursor and mouse) was used to measure leaf length (LL), leaf maximal width (LMW), apex length (AL), apex angle (AA) and distance from the base of the leaflet to the point of maximum width (PMW). To compute specific leaf mass (SLM) in paper I, the leaflets were oven-dried at a temperature of approximately 40°C for three days to maintain a consistent weight and moisture content. The leaves were then weighed and their respective dry weights were divided by leaf area (LA).

**Table 1.** List of measured or calculated descriptors of leaf morphology.

| | **Primary variables** |
|---|---|
| LL: | Leaflet length (cm) |
| BL: | Leaflet lamina (proxy to distance between two prominent vein (cm) |
| LPD: | Leaflet petiole diameter (cm) |
| LPL: | Leaflet petiole length (cm) |
| LMW: | Leaflet maximal width (cm) |
| PMW: | Distance from base of the leaflet to the point maximal width (cm) |
| AL: | Apex length (cm) |
| LA: | Leaflet surface area ($cm^2$) |
| AA: | Apex angle ($\Theta^{o}$) |
| SLA: | Specific leaflet area ($cm^2\ g^{-1}$) |
| | **Synthetic variables and ratios (or calculated variables)** |
| PO: | Petiole length to the ratio of leaflet length, LPL/LL |
| LO: | Maximal width of leaflet to the ratio of leaflet lamina, LMW/BL |
| PR: | Petiole percentage to total leaflet length, 100 x LPL/(LL+LPL) (%) |
| $LW^{3}/_{4}$: | Leaflet width at three-quarters of leaflet length, LMW x 3/4 |

**Figure 2.** Leaf image acquisition and analysis hardware. The setup is based on high-resolution desktop scanners for image acquisition and the WinFOLIA computer program.

### 2.3 Experimental design and data collection (Paper IV)

Six permanent plots of dimensions 100 m X 100 m for a total area of 6 ha were established in 2000 with *K. anthotheca* and *E. utile* seedlings in a degraded section of the Pamu-Berekum Reserve. At the time of planting, the seedlings had an approximate average height of 50 cm and an age of one year. The planting distance between each pair of seedlings within the strip was 3 m, and the dimensions of the strip or gap were 10 m by 2 m. The strips had an E-W orientation to ensure adequate light interception and reduce the shade cast onto the seedlings by taller overstory trees (Lamprecht 1989). The beating up and maintenance of the seedlings was performed up to the third year after planting, and two scheduled weedings were conducted per year during that period. However, after the third year, no further maintenance was conducted, and the young mahogany trees were left on their own to compete with other species. In the ninth year after planting, inventories were conducted in 150 subplots to generate data with which to run a Poisson regression model. The sampling design involves dividing the six plots (6 ha) into 20 m X 20 m subplots. Every second subplot was systematically sampled along a square grid in the east direction. Censuses were conducted on the selected subplots for all tree species and shrubs with dbh (Diameter at Breast Height; girth at 1.5 m) ≥ 10 cm. In addition, dominant height (H*d*) was determined by computing the average height of the four tallest trees within the subplot. Species density per unit area was also computed. The number of African mahogany species in each subplot that survived at the end of the period was counted, in addition to other major timber species belonging to different families. Diameter at breast height measurements were obtained for all of the sampled trees above a dbh of 10 cm with the aid of fibreglass tape and callipers.

### *2.3.1 Modelling recruitment in enrichment plantings (Paper IV)*

In paper IV, 30 species from 9 families were used in the analytical model. The species were classified into ten groups based on their families (e.g., Vanclay 1991); however, only six groups were incorporated into the analytical model because of the limited data available to evaluate the effect of species numbers on the recruitment of African mahoganies. The effects of stand structure and native species diversity on the recruitment of African mahoganies per unit area were specified using a Poisson regression model, which was selected because the dependent variable is a discrete, or count, variable (Pudney 1989, Cameron and Trivedi 1998).

The model is written as:

$$y_i = e^{x_i\beta} + \varepsilon_i = e^{(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{2i} ..+.....+\beta_k x_k .)} + \varepsilon_i$$

Here, $y_i$ is the number of African mahoganies per unit area; the $x_i$s are the independent variables that represent the populations of the six included groups (Fabaceae, Moraceae, Combretaceae, Sapindaceae, Sterculiaceae and Rubiaceae) of native species as well as stand structure characteristics (BA, SDI, H*d*, S, and C*d*). The variables in stand structure characteristics are defined as follows: the height of the dominant or tallest trees in the stand (H*d*), basal area (BA), the stand density index (SDI), growing space (S) and crown diameter (C*d*); β is the parameter estimate and ε the error term.

## 2.4 Species diversity inventory design and soil sample collection (Papers V, VI)

In 2000, 8 study plots of dimensions 100 m X 100 m each and a total area of approximately 8 ha were demarcated to assess the effect of mixed mahogany species on the diversity and structure of resident tree species (paper VI) and soil chemical characteristics (paper V). These plots consist of 4 plots (4 ha) of mixed mahogany species (*Khaya anthotheca* (Welw.), *Entandrophragma utile* (Dawe and Sprague), and *Khaya grandifoliola* (Welw.) C.DC.) and 4 plots (4 ha) in an adjacent degraded site that was undergoing natural regeneration, primarily of secondary forest interspersed with grasses. The mahoganies were initially planted at a spacing of 3 m x 3 m with a substitution design (papers V, VI) (Kelty and Cameron 1995).

The design used for the studies (papers V, VI) was a completely randomised design (CRD) with two treatments and four replicates. The treatments were plantings of mixed mahogany species and naturally regenerating forest. The plots of the treatments were established on a formerly fire-degraded forest site with the same environmental conditions among the plots. The mixed mahogany plantation did not receive any silvicultural attention for 10 years after its initial establishment. However, additional fire outbreaks were prevented during the period under consideration.

For the purposes of inventorying species diversity (paper VI) and obtaining soil samples for chemical analyses (paper V), the 100 m X 100 m plots were each partitioned into 25 subplots (20 m X 20 m) (papers V, VI). Ten out of the 25 subplots per plot were then randomly selected (100 m X 100 m) (papers V, VI). The selected subplots were subsequently divided into grids or arrays of dimensions 5 m X 5 m for paper VI and 4 m X 4 m for paper V, respectively. However, with the aid of a handheld GPS unit, every second (paper V) or third (paper VI) grid cell from the west to the east direction was systematically selected. The selected grids were inventoried for all tree species with dbh ≥ 5 cm (paper VI). The trees were identified to species and classified into three dbh size classes, 5-10 cm, 10-20 cm, and >20 cm, and three height classes, 1-10 m, 10-15 m, and >15 m (paper VI). Composite soil samples were obtained from the centre of each selected grid with the aid of an auger from depths of 0-10 cm, 10-20 cm and 20-30cm (paper V). The soil samples were then sent to the laboratories of the Soil Research Institute, Council for Scientific and Industrial Research (CSRI), of Ghana for chemical analyses. The detail laboratory standard protocols for measuring and calculating the soil chemical parameters are given in paper V.

### *2.4.1 Measures of species diversity (Paper VI)*

In paper VI, the treatments consist of the site that was restored with a mixed mahogany plantation and the natural regeneration site. Alpha diversity (α-diversity) indices were employed to compare the species diversity and richness of these two contrasting sites. The Shannon-Wiener diversity index (H), Pielou's evenness index (J) and Simpson's diversity index (D -1) (Magurran 2004) were also used in the investigation. The H, J, and D values were calculated for each species per subplot (i.e., subplots 1–40 in the mixed mahogany plantations and 1-40 in the natural regeneration area). Species richness (S) was estimated as a count index, that is, the number of species per unit area. The relative importance of the species and the families present in both the mixed mahogany plantation and the natural regeneration plots was analysed using the importance value index (*IVI*) ( Romero-Dugue et al. 2007, Gonzalez-Iturbe et al. 2002) and the family importance value index (FIV)(Gonzalez-Rivas et al. 2006), respectively. The β-diversity index of similarity for the species compositions of the two sites was evaluated using the Sorensen similarity index ($C_s$) (Magurran 2004).

## 2.5 Statistical analyses

Size correction was conducted through the transformation of all linear leaflet parameters. The overall leaflet size is computed as the square root of the product of total leaflet length and leaflet width. The result of this computation is then regressed against all of the linear leaflet parameters (papers I, II, III). The residuals from the regression are then used to represent the original linear leaflet parameters as input data for further statistical analyses

(Blue and Jensen, 1988, McCoy et al. 2006) (papers I, II, III). This transformation of the variables eliminates the problem of allometric effects, which would reduce the reliability of statistical estimates derived from the parameters and impact the level of significance.

In studies II and III, multivariate statistics were employed in the analyses of the data. The application of multivariate techniques or statistics is particularly formidable in studies that involve taxonomic analyses. In addition, multivariate statistics are suitable in instances where comparisons of samples of organisms taken from different locations or from different taxa are to be made in relation to certain environmental factors (Borazan and Babac 2003, Ter Braak 1986). Principal Component Analysis (PCA) was employed to determine the variation in leaf morphometric characters or traits in papers II and III. Thirteen morphological characters were included in the PCA in paper III and ten in paper II. Discriminant function analysis (DFA) and the unweighted-pair group method with arithmetic average algorithm (UPGMA) were used to evaluate the similarity or dissimilarity among the populations of each taxon (*K. ivorensis* and *K. anthotheca*) from different provenance sites (Cristofolini and Crema 2005) (paper III). In addition, a cluster analysis was performed on six leaflet characteristics using an UPGMA based on the matrix of Euclidean distances between sites (Cristofolini and Crema 2005) (paper III). Loading from the first four principal components (PC1 to PC2) were used as input data for a two-way analysis of variance (ANOVA) with ecological zones and populations as factors (paper III).

However, the loadings from PC1 were also regressed against ecogeographical variables (paper II) to evaluate geographic variation in leaf morphology. Climate data collected over a period of sixteen years (paper II) for each provenance location were obtained from the Ghana Meteorological Department and used in the analyses. PC1 was regressed against mean annual precipitation (MAP), altitude and latitude, the annual aridity index (AAI) and annual potential evapotranspiration (APET) (paper II). The calculation of AAI and APET followed the procedures of Uribe-Salas et al. (2008) and Malmstrom (1969), respectively (paper II). Phenotypic plasticity in leaf morphology along the environmental gradient among populations of *K. ivorensis* was estimated with the environmentally standardized plasticity index (ESPI) (paper I) (Valladares et al. 2006). The environmental factors incorporated into the ESPI were the mean annual precipitation, mean maximum temperature, latitude and altitude for each provenance location.

The ESPI of leaflet length (LL) was regressed against environmental variables (paper I). The variability of the ESPI of leaflet length among populations with respect to environmental factors were evaluated with a one-way ANOVA, and a post-hoc Tukey's test was conducted considering populations as a factor (paper I). In paper IV, a two-stage estimation of the parameters in the Poisson model (3) was tested in quasi-maximum likelihood (QML) estimation within the framework of a Newton-Raphson optimisation algorithm (Stata version 11, data analysis and statistical software, StataCorp LP, 2010). In running the algorithm with Stata statistical software, the robust standard error option was selected for parameter estimation (Cameron and Trivedi 2009).

In paper VII, the mean values of H, S, J and 1-D as well as stand structure variables (DBH and height) for the trees measured in the restored and natural regeneration sites were compared using a t-test. In addition, a t-test was used to compare the differences in the mean values of soil chemical characteristics between soils beneath natural regeneration and mixed mahogany plantation sites (paper V). Afterwards, one-way ANOVA was conducted to evaluate the variability in the soil chemical parameters with soil depth as the main factor (paper V). Most of the statistical analyses were performed with the XLSTAT software package (Addinsoft SARL, Paris, France, 2009) on an Excel platform, whereas the ANOVAs (III) were calculated using SPSS version 17.0 (SPSS Incorporated an IBM Company, Chicago, USA, 2010).

# 3 RESULTS

## 3.1 Phenotypic plasticity and ecogeographic variation in leaf morphology (Papers I, II)

In general, the phenotypically plastic response in *K. ivorensis* in relation to environmental factors varied significantly among the populations (Table 2). The study revealed that the environmentally standardized plasticity index (ESPI) among *K. ivorensis* populations increased with mean annual precipitation and decreased with mean annual temperature, altitude and latitude (Table 2). However, in terms of variations in leaf morphological characteristics with respect to ecogeographical variables, leaf size (PC1) increased in both *K. ivorensis* and *K. anthotheca* with mean annual precipitation and decreased with annual potential evapotranspiration (APET), annual aridity index (AAI) and latitude (Table 3). The main findings were that both the ESPI and PC1 exhibited the same relationships with mean annual precipitation and latitude. These findings suggest clinal relationships to the environmental gradient. However, significant differences in ESPI at the population level were observed. The highest ESPI values with respect to mean annual precipitation and latitude were recorded for Ankasa Conservation (ANK), followed by the Tano Nimiri forest reserve (TNM). The lowest ESPI in relation to precipitation and latitude among the populations was recorded for the Bobiri Butterfly Sanctuary (BBS) (Figure 2, paper I). These results indicated a south-to-north clinal relationship between leaf morphology and the environmental variables, suggesting that leaf size decreases from south to north. A similar pattern was also observed in other ecogeographical variables in relation to leaf morphological traits in paper II. The highest phenotypically plastic response of leaf length to altitudinal gradient and temperature was recorded in Tano Nimiri and the lowest ESPI values in terms of temperature and altitude were registered for the Bobiri Butterfly Sanctuary and Ankasa Conservation, respectively. However, the ESPIs for all of the environmental variables evaluated in the analyses (temperature, precipitation, latitude and altitude) differed significantly among the populations of *K. ivorensis* (Table 2).

## 3.2 Morphometric variation and similarity among the populations

The two hierarchal factors considered in the analyses of variance contributed significantly to the variation in the leaf morphology of the two species of African mahogany, *K. anthotheca* and *K. ivorensis* (Table 4). However, the results were inconsistent; at the ecological level, PC4 was not significantly different in *K. ivorensis*; similarly, PC1, PC2 and PC4 did not differ significantly in *K. anthotheca* at the ecological level.

Conversely, a significant difference was recorded for *K. anthotheca* in PC1 and PC2 at the population level (Table 4). This observation might stem from the fact that inner and outer zones of the dry semideciduous ecological zone are less heterogeneous and differentiated in characteristics. Thus, partitioned them into two components do not confer much variability at the ecological zone level in *K. anthotheca* populations. The discriminant function analysis separated the populations of *K. ivorensis* and *K. anthotheca* into two distinct groups (Figure 3, paper III). There was a limited zone of convergence among the populations of these two species. The level of interaction is too minimal to ascribe any hybridisation to the observed convergence. To be absolutely certain, an investigation at the molecular level will be required.

**Table 2.** Summary results of a one-way ANOVA of the Environmental Standardized Plasticity index (ESPI) and the linear relationship between the ecogeographic variables of six provenance sites of *Khaya ivorensis*: Pra-Anum Headwaters (PAH), Bobiri Butterfly Sanctuary (BBS), Subiri Forest Reserve (SFR), Ankasa (ANK), Tano Nimiri (TNM) and Kajeas Forest Reserve (KFR) (**Paper I**).

| | **Variance Components** | | | **Linear regression fits of ESPI of leaf length and ecogeographic variables** | | | | |
|---|---|---|---|---|---|---|---|---|
| **ESPI** | **Population (%)** | **Error (%)** | **P-value** | **Direction ESPI** | **X** | **Equation *** | **P-value** | **$R^2$** |
| Precipitation | 94.64 | 5.36 | <0. 0001 | ↑ | ↑ | Y=1E-06X - 0.0002 | <0.001 | 0.7954 |
| Temperature | 97.66 | 2.34 | <0. 0001 | ↓ | ↑ | Y=-0.0083X+0.4195 | <0.001 | 0.7811 |
| Altitude | 96.50 | 3.50 | <0. 0001 | ↓ | ↑ | Y=-2E-06X + 0.0018 | <0.001 | 0.8198 |
| Latitude | 97.63 | 2.70 | <0. 0001 | ↓ | ↑ | Y=-0.3324X + 2.914 | <0.001 | 0.6105 |

*Where Y is ESPI and X represents the ecogeographic variables (Precipitation, Temperature, Altitude and Latitude) within a row.

**Table 3.** Results of the linear relationship between the individual scores of the first principal component (PC1) and ecogeographic variables: Latitude, Precipitation, Annual Potential Evapotranspiration (APET) and Annual Aridity Index (**Paper II**).

| | **Latitude** (Ө$^o$) | **Precipitation** (mm) | **Annual Potential Evapotranspiration** (mmday$^{-1}$) | **Annual Aridity Index** (Cmm$^{-1}$) |
|---|---|---|---|---|
| ***Equation** | | | | |
| *Khaya anthotheca* | Y = -3.1433X+23.143<br>$R^2$ = 0.9271 | Y = 0.0472X-61.091<br>$R^2$ = 0.9526 | Y = -63.28X+12.466<br>$R^2$ = 0.5682 | Y = -6.0774X+22.532<br>$R^2$ = 0.8312 |
| *Khaya ivorensis* | Y = -2.925X+16.854<br>$R^2$ = 0.6173 | Y = 0.0065X-10.86<br>$R^2$ = 0.5908 | Y = -18.209X+0.7365<br>$R^2$ = 0.7365 | Y = -3.2603X+15.81<br>$R^2$ = 0.8576 |
| PC1 | (-)↓ | (+)↑ | (-)↓ | (-)↓ |
| Eco-geographic variables | (+)↑ | (+)↑ | (+)↑ | (+)↑ |

The signs in parentheses and the arrows depict the direction of the association between PC1 and the geographic variables. A positive sign indicates increase and negative decrease. *Y denotes PC1 in the linear regression fit and X represents any of the ecogeographic variables in a column of the table.

Nevertheless, the two *Khaya* species have complementary distributions with *K. anthotheca* restricted to the dry semi-deciduous ecological zone and *K. ivorensis* confined more or less to humid environments. Moreover, the cluster analysis divided these two primary groups into subunits based on either the similarity or dissimilarity of their morphological characters (Figure 4, paper III). The first group consists of six subunits, primarily populations of *K. ivorensis,* and the second cluster has five subunits or sets comprised of *K. anthotheca* populations (Figure 4, paper III). The Bobiri Butterfly Sanctuary (BBS) and Kajeas Forest Reserve (KFR) populations of *K. ivorensis* were considered phenetically closely related in terms of leaf morphological characteristics, whereas the rest of the four populations (Subiri Forest Reserve (SFR), Tano Nimiri (TNM), Pra-Anum Headwaters (PAH) and Ankasa Conservation (ANK)) were dissimilar based on the UPGMA analysis. However, in *K. anthotheca,* the UPGMA analysis identified two sets of populations considered to be phenetically related; the Boma forest reserve (BOMA) and Afram Headwaters forest reserve (AHF) comprised one set and the Boabeng-Fiema Monkey Sanctuary (BFM) and Aparapa Shelterbelt (ASB) comprised the second set of populations. The Northern Scape East Forest (NSE) was a distinct population (Figure 4, paper III).

### 3.3 Effects of stand structure and tree species diversity on recruitment

The effects of stand structure variables and the abundances of resident tree species from various family groups on the recruitment of mahogany species in enrichment plantings were analysed with a two-stage Poisson regression model (Paper IV). The summary of the estimated parameter is given in table 4.The key stand structural variables that were evaluated in the model significantly influence recruitment in Africa mahoganies. The results indicated that basal area (BA), growing space (S) and crown diameter (C*d*) were positively associated with the recruitment of African mahoganies in line-enrichment plantings. However, increasing dominant height (H*d*) of the remnant stand was correlated with decreased recruitment in mahogany species (Table 4). In addition, the abundances of the species belonging to the six groups considered in model, Fabaceae, Moraceae, Combretaceae, Spinadaceae, Sterculiaceae and Rubiaceae, were significantly negatively associated with the recruitment of African mahoganies (Table 4). The behaviour of the model is best understood from the principle of static analysis, for instance, based on the parameter estimate (i.e., coefficient ′′β′′; 0.053496) of BA; a unit change in this variable will lead to a 5.3% increase in recruitment (Table 4). Similarly, a unit change in the coefficient of the parameter estimate of Fabaceae will decrease recruitment by 9.2% (Table 4). The direction of the change in recruitment depends on the sign and size of the coefficient of the parameter estimate of the variable in the model.

**Table 4.** The first part of the table provides summary statistics of two-way ANOVA for the first four principal components of foliar morphological characteristics in *Khaya ivorensis* and *Khaya anthotheca*. The variance components have been partitioned as percentages at two hierarchical levels, ecological zones and populations. The second part of the table provides a summary of the results of Poisson regression modelling of the effects of stand characteristics and species diversity on the recruitment of African mahoganies. The model is based on the mean annual numbers of African mahoganies recruited per unit area. The parameter estimates, their standard errors and the Wald test of significance (Z) are also given in the table. (**Paper III, IV**).

| **Species** | **Trait** | **Variance Components** | | | | |
|---|---|---|---|---|---|---|
| | | **Ecological zones** | | **Populations** | | **Error** |
| | | **%** | **P** | **%** | **P** | **%** |
| **Khaya ivorensis** | PC1 | 34.28 | **0.000** | 61.47 | **0.000** | 4.25 |
| | PC2 | 71.32 | **0.000** | 27.91 | **0.000** | 0.77 |
| | PC3 | 49.71 | **0.000** | 47.61 | **0.000** | 2.68 |
| | PC4 | 36.31 | 0.076 | 49.64 | **0.015** | 14.05 |
| **Khaya anthotheca** | PC1 | 12.33 | 0.276 | 77.30 | **0.000** | 10.37 |
| | PC2 | 1.00 | 0.621 | 94.93 | **0.000** | 4.07 |
| | PC3 | 83.92 | **0.000** | 10.80 | 0.107 | 5.80 |
| | PC4 | 15.83 | 0.450 | 56.47 | 0.107 | 24.70 |

| **Poisson regression models** | **Variable** | **Coefficient (β)** | **Std. Error** | **Z-Statistic** | **P>\|Z\|** | **R$^2$** |
|---|---|---|---|---|---|---|
| | Constant | 4.049070 | 0.970377 | 4.172679 | **0.0000** | **0.24** |
| | BA | 0.053496$^{**}$ | 0.020969 | 2.551198 | **0.0107** | |
| | H*d* | -0.042561$^{*}$ | 0.020117 | -2.115650 | **0.0344** | |
| | SDI | 0.000103 | 5.63E-05 | 1.822386 | 0.0684 | |
| | S | 1.964375$^{***}$ | 5.279203 | 3.720969 | **0.0002** | |
| | C*d* | 1.037160$^{*}$ | 0.486409 | 2.132281 | **0.0330** | |
| **Goodness-of-fit chi$^2$** = 98.510<br>**Prob > Chi$^2$ (70) =** 0.067 | | | | | | |
| | Constant | 2.696157 | 0.194713 | 13.85 | **0.003** | **0.28** |
| | Fabaceae | -0.092743$^{***}$ | 0.031170 | -2.98 | **0.000** | |
| | Moraceae | -0.079981$^{***}$ | 0.018994 | -4.21 | **0.000** | |
| | Combretaceae | -0.116415$^{***}$ | 0.026457 | -4.71 | **0.000** | |
| | Spinadaceae | -0.099915$^{***}$ | 0.026457 | -3.78 | **0.000** | |
| | Sterculiaceae | -0.010281 | 0.039198 | 0.26 | 0.793 | |
| | Rubiaceae | -0.075033$^{***}$ | 0.020170 | -3.72 | **0.000** | |
| **Goodness-of-fit chi$^2$** = 60.233<br>**Prob >Chi$^2$ (61)** = 0.5039 | | | | | | |

Significance levels: **P*<0.05; ***P*<0.01; ***< 0.001. The P-values in bold are significantly different (*P*<0.05)

## 3.4 Effects of mixed mahogany plantation on tree diversity and soil chemical properties

The plots restored with mixed mahogany plantation and the control that is, the previously degraded site that had undergone natural regeneration, registered significant differences in most of the soil chemical properties analysed at the end of the 10 year study. On the whole, the plantation plots performed better than the natural regeneration plots. The soils beneath the mixed mahogany plantation recorded the highest mean values of most of the soil chemical properties considered in paper V. In particular, Mg, Ca, total N, base saturation, total exchangeable bases (TEB), CEC, organic C and organic matter were significantly higher underneath mixed plantation compared to the degraded natural regeneration site (Table 5). Soil pH was relatively higher in the soils beneath mixed mahogany plantation plots and lower in the soils beneath degraded natural regeneration plots. However, the mean concentrations of Al, K and Na were significantly higher in the soils underneath the degraded natural regeneration plots compared to the mixed mahogany plantation plots (Table 5). In general, soil chemical properties declined moving down the soil profile (increasing soil depth) at both sites (Table 2, paper V).

The four diversity indices used in study VI to assess tree species diversity and composition differed significantly between the mixed mahogany and natural regeneration plots. In all cases, the mixed mahogany plantation plots registered the highest values for all four of the diversity indices used in the evaluation compared to the natural regeneration plots (Table 5). However, Pielou's index of evenness was not significantly different between the two sites. In comparing the two contrasting sites (i.e., mixed mahogany plantation and natural regeneration plots) at the community level in terms of the similarity in tree species assemblages over time, a relatively low Sorensen similarity index (70.3%) between the communities was recorded for tree species (Table 5). Nevertheless, 17 unique species were found to be solely associated with the mixed plantation plots compared to 5 species for the natural regeneration plots (Table 3, paper VI). Index (IVI) values, were *Ficus exasperate*, *Terminalia superba*, *Morida lucida*, *Antiaris toxicaria, Trema occidentalis* and *Vernonia amygdalina* (Table 4, paper VI). Moraceae, Fabaceae, Mimosaceae, Euphorbiaceae and Combretaceae were the top five families in terms of the Family Importance Value (FIV). The most specious families at both sites were Moraceae and Fabaceae (Table 5, paper VI). The structural distributions of diameter class and height class were skewed toward a relatively large proportion of smaller woody tree species, an indication that succession is ongoing and a stable climax state has yet to be attained. However, the average dbh and height differed significantly between the mixed mahogany plots and natural regeneration plots. Mixed mahogany plots recorded the highest mean values of species diameter and height compared to natural regeneration plots (Table 5).

**Table 5.** Summary results of t-test statistics on the top soil (bulk sample) chemical properties, plant community structure characteristics and measures of diversity for the two sites (planted: mixed mahogany and natural regeneration) of regenerated dry semi-deciduous secondary forest at the Pamu-Berekum Forest Reserve in Ghana. The reported measures are means and corresponding standard errors (SE). (**Paper V, VI**)

| **Measures** | **Mixed plantation site** | **Degraded forest/ natural regeneration site** | **Significance Level** |
|---|---|---|---|
| **Soil Parameters** | **Mean± SE** | **Mean ±SE** | **P-value** |
| pH($H_2O$) | 6.23±0.12 | 4.96±0.11 | 0.0001 |
| Organic C (%) | 2.94±0.32 | 1.03±0.07 | 0.0001 |
| Organic Matter (%) | 5.07±0.54 | 1.78±0.13 | 0.0001 |
| N (%) | 0.25±0.03 | 0.19±0.01 | 0.0250 |
| P (ppm)* | 0.17±0.07 | 0.33±0.08 | 0.1650 |
| K (meq/100 g) | 0.12±0.01 | 0.59±0.07 | 0.0001 |
| Na (meq/100 g) | 0.04±0.01 | 0.10±0.01 | 0.0001 |
| Ca (meq/100 g) | 12.43±1.28 | 4.33±0.62 | 0.0001 |
| Mg (meq/100 g) | 14.00±2.04 | 0.80±0.09 | 0.0001 |
| Al (meg/100 g) | 0.10±0.01 | 2.16±0.26 | 0.0001 |
| TEB (meq/100 g) | 26.59±2.57 | 5.82±0.76 | 0.0001 |
| ECEC (meq/100 g)[#] | 26.69±2.57 | 7.97±0.55 | 0.0001 |
| Base saturation (%) | 99.57±0.04 | 68.99±4.37 | 0.0001 |
| ****Diversity indices** | | | |
| Simpson's index of diversity (D–1) | 0.835±0.021 | 0.768±0.016 | 0.0370 |
| Shannon-Wiener diversity Index (H´) | 1.906±0.074 | 1.596±0.062 | 0.0030 |
| Species richness (S) | 10.10±0.566 | 7.926±0.370 | 0.0030 |
| Pielou's evenness index (J) | 0.821±0.017 | 0.776±0.017 | 0.0600 |
| Sorensen's similarity index ($C_s$)[e] | 70.30 | 70.30 | - |
| *****Stand structure** | | | |
| DBH (5-10cm) | 12.90±0.731 | 9.04±0.670 | 0.0001 |
| DBH (10-20cm) | 12.63±0.705 | 9.78±0.553 | 0.0030 |
| DBH (≥20cm) | 9.63±0.834 | 4.82±0.527 | 0.0001 |
| Mean DBH (cm) | 16.28±0.456 | 13.04±0.325 | 0.0001 |
| Height (1-10m) | 18.70±0.795 | 13.33±0.986 | 0.0001 |
| Height (10-15m) | 11.63±0.925 | 9.78±0.701 | 0.1220 |
| Height (≥15m) | 3.93±0.669 | 1.85±0.313 | 0.0090 |
| Mean height (m) | 11.17±0.244 | 9.82±0.195 | 0.0001 |

*Available Brays phosphorous (P); [#]Effective cation exchange capacity; [e] Sorensen similarity index was calculated for the entire 8 ha study plots;**Calculation is based on 20 m X 20 m subplots; ***Number of individual tree species observed for the specified interval (of diameter or height) per hectare.

The six most dominant and abundant tree species at both sites, which were assigned the highest Importance Value.

# 4 DISCUSSION

## 4.1 Phenotypic plasticity and ecogeographic variation in leaf morphology (papers I, II)

In this study (I), *K. ivorensis* depicted a phenomenal, highly phenotypically plastic response of leaf morphology, in particular leaflet length, to the environmental variables considered in the investigation. Variability in the magnitude of the phenotypically plastic response was observed among the populations of *K. ivorensis*. In general, the highest magnitudes of the ESPI in relation to mean annual precipitation, mean annual temperature and latitude were recorded for the Tano Nimiri Forest Reserve and Ankasa Conservation (paper I). These strong associations of the ESPI with environmental variables followed south to north clinal relationships. In addition, the ESPI of leaflet length in *K. ivorensis* declined with increasing altitude (paper I). This interesting observation is not uncommon for forest tree species (e.g., see commentary in Thomas 2011, Cordell et al. 1998). Moreover, leaflet morphological traits were observed to vary with precipitation, the annual aridity index, annual potential evapotranspiration and latitude in *K. ivorensis* and *K. anthotheca* (paper II). Nevertheless, there are intimate interrelationships among these three key ecogeographical variables. The interdependence of these variables is directly connected to precipitation dynamics (Arora 2002). In Ghana, there is a strong association between the characteristics of forest tree species and the ecological zones as defined by the precipitation gradient (Swaine 1996). In paper II, among the populations of the two *Khaya* species investigated, it was observed that the measurements of leaf morphological traits increased with average precipitation and declined with increases in the annual aridity index, evapotranspiration and latitude across the distributional range in Ghana. These findings are consistent with other studies involving different forest tree species (Fonseca et al. 2000, Uribe-Salas et al. 2008). The direct relationship between leaf morphological traits and average precipitation has been described as one of the mechanisms employed by plants to reduce desiccation and maximise water use efficiency (e.g., Picotte et al. 2009, Picotte et al. 2007).

Almost all of the environmental variables investigated vary along a latitudinal gradient. In general, the southern populations of *K. ivorensis and K. anthotheca* have larger measurements for morphometric traits compared to those in the north, possibly differentiated along an environmental gradient (paper II). These variations in morphological traits along an environmental gradient are also reflected in the magnitude of the phenotypically plastic response in *Khaya* species (paper I). In Ghana, there is a gradient in the amount of rainfall from the south to the north; it is wetter in the south than in the north of the country. The differentiation of the populations of African mahogany species along a geographic gradient suggests the capacity of the populations to adapt to local environmental conditions. The underlying cause of population differentiation could be the phenotypically plastic response in the species and/or genetic variation (e.g., Byars et al. 2007). Thus, this provides a suitable framework for delineating provisional zones for seed collection and movement in the country (e.g., Uribe-Salas et al. 2008). This is under the premise that the level of adaptedness in the populations of *K. ivorensis* and *K. anthotheca* is closely related to the observed variation in the environmental gradient. Hence, populations at high latitudes could be provided with assisted migration to lower latitudes in anticipation of climate change, or seeds collected from higher latitudes could be used for reforestation or restoration activities within the same zone or moved to wetter and more productive lower latitudes (Figure 1, paper II). Moreover, it is plausible to suggest that those populations with high ESPIs, such as the Tano Nimiri Forest Reserve and Ankasa Conservation, may exhibit a low level of fitness in dry environments due to the cost of phenotypic plasticity

(DeWitt et al. 1998, Auld et al. 2010). In contrast, those populations with low ESPIs are predicted to function optimally under wet environmental conditions.

## 4.2 Morphometric variation and similarity among the populations (paper III)

The general pattern observed was that the two species of African mahogany, *K. anthotheca* and *K. ivorensis,* exhibited significant leaflet morphometric variation at all of the hierarchal levels considered in the analyses (paper III). However, most of the variations were observed at the ecological zone level, indicating that environmental heterogeneity in terms of resource availability might have contributed to the variation (Picotte et al. 2009). Nevertheless, a portion of the leaf morphometric variation was registered at the population level. These results are consistent with other studies (Blue and Jensen 1988, Bruschi et al. 2003). Furthermore, the ordination analyses separated all populations and individuals of the two *Khaya* species investigated into two separate and unique phenetic groups without any intermediates.

On the bases of the results from the leaf morphometric analyses, it could be presumed that hybridisation between the two *Khaya* species has not occurred despite the fact that they have overlapping distributions in Ghana. However, as morphometric analyses alone cannot be used to ascribe hybridisation, the application of molecular markers is necessary in this regard. Moreover, the cluster analysis suggested the existence of two major phenetic groups constituting *K. ivorensis* and *K. anthotheca.* Within the *K. ivorensis* phenetic group, the Bobiri Butterfly Sanctuary and Kajeas populations were considered morphologically similar and the remaining four populations were considered dissimilar or to be a distinct cluster. This differentiation among the populations is closely related to ecological zone. The ecological zones are defined by the precipitation gradient in the country. With the exception of the Pra-Annum forest reserve, each of the dissimilar populations falls within the moist and wet evergreen forest ecological zones, where the highest amounts of precipitation in the country are recorded. In the case of *K. anthotheca,* the projection consisted of two subsets, which were considered to be phenetically or morphologically similar. However, the Northern Scape East forest reserve (NSE) was considered to be distinct from all other populations of *K. anthotheca*. This distinctiveness of NSE is primarily due to geographic isolation. NSE is located on top of one of the highest mountain ranges in the country. The implications of these observations for seed zonation are that, for instance, seeds from NSE should be planted at higher altitudes. Seeds from the distinct populations of *K. ivorensis* in the moist and wet evergreen forest zones should be planted in the same ecological zone from which they were derived. However, seeds from the moist evergreen forest zone could be sent to either the wet evergreen forest zone or the moist evergreen ecological zone.

## 4.3 Effects of stand structure and tree species numbers on recruitment (paper IV)

The key stand-level variables evaluated in the model had significant influences on the recruitment of mahogany species in various directions. In study IV, basal area (BA) had a significant positive influence on the number of African mahoganies recruited during the period under consideration. The positive association of BA and the recruitment of African mahoganies reflects the characteristics of so-called non-pioneer light demander species (Hawthorne 1993). However, the relationships between BA and recruitment in forest trees are inconsistent and species-specific, different responses having been reported (Noguchi and Yoshida 2009, Kariuki et al. 2006). In general, the BA of a stand is considered a parameter for measuring population density, which invariably captures space and resource availability, both of which facilitate recruitment in forest tree species (e.g., Eriksson and Ehrlen 1992). In particular, light availability at the ground level is strongly influenced by incremental changes in basal area and hence recruitment (Espelta et al. 1995).

In study IV, the dominant height (H*d*) was found to be negatively related to recruitment, which is indicative because H*d* captures the amount of shadow or shade that can be cast on the young mahogany species. However, it has been suggested that the greater the height of the stand the more unfavourable the light conditions on the ground in line-enrichment plantings (Lamprecht 1989, page 117). Moreover, in enrichment plantings, light is one of the major limiting factors for recruitment and invariably depends on the width of the strips and their orientation in space (Pena-Claros et al. 2002, Lamprecht 1989).

The crown width (C*d*) and growing spaces (S) are measures of competition and resource availability in the stand (e.g., Krajicek et al. 1961, Condes and Sterba 2005). Additionally, C*d* and S determine the level of canopy openness and growth efficiency, which are functions of the amount and quality of light energy reaching the understory. Furthermore, these two variables (Cd & S) provide an indication as to the intensity of competition for and the availability of below-ground resources, particularly water and nutrients (e.g., Palik et al. 1997). In this study, S and C*d* were found to be positively related to the recruitment and establishment of African mahoganies. These relationships are concordant with the findings of Palik et al. (1997). Light energy and below-ground resources depend on C*d* and S; therefore, a reduction in these parameters will limit their availability and subsequently recruitment and establishment. All things being equal within the context of this study and the limitations of the model, it is notable that silvicultural manipulations of these stand variables will facilitate recruitment and enhance the establishment of mahogany species in line-enrichment plantings.

The interactions of the African mahoganies with various tree species groupings (families) were negative and asymmetrical. The intensity of the observed interactions increased with the density of the other species groupings according to the analytical model, leading to reductions in the numbers of African mahoganies recruited. These findings are, to some extent, consistent with the findings of Weiner (1985), which indicated that size inequality increases with increasing density and is usually profound at a high level of productivity. In general, the mechanism behind such interactions within the plant community is usually competition (Brand and Magnussen 1988).

### 4.4 Effects of African mahoganies on soil chemistry and resident native tree diversity and composition (papers V, VI)

This study (paper V) confirms the important role of native forest tree plantation in improving soil chemical properties. The mahogany mixed plantation exhibited differential effects on soil chemical properties, thus suggesting mixed mahogany plantation as an ideal tool to facilitate the restoration of degraded soils in tropical dry semi-deciduous forest ecosystems in Ghana. Surprisingly, there was a slight elevation in the pH of the soil beneath mixed mahogany plantation compared to the degraded natural regeneration site. However, another study has reported a slight pH elevation in the soils upon the establishment of a native forest tree plantation with the objective of restoring a degraded forest ecosystem (Goma-Tchimbakala et al. 2008). In general, a decline in soil pH as a result of a forest tree planting is not uncommon (Rhodes and Binkely 1996). Moreover, it has been indicated elsewhere that the direction and effect of forest tree plantations on soil chemical reaction, particularly pH, depend on the type of forest tree species being planted (Hagen-Thorn et al.

2004). The result of study V with respect to pH has significant importance, especially in the humid tropics and, for that matter, Ghana, where low-pH soils and the associated aluminium toxicity are common occurrences. African mahogany species have the potential to be employed in ecosystem engineering to address problems of low acidity.

The CEC, TEB, Ca and Mg values were particularly high in the soils beneath mixed mahogany plantation compared to the natural regeneration forest site, differing significantly. The high amounts of Ca and Mg beneath the mixed mahogany plantation might have resulted from continuous recycling and accumulation through the biomass (e.g., Adams and Attiwill 1986). The relatively high amounts of base-forming cations in the soil beneath the mixed mahogany plantation might be the reason behind the previously discussed pH elevation in these soils. The higher amounts of Ca and Mg observed in this study (paper V) in the soil beneath the mixed mahogany plantation are consistent with studies involved different species of mixed forest tree plantation (Parrotta 1999, Boley et al. 2009). In general, the high CEC recorded beneath the soils of mixed mahogany plantation might have been mediated by high inputs of organic matter into the soil through litter recycling from the mixed planting stand (for a review see Haynes and Naidu 1998).

The high base-saturation values recorded in the soil beneath the mixed mahogany plantation has directly relationship to the high concentration of Ca recorded at the mixed plantation site. Nevertheless, incremental change in base saturation after pasture land was reverted back to native forest via tree plantation has been reported (Boley et al. 2009). Furthermore, the low level of K concentration under mixed mahogany plantation suggests that either the element is actively extracted from the soil by the mahogany species or it is more mobile in the plant-soil matrix. In this study, the low concentration of Al recorded at mixed mahogany plantation site as compared to the natural regeneration site is imperative due to direct intimate link of soil pH and the Al concentration in the soil (Abreu et al. 2003). At a high pH, the activities of $Al^{+3}$ ions decline in the soil solution in addition to Al availability (for a review see Haynes and Naidu 1998).

The high levels of carbon and organic matter reported in this study in the soils beneath the mixed mahogany plantation are consistent with other studies involving native forest tree plantation employed to catalyse the restoration of degraded forest lands (e.g., Paul et al. 2002, Singh and Zeng 2008). Moreover, the levels of organic carbon and organic matter content in the soil depend directly on the quantity and quality of organic material that could be incorporated in the soil. In general, mixed native forest tree plantations tend to have higher above- and below-ground biomass, which affect soil carbon and organic matter dynamics (Singh and Singh 2006). The soil P was not significantly different between the mixed mahogany plantation site and natural regeneration site. P is generally deficient in tropical soils, especially in Ghanaian soils. Total organic N levels in the soils at mixed mahogany plantation site were higher as compared to natural regeneration site. The present study V, provides additional evidence that mixed forest tree plantation improve soil N pools dynamics compared to mono-specific stands or natural regeneration in a disturbed ecosystem (Parrotta 1999). In general, forest tree species usually exert a tremendous influence on soil nitrogen pools because of their high biomass productivity (Parrotta 1992).

The role of forest tree plantation in aiding the restoration of degraded dry semideciduous forest ecosystems in Ghana has been clearly demonstrated in this study (VI). The mixed mahogany plantation site performed better than the degraded natural regeneration site with respect to all of the indices of diversity employed in the analyses. In study VI, it is clear that the mixed mahogany plantation might have removed the perturbation at the degraded site and facilitated the natural regeneration of a diversity of tree species. The results of study VI support the findings that forest tree catalyse natural regeneration and recruit diverse native tree species (Parrotta et al. 1997a) as well as create the necessary microclimatic conditions for the recolonisation of other native woody species (Wunderle Jr. 1997).

However, in study VI, the major constraint to the recolonisation of the degraded natural regeneration site by diverse woody tree species is the invasion of noxious weeds such as *Chromolaena odorata* and *Imperata cylindrica* (Awanyo et al. 2011). Weed invasion following anthropogenic disturbances in forest ecosystems generally slows down natural regeneration (see, e.g., Kaewkrom et al. 2005). The mixed mahogany plantation is able to modify the prevailing substrate conditions, in contrast with the degraded natural regeneration site, and in the process reduce the incidence of weeds.

The most striking aspect of study VI is the high proportion of woody tree species that were within the low diameter and height classes, an indication that succession is still ongoing and a stable climax state has yet to be attained at both contrasting sites. However, the most dominant and abundant tree species, which recorded the highest Importance Value Index (IVI) values, were *Ficus exasperate* and *Antiaris toxicaria* in the mixed mahogany plantation and natural regeneration sites, respectively. The five families that registered the highest Family Importance Values (FIV) were Moraceae, Fabaceae, Mimosaceae, Euphorbiaceae and Combretaceae. However, the most speciose families at both sites were Moraceae and Fabaceae. The high proportion of species belonging to Fabaceae and Moraceae suggests the role of these families in enhancing soil amelioration. In general, Fabaceae (e.g., *Albizia* species) are nitrogen fixers (e.g., Swaine et al. 2005), whereas Moraceae species of genera such as *Ficus* and *Antiaris* have fast growing habits that enable these species to out-compete weeds in disturbed ecosystems. Additionally, Moraceae have an inherent capacity to conserve moisture by virtue of their morphological characteristics, thus creating the necessary conditions for late arrivals to make succession self-sustaining. It has been suggested that Fabaceae species modify the conditions of the soil microenvironment, thus acting as facilitators in recruiting other tree species to the site (Camargo-Ricalde et al. 2002). The relatively high proportion of *Ficus exasperate* at both sites is because the fruits are easily dispersed by animals (Kaewkrom et al. 2005). *Trema occidentalis* is noted for its role as a pioneer species and has an inherent ability to invade gaps and disturbed secondary forest at early successional stages (Swaine and Hall 1983).

# 5 CONCLUSIONS

This study supported the existence of a highly phenotypically plastic response of leaf morphology to an environmental gradient in *K. ivorensis.* In general, the leaf morphometric variables in *K. ivorensis* and *K. anthotheca* vary with ecogeographic parameters and exhibit a south-to-north clinal relationship. The southern populations have larger measurements of morphological parameters compared to the northern populations, the populations being differentiated along a precipitation gradient that crosses the country. This finding provides a preliminary suitable framework for phenotype-environmental matching to each ecological zone in the country. In terms of similarity among the populations, two sets of *K. anthotheca* and one set of *K. ivorensis* populations were considered to be morphologically related. However, distinctiveness or dissimilarity in leaf morphology among the populations of *Khaya* species in the country is closely associated with ecological zone, which is more or less defined by precipitation amounts. The implication is that seed movement and collection for restoration should be guided by the precipitation regimes of the sources or provenance sites. The success of the recruitment and establishment of mahogany species in line-enrichment plantings depends directly on the stand structure of the remnant forest and the interactions with resident tree species. Within the context of a Poisson regression model, the stand structure variables of dominant height, growing spaces, crown width and basal area exhibited strong influences on the recruitment of African mahoganies. Thus, the silvicultural manipulation of these variables would enhance the recruitment and establishment of mahoganies in enrichment plantings. In addition, due to the asymmetric interactions between mahogany species and other native timber species from six selected family groups, from a practical perspective a reduction in the numbers of those other species per unit area will ensure a high recruitment of African mahoganies.

The study showed that mixed mahogany species could serve as an ideal tool for the restoration of soil chemical properties in degraded dry semi-deciduous forest ecosystems and accelerate the colonisation, recruitment and establishment of native tree species at the site. However, the major constraint to the successful restoration of dry semi-deciduous ecosystems in Ghana is the incidence of recurrent wildfires, which must be curtailed. This could be achieved through a conscientious effort in terms of public education about the detrimental effects of wildfires on forest ecosystem functioning and biodiversity conservation. In addition, the identification and use of fire-resistant indigenous tree species as a greenbelt around forest reserves and forest tree plantations should be encouraged.

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