EVALUATION OF TREE AND SHRUB RESPONSES TO SOIL MOISTURE STATUS AND THEIR POTENTIAL FOR AFFORESTATION IN THE SEMI-ARID RANGELANDS OF MAKUENI DISTRICT, KENYA

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A thesis submitted to the Graduate School in fulfillment for the requirements of the Doctor of Philosophy Degree in Natural Resources Management of Egerton University

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and I wish to declare that the said work has not been submitted elsewhere for a degree.

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Recommendation

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DEDICATION

This thesis is dedicated to my immediate and extended families. In particular to my elder brother Alexander Mengich and Sister-in-law Teriki Mete who took me into their custody following the loss of both my late parents Tarkok Chelagat and Kimengich Arap Kandagor at an early age.

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ABSTRACT

This study was conducted to evaluate responses of trees and shrubs to soil moisture status with the aim of determining drought tolerance indicators for their survival in the semi-arid rangelands of Makueni District, Kenya. Study sites were identified in three major agro-ecological zones, namely, Nthangu, Kathonzweni and Kibwezi forests of Makueni district using existing vegetation, agro-ecological maps and Landsat Imageries. Sample tree and shrub species were identified during field surveys conducted between August and September 2002. Data on vegetation species, soils, and plant and soil moisture parameters were taken for one year between July 2003 and June 2004 to compare the three zones. Collected data was analysed using various parametric and non-parametric tests. The number of tree families, genera and species were largest at Nthangu forest (33, 60, 77) followed by Kibwezi (30, 48, 70) and Kathonzweni (28, 42, 69), respectively. There were significant differences in DBHs (Kruskallis Wallis test, X^2=97.56, d.f=2, $p<0.05$) and heights (Kruskallis Wallis test, X^2=100.9, d.f=2, $p<0.05$) between the three sites. Mean DBHs and heights were 4.6 cm, 6.4 cm and 7.6 cm, and 4.4 m, 5.1 m and 5.3 m, for Nthangu, Kathonzweni and Kibwezi forests, respectively.

Plant water potentials (ψ) were significantly higher ($P<0.05$) at Nthangu forest (ψ=-1.23) than at Kathonzweni (ψ=-1.31) and Kibwezi (ψ=-2.64). Similarly, plant water potentials were significantly lower during the dry seasons than during the rainy seasons, and higher in the morning hours than in the afternoon hours. Transpiration rates (Ti) were significantly lower ($p<0.05$) at Nthangu (Ti=10.24) than at Kathonzweni (Ti=11.35) and Kibwezi (Ti=11.73) forests, significantly lower during the dry seasons than during the rainy seasons, and lower in the morning hours than in the afternoon hours. Stomatal conductances (g) were significantly higher ($P<0.05$) at Nthangu (g=0.88) than at Kathonzweni (g=0.77) and Kibwezi (g=0.62) forests. It was also significantly lower for the exotic species than for the indigenous species ($p<0.05$). Soil moisture contents were highest at Kibwezi (54.2 Kg/m^3) followed by Nthangu (51.2 Kg/m^3) and Kathonzweni (45.1 Kg/m^3) forests. Spatial distributions, size characteristics and water potentials of trees and shrubs were identified as potential indicators of stress and adaptation, based on which *A. tortilis*, and *S. siamea* were recommended for planting to rehabilitate degraded sites in these areas. It was also recommended that more studies be carried out on a wider variety of species and sites, and with more emphasis on water and osmotic potentials.

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ABA	-	Abscisic acid
ACZ	-	Agro-climatic zone
AGB	-	Above-ground biomass
AMF	-	Arbuscular mycorrhizal fungi
ANOVA	-	Analysis of Variance
ANPP	-	Above-ground Net Primary Production
ARIDSAK	-	Agroforestry for Integrated Development in Semi-arid Areas of Kenya
ASALs	-	Arid and Semi-arid Lands
BTC	-	Belgian Technical Cooperation
BGB	-	Below-grour d biomass
DAAD	-	Deutscher Akademischer Austauschdienst (German Academic Exchange Service)
DAEO	-	Divisional A gricultural Extension Office
DBH	-	Diameter at Breast Height
DFO	-	District Fores t Officer
DRSRS	-	Department c f Resource Surveys and Remote Sensing
FERD	-	Faculty of Environment and Resources Development
GoK	-	Government of Kenya
IAEA	-	International Atomic Energy Agency
IDRDU	-	Institute of Dryland Research, Development and Utilization (UoN)
ICRAF	-	International Centre for Research in Agroforestry
ICRISAT	-	International Crops Research Institute for the Semi-arid Tropics
ITCZ	-	Inter-tropical Convergence Zone
IVI	-	Important Value Index
KARI	-	Kenya Agricultural Research Institute
KEFRI	-	Kenya Forestry Research Institute
MAFF	-	Ministry of Agriculture, Fisheries and Food
MPa	-	Mega Pascals

NAD	-	Nicotinamide adenine dinucleotide
NADP	-	Nicotinamide adenine dinucleotide phosphate
NARE	-	Natural Resources Department of Egerton University
PAM	-	Plant-available Moisture
PAN	-	Plant-available Nutrients
PCA	-	Principal Components Analysis
PEP	-	Phosphoenolpyruvic acid (Phosphoenolpyruvate)
PRD	-	Partial Root Drying
RA	-	Relative abundance
R_b	-	Boundary layer resistance
R_c	-	Cuticular resistance
RD	-	Relative dominance
RDI	-	Regulated Deficit Irrigation
RF	-	Relative frequency
R_s	-	Stomatal resistance
R_t	-	Root resistance
R_x	-	Xylem resistance
RSA	-	Root system architecture
SPAC	-	Soil-plant-atmosphere continuum
UNESCO	-	United Nations Educational Scientific and Cultural Organisation
π	-	Osmotic potential
ψ	-	Water potential
g_w	-	Stomatal conductance
Ti	-	Transpiration rate
RGR	-	Relative growth rate
ULR	-	Unit Leaf Rate
UoN	-	University of Nairobi
LAR	-	Leaf Area Ratio
SLA	-	Specific Leaf Area
LWR	-	Leaf Weight Ratio

CHAPTER ONE

INTRODUCTION

1.1 Background

The Arid and Semi-arid Lands (ASALs) cover over 80% of Kenya's land area. In these areas, trees and shrubs contribute significantly to ecosystem biodiversity, structural complexity, and spatial heterogeneity (Belsky et al., 1993b; Banda et al., 2006; Back'eus et al., 2006; L'opez-Pintor et al., 2006). They also increase faunal diversity by providing forage and shade for animals requiring browse and protection from full sunlight.

The occurrence of various species, combinations and proportions of woody and herbaceous plants give rise to different vegetation categories; woodlands, bushlands, shrublands and their intermediates identified based on tree/shrub and herbaceous layer densities, cover and production (Pratt and Gwynne, 1977; Pratt et al., 1966). According to Fleming et al. (2002), woodlands may also be classified under forest types. ASALs socio-economically support about a third of Kenya's over 30 million people, over half of the domestic livestock populations and most (80-90%) of the country's wildlife resources (GoK, 2003; GoK, 2006). Wood and non-wood products and services harvestable from these areas include gums and resins, aloe, charcoal, indigenous fruits, honey, essential oils, silk, edible oil, commercial juices, frankincense, timber, poles, fuelwood, wood for implements, edible herbs, grass for brushes, and insects (Republic of Kenya, 2005; Shackleton et al., 2002). Additionally, woodlands, together with forests provide about 70% of the energy consumed annually and act as sources for fuelwood and charcoal. The demand is currently 31 million m^3 (Ogolla and Mugabe, 1997; Republic of Kenya, 2005).

Rapid human population increase in the ASALs have recently increased pressure on land productivity and resources, and disrupted the ecological balance that has evolved over a long period of time (Republic of Kenya, 2005; GoK, 2006). Vast areas of forest and woodland have been cleared to give way to cultivation and settlement, and to meet the ever-increasing demand for wood products and services. For instance, since the middle of the 20^{th} century, large areas of *Commiphora-Acacia* woodlands and shrublands in Tsavo National park were converted to open savanna, grasslands and open ground through over-exploitation owing to human activities coupled with elephant feeding habits (Glover, 1963).

Likewise, significant proportions of rangeland have been overstocked, selectively grazed and overgrazed due to sudden increases in domestic livestock populations (Odera, 1998). As a result, land degradation has occurred, and the dryland ecosystem has been changed and impoverished (GoK, 2006; Too, 1995). Degraded sites are low in fertility, poor in both floral and faunal biodiversity and often infested and colonized by undesirable plant species of little value to human welfare (Lemenih et al., 2005; Walter, 1971; Fasona and Omojola, 2009). In order to improve land productivity, conserve biodiversity and enhance sustainable environmental and dryland natural resources management (Republic of Kenya, 2005), it is crucial that this land degradation be arrested and the degraded sites rehabilitated. One of the fastest ways of rehabilitating deforested and degraded areas is through tree planting and sustainable management of adapted tree and shrub species. In this study, responses to soil moisture variation of selected woody vegetation species was assessed with the aim of determining drought tolerance indicators for their survival.

1.2 Statement of the problem

Woody vegetation cover in the semi-arid areas of Kenya has continued to decline over time because of over-exploitation due to increased demand for various products and services which has resulted in loss of valuable tree and shrub species. In addition, the number of tree and shrub vegetation that can tolerate drought stress conditions have diminished because of constant use and frequent outbreaks of bushfires, and due to climate change which has resulted in harsher and drier conditions in rangelands (Omambia et al., 2009). Although these species have different morpho-physiological adaptations, and respond differently to soil moisture stress, these adaptations are not well understood. This is because they have not been adequately studied and documented for many of the species in the semi-arid areas of Kenya. Consequently, identification of appropriate tree and shrub species for rehabilitation of degraded sites based on drought resistance is a difficult task. This is due to lack of morpho-physiological adaptation indicators for these tree and shrub species, and failure to recognize and gainfully apply important forces of natural selection such as the r- and k- selectivity (McNaughton, 1975). This limits opportunities for the selection of specific tree species for different agro-ecological zones.

1.3 Justification

The declining woody vegetation cover in arid and semi-arid areas should be minimized. This could include rehabilitation through tree planting. However, for the success of rehabilitation programmes under arid and semi-arid conditions, several conditions need to be met; tree and shrub species most adapted to soil moisture deficiency, and low and poorly distributed rainfall should be identified. This necessitates an understanding of the types and mechanisms of adaptation to moisture stress, the morpho-physiological indicators, and the techniques of studying these mechanisms. This study sought to identify indicators of adaptation using plant and soil moisture dynamics and relationships during wet and dry seasons in Makueni district, Kenya. The results of this study are intended to guide decisions regarding identification of exotic and indigenous trees and shrubs adapted and having potential for survival in the arid and semi-arid rangelands of Kenya.

1.4 Study objectives

1.4.1 Broad objective

The broad objective of this study was to assess the physiological responses of trees and shrubs to soil moisture status with the aim of identifying morpho-physiological adaptation indicators that would guide in identification of appropriate tree and shrub species for rehabilitation of degraded sites in the semi-arid rangelands of Makueni district, Kenya.

1.4.2 Specific objectives

i) To investigate the spatial distribution of indigenous tree and shrub species based on the soil moisture status of major agro-ecological zones of a semi-arid rangeland in Makueni district, Kenya;

ii) To measure the size characteristics (heights and diameters at breast height) of indigenous tree and shrub species based on soil moisture status of the major agro-ecological zones of a semi-arid rangeland in Makueni district, Kenya;

iii) To assess plant and soil moisture dynamics during wet and dry seasons, and at pre-dawn and midday in three major agro-ecological zones of a semi-arid rangeland in Makueni district, Kenya;

iv) To identify morpho-physiological indicators of stress and adaptation in trees and shrubs based on plant and soil moisture dynamics and relationships.

1.5 Study hypotheses

The following hypotheses were tested:

H_{O1} The spatial distribution of indigenous tree and shrub species in semi-arid rangelands has no significant relationship with agro-ecological zonation;

H_{O2} The size characteristics of indigenous tree and shrub species in semi-arid rangelands have no significant relationship with agro-ecological zonation;

H_{O3} Plant and soil moisture characteristics in different agro-ecological zones of semi-arid rangelands do not vary significantly during wet and dry seasons, and at pre-dawn and midday;

H_{O4} There is no relationship between plant-soil moisture and morpho-physiological indicators of stress and adaptation in trees and shrubs in semi-arid rangelands.

CHAPTER TWO

LITERATURE REVIEW

2.1 Soil and plant moisture dynamics

2.1.1 Soil moisture

In reference to soil-plant-water relationships, soil is an important medium for water storage and root growth (Kramer, 1969; Fitzpatrick, 1983; Snyder et al., 2003; Radersma and Ong, 2004; Dolling et al., 2006; Ward and Micin, 2006; Gaza et al., 2006). In soils, the water readily available for uptake by plants occurs in the range between field capacity and permanent wilting point (Okalebo et al., 1993; Cass, 1999). Field capacity, also referred to as the field-carrying capacity, the normal moisture capacity, or the capillary capacity, is the water content after drainage of gravitational water has become very low and water content has become relatively stable (Hillel, 1979). The situation usually exists for 1 to 3 days (about 48 hrs) after the soil has been thoroughly wetted by rain or irrigation and represents a water potential of –0.03 MPa or less (Okalebo et al., 1993; Cass, 1999). Field capacity has been widely used to refer to the upper limit of soil water storage for plant growth (Hillel, 1979). Permanent wilting point, on the other hand, is the water content at which plants become permanently wilted (assuming that the leaves exhibit visible wilting), unless water is added to the soil (Fitzpatrick, 1983). It is widely used to refer to the lower limit of soil water storage for plant growth and corresponds to a water potential of –1 to –2 MPa (i.e. approx. –1.5 MPa on average) (Fitzpatrick, 1983; Okalebo et al., 1993). The range between field capacity and permanent wilting percentage has considerable practical significance in assessments of the agricultural value of soils and constitutes an important field soil parameter (IAEA, 2003). As the water content diminishes within this range, the soil water suction increases and so the plant has greater and greater difficulties in obtaining water, thus experiencing ever-increasing water stress (Fitzpatrick, 1983).

2.1.2 Plant moisture

Water is mainly absorbed by plants as liquid through the roots. A small quantity is absorbed through the leaves and even through twigs (Kramer, 1969). Absorption of water occurs along gradients of decreasing water potential from soil to roots (Fitter and Hay, 1987).

Transpiration produces the energy gradient that causes transpiration pull that in turn controls the rate of absorption and the ascent of sap (Salisbury and Ross, 1978; Kramer, 1969). This often produces midday leaf water deficits. Where drying soil cause absorption to lag behind water loss, permanent water deficits develop causing injury and death by desiccation.

Absorption and transpiration are linked by the continuous water columns in the xylem system of plants i.e. the soil-plant-air continuum (SPAC) (Fitter and Hay, 1987; Kramer, 1969). Movement of water through the soil-plant-atmosphere continuum occurs in both the liquid and gaseous states (Fitter and Hay, 1987). Flow from soil to roots as well as from the root surfaces to the liquid-air menisci at the evaporating sites in the leaves occur in the liquid state along gradients of water potential. Similarly, this occurs over short distances in cells of other tissues in all plant organs.

Flow from the evaporating surfaces within the leaf to the bulk air occurs in the vapour state along gradients of water vapour concentration through the stomata and the cuticle, and to a slight extent in liquid form (guttation). It is assumed that most of the water loss occurs through the stomata, but the cuticular component becomes increasingly important as stomata close (Lawlor, 1987; Willmer, 1983). On its way from the surface of the plant to the bulk air, the vapour moves into the adjacent layer of air (the boundary layer) and then into the open air by diffusion (Lawlor, 1987). The difference in vapour pressure of water within the leaf and in the atmosphere beyond the boundary layer i.e. the atmospheric evaporative demand (Lawlor, 1987; Gaza et al., 2006) is the driving force for transpiration.

2.1.3 Measurement of soil and plant moisture

Moisture in soils and plants may be expressed in terms of either water content or water potential (Fitter and Hay, 1987). The water content is a measure of the amount of water available in the soil or plant, and may be estimated gravimetrically on a weight or a volume basis (IAEA, 2003). Water in the soil-plant-atmosphere continuum can better be understood with the help of the water potential concept. Water potential (symbolized by the Greek letter Psi (ψ)) may be defined as the potential energy (joules) per unit mass of water (m^3) with reference to pure water at zero potential. According to Fitter and Hay (1987),

$$\psi = (R.T.\ln(a_w))/V_w; \quad \text{---------- 1}$$

Where;

R is the gas constant,

T is the absolute temperature,

V_w is the partial molar volume of water and a_w is the activity of water.

As 1.0 Newton = 1.0 J m^{-2}, water potential is expressed in units of pressure (N m^{-2} = Pascals, symbol Pa or more commonly MPa).

Soil water potential (ψ_{Soil}) measures the energy status of the soil water and therefore the amount of force required of the plant to absorb this water. The major component of water potential in non-saline soils is the matric potential, τ, a measure at atmospheric pressure of the tendency for the matrix to adsorb additional water molecules and which is expressed in the units of water potential (Pallardy et al., 1991; Salisbury and Ross, 1978). In saline soils, there is a significant osmotic component, π_{soil} which may reduce the soil water potential by up to –0.2 MPa (Tattini et al., 2002; Bayuelo-Jim'enez et al., 2003; Ebert, 1998; Olukoye et al., 2003; Ali-Dinar et al., 1998; 1999). The contribution of gravitational component potential varies with height at a rate of 0.1 MPa per 10 m (Pallardy et al., 1991). Soil water potential may therefore be expressed as:

$$\psi_{Soil} = \tau + \pi_{soil} + g \quad \text{---------- 2}$$

Where;

ψ_{Soil} is the soil water potential,

τ is the matric potential,

π_{soil} is the soil osmotic potential and g is the gravitational potential.

The water potential (ψ) of a plant (or leaf) mainly consists of osmotic pressure (potential) (ψ_π), which arises from the presence of dissolved solutes in the cell and lowered activity of water attributable to interaction with charged surfaces, and pressure (turgor) potential (ψ_p), which arises from tension in the xylem and the development of positive internal pressures within cells

as water presses against cell walls (Slatyer, 1967; Kramer, 1969; Bayuelo-Jim'enez et al., 2003; Tattini et al., 2002). Each is expressed in pressure units (MPa). Thus:

$$\psi = \psi_{\pi} + \psi_{p}. \quad \text{---------- 3}$$

Pressure potential may have any value. By convention, it equals to zero at atmospheric pressure (i.e. ψ_p=0). Addition of pressure results in a positive pressure potential, and tension (pulling; the opposite of pressure) results in a negative pressure potential. Pressure potential is usually positive in living cells but is often negative in dead xylem elements. The osmotic potential is always zero in pure water and negative when solute particles are added. Since pressure potential can be positive and very high, and osmotic potential can be either zero or negative, water potential can be either negative (osmotic potential is more negative than pressure potential), zero (pressure potential equals osmotic potential but is positive in sign), or positive (pressure potential is more positive than osmotic potential). Water potential of pure water at atmospheric pressure is defined as zero (Salisbury and Ross, 1978). In a solution at atmospheric pressure, water potential will be negative. In pure water under some external pressure above atmospheric, water potential will be positive.

In order for water to flow from the soil to the leaf, the ψ of the bulk soil must exceed the ψ of the root surface which must exceed the ψ of the leaf (i.e. $\psi_{bulk\ soil} > \psi_{root\ surface} > \psi_{leaf}$). Under most conditions, water potential is highest in the soil and lowest in the atmosphere, with intermediate values in the plant; that is, there is a gradient from the soil through the plant to the atmosphere. But the components of water potential vary considerably in the soil-plant-atmosphere continuum (Salisbury and Ross, 1978).

2.1.4 Diffusive resistances

Overall resistance to water movement in plants is of significant importance as it contributes to the determination of the rate at which water flows from the soil to the leaf through the soil-plant-atmosphere continuum. Resistance is highest in the roots, intermediate in the leaves, and lowest in the stems. The series of resistances that may be encountered at any of the various phases of the system are: root resistance (R_r), xylem resistance (R_x), cuticular resistance (R_c), stomatal resistance (R_s) and boundary layer resistance (R_b) (Kramer, 1969).

The resistance to water movement through plant roots (R_t) occurs at the outer cambial and cork layers and at the endodermis in roots with and without secondary thickening, respectively. Cuticular diffusion resistance (R_c) occurs in leaves where the waxy cuticle is a very effective barrier to water loss with small conductances of 0.005 $molm^{-2}s^{-1}$ or smaller (Lawlor, 1987). Stomatal resistance (R_s), the restriction of CO_2 and water vapour (H_2O) transfer between the atmosphere and the internal tissue of the leaf is variable depending on the size of stomatal aperture. Stomatal resistance may be obtained by obtaining the reciprocal of the stomatal conductance as fluxes are inversely proportional to resistances and directly proportional to conductances. Stomatal conductance can be obtained by determining the size of the stomatal aperture or by measuring the rate of gaseous water vapour loss. The air layer surrounding the leaf causes the boundary layer resistance (R_b). Boundary layer thickness, and therefore, conductance (g) at the leaf surface varies with wind speed, surface dimensions and characteristics such as hairiness (Berry and Downton, 1982). According to Lawlor (1987), stomatal pathways operate in parallel with cuticular pathways, and both are in series with the boundary layer. However, maximum stomatal conductance is much greater than cuticular conductance, and much of the gaseous exchange occurs via the stomatal pore.

2.2 Effects of soil moisture deficits on plants in semi-arid areas

In semi-arid areas, long-term and severe water deficits develop when decreasing soil water potential and hydraulic conductivity cause decreased absorption of water. Under these conditions soil suction becomes higher than root suction, causing plant water uptake to decrease or cease altogether and leading to water deficit stress in plants (Radersma and Ong, 2004). There are far-reaching effects of water stress on many plant characteristics and processes (Hsiao, 1973; Salisbury and Ross, 1978; King et al., 2006).

Water deficit stress affects growth and productivity either directly by desiccation (dehydration) (Hsiao, 1973) or through reduced CO_2 assimilation (Hillel, 1979). Hsiao (1973) divides the effects of water stress into 3 levels of dehydration: *mild*, a lowering of the cell water potential by several bars, or up to 8-10% dehydration below saturation, *moderate*, -1.2 to –1.5 MPa or 10-20% below saturation, and *severe*, beyond –1.5 MPa. Mild and moderate dehydrations occur within the zone of cell turgor (including guard cell turgor). They do not quite

decrease cell turgor to zero and are basically elastic and reversible osmotic dehydrations. Severe dehydrations are those which occur within the zone of cell flaccidity.

Cell expansion (growth) is the first growth response to be inhibited by increasing water stress. This is because dehydration induces lack of turgor (a decrease in cell water potential) and reduces (or inhibits) cell growth (enlargement). In common bean (*Phaseolus vulgaris* L.), for instance, significant decreases in leaf water potential were observed for both partial root drying (PRD) and regulated deficit irrigation (RDI) treatments compared to well-watered (WW) treatments (Wakrim et al., 2005). In Canola (*Brassica napus* L.), water deficiency reduced plant growth and altered water relations (King et al., 2006). The minimum turgor pressure for growth occurs at some point above zero turgor, since small turgor pressures produce an elastic (reversible) cell expansion rather than the plastic irreversible characteristic of growth. Short drought periods reduce plant growth rates both during and after the stress or only after the stress (Plodowski et al., 1989). The severity of the effects of moisture stress varies according to the development stage of the plant. i.e. cell division, enlargement or differentiation. Cell enlargement is more sensitive to water stress than cell division as it requires more water when cells are enlarging to several fold their original size during cell enlargement, and only to double their size during cell division.

Elsewhere, Hoffman (2002), radial stem growth of four common tree species closely tracked seasonal patterns of precipitation with peak growth occuring in the middle of the wet season and little or no growth occuring in the dry season. In environments where phosphorus (P) is the main limitation to crop growth, water deficiency can be an important limitation to crop growth because transport of P in soils is highly dependent on soil water content. On a P-fixing Oxisol/Ferralsol in western Kenya, Radersma and Ong (2004) found that a significant absolute soil water content reduction of 2-3% at relatively high soil water retention (pF), caused a decrease in maize production of 30-40% due to soil-drying induced P-deficiency. Water stress also affects many enzyme-mediated processes such as respiration, the dark reactions of photosynthesis, the formation of chlorophyll (Alberte et al., 1975; Li et al., 2006), and carbohydrate and nitrogen metabolism (Vieira de Silva et al., 1974). In North America, the net photosynthesis and stomatal conductance of Cattail (*Typha latifolia*), an important species of freshwater wetlands, were enhanced by continuous and periodic flooding, but reduced under periodic drought (Li et al., 2006). Reduced turgor due to water deficit stress of both the guard

cells of the stomata and of the other epidermal cells induces stomatal closure in plants (Hsiao, 1973). Stomatal closure cuts off the diffusion of CO_2 into the intercellular spaces of the leaf, thereby, along with the direct effects of water stress on chloroplast processes, inhibits photosynthesis (Hillel, 1979; Beadle et al., 1985).

Stomatal closure also prevents the diffusion of O_2 into the leaf, and may inhibit respiration. A concomitant increase in the endogenous level of abscisic acid (ABA) often occurs in water-stressed tissue (Wakrim et al., 2005; Liu et al., 2005; Hartung et al., 2005), suggesting that hormonal modulation of stomatal response to water stress may be an important regulatory mechanism in the ability of plants to withstand temporal water deficits (Liu et al., 2005). Stress ABA serves as a long distance signal regulating the water relations of shoots (stomata, meristems) and roots (hydraulic conductivity, root development, desiccation tolerance (Hartung et al., 2005). Wakrim et al. (2005), however, concluded that ABA might not be directly involved in the initial stages of stomatal control under partial root drying (PRD) and regulated deficit irrigation (RDI).

The level of ABA in fully turgid leaves increases in response to the stress treatments (Hartung et al., 2005). Repetitive cycles of water stress decreased the threshold leaf water potential required for initiating stomatal closure in cotton leaves (Ackerson, 1980; Zabadal, 1974). Synthesis of protein and cell walls is quite sensitive; at higher stress levels where nitrogen metabolism and other processes are reduced. At fairly high stress levels, the amino acid proline begins to accumulate, and in some cases sugar accumulates. These compounds decrease osmotic potential and may provide storage for reduced sugars and nitrogen during stress.

Chronic water stress may cause a reduction in plant productivity due to a decrease in the amount of solar radiation intercepted by the canopy, and lower efficiency of conversion of the intercepted radiation to biomass (Atwell et al., 1999). A lower conversion efficiency results mainly from lower net photosynthetic rates and increased mortality rates of plant parts (e.g. leaves and fine roots). The strong positive relationship commonly observed between plant primary productivity and precipitation in China clearly implies that water is a significant factor limiting the productivity of spring wheat (Wei and Zhao, 1995). Water deficits can drastically reduce the harvest index of biological yield from its genetic potential to zero (Pan et al. (2003), and worldwide losses in crop yields from water deficits probably exceed the losses from all other

causes combined (Kramer, 1980). According to Pan et al. (2003), drought stress decreases mean plant biomass and increases both the relative variation in plant biomass and the concentration of mass within a small fraction of the population.

2.3 Salinity-induced soil moisture deficits

Plants that can grow on soils of high salt content are termed halophytes. In order to survive these conditions, these plants must overcome problems related to osmotic differences, specific ion toxicity and extreme site conditions (Fitter and Hay, 1987). In order to overcome these problems, halophytes achieve a lower intracellular solute potential than the soil solution, exclude toxic compounds from plants in favour of non-toxic compounds, and develop appropriate internal mechanisms to adapt to extreme site conditions. There is substantial evidence that glycophytic as well as halophytic species adjust to high salt concentrations by lowering tissue osmotic potentials with an increase of inorganic ions from the external solution and/or compatible solutes (Cachorro et al., 1995; Kamel, 2008).

Salinity is an important physiological and agronomic problem in arid and semi-arid regions. Under conditions of low rainfall, restricted drainage, high temperatures, low relative humidities and high wind speeds, high salt concentrations result and interfere with soil water uptake and growth of plants (Madsen and Mulligan, 2006; Olukoye et al., 2003; Oba et al., 2001). The degree of salt accumulation depends on the degree of leaching of soil (thus its permeability (Fitzpatrick, 1983)), the presence of vegetation (evapotranspiration) and the amount and seasonal distribution of rainfall (Shaw, 1999). Saline soils are frequently alkaline, containing less soluble sulphates and carbonates of Na, Mg and Ca, in addition to the more neutral chlorides (Choi et al., 2006; McBride, 1994). High salt concentrations cause surface sealing and reduce water infiltration, leading to flash floods (Olukoye et al., 2003).

Most plants respond to total salinity as an osmotic effect and to ion toxicity (most often involving sodium, chloride and boron ions) as necrotic spots in the leaf, leaf bronzing and, in highly toxic cases, defoliation (Shaw, 1999; Choi et al., 2006). Salinity is known to depress nutrient balances, water and osmotic potentials, and physiological processes (Tattini et al., 2002; Bayuelo-Jim'enez et al., 2003). These effects of high salt concentrations in the soil are due to an excessive uptake and translocation of salt ions into the leaf tissue, where enzymes and/or organelles are denatured (Munns and Termaat, 1986).

Salinity has a significant effect on tissue concentrations and uptake rates of Na^+, K^+, Ca^{2+} and Cl^-. Salinity-induced declines of CO_2 assimilation and net photosynthesis in fruit trees can be attributed to a partial stomatal closure as well as to toxic effects of Na and Cl ions in the mesophyll cells (Lloyd et al., 1987; Cachorro et al., 1993). Interferance with these physiological processes, leads to reductions in biomass production and growth in plants (Choi et al., 2006).

Different plant species and provenances at various growth stages are known to respond differently to salinity stress (Bayuelo-Jim'enez et al., 2003). In central Queensland, *Acacia salicina* was found to be superior to three Eucalyptus species in its ability to emerge and survive under saline conditions (Madsen and Mulligan, 2006). Similarly, established plants survived the range of salt treatments far better than emerging seedlings (Madsen and Mulligan, 2006). In the semi-desert zone of North Horr in Northern Kenya, survival rates for indigenous plants growing on highly saline soils were higher than those of exotic ones (Olukoye et al., 2003). Using the growth analysis, ion uptake characteristics and the gas exchange parameters in a greenhouse experiment conducted in Berlin, it was concluded that *Annona muricata* had a higher salt tolerance than *A. cherimola* (Ebert, 1998).

There is evidence that some of the effects of salinity stress in plants may be reversible. Tattini et al. (2002) concluded that salt-induced water stress primarily controlled gas exchange of salt treated *P. latifolia* leaves, whereas the salt load in the leaf did not cause irreversible damage to the photosynthetic apparatus. From the investigation by Ali-Dinar et al. (1998), it is reasonable to assume that salinity effects on leaf and shoot dry weight in guava can be alleviated by increasing nitrate N application rates from low to moderate. This is because higher N rates improved the efficiency of plants for proper nutrient uptake and decreased the capacity of salt ions such as Na^+ and Cl^-. Tattini et al. (2002) demonstrated that photosynthetic performance of salt-treated plants fully recovered once salt was leached from the root zone, with the recovery rate depending on the severity of the salt stress previously experienced by the plants.

2.4 Plant adaptations to water deficit stress

In arid and semi-arid lands, it is important for plants of all species to develop adaptations in structure and function that enable them survive through prevailing environmental

conditions e.g. high temperatures, high radiation, low humidity and low water availability (Kramer, 1980; Connor, 2005; Liu et al., 2005). These adaptations, both physiological and morphological, are partially a result of long-term effects of natural selection forces such as the r- and k- selectivity (McNaughton, 1975). Such comprise either avoidance of water stress and extreme temperatures or evolution of anatomical and biological adaptations to ameliorate or tolerate water stress and maintain relatively low leaf temperatures (Kramer, 1980; Salisbury and Ross, 1978; Bolger et al., 2005; Connor, 2005).

In r/k selection theory, selective pressures are hypothesized to drive evolution in one of two generalized directions; r- or k- selection. These terms, r and k, are derived from standard ecological algebra, as illustrated in the simple Verhulst equation of population dynamics: $dN/dt = rN(1-N/K)$ (Verhulst, 1838; cited in Pianka, 1970);

where, r is the growth rate of the population (N) and K is the carrying capacity of its local environmental setting.

The theory relates to the selection of combinations of traits in an organism that trade off between quantity and quality of offspring. Typically, r-selected species exploit less crowded ecological niches, and produce many offspring, each of which has a relatively low probability of surviving to adulthood. In contrast, k-selected species are strong competitors in crowded niches, and invest more heavily in fewer offspring, each of which has a relatively high probability of surviving to adulthood. In scientific literature, r-selected species are occasionally referred to as "opportunistic", while k-selected species are described as "equilibrium".

Although some organisms are identified as primarily r- or k- strategists, no genotype is likely to be completely r-selected or completely k- selected. Rather, we expect an r-k continuum, the former occurring in a perfect ecological vacuum with no density effects and no competition, the latter occurring in a completely saturated ecosystem where density is high and competition for resources is intense (McArthur and Wilson, 1967). The position of a population on the evolutionary r-k continuum depends upon both the properties of the ecosystem and the ecological role of the population in that ecosystem. In a forest, for instance, the trees may be subject to k- selection while foliage-feeding insects suffering high annual mortality may be

subject to r-selection. Gadgil and Solbrig (1972) argued that the most important determinant of the position of a population on the r-k continuum is the magnitude of density-independent mortality. Where this is high, r- selection should prevail, where this is low, k- selection should prevail.

In an ecological void, the optimal adaptive strategy channels all possible resources into progeny, thereby maximizing the rate at which resources are colonized. At ecological saturation, the optimal strategy channels all possible resources into survival and production of a few offspring of extremely high competitive ability.

Drought avoidance by plants is achieved through rapid growth and completion of life cycles before drought sets in and is a characteristic of only a few plants, such as desert ephemerals and some plants growing in areas possessing well-defined wet and dry seasons (Kramer, 1980). Trees cannot avoid drought because they are perennials, and the only mechanism by which they can survive is through tolerance.

Drought tolerance is achieved through two main strategies, namely; dehydration postponement and dehydration tolerance (Kramer, 1980; Levitt, 1980; Turner, 1986). Dehydration postponement is achieved either through increased water uptake, reduced water loss, or both (Liu et al., 2005; Connor, 2005; Kramer, 1980). Adaptations that lead to dehydration postponement, therefore, include early leaf abscission, low leaf area, thick cuticle, hairy and waxy leaves and stems, sunken stomata, stomatal sensitivity and extensive root systems. Liu et al. (2005) discuss the role of ABA-based drought stress chemical signaling in regulating crop vegetative and reproductive development and its contributions to crop drought adaptation.

Increased concentrations of ABA in the root induced by soil drying may maintain root growth and increase root hydraulic conductivity; both lead to an increase in water uptake and thereby postpone the development of water deficit in the shoot (Liu et al., 2005). These adaptations help the plant to endure periods without significant rainfall whilst maintaining high plant water status (Kramer, 1980). However, some of the factors that contribute to dehdration postponement by reducing water loss, such as decreasing stomatal conductance, leaf rolling and decrease in leaf area are all processes that are likely to lead to decrease in growth (Turner, 1979).

Dehydration tolerance (Bolger et al., 2005) refers to the ability of a plant to endure drought and low tissue water status (Kramer, 1980). The two main mechanisms involved

are turgor maintenance and dessication tolerance. The maintenance of turgor during a drop in plant water status is thought to maintain plant metabolic processes and aid in its growth and survival during growth (Osonubi and Davis, 1978; Ranney et al., 1990). Plants that maintain turgor in their leaves will therefore grow and photosynthesize faster when exposed to drought than those that do not (Hsiao, 1973). Turgor maintenance at lower tissue water potential can be achieved through changes in osmotic potential (osmotic adjustment) (Bayuelo-Jim'enez et al., 2003; Tattini et al., 2002; Ma et al., 2006) or tissue elasticity (elastic adjustment) (Tyree and Jarvis, 1982). Osmotic adjustment has been cited as a major drought tolerance mechanism (Kramer, 1980; Levitt, 1980; Kozlowski, 1982). It has been demonstrated in many species (Bayuelo-Jim'enez et al., 2003; Turner and Jones, 1980; Ma et al., 2006; Kamel, 2008) and has been observed to maintain stomatal opening and photosynthesis to lower water potentials (Ludlow et al., 1985; Turner and Jones, 1980; Bayuelo-Jim'enez et al., 2003). Osmotic adjustment, therefore, has important implications for productivity because it confers drought tolerance without necessarily reducing photosynthesis and growth (Kozlowski, 1982). However, osmotic adjustment will only be effective in maintaining growth processes of the shoot during drought if it also occurs in the roots (Turner, 1986). There is, therefore, no consensus on the role of osmotic adjustment in growth maintenance under drought. With regard to achieving turgor maintenance through changes in tissue elasticity (Tyree and Jarvis, 1982), an increase in cell wall elasticity results in smaller changes in turgor pressure for a given change in relative water content (R*). High cell wall elasticity in *E. globules*, for instance, facilitated maintenance of turgor over a wide range of R* and allowed it to tolerate moderate water stress (Lemcoff et al., 1994). In some cases, however, no osmotic adjustment (lowering of osmotic Potential) and no change in tissue elastic properties were observed in response to increasing summer drought and intensity of water stress (Borghetti et al., 2004).

Tolerance to desiccation depends on the ability of cells to withstand injury during severe drought stress (Turner, 1986). Dehydration tolerance has been thought to occur in concert with dehydration postponement abilities (Blum and Ebercon, 1984). The role of desiccation tolerance in species survival is cited by Martin et al. (1987). However, Levitt (1980) contended that dehydration tolerance is rarely a significant factor in successful drought endurance by higher plants. Majority of trees exhibit little variation in desiccation tolerance (Hinkley et al., 1979).

2.5 Soil moisture as primary determinant of rangeland vegetation structure and function

Trees, shrubs, grasses and herbs adapted to arid and semi-arid rangelands exist in various combinations and formations that comprise the savanna. It is hypothesized that the origin of the large variety of these formations may be traced to four selective forces (determinants) that control the common features and differences in structure and function, and are responsible for the existing variety of savanna formations. These are: available moisture (PAM), available nutrients (PAN), fire, and herbivory (Solbrig et al., 1996; Sankaran et al., 2005). PAM and PAN are commonly referred to as primary determinants, while fire and herbivory are secondary determinants. PAM integrates rainfall, water infiltration, evapotranspiration, soil texture, and hydrologic regime into a single measure of the soil moisture available to plants. PAN is a measure of the nutrients available to plants during their period of growth. Research findings show that respective contributions of the four determinants to ecosystem structure and function are variable (Birkett and Stevens-wood, 2005; Picard et al., 2005). According to Cole (1986), the height and spacing of trees/shrubs, which determine the categories of savanna is influenced mainly by soil moisture conditions, while the rates of biomass accumulation and the composition of the vegetation units in terms of chemistry of the leaves and species, within each category varies with nutrient status. On a global basis, in undisturbed natural terrain, the change from tropical forest to savanna occurs where the availability of moisture and nutrients throughout the year is inadequate to sustain closed forests with well-developed shrub layers.

Frequent fires result in reduced soil moisture in the upper soil horizons and increased clay dispersion, decreased aggregate stability, and increased soil crusting, which lead to decreased water infiltration, increased run-off, and overall greater moisture limitation for plants. This moisture limitation strongly affects, among other things, root colonization by arbuscular mycorrhizal fungi (AMF) and root system architecture (RSA) (Hartnett et al., 2004; Lopez-Gutierrez et al., 2004). At the woodland/forest boundary, deliberate use of fire may extend the savanna, and protection from it may encourage the regeneration of forest. The existence of various savanna formations within the East African region, are sometimes attributed to the influence on plant evolution of large populations of wild herbivores (Pratt and Gwynne, 1977).

In the Miombo woodland of northwestern Zimbabwe, elephants caused 48% decline in proportions of large trees (>11 cm diameter), significant reductions (30.9-90.9%) in tree heights,

reductions in stem areas (43.5%) and densities (2.5%) of all trees (Mapaure and Moe, 2009). Likewise, in an enclosed fire-free wooded grassland habitat in the Laikipia region of Kenya, elephants were responsible for the loss of 40% of *Acacia drepanolobium* trees, black rhinos 33%, while heavy browsing by giraffes reduced tree growth rates and increased their susceptibility to drought (Birkett and Stevens-wood, 2005). In the 1960s, large populations of elephants converted over 12,000 km^2 of woodlands and shrublands of the 20,000 km^2 Tsavo National Park into open savanna grasslands (Glover, 1963; Agnew, 1968).

Savannas are rarely stable and can experience rapid local changes from dense woodlands to open plains (Birkett and Stevens-wood, 2005). The dominant grasses in the grass stratum of all savanna areas are known to belong to the C_4 group, i.e. those exhibiting the C_4 photosynthetic pathway (Chinthapalli et al., 2003). In C_4 photosynthesis, the first product of the photosynthetic carbon reduction (PCR) cycle is a 4-carbon compound (carboxylic acid), oxalo acetic acid (OAA). Plants exhibiting this photosynthetic pathway usually occur in adverse environments and are adapted to high light intensities, high temperatures, high evapotranspiration rates, and high salinity (Raghavendra and Rama Das, 1993; Hall and Rao, 1987; Bassham and Buchanan, 1982; Macharia, 1981).

C_4 plants differ from C_3 plants in that the later usually occur in high altitude areas, temperate lands and semi-deciduous tropical forests with low temperatures and high soil moisture (Still et al., 2003; Chinthapalli et al., 2003; Snyder et al., 2003). In C_3 photosynthesis, the first primary product of the PCR cycle is a 3-carbon compound, phosphoglyceric acid (PGA) (Hall and Rao, 1987; Beadle et al., 1985; Lawlor, 1987; Macharia, 1981). The rate of CO_2 fixation by C_4 plants is not affected by atmospheric concentrations of O_2 (high) and CO_2 (low) both factors which normally enhance the photorespiration rate of C_3 plants. This is due to insensitivity of the the carboxylating enzyme, phosphoenol pyruvate carboxylase to these changes in C_4 photosynthesis unlike Ribulose 1,5 Biphosphate carboxylase (RUBISCO) in C_3 cycle of photosynthesis. The water use efficiency, i.e. the ratio of the mass of CO_2 assimilated to water transpired, in C_4 plants is often twice that of C_3 species. There is usually a spatial C_3-C_4 species displacement showing a decrease in C_4 species and an increase in C_3 species at high altitudes, and an increase in C_4 species at the expense of C_3 species at lowland sites (Macharia, 1981; Still et al., 2003).

It has also been reported that salinity tolerance is a common feature of many C_4 species (Hall and Rao, 1987). There are three sub-types of C_4 photosynthesis depending on the reaction sequence of C_4 acids decarboxylation in bundle sheath cells (Lawlor, 1987; Raghavendra and Rama Das, 1993; Bassham and Buchanan, 1982;). These are NADP-me (malate formers), PEP-ck, and NAD-me (aspartate formers). Within the savannas, aspartic acid forming C_4 grasses predominate in the drier areas where there is a higher nitrogen availability in the soils, whereas malate forming C_4 grasses predominate in the moister areas.

Trees in the savanna are thought to reduce understorey plant productivity through competition for water (Walter, 1971; McMurtrie and Wolf, 1983), although recent research on interactions between the two basic components: trees and grasses (Douglas et al., 2006; Paris et al., 2005; Picard et al., 2005), have indicated that herbaceous layer productivity may be higher under tree canopies than in nearby open grasslands (Holland, 1980; Maranga, 1984). This increase in productivity is localized under or near tree crowns and is found most often in communities with low tree density, low rainfall, and moderate soil fertility (e.g. Knoop and Walker, 1985; Belsky and Amundson, 1992; Belsky et al., 1993a, b). Belsky et al. (1989; 1993a, b) reported that above-ground herbaceous productivity under crowns of a common African tree species, *Acacia tortilis* (Forsk) Hayne subsp. Spirocarpa (Hochst. Ex A. Rich). Brenan (Leguminosae), was significantly greater than that measured in adjacent grasslands both at low-rainfall and at high-rainfall savannas in Tsavo National Park, Kenya.

The increase in herbaceous productivity below tree crowns relative to the grassland was greater at the low rainfall than the high rainfall site (95 vs 52%), respectively. Belsky (1994) suggests that savanna trees competed more intensely with understorey plants at wetter sites, where their roots terminated in or near crown zones, than at drier sites, where their roots extended further into open grasslands. A number of recent studies show that isolated trees can improve understorey productivity (Holland, 1980; Belsky et al., 1989; 1993a, b; Frost and McDougald, 1989; Weltzin and Coughenour, 1990). Patterns of above-ground net primary productivity (ANPP) under and near trees of *A. tortilis* and *A. digitata* in Tsavo National Park, Kenya were similar, with significantly greater ANPP in their canopy zones (705 ± 39 g m^{-2}) than in their root (430 ± 23 g m^{-2}) or grassland (361 ± 21 g m^{-2}) zones (Belsky et al., 1989).

The shade from tree crowns reduces soil and plant temperatures and evapotranspiration in below-crown environments. Such reductions are thought to improve below-crown plant water

relations (Frost and McDougald, 1989; Weltzin and Coughenour, 1990). In a study conducted to investigate the effects of trees on their environment in a semi-arid tropical savanna of southern Kenya, tree canopies of both *A. tortilis* and *A. digitata* reduced solar irradiance by 45-65%, soil temperatures by 5-11^{0}C and rainfall by 0-50% compared to open grassland (Belsky et al., 1989).

2.6 Degradation in Arid and Semi-arid Lands (ASALs)

The majority of the population in the Arid and Semi-arid Lands (ASALs) of Kenya are pastoralists and agro-pastoralists but increasingly, farmers from the overcrowded higher potential areas have migrated into the drylands causing changes in land use, privatization of communal land and increasing pressure on land and water resources. Demands placed on these resources and the fragile ecosystems by the rapidly expanding populations, through agricultural intensification, urbanization, and industrialization have combined to intensively exploit the natural resources in these areas. This has resulted in moderate to severe land degradation and desertification.

Land degradation is defined as the reduction in the capacity of the land to provide ecosystem goods and services and assure its functions over a period of time for the beneficiaries of these. It is a serious environmental and socio-economic problem that affects large areas and many people in dryland regions and manifests in forms of impoverishment and depletion of vegetation cover, loss of biophysical and economic productivity, wind and water erosion, salinization and deterioration of physical, chemical and biological soil properties. Biological diversity is being eroded at an alarming rate due to the consumptive uses of species as well as the excessive alteration of habitats owing to human activities such as cultivation, pastoralism and urbanization. The increase of human population also accelerates species extinction as such population exerts more pressure on available resoures. Degraded land is costly to reclaim and if severely degraded, may no longer provide a range of ecosystem functions and services with a loss of the goods and many other potential environmental, social, economic and non-material benefits that are critical for society and development. The consequences of land degradation are reduced land productivity, socio-economic problems, including uncertainty in food security, migration, limited development and damage to ecosystems.

Kenya is representative of drylands in sub-saharan Africa in terms of pressures on land resources and severity of degradation. Continuing to ignore the specific needs of ASALs will

result in increased poverty and environmental degradation. Where no remedial action is taken, continued degradation will lead to the breakdown of the entire production systems. The removal of the protective cover to reduce competition for water and nutrients, ploughing, heavy grazing and deforestation all leave the soil highly vulnerable to wind erosion, particularly during severe droughts. Heavy grazing around water points or during long droughts prevents or delays the re-growth of vegetation or favours only unpalatable shrubs. Consequently, there is commitment of the government to overcome degradation in view of its implications on poverty and food security. The draft national policy for the sustainable development of Arid and Semi-arid Lands of Kenya (Republic of Kenya, 2004) signifies government commitment to the development of ASALs taking cognisanse of the fact that "Kenya will not achieve sustained growth in her national economy as long as the ASALs and their enormous resources are not factored into effective national planning and development". The challenge is to develop an innovative approach to sustainable land management (SLM) where resource conservation and land rehabilitation can be combined with improved livelihoods and income generation for local communities and farmers/herders.

2.7 Knowledge gap

Successful rehabilitation through tree planting of deforested and degraded sites in semi-arid rangelands of Kenya where rainfall is low and poorly distributed requires the use of species that are most adapted to soil moisture stress. Selection of appropriate species requires an understanding of the types, levels and mechanisms of adaptation by candidate trees and shrubs and knowledge of the morpho-physiological indicators of these adaptations that would guide their identification. Information on these indicators is not available as they have not been adequately studied and documented for most of the tree and shrub species in semi-arid Kenya.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

3.1.1 Geographical location

The study was conducted in Makueni District of Kenya. It covers an area of 7,965.8 km^2 (Fig. 1; Republic of Kenya, 1997). It lies between Latitude 1^0 35′ South and 2^0 35' South, and Longitude 37^0 10′East and 38^0 30′ East. The district is generally low-lying with altitude ranging between 600 m a.s.l at Tsavo and 1,900 m on the Kilungu hills.

3.1.2 Topography, climate and soils

Major land forms comprise the Chyulu hills situated along the southwestern border in Kibwezi division, and the Mbooni and Kilungu hills to the west. The district is characterized by arid and semi-arid climates (Pratt et al., 1966; Maundu and Tengnas, 2005; Van den Abeele et al., 2005). Annual rainfall is generally low and unreliable, ranging between 200 — 900 mm in the low-lying areas and 800 — 1,200 mm in the hills (Republic of Kenya, 1997). The rainfall is bimodally distributed and occurs in March/April (long rains) and November/December (short rains). The latter are usually more reliable both in amount and distribution, and accounts for 58% of the annual total precipitation (Musembi, 1986).

There are three main soil types in the district: the red clay soils found on the hill masses and some parts of the lowland which form the agro-ecological zone UM2; the sandy soils found mainly in the central parts of the district including Wote and Kathonzweni divisions; and the black cotton soils found in the southern divisions of Kibwezi, Makindu, Mtito-Andei and some parts of Kilome, which form agro-ecological zone LM2. The UM5 and LM5 agro-ecological zones are covered by red clay soils and black cotton soils, which are suitable for cotton and sisal production.

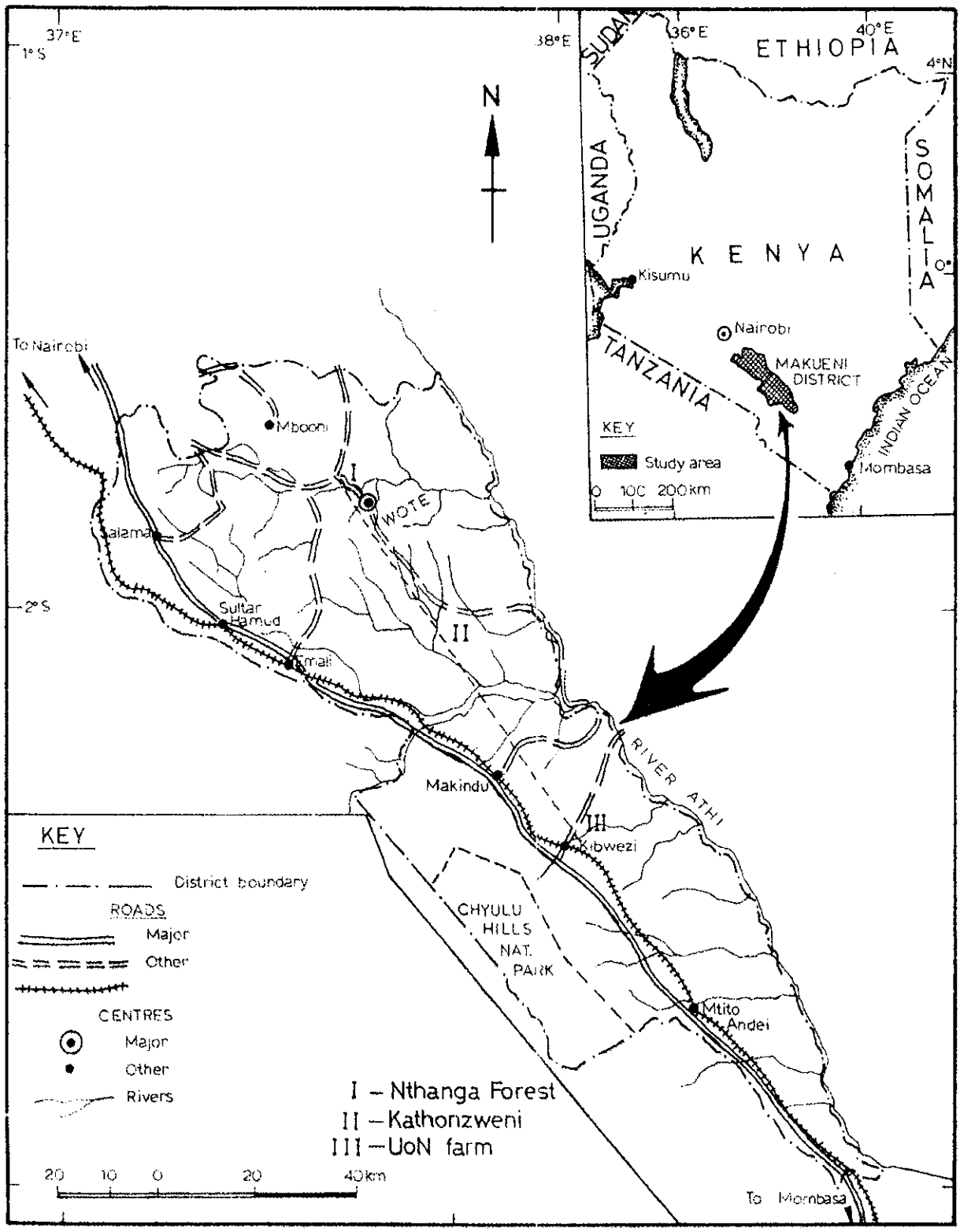


Fig. 1: Location of study area (source: Survey of Kenya, 1998)

3.1.3 Agro-ecological zones and land use patterns

Makueni district is divided into six agro-climatic zones using a moisture index based on annual rainfall expressed as a percentage of potential evaporation (Jaetzold and Schmidt, 1983). Areas with indexes greater than 50% have high potential for cropping and are designated zones I, II and III. The sub-humid to arid zones (zones IV, V and VI) have indexes of less than 50% and a mean annual rainfall of less than 1100 mm (Figure 2). The six agro-climatic zones are each sub-divided according to mean annual temperature to identify areas suitable for growing each of Kenya's major food and cash crops. Agro-ecological zones are defined by relevant agro-climatic factors and differentiated by soil patterns. Nationally, the main zones are: Tropical Alpine zones (TA), Upper Highland zones (UH), Lower Highland zones (LH), Upper Midland zones (UM), Lower Midland zones (LM), Lower zones (L), and Coastal Lowland zones (CL) (Jaetzold and Schmidt, 1983). These zones are associated with corresponding temperature variations ranging from freezing to 40 ^{0}C. In Makueni district, there are two of these major agro-ecological zones, namely: Upper Midland (UM) and Lower Midland (LM). These are further divided into sub-zones depending on humidity levels and water supply (1=wet, 6=very dry).

According to these AEZs, land in Makueni is classified broadly into three categories: high potential, medium potential and low potential based mainly on the rainfall received. The high potential areas receive an annual average rainfall of over 750 mm, and include LM2. The medium potential areas receive an annual average rainfall of 500-750 mm, and include LM3, UM3, UM4 and LM4. The low potential areas receive an annual average of less than 500 mm, and include LM5, LM6, UM6 and UM5 (Republic of Kenya, 2002; Van den Abeele et al., 2005). The high and medium potential areas are suitable for arable rain-fed agriculture, while the low potential areas are dominated by nomadic pastoralism, ranching and agriculture (including irrigated agriculture). Appendix 1 (pg 126) describes each agro-ecological zone by percentage area under agriculture, location, and major land use.

3.2 Study sites

Three study sites (one per agro-ecological zone) were randomly selected with the help of agro-Climatic maps and Landsat Imageries and on the basis of existing vegetation (Lambrecht, 1989; Shiver and Borders, 1996; Fasona and Omojola, 2009) (Fig. 2). The maps and satellite pictures were obtained from the Survey of Kenya and the Department of Resource Surveys and

Remote Sensing (DRSRS) (GoK, 2006). Using the maps, the three agro-ecological zones of the district (i.e. high, medium, and low potential zones) were identified and demarcated. Actual study sites in each of these zones were subsequently selected after a tour of the district and an extensive survey of the vegetation. Minimally disturbed natural forests, woodlands and bushlands were selected. It was difficult to find completely undisturbed areas because of encroachment by the local people who have long been using these areas to graze, obtain wood and charcoal for fuel, and harvest poles and timber for house construction and furniture.

Selected sites were located at the lower parts of zone III in Nthangu Forest (1,575 m a.s.l.) (site I), at the lower parts of zone IV in Mavindini location of Kathonzweni division (1,250 m a.s.l.) (site II), and at the boundary of zones V and VI at Kibwezi Forest (900 m a.s.l.) (site III) (Fig. 2).

Site I: Nthangu Forest

Nthangu Forest is located 14 km north of Wote town off the Makueni-Machakos road on the boundary between Kaiti and Kisau divisions. Gazetted in 1960 (Gazettement # 532/1960), the forest covers a total area of 2,697.8 hectares and is made up of 6 blocks, namely; Nthangu (843.8 ha), Kitondo (1,086.4 ha), Kyai (106 ha), Kithendu (218.9 ha), Waiya (263 ha) and Kalimani (179.7 ha). The Nthangu Forest block lies between longitude 37^0 37'E and latitude $1^0$43'S. The highest point is found at 1,575 m above sea level. On this site, *Combretum molle*, *Croton dichogamus* and shrubs such as the Rhus spp. dominated the original indigenous vegetation (Ojiambo et al., 2001). Currently, the original spp. are mainly represented by coppices as in 1996, part of the forest was clear-felled and planted with plantation tree species that included Cypress (*Cupressus lusitanica*) (124.5 ha), Pines (*Pinus radiata* and *Pinus patula*) (447 ha), Eucalyptus spp (41 ha), and others such as *Calitris robusta* (14 ha). The forest is managed by the Ministry of Forestry and Wildlife (Kenya Forest Service) and access is restricted. During severe drought, neighbouring farmers may be allowed to graze their livestock (cattle, sheep and donkeys only) for controlled periods of time. Goats are never allowed in the forest. Women and children may also be allowed to collect dried and fallen branches for firewood.

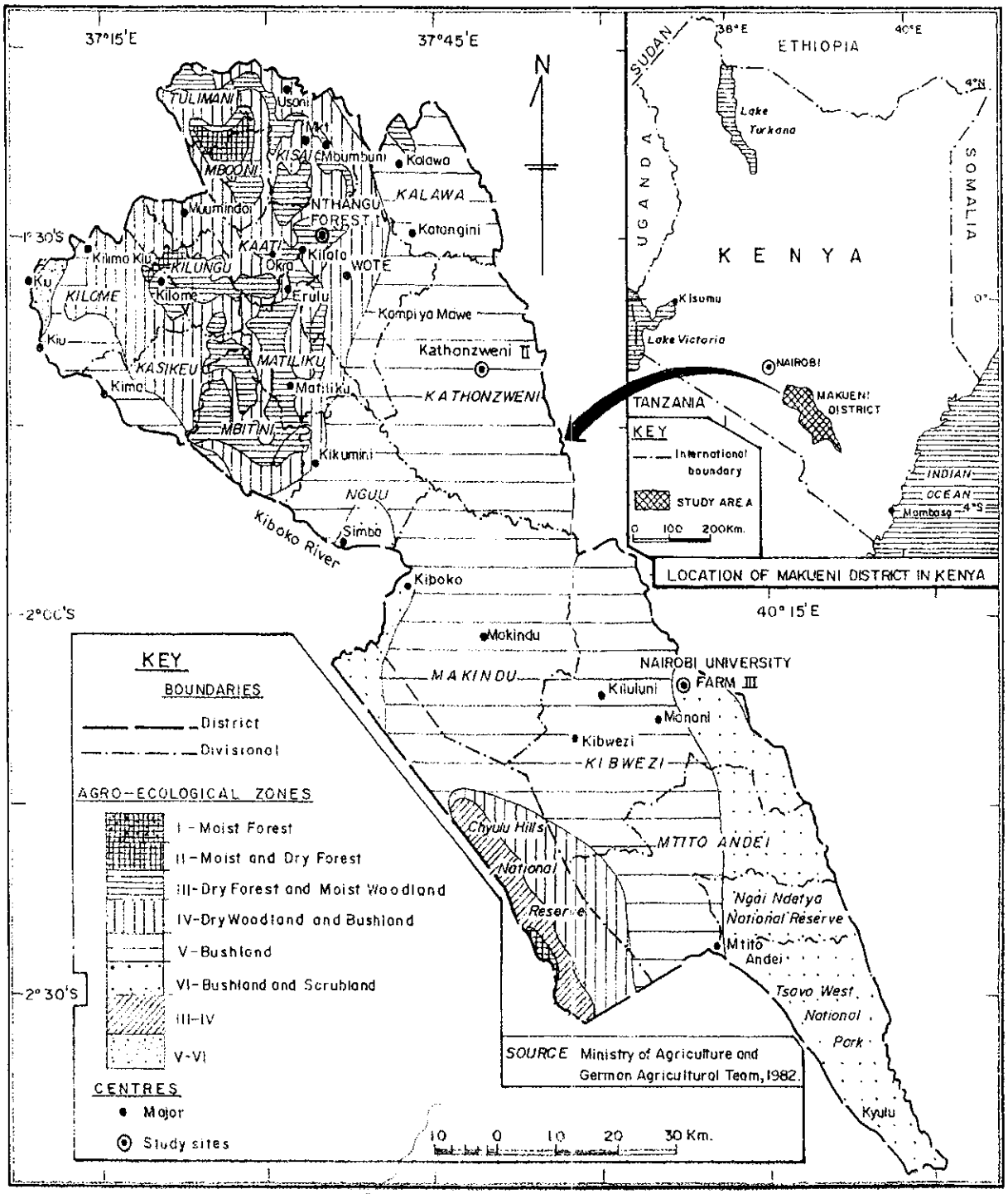


Fig. 2: Agro-ecological zones and vegetation of Makueni district (Source: Jaetzold and Schmidt, 1983)

Site II: Mavindini

Study sites in Kathonzweni division were located at Muusini, Mathemba and Miangeni villages of Mavindini, one of the 6 administrative locations of the division. The sites were about 40 km south of Wote town near Kathonzweni township east of the Wote-Kibwezi road. Muusini and Mathemba villages where the first 3 sample plots were located are at a higher elevation where members of the genus *Combretum* dominate the vegetation. The villages border KARI's Kambi-ya-Mawe dryland research sub-station (approx. 1,230 m a.s.l., 1^0 57' S latitude and 37^0 40' E longitude) which receives a mean annual rainfall of between 400 and 500 mm. Miangeni village where the fourth plot was located lies at a lower elevation near the river Athi. It is hotter and drier, with environmental conditions similar to those of Kibwezi. In all cases, the plots were located on farmers' fields and school compounds where security of plants and equipment was guaranteed.

Site III: Kibwezi Forest

The total area of Kibwezi division is 1,251 km^2 and comprises four administrative locations, namely Kikumbulyu, Masongaleni, Utithi and Kinyambu. Most of it is covered by natural woodland. The estimated population in the division is 18,858 persons with 13,642 households spread over 16 sub-locations. The current population density is 50 persons/km^2. The average number of persons per household is six (Republic of Kenya, 2002).

The study site occupied the part of the expansive Kibwezi Forest land owned by the University of Nairobi's Institute of Dryland Research, Development and Utilization (IDRDU). This is a 12,000-acre land mainly used for research and training by the University. Of this total land area, 120 acres was irrigated land used to produce horticultural crops, while the rest was composed of a small scale livestock ranch with cattle, sheep, goats and camels, and limited office, laboratory, and accommodation/residential facilities. The study site was located within the forest about 20 km away from Kibwezi township off the Kibwezi-Kasayani road along the Kasayani-Kyanginywa road. Kibwezi lies at an altitude of about 900 m a.s.l., and has annual rainfall of about 600 mm/yr and a mean annual temperature of 27 ^{0}C.

Land use outside and around the forest (ACZ V and VI) (semi-arid) is mixed farming, mainly, sedentary along the Kibwezi and Athi rivers, where growing of vegetables and fruits (horticultural crops) is carried out. Important crops are drought escaping/tolerant varieties of

maize, beans, pigeon peas, cassava, sweet potatoes, cowpeas, sorghum and millet. The major livestock types kept include poultry, goats, cattle and sheep (Ngoda and Obwoyere, 2001). The south-eastern part of Kibwezi forest forms part of Tsavo National Park and is therefore set aside for wildlife conservation. Vegetation is mainly dominated by *Acacia* and *commiphora* species dotted with *Adansonia digitata* (Baobab trees).

3.3 Climate, soils and woody vegetation

It was necessary to collect data on some climatic factors and soil physical and chemical properties as both had significant effects on soil moisture content and the morpho-physiological characteristics of the local vegetation. Indigenous tree and shrub species occurring in each of the three main agro-ecological zones of the district were identified and data was collected by establishing transects and systematic sample plots.

3.3.1 Establishment of transects and sample plots

Transects and sample plots were established by strata according to the methods described by Lambrecht (1989) and Shiver and Borders (1996). At Nthangu Forest, the transect ran along a 15-km line running from the forester's office in the north to Mitubu hill which overlooks Wote township in the south (Fig 3). Plots A-D were established at Mbenza, Kyamboo, Kangea and Mitubu points of the forest, respectively.

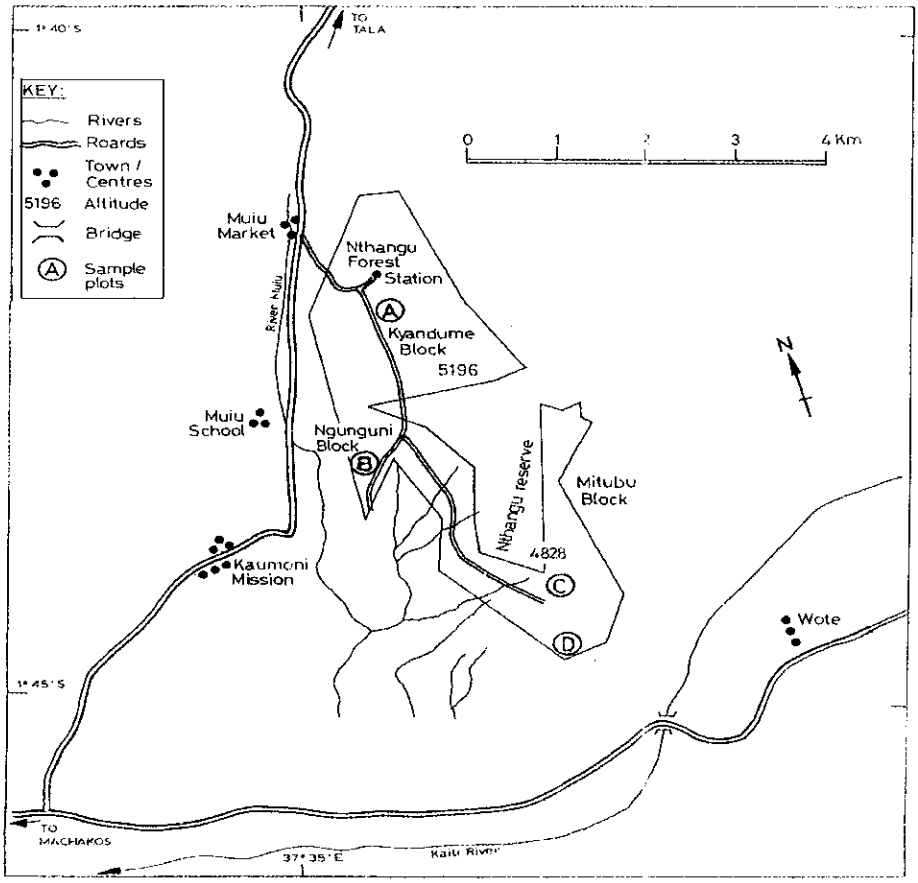


Figure 3: Map showing plots used to assess vegetation at Nthangu forest, Makueni district.

A 40-km transect connecting Kambi-ya-mawe market along Kathonzweni-Wote Road and Miangeni market near Athi river was established in Mavindini (Fig 4).

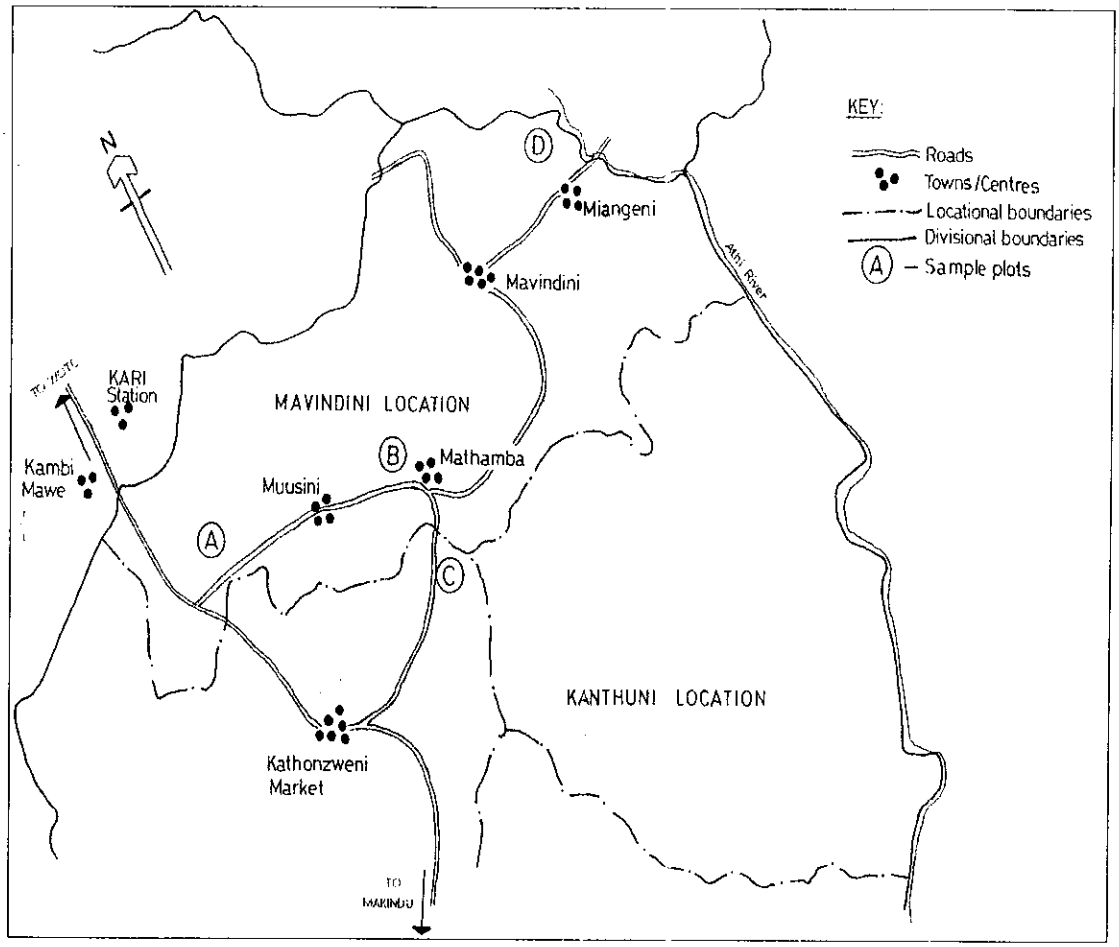


Figure. 4: Sketch map (not drawn to scale) showing plots used to assess vegetation at Kathonzweni, Makueni district.

Similarly, at Kibwezi, a transect was laid out between the junction of Kibwezi-Kisayani and Kisayani-Kyanginywa roads, and Kyanginywa market on the Kibwezi river (Fig 5).

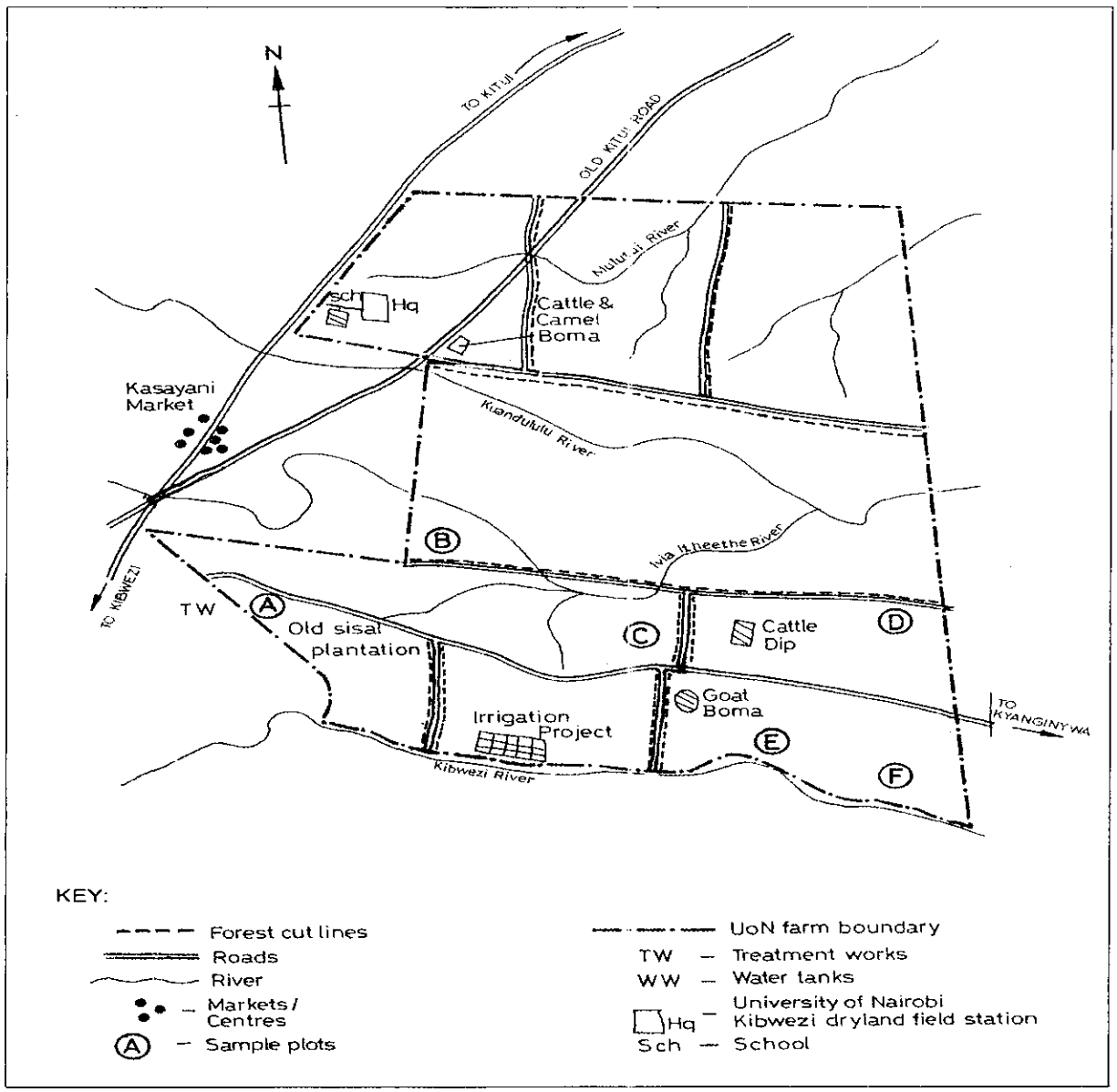


Figure. 5: Sketch map (not drawn to scale) showing plots used to assess vegetation at Kibwezi forest, Makueni district.

Along each transect, a total of four benchmarks were established at 4-5 km intervals. An exception was the case of Mavindini where the last benchmark at Miangeni was much further away from its nearest benchmark at Mathemba. One to three (1-3) kms away from each benchmark in alternate directions either to the right or to the left, 50 m x 50 m (2,500 m^2) plots were established (Lambrecht, 1989). The fifth and sixth plots were established at Kibwezi.

3.3.2 Climatic data

Information on rainfall and temperature was collected on a daily basis throughout the period of data collection. This was done by installing mini weather stations with a rain gauge and thermometer at strategic points within each study site. At Kibwezi and Nthangu forests, some of the weather information was collected with the help of equipment belonging to the University of Nairobi's Institute of Dryland Research, Development and Utilization (IDRDU), and Forest Department. This made it possible to collect additional climatic data (radiation, sunshine hours, wind speed and relative humidity) at Kibwezi.

3.3.3 Soil physical and chemical properties

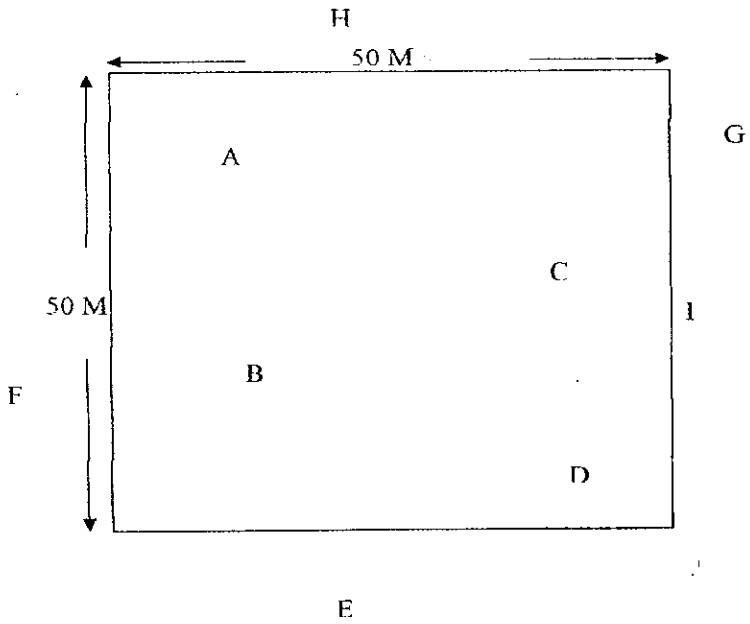
3.3.3.1 Soil sampling

Soil samples were taken from each site and around each tree at different soil depths. Ten sampling points were identified per site. Soil samples were taken at depths of 10 – 15 cm and 80 – 85 cm. Four of the sampling points were randomly located within each of the 2,500 m^2 plots while the rest were randomly located at various points outside the plots but in the neigboughood (Figure 6). Each fresh sample was carefully mixed and 1 kg parts packed separately in labeled polythene bags (a total of 20 samples/site and 60 samples (60 kg) in total).

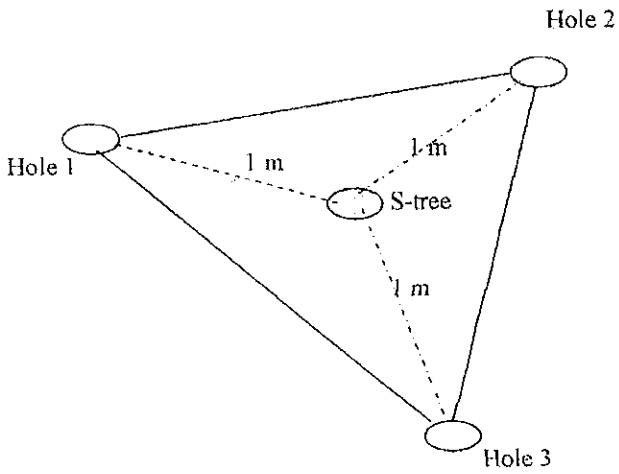
More soil samples were taken by sinking three holes around each tree at distances of 1 m from the tree and at equal distances from each other (forming a triangular shape) (Figure 6). This was done using a measuring tape, soil auger and a plastic hammer. In this case, soil samples were taken at 6 different depths, i.e. 15 - 20 cm, 30 - 35 cm, 60 - 65 cm, 90 - 95 cm, 120 – 125 cm and 150 - 155 cm (18 samples * 10 trees = 180 samples in total). These depths were selected to correspond with the depths at which soil moisture readings were taken. Fresh samples, 500 g – 1 kg each were also collected from these depths in labeled polythene bags.

Samples were transported to Kenya Forestry Research Institute's (KEFRI's) field laboratories at Kibwezi for air-drying. The three samples from similar depths around each tree were combined and mixed into a composite (60 samples in total).

Pits of up to 1.6 m depth each were also dug a few metres from sample trees at each site to expose the soil profile. At each of the six different soil depths, soil cores were extracted with steel rings from the sidewall of the pits (60 in total).



(a) Sample points (A-J) in and around sample plot



(b) Holes sunk around sample trees and shrubs (S-tree)

Figure 6: Diagram showing sample points within and around (a) sample plots, and (b) sample trees and shrubs.

3.3.3.2 Soil analysis

Soil samples were transported to KEFRI headquarters for chemical and physical analyses. The following parameters were assessed:

i) Available phosphorus (P), measured using the Olsen Method (Okalebo et al., 1993).

ii) Exchangeable bases. Soil samples were extracted with Ammonium acetate solution and the amounts of exchangeable Na and K were measured by flame photometry, while Ca and Mg by atomic absorption spectrophotometry (Okalebo et al., 1993).

iii) Trace elements (Cu, Zn, Mn and Fe) were extracted by the EDTA method and their contents measured by Atomic Absorption Spectrophotometry (Okalebo et al., 1993).

iv) Soil texture was assessed by dispersing soils into individual particles using 10% calgon (Sodium hexametaphosphate) solution, measuring fractions using the hygrometer method and assigning textural classes on the basis of soil textural triangle (Brady, 1974: Okalebo et al., 1993).

v) Soil organic carbon (C) was determined using the Walkley-Black method (Okalebo et al., 1993).

vi) Nitrogen (N) was extracted by wet acid digestion method based on Kjeldahl oxidation and determined according to the procedures outlined by Okalebo et al. (1993).

vii) pH (H_2O, $CaCl_2$) and electro-conductivity (E.C) were subsequently determined from the same solution according to the procedures described by Okalebo et al. (1993).

For the macro- and micro-nutrients, exchangeable cation contents (plant-available cations) rather than total contents were assessed due to their relevance to plant nutrition.

3.3.4 Spatial distribution and size characteristics of indigenous tree and shrub species based on soil moisture status

3.3.4.1 Identification and inventory of trees and shrubs

With the help of a forester and a parataxonomist, all trees and shrubs in each plot were initially identified by their local names and later by their botanical names using available

literature (Dale and Greenway, 1961; Beentje, 1994; Maundu and Tengnas, 2005). Trees and shrubs were counted and recorded by species, diameter (3-cm) and height (2-m) classes.

3.3.4.2 Assessment of size (DBH and height) characteristics

Size characteristics were described in terms of diameters at breast height (DBHs), heights, and diameter and height distributions. Trees and shrubs were measured for heights using SUUNTO clinometers for trees above 5.0 m, and measuring poles in the case of younger ones. Tree height was assumed to be the height of the main tree crown, ignoring any stems protruding from the crown. Diameters at breast height (1.30 m above ground) were measured for trees and shrubs above this height using diameter tapes.

3.3.4.3 Determination of Important Value Indices (IVIs)

The above measurements were used to calculate Important Value Indices (IVIs) — indices of the ecological importance of tree and shrub species, genera and families. According to Misra (1968), IVIs can be determined as follows:

IVI = Relative abundance (RA) + Relative dominance (RD) + Relative frequency (RF) - 4

Where: Abundance (A) = number of individuals/hectare (N/ha)

RA = Abundance of a given species/total abundance of all species x 100

Dominance (D) = basal area (m^2/ha)

RD = Basal area of a given species/total basal area of all species x 100

Frequency (F) = Percentage (%) of subplots in which the species is represented

RF = Frequency of a given species/total frequency of all species x 100.

The DBH data was used to calculate densities in terms of basal areas, which were in turn used to determine species dominances, and to calculate the IVIs.

The stand basal area (G), defined as the sum of the cross sections of all the trees of a population measured at 1.30 m height (Van Laar and Akca, 1997), was calculated as follows:

$$G = \sum_{i=1}^{n} gi \quad \text{----------} \quad 5$$

Where n = total number of trees of the population

gi = basal area of the individual (i^{th}) tree.

Van Laar and Akca (1997) and Brodbeck (2003) described and contrasted three types of mean heights and diameters that may be compared. These were; arithmetic mean, quadratic mean and mean according to Weisse (1880) (cited in Van Laar and Akca, 1997). Each of these types of means had advantages and disadvantages. However, despite some limitations, arithmetic mean was the simplest and easiest to measure compared to the others. It considered a weighted average of all the trees and shrubs measured.

Arithmetic mean diameters (d) of tree and shrub species assessed during the survey were calculated as:

$$d = 1/n \sum_{i=1}^{n} di \quad \text{----------} \quad 6$$

Where di = diameter of the individual (i^{th}) tree

n = total number of trees of the stand.

For standardization purposes, all plot data were converted to values per hectare (ha).

3.4 Plant and soil moisture dynamics

3.4.1 Plant moisture parameters i.e. leaf water potential (ψ), transpiration rates (Ti) and stomatal conductance (gw)

Leaf water potential (ψ_l) was measured under field conditions by use of the Scholander-type pressure chamber (Boyer, 1995; Ritchie and Hinckley, 1975; Cochard *et al.*, 2001) (Fig. 7) for selected plant species and repeated for diurnal variation at pre-dawn, early morning, midday and evening. Data was taken for one year (two dry seasons and two rainy seasons) at intervals of 1-2 months between July 2003 and June 2004. During each measurement, three leaves from

different branches about the same height and exposition were sampled per tree and shrub. Pre-dawn measurements were made between 4.00 am and 6.00 am, early morning measurements were made between 9.00 am and 10.00 am, midday measurements were made between 12.00 noon and 2.00 pm, while evening measurements were made between 3.00 pm and 4.00 pm. It was assumed that at pre-dawn, plant and soil water potentials approached equilibrium, while at midday, transpiration rates were at their highest and plants experienced the worst daily situation with regard to water deficit stress.

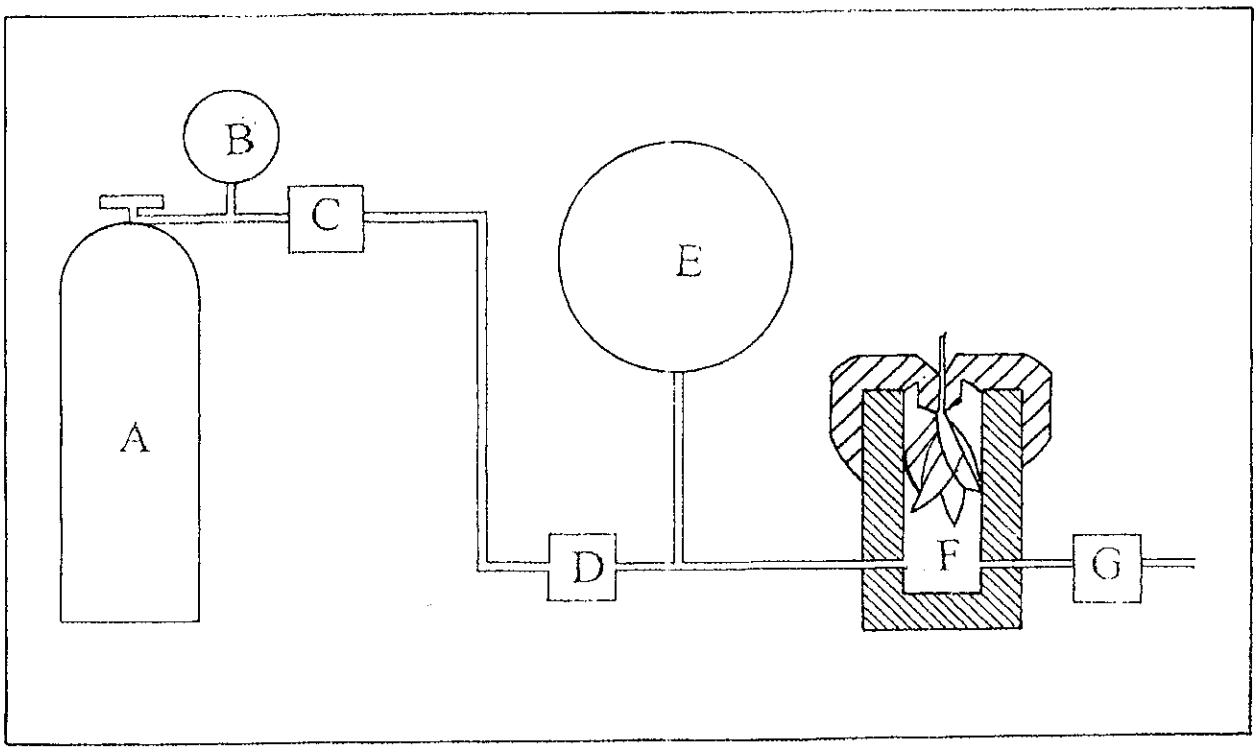


Figure 7: The Scholander Pressure Chamber: **A**=cylinder with compressed air, **B**=pressure gauge, **C**=stopcock, **D**=adjustment valve, **E**=pressure gauge, **F**=pressure chamber, **G**=outlet, excess pressure valve (Mitloehner, 1998).

Transpiration rates (Ti) ($mmolm^{-2}s^{-1}$) and stomatal conductances (gw) ($molm^{-2}s^{-1}$) were measured using a LI-1600 Steady State Porometer (Li-Cor, Inc. Lincoln, NE; Appendix 1).

Additional data concurrently obtained from the same instrument included leaf temperature, air temperature within the cuvette, and photosynthetic photon flux density (µg mol m^2s^{-1}).

Osmotic potentials were measured following the standard procedures described by Kreeb (1990). As water potential measurements were taken during pre-dawn and midday, leaf samples each amounting to 7-10 g fresh weight under field conditions were taken using a precision balance and immediately and carefully shock-dried using a frying pan and a cooking stove. This was to kill chlorophyll and avoid further enzymatic changes. Dried samples were properly packed in carefully labeled polythene bags and transported to the University of Goettingen in Germany where further processing and laboratory analysis for the determination of dry matter and osmotic potentials (π) were done at the Institute of Silviculture.

The leaves were oven-dried at 105 ^{0}C and the kiln dry leaves powdered. A sample of 1 gram each was mixed with 8 ml of distilled water. This mixture was soaked overnight in a water bath at 55 ^{0}C to fully dissolve the osmotically active solubles (salts, organic acids, sugars). The samples were then centrifuged (using Labofuge III, Heraeus GmbH, Germany) for 15 minutes at 4,000 rotations/min in order to separate coarse leaf material from liquid. Finally, the freezing point of this liquid was measured using a cryoscope (Semi-Micro Osmometer, Knauer GmbH, Germany). Considering the added 8 ml of distilled water, this value was recalculated towards the original water content at the natural site.

The freezing point of the solution is proportional to the osmotic potential of this solution. According to Kreeb (1990), the relationship between the freezing-point depression (Δt in ^{0}C) and the osmotic potential (π^* in atm) is as follows:

$$\pi^*(\text{atm}) = 0.021\ (\Delta t)^2 - 12.06\ \Delta t \qquad \text{---- ---------- 7}$$

This value is referred to a temperature of 20 ^{0}C and expressed in megapascal (MPa). Following the potential concept (e.g. Kramer, 1969), osmotic potentials as well as water potentials are given in negative values.

Soil moisture was measured using the Neutron Soil Moisture Probe (type I.H III, SR. No. 326, source No. 2869 NK) (IAEA, 2003; Bell, 1987; Pallardy et al., 1991; Fig. 8). On the days when the plant moisture parameters were measured, soil moisture was also determined once at midday at the six different soil depths.

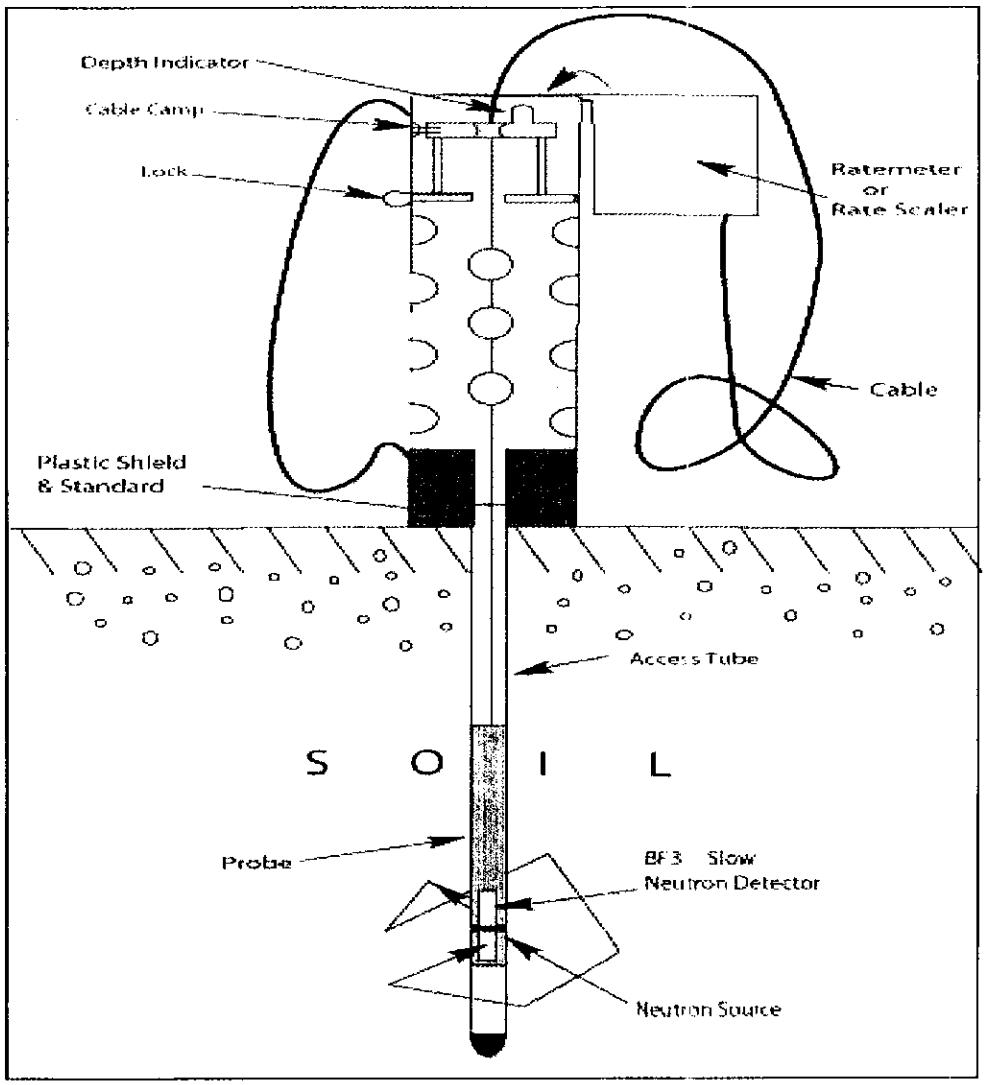


Fig. 8: The Wallington soil moisture probe used to measure soil moisture

3.4.2 Selection of trees and shrubs

Five evergreen sample tree and shrub species: *Pachystigma schumannianum*, *Maerua decumbens*, *Cadaba farinosa*, *Boscia coriacea* and *Senna siamea* were selected during field surveys conducted at the height of the dry season between August and September 2002. Selection was based on the natural distribution of species in the three agro-ecological zones, their ability to maintain green foliage during all seasons, and their perceived drought tolerance and potential for rehabilitation tree planting in semi-arid rangelands. During the selection, representatives of both trees and shrubs were considered because of their inherent differences in rooting characteristics. Shrubs have shallow rooting systems and are likely to show more

pronounced responses to changes in soil moisture status than deep-rooted trees. They are also short and bushy, making it possible to sample leaves and young twigs more conveniently during data collection. It was also desirable to have at least one tree/shrub of exotic origin for comparison purposes and to represent the introduced species.

P. Schumannianum and *B. coriacea* were found in sites I (Nthangu forest) and III (Kibwezi), respectively, *M. decumbens* and *C. farinosa* were found in both sites II (Kathonzweni) and III, and *S. siamea* was grown in farms and fields close to the other sample trees and shrubs in all the 3 sites.

In the complementary study, 3-4 tree and shrub species per study site were selected for assessment from among the dominant and ecologically important tree and shrub species identified in section 3.3.4.1 above. Selection from among the species was further made on the basis of distribution (proximity) between and within sites, presence or absence of leaves at time of measurement, and size characteristics of the leaves. At Nthangu forest, it was not possible to select from the dominant species because of the great force required by these species for the water potential measurement, but could not be provided by the scholander apparatus in use. Instead, two indigenous species that occurred widely around neighbouring farmlands and closer to the *S. siamea* sample trees were selected. The species selected for this part of the study were:

Nthangu forest: *Acacia tortilis*, *Acacia polyacantha*, *Senna siamea*
Kathonzweni: *Acacia tortilis*, *Combretum collinum*, *Terminalia brownii*, *Senna siamea*
Kibwezi: *Acacia tortilis*, *Commiphora campestris*, *Senna siamea*

3.4.3 Morphophysiological indicators of stress and adaptation based on plant and soil moisture dynamics and relationships

Results of the spatial distribution of woody vegetation, size characteristics of tree and shrub species, and the dynamics and relationships of plant and soil moisture during wet and dry seasons, and at pre-dawn and midday were used as a basis to identify morpho-physiological indicators of stress and adaptation in trees and shrubs.

3.5 Statistical Analysis

Soil physical and chemical compositions, plant water and osmotic potentials, transpiration rates and stomatal conductances per season and different day times in each site at different depths were analysed using generalized linear model and ANOVA procedures (Fisher's and Student t-test). Mean comparisons were done using orthogonal contrasts, Turkey's Honestly significant differences, LSD and standard error of difference of means (s.e.d) test between and within study sites. Additionally, Principal Component and discriminant Analysis (PCA) procedures were used to analyse the correlation between water potential, transpiration rate, conductance, light intensity, relative humidity, leaf temperature and cuvette temperature between and within selected study areas.

On the spatial distribution and size characteristics of indigenous tree and shrub species where individual counts were done and DBH and height measured, log linear modeling procedures were used to analyse count data following Poisson distribution where comparisons between sites and common tree species were carried out. Mean DBH and height were analysed using analysis of variance (ANOVA) by first checking whether ANOVA assumptions were obeyed. Whenever the normal distribution of the data was not observed, non-parametric tests mainly Mann Whitney U and Kruskallis Wallis were used. The former was used instead of t-test for comparing two independent variables especially for measurements of some species that occurred in only two study sites. The latter was used to compare measurements of more than two independent variables instead of one-way ANOVA. For these non-parametric tests, mean ranks of the response variate for comparison of independent variables were used and statistical differences were declared using Z-score and Chi-square tests for Mann Whitney U and Kruskallis Wallis, respectively. Additionally, dominance/abundance, DBH and height class distributions, basal areas, important value indices (IVIs) and frequencies of tree and shrub species were computed for each study site and comparisons done where necessary. For the case of basal area between tree species at each site, the data was log transformed to satisfy the normality assumption of ANOVA. Regression and correlation analysis were done for DBH and height of various tree and shrub species at Kibwezi, Kathonzweni and Nthangu study sites. Coefficients of determination (R^2) were used to identify the strength of the goodness of fit.

All field and laboratory data was compiled and entered into Ms-excel 2003-2007 where data management techniques like data checking for errors, exploration and general pattern of the

data were done. Subsequently data was analysed using Genstat-general statistical software V10 and all statistically significant differences were declared at five percent level of significance ($p<0.05$), unless stated otherwise.

CHAPTER FOUR

RESULTS

4.1 Climatic factors and soil physical and chemical properties

4.1.1 Rainfall

The climatic data collected at the three sites during the study period are shown in appendix 2. The mean monthly values of rainfall for Nthangu, Kathonzweni and Kibwezi forests were 80.6 mm, 40.4 mm and 52.6 mm, and the number of rainy days were 6.0, 4.0 and 5.0, respectively. Monthly amounts of rainfall for the three sites are graphically shown in Fig. 9.

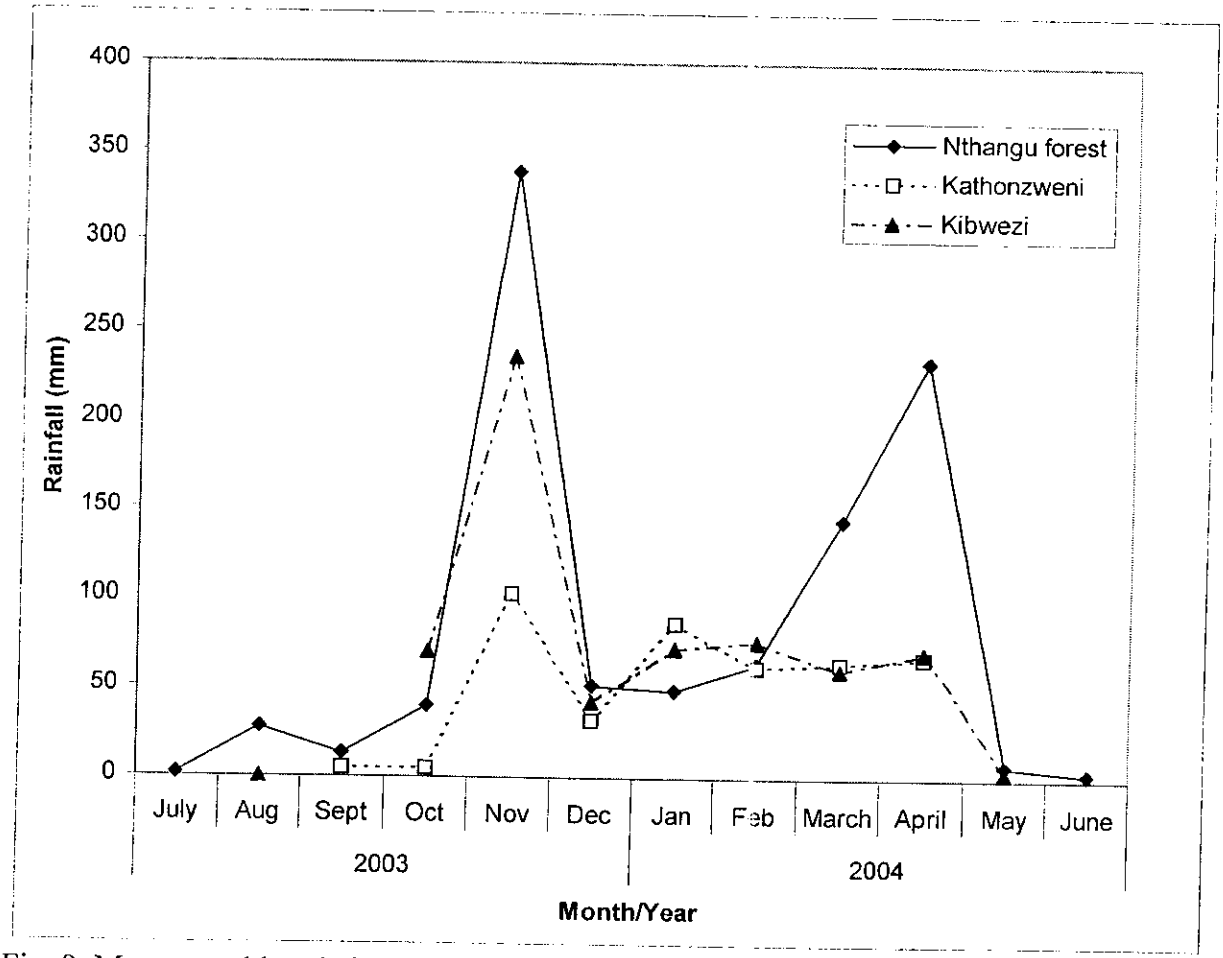


Fig. 9: Mean monthly rainfall for Nthangu, Kathonzweni and Kibwezi forests of Makueni District (July 03-June 04)

4.1.2 Soil physical and chemical properties

The results of soil physical and chemical analyses for the three study sites (Nthangu, Kathonzweni and Kibwezi) and two soil depths (10 cm and 80 cm) are shown in Tables 1, 2 and 3. It was consistently observed that the range of values for electro-conductivity (E.C), P, K, Ca, Mn and Fe were higher at Kibwezi, the site that had the driest weather conditions, compared to both Nthangu and Kathonzweni forests that had more favourable weather conditions. Carbon (C), N and Zn had higher values at the more moist sites compared to the drier sites. Carbon (C), N, K, Ca, Mn and Zn had higher values at shallower soil layers than at the deeper soil layers. Sodium (Na) seemed to have higher values at the lower soil depths than the higher ones.

Table 1: Mean textural and electro-conductivity properties of soil samples taken at two soil depths at Nthangu, Kathonzweni and Kibwezi sites of Makueni district.

Study site	Depth (cm)	Parameter			
		Sand (%)	Clay (%)	Silt (%)	E.C. (μS/cm)
Nthangu (n=10)	10	66.6	25.2	8.2	28.8
	80	66.7	23.1	10.2	15.5
Kathonzweni (n=11)	10	80.4	14.8	4.8	24.3
	80	76.4	19.4	4.2	16.2
Kibwezi (n=10)	10	76.8	17.0	6.2	38.5
	80	71.6	21.8	6.6	44.9
S.e.d		3.61	3.70	1.201	9.31

Table 2: Mean macro-element contents of soil samples taken at two soil depths at Nthangu, Kathonzweni and Kibwezi sites of Makueni district.

Study site	Depth	Parameter						
		P (ppm)	C (%)	N (%)	K (ppm)	Ca (ppm)	Na (ppm)	Mg (ppm)
Nthangu (n=10)	10	2.20	1.18	0.19	226.0	202	71.9	300
	80	2.22	0.44	0.10	66.0	137	86.7	184
Kathonz (n=11)	10	2.20	0.59	0.09	201	237	98.9	226
	80	2.10	0.30	0.08	159	164	102.8	239
Kibwezi (n=10)	10	6.00	0.55	0.07	301	474	74.3	232
	80	5.30	0.35	0.10	263	701	78.6	261
S.e.d		1.215	0.114	0.0503	67.6	189.9	15.43	66.7

Table 3: Micro-element and pH values of soil samples taken at two soil depths at Nthangu, Kathonzweni and Kibwezi sites of Makueni district

Study site	Depth	Parameter					
		Cu (ppm)	Zn (cm)	Mn (ppm)	Fe (ppm)	pH (H_2O)	pH ($Ca\ Cl_2$)
Nthangu (n=10)	10	3.11	8.27	63.0	157	-	-
	80	2.35	8.33	38.0	111	-	-
Kathonz (n=11)	10	3.38	4.29	199	139	-	-
	80	3.22	5.03	92.0	166	-	-
Kibwezi (n=10)	10	3.34	0.48	225	324	-	-
	80	3.37	0.72	164	334	-	-
S.e.d		0.591	1.177	36.1	40.1		

4.1.2.1 Soil physical and chemical properties by site

The results (Tables 4a, 4b and 4c) show the p values associated with statistical analysis of each parameter. Overall mean values of all parameters measured, except N% ($F_{(2,53)}$ = 1.97, p=0.150), Na (ppm) (F(2,53) = 3.02, p=0.057) and Mg (ppm) ($F_{(2,53)}$ = 0.05, p=0.953) were significantly different between sites ($p<0.05$).

Site variations shown by some of the properties were extremely wide. The values for E.C. ($F_{(2,53)}$ = 6.36, $p<0.05$) and P ($F_{(2,53)}$ = 10.56, $p<0.05$), for instance, were significantly higher at

Kibwezi (41.7 µS/cm and 5.65 ppm, respectively) than at the other sites (20.2-22.2 µS/cm and 2.15-2.21 ppm, respectively). The contents of carbon ($F_{(2,53)}$ = 12.79), N ($F_{(2,53)}$ = 1.97) and Zn ($F_{(2,53)}$ = 40.94) were significantly higher ($p<0.05$) at Nthangu forest than at the other sites.

Table 4: Soil physical and chemical properties by site

(a) Textural and electro-conductivity properties

Parameter	Nthangu	Kathonzweni	Kibwezi	Mean	S.e.d	Fpr
Sand (%)	66.6^a	78.4^b	74.2^c	73.2	2.55	<0.001
Clay (%)	24.2^a	17.1^b	19.4^b	20.1	2.62	0.030
Silt (%)	9.2^a	4.5^b	6.4^c	6.6	0.849	<0.001
E.C(µS/cm)	22.2^a	20.2^a	41.7^b	27.8	6.59	0.003

Means followed by the same superscript on the same row are not significantly different ($p>0.05$).

(b) Macro-element contents

Parameter	Nthangu	Kathonzweni	Kibwezi	Mean	S.e.d	Fpr
P (ppm)	2.21^a	2.15^a	5.65^b	3.3	0.859	<0.001
C (%)	0.81^a	0.45^b	0.45^b	0.56	0.0809	<0.001
N (%)	0.15^a	0.08^b	0.09^b	0.11	0.0356	0.150
K (ppm)	146.0^a	180.0^a	282.0^b	202	47.8	0.020
Ca (ppm)	170.0^a	201.0^a	588.0^b	316	133.7	0.005
Na (ppm)	79.3^a	100.8^b	76.4^a	86.0	10.91	0.057
Mg (ppm)	242.0^a	232.0^a	246.0^a	240	47.2	0.953

Means followed by the same superscript on the same row are not significantly different ($p>0.05$).

(c) Micro-element and pH values

Parameter	Nthangu	Kathonzweni	Kibwezi	Mean	S.e.d	Fpr
Cu (ppm)	2.73^a	3.30^b	3.85^b	3.3	0.418	0.039
Zn (ppm)	8.30^a	4.66^b	0.60^c	4.5	0.832	<0.001
Mn (ppm)	50.0^a	146^b	195^c	131	25.5	<0.001
Fe (ppm)	134.0^a	153.0^a	329.0^b	203	28.3	<0.001
pH (H_2O)	6.7^a	6.7^a	7.0^b	6.8	0.0759	<0.001
pH ($CaCl_2$)	5.9^a	6.0^b	6.4^c	6.1	0.0645	<0.001

Means followed by the same superscript on the same row are not significantly different ($p>0.05$).

Copper (Cu) content was significantly lower ($F_{(2,53)}$ = 3.46, $p<0.05$) at Nthangu forest (2.73 ppm) than at Kathonzweni (3.30 ppm) and Kibwezi (3.85 ppm). Iron (Fe) content was significantly higher ($F_{(2,53)}$ = 27.91, $p<0.05$) at Kibwezi (329.0 ppm) than at the other sites (134.0-153.0 ppm). Potassium (K) and Ca contents were significantly higher at Kibwezi (282.0 and 588.0 ppm) than at Nthangu (146 ppm and 170 ppm) and Kathonzweni (180 ppm and 201

ppm), respectively. There was a gradual increase in the concentration of Mn (ppm) from Nthangu through Kathonzweni to Kibwezi.

4.1.2.2 Soil physical and chemical properties at six different depths around trees and shrubs

Averages for the soil properties at six different soil depths around the ten individual sample trees combined for different points at Nthangu, Kathonzweni, and Kibwezi sites showed varying values between sites (Tables 5a, 5b and 5c; Appendix 8). However, it was not possible to confirm whether the differences were significant as the samples taken were not adequate in terms of both the number and replication to enable statistical analysis.

Table 5: Physical and chemical properties of soil samples at six different depths around tree and shrub species in three sites of Makueni district

(a) Textural and electro-conductivity properties

Soil depth (cm)	Parameter			
	Sand (%)	Clay (%)	Silt (%)	E.C. (μS/cm)
10-15	68.4	26.2	5.4	41.9
30-35	65.8	28.4	6.4	37.9
60-65	63.0	29.2	8.7	31.6
90-95	63.2	29.8	7.5	32.1
120-125	63.2	29.2	7.6	43.0
150-155	62.3	30.3	8.7	41.1

(b) Macro-element contents

Soil depth (cm)	Parameter						
	P (ppm)	C (%)	N (%)	K (ppm)	Ca (ppm)	Na (ppm)	Mg (ppm)
10-15	7.2	0.74	0.09	575	254	49.5	337
30-35	3.7	0.62	0.11	473	239	46.8	347
60-65	4.2	0.54	0.08	308	195	59.9	390
90-95	3.5	0.42	0.08	290	159	55.8	367
120-125	4.9	0.42	0.09	278	212	64.8	395
150-155	4.0	0.43	0.08	278	128	62.6	367

(c) Micro-element and pH values

Soil depth (cm)	Parameter					
	Cu (ppm)	Zn (ppm)	Mn (ppm)	Fe (ppm)	PH (H_2O)	PH ($CaCl_2$)
10-15	5.8	1.72	174	77.4	6.5	6.1
30-35	5.0	1.61	134	74.7	6.7	6.1
60-65	2.9	1.61	101	144	6.7	6.0
90-95	2.7	1.73	78	98.8	6.5	5.9
120-125	3.2	2.34	86	55.5	6.6	6.0
150-155	2.4	1.73	60	46.1	6.6	6.0

Raw data generated from soil samples collected from the different depths around each sample tree per site are shown in Appendix 3.

4.2 Spatial distribution of indigenous tree and shrub species

Results of the vegetation survey conducted at the three study sites (Nthangu Forest, Kathonzweni and Kibwezi) were summarized in terms of species composition, size distribution and Important Value Indices (IVIs). Tree and shrub species were listed by both their local and botanical names, their respective family names and life forms (i.e. tree, shrub, liana, bush or climber). The density, dominance and frequency of each of the identified species was calculated and used to determine the IVI of individual species and families. The results were as discussed in the sections below.

4.2.1 Species composition and other attributes

4.2.1.1 Species characterising various sites

Vegetation at Nthangu Forest was found to consist of Seventy-seven (77) different tree and shrub species. These species can be categorized into 33 families and 60 genera (Appendix 4). The most common genera in order of frequency were Combretum (6), Acacia (5), Grewia (4), Cassia (2), Rhus (2), Terminalia (2), Croton (2) and Indigofera (2). The most common families were Papilionaceae (8), Euphorbiaceae (7), Combretaceae (6), Mimosaceae (6), Tiliaceae (5), Anarcadiaceae (4), Caesalpiniaceae (3), Rubiaceae (3), Sapindaceae (2), Rhamnaceae (2), Apocynaceae (2), Verbenaceae (2), Labiatae (2) and Simaraubaceae (2). In appendix 5,

Important Value Indices were calculated and reported for those species whose height and DBH were above 1.3 m and greater than 1.0 cm, respectively. Ecologically important tree and shrub species according to descending order of their Important Value Indices (IVI)s) were as shown in table 6. Rhus spp. included two different tree species, namely: *Rhus natalensis* and *Rhus vulgaris*.

Vegetation at Kathonzweni was found to consist of sixty-nine (69) different tree and shrub species. These species can be categorized into 28 families and 42 genera (appendix 4). The most common genera in order of frequency were Commiphora (6), Combretum (6), Acacia (6), Grewia (4), Boscia (3), Terminalia (2), Albizia (2) and Lannea (2). The most common families were Mimosaceae (10), Combretaceae (8), Burseraceae (6), Papilionaceae (5), Tiliaceae (5),Capparaceae (3), Euphorbiaceae (3), Verbenaceae (3), Capparidaceae (2), Anacardiaceae (2) and Caesalpiniaceae (2). Ecological importance of tree and shrub species by their IVIs could be determined for only 31 of the species. According to descending order of their IVIs, ecologically important species were as shown in table 6.

Vegetation at Kibwezi was found to consist of seventy (70) different tree and shrub species. These species may be categorized into 30 families and 48 genera (appendix 4). The most common genera in order of frequency were Acacia (8), Commiphora (6), Grewia (5), Combretum (3), Boscia (3), Maerua (2) and Lannea (2). The most common families were Mimosaceae (11), Burseraceae (6), Tiliaceae (6), Euphorbiaceae (5), Capparaceae (4), Combretaceae(4), Anacardiaceae (3), Papilionaceae (3), Sterculiaceae (2), Caesalpiniaceae (2) and Verbenaceae (2). Ecologically important tree and shrub species according to descending order of their IVIs were as shown in table 6.

Table 6: Important tree and shrub species at Nthangu, Kathonzweni and Kibwezi forests of Makueni district.

Study site	Species	Species type	Rank	Dominance (m^2/ha)	Abundance (N/ha)	Frequency (%)	IVI
Nthangu Forest	Rhus spp	S, T	1	1.40	290	100	29.1
	C. molle	T	2	2.74	74	75	23.2
	A. hockii	S,T	3	1.15	145	100	18.7
	D. mespilifor.	T	4	1.22	127	100	18.0
	P. viridiflor.	T, S	5	1.90	57	75	17.1
	T. brownii	T	6	1.03	60	100	12.9
	E. divinorum	T	7	1.02	57	100	12.6
	P. schuman.	S, T	8	0.39	99	100	11.3
	F. saligna	T	9	0.93	39	25	8.8
	Other species		10-52				149.5
Kathonzweni	*C. collinum*	S, T	1	4.0	319	75	60.7
	T. brownii	T	2	1.0	19	100	34.8
	A. tortilis	T	3	4.2	63	100	33.8
	C. apiculatum	T	4	2.3	89	75	25.7
	C. baluensis	T	5	1.3	24	75	16.3
	C. Campestris	T	6	1.2	39	100	15.4
	A. nilotica	T	7	0.2	44	75	14.8
	L. triphylla	S, T	8	0.9	65	50	14.6
	S. africana	T	9	0.6	18	100	10.3
	Other species		10-52				98.6
Kibwezi	*A. digitata*	T	1	33.9	3.0	33	45.7
	A. tortilis	T	2	8.7	152	100	33.4
	A. mellifera	S, T	3	2.8	88	83	17.4
	C. africana	T	4	3.5	61	83	15.0
	C. dichogam.	S, T	5	0.9	64	50	10.7
	D. elata	T	6	6.9	5.0	17	10.1
	A. elliator	T	7	2.2	23	67	8.1
	A. nilotica	T	8	0.8	25	100	7.8
	S. incanum	S	9	0.4	45	50	7.7
	Other species		10-52				142.5

S=shrub, T=Tree, IVI=Important Value Index

4.2.1.2 Commonly occurring tree and shrub species in the three sites of Makueni district

The tree and shrub species that occurred commonly in all the three study sites were compared and ranked at each site based on their IVIs (Table 7). Predominant species with the highest IVIs were *Acacia nilotica* at Nthangu (6.8) and *Acacia tortilis* at Kathonzweni (33.8) and Kibwezi (33.4). *Acacia mellifera* had the second highest IVI at Kibwezi.

Table 7: Important Value Indices (IVIs) of commonly occurring tree and shrub species at Nthangu, Kathonzweni and Kibwezi forests of Makueni district.

Species	Important value index (IVI)		
	Nthangu	Kathonzweni	Kibwezi
Acacia tortilis	3.6	33.8	33.4
Acacia nilotica	6.8	14.8	7.8
Acacia mellifera	1.7	5.0	17.4
Grewia spp.	2.2	4.4	2.8
S. erialiacea	1.7	3.3	2.5
Total	16.0	61.3	63.9

4.2.1.3 Ecologically important tree and shrub families

The most important families with IVIs of at least 10.0 and according to descending order of their IVIs at each study site were as shown in table 8.

Table 8: Important tree and shrub families at Nthangu, Kathonzweni and Kibwezi forests of Makueni district

Study site	Tree family	Rank	Dominance (m^2/ha)	Abundance (N/ha)	Frequency (%)	IVI
Nthangu Forest	Combretaceae	1	4.7	215	100	60.9
	Anacardiaceae	2	1.9	354	100	42.7
	Mimosaceae	3	2.0	209	100	40.0
	Rubiaceae	4	0.4	107	75	19.5
	Pittosporaceae	5	1.9	57	50	19.1
	Papilionaceae	6	0.5	47	75	15.8
	Tiliaceae	7	0.4	71	50	15.8
	Ebenaceae	8	1.0	57	75	14.1
	Proteaceae	9	0.9	39	25	9.7
	Other families	10-25				62.5
Kathonzweni	Combretaceae	1	7.5	460	75	109.4
	Mimosaceae	2	5.0	138	100	66.4
	Burseraceae	3	3.0	94	75	41.7
	Anacardiaceae	4	0.9	65	50	14.9
	Sterculaceae	5	0.6	18	100	10.4
	Papilionaceae	6	0.4	35	25	8.8
	Labiatae	7	0.2	12	25	7.1
	Umbelliferae	8	0.4	11	25	6.9
	Ochnaceae	9	0.04	15	25	5.6
	Other families	10-17				28.9
Kibwezi	Mimosaceae	1	17.0	328	100	89.8
	Bombaceae	2	33.9	3.0	33	46.5
	Burseraceae	3	7.4	94	100	34.6
	Caesalpiniaceae	4	7.0	16	50	15.2
	Tiliaceae	5	0.4	21	67	15.0
	Combretaceae	6	0.8	57	67	14.5
	Solanaeae	7	0.4	45	17	8.5
	Boraginaceae	8	0.4	34	33	8.3
	Sterculiaceae	9	0.6	25	50	8.0
	Other families	10-24				59.6

4.2.2 Tree and shrub species densities at each site

Tree and shrub species densities at each of the three sites; Nthangu forest, Kathonzweni and Kibwezi were described in terms of their basal areas.

The mean basal areas reported here were based on trees and shrubs that were 3 m and above in height. The mean basal areas of nine ecologically most important tree and shrub species which accounted for 70.7%, 86.5% and 78.3% of the overall mean basal area of woody perennials at Nthangu forest, Kathonzweni and Kibwezi study sites, respectively are shown in

table 9. Values are reported on per hectare basis. The overall mean basal areas for these sites in the same order were 16.7 m^2/ha, 19.3 m^2/ha and 76.8 m^2/ha. There were no significant differences in basal area between pairs of the four tree species with the highest basal areas at Nthangu forest: *T. brownii* (0.17 m^2/ha), *C. molle* (0.13 m^2/ha), *F. saligna* (0.13 m^2/ha) and *P. viridiflorum* (0.13 m^2/ha) ($F_{(1, 203)}$ =3.04; p>0.05). There were also no significant differences in basal areas between pairs of the three species with the highest basal areas at Kathonzweni: *Acacia tortilis* (0.09 m^2/ha), *C. baluensis* (0.08 m^2/ha) and *T. brownii* (0.07 m^2/ha) (p>0.05). At Kibwezi, the basal area of *A. digitata* (8.47 m^2/ha) was significantly higher than that of *D. elata* (0.86 m^2/ha) ($F_{(1,612)}$ = 40.84, P<0.05).

Among the three species, each occurring in at least two of the study sites, it was observed that mean basal areas were higher at more moist sites (Table 9). For instance, the basal area of *T. brownii* was higher at Nthangu forest (0.17 m^2/ha) than at Kathonzweni (0.07 m^2/ha) although the differences were not significant ($t_{(1,19)}$ = -1.26, p>0.05), while those of *A. tortilis* ($t_{(1,252)}$ = 3.83, p<0.05) and *A. nilotica* ($t_{(1,71)}$ = 1.96, p<0.05) were both significantly higher at Kathonzweni (0.09 m^2/ha, 0.04 m^2/ha, respectively) than at Kibwezi (0.04 m^2/ha, 0.02 m^2/ha, respectively). At the Kathonzweni site, A. *tortilis* had the highest basal area (0.09 m^2/ha) followed by *T. brownii* (0.07 m^2/ha) and *A. nilotica* (0.04 m^2/ha) in that order. The former and the later were significantly different ($t_{(1,252)}$ = 3.83, p<0.05). At Kibwezi, *A. tortilis* had a basal area (0.04 m^2/ha) twice higher than that of *A. nilotica* (0.02 m^2/ha). However, the differences were not statistically significant ($t_{(1,71)}$ = 1.96, p>0.05).

Table 9: Mean basal areas (BA) of nine important tree and shrub species at Nthangu, Kathonzweni and Kibwezi forests of Makueni district

Study site	Species	Mean BA (m^2/ha)	Max.	Min.	Range	S.E	n
Nthangu	Rhus spp	0.02	0.102	0.001	0.101	0.000	67
	C. molle	0.13	0.608	0.001	0.607	0.014	21
	A. hockii	0.04	0.212	0.005	0.207	0.001	24
	D. mespilifor.	0.04	0.385	0.004	0.381	0.004	32
	P. viridiflor	0.13	0.363	0.006	0.358	0.004	15
	T. brownii	0.17	0.407	0.014	0.393	0.007	5
	E. divinorum	0.07	0.349	0.008	0.341	0.005	15
	P. schumann	0.01	0.031	0.009	0.031	0.000	26
	F. saligna	0.13	0.385	0.014	0.371	0.008	7
Kathonzweni	*C. collinum*	0.02	0.332	0.001	0.332	0.000	257
	T. brownii	0.07	0.266	0.006	0.256	0.002	14
	A. tortilis	0.09	0.369	0.004	0.365	0.024	47
	C. apiculatum	0.04	0.132	0.002	0.130	0.000	65
	C. baluensis	0.08	0.231	0.001	0.230	0.002	16
	C. campestris	0.04	0.224	0.004	0.220	0.001	27
	A. nilotica	0.04	0.138	0.004	0.135	0.000	33
	L. triphylla	0.02	0.053	0.003	0.050	0.000	47
	S. africana	0.06	0.167	0.003	0.165	0.001	11
Kibwezi	*A. digitata*	8.47	20.79	2.290	18.50	27.09	4
	A. tortilis	0.04	0.342	0.001	0.341	0.001	205
	A. mellifera	0.02	0.302	0.001	0.301	0.001	123
	C. africana	0.05	0.363	0.001	0.362	0.001	75
	C. dichogam	0.01	0.046	0.001	0.045	0.000	95
	D. elata	0.86	2.684	0.001	2.683	0.300	8
	A. elliator	0.09	0.622	0.001	0.622	0.016	24
	A. nilotica	0.02	0.091	0.004	0.087	0.000	38
	S. incanum	0.01	0.023	0.001	0.023	0.000	51

4.2.3 Size characteristics of indigenous tree and shrub species

4.2.3.1 Mean diameter

The results showed that the mean site DBH for all species was 6.4 cm, 7.6 cm and 4.6 cm for Kathonzweni, Kibwezi and Nthangu, respectively. Following Kruskallis Wallis test one way ANOVA, there was significant difference (χ^2=97.56, d.f=2, $p<0.05$; Kathonzweni mean rank=1263.3, Kibwezi=1233.8 and Nthangu=897.2) in mean DBH. This difference was mainly as a result of Nthangu as further comparisons showed that there was no significant difference ($p>0.05$) on mean DBH between Kathonzweni and Kibwezi. Tree and shrub species with the highest mean diameters at Kibwezi, Kathonzweni and Nthangu were *A. digitata* (148.4 cm), *C.*

abbreviata (14.9 cm) and *E abyssinica* (12.0 cm) while those with the lowest means were *Indigofera spp* (2.0 cm), *G. tembensis* (1.6 cm) and *S. eraliacea* (3.5 cm), respectively.

Consequently, among the common species across sites, *A. tortilis* significantly (p=0.003) performed better at Kathonzweni with mean DBH of 12.1 cm as compared to Kibwezi whose mean DBH was 9.6 cm. Similarly, *A. nilotica* significantly (p=0.008) performed better at Kathonzweni with mean DBH of 9.6 cm as compared to Kibwezi whose mean DBH was 7.7 cm. Equally, *T. brownii* significantly (p=0.003, Mann Whitney U test=46, Kathonzweni mean rank=21.2 and Nthangu=11.7) performed better at Kathonzweni with mean DBH of 10.1 as compared to 5.2 cm at Nthangu.

Table 10: Arithmetic mean diameters of dominant tree and shrub species at three sites of Makueni district

Study site	Species	Mean DBH (cm)	Max.	Min.	Range	n
Nthangu	Rhus spp	3.81	9.0	1.5	8.0	67
	C. molle	8.05	22.0	1.0	21.0	21
	A. hockii	5.51	13.0	2.5	10.5	24
	D. mespilifor.	5.22	21.0	2.0	19.0	32
	P. viridiflorum	9.84	18.0	2.5	15.5	15
	T. brownii	10.98	18.0	4.0	14.0	5
	E. divinorum	6.94	20.0	3.0	17.0	15
	P. schumann	3.46	6.0	1.0	5.0	26
	F. saligna	10.57	21.0	4.0	17.0	7
Kathonzweni	*C. collinum*	4.83	32.5	0.3	32.2	257
	T. brownii	10.05	20.0	3.0	17.0	14
	A. tortilis	12.09	24.0	2.5	21.5	47
	C. apiculatum	7.48	20.5	2.0	18.5	65
	C. baluensis	9.25	19.0	1.5	17.5	16
	C. campestris	8.65	18.5	3.5	15.0	27
	A. nilotica	9.65	21.0	3.5	17.5	33
	L. triphylla	7.41	13.0	3.2	9.8	47
	S. africana	8.05	16.0	2.0	14.0	11
Kibwezi	*A. digitata*	148.4	257.3	85.0	172.3	4
	A. tortilis	10.18	33.0	1.9	31.1	205
	A. mellifera	6.95	31.0	1.5	29.5	123
	C. africana	9.84	34.0	2.0	32.0	73
	C. dichogamus	5.03	12.1	1.5	10.6	95
	D. elata	34.57	92.0	2.0	90.0	8
	A. elliator	10.75	44.5	1.0	43.50	24
	A. nilotica	7.69	17.0	3.5	13.5	38
	S. incanum	4.33	8.6	1.3	7.3	51

4.2.3.2 Diameter distribution

According to the raw data obtained from this study and on which all calculations are based, DBH sizes ranged from 1.0-22.0, 0.3-32.5 and 1.0-257.3 cm at Nthangu Forest, Kathonzweni and Kibwezi sites, respectively. In order to construct diameter distribution bar graphs, the diameter sizes were divided into 3-cm classes for both overall distributions (Fig 10) and distributions of dominant species (Appendix 6). Diameters above 46 cm such as those of *D. elata* and *A. digitata* were combined to allow easier construction of the overall distribution curve. Each diameter class was plotted against the density (individuals per hectare (ind ha^{-1})) of species occurring within that class.

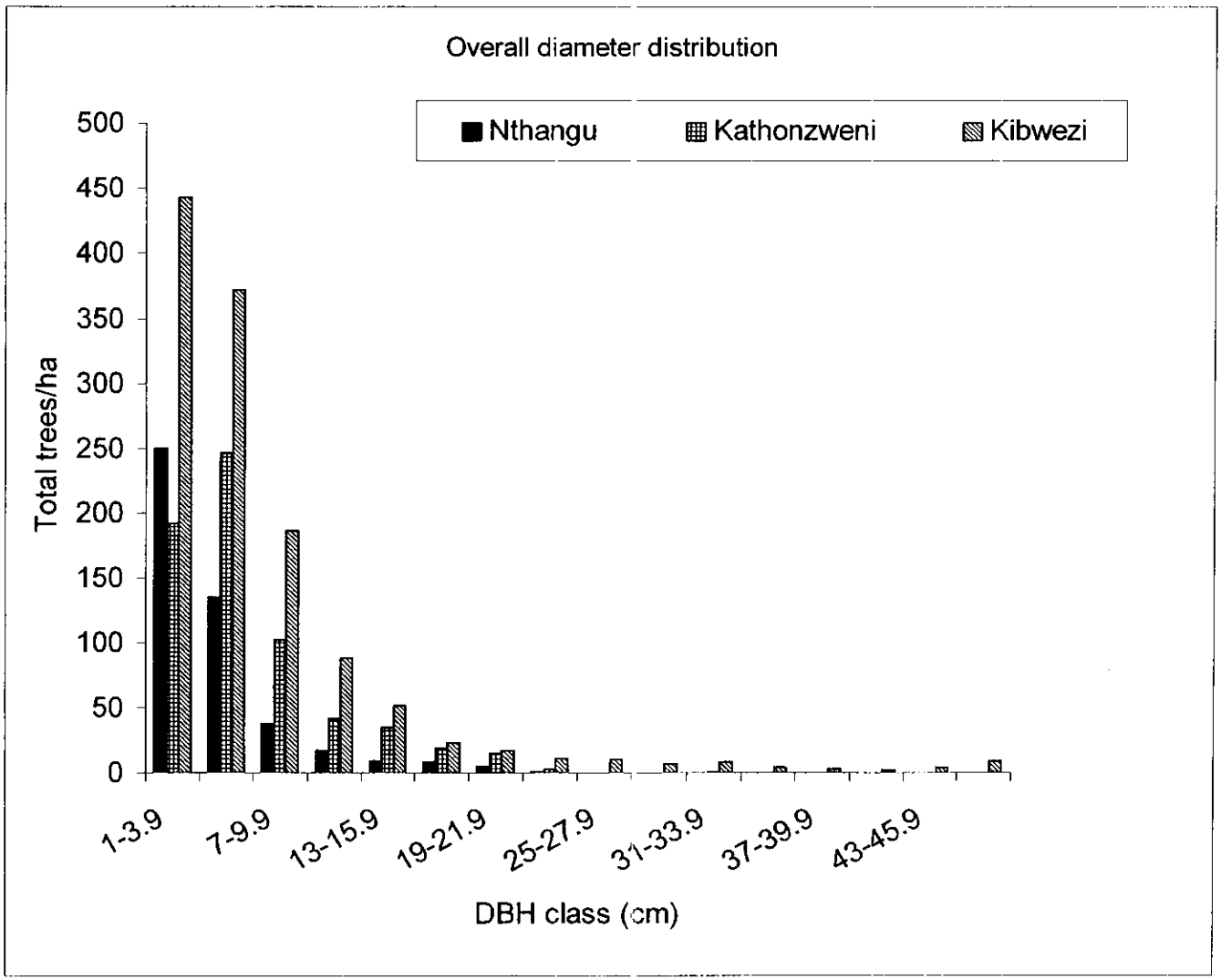


Fig. 10: Overall diameter distributions of tree and shrub species occurring at Nthangu forest, Kathonzweni and Kibwezi sites of Makueni district

Majority of the trees and shrubs occurring at Nthangu, Kathonzweni and Kibwezi forests of Makueni district fell within the lowest diameter classes (Fig. 10, Appendix 6). Since figure 10 shows absolute numbers of trees and shrubs in each diameter class per hectare, it was not possible to include error bars in the graph, as these are usually associated with mean values of data. Unlike at Nthangu and Kibwezi forests where the lowest diameter class had larger number of plants than the second-lowest (thus, showing near-perfect inverted J-shaped distributions), the number of plants in the lowest diameter class (1.0-3.9 cm) at Kathonzweni was lower than in the second lowest diameter class (4.0-6.9 cm). From the latter diameter class onwards, the trend was similar to that of the other two sites. The range of diameters at Kibwezi was wider than that at the other sites. Some of the plants growing at this latter site were large with diameters exceeding 46.0 cm recorded.

Among the dominant tree and shrub species at Nthangu forest, only *C. molle* and *P. viridiflorum* did not follow the inverted J-shaped distribution shown by the other species at the same site. Among the different species assessed at Kathonzweni, all, except *S. africana*, had a lower number of individuals in the lowest diameter class (1.0-3.9 cm) than in the second lowest. Distributions in the higher diameter classes showed trends that were similar to those in the other sites. At Kibwezi, most of the species comprising the dominant group belonged to the acacia family which also contributed the largest number of trees and shrubs per hectare.

According to the DBH distributions of the tree and shrub species that occurred commonly in at least two study sites, the largest number of *A. tortilis* plants was found in Kibwezi where they were represented in all the diameter classes except the 28.0-30.9 cm class. At Kathonzweni, *A. tortilis* was also represented in most of the diameter classes (Appendix 6). *Acacia nilotica* was represented in all diameter classes up to 18.9 cm and 2.19 cm at both Kathonzweni and Kibwezi (Appendix 6). *T. brownii* was represented in all diameter classes up tp 7.0-9.9 cm and in the 16.0-18.9 cm diameter class both at Kathonzweni and Nthangu (Appendix 6).

4.2.3.3 Mean height

According to the results, overall mean heights at Kibwezi, Kathonzweni and Nthangu were 5.3 m, 5.1 m and 4.4 m, respectively. These were found to be significantly different (Kruskalli Wallis Test, χ^2=100.9, d.f=2, $p<0.05$; Kathonzweni mean rank=1302.7, Kibwezi=1211.0 and Nthangu=902.6). This difference was mainly as a result of Nthangu as

further comparisons showed that there was no significant difference ($p>0.05$) on mean height between Kathonzweni and Kibwezi.

Tree and shrub species with the highest mean heights at Kibwezi, Kathonzweni and Nthangu were *A. digitata* (17.0 m), *C. paniculatum* (7.4 m) and *Grewia spp* (7.8 m) while those with the lowest means were *T. africanum/O. kirkii* (2.8 m), *A. mellifera* (2.4 m) and *S. eraliacea.* (1.7 m), respectively.

Consequently, among the common species across sites, *T. brownii* significantly ($p<0.05$, Mann-Whitney U test =39.0, Kathonzweni mean rank=21.7 and Nthangu=11.3) performed better at Kathonzweni with mean height of 7.2 m as compared to Nthangu whose mean height was 3.4 m. On the other hand the mean height of *A. nilotica* and *A. tortilis* at Kathonzweni and Kibwezi were 5.5 m, 5.9 m and 4.7 m and 5.8 m, respectively. These were found not to be significantly different ($p>0.05$).

Mean heights of the three commonly occurring tree species did not show substantial variation both within and between respective sites (Table 11). *T. brownii* had a lower mean height of 6.6 m at Nthangu than at Kathonzweni (7.2 m). *A. tortilis* had a lower mean height (5.9 m) at Kathonzweni than at Kibwezi (6.1 m), while *A. nilotica* had a higher mean height at Kathonzweni (5.5 m) than at Kibwezi (4.7 m).

Table 11: Arithmetic mean heights of dominant tree and shrub species at three sites of Makueni district

Study site	Species	Mean ht (m)	n
Nthangu	Rhus spp	4.44	67
	C. molle	5.57	21
	A. hockii	4.49	24
	D. mespilifor.	5.08	32
	P. viridiflorum	6.27	15
	T. brownii	6.64	5
	E. divinorum	5.67	15
	P. schumann	4.66	26
	F. saligna	7.31	7
Kathonzweni	*C. collinum*	5.25	257
	T. brownii	7.18	14
	A. tortilis	5.94	4.7
	C. apiculatum	5.08	65
	C. baluensis	5.43	16
	C. campestris	4.77	27
	A. nilotica	5.48	33
	L. triphylla	4.86	47
	S. africana	5.54	11
Kibwezi	*A. digitata*	17.0	4
	A. tortilis	6.11	205
	A. mellifera	5.69	123
	C. africana	5.91	73
	C. dichogamus	4.53	95
	D. elata	9.70	8
	A. elliator	7.39	24
	A. nilotica	4.67	38
	S. incanum	3.53	51

4.2.3.4 Height distribution

According to the raw data obtained from this study and on which all calculations were based, the woody stratum ranged in height from 0.3-15 m, 1.1-14.1 m and 0.5-24 m for Nthangu, Kathonzweni and Kibwezi sites, respectively. In order to construct height distribution bar graphs, these height sizes were divided into 2-m classes for both overall distributions (Fig 11) and distributions of dominant species (Appendix 7). Each height class was plotted against the density (individuals per hectare (ind ha^{-1})) of species occurring within that class.

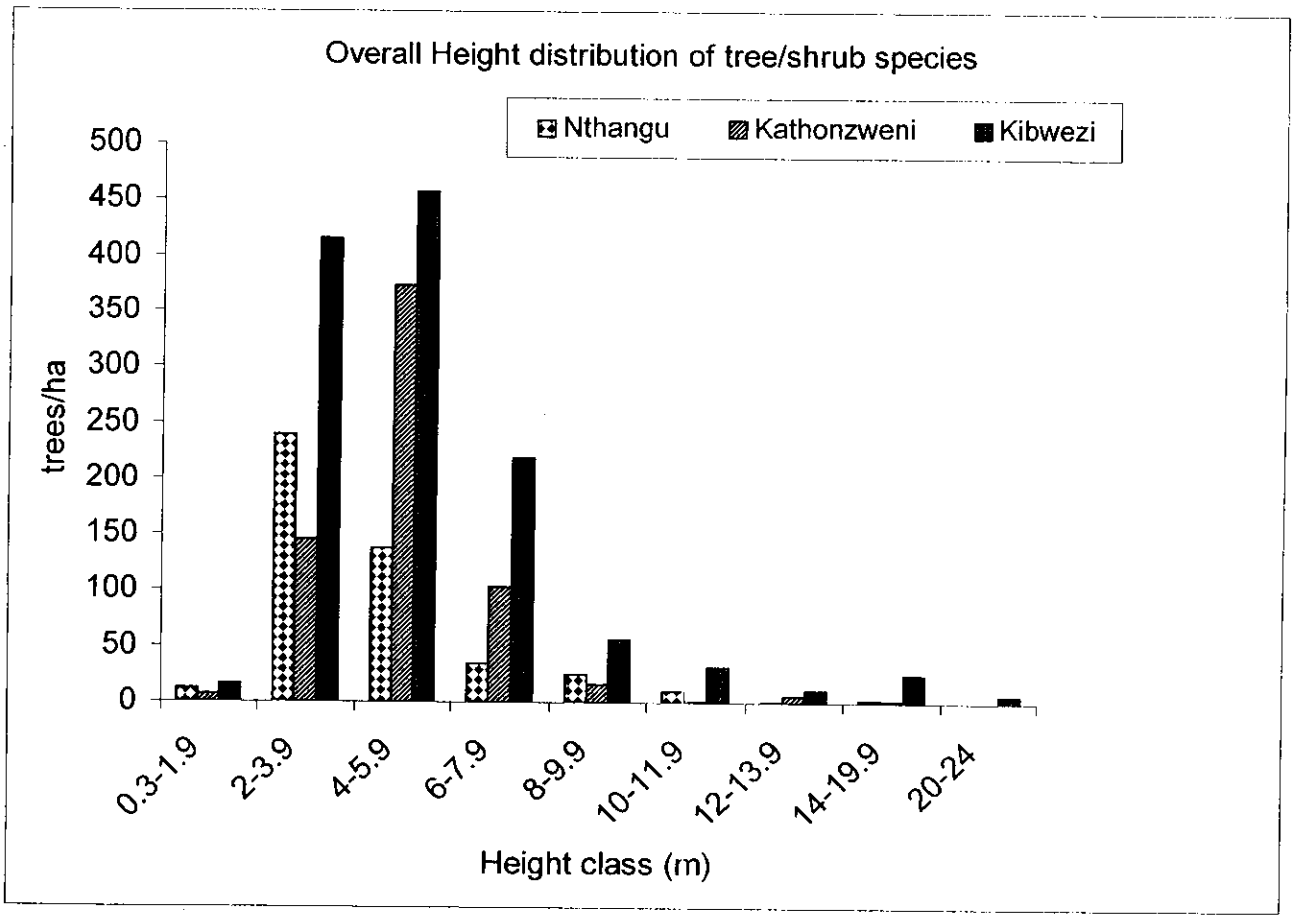


Fig. 11: Overall height distributions of tree and shrub species at Nthangu forest, Kathonzweni and Kibwezi sites of Makueni district

According to figure 11, the largest number of trees per hectare at Nthangu forest (approx. 400) fell in heights between 2.0 m and 5.9 m. Those at Kathonzweni fell between 2.0 m and 7.9 m with the 4.0-5.9-m height class having the largest number of individuals per ha (approx. 380), and those at Kibwezi between 2.0 m and 7.9 m with the largest number of individuals per hectare (approx. 450) occuring in the 4.0-5.9-m height class. Thereafter, the numbers in all sites decreased with increasing height class. The Kibwezi site had trees and shrubs that attained higher heights than those at the other sites.

Height distributions of many dominant tree and shrub species at each site (Appendix 7) were similar to those of overall distributions. At Nthangu forest, majority of these trees and shrubs mainly belonged to three of the dominant species, i.e. Rhus spp., *A. hockii*, *D. mespiliformis* and *P. schumannianum*. At Kathonzweni, *C. collinum* was the most dominant (frequent) tree species. Others were: *A. tortilis*, *C. apiculatum*, *C. campestris*, *L. triphyla* and *C. africana*. *T. brownii* showed a distribution in which the number of individuals increased with

height class up to 8.0-9.9 m height class. The reverse was shown by *C. baluensis* (Appendix 7). The Majority of ecologically important trees and shrubs at Kibwezi mainly belonged to the species; *A. tortilis*, *A. mellifera*, *C. africana*, *C. dichogamus* and *S. incanum*.

In all sites, majority of the trees belonging to *A. tortilis* fell in height classes ranging from 2.0 m-5.0 m. At Kibwezi, the species was represented in all, but the lowest (0.3 m-1.9 m) height classes. At Kathonzweni, they were represented in height classes between 2.0 m and 6.0 m. In both the sites, the lowest height class had lower number of trees than the second or third lowest height classes (Appendix 7).

Kathonzweni seemed to have taller *A. nilotica* trees than Kibwezi (Appendix 7). At Kathonzweni, the species was generally represented in diameter classes between 4.0 and 12.0 m. At Kibwezi, they were represented in classes between 2.0 and 10.0 m. Nthangu forest had a larger number of *T. brownii* trees than Kathonzweni, particularly in the 2.0-3.9 m height class. At Kathonzweni, the species was represented in the higher classes where the number of trees per hectare increased with increasing height class.

4.2.3.5 Relationship between DBHs and heights of dominant tree and shrub species

Results for regression and correlation analyses between DBH and height of all of the important tree and shrub species in each of the three sites showed positive significant correlations between the two variates, implying that for a unit increase in DBH, there was some unit increase in height. Line graphs showing equations, R^2, correlation coefficients and p values of one of the important tree species at each site are presented in figures 12-14.

The regression equation in figure 12 showed a significant positive relationship ($p<0.05$) between the height and DBH of *E. divinorum* at Nthangu forest in which a unit increase in the DBH resulted in some increase in height. The relationship between the two parameters was represented by the regression equation: $Ht = 0.4489DBH + 2.4513$. There was a strong positive correlation with a coefficient of 0.7737 and a R^2 of 0.5986 meaning that the DBH of the species explained 60% of the variation in its height.

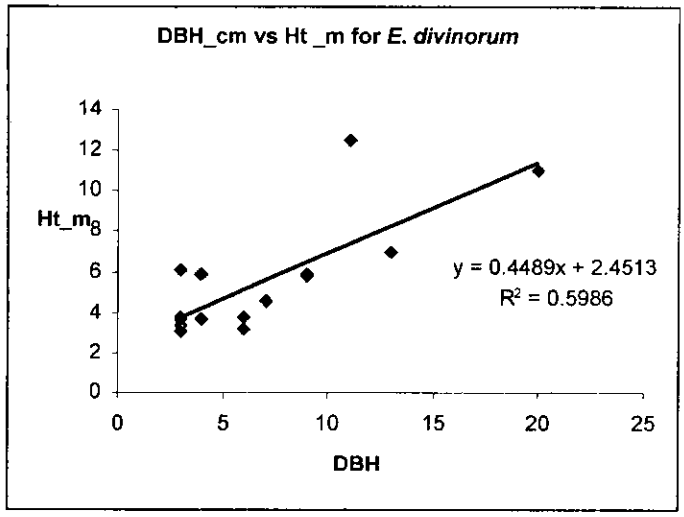


Figure 12: Regression and correlation between DBH (cm) and height of *E. divinorum* at Nthangu forest.

The regression equation in figure 13 showed a significant positive relationship ($p<0.05$) between the height and DBH of *A. tortilis* at Kathonzweni in which a unit increase in the DBH resulted in some increase in height according to the regression equation: Ht = 0.1218DBH + 4.4678. The relationship had a correlation coefficient of 0.5646 and a R^2 of 0.3188, meaning that the DBH of the species explained 31.9% of the variation in its height.

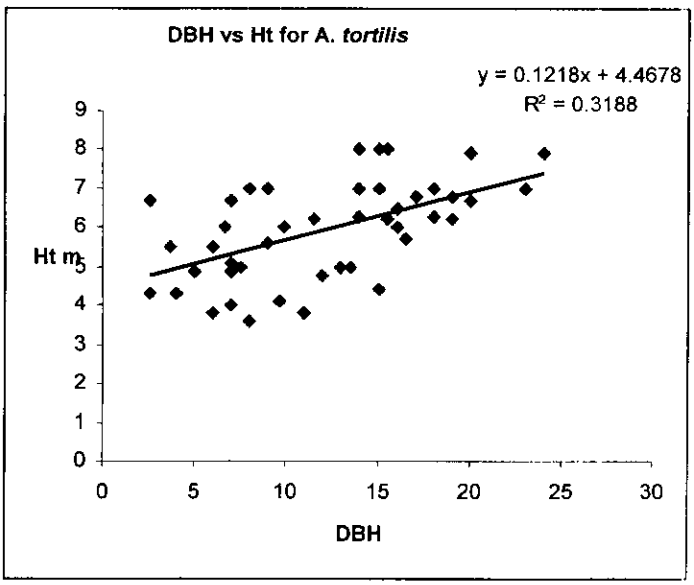


Figure 13: Regression and correlation between DBH (cm) and height of *A. tortilis* at Kathonzweni.

The regression equation in figure 14 showed a significant positive relationship ($p<0.05$) between the height and DBH of *A. eliatior* at Kibwezi in which a unit increase in the DBH resulted in some increase in its height according to the regression equation: Ht = 0.4736DBH + 2.30. The relationship had a correlation coefficient of 0.9727 and a R^2 of 0.9462, meaning that the DBH explained 94.6% of the variation in the height of the species.

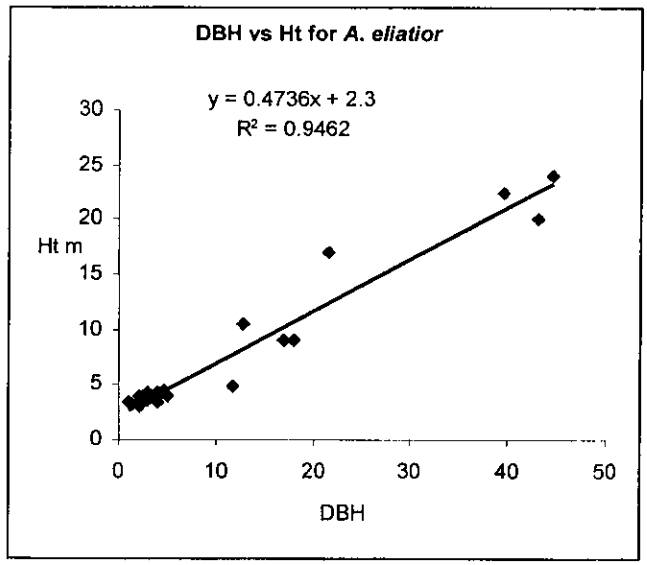


Figure 14: Regression and correlation between DBH (cm) and height of *A. eliatior* at Kibwezi.

4.3 Plant and soil moisture during wet and dry seasons

4.3.1 Plant water potentials

4.3.1.1 Plant water potentials by site

Of the two tree and shrub species (*P. schumannianum* and *S. siamea*) assessed for water potential, *P. schumannianum* was not naturally distributed in all the three study sites, but was only found at Nthangu forest. In November 2003, no water potential measurements were taken on this species because climatic conditions were extremely dry, and the tree had lost most of its leaves through abscission. *S. siamea* as an introduced species was available somewhere in each of the three sites and was used to compare sites with regard to this parameter. The effect of site on the water potential of *S. siamea* was highly significant ($F_{(2,169)} = 152.18$, $p<0.05$), accounting for 62% of the variability. The results are summarized in Table 12.

According to a regression analysis for the comparison of means, mean water potentials of *S. siamea* were significantly higher (less negative) at Kathonzweni than at Kibwezi ($t_{(1,169)}$ =

15.02, $p<0.05$). However, they were not significantly different between Kathonzweni and Nthangu forest ($t_{(1,169)} = 0.77$, $p>0.05$). It also followed that the same was significantly higher at Nthangu forest than at Kibwezi ($p<0.05$).

Table 12: Mean water potentials (MPa) of *S. siamea* trees growing at Nthangu, Kathonzweni and Kibwezi sites of Makueni district during wet and dry seasons

Study site	Mean water potential (MPa)	n
Nthangu forest	-1.23[a]	63
Kathonzweni	-1.31[a]	60
Kibwezi	-2.64[b]	52
Overall	-1.73	175

S.e.d = 0.0893; Mean water potentials followed by the same superscript on the same column were not significantly different ($p>0.05$)

4.3.1.2 Plant water potentials by season

According to the data (Table 13), the seasonal differences of water potential for *P. schumannianum* were statistically significantly ($t_{(1,169)} = 12.43$, $p<0.05$). However, those for *S. siamea* were not statistically significant and showed higher (less negative) water potentials during the dry season than during the wet season.

Table 13: The effect of season on daily water potential (MPa) measurements of *P. schumannianum* and *S. siamea* in three sites of Makueni district, Kenya.

Species	Season	Mean water potential (MPa)	n
P. schumannianum	Dry	-3.52[a]	36
	Wet	-1.56[b]	27
S. siamea	Dry	-1.17[a]	36
	Wet	-1.32[a]	27

S.e.d = 0.1466; Means of each species followed by the same superscript on the same column were not significantly different ($p>0.05$).

4.3.1.3 Plant water potentials by time of day

The regression analysis for the comparison of means showed that overall mean water potentials of *P. schumannianum* and *S. siamea* at 12.00 noon were not significantly different from both those at 9.00 am ($t_{(1,113)}$ = 0.34, p=0.735) and those at 3.00 pm ($t_{(1,113)}$ = -1.30, p=0.198). However, the results summarized in Table 14 show that individual mean water potentials for both species were significantly higher (less negative, p<0.05) at 9.00 am than at both 12.00 noon and 3.00 pm. Mean water potentials during the latter two times were not significantly different (p>0.05).

Table 14: One-to-two monthly water potential (ψ_w) measurements of *P. schumannianum* and *S. siamea* during morning and afternoon hours in Makueni district of Kenya.

Species	Time	Mean water potential (MPa)	n
P. schumannianum	9.00 am	-2.50[a]	21
	12.00 noon	-2.69[b]	21
	3.00 pm	-2.85[b]	21
S. siamea	9.00 am	-0.96[a]	21
	12.00 noon	-1.40[b]	21
	3.00 pm	-1.33[b]	21

S.e.d = 0.1777; Means of the same species followed by the same superscript on the same column were not significantly different (p>0.05).

4.3.1.4 Plant water potentials by species

Overall mean water potentials (ψ_w) of *P. schumannianum* and *S. siamea* were significantly different ($t_{(1,113)}$ = 35.64, p<0.05), with the species accounting for 40.6% of the variability. This was confirmed by the regression analysis for the comparison of means (p<0.05). According to the results, the mean ψ_w of *P. schumannianum* (-2.68, n=63) was significantly lower ($t_{(1,113)}$ = 9.11, p<0.05) than that of *S. siamea* (-1.33, n=63).

According to the accumulated analysis of variance for *S. siamea* (Appendix 8), the interaction between site, season and time was not significant ($F_{(6,124)}$ = 1.12, p=0.357), implying that each of these sources of variation influenced the water potential of *S. siamea* independently. However, the effects of interaction between site and each of the weather variables (light

intensity, relative humidity, leaf temperature and cuvette temperature) were highly significant ($p<0.05$), implying that site did not influence the water potential independently of any of these variables.

4.3.2 Transpiration rates and stomatal conductances

Majority of the sample trees and shrubs were found in one and/or at most two sites. Only *S. siamea* was common to all the three sites. A summary for the transpiration rates and stomatal conductances of *S. siamea* at the three sites, during the two seasons and at various times is provided in Table 15. The various factors fitted in the regression model contributed 42.6% of the variation in transpiration rate with a s.e of 1.69.

The interaction between site, season and time was highly significant, implying that the individual influences of each of these sources of variation on the transpiration rate ($F_{(12,136)} = 4.98$, $p<0.05$) and stomatal conductances ($F_{(12,136)} = 2.65$, $p<0.05$) of *S. siamea* were not independent. Indications for the effects of each of these sources of variation are highlighted below.

Table 15: Mean transpiration rates ($mmolm^{-2}s^{-1}$) and stomatal conductances ($molm^{-2}s^{-1}$) of *S. siamea* at various times during dry and wet seasons at Nthangu, Kathonzweni and Kibwezi sites of Makueni district.

Parameter	Time	Site/Season					
		Nthangu		Kathonz		Kibwezi	
		Dry	Wet	Dry	Wet	Dry	Wet
Mean transpiration rate	9.00 am	9.24^{a}	8.85^{a}	12.18^{a}	9.19^{a}	9.89^{a}	10.15^{a}
	12.00 noon	12.87^{b}	10.64^{a}	13.05^{ab}	10.33^{b}	13.32^{bc}	12.40^{bc}
	3.00 pm	10.17^{c}	9.64^{a}	13.16^{b}	9.45^{ab}	12.73^{c}	11.78^{c}
	S.e.d = 0.890		n= 9				
Mean stom. conductance	9.00 am	1.22^{a}	0.90^{a}	0.93^{a}	0.89^{a}	0.71^{a}	0.69^{a}
	12.00 noon	1.61^{b}	$0.65b^{c}$	0.76^{bc}	0.71^{bc}	0.58^{ab}	0.67^{a}
	3.00 pm	0.68^{c}	0.69^{c}	0.75^{c}	0.62^{c}	0.53^{b}	0.55^{a}
	S.e.d = 0.1357		n=9				

Means followed by the same superscript on the same column, during the same season and at the same site were not significantly different ($p>0.05$).

4.3.2.1 Transpiration rates and stomatal conductances by site

Of the sample tree and shrub species, *P. schumannianum* and *B. coriacea* were each found in only one site (Nthangu forest and Kibwezi, respectively). *M. decumbens* and *C. farinosa* were each found in two sites (Kathonzweni and Kibwezi), while only *S. siamea* was distributed in all the three sites. Consequently, it was possible to compare the effect of site on the transpiration rates and stomatal conductances of sample trees and shrubs using the latter species. The overall mean transpiration rate and stomatal conductance of *S. siamea* for all the sites were 11.11 $mmolH_2Om^{-2}s^{-1}$ and 0.76 $molm^{-2}s^{-1}$, respectively. The effects of site on the transpiration rate ($F_{(2,136)}$ = 10.79) and stomatal conductance ($F_{(2,136)}$ = 13.30) of *S. siamea* were highly significant ($p<0.05$), although it accounted for only 8.1% of the variation in transpiration rate (Table 16). According to regression analysis for the comparison of means, transpiration rates at Kathonzweni were not significantly different from those at either Nthangu ($t_{(1,136)}$ = 0.824, $p>0.05$) or Kibwezi ($t_{(1,136)}$ = 0.732, $p>0.05$). At Nthangu forest, stomatal conductances of *S. siamea* were significantly higher than those at Kathonzweni and, which were also significantly higher than those at Kibwezi.

Table 16: Overall mean transpiration rates (mmol m^{-2} s^{-1}) and stomatal conductances ($molm^{-2}$ s^{-1}) of *S. siamea* at Nthangu, Kathonzweni and Kibwezi.

Parameter	Site			
	Nthangu	Kathonzweni	Kibwezi	S.e.d
Mean transpiration rate	10.24^a (n=51)	11.35^b (n=51)	11.73^c (n=52)	0.333
Mean stomatal conductance	0.88^a (n=51)	0.77^b (n=51)	0.62^c (n=52)	0.0507

Means followed by the same superscript on the same row were not significantly different ($p>0.05$)

Combined transpiration rates ($t_{(1,231)}$ = -0.18, $p>0.05$) and stomatal conductances ($t_{(1,231)}$ = -0.64, $p>0.05$) of *C. farinosa* and *S. siamea* at Kathonzweni were each not significantly different from those at Kibwezi. The interaction between site, species, season and time in each case was not significant ($p>0.05$), implying that the individual influence of each of these sources of variation on both the transpiration rates and stomatal conductances of the two species was independent.

4.3.2.2 Transpiration rates and stomatal conductances by season

The effect of season on the combined transpiration rate of tree and shrub species at each site was highly significant at Nthangu ($F_{(1,83)} = 9.49$, $p<0.05$) and Kathonzweni ($F_{(1,197)} = 82.72$, $p<0.05$) where they contributed 11% and 42% of the variation, respectively. At Kibwezi, it was not significant ($F_{(1,140)} = 2.09$, $p=0.151$) and accounted for only 1.5% of the variation. At each of the three sites, mean transpiration rates of *S. siamea* were significantly different ($p<0.05$) between dry and wet seasons. According to Table 17 below, they were higher during the former than during the latter seasons.

Table 17: Transpiration rates and stomatal conductances of *S. siamea* during dry and wet seasons in three sites of Makueni district

Parameter	Site/season						S.e.d
	Nthangu		Kathonz		Kibwezi		
	Dry	Wet	Dry	Wet	Dry	Wet	
Mean transp. rate	10.83^a	9.71^b	12.80^a	9.71^b	11.98^a	11.46^b	0.474
(mmol m-2 s-1)	(n=24)	(n=27)	(n=27)	(n=24)	(n=27)	(n=25)	
Mean stom. conductance	1.03^a	0.75^b	0.81^a	0.72^b	0.60^a	0.63^a	0.0722
(mol m-2 s-1)	(n=24)	(n=27)	(n=27)	(n=24)	(n=27)	(n=25)	

Means at the same site followed by the same superscript on the same column were not significantly different ($p>0.05$).

The effect of season on the stomatal conductances of tree and shrub species at each site was not significant ($p>0.05$) in all the sites and accounted for only 1.8%, 0.02% and 0.15% of the variation at Nthangu ($F_{(1,83)} = 2.67$, $p=0.106$), Kathonzweni ($F_{(1,197)} = 0.04$, $p=0.833$) and Kibwezi ($F_{(1,140)} = 2.09$, $p=0.151$) sites, respectively. At the three sites, the interaction between site and season was significant ($F_{(2,83)} = 6.62$, $p<0.05$; $F_{(4,197)} = 1.11$, $p>0.05$; $F_{(4,140)} = 1.14$, $p>0.05$ for Nthangu, Kathonzweni and Kibwezi, respectively). Stomatal conductances per site of *S. siamea* during dry and wet seasons are shown in table 17.

4.3.2.3 Transpiration rates and stomatal conductances by time of day

The effect of time of the day on the combined transpiration rate of tree and shrub species at each site was highly significant and accounted for 24%, 14% and 20.4% of the variation at the sites, respectively. At Nthangu and Kathonzweni, mean transpiration rates were significantly lower ($p<0.05$) at 9.00 am than at 12.00 noon, but there were no significant differences ($p>0.05$)

between 12.00 noon and 3.00 pm. At Kibwezi, the differences between transpiration rates at 12.00 noon and both 9.00 am ($t_{(1,140)}$ = -1.99) and 3.00 pm ($t_{(1,140)}$ = -2.07) were statistically significant ($p<0.05$). In each of the three sites, mean transpiration rates of *S. siamea* were in most cases significantly lower ($p<0.05$) at 9.00 am than at the other times of the day (Table 18).

Table 18: Overall transpiration rates of *S. siamea* during morning and afternoon hours at three sites in Makueni district.

Time	Site		
	Nthangu	Kathonzweni	Kibwezi
9.00 am	9.05^{a} (n=18)	10.69^{a} (n=15)	10.07^{a} (n=17)
12.00 noon	11.76^{b} (n=18)	11.69^{b} (n=18)	12.86^{b} (n=17)
3.00 pm	9.91^{a} (n=15)	11.31^{ab} (n=18)	12.26^{b} (n=18)

S.e.d =0.890; Means at the same site followed by the same superscript are not significantly different ($p>0.05$)

The effect of time on the stomatal conductances of tree and shrub species at Nthangu forest was not significant ($F_{(2,83)}$ = 3.02, $p>0.05$) and accounted for only 4.1% of the variation. At Kathonzweni ($F_{(2,197)}$ = 17.30, $p<0.05$) and Kibwezi ($F_{(2,140)}$ = 23.31, $p<0.05$), it was highly significant and accounted for 13.9% and 23.1% of the variation, respectively. At Kathonzweni, mean stomatal conductance was significantly higher ($t_{(1,197)}$ = 3.25, $p<0.05$) at 9.00 am than at 12.00 noon, but there were no significant differences ($t_{(1,197)}$ = -0.39), $p>0.05$) between 12.00 noon and 3.00 pm. At Kibwezi, the differences between stomatal conductances at 12.00 noon and both 9.00 am ($t_{(1,140)}$ = 1.00) and 3.00 pm ($t_{(1,140)}$ = -1.65) were not significantly ($p>0.05$) different. According to Table 15 above, mean stomatal conductances of *S. siamea* at various sites were significantly higher ($p<0.05$) at 9.00 am than at the other times of the day.

4.3.2.4 Transpiration rates and stomatal conductances by species

Comparisons at each site were first made between indigenous species alone and then between indigenous and exotic species (*S. siamea*). Comparisons between indigenous species alone were done at Kathonzweni and Kibwezi sites. At Kathonzweni, the mean transpiration rates ($t_{(1,197)}$ = 1.73, p=0.085) and the mean stomatal conductances ($t_{(1,197)}$ = -0.31, p=0.753) of *C. farinosa* were not significantly different from those of *M. decumbens*. At Kibwezi, transpiration rates of *C. farinosa* and *B. coriacea* were significantly different from each other ($t_{(1,140)}$ = 23.30,

p=0.046). Stomatal conductances of the two species were not significantly different from each other ($t_{(1,140)} = 0.09$, p=0.925).

Comparisons between indigenous and exotic species were done in all sites. At Nthangu forest, the transpiration rates and stomatal conductances of *P. schumannianum* were not significantly different from those of *S. siamea* ($t_{(1,83)} = 1.57$, p=0.120 and $t_{(1,83)} = 0.50$, p=0.621, respectively). At Kathonzweni, the transpiration rate and stomatal conductance of *C. farinosa* were not significantly different ($t_{(1,197)} = 0.49$, p=0.627 and $t_{(1,197)} = 0.92$, p=0.359, respectively) from those of *S. siamea.* At Kibwezi, the transpiration rate and stomatal conductance of *C. farinosa* were not significantly different ($t_{(1,140)} = 1.05$, p=0.294 and $t_{(1,140)} = -0.30$, p=0.766, respectively) from those of *S. siamea.*

4.3.3 Relationships between plant moisture parameters and weather variables

Interactions between the various moisture parameters in *S. siamea* and the weather variables measured during the dry season were tested using a two-sided test of correlations procedure for correlations different from zero, and the Principal components analyses (PCA). The results of the analyses are shown in Tables 19, 20 and 21, and Figure 15 for Nthangu forest, Kathonzweni and Kibwezi sites, respectively. According to Table 19, significant correlations ($p<0.05$) were observed between the water potential of *S. siamea* and light intensity, leaf temperature and cuvette temperature. It was also observed between stomatal conductance and light intensity, leaf temperature and cuvette temperature. No other significant correlations were observed.

Following the Principal Components Analysis of all variables in all sites (water potential, transpiration rate, stomatal conductance, light intensity, relative humidity, leaf temperature and cuvette temperature), the results showed that PCA1 accounted for 99.99% of the total variability on variance sum of squares and products at Nthangu forest as compared to PCA2 and PCA3. This implied that PCA1 significantly provided information on plant moisture relationships of *senna siamea* at this site. These were consistent with correlation matrix on PCA where PCA1 accounted for 66.8% followed by PCA2 (20.6%) and PCA3 (10.2%). This showed that PCA procedures provided nearly all total variability of the interrelationship between the measurement variables leaving about 2.4% unexplained (Fig 15). Therefore this affirms the correlations as in Table 19.

Table 19: Two sided test of correlations between plant moisture parameters and weather variables at Nthangu forest with reference to *S. siamea*

	ψ	Ti	gi	Li	Rh	Lt	Ct
ψ	1.00						
Ti	-0.273	1.00					
gi	0.543	0.612	1.00				
Li	-0.819*	-0.083	-0.784*	1.00			
Rh	-0.396	-0.242	-0.450		1.00		
Lt	-0.776*	-0.305	-0.939*			1.00	
Ct	-0.883*	-0.048	-0.818*				1.00

ψ=Water potential, Ti=Transpiration rate, gi=Stomatal conductance, Li=Light intensity, Rh=relative humidity, Lt=Light intensity, Ct=Cuvette temperature; Correlation coefficients preceeded by an asterisk (*) were significantly different ($p<0.05$)

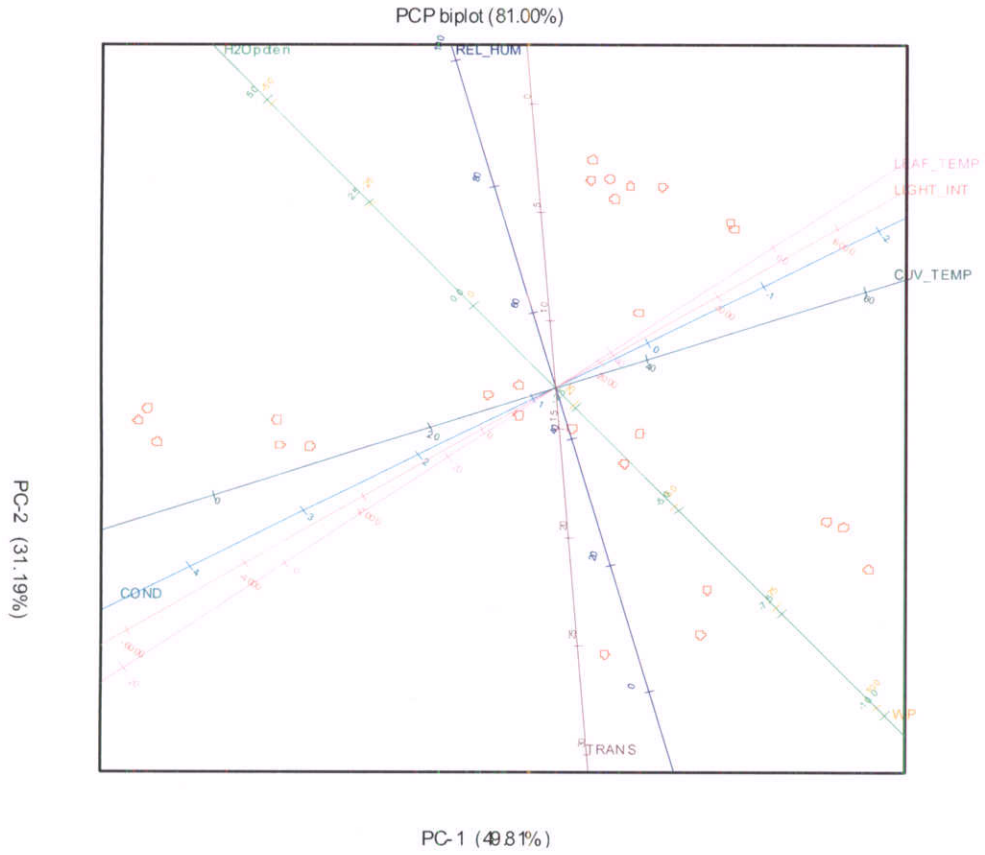


Figure 15: Principal Components Analysis and scores scatter diagram using correlation matrix for Nthangu, Kathonzweni and Kibwezi forests

In Table 20, significant correlations were only observed between stomatal conductances and light intensity, leaf temperature and cuvette temperature.

Table 20: Two sided test of correlations between plant moisture parameters and weather variables at Kathonzweni with reference to *S. siamea*

	ψ	Ti	gi	Li	Rh	Lt	Ct
ψ	1.00						
Ti	-0.535	1.00					
gi	-0.536	0.019	1.00				
Li	-0.503	0.021	-0.940*	1.00			
Rh	0.164	-0.499	-0.610		1.00		
Lt	-0.462	0.045	-0.974*			1.00	
Ct	-0.596	0.235	-0.953*				1.00

ψ=Water potential, Ti=Transpiration rate, gi=Stomatal conductance, Li=Light intensity, Rh=relative humidity, Lt=Light intensity, Ct=Cuvette temperature; Correlation coefficients preceeded by an asterisk (*) were significantly different ($p<0.05$)

Following the Principal Components Analysis of all variables, the results showed that PCA1 at Kathonzweni accounted for 99.99% of the total variability on variance sum of squares and products as compared to PCA2 and PCA3. This implied that PCA1 significantly provided information on plant moisture relationships of *senna siamea* at this site. These were consistent with correlation matrix on PCA where PCA1 accounted for 65.69% followed by PCA2 (26.37%) and PCA3 (5.51%). This showed that PCA procedures provided nearly all total variability of the interrelationship between the measurement variables leaving about 2.43% unexplained (Fig 15). Therefore this affirms the correlations as in Table 20.

Significant correlations occurred between water potential and transpiration rate, stomatal conductance, relative humidity and leaf temperature (Table 21).

Table 21: Two sided test of correlations between plant moisture parameters and weather variables at Kibwezi with reference to *S. siamea*

	ψ	Ti	gi	Li	Rh	Lt	Ct
ψ	1.00						
Ti	-0.935*	1.00					
gi	-0.880*	0.760*	1.00				
Li	0.089	0.042	-0.432	1.00			
Rh	0.948*	-0.828*	-0.953*		1.00		
Lt	0.760*	-0.564	-0.960*			1.00	
Ct	0.347	-0.034	-0.622				1.00

ψ=Water potential, Ti=Transpiration rate, gi=Stomatal conductance, Li=Light intensity, Rh=relative humidity, Lt=Light intensity, Ct=Cuvette temperature; Correlation coefficients preceeded by an asterisk (*) were significantly different ($p<0.05$)

It also occurred between transpiration rate and both stomatal conductance and relative humidity, and between stomatal conductance and both relative humidity and leaf temperature.

Following the Principal Components Analysis of all variables, the results showed that PCA1 at Kibwezi accounted for 99.99% of the total variability on variance sum of squares and products as compared to PCA2 and PCA3. This implied that PCA1 significantly provided information on plant moisture relationships of *senna siamea* at this site. These were consistent with correlation matrix on PCA where PCA1 accounted for 69.3% followed by PCA2 (22.2%) and PCA3 (7.6%). This showed that PCA procedures provided nearly all total variability of the interrelationship between the measurement variables leaving about 0.9% unexplained (Fig. 15). Therefore this affirms the correlations as in Table 21.

As shown by the two-sided tests of correlations carried out above, it was only at the Kibwezi site, and not at Nthangu forest or Kathonzweni that correlations between pairs of all the three moisture parameters measured (water potential and transpiration rates: $r=-0.935$, $p<0.05$; water potential and stomatal conductances: $r=-0.880$, $p<0.05$; and transpiration rates and stomatal conductances: $r=0.760$, $p<0.05$) were significant (Tables 19, 20 and 21). Higher temperatures, drier conditions and clearer skies characterised conditions at Kibwezi more than the other sites. It is suggested that prolonged exposure to these conditions favoured high transpiration rates, water deficit stresses and expression of clearer relationships between the parameters. Nthangu and Kathonzweni were characterised by moist, misty and cloudy conditions

that may have resulted in irregular and unreliable measurements with erratic trends. The significant negative correlation (-0.935) between water potential and transpiration rate of *S. siamea* at Kibwezi indicate that the former decreased (became more negative) with increase in the later and vice versa. The significant negative correlation (-0.880) between water potential and stomatal conductance of *S. siamea* indicate that the former decreased (became more negative) with an increase in the later. It is suggested that an increase in stomatal aperture (stomatal conductance) led to increased tension and decreased (more negative) water potential in plant tissues. The significant positive correlation (0.760) between the transpiration rate and stomatal conductance of *S. siamea* indicates that the former increased with increase in the later. It is thought that when stomatal conductance, which is synonymous with stomatal arpeture increase, more water vapour is lost per unit leaf area through the process of transpiration.

4.3.4 Soil moisture content

Data collected from the five soil depths during the two seasons and at the three sites are summarized in Appendix 9. Regression coefficients of mean soil moisture contents at each site showed that differences were highly significant ($F_{(2,2643)} = 200.77$, $p<0.05$). At Nthangu forest, soil moisture content around *S. siamea* was significantly higher than around *P. schumannianum* ($t_{(1,568)} = 16.20$, $p<0.05$). At Kathonzweni, soil moisture around *C. farinosa* was significantly lower than that around *S. siamea* ($t_{(1,1311)} = 5.95$, $p<0.05$), but not significantly different from that around *M. decumbens* ($t_{(1,1311)} = -1.80$, $p=0.073$). According to Appendix 9, average soil moisture contents around *S. siamea* (48.1 Kg/m^3) were higher than those around *M. decumbens* (41.6 Kg/m^3). At Kibwezi, soil moisture content around *C. farinosa* was significantly lower than that around both *S. siamea* (54.5 Kg/m^3) ($t_{(1,716)} = 6.24$, $p<0.05$) and *B. coriacea* (60.9 Kg/m^3) ($t_{(1,716)} = 6.61$, $p<0.05$).

4.3.4.1 Soil moisture content by site

A regression analysis for the comparison of means showed that mean soil moisture content at Kathonzweni (45.1 Kg/m^3) was significantly lower ($F_{(2,2643)} = 200.77$, $p<0.05$) than that at Kibwezi (54.2 Kg/m^3). According to the estimates, no significant differences in soil moisture contents existed between Kathonzweni and Nthangu forest ($t_{(1,2643)} = -0.86$, $p=0.391$). There was also no significant difference in soil moisture content between Kibwezi and Nthangu forest.

Table 22: Soil moisture contents (Kg/m^3) during two seasons at Nthangu, Kathonzweni and Kibwezi sites of Makueni District .

Season	Site		
	Nthangu	Kathonzweni	Kibwezi
Dry	46.4^a (n=318)	42.3^a (n=705)	50.9^a (n=378)
Wet	56.8^b (n=270)	48.3^b (n=636)	57.7^b (n=366)

S.e.d=0.746; Means on the row and in the same column followed by the same superscript are not significantly different ($p>0.05$)

4.3.4.2 Soil moisture content by season

Overall mean soil moisture contents during wet and dry seasons at Nthangu, Kathonzweni and Kibwezi forests are shown in Table 22 above. According to the data, overall mean soil moisture contents during dry seasons were significantly lower ($F_{(1,2643)} = 321.22$, $p<0.05$) than during wet seasons.

The strong effects of season were supported by 77.5%, 50.5% and 61.4% total variances accounted for at Nthangu, Kathonzweni and Kibwezi. respectively.

Figures 16, 17 and 18 represent variations in mean soil moisture content at each of the three sites during the study period between July 2003 and May 2004. At Nthangu forest (Fig 16), moisture contents peaked at the beginning of the short rains in November 2003. This was seen as an increase of moisture contents in the first three soil depths (15 cm, 30 cm and 60 cm). It was suspected that as moisture continued to diffuse down the soil profile, soil moisture in lower soil depths would subsequently be increased. The long rains were low in amounts, and did not cause substantial increases of soil moisture in March and May 2004. In all cases of data collection, soil moisture contents steadily decreased with increasing soil depth. This was evident during the rainy seasons (November, January, March and May) compared to the dry seasons (July, August and September).

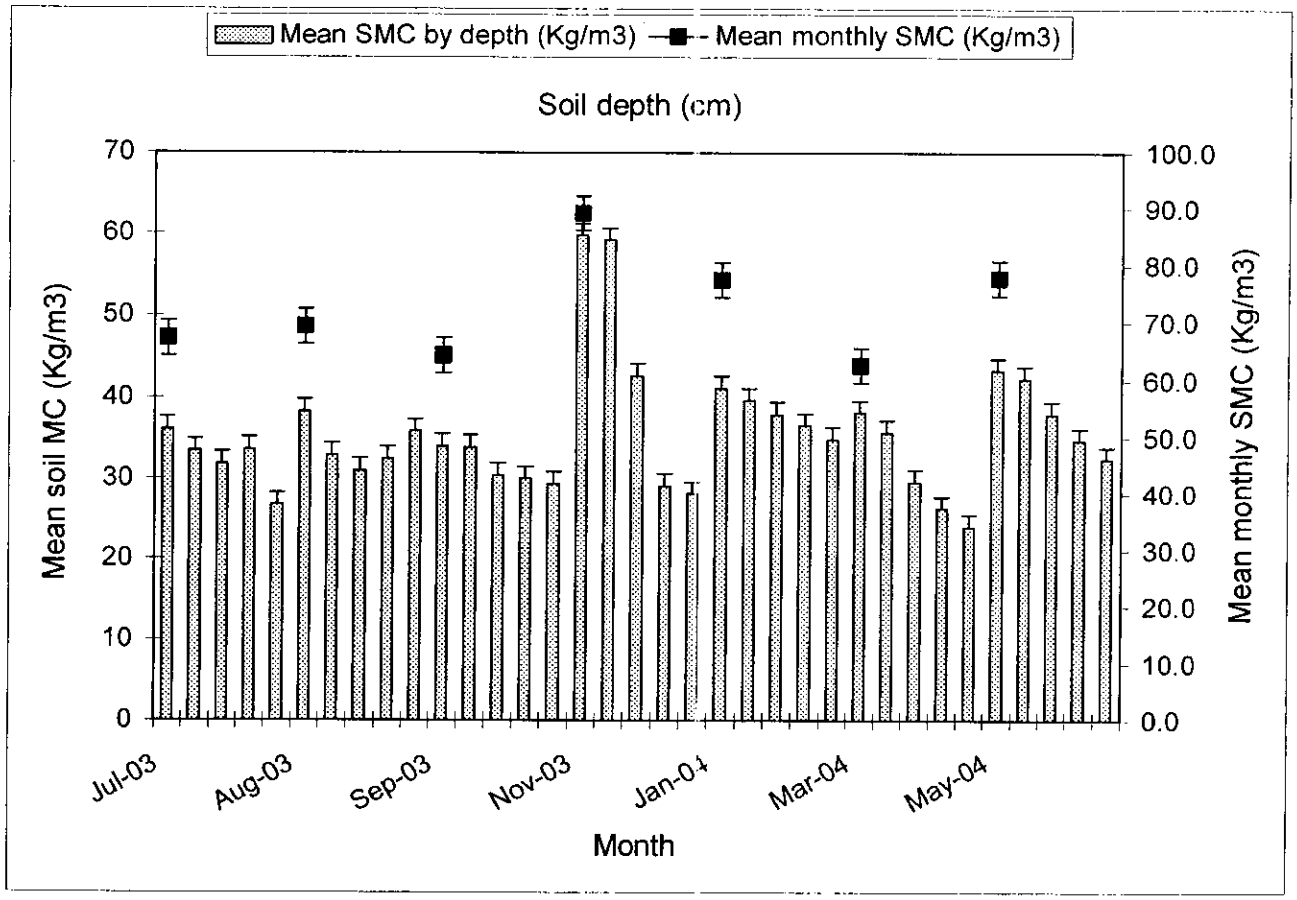


Figure 16: Soil moisture profile at the Nthangu site of Makueni district during wet and dry seasons (July 03-May 04).

At Kathonzweni (Fig 17), there were no substantial variations observed in the amounts of rainfall received between the dry season and the rainy season. However, the small, though erratic, amounts of rainfall following the short rains in March-May 2004 were seen as a slight increase in overall amounts during these months. Soil moisture contents increased with increasing soil depth in all cases of data collection, except November 2003, when higher rainfall wetted the upper layers of the soil profile, upsetting the trend within the first three depths.

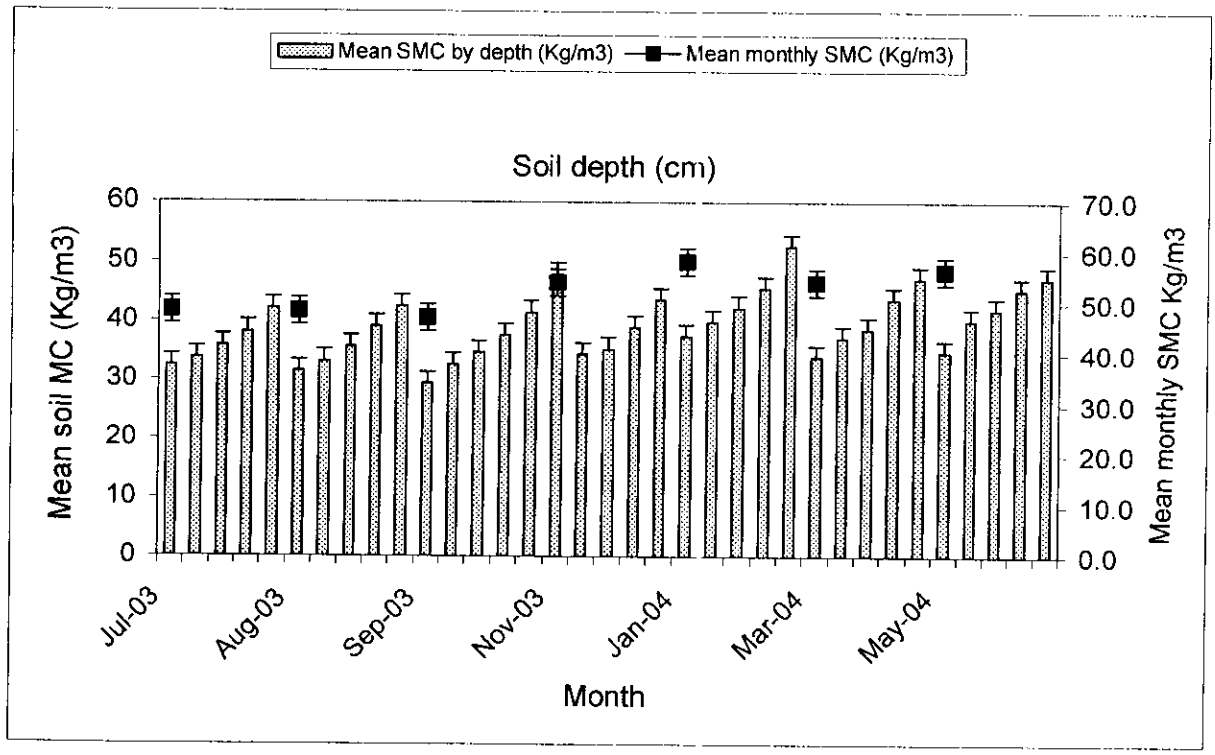


Figure 17: Soil moisture profile at the Kathonzweni site of Makueni district during wet and dry seasons (July 03-May 04).

Soil moisture contents at Kibwezi (Fig 18) varied differently with depth. During the dry months (August and September 2003), soil moisture contents increased with increasing depth. A similar trend was observed in the usually rainy months of March and May 2004. This was because the amount of rainfall received was small and did not cause a substantial effect on the trends in soil moisture. During the short rainy season (November 2003 – January 2004), the opposite trend was observed.

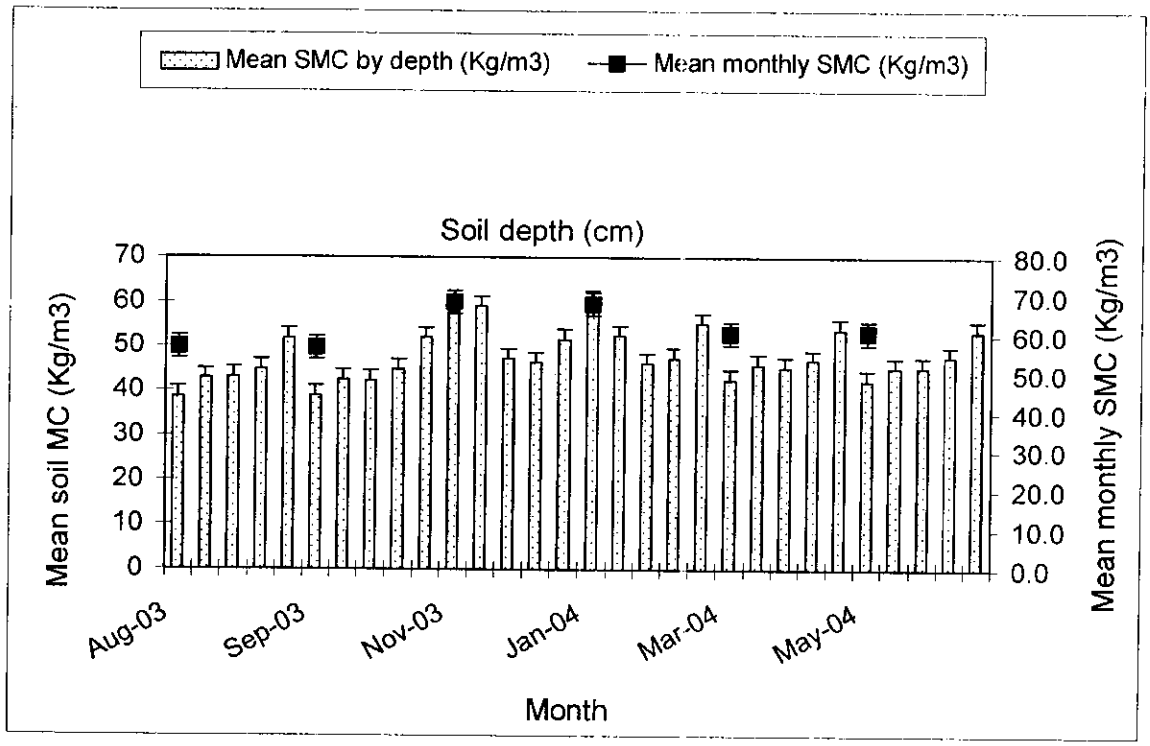


Figure 18: Soil moisture profile at the Kibwezi site of Makueni district during wet and dry seasons (July 03-May 04).

4.3.4.3 Soil moisture content by depth

According to the data, soil moisture content was significantly different between depths ($F_{(4,2643)} = 14.31$, $p<0.05$) (Table 23). It was significantly higher at 150 cm than at 120 cm ($t_{(1,2643)} = 3.49$, $p<0.05$). Moisture content at 120 cm was significantly higher than at 90 cm, but not significantly different from that at 30 cm and 60 cm. The variations in the soil moisture contents at different depths observed at the different points around each of the sample trees and shrubs are shown in Appendix 10.

Table 23: Mean soil moisture contents at five soil depths in the three sites of Makueni District

Soil depth (cm)	Moisture content (Kg/m^3)	n
30	48.7^a	567
60	48.7^a	567
90	47.3^b	567
120	48.8^a	558
150	52.3^c	414
Overall mean	49.2	2,673

S.e.d = 0.673; Means followed by the same superscript on the same column were not significantly different (P>0.05)

4.3.4.4 Soil moisture contents around sample trees and shrubs at different sites

Mean soil moisture contents around specific tree and shrub species varied considerably. Soils at Kaumoni (near Nthangu forest), Muusini at Kathonzweni and at two points closest to the cattle boma at Kibwezi all had mean moisture contents much higher than the other points i.e. 58.7, 53.7, 54.7 and 60.2 Kg/m^3, respectively (Table 24). All the other points had mean soil moisture contents ranging from 37.1 Kg/m^3 (Miangeni) to 48.7 Kg/m^3 (Kibwezi). Sample trees located at the first three points were *S. siamea*, while that at the fourth point was *B. coriacea*.

Table 24: Mean soil moisture contents at various points around sample trees and shrubs in Makueni District .

Point (site)	Species	Moisture content (Kg/m^3)	n
1 (Nthangu)	*P. schumannianum*	44.5^{c}	309
2 (Kaumoni)	*S. siamea*	58.7^{g}	279
3 (Muusini)	*S. siamea*	53.7^{f}	285
4 (Mathemba B)	*M. decumbens*	42.9^{b}	300
5 (Mathemba B)	*C. farinosa*	45.8^{d}	285
6 (Miangeni)	*M. decumbens*	37.1^{a}	225
7 (Miangeni)	*C. farinosa*	44.2^{c}	246
8 (Kibwezi)	*S. siamea*	54.7^{f}	270
9 (Kibwezi)	*B. coriacea*	60.2^{h}	270
10 (Kibwezi)	*C. farinosa*	48.7^{e}	204
Overall mean			267.3

S.e.d = 0.950; Means followed by the same superscript on the same column were not significantly different (P>0.05)

In all the three sites (Nthangu, Kathonzweni and Kibwezi), there were significant interactions ($p<0.05$) between species and season and species and depth (Table 25), implying that either soils around each species had different water retention capacities during different seasons and at different depths, or the species had different water conservation/consumption abilities during different seasons and at different depths. Interactions between season and depth for the three sites were also significant ($p<0.05$), implying that the effects of season and depth on soil moisture around tree species were not independent. Interactions between species, season and depth were highly significant at Kibwezi, but were not significant at Nthangu and Kathonzweni ($p<0.05$), implying that effects of the various factors at Kibwezi were not independent.

Table 25: ANOVA attributes for interactions between various factors at the three sites

Type of interaction	ANOVA attribute	Site		
		Nthangu	Kathonzweni	Kibwezi
Species x season	df	1	2	2
	Residuals	568	1311	716
	F (v.r)	19.62	42.47	12.49
	F_{pr}	<0.001	<0.001	<0.001
Species x depth	df	4	8	7
	Residuals	568	1311	716
	F (v.r)	190.85	18.35	27.01
	F_{pr}	<0.001	<0.001	<0.001
Season x depth	df	4	4	4
	Residuals	4,568	1311	716
	F (v.r)	32.72	7.04	38.69
	Fpr	<0.001	0.001	<0.001
Species x season x depth	df	4	8	7
	Residuals	568	1311	716
	F (v.r)	2.24	1.15	4.91
	F_{pr}	0.063	0.330	<0.001

4.4 Plant moisture levels at pre-dawn and at midday during the dry season

4.4.1 Plant water potentials

Pre-dawn and midday water potentials measured during the study were analysed according to site and species. According to the results, differences between mean pre-dawn water potentials for different tree and shrub species at various sites (Nthangu: $F_{(1,4)} = 72.25$; Kathonzweni: $F_{(1,6)} = 288.46$; Kibwezi: $F_{(2,6)} = 73.21$) were statistically significant ($p<0.05$) (Table 26). This was further supported by 93.4%, 97.6% and 94.8% of total variance of pre-dawn water potential accounted for by species at Nthangu forest, Kathonzweni and Kibwezi sites, respectively. At Nthangu forest, pre-dawn water potential of *A. polyacantha* was significantly higher (less negative) ($t(1,4) = 8.50$, $p<0.05$) than that of *S. siamea*. At Kathonzweni, pre-dawn

water potential of *A. tortilis* was not significantly different from that of *S. siamea* ($t_{(1,6)}$ = -0.70, p=0.510). At Kibwezi, the mean pre-dawn water potential of *A. tortilis* was significantly ($t_{(1,6)}$ = -28.04, p<0.05) lower (more negative) than that of *C. campestris*. However, it was not significantly ($t_{(1,6)}$ = 1.37, p>0.05) different from that of *S. siamea*.

Mean midday water potentials for the various species were significantly different (p<0.05) at Nthangu forest ($F_{(1,4)}$ = 276.57, p<0.05) and Kibwezi ($F_{(2,6)}$ = 551.26, p<0.05), where species accounted for 98.2% and 99.3% of the total variance, respectively. However, they were not significantly different ($F_{(1,6)}$ = 0.49, p=0.510) at Kathonzweni. At Nthangu forest, mean midday water potential for *A. polyacantha* was significantly lower (more negative) ($t_{(1,4)}$ = -16.63, <0.05) than that of *S. siamea*. At Kibwezi, mean midday water potential of *A. tortilis* was significantly lower (more negative) than that of *C. campestris* ($t_{(1,6)}$ = -28.04, p<0.05), but not significantly different from that of *S. siamea* ($t_{(1,6)}$ = 1.37, p<0.05).

Table 26: Mean midday and pre-dawn water potentials (ψ_w) (MPa) of dominant tree and shrub species at Nthangu forest, Kathonzweni and Kibwezi sites of Makueni district.

Study site	Species	Mdd ψ_w	n	Pdd ψ_w	n	Diurnal range
Nthangu	*A. polyacantha*	-2.90[a]	3	-0.90	3	2.00
	S. siamea	-2.17[b]	3	-1.18	3	0.98
	s.e.d	0.0441				0.0441
Kathonzweni	*A. tortilis*	-3.20[a]	4	-1.05	4	2.15
	S. siamea	-3.08[a]	4	-2.30	4	0.78
	s.e.d	0.1785				0.1909
Kibwezi	*A. tortilis*	-3.12[a]	3	-1.12[a]	3	2.00[a]
	C. campestris	-0.73[b]	3	-0.05[b]	3	0.68[b]
	S. siamea	-3.23[c]	3	-2.70[c]	3	0.53[c]
	s.e.d	0.0850	3	0.1876	3	0.1967

Means followed by the same superscript on the same column at each site were not significantly different (p>0.05)

Because of the variability in absolute pre-dawn and midday water potentials associated with different tree and shrub species, which also varied from site to site in composition and density, the use of overall means of these parameters to compare sites were not appropriate. To improve the validity of comparisons between sites using mean water potential values, data for *S. siamea*, the only sample tree species represented in all the sites was used. Results are summarized in Table 27.

Table 27: Mean pre-dawn and midday water potentials of *S. siamea* at Nthangu, Kathonzweni and Kibwezi sites of Makueni District .

Site	Mean pre-dawn ψ_w (MPa)	Mean mdd ψ_w (MPa)	n
Nthangu	-1.18[a]	-2.17[a]	3
Kathonzweni	-2.30[b]	-3.08[b]	4
Kibwezi	-2.70[c]	-3.23[b]	3
S.e.d	0.0874	0.1635	

Means followed by the same superscript on the same column were not significantly different (p>0.05)

The results showed that there was a strong evidence (p<0.05) that pre-dawn water potential for *S. siamea* differed between the three sites. This was further buttressed by 96.9% of total variance accounted for. In addition, regression analysis for comparing the estimates of the sites showed that there was highly significant differences (p<0.05) in pre-dawn water potential between Nthangu and Kathonzweni. Similarly, there was sufficient evidence to declare difference (p=0.003) in pre-dawn water potential between Kathonzweni and Kibwezi. It then followed that by default, there was highly significant difference (p<0.05) in pre-dawn water potential between Kibwezi and Nthangu (Table 27)

Similarly, there was every reason to believe (p<0.05) that midday water potential of *S. siamea* differed between Nthangu, Kathonzweni and Kibwezi. This was further evidenced by sites contributing 82.6% of the total variance. However, there was no significant difference (p=0.365) in midday water potential for *S. siamea* between Kathonzweni and Kibwezi (Table 27).

4.4.2 Plant osmotic potentials

Midday and standardised (pre-dawn) osmotic potentials collected during the study were also analysed according to site and species. A summary of the results according to species at each site is presented in Table 28.

Table 28: Mean standardised and midday osmotic potentials(π) of dominant tree and shrub species at Nthangu forest, Kathonzweni and Kibwezi sites of Makueni District

Study site	Species	Std π	Mdd π	Diurnal range
Nthangu	*A. polyacantha*	-2.29[a]	-2.43[a]	0.23[a]
	A. tortilis	-2.30[a]		-
	S. siamea	-1.80[b]	-2.12[b]	0.32[a]
	s.e.d	0.1053	0.1168	0.0933
Kathonzweni	*A. tortilis*	-2.01[a]	-2.37[a]	0.36[a]
	C. collinum	-3.20[b]	-3.93[b]	0.74[b]
	S. siamea	-2.10[a]	-2.32[a]	0.34[a]
	T. brownii	-1.99[a]	-2.98[c]	0.98[c]
	s.e.d	0.1332	0.0943	0.1664
Kibwezi	*A. tortilis*	-1.90[a]	-2.61[a]	0.73[a]
	C. campestris	-0.93[b]	-1.13[b]	0.26[b]
	S. siamea	-1.79[c]	-2.15[c]	0.37[b]
	s.e.d	0.0923	0.1484	0.1373

Means at each site followed by the same superscript on the same column were not significantly different ($p>0.05$); n=6

The values from the pre-dawn (standardised) and midday osmotic potentials varied with individual tree and shrub species in all the sites. At Nthangu forest, *S. siamea* had the highest (least negative) standardised osmotic potential (-1.80 MPa), while *A. tortilis* had the lowest (-2.30 MPa). At Kathonzweni, *T. brownii* had the highest (least negative) pre-dawn osmotic potential followed by *A. tortilis*, *S. siamea* and *C. collinum* in that order. At Kibwezi, *C. campestris* had the highest (least negative) pre-dawn osmotic potential followed by *S. siamea* and *A. tortilis*, also in that order.

With regard to mean midday osmotic potentials, *S. siamea* had a higher (less negative) value (-2.12 MPa) than *A. polyacantha* (-2.43 MPa) at Nthangu forest. At Kathonzweni, midday osmotic potentials of *A. tortilis* (-2.37 MPa) and *S. siamea* (-2.32 MPa) were not significantly different ($t_{(1,20)} = -0.53$, $p>0.05$) from each other. However, both had significantly higher ($t_{(1,20)} = 6.41$, $p<0.05$) midday osmotic potentials than *T. brownii* (-2.98 MPa) which in turn had significantly higher midday osmotic potentials than *C. collinum* (-3.93 MPa). At Kibwezi, *C. campestris* (-1.13 MPa) had a significantly higher ($p<0.05$) midday osmotic potential than both *S. siamea* (-2.15 MPa) and *A. tortilis* (-2.61 MPa) ($t_{(1,14)} = -9.56$, $p<0.05$).

To be able to make a valid and appropriate comparison between the three study sites, a separate analysis was conducted on the pre-dawn and midday osmotic potentials data for *S. siamea* which was sampled in all the three sites. The results are summarized in Table 29 below.

Table 29: Mean standardised (pre-dawn) and midday osmotic potentials of *S. siamea* at Nthangu, Kathonzweni and Kibwezi sites of Makueni District .

Site	Mean standardised π (MPa)	Mean midday π (MPa)
Nthangu	-1.80^{a}	-2.12^{a}
Kathonzweni	-2.10^{b}	-2.32^{b}
Kibwezi	-1.79^{a}	-2.15^{a}
S.e.d	0.0954	0.0983

Means followed by the same superscript on the same column were not significantly different ($p>0.05$); n=6

According to these results, pre-dawn osmotic potentials of *S. siamea* significantly ($p<0.05$) differed between the three sites. This was supported by 40.3% of total variance accounted for. A regression analysis for the comparison of estimates of sites showed that there was highly significant ($p<0.05$) difference between Kathonzweni and both Nthangu ($p=0.008$) and Kibwezi ($p=0.005$). According to Table 29, mean standardised osmotic potentials were significantly lower at Kathonzweni than at both Nthangu and Kibwezi. However, mean pre-dawn osmotic potentials at Nthangu and Kibwezi were not significantly ($p>0.05$) different.

There was every reason to believe that the midday osmotic potential of *S. siamea* was not significantly ($p<0.132$) influenced by site, with the later accounting for 13.5% of the variation. Table 29 shows that midday osmotic potentials were significantly lower at Kathonzweni than at both Kibwezi and Nthangu. However, no significant differences in this regard were observed between Kibwezi and Nthangu.

CHAPTER FIVE

DISCUSSION

5.1 Soil physical and chemical Properties

The results obtained from the textural analysis of the soils sampled during the study were largely similar to those previously reported from various sites within the region (Nyadzi et al., 2003; Mbuvi, 2000). Soils which are mostly loamy as in the study area have more or less equal amounts of sand, silt and clay, and therefore, have properties that are intermediate between those of clay and those of sand, and are considered most favourable for plant growth because they hold more available water and cations than sand and because they are better aerated and easier to work than clay (Slatyer, 1967; Williams et al., 1996).

The phosphorus contents determined for various sites in the study area were low. Lopez-Gutierrez et al. (2004) identified phosphorus as one of the most limiting macronutrients under similar conditions elsewhere in Venezuela. At Katumani in the nearby Machakos district and with environmental conditions similar to those of the study area, nitrogen and phosphorus contents were less than optimal but like other nutrients, were considered adequate for plant growth (Mathuva et al., 1998). Likewise, Macharia (1981) reported low soil phosphorus and manganese contents at Amboseli National Park. These suggest a P-poor parent material and indicate P-deficiency in the study area.

It is suggested that the C and N contents at Nthangu forest were highest compared to the other sites most likely because the point where the soil sampling was done was under forest and the higher amount of litter and organic matter associated with it were in various stages of decomposition to yield higher C and N contents. Soils located below tree crowns are often known to have significantly higher concentrations of organic matter, N, Ca, P and K, high microbial biomass, reduced bulk density and increased infiltration than open grassland soils (Vetaas, 1992; Ludwig et al., 2003). Such high nutrient concentrations enable soils to support higher biomass productivity and a greater diversity of species. It has been shown that moderate N supply improved the photosynthetic capacity, transpiration and stomatal conductance of plants (Ali-Dinar et al., 1999; Norton and Wachsmann, 2006) and that 90% of dry matter is composed of Carbon compounds that are generated through the photosynthetic process (Marschner, 1986).

Increasing N rate from low to moderate, alleviates NaCl effects and improves leaf and shoot dry weight (Ali-Dinar et al., 1998). It is suggested that the additional nitrogen enabled roots to grow deeper into the soil profile, and to develop stronger suction force to extract water at higher tension (Norton and Wachsmann, 2006).

According to comparative ratings made by Okalebo et al. (1993), the nitrogen content of soils in the study area was moderate to low, while that of carbon was low to very low. Similarly observations were made by Macharia (1981) who reported that soil carbon and nitrogen in four grassland ecosystems in Kenya were either low or deficient. These low concentrations may be attributed to the fact that the area receives low and erratic rainfall, which does not provide enough vegetative material for decomposition and does not lead to significant differences in soil properties between wet and dry seasons (Mbuvi, 2000). This was the case in the semi-desert zone of North Horr in Northern Kenya (mean annual rainfall of 157 mm) where soil carbon contents at the soil surface (0-15 cm depth) was even lower and ranged between $0.09\pm0.01\%$ and $0.21\pm0.02\%$ at various sites (Olukoye et al., 2003). The abundance of termites in the area aggravates the situation and leads to more shortages in the two nutrients. Furthermore, the area experiences very hot and dry conditions, both of which provide an environment conducive for quick decomposition of any litter fall and rapid reduction in the supply of both organic matter and nitrogen.

In this study, there were no substantial differences between cultivated and uncultivated sites in terms of these and other nutrients measured during the study. This observation was not consistent with the findings of other researchers where C and N contents in the soil declined significantly and exponentially with increasing years under cultivation (Lemenih et al., 2005; Woomer et al., 1994). Mbuvi (2000) reported significantly more organic carbon in uncultivated (bush) soils than in cultivated soils, but no significant differences in nitrogen and phosphorus contents.

The pH values observed in this study showed that soils in this area were slightly acidic (6.0-7.0 in H_2O and 5.8-6.4 in $CaCl_2$) and did not vary substantially from those observed elsewhere within the region (Macharia, 1981; Odhiambo et al., 2001; Nyadzi et al., 2003). During an assessment of various germination media in Kibwezi division, Juma (2002) measured slightly higher pH values ranging from 7.5-9.0. Soil pH is a major factor of soil fertility and an indicator of soil nutrient availability. It may influence nutrient absorption and plant growth

through the direct effect of the hydrogen ion, or through the indirect influence on nutrient availability and the presence of toxic ions (Brady, 1974). More acid soils have less available nutrients.

In this study, electro-conductivity (E.C.) of the 1:5 soil/water suspension ($E.C_{1:5}$) was variable between sites with significantly higher values recorded at Kibwezi (38.5 μS/cm at 10 cm and 45.0 μS/cm at 80 cm below ground level). As electro-conductivity (E.C) is a useful indicator of the total concentration of solutes in a soil (Madsen and Mulligan, 2006; Okalebo et al., 1993; Shaw, 1999; Fitzpatrick, 1983), it is suspected that these high values occurred because this site receives lower mean annual rainfall than the other sites and therefore, was less severely leached of salts compared to the other sites (Fitzpatrick, 1983). This may further be supported by the fact that the concentrations of most of the nutrients i.e. P, Cu, Mn, Fe, K, Ca and Mg were higher at the drier site (Kibwezi) and lower at the wetter sites (Nthangu and Kathonzweni). According to Brown (1999) and Madsen and Mulligan (2006), E.C. varies between sites and throughout profiles depending on level and nature of salting.

According to exchangeable magnesium ratings by MAFF (1967) (<30 ppm = low, 30-60 ppm = medium and >60 ppm = high), soils in all the study sites could be rated to be high in Mg, that is, usually sufficient in soils. According to Landon (1984), Mg controls the availability of Ca and the strength of soil structure. According to the critical values summarized by Cox and Kamprath (1972), Makueni district generally had sufficient levels of the micro-elements assessed in this study. According to these authors, defficiency levels of Cu, Zn, Mn and Fe were (0.2-100 ppm), 0.3-7.5 ppm, 2.0-65 ppm and 2.0-45 ppm, respectively) which were on average lower than those measured in this study. It was Kibwezi with the mean Zn content of 0.48 ppm and 0.72 ppm at 10 and 80 cm depths, respectively, which approached deficiency. Plants vary in their micro-nutrient requirements as well as their abilities to extract them from the soil.

The results of soil physical and chemical analysis at different depths were consistent with those reported from elsewhere. The significant decrease in carbon content with depth has been reported under sub-humid conditions in Western Kenya where soil organic carbon decreased from 1.7% in the top soil to 0.3% at 2-3 m depth (Radersma and Ong, 2004). There were no significant differences in most soil properties between soils taken at various soil depths. Similar observations have been reported for soil texture (Ludwig et al., 2003), bulk density (McIntyre et al., 1996) and soil pH (Radersma and Ong, 2004). However, Radersma and Ong (2004) recorded

a decrease in Olsen-P from 1.2 mg kg^{-1} in the top 15 cm to 0.3 mg kg^{-1} at lower soil depths. This was in agreement with the results obtained from this study where mean P content decreased from 7.2 ppm at the 10-15 cm soil depth to 4.0 ppm at the 150-155 cm soil depth. Brown (1999) noted that extractable P is almost always concentrated near the surface or where fertilizer P is applied or derived from organic matter. He also noted that total N was associated with organic matter and tended to be highest near the surface. In this study, N contents were similar at all depths, and this trend was not observed.

These results show that soil moisture had a strong effect on the soil physical and chemical properties of the study area, with N and C contents being low due to low vegetation cover, and most of the other macro and micro elements being high in lower rainfall areas due to minimal leaching. Soil texture was mostly loamy, being favourable for plant growth. The P deficiency observed was attributed to P-poor parent material.

5.2. Spatial distribution of indigenous tree and shrub species

About 2,000 out of the estimated 8,000 – 9,000 species of plants found in Kenya are trees and shrubs existing among other vegetation types mainly in the ASALs (Ogolla and Mugabe, 1997; Maundu and Tengnas, 2005). Many of these species exist outside the gazetted forests in the extensive woodlands and on land devoted to pastoralism and agriculture. The total number of species identified in this study (139), therefore, represents less than a tenth of the trees and shrubs that may be encountered somewhere in the diverse ASAL landscape. In a similar study covering an area comprising four districts of Ukambani, namely, Makueni, Machakos, Kitui and Mwingi, the Department of Resource Surveys and Remote Sensing (DRSRS) identified a total of 300 tree and shrub species which were used to describe the local vegetation (Ojiambo et al., 2001). In a botanical inventory and diversity assessment of Mt. Marsabit forest in northern Kenya, Githae et al. (2007) recorded 52 species of trees and shrubs, twelve species of herbs and six species of climbers and lianas. Likewise, in the nearby Miombo woodland area of eastern Tanzania, a total of 86 tree species were identified (Back'eus et al., 2006). The low species numbers observed in this and previous studies may be attributed to: (i) intensified human activities that may have led to elimination of some of the tree and shrub species through wood harvesting, fires, livestock browsing/grazing and agricultural activities (Back'eus et al., 2006), (ii) natural phenomena such as frequent droughts and wildlife damage (Birkett and Steven-

woods, 2005) that may have led to loss of some of the more susceptible tree and shrub species, and iii) salinity of soils which can only support a limited number of hardy and adapted species (Macharia, 1981).

Nthangu forest had the largest number of species, families and genera (77, 33, 60) followed by Kibwezi (70, 30, 48) and Kathonzweni (69, 28, 42) in that order. Similar gradients have been documented within the study area and its immediate surroundings by other researchers such as Ego et al. (2001). It is suggested that the gradients were a function of the long-term effects of rainfall and soil moisture that favoured Nthangu rather than the other two sites. Climate provides one of the strongest controls on the species composition and characteristics of vegetation, and Kenya is thought to owe its high biological diversity to the enormous variation in climate and topography which result in a great range of habitats (Yimer et al., 2006; Back'eus et al., 2006; Coughenour and Ellis, 1993;). According to Van den Abeele et al. (2005), vegetation in Makueni district ranges from the forests on hill tops (Mbooni, Kilungu) in the high potential areas to the Acacia-Commiphora complex of the ASALs of Makindu, Kibwezi and Mtito Andei in the low potential areas. In the Turkana district of Kenya, the regional herbaceous vegetation biomass reflects a gradient in which the highest levels of biomass occur where rainfall was >600 mm, and the lowest levels occur where rainfall was estimated at 150-200 mm (Coughenour and Ellis, 1993). Similar gradients have been observed at the Nairobi National Park in southern Kenya (Helsa et al., 1985) and in a geologically homogeneous area in Australia (Myers and Neales, 1984).

Trees, shrubs and other vegetation in this study were observed to combine in different ways at different sites to form different species assemblages and vegetation structures. According to the results and the physiognomic classifications described in literature (Pratt and Gwynne, 1977), the vegetation at Nthangu forest, Kathonzweni and Kibwezi may be categorized as *Rhus-Combretum-Acacia* thicket, *Combretum-Terminalia-Acacia* woodland, and *Acacia-Commmiphora* woodland, respectively. In a vegetation survey conducted at sites located at various points within Makueni district, DRSRS identified different vegetation associations (physiognomies) dominated by different plant species and genera as this study (Ojiambo et al., 2001). In a separate study, it was difficult to delineate the dominant species in Kikumbulyu location of Kibwezi division due to severe clearing and high population density (Ngoda and Obwoyere, 2001). In Kajiado and Makueni districts, dominant tree and shrub species included

Acacia senegal, *Grewia bicolor*, Justicia spp., *Grewia villosa*, *Abutilon mauritianum*, *Solanum incanum* and *Aspilia mossambicensis* (Ego et al., 2001).

Acacia was the most common genus represented in all the sites. The genus belongs to the family Mimosaceae which was ecologically the most important at Kibwezi, second most important at Kathonzweni and the third most important at Nthangu forest. Among the Acacias, *A. tortilis* was ecologically the most important followed by *A. nilotica* and *A. mellifera*. It was among the first three dominant tree species at Kathonzweni and Kibwezi sites. The observations were consistent with results obtained in arid northern Kenya, where the genus *Acacia* was common and usually dominant in twenty-nine (29) out of thirty (30) sites sampled for a vegetation survey (Coughenour and Ellis, 1993). *T. brownii* was ecologically the sixth and the second most important at Nthangu and Kathonzweni, respectively, while *C. collinum* was the most important at Kathonzweni. The family Combretaceae was widely represented at Nthangu and Kathonzweni where it was ecologically the most important at both the sites, and the sixth most important at Kibwezi. *C. campestris* was the sixth most important at Kathonzweni, but was not among the nine most important species at the other sites.

The family *Burseraceae* to which it belongs was not among the nine most important families at Nthangu, but was the third most important at both Kathonzweni and Kibwezi. The three sample tree and shrub species; *M. decumbens*, *C. farinosa* and *B. coriacea* were not among the nine important tree species in all the sites. Likewise, the families *Capparidaceae* and *Capparaceae* to which they belong were not among the nine most important families in all the three sites. *S. siamea* was not captured in all the sites as it was exotic and did not grow naturally in rangelands. However, the family *Caesalpinaceae* to which it belongs was represented at Kibwezi where it was the fourth most important.

Despite evidence of disturbances attributed to intensified human activities, the spatial distribution of trees and shrubs observed in this study showed that different sites (agro-ecological zones) supported different species and categories of woody vegetation probably due to different rainfall regimes and soil moisture levels. The fact that these vegetation categories grew naturally and dominated the various sites was an indication that conditions prevailing at the sites were favourable for the survival and growth of these species.

5.3 Size characteristics of indigenous tree and shrub species

Tree and shrub species at Nthangu, Kathonzweni and Kibwezi forests had overall mean basal areas of 16.7 m^2/ha, 19.3 m^2/ha and 76.8 m^2/ha, mean DBHs of 4.6 cm, 6.4 cm and 7.6 cm, and mean heights of 4.4 m, 5.1 m and 5.3 m, respectively. Only a few of the individual species reached higher heights over 20.0, 15.0 and 26.0 m at the three sites, respectively. The small size dimensions may be attributed to the long-term effects of the low and poorly distributed rainfall in the area (Coughenour and Ellis, 1993). It was suggested that rainfall amounts over the vast majority of the study area were too low to support large trees, which only occurred in association with some sort of water concentration zones such as riparian zones and micro-drainages. The mean heights measured in this study were within the range expected for various vegetation categories in rangelands where woodlands, bushlands and shrublands are described as stands of trees up to 20 m, assemblages of trees and shrubs not exceeding 10 m, and stands and shrubs not exceeding 6 m, respectively (Pratt and Gwynne, 1977). During a vegetation survey conducted by DRSRS between April and June 2000 at various points of the study area, Ojiambo et al. (2001) measured tree and shrub heights ranging from 3 m to 7 m at various points between Nthangu forest and Kibwezi. Only five trees, namely; *A. digitata* (17.0 m), *D. elata* (9.7 m), *A. elliator* (7.4 m), *F. saligna* (7.3 m) and *T. brownii* (7.2 m) had mean height values substantially higher than the average.

Mean size dimensions obtained for the three sites indicate that trees and shrubs at the Kibwezi site were larger than those at Kathonzweni and Nthangu sites. This was not consistent with information reported in literature in which sites characterised by higher rainfall regimes have larger trees (Coughenour and Ellis, 1993; Myers and Neales, 1984). It is suggested that the occurrence of larger tree and shrub species at the drier site compared to the wetter sites may partly be attributed to the presence of genetically larger tree species such as *A. digitata*, *D. elata* and *A. tortilis* in the population at the former site, which are less widespread at the other sites. The observation may also be as a result of the clear-felling incident that occurred at Nthangu forest in 1996 and affected natural vegetation from the more productive parts of the forest. As re-planting was done with exotic species, the vegetation survey was conducted on a less productive section with smaller size natural vegetation.

On the other hand, trees and shrubs at Kibwezi forest were possibly largest because of the protection provided by the university against any encroachment, and probably because trees at

this site may have had their root systems approaching or reaching the water table. Trees and shrubs at Kathonzweni were exposed to adverse human interferences, and did not benefit from the effects of higher rainfall as Nthangu or the proximity to a water table as Kibwezi. Hence, they were generally small. Alteration of natural ecosystems by human influences is a common problem the world over (Walker and Langridge, 1997). According to Ward and Micin (2006) and Gaza et al. (2006), plants with access to ground water are larger, less stressed and characterised by higher evapotranspiration (ET) rates than plants without access to ground water.

Size distributions of tree and shrub species in this study showed that the majority of individuals fell within the small diameter and height classes. At both Nthangu forest and Kibwezi sites, the DBH frequency bar graphs were high at the smallest diameter classes and declined smoothly to maximum diameters of 25.0 and over 46.0 cm, respectively. This is consistent with results of other studies which concur that most plant populations consist of relatively few large individuals and many small ones, and the few large individuals account for most of the population biomass (Weiner, 1985; Benjamin and Hardwick, 1986). Similar observations were made in the Miombo ecosystem of western Tanzania where four different land management areas had size class distributions with greater numbers of juvenile trees (2-10 cm DBH) than adults (Banda et al., 2006).

Overall DBH distribution at Kathonzweni and overall height distributions in all the sites showed trends in which there were few individuals in the lowest size classes compared to the middle classes. Juma (2002) observed similar distributions on *Melia volkensii* that showed age and size class distributions with a high frequency of mature trees, and no seedlings. Such size distributions suggest either that climatic conditions for establishment of at least a section of the population have been unfavourable, or that there have been recent increases in over-exploitation due to unchecked human interference and livestock browsing. In the case of Kathonzweni in this study, the later may be possible because the site was not under protection by any lawful authority, and was subject to cases of encroachment. The local people usually cut trees for purposes of firewood, charcoal, poles, and browse, while livestock species such as cattle, goats and donkeys roam about mostly unrestricted. Browsing has the greatest negative effect on the younger members of the population, while other human activities cut across the board. Levitt (1972) attributed a typical age and size-class distribution to the browsing effect of goats, giraffe, orix, lesser kudu, and on farms, lopping or pruning for fodder. Such distributions are risky as

they indicate a situation where populations decline in size and, if remedial measures are not taken urgently, eventually disappear with time. It is also suggested that in the present case, the unexpected absence or reduced number of individuals within small height classes occurred because heights were only measured on trees and shrubs with DBHs $\geq$1.0 cm. Moreover, the number of young trees at this DBH was underestimated because some were either ignored on the assumption that they were too small or were not measurable. Weiner (1985) suggests that the reduced number or absence of small individuals in a population may be attributed to density-dependent mortality of the smallest plants, and that within a population, size appears to be correlated with fitness.

Of the two size characteristics, DBHs were easier to measure and were more reliable and consistent than heights. Tree and shrub species with DBH distributions in which frequency bar graphs are high at the smallest size classes and decline smoothly were *P. schumannianum* and *T. brownii* at Nthangu. *C. collinum* and *C. campestris* at Kathonzweni showed this trend from the second lowest diameter class onwards. *C. collinum* and *A. tortilis* had the largest number of individuals at Kathonzweni and Kibwezi, respectively, where they were represented in most of the diameter classes. There was evidence of interferences on the natural state of vegetation by humans and livestock. Hence, there were no clear trends as those observed under natural conditions (Coughenour and Ellis, 1993).

The size characteristics in which trees and shrubs had small height and DBHs may be attributed to the low soil moisture levels associated with different agro-ecological zones of the district that resulted from the low and poorly distributed rainfall in the study area. Tree and shrub species with size distributions in which small size classes had large numbers of individuals and large size classes had small numbers of individuals were considered to be adapted to respective sites as they showed that they could successfully propagate, grow and survive under the conditions prevailing in these sites. However, clear differences in size distributions between and within sites were over-shadowed by human disturbances, genetic differences in tree and shrub species, and access to ground water.

5.4 Plant and soil moisture dynamics during wet and dry seasons

5.4.1 Plant moisture by site

Sample tree and shrub species at Nthangu forest/Kaumoni area were characterised by significantly higher (less negative) plant water potentials, lower transpiration rates, and higher stomatal conductances than the other sites. As plant moisture parameters are known to be dependent on environmental and plant internal factors (De Rocher et al., 1995; Nyadzi et al., 2003), it is suggested that, being situated at a higher altitude than the other sites, Nthangu forest/Kaumoni area had a higher mean annual rainfall, lower light intensities, lower atmospheric temperatures and higher atmospheric relative humidities which had direct effects on soil and plant moisture relationships.

The more rainfall received at Nthangu forest during the study period compared to the other sites meant more soil moisture being available for absorption by growing plants, and increased turgidity of plant cells including guard cells. Increased turgidity of guard cells leads to increase in stomatal opening, a process that may be termed "hydroactive opening" (Salisbury and Ross, 1978). At low temperatures, the cuticular diffusion resistance increases, maintaining a higher potential of guard cells and increasing stomatal aperture (stomatal conductance). A higher atmospheric relative humidity at the site meant lower vapour pressure gradient between the leaves and the atmosphere, which in turn led to reduced loss of water vapour through transpiration, a higher water potential and higher turgidity in cells, and increased stomatal aperture. Field observations by Myers and Neales (1984) suggested that stomatal conductances (g_s) are decreased at high values of leaf-to-air vapour pressure difference (VPD) (Δ_e).

The combined effect of a high plant water potential and high atmospheric relative humidity at Nthangu was a low water vapour pressure gradient between the leaf and the surrounding air, resulting in reduced transpiration rates. This was not consistent with observations made in North Australia where transpiration rates were significantly lower in trees at the driest site than at the other sites (Eamus et al., 2000). The inconsistency may have occurred due to several reasons. Low light intensities, for instance, fail to provide sufficient warmth to the surfaces of the leaf, leading to a low vapour pressure gradient and to less rapid evaporation (transpiration). Soil temperatures influence water uptake by plants in that both the capacity of the roots to absorb and the resistance to movement of water through the soil are temperature-

dependent (Br'eda et al., 1995). Plants can extract water from cold soils less readily than from warm soils. At low temperatures, the permeability of protoplasm to water falls, and the cuticular diffusion resistance increases, further reducing the rates of transpiration.

At Kathonzweni and Kibwezi sites, annual rainfall and soil moisture were low, light intensities and atmospheric temperatures were high, and atmospheric relative humidities were low. These conditions favoured low soil and plant water potentials, high transpiration rates, low stomatal conductances as observed in this study, and increased moisture stress among plants which required great force to extract water from soils at their growing sites. Consequently, the scholander pressure chamber used in this study could not provide sufficient external pressure (≥4.0 MPa) to cause reverse flow of xylem sap from freshly cut leaves of three of the sample tree and shrub species: *M. decumbens*, *C. farinosa* and *B. coriacea*. Such low water potentials among plants in rangeland ecosystems are not uncommon (Cresswell et al., 1982) and many of the plants are capable of surviving down to much lower water potentials, but under such conditions, there is no growth.

While *M. decumbens* and *C. farinosa* were widely distributed at the two sites, *B. coriacea* occurred only at Kibwezi. None of the three species was found at Nthangu forest where the local sample tree; *P. schumannianum* was widely distributed. Morphologically, the later was deciduous, dropping its leaves during extreme dry seasons, and its leaves were hairy, meaning that they showed high boundary layer resistances. Both these important morphological adaptations are likely to have contributed to the low transpiration rates, and the maintenance of high water potentials during the study period. Consistent with these observations, Gebrekirstos et al. (2006) reported very low water potentials in evergreen tree and shrub species growing in Ethiopia compared with deciduous counterparts. The significantly lower (more negative) water potentials shown by *S. siamea* at Kibwezi compared to the other two sites may be attributed to the harsher climatic conditions, and probably the fact that it was older in age. Physiological and morphological differences between younger and older plant parts have been reported from spain where young and green parts of leaves showed five times higher chlorophyll concentration and greater photosynthetic capacity than the senescent parts of the foliage (Ramirez et al., 2006).

5.4.2 Plant moisture by season

Significantly lower (more negative) water potentials, higher transpiration rates and significantly lower stomatal conductances were recorded for sample tree and shrub species during the dry seasons as compared to the rainy seasons. Similar observations were made in southern Italy where large seasonal fluctuations have been observed for both pre-dawn and afternoon water potentials. Although minimum values down to -4.0 MPa have been measured, plant water potentials always recovered to less negative values after drought. In North Australia, mean daily transpiration rates of five indigenous Eucalyptus spp. were generally higher in the dry season than in the wet season (Eamus et al., 2000). Elsewhere, transpiration did not show any significant effect of irrigation treatments during the first ten days of drought stress application, and thereafter decreased in PRD and RDI to a level around 50% of ww (Wakrim et al., 2005).

During the rainy season, the soil moisture status was more favourable, more soil moisture was available for absorption by growing plants, and plant water potentials were higher. During the dry season, the low soil moisture availability led to low plant water potentials. Prevailing climatic conditions favoured a high water vapour pressure gradient between plant leaves and the dry air and an increased evaporative demand, leading to the high rates of transpiration, increased xylem tension and low plant water potentials. During the peak dry period prior to the summer rainy season in the USA, trees at an intermittent stream site exhibited greater water stress as transpiration did not increase beyond its mid-morning peak with increasing vapour pressure deficit which was likely due to leaf stomatal closure (Gaza et al., 2006). This stress was alleviated after significant monsoonal rains and runoff events had recharged soil moisture and raised ground water levels. Field measurements made in Australia indicated that leaf conductance decreased at high values of leaf-to-air vapour pressure difference (VPD) (Δe) (Myers and Neales, 1984). This was attributed to reduced stomatal aperture and stomatal conductance.

The sample tree and shrub species in all the study sites did not show significant differences in stomatal conductances between seasons. The slightly different trend shown by *B. coriacea* may be due to its sclerophyllous (hard and brittle) leaves. *S. siamea* showed significant differences in stomatal conductances between the seasons at Nthangu/Kaumoni area and at Kathonzweni, but not at Kibwezi. It is suggested that, compared to the Kibwezi site, the annual rainfall amount received at the two sites was sufficient to cause a significant impact on the soil

and plant moisture status, which in turn led to a significant difference in stomatal behaviour. During the rainy season, cell water potentials were high enough to cope with diurnal loss of water by transpiration from guard cells and keep turgidity high enough to maintain more open stomata and higher stomatal conductances. During the dry season, reduced soil and plant moisture status led to less turgid guard cells and reduced stomatal aperture and stomatal conductances. At Kibwezi, the differences between dry season and wet season rainfall was not sufficient enough to cause significant differences in stomatal behaviour.

5.4.3 Plant moisture by time of day

Plant moisture parameters showed daily fluctuations that were sometimes irregular due to sudden changes in weather. Although observations were not significantly different, plant water potentials were highest (least negative) in the morning compared to the afternoon hours. Transpiration rates of the test species were significantly lower during the morning hours than in the afternoon hours, while stomatal conductances were significantly higher in the morning than in the afternoon. Similar observations were made in Western Tanzania (Nyadzi et al., 2003), South Carolina in the USA (Collins and Wein, 1990) and Australia (Myers and Neales, 1984).

In the seasonal savannas of Central Brazil, four out of five local tree species sampled for studies on diurnal patterns of some physiological parameters showed strong stomatal control and attained maximum stomatal conductances in the morning hours (Franco and Luttge, 2002). Among seedlings of outcrossed and selfed jack pine (*Pinus banksiana* Lamb.) plants, xylem pressure potentials varied diurnally approaching the point of hydroactive stomatal closure at –1.7 MPa during early afternoon and –0.5 MPa around midnight (Blake and Yeatman, 1989). Other research reports showing similar fluctuations include those of the shrub *Artemisia tridentata* (Richards and Caldwell, 1987) and *Acacia tortilis* (Ludwig et al., 2003).

P. schumannianum and *B. coriacea*, which were only found in extreme sites (I and III), respectively, had additional morphological characters which were thought to have interacted with the environment to yield the physiological variations observed in this study. The former was located at a site surrounded by a forest of taller tree and shrub species so that the same was partly under shade and some environmental conditions affecting it may have varied little during the day. Leaves belonging to this species were hairy, suggesting that their boundary layer resistance to transpiration was higher, leading to lower transpiration rates. As air movement (wind) at the

site was restricted due to abstraction by surrounding trees and shrubs, this boundary layer resistance also varied little during the day. The later was characterised by sclerophyllous (hard and brittle) leaves, an adaptation which suppressed adverse effects of daily variations in environmental conditions.

Consistent with results of experiments conducted elsewhere (Collins and Wein, 1990; Franco and Luttge, 2002), light intensity and atmospheric temperature were low in the morning, rose to a peak after midday and decreased again in the late afternoon. Atmospheric relative humidity (RH) on the other hand was high in the morning but dropped in the afternoon. In a study conducted in four grassland ecosystems in Kenya, it was evident that rates of transpiration increased with increasing light intensity until a certain level; dependent on species; above which it decreased (Macharia, 1981). Similar fluctuations were observed for transpiration and light intensity in field and greenhouse trials in Australia and the USA (Eamus et al., 2000; De Rocher et al., 1995; Collins and Wein, 1990). It is suggested that as light intensity increased in the afternoon, it warmed up the leaf surfaces of sample trees and shrubs leading to increased leaf-air vapour pressure difference and to higher evaporation (transpiration rates). Likewise, stomatal apertures are more open in the morning hours because plant water potentials were high and guard cells were turgid (hydropassive opening). In the afternoon hours, high transpiration rates resulted in more rapid loss of water from the guard cells than was being replenished. Thus the stomatal opening, and therefore, the stomatal conductance were reduced. In the study presented here, it is suggested that measurements recorded at 9.00 am were taken at a point of the fluctuation curve when the plant water potentials were decreasing while transpiration rates were increasing. At the point of lowest water potential around midday, transpiration rates and xylem tension are highest, while at the point of highest water potentials around midnight, the same are lowest. At this point, the plant and soil water potentials approach equilibrium.

5.4.4 Plant moisture by Provenance (geographic origin)

The results of this study showed that the morpho-physiological characteristics of the exotic species *S. siamea* and the indigenous species *P. schumannianum* were similar, both dropping their leaves during extreme dry seasons. Likewise, plant moisture parameters in the exotic tree species *S. siamea* and those in the indigenous tree and shrub species (*P. schumaniannum, C. farinosa, M. decumbens* and *B. coriacea*) were mostly not significantly

different. Although water potentials of *P. schumannianum* at Nthangu forest were significantly lower than those of *S. siamea*, the same may be as a result of the influence by the surrounding denser forest and the characteristic hairy leaves associated with the former species. The fact that *S. siamea* can grow well in most of the study area, and that there were no striking differences between moisture parameters of this species and those of the indigenous ones, show that the species is potentially adapted to most of the study area, and that not all exotic species are poorly adapted to semi-arid areas as is commonly believed. It is more important to consider the conditions prevailing at the points of origin as compared to those at the target areas.

5.4.5 Soil moisture

According to the results obtained from this study, Kibwezi had the highest mean soil moisture content, followed by Nthangu forest and Kathonzweni, respectively. This was not consistent with the amounts of rainfall received during the study period in which Nthangu forest recorded the highest amount (966.6 mm) followed by Kibwezi (632.4 mm) and Kathonzweni (484.5 mm). This inconsistency may be attributed to several factors. First, the combined effects of rocky soils and steeper slopes at Nthangu forest meant that much of the rain water received at any one time was lost as run-off and less infiltrated into the soil. The limited amount that entered the soil was readily absorped by the large population of plants and some might have been lost to the atmosphere through evapotranspiration. Hence the amount of soil moisture was comparatively low. Secondly, rainfall within the study area is known to be erratic and poorly distributed. Rain may fall from time to time, but the amounts may be too low to allow infiltration to significant depths. This situation is worsened and infiltration is further restricted where soils are characterised by surface crusts and sub-surface hard pans due to poor structure (Lal, 1979; Acuna and Wade, 2005). Because of excessive radiation and high atmospheric temperatures, this water is quickly diffused out of the soil and lost to the atmosphere through evapotranspiration. The variation in rainfall amounts and frequency, and in radiation and temperatures at different sites may have contributed to the observed differences. Thirdly, the different soil types associated with the different sites may have contributed differently to water transport and retention in the soils (Lal, 1979; Fitzpatrick, 1983). Soil in parts of the study area have a potential of forming a surface soil crust or hard pan which favour loss of water through run-off

rather than infiltration into deeper soil layers (Michieka and Van der Pouw, 1977; Lal, 1979; Acuna and Wade, 2005).

The seasonal variation in soil moisture contents recorded in this study was similar to that observed in other areas. In Kenya's Tsavo National Park (West), soil moisture at depths of 5-10 cm, 15-20 cm, and 25-30 cm fluctuated with seasonal rainfall (Belsky et al., 1989). In sub-humid western Kenya, the amplitude and average level of soil moisture contents during the dry and wet seasons differed from the different layers, being largest at the upper soil layer and lower at the lower soil layers (Radersma and Ong, 2004).

Definite trends in soil moisture contents in relation to soil depth were not clear although differences in soil moisture contents at various depths were statistically significant. This is probably because the amounts of rainfall received were too low, and also that soils at the various sites may have varied in their capacity to transport and retain water. The transfer of water from wet topsoil to deeper, dry layers prevents shallow-rooted competitors from utilizing the water and also reduces losses by soil evaporation. According to Dolling et al. (2006), evaporation and transpiration losses are concentrated in the surface 0.3 m. This allows plants to maximize their resource acquisition during periods of high water availability and to "store" the water for use later in the season when the shallow soil layers are dry. This may be an important mechanism for drought avoidance by plants growing in climates having a short, intense wet-season such as semi-arid, Mediterranean and sub-tropical climates. In this study, tree and shrub species growing at various sites may have had some effect on the soil moisture as did four agroforestry tree and shrub species growing in western Kenya (Broadhead et al., 2003). Consequently, soil moisture contents were greater under *S. siamea* and *B. coriacea* than under the other sample species. This suggests possession of higher capacities for water conservation by these two species compared to the others.

The soil moisture contents recorded during this study were considered low, consistent with those reported by other researchers within the region, and reflected the amounts of rainfall received in the study area. Macharia (1981), for instance, reported low soil moisture levels for much of the year in three of four grassland ecosystems in Kenya. Considering the amounts of rainfall received by each of the three research sites, a soil moisture gradient should have been observed where soils at Nthangu forest contained the highest overall mean moisture compared to the other two sites. This is because similar studies conducted elsewhere have shown a close

positive correlation between rainfall and soil moisture (Ludwig et al., 2003; Belsky et al., 1989). A similar gradient was not clearly observed in this study, probably because of rocky soils, steep slopes and rapid water uptake by the large population of plants at Nthangu forest as explained in earlier paragraphs, which led to depressed mean moisture content at this site despite a higher rainfall compared to the other sites.

The results showed significant variations in plant and soil moisture levels between sites (agro-ecological zones) and seasons. Soil moisture levels varied with the amounts of rainfall, local terrain and soil condition, while plant moisture levels varied according to soil moisture status, plant internal factors and climatic conditions. The rapid changes in transpiration rates and stomatal conductances that occurred from time to time mostly due to changes in weather made it difficult to follow the effects of soil moisture status on these parameters. Water potential was simpler to measure, did not vary rapidly with environmental factors and was easier to follow, being higher at the higher potential site, during the wet season than during the dry season, and in the morning hours than in the afternoon hours. During dry seasons, when water potentials were lowest, tree and shrub species, particularly at the drier site, were exposed to severe water deficiency stress and responded by developing morpho-physiological strategies to reduce transpiration water loss and adapt to local conditions.

5.5 Tree and shrub moisture levels at pre-dawn and midday during the dry season

In this study, the varying ranges of pre-dawn and midday water potentials for different tree and shrub species influenced the overall means which in turn made it difficult to make comparisons of various sites in terms of these parameters. For instance, the low midday water potentials of *A. tortilis* at Kathonzweni may have contributed to the very low overall means at this site. At the Kibwezi site, the extremely high pre-dawn water potentials for *C. campestris* may have raised the overall means to values above those of Kathonzweni. It was suggested that the water potentials of *S. siamea* were better parameters to compare sites as this tree occurred in all the three sites. Both pre-dawn and midday water potentials of *S. siamea* were higher at Nthangu/Kaumoni area than both Kathonzweni and Kibwezi. Mean pre-dawn water potentials of the latter declined from Nthangu forest/Kaumoni area (-1.18 MPa) to Kathonzweni (-2.30 MPa) and to Kibwezi (-2.70 MPa). According to Sellin (1999), it is assumed that plant and soil come into equilibrium overnight because of stomatal closure, although there is increasing evidence that

some species maintain substantial stomatal conductance and transpirational water loss at night (Snyder et al., 2003). The conditions of the equilibrium are presumed to correspond to the daily maximum level of ψ_l which is reached, usually just before sunrise (Sellin, 1999). At this point, it is expected that $\psi_l = \psi_{root} = \psi_{soil}$, and therefore that the pre-dawn ψ_l can be used to estimate the soil water availability or the ψ_{soil} in the immediate vicinity of the roots (Mitloehner, 1997). In this regard, it may be suggested, based on these measurements, that soil moisture availability at Nthangu forest/Kaumoni area was higher than at both Kathonzweni and Kibwezi. For the re-saturation at pre-dawn, *S. siamea* trees at Nthangu forest/Kaumoni area needed apply about a half of the suction force for midday compared to about three quarters at Kathonzweni and about four-fifths at Kibwezi. The suction force applied for re-saturation at Kathonzweni was about 90% that applied at Kibwezi, while that applied at Nthangu forest/Kaumoni area was about 73% that applied at Kathonzweni.

The observations were consistent with the amounts of rainfall received which were higher at Nthangu/Kaumoni area than at Kathonzweni and Kibwezi. Comparable results were obtained at three different study sites in Northern Australia where pre-dawn water potentials increased significantly at the start of the rainy season when the rains came after a drought of up to 6 months (Eamus et al., 2000). This suggests that pre-dawn water potential measurements in trees and shrubs can be used as biological indicators of site soil water availability, and by extension, agricultural potential. This has successfully been done in Latin America and Southern Africa (Mitloehner, 1997; Krug, 2004). The small, though statistically significant variation in pre-dawn water potential between sites may be attributed to the small and similar amounts of rainfall received in all the sites which did not significantly affect soil moisture availability. It is also suspected that the higher soil moisture availability was not only because of the higher amounts of rainfall received at the site, but also because the site had a gently sloping terrain and deep soils which allowed better infiltration and storage of water. Under certain conditions (Sellin, 1996), daily maximum water potentials may not always be evident just prior to dawn, but an hour or two later. Therefore, it is sometimes considered more exact to use the term "base water potential (ψ_b)" rather than "pre-dawn water potential" (Sellin, 1999). The base water potential is also of paramount physiological importance as it has been reported to control a daily maximum level of stomatal conductance for a variety of species (Gucci et al., 1996), thereby influencing the plants'

productivity and performance. Pre-dawn ψ_l may be useful as a "baseline" water stress at the whole-plant level.

Midday water potential measurements were taken when the trees and shrubs were experiencing the worst possible circumstances as this was the driest time of the day when transpiration rates were highest and the plant experienced the greatest water deficit stress. According to Mitloehner (1997) and Gebrekirstos et al. (2006), the difference between the pre-dawn value and the midday value of the plant water potential reflects the range of plant water potential to overcome the soil water potential. This daily amplitude of water potential decreases with increasing plant water stress (Borghetti et al., 2004), and when drying soil causes absorption to lag behind water loss, permanent water deficits develop which cause injury and even death by desiccation. In this study, it was not possible to measure pre-dawn and midday water potentials of *C. collinum* and *T. brownii* because of the excessively high pressures required to cause reverse flow of xylem sap from leaf samples.

According to the data, *A. polyacantha*, *A. tortilis* and *C. campestris* had high pre-dawn water potentials indicating possibility of accessibility to some constant source of soil water which always ensured rapid overnight make-up for daily water loss (Abdallah and Chaieb, 2007). The large diurnal ranges shown by the two Acacias indicate a lag possibly due to absorption of water from distant locations – low water table at a far vertical distance or a horizontal point far from the position of the tree. In this regard, *A. tortilis* is known to have both very deep tap roots and far-reaching lateral roots that extend down to the water table and ensure a constant supply of soil water to the plant (Belsky et al. 1989; Belsky, 1994). This type of adaptation may be reffered to as dehydration postponement (Kramer, 1980; Levitt, 1980; Turner, 1986) and partly explains why *A. tortilis* is widely distributed in the study area despite harsh climatic conditions in some of the study sites. In the open savanna woodlands of southern and eastern Ethiopia, *A. tortilis* was among three tree and shrub species with wide capacities to withstand variations in soil moisture that exhibited low midday (-3.05 to -4.85 MPa), low pre-dawn (-1.98 to -3.0 MPa) and wide diurnal (1.16 to 2.25 MPa) plant water potential ranges, and which were considered suitable candidates for reforestation in drought prone areas (Gebrekirstos et al., 2006).

C. campestris had the lowest amplitude (diurnal range) of water potential , possibly because, although it was not accessible to ground water, water was available from its succulent

stems and no lag was experienced between absorption and loss of water. It exhibited the highest midday (-0.73 MPa), highest pre-dawn (-0.05 MPa) and narrow diurnal (0.68 MPa) plant water potential ranges, suggesting narrow capacity to withstand variations in soil moisture and showing likely low adaptation to the study area. That *S. siamea* had a low pre-dawn water potential disqualifies possibility that it was in contact with any ground water, and the low diurnal range of water potential suggests exposure to drier soil moisture conditions. It exhibited a low midday (-2.17 to –3.23 MPa), low pre-dawn (-1.05 to –2.70 MPa) and narrow diurnal (0.53 – 0.98) plant water potential ranges, which also show narrow capacity to withstand variations in soil moisture and low adaptation to the study area. There were indications that under severe conditions, these species displayed other types and mechanisms of adaptation. Most of these adaptations may also be categorized under dehydration postponement (Connor, 2005).

It may likewise be stated that by measuring pre-dawn (standardised) osmotic potentials of local trees and shrubs, it is possible to reflect the solute conditions of a site, while by measuring midday plant osmotic potentials, it is possible to reflect the adaptation of tree and shrub species to these solute conditions (Mitloehner, 1997; Krug, 2004). According to the results, mean pre-dawn osmotic potentials of *S. siamea* were significantly lower at Kathonzweni than at both Nthangu forest and Kibwezi, suggesting a higher total concentration of solutes at this site. In the present study, the concentrations of most of the nutrients measured (P, Cu, Mn, Fe, K, Ca and Mg) were higher at the drier site (Kibwezi) and lower at the wetter sites (Nthangu and Kathonzweni). The drier site received the least amount of annual rainfall, and was likely less severely leached of salts compared to the other sites (Fitzpatrick, 1983).

According to Krug (2004), the bigger the difference between the pre-dawn (standardised) and midday osmotic potential values, the more the tree internal osmotic potential manages to cope with edaphic constraints relating to soil solutes. When the water stress phase at noon (midday) and the plant relaxation phase at night (pre-dawn) approach the same value, like in the late dry season, the plant internal potentials (water potential and respective osmotic potentials) would have the same value, indicating the same pre-dawn (with regard to osmotic potentials; standardised) as midday. At this point, the leaves no longer have the ability to take up water from the soil system or to overcome the soil's concentration of solutes.

Consequently, all those tree and shrub species that were accessible to water, by virtue of their presumed proximity to the water table (*A. tortilis* (0.30) and *A. polyacantha* (0.23)) had

very low diurnal ranges of plant osmotic potentials. This may be attributed to the sustained dilution effect of plant solutes by the abundantly available water. *S. siamea* had low osmotic potential ranges, but as discussed earlier, it possibly had other types and mechanisms of adaptation. The small osmotic potential range of *C. campestris* was likely as a result of water in the succulent stems which maintained the low concentration of solutes. The larger osmotic potential ranges shown by *C. collinum* (0.74), and *T. brownii* (0.98) at Kathonzweni, and *A. tortilis* at Kibwezi where conditions were drier (0.73), were probably partly as a result of osmotic adjustment, an adaptation that results in increased concentration of solutes in plants, that in turn enables them absorb soil moisture with heightened suction force.

Results of this study showed that compared to midday measurements, pre-dawn water potentials were high due to minimal transpirational water loss at night, and were in equilibrium with soil water potentials, such that they could be used as biological indicators of water potentials of the sites where the trees and shrubs grew. Midday water potentials were low as they were taken when transpiration was highest and when the trees were experiencing the worst moisture deficiency stress. When the two measurements were taken during the dry season, they reflected the moisture status of the sites and the worst internal moisture situations that the trees and shrubs attained, and needed to overcome, hence providing indication of possible adaptations of tree and shrub species to growing sites. Pre-dawn and midday measurements and their variations were consistent with the morphological changes that occurred in various tree and shrub species during the dry season. As an important component of water potential, plant osmotic potential was a useful indicator of solute concentrations in plants and soils and provided indication of possible adaptation to these sites based on this parameter.

5.6 Morpho-physiological indicators of adaptation and stress

All the parameters assessed in this study were potential indicators of stress and adaptation in woody vegetation. Trees and shrubs that were widely distributed and dominated various sites in the study area were thought to be adapted to those areas. They showed that conditions prevailing in those areas were favourable for their survival and growth. Consequently, *T. brownii* and *C. collinum* were found at Nthangu and Kathonzweni, while *A. tortilis* was adapted to most of the study area. Trees and shrubs that had size distributions in which frequency bar graphs were high at the smallest size classes and declined smoothly had the potential to survive and

sustain production as they represented resilient populations in which ageing members were adequately and promptly replaced by younger ones. It is suggested that under natural conditions where human disturbances were minimal, these trend would be clearly observed. Of the growth parameters measured, DBH was easier to measure and more reliable than height. Tree and shrub species that maintained high water potentials despite changes in environmental condition had the potential to survive and grow under conditions of severe stress. This is probably the reason why all the trees and shrubs assessed in this study developed short and long term strategies of water loss reduction and increased water uptake during periods of moisture deficiency stress.

In this regard, *P. schumannianum* and *T. brownii* were characterised by hairy leaf surfaces, while *B. coriacea* was characterised by hard and brittle (sclerophyllous) leaves with sharp apices. *C. collinum*, *S. siamea*, *C. farinosa* and *B. coriacea* had smooth and shiny leaves that possibly reflected some of the incoming radiation. *A. tortilis* and *C. farinosa* had many small leaves, while *M. decumbens* was charactertised by a swollen succulent tap root system with very few lateral rootlets. *C. campestris* was characterised by a succulent stem that retained water for use by the plant during dry seasons. *P. schumannianum* at Nthangu forest and *C. campestris* at Kibwezi dropped most of their leaves during severe dry seasons. *S. siamea* retained its entire leaf biomass at Nthangu forest and at Kathonzweni, but lost a large percentage of it at Kibwezi where conditions were harshest. It is suspected that these visible morphological features complemented other invisible ones to enable the rangeland tree and shrub species survive under semi-arid conditions. Consequently, *T. brownii*, and *C. collinum* at Kathonzweni, *M. decumbens* and *C. farinosa* at Kathonzweni and Kibwezi, and *B. coriacea* at Kibwezi were mostly green during the entire study period possibly due to other adaptive features that were not clearly visible.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

1. The different sites (agro-ecological zones) of Makueni district supported different species and categories of woody vegetation that grew naturally and dominated the various sites probably due to different rainfall regimes and soil moisture levels. This suggested that spatial distribution may possibly be one of the main indicators of adaptation as species that can grow and survive under conditions prevailing at various sites were likely to spread and dominate such sites.

2. The small size characteristics of woody vegetation, and their variation from site to site were mainly as a result of low soil moisture levels associated with different agro-ecological zones. However, clear distributions were over-shadowed by human disturbances, genetic differences in tree and shrub species, and access to ground water.

3. There were significant variations in plant and soil moisture levels at different sites (agro-ecological zones) and during various seasons to which tree and shrub vegetation responded by developing different morpho-physiological strategies to survive and grow during severe moisture deficiency stress.

4. Measurements of pre-dawn and midday water potentials may provide indication of site moisture availability and tree adaptations to the sites. The consistency shown by these measurements and their variation with morphological changes in trees and shrubs during the dry season shows that these measurements may be used to complement morphological changes and as a rapid method of identifying types and mechanisms of adaptation in woody vegetation.

5. Of the parameters assessed in this study, spatial distribution, size distribution and water potential were potential indicators of adaptation and stress in semi-arid rangeland woody vegetation. Based on these indicators, *A. tortilis* was identified as adapted to majority of sites in the study area. *S. siamea* was recommended based on its performance in various sites and its water use and conservation.

6.2 Recommendations

1. Studies to determine spatial distribution of woody vegetation based on soil moisture status should be replicated under more natural conditions (conditions of more minimal human interference) in similar agro-ecological zones in and outside the region.

2. Studies to determine the size characteristics of woody vegetation in relation to soil moisture should be replicated under conditions where human and other influences are minimal in similar agro-ecological zones in and outside the region.

3. There is need for more research to identify more tree and shrub species whose internal moisture statuses vary minimally regardless of zonal and seasonal variations in soil moisture as such trees can survive and grow under conditions of severe moisture deficiency stress.

4. More studies on pre-dawn and midday water potentials using more powerful equipment are recommended on a wider range of tree and shrub species and at a variety of semi-arid rangeland sites. In these studies, greater consideration should be given to plant osmotic potentials, as soil solutes have significant influences on soil moisture uptake, and trees and shrubs must develop adaptations to these influences in these areas.

5. More studies should be conducted on a wider variety of semi-arid rangeland sites to identify more indicators of stress and adaptation, as these will further assist in the identification of appropriate tree and shrub species for rehabilitation of degraded rangeland sites.

CHAPTER SEVEN

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APPENDICES

Appendix 1: Major land uses in various agro-ecological zones of Makueni district (Source: District Agriculture Office, Wote, 1996).

Agro-ecological Zone	% of district agric. Area	Description of area	Main land use activities
High potential LM2	19.3	Hill masses of Mbooni and Kilungu	Coffee, Maize, Peas, Citrus, fruits, afforest
Medium potential LM3, UM3, LM4, UM4	2.4	Lower slopes of hills adjacent areas of Nzui, Ukia.	Coffee, Maize, cotton, beans, pigeon peas, sun-Flower, sorghum, fruits
Lower potential LM5, LM6, UM6,	56.7	Wote, Matiliku	Livestock, Maize, beans, sorghum cotton, sunflower, pigeon peas, forests

Appendix 2: Climatic data for Nthangu, Kathonzweni and Kibwezi sites of Makueni district between July 2003 and June 2004

Study site	Parameter		Month													
			July 03	Aug 03	Sept 03	Oct 03	Nov 03	Dec 03	Jan 04	Feb 04	March 04	April 04	May 04	June 04	Total	Mean
Nthangu	Rainfall (mm)		1.6	27.5	13.0	39.0	338.4	50.8	48.5	63.6	143.9	233.6	7.7	3.0	966.6	80.6
	Rainy days		1	4	5	8	13	9	9	9	5	13	4	1	81	6.0
	Mean max. Temp (^{0}C)		-	24.2	26.0	28.5	25.4	26.4	26.9	27.8	29.2	27.1	25.8	23.8	291.1	26.5
	Mean min. temp (^{0}C)		-	20.2	20.2	21.7	21.4	22.2	22.5	22.8	23.9	22.6	21.5	20.3	239.3	21.8
Kathonzweni	Rainfall (mm)		-	-	5.0	5.0	102.2	31.5	86.0	62.0	64.0	67.3	-	-	484.5	40.4
	Rainy days		-	-	2	1	6	3	9	5	3	7	-	-		4.0
	Mean max. Temp (^{0}C)		-	26.1	28.1	30.3	28.1	-	-	-	-	-	-	-	112.6	28.2
	Mean min. temp (^{0}C)		-	23.1	24.7	26.1	24.6	-	-	-	-	-	-	-	98.5	24.6
Kibwezi	Rainfall (mm)		0.0	0.1	0.0	69.9	235.7	42.0	71.8	75.9	60.0	70.0	4.0	0.0	632.4	52.6
	Rainy days															5.0
	Mean max. Temp (^{0}C)		28.4	28.2	30.4	28.9	30.4	30.5	30.8	30.8	33.1	30.7	31.0	28.7	331.1	27.6
	Mean min. temp (^{0}C)		14.7	15.0	16.6	18.9	19.2	17.6	18.8	19.5	20.8	20.1	18.1	15.6	214.9	17.9
	Radiation (Langleys)		389.4	372.5	472.4	404.4	523.5	515.1	-	444.4	479.3	442.8	444.0	-	4487.8	448.8
	Sunshine hrs		6.6	6.2	9.3	6.8	8.4	-	6.4	-	-	-	-	-	43.7	7.3
	Wind run		-	152.6	181.6	85.1	87.2	76.6	-	-	-	-	-	-		
	RH (%)	6.00 am	-	-	-	-	-	-	-	-	47.4	54.7	46.4	44.9	193.4	48.4
		9.00 am	-	-	-	-	-	-	-	-	38.2	49.5	39.9	39.8	167.4	41.9
		3.00 pm	-	-	-	-	-	-	-	-	71.8	74.9	69.8	66.5	283	70.8

Appendix 3: Soil chemical and physical properties at six depths around sample tree and shrub species in three sites of Makueni district

Study site	Species/sub-site	Depth (cm)	Soil property															
			Sand (%)	Clay (%)	Silt (%)	pH (H_2O)	pH ($CaCl_2$)	E.C (u/cm)	P (ppm)	C (%)	N (%)	Cu (ppm)	Zn (ppm)	Mn (ppm)	Fe (ppm)	K (ppm)	Ca (ppm)	Na (ppm)	Mg (ppm)
Nthangu	*P. schuman* (Nthangu)	15	64	30	6.0	6.5	6.0	34.3	16.0	1.15	0.19	6.43	1.75	65.0	144	378	360	37.0	443
		30	60	30	10	6.6	6.1	31.0	5.0	1.01	0.05	3.29	2.03	46.0	127	341	249	62.0	398
		60	64	24	12	6.7	6.1	17.3	1.0	0.51	0.08	1.70	1.17	42	83	189	242	71	384
		90	70	22	8.0	6.9	6.1	40.2	4.0	0.19	0.08	0.87	3.54	28	60	114	199	6.0	343
		120	74	12	14	6.8	6.1	10.4	2.0	0.14	0.11	0.65	1.23	34	64	151	167	95	416
		150	76	10	14	6.6	6.2	11.5	4.0	0.08	0.11	0.44	0.97	37	34	132	173	72	718
		Mean	68	21.3	10.7	6.7	6.1	24.1	5.3	0.51	0.10	2.23	1.78	42	85.3	217.5	231.7	57.2	450.3
	S. siamea (Kaumoni)	15	68	30	2.0	6.3	5.8	30.6	4.0	0.86	0.11	3.26	2.69	193	85	492	357	48	307
		30	62	36	2	7.1	6.0	10	2.0	0.7	0.11	1.21	1.07	127	108	95	315	99	280
		60	60	40	-	6.6	6.0	16.2	2.0	0.85	0.08	2.60	2.77	89	59	57	217	79	205
		90	62	38	-	7.0	6.2	11.2	2.0	0.67	0.08	1.02	1.72	83	89	284	194	73	223
		120	58	40	2.0	6.6	6.1	12.3	3.0	0.66	0.11	0.81	2.04	78	63	57	106	20	206
		150	62	30	8.0	7.0	6.2	13.4	2.0	0.58	0.04	1.93	0.93	35	102	57	127	57	251
		Mean	62	35.7	3.5	6.8	6.1	15.6	2.5	0.72	0.09	1.81	1.87	100.8	84.3	173.7	219.3	62.7	245.3
Kathonzweni	*S. siamea* (Muusini)	15	62	34	4.0	6.4	6.0	33.5	2.0	0.81	0.04	3.76	1.35	175	47	719	333	68	512
		30	60	36	4.0	6.7	6.2	38.1	1.0	0.71	0.08	2.93	1.06	132	60	568	197	9.0	375
		60	56	20	24	6.5	6.0	24.2	3.0	0.67	0.11	2.58	1.14	92	72	397	275	43	628
		90	56	38	6.0	6.5	6.1	21.6	2.0	0.61	0.04	2.14	1.13	78	48	284	164	65	522
		120	54	40	6.0	6.2	5.8	44.6	3.0	0.53	0.04	1.68	1.30	33	75	359	157	89	544
		150	56	38	6.0	6.7	6.1	119.6	1.0	0.55	0.04	3.68	1.44	179	84	341	223	80	620
		Mean	57.3	34.3	8.3	6.5	6.0	47.0	2.0	0.65	0.06	2.80	1.24	114.8	64.3	444.7	224.8	59.0	533.5
	M. decumb (Mathem b)	15	76	20	4.0	6.6	6.0	58.5	3.0	0.83	0.04	1.52	1.34	187	91	341	153	2.0	182
		30	68	30	2.0	6.6	5.8	43	2.0	0.58	0.08	1.06	1.42	104	52	265	147	13	227
		60	62	34	4.0	6.6	5.8	26.1	3.0	0.61	0.08	0.75	0.46	21	19	246	120	11	239
		90	62	34	4.0	6.1	5.7	18.9	3.0	0.52	0.08	0.47	0.56	126	57	227	95	2.0	287
		120	62	36	2.0	6.5	5.8	22.2	3.0	0.55	0.08	0.58	0.18	4.0	6.0	227	56	47	291
		150	62	38	-	6.6	5.8	21.9	4.0	0.50	0.08	2.98	0.88	1.0	8.0	208	41	74	249
		Mean	65.3	32	3.2	6.5	5.8	31.8	3.0	0.60	0.07	1.23	0.81	73.8	38.8	252.3	102.0	24.8	245.8
	C. farinosa (Mathem b)	15	66	32	2.0	6.6	6.2	63.1	5.0	0.72	0.11	2.02	1.13	99	64	832	163	15	253
		30	66	34	-	6.2	5.8	51.3	7.0	0.53	0.11	1.06	1.49	78	32	662	147	22	243
		60	62	36	2.0	6.5	5.8	56.1	9.0	0.55	0.08	0.44	0.75	25	4	227	304	31	319
		90	64	36	-	6.3	5.9	57.1	4.0	0.49	0.04	0.74	0.35	22	28	549	136	30	371
		120	60	32	8.0	6.6	6.1	74.5	7.0	0.55	0.08	1.29	2.08	28	3.0	322	150	38	319
		150	60	38	2.0	6.3	5.9	84.6	4.0	0.62	0.08	1.72	3.14	44	5.0	397	195	64	347

		Mean	63	34.7	3.5	6.4	6.0	64.5	6.0	0.58	0.08	1.21	1.49	49.3	22.7	498.2	182.5	33.3	308.7
	M. decumb	15	70	22	8.0	6.8	6.2	32.3	3.0	0.61	0.08	12.51	2.64	298	80	416	178	82	375
	(Miangeni)	30	68	22	10	7.0	6.3	29.3	1.0	0.31	0.11	13.48	2.23	300	91	303	160	83	394
		60	66	22	12	6.8	6.2	25.7	3.0	0.15	0.08	1.43	1.28	361	113	151	93	67	555
		90	62	24	14	6.6	6.1	19.4	2.0	0.19	0.08	-	-	-	-	114	100	89	587
		120	64	24	12	6.6	6.2	13.6	2.0	0.19	0.08	10.22	5.24	231	79	189	160	86	863
		150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Mean	66	22.8	11.2	6.8	6.2	24.1	2.2	0.30	0.09	9.66	2.85	297.5	90.8	234.6	138.2	81.4	554.8
	C. farinosa	15	70	22	8.0	6.6	6.1	14.6	7.0	0.65	0.08	16.99	2.06	389	95	776	201	62	441
	(Miangeni)	30	68	26	6.0	6.9	6.3	53.3	2.0	0.49	0.08	14.7	1.76	311	102	568	162	66	400
		60	66	26	8.0	7.0	6.3	32.9	4.0	0.62	0.08	10.93	0.64	225	96	284	119	84	491
		90	66	26	8.0	6.8	6.3	34.8	4.0	0.22	0.11	10.05	1.64	206	96	132	73	86	616
		120	62	28	10	7.0	6.6	36.7	12	0.28	0.11	11.3	5.31	218	103	151	116	78	435
		150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Mean	66.4	25.6	8	6.9	6.3	34.5	5.8	0.45	0.09	12.79	2.28	269.8	98.4	382.2	134.2	75.2	476.6
Kibwezi	*S. siamea*	15	60	34	6.0	6.3	6.0	44.2	8.0	0.46	0.08	4.46	2.47	23	45	454	153	38	220
	(Kibwezi)	30	68	26	6.0	6.4	6.0	32.4	9.0	0.88	0.08	3.61	1.89	57	57	587	238	32	220
		60	66	30	4.0	6.4	5.8	44.1	7.0	0.68	0.08	0.25	1.43	24	50	454	103	107	132
		90	62	32	6.0	6.4	5.6	20.2	5.0	0.52	0.11	2.91	3.96	7.0	40	359	15	99	77
		120	64	30	6.0	6.4	5.7	21.6	8.0	0.71	0.11	0.67	0.94	113	76	530	74	85	152
		150	58	35	6.0	6.2	5.6	12.7	6.0	0.53	0.11	2.57	1.07	8.0	30	284	27	44	142
		Mean	63	31.3	5.7	6.4	5.8	29.2	7.2	0.63	0.10	2.41	1.96	38.7	49.7	444.7	101.7	67.5	157.2
	B. coriacea	15	70	24	6.0	6.7	6.2	18	20	0.44	0.08	2.14	0.68	87	60	776	384	62	372
	(Kibwezi)	30	64	30	6.0	6.7	6.1	32	5.0	0.31	0.15	3.79	1.54	49	43	681	368	35	417
		60	58	36	6.0	6.5	5.8	33	7.0	0.21	0.11	1.7	1.56	18	35	568	192	35	417
		90	60	34	6.0	6.3	5.6	26	1.0	0.16	0.11	0.33	0.78	16	38	378	130	18	206
		120	62	34	4.0	6.4	5.7	14	6.0	0.12	0.08	2.02	2.55	20	38	378	225	49	293
		150	62	22	16	6.5	6.0	24	7.0	0.16	0.08	3.15	3.66	118	60	530	109	47	243
		Mean	62.7	28.3	7.3	6.5	5.9	24.5	7.7	0.23	0.10	2.19	1.80	51.3	45.7	551.8	234.7	41.0	346.0
	C. farinosa	15	78	14	8.0	6.6	6.0	89.8	4.0	0.84	0.11	4.56	1.13	221	63	568	257	81	262
	(Kibwezi)	30	74	14	12	6.7	6.0	58.6	3.0	0.68	0.26	-	-	-	-	662	410	47	514
		60	70	24	6.0	6.9	6.1	40.4	3.0	0.55	0.04	5.37	1.58	110	908	511	285	71	399
		90	68	24	8.0	6.5	5.8	72	8.0	0.62	0.04	5.42	1.89	136	433	454	486	90	436
		120	72	16	12	6.8	6.0	180.1	3.0	0.49	0.08	3.21	2.52	97	48	416	912	61	428
		150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Mean	72.4	18.4	9.2	6.7	6.0	88.2	6.2	0.64	0.11	4.64	1.78	141.0	363.0	522.2	470.0	70.0	407.8

Appendix 4: The tree and shrub species in three sites of Makueni district

Study site	Species local name	Botanical name	Family name	Species type
Nthangu forest	Itithyo	*Combretum collinum*	Combretaceae	S, T
	Kaluma	*Pithosporum viridiflorum*	Pithosporaceae	T, S
	Kiama	*Combretum molle*	Combretaceae	T
	Kithauna	*Lannea schimperi*	Anacardiaceae	T
	Kithongoi	*Dodonea angustifolia*	Sapindaceae	S, T
	Kithunzi	*Maytenus heterophylla*	Celastraceae	S, T
	Kitolousuu	*Ziziphus abyssinica*	Rhamnaceae	T, S, C
	Kiba	*Pappea capensis*	Sapindacea	S, T
	Kivuti	*Erythrina abyssinica*	Papilionaceae	T
	Kiaa	*Euphorbia candelabrum*	Euphobiacea	T
	Lunguyu	Indigofera spp.	Papilionaceae	S, H
	Mutote	*Carissa edulis*	Apocynaceae	S
	Mwaanzia	*Bridelia taitensis*	Euphorbiaceae	S, T
	Mwindenguwe	*Triumfetta* flavescens	Tiliaceae	S
	Mukaati	*Faurea saligna*	Proteaceae	S, T
	Mukakaa	*Premna resinosa*	Verbenacea	S
	Mukala	*Antidesma venosum*	Euphorbiacea	T
	Mukandu	*Ocimum suave*	Labiatae	H, S
	Mukayau	Salvadora spp.	Salvadoraceae	T, S
	Mukenea	*Zanthoxylum chalybeum*	Rutaceae	S, T
	Mukengeka	*Cassia senguana*	Caesalpiniaceae	T
	Muketa	*Myrsine africana*	Myrsinaceae	S, T
	Mukiliuli	*Harrisonia abyssinica*	Simaraubaceae	S, T
	Mukinyai	*Euclea divinorum*	Ebenaceae	T
	Mukokola	*Combretum exalatum*	Combretaceae	T
	Mukomoa	*Vangueria infausta*	Rubiaceae	S, T
	Mukongoo	*Diospyrus mespiliformis*	Ebenaceae	T
	Mukukuma	*Uvaria scheffleri*	Annonaceae	T, L
	Mukuluu	*Securinega virosa*	Euphorbiaceae	S
	Mukulwa	*Acalypha fruticosa*	Euphorbiacea	S
	Mukubu	*Craibia brownii*	Papilionoidiae	T
	Mulawa isamba	Grewia spp.	Tiliaceae	T
	Mulawa muka	*Grewia bicolor*	Tiliaceae	S, T
	Mulului	*Balanites aegyptiaca*	Simaraubaceae	
	Mungendia nthenge	*Kleinia squarrosa*	Compositae	S
	Mongolli	*Acacia senegal*	Mimosaceae	S, T
	Mung'uthe	*Lonchocarpus eriocalyx*	Papilionaceae	S, T
	Munoa mathoka	*Dicrostachys cinerea*	Mimosaceae	T, S
	Munyua	*Acacia hockii*	Mimosaceae	S, T
	Munyunga-mai	*Cassia didymobotrya*	Caesalpiniaceae	S, T
	Musemei	*Acacia nilotica*	Mimosaceae	T
	Musensili	*Gnidia latifolia*	Thymelaeaceae	S

	Musomolo	*Lantana camara*	Verbenaceae	S
	Musovi	*Hoslundia opposita*	Labiatae	S
	Musuusuu	Crotalaria spp.	Papilionaceae	H, S
	Mutandi	*Ochna inermis*	Ochnaceae	T
	Mutheu	*Rhus natalensis*	Anacardiaceae	S,T
	Mutheu	*Rhus vulgaris*	Anarcardiaceae	S,T
	Muthia	*Acacia mellifera*	Mimosaceae	S, T
	Muthika	Indigofera spp	Papilionaceae	S
	Muthingii	*Ormocarpus kirkii*	Papilionaceae	T
	Muthulu	*Croton megalocarpus*	Euphorbiacea	T
	Muthumula	*Tamarindus indica*	Caesalpiniaceae	T
	Muti	*Aspilia mossambisensis*	Compositae	S
	Mutongu	*Solanum incanum*	Solanaceae	S
	Mato (Mutoo muka)	*Azanza garckeana*	Malvaceae	T
	Mutoo	*Terminalia prunoides*	Combretaceae	T
	Mutote	*Carissa edulis*	Apocynaceae	S
	Mutotoo	*Pachystigma schumannian*	Rubiaceae	S,T
	Mutula	*Ximenia americana*	Olacaceae	T,S
	Mutumbuu	*Scutia myrtina*	Rhamnaceae	S,T
	Mutungate	*Commiphora habessinica*	Burseraceae	S,T
	Mutungu	Commiphora spp.	Burseraceae	T
	Mutunguu	*Thylachium thomasii*	Capparaceae	S,T
	Mutuva	*Grewia tembensis*	Tiliaceae	S
	Muua	*Sclerocarya birrea*	Anacardiaceae	T
	Muuku	*Terminalia brownii*	Combretaceae	T
	Muuwa nzuki	*Combretum apiculatum*	Combretaceae	T
	Muvatha	*Vernonia lesiopus*	Compositae	H,S
	Muvau	*Dombeya kirkii*	Sterculiaceae	S,T
	Mpingo	*Dalbergia melanoxylon*	Papilionoideae	S,T
	Muvuu	*Grewia villosa*	Tiliaceae	S
	Muvuavoi	*Steganotaenia araliaceae*	Umbelliferae	T
	Mwaa	*Acacia tortilis*	Mimosoidiae	T
	Mwaalika	*Heeria reticulata*	Anacardiacea	T
	Mwalula	*Croton dichogamus*	Euphorbiacea	S,T
	Mwinthongoi	*Pavetha gardeniifolia*	Rubiaceae	S
	Utithi	*Combretum collinum*	Combretaceae	S,T
Kathonzweni	Ikuu	*Commiphora africana*	Burseraceae	T
	Iliva	*Commiphora rostrata*	Burseraceae	S,T
	Isivu	*Boscia coriacea*	Capparaceae	S,T
	Ithityo	*Combretum zeyheri*	Combretaceae	T
	Itula	*Commiphora baluensis*	Burseraceae	T
	Itumbukyamuu	*Faurea saligna*	Proteaceae	S,T
	Iulu	*Commiphora campestris*	Burseraceae	T
	Mupopotwe	*Maerua kirkii*	Capparidaceae	S,T
	Kiluli	*Boscia angustifolia*	Capparaceae	S,T
	Kiongwa	*Combretum paniculatum*	Combretaceae	S,L
	Kithea	*Cordia monoica*	Boraginaceae	S,T

Kithunzi	*Maytenus heterophylla*	Celastraceae	S,T
Kiva	*Pappea capensis*	Sapindaceae	T
Kyenzenze	Boscia spp.	Capparaceae	T
Kyoa isamba	*Albizia anthelmintica*	Mimosaceae	T,B
Kyoa kikaa	*Commiphora ovalifolia*	Burseraceae	S,T
Kiongwa	*Combretum paniculatum*	Combretaceae	S,L
Kyuasi	*Lannea stuhlmanii*	Anacardiaceae	S,T
Kyundua	*Albizia amara*	Mimosoideae	T
Kiusia	*Sterculia africana*	Sterculiaceae	T
Lunguyu	Indigofera spp.	Papilionaceae	S
Mutungu	*Solanum incanum*	Solanaceae	S
Mutunguu	*Thylachium thomasii*	Capparaceae	S,T
Mwaanzia	*Bridelia taitensis*	Euphorbiaceae	S,T
Mwai	*Platycelyphium voense*	Papilionaceae	T
Mwindenguwe	*Triumfetta macrophyla*	Tiliaceae	S
Mukakaa	*Premna resinosa*	Verbenaceae	S
Mukayau	*Salvadora persica*	Salvadoraceae	T,S
Mukigeka	*Cassia sengueana*	Caesalpiniaceae	T
Mukiliuli	*Harrisonia abysinica*	Simaraubaceae	S,T
Mukokola	*Combretum exalatum*	Combretaceae	T
Mukuluu	*Securinega virosa*	Euphorbiaceae	S
Mukulwa	*Acalypha fruticosa*	Euphorbiaceae	S
Mukume	*Haplocoelum foliolosum*	Sapindaceae	S,T
Mukuswi	*Acacia brevispica*	Mimosaceae	S,T
Mulawa isamba	Grewia spp.	Tiliaceae	T
Mulawa muka	*Grewia bicolor*	Tiliaceae	S,T
Mongolli	*Acacia senegal*	Mimosaceae	S,T
Munoa mathoka	*Dicrostachys Cinerea*	Mimosaceae	S,T
Munyua	*Acacia hockii*	Mimosaceae	S,T
Musemei	*Acacia nilotica*	Mimosaceae	T
Musensili	*Gnidia latifolia*	Thymealaeaceae	S
Musomolo	*Lantana camara*	Verbenaceae	S
Musovi	*Hoslundia opposita*	Labiatae	S
Mutaavesi	*Lantana camara*	Verbenaceae	S
Mutandi	*Ochna inermis*	Ochnaceae	T
Muthaalwa	*Lannea triphylla*	Anacardiaceae	S,T
Muthia	*Acacia mellifera*	Mimosoideae	S,T
Muthika	Indigofera spp.	Papilionaceae	S,H
Muthuigi	*Ormocarpus kirkii*	Papilionaceae	T
Muthito	*Cadaba farinosa*	Capparidaceae	S,T
Mutongu	*Solanum incanum*	Solanaceae	S
Mato (Mutoo muka)	*Azanza garckeana*	Malvaceae	T
Mutoo	*Terminalia prunoides*	Combretaceae	S,T
Mutotoo	*P. Schumannianum*	Rubiaceae	S
Mutungate	*Commiphora habessinica*	Burseraceae	T
Mututi	*Thunbergia holstii*	Acanthaceae	S
Mutuba	*Grewia tembensis*	Tiliaceae	S

	Muuku	*Terminalia brownii*	Combretaceae	T
	Muuwa nzuki	*Combretum apiculatum*	Combretaceae	T
	Mpingo	*Dalbergia melanoxylon*	Papilionaceae	S,T
	Muvuu	*Grewia villosa*	Tiliaceae	S
	Muvuavoi	*Steganotaenia araliacea*	Umbelliferae	T
	Muvuluvulu	*Opilia celtidifolia*	Opiliaceae	L
	Mwaa	*Acacia tortilis*	Mimosoideae	T
	Mwaitha	*Entada leptostachya*	Mimosaceae	C
	Mwalanthate	*Cassia abbreviata*	Caesalpinioideae	T
	Utithi	*Combretum collinum*	Combretaceae	S,T
	Yongwa	*Commiphora riparia*	Burseraceae	T
Kibwezi	Ikindu	*Phoenix reclinata*	Palmae	T
	Ikuu	*Commiphora africana*	Burseraceae	T
	Iliva	*Commiphora rostrata*	Burseraceae	S,T
	Isivu	*Boscia coriacea*	Capparaceae	S,T
	Itula	*Commiphora baluensis*	Burseraceae	T
	Iulu	*Commiphora campestris*	Burseraceae	T
	Mupopotwe	*Maerua kirkii*	Capparidaceae	S,T
	Kikaiki	*Acacia thomasii*	Mimosaceae	T
	Kiluli	*Boscia angustifolia*	Capparaceae	T
	Kinatha	*Maerua decumbens*	Capparaceae	S
	Kiongwa	*Combretum paniculatum*	Combretaceae	S,L
	Kisaya	*Bechermia discolor*	Rhamnaceae	T,S
	Kitanda mboo	*Capparis tomentosa*	Capparaceae	S,C
	Kithea	*Cordia sinensis*	Boraginaceae	S,T
	Kiaa	Euphorbia spp.	Euphorbiaceae	T
	Kyaakyusi	*Combretum schumannii*	Combretaceae	T
	Kyenzenze	Boscia spp.	Capparaceae	S,T
	Kyoa isamba	*Albizia anthelmintica*	Mimosaceae	T,B
	Kyoa kikaa	*Commiphora ovalifolia*	Burseraceae	S,T
	Kyuasi	*Lannea schumanii*	Anacardiaceae	S, T
	Kiusia	*Sterculia africana*	Sterculiaceae	T
	Mwaanzia	*Bridelia taitensis*	Euphorbiaceae	S,T
	Mwambo	*Adansonia digitata*	Bombaceae	T
	Mwangi	*Delonix elata*	Caesalpinioideae	T
	Mwindenguwe	*Triumfetta macrophylla*	Tiliaceae	S
	Mukakaa	*Premna resinosa*	Verbenaceae	S
	Mukami	*Neutonia hildbrandii*	Mimosaceae	T
	Mukangakanywa	*Garcinia livingstonii*	Gittiferae	S,T
	Mukaiao	*Salvadora persica*	Salvadoraceae	T,S
	Mugea	*Anisotes ukambensis*	Acanthaceae	S
	Mukokola	*Combretum exalatum*	Combretaceae	T
	Mukulwa	*Acalypha fruticosa*	Euphorbiaceae	S
	Mukuswi	*Acacia brevispica*	Mimosoideae	S,T
	Mulalambila	Hibiscus spp.	Malvaceae	S
	Mulawa isamba	Grewia spp.	Tiliaceae	T
	Mulawa muka	*Grewia bicolor*	Tiliaceae	S,T

Mulela	*Acacia xanthophloea*	Mimosoideae	T
Mongolli	*Acacia senegal*	Mimosoideae	S,T
Mukulwa	*Acalypha fruticosa*	Euphorbiaceae	S
Mung'uthe	*Lonchocarpus eriocalyx*	Papilionaceae	S,T
Munina	*Acacia elatior*	Mimosoideae	T
Munoa mathoka	*Dicrostachys cinerea*	Mimosoideae	T
Musemei	*Acacia nilotica*	Mimosoideae	T
Musilingu	*Grewia fallax*	Tiliaceae	S,T
Musomolo	*Lantana camara*	Verbenaceae	S
Musovi	*Hoslundia opposita*	Labiatae	S
Mutandi	*Ochna inermis*	Ochnaceae	T
Muthaalwa	*Lannea triphylla*	Anacardiacea	S,T
Muthia	*Acacia mellifera*	Mimosoideae	S,T
Muthika	Indigofera spp.	Papilionaceae	S,H
Muthuigi	*Ormocarpus kirkii*	Papilionaceae	T
Mutiligo	*Lawsonia inermis*	Lythraceae	S,T
Mutongu	*Solanum incanum*	Solanaceae	S
Mutoo	*Terminalia prunoides*	Combretaceae	S,T
Mutungate	*Commiphora habessinica*	Burseraceae	T
Mutungu	*Lannea alata*	Anacardiaceae	S,T
Mutunguu	*Thylachium africanum*	Capparaceae	S,T
Mututi	*Thunbergia holstii*	Acanthaceae	S
Mutuba	*Grewia tembensis*	Tiliaceae	S
Muvatha	Vernonia spp.	Compositae	S
Muvau	*Dombeya kirkii*	Sterculiaceae	S,T
Muvuu	*Grewia villosa*	Tiliaceae	S
Muvuavoi	*Steganotaenia eraliacea*	Umbelliferae	T
Muvuluvulu	*Opilia celtidifolia*	Opiliaceae	L
Mwaa	*Acacia tortilis*	Mimosoidiae	T
Mwaitha	*Entada leptostachya*	Mimosaceae	C
Mwalanthate	*Cassia abbreviata*	Caesalpinioidiae	T
Mwalula	*Croton dichocamus*	Euphorbiaceae	S,T
Yongoa	*Commiphora hildbraedii*	Burseraceae	T
Yumbu	Ficus spp.	Moraceae	T

Species type: T=tree, S=shrub, H=herb, L= liana, C=climber, B=bush

Appendix 5: Important value indices (IVIs) for tree and shrub species in three sites of Makueni district

Study site	Species	Dominance (m^2/ha)	RD (N/ha)	Adundance	RA (%)	Frequency	RF	IVI
Nthangu forest	Rhus spp.	1.40	8.4	290	17.7	100	3.0	29.1
	C. molle	2.74	16.4	74	4.5	75	2.3	23.2
	A. hockii	1.15	6.9	145	8.8	100	3.0	18.7
	D. mespilifor.	1.22	7.3	127	7.7	100	3.0	18.0
	P. viridiflor.	1.9	11.3	57	3.5	75	2.3	17.1
	T. brownii	1.03	6.18	60	3.7	100	3.0	12.9
	E. divinorum	1.02	6.1	57	3.5	100	3.0	12.6
	P. schumann.	0.39	2.3	99	6	100	3.0	11.3
	F. saligna	0.93	5.55	39	2.4	25	0.8	8.8
	G. latifolia	0.16	0.96	57	3.5	100	3.0	7.5
	C. apiculaum.	0.38	2.26	35	2.1	100	3.0	7.4
	A. nilotica	0.49	2.91	14	0.9	100	3.0	6.8
	H. reticulata	0.45	2.54	57	3.5	25	0.8	6.8
	G. tembensis	0.15	0.93	46	2.8	100	3.0	6.7
	A. garckeana	0.35	2.07	25	1.5	100	3.0	6.6
	M. africana	0.39	2.34	50	3.1	25	0.8	6.2
	D. cinerea	0.1	0.59	39	2.4	100	3.0	6.0
	D. melanoxyl.	0.08	0.49	21	1.3	100	3.0	4.8
	C. collinum	0.38	2.27	14	0.9	50	1.5	4.7
	C. zeyheri	0.11	0.65	28	1.7	75	2.3	4.7
	L. eriocalyx	0.20	1.21	11	0.7	75	2.3	4.2
	Muvuia	0.02	0.14	14	0.9	100	3.0	4
	B. taitensis	0.04	0.24	11	0.7	100	3.0	3.9
	C. sengueana	0.04	0.22	21	1.3	75	2.3	3.8
	G. bicolor	0.02	0.12	7	0.4	100	3	3.5
	Mutuma	0.11	0.63	35	2.1	25	0.8	3.5
	Z. abyssinica	0.09	0.55	7	0.4	75	2.3	3.3
	P. gardeniifol.	0.01	0.08	4	0.2	100	3.0	3.3
	Muisya	0.13	0.76	25	1.5	25	0.8	3.1
	U. scheffleri	0.02	0.13	11	0.7	75	2.3	3.1
	Crotalaria spp.	0.02	0.12	11	0.7	75	2.3	3.1
	A. tortilis	0.26	1.55	11	0.7	25	0.8	3.1
	S. persica	0.11	0.68	11	0.7	50	1.5	2.9
	C. edulis	0.01	0.07	4	0.2	75	2.3	2.6
	V. infausta	0.01	0.05	4	0.2	75	2.3	2.6
	Ukomo	0.04	0.22	11	0.7	50	1.5	2.4
	D. angustifol.	0.08	0.51	14	0.9	25	0.8	2.2
	Grewia spp.	0.17	1.03	7	0.4	25	0.8	2.2
	X. americana	0.06	0.33	7	0.4	50	1.5	2.2
	E. abyssinica	0.18	1.08	4	0.2	25	0.8	2.1
	Mus mzue	0.04	0.25	14	0.9	25	0.8	2.0
	D. kirkii	0.04	0.26	4	0.2	50	1.5	2.0
	P. capensis	0.01	0.05	4	0.2	50	1.5	1.8
	C. exalatum	0.01	0.08	4	0.2	50	1.5	1.8
	S. incanum	0.02	0.11	4	0.2	50	1.5	1.8
	V. lesiopus	0.01	0.08	4	0.2	50	1.5	1.8

	A. mellifera	0.04	0.22	11	0.7	25	0.8	1.7
	G. villosa	0.03	0.18	11	0.7	25	0.8	1.7
	S. eraliaceae	0.01	0.03	4	0.2	50	1.5	1.7
	L. schimperi	0.04	0.21	7	0.4	25	0.8	1.4
	C. megaloc.	0.07	0.42	4	0.2	25	0.8	1.4
	B. aegyptiaca	0.01	0.07	4	0.2	25	0.8	1.1
Kathonzweni	*C. collinum*	3.99	20.64	319	36.4	75	3.7	60.7
	T. brownii	1.00	5.18	19	24.7	100	4.9	34.8
	A. tortilis	4.20	21.74	63	7.2	100	4.9	33.8
	C. apiculatum	2.30	11.9	89	10.1	75	3.7	25.7
	C. baluensis	1.34	6.93	24	2.7	75	3.7	16.3
	C. campestris	1.17	6.06	39	4.4	100	4.9	15.4
	A. nilotica	0.18	6.1	44	5.0	75	3.7	14.8
	L. triphylla	0.91	4.7	65	7.4	50	2.5	14.6
	S. africana	0.63	3.25	18	2.1	100	4.9	10.3
	C. africana	0.34	1.77	20	2.3	100	4.9	9.0
	H. opposita	0.15	0.76	12	1.4	100	4.9	7.1
	P. voense	0.41	2.15	31	3.5	25	1.2	6.9
	C. ovalifolia	0.35	1.83	11	1.3	75	3.7	6.8
	A. amara	0.55	2.86	12	1.4	50	2.5	6.8
	C. zeyheri	0.18	0.94	32	3.6	25	1.2	5.7
	A. brevispica	0.04	0.2	16	1.8	75	3.7	5.7
	O. inermis	0.04	0.23	15	1.7	75	3.7	5.6
	P. resinosa	0.01	0.06	3	0.3	100	4.9	5.3
	G. latifolia	0.12	0.63	8	0.9	75	3.7	5.2
	B. angustifol.	0.02	0.12	1	0.1	100	4.9	5.1
	A. mellifera	0.01	0.01	1	0.1	100	4.9	5.0
	Grewia spp.	0.01	0.07	5	0.6	75	3.7	4.4
	S. eraliaceae	0.06	0.29	4	0.5	50	2.5	3.3
	C. rostrata	0.11	0.58	11	1.3	25	1.2	3.1
	A. hockii	0.01	0.01	1	0.1	50	2.5	2.6
	T. prunoides	0.01	0.04	1	0.1	50	2.5	2.6
	C. abbreviata	0.14	0.72	3	0.3	25	1.2	2.2
	B. taitensis	0.01	0.07	4	0.5	25	1.2	1.8
	Indigofera spp.	0.01	0.04	4	0.5	25	1.2	1.7
	O. celtidifol.	0.02	0.08	1	0.1	25	1.2	1.4
	A. anthelmint.	0.01	0.04	1	0.1	25	1.2	1.3
Kibwezi	*A. digitata*	33.87	44.13	3	0.4	33	1.2	45.7
	A. tortilis	8.66	11.28	152	18.4	100	3.7	33.4
	A. mellifera	2.8	3.65	88	10.7	83	3.0	17.4
	C. africana	3.49	4.55	61	7.4	83	3.0	15.0
	C. dichocam.	0.92	1.20	64	7.7	50	1.8	10.7
	D. elata	6.87	8.94	5	0.6	17	0.6	10.1
	A. elatior	2.20	2.87	23	2.8	67	2.4	8.1
	A. nilotica	0.82	1.07	25	3	100	3.7	7.8
	S. incanum	0.41	0.53	45	5.4	50	1.8	7.7
	C. sinensis	0.37	0.48	34	4.1	83	3.0	7.6
	C. baluensis	2.52	3.28	9	1.1	83	3	7.4
	C. ovalifolia	1.09	1.41	21	2.5	83	3.0	6.9
	A. ukamben.	0.39	0.50	26	3.1	83	3.0	6.6
	B. discolor	2.31	3.01	6	0.7	67	2.4	6.1

G. bicolor	0.19	0.24	13	1.6	100	3.7	5.5
C. schuman.	0.48	0.62	31	3.8	17	0.6	5.0
Euphorb. spp.	2.68	3.49	5	0.6	17	0.6	4.7
T. prunoides	0.28	0.37	15	1.8	67	2.4	4.6
D. kirkii	0.23	0.29	21	2.5	50	1.8	4.6
C. abbrev.	0.09	0.11	11	1.3	83	3.0	4.4
A. xanthophl.	1.88	2.45	9	1.1	17	0.6	4.2
C. campestris	1.2	1.56	8	1.0	33	1.2	3.8
B. angustifol.	0.03	0.03	10	0.1	100	3.7	3.8
Boscia spp.	0.06	0.08	11	1.3	67	2.4	3.8
D. cinerea	0.06	0.08	16	1.9	50	1.8	3.8
A. thomasii	0.55	0.71	10	1.2	50	1.8	3.7
C. paniculat.	0.02	0.03	11	1.3	67	2.4	3.7
M. kirkii	0.04	0.06	3	0.4	83	3.0	3.5
L. triphylla	0.14	0.19	12	1.5	50	1.8	3.5
G. livingston.	0.21	0.27	21	2.5	17	0.6	3.4
T. africanum	0.02	0.03	7	0.8	67	2.4	3.2
G. villosa	0.01	0.01	1	0.1	83	3	3.1
S. africana	0.34	0.45	4	0.5	50	1.8	2.8
Grewia spp.	0.20	0.26	5	0.7	50	1.8	2.8
A. senegal	0.03	0.04	3	0.4	67	2.4	2.8
G. taitensis	0.01	0.01	1	0.1	67	2.4	2.5
S. erialiacea	0.08	0.11	5	0.6	50	1.8	2.5
C. habessin.	0.03	0.03	4	0.5	50	1.8	2.3
Indigofera spp.	0.01	0.01	3	0.4	50	1.8	2.2
L. camara	0.01	0.01	2	0.2	50	1.8	2.0
C. hildbraedii	0.02	0.03	2	0.2	50	1.8	2.0
C. rostrata	0.11	0.14	10	1.2	17	0.6	1.9
A. anthelmint.	0.01	0.01	1	0.1	50	1.8	1.9
O. kirkii	0.01	0.01	3	0.4	33	1.2	1.6
Muvuia	0.01	0.01	2	0.2	33	1.2	1.4
L. schumannii	0.38	0.50	1	0.1	17	0.6	1.2
S. persica	0.15	0.20	3	0.4	17	0.6	1.2
L. inermis	0.02	0.03	3	0.4	17	0.6	1.0
P. reclinata	0.17	0.22	1	0.1	17	0.6	0.9
Ficus spp.	0.15	0.20	1	0.1	17	0.6	0.9
N. hildbrand.	0.03	0.03	1	0.1	17	0.6	0.7

Appendix 6: Diameter distributions (n) of dominant tree and shrub species at Nthangu, Kathonzweni and Kibwezi sites of Makueni district

Site	Species	Diameter class (cm)															
		1.0-3.9	4.0-6.9	7.0-9.9	10.0-12.9	13.0-15.9	16.0-18.9	19.0-21.9	22.0-24.9	25.0-27.9	28.0-30.9	31.0-33.9	34.0-36.9	37.0-39.9	40.0-42.9	43.0-45.9	>46.0
Nthangu	Rhus spp.	184	85	22	-	-	-	-	-	-	-	-	-	-	-	-	-
	C. molle	22	28*	8	-	4	4	8	4	-	-	-	-	-	-	-	-
	A. hockii	78	43	19	4	4	-	-	-	-	-	-	-	-	-	-	-
	D. melispiform.	67	36	14	4	4	-	4	-	-	-	-	-	-	-	-	-
	P. viridiflorum	15	7	12	11	8	12	-	-	-	-	-	-	-	-	-	-
	T. brownii	39	11	4	--	-	8	-	-	-	-	-	-	-	-	-	-
	E. divinorum	22	14	11	4	4	-	4	-	-	-	-	-	-	-	-	-
	P. Schumann.	67	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F. saligna	14	8	8	4	-	4	4	-	-	-	-	-	-	-	-	-
	Total	508	264	98	27	24	28	20	4								
Kathonzweni	*C. collinum*	115	172	10	5	2	9	1	-	-	-	1	-	-	-	-	-
	T. brownii	3	4	1	6	2	1	1	-	-	-	-	-	-	-	-	-
	A. tortilis	4	6	17	4	14	8	6	4	-	-	-	-	-	-	-	-
	C. apiculatum	15	28	25	8	4	3	4	-	-	-	-	-	-	-	-	-
	C. baluensis	8	4	1	1	2	1	4	-	-	-	-	-	-	-	-	-
	C. campestris	1	13	12	7	4	1	-	-	-	-	-	-	-	-	-	-
	A. nilotica	3	11	14	5	5	1	4	-	-	-	-	-	-	-	-	-
	L. triphylla	4	22	28	7	1	-	-	-	-	-	-	-	-	-	-	-
	S. africana	8	-	3	2	2	1	-	-	-	-	-	-	-	-	-	-
	Total	161	265	111	45	36	25	20	4	-	-	1	-	-	-	-	-
Kibwezi	*A. digitata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
	A. tortilis	18	35	36	26	20	8	3	2	2	-	2	-	-	-	-	-
	A. mellifera	27	31	15	9	4	-	-	-	2	-	1	-	-	-	-	-
	C. africana	23	15	6	1	5	4	6	3	-	-	-	1	-	-	-	-
	C. dichogamus	21	28	13	3	-	-	-	-	-	-	-	-	-	-	-	-
	D. elata	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	3
	A. elliator	12	6	-	2	-	2	1	-	-	-	-	-	1	-	2	-
	A. nilotica	3	9	9	4	1	1	-	-	-	-	-	-	-	-	-	-
	S. incanum	23	18	2	-	-	-	-	-	-	-	-	-	-	-	-	-
	Total	129	142	83	45	30	15	10	5	4	-	3	1	1	-	2	7

Appendix 7: Height distributions (n) of dominant tree and shrub species at Nthangu, Kathonzweni and Kibwezi sites of Makueni district

Site	Species	Height class													
		0.0-1.9	2.0-3.9	4.0-5.9	6.0-7.9	8.0-9.9	10.0-11.9	12.0-13.9	14.0-15.9	16.0-17.9	18.0-19.9	20.0-21.9	22.0-23.9	24.0-25.9	26.0-27.9
Nthangu	Rhus spp.	7	181	89	-	4	-	-	11	-	-	-	-	-	-
	C. molle	-	4	50	7	8	7	-	-	-	-	-	-	-	-
	A. hockii	-	100	32	4	11	-	-	-	-	-	-	-	-	-
	D. melispiform.	7	57	39	4	21	-	-	-	-	-	-	-	-	-
	P. viridiflorum	-	14	4	25	18	-	-	-	-	-	-	-	-	-
	T. brownii	11	35	4	-	11	-	-	-	-	-	-	-	-	-
	E. divinorum	4	25	14	7	-	4	4	-	-	-	-	-	-	-
	P. Schumann.	-	46	42	-	-	11	-	-	-	-	-	-	-	-
	F. saligna	-	18	4	-	18	-	-	-	-	-	-	-	-	-
	Total	29	480	278	47	19	22	4	11	-	-	-	-	-	-
Kathonzweni	*C. collinum*	4	45	218	40	2	-	8	3	-	-	-	-	-	-
	T. brownii	-	2	4	7	8	-	-	-	-	-	-	-	-	-
	A. tortilis	-	4	13	32	4	-	-	-	-	-	-	-	-	-
	C. apiculatum	-	16	59	13	-	-	-	-	-	-	-	-	-	-
	C. baluensis	-	8	8	5	3	-	-	-	-	-	-	-	-	-
	C. campestris	-	8	27	4	-	-	-	-	-	-	-	-	-	-
	A. nilotica	-	-	39	4	-	2	-	-	-	-	-	-	-	-
	L. triphylla	-	18	40	7	-	-	-	-	-	-	-	-	-	-
	S. africana	-	8	2	8	-	-	-	-	-	-	-	-	-	-
	Total	4	109	410	120	17	2	8	3	-	-	-	-	-	-
Kibwezi	*A. digitata*	-	-	-	-	-	-	-	-	-	1	1	1	1	-
	A. tortilis	-	34	57	45	8	6	2	3	-	-	-	-	-	-
	A. mellifera	2	15	40	27	2	2	-	2	-	-	-	-	-	-
	C. africana	1	27	17	8	2	6	2	-	-	-	-	-	-	-
	C. dichogamus	-	17	39	5	-	-	-	-	-	-	-	-	-	-
	D. elata	-	2	2	-	-	-	-	1	1	-	-	-	1	-
	A. elliator	-	14	4	-	2	1	-	-	1	-	1	1	1	1
	A. nilotica	-	7	15	2	2	-	-	-	-	-	-	-	-	-
	S. incanum	1	37	7	-	-	-	-	-	-	-	-	-	-	-
	Total	4	153	181	87	16	15	4	6	2	1	2	2	3	1

Appendix 8: Accumulated analysis of variance for water potentials of *S. siamea* in three sites of Makueni district

Change	d.f	s.s	m.s	v.r	F pr.
+ SITE	2	62.09	31.05	455.23	<0.001
+ SITE.Season	3	9.76	3.25	47.68	<0.001
+ SITE.TIME	6	2.46	0.41	6.00	<0.001
+ LIGHT_INT.SITE	3	1.11	0.37	5.42	0.002
+ REL_HUM.SITE	3	8.06	2.69	39.39	<0.001
+ LEAF_TEMP.SITE	3	6.87	2.29	33.58	<0.001
+ CUV_TEMP.SITE	3	2.50	0.83	12.24	<0.001
+ SITE.Season.TIME	6	0.46	0.08	1.12	0.357
Residual	124	8.46	0.07		
Total	153	101.76	0.67		

Appendix 9: Soil moisture contents (Kg/m^3) by depth around tree species during wet and dry seasons in three sites of Makueni district

Study site	Season	Species	Soil depth (cm)	Moisture content (Kg/m^3)
Nthangu	Dry	*P. schumannianum*	30	54.5
			60	46.5
			90	36.8
			120	30.4
			150	24.0
		S. siamea	30	49.7
			60	51.3
			90	52.9
			120	60.9
			150	64.1
	Wet	*P. schumannianum*	30	75.3
			60	70.5
			90	52.9
			120	33.6
			150	25.6
		S. siamea	30	62.5
			60	64.1
			90	59.3
			120	60.9
			150	65.7
Kathonzweni	Dry	*C. farinosa*	30	38.4
			60	40.0
			90	41.6
			120	44.8
			150	48.0
		M. decumbens	30	36.8
			60	36.8
			90	38.4
			120	41.6
			150	44.8
		S. siamea	30	35.2
			60	41.6
			90	48.0
			120	54.5
			150	59.3
	Wet	*C. farinosa*	30	49.7
			60	44.8
			90	46.4
			120	48.0
			150	51.3
		M. decumbens	30	40.0

			60	40.0
			90	40.0
			120	44.8
			150	46.4
		S. siamea	30	52.9
			60	52.9
			90	57.7
			120	79.5
			150	72.1
Kibwezi	Dry	*B. coriacea*	30	56.1
			60	54.5
			90	52.9
			120	56.1
			150	59.6
		C. farinosa	30	40.0
			60	48.0
			90	44.8
			120	44.8
			150	-
		S. siamea	30	41.6
			60	46.4
			90	51.3
			120	56.1
			150	59.3
	Wet	*B. coriacea*	30	78.5
			60	70.5
			90	54.5
			120	57.7
			150	60.9
		C. farinosa	30	46.4
			60	49.7
			90	48.0
			120	44.8
			150	-
		S. siamea	30	57.7
			60	59.3
			90	56.1
			120	57.7
			150	60.9

Appendix 10: Soil water content (Kg/m^3) around sample tree and shrub species at 1-2 monthly intervals for a period of one year in three sites of Makueni district

Study site	Sub-site/Species	Soil depth (cm)	Month/Year						
			July 03	Aug 03	Sep 03	Nov 03	Jan 04	March 04	May 04
Nthangu forest	Nthangu	30	51.3	60.9	51.3	92.9	60.9	52.9	70.5
	(*P. schum.*)	60	41.6	44.8	48.0	91.3	56.1	49.7	64.1
		90	35.2	36.8	36.8	59.3	48.0	38.4	51.3
		120	28.8	32.0	30.4	30.4	36.8	30.4	35.2
		150	22.4	30.4	22.4	22.4	28.8	24.0	25.6
	Kaumoni	30	51.3	48.0	44.8	76.9	56.1	56.1	52.9
	(*S. siamea*)	60	52.9	49.7	49.7	76.9	57.7	56.1	57.7
		90	56.1	51.3	49.7	62.5	57.7	54.5	57.7
		120	67.3	60.9	56.1	52.9	68.9	57.7	62.5
		150	70.5	65.7	60.9	57.7	72.1	65.7	67.3
Kathonzweni	Muusini	30	35.2	33.6	32.0	60.9	57.7	40.0	36.8
	(*S. siamea*)	60	41.6	38.4	36.8	44.8	68.9	48.0	43.2
		90	52.9	46.4	43.2	49.7	76.9	54.5	48.0
		120	60.9	51.3	49.7	59.3	86.5	60.9	54.5
		150	67.3	56.1	52.9	64.1	91.3	68.9	60.9
	Mathem B	30	44.8	44.8	40.0	48.0	41.6	41.6	40.0
	(M. decum)	60	38.4	38.4	41.6	40.0	44.8	43.2	43.2
		90	38.4	38.4	38.4	36.8	43.2	40.0	38.4
		120	44.8	46.4	44.8	43.2	48.0	44.8	44.8
		150	44.8	44.8	44.8	44.8	48.0	46.4	46.4
	Mathem B	30	41.6	40.0	38.4	54.5	52.9	43.2	44.8
	(*C. farinosa*)	60	46.4	44.8	44.8	44.8	49.7	46.4	49.7
		90	43.2	43.2	43.2	43.2	46.4	44.8	46.4
		120	44.8	44.8	44.8	44.8	46.4	46.4	44.8
		150	48.0	48.0	46.4	46.4	48.0	48.0	48.0

	Miangeni (*M. decum*)	30	30.4	30.4	27.2	51.2	28.8	28.8	33.6
		60	33.6	35.2	32.0	32.0	33.6	32.0	43.2
		90	38.4	38.4	36.8	36.8	38.4	38.4	48.0
		120	40.0	36.8	38.4	38.4	40.0	40.0	51.3
		150	-	-	-	-	-	-	-
	Miangeni (*C. farinosa*)	30	35.2	35.2	35.2	65.7	36.8	38.4	46.4
		60	36.8	36.8	35.2	38.4	36.8	36.8	52.9
		90	41.6	41.6	40.0	40.0	41.6	40.0	62.5
		120	43.2	46.4	43.2	41.6	44.8	44.8	68.9
		150	-	-	46.4	44.8	48.0	48.0	70.5
Kibwezi	Kibwezi (*S. siamea*)	30	-	40.0	40.0	65.7	64.1	43.2	41.6
		60	-	44.8	46.4	72.1	56.1	49.7	48.0
		90	-	49.7	49.7	62.5	52.9	52.9	51.3
		120	-	54.5	54.5	59.3	57.7	57.7	56.1
		150	-	59.3	59.3	57.7	64.1	60.9	60.9
	Kibwezi (*B. coriacea*)	30	-	52.9	52.9	94.5	83.3	60.9	57.7
		60	-	54.5	52.9	84.9	67.3	57.7	57.7
		90	-	51.3	51.3	54.5	56.1	54.5	54.5
		120	-	54.5	56.1	56.1	59.3	57.7	57.7
		150	-	59.3	59.3	59.3	62.5	60.9	60.9
	Kibwezi (*C. farinosa*)	30	-	38.4	40.0	36.8	57.7	41.6	43.2
		60	-	46.4	46.4	44.8	56.1	49.7	46.4
		90	-	46.4	43.2	44.8	49.7	48.0	46.4
		120	-	43.2	43.2	43.2	44.8	44.8	46.4
		150	-	-	-	-	-	-	-