1.0 INTRODUCTION

1.1 Background

Interspersed trees in a continuous grass matrix characterize savanna biomes (Frost *et al.,* 1986). Savanna structure and dynamics is primarily determined by soil moisture, soil nutrients, fire and herbivory, which together act on the interrelationships of the tree and grass layers (Skarpe, 1992). Both layers develop competitive interactions (Knoop and Walker, 1985). However, by modifying resource availability to understorey species (Vetaas, 1992), trees can produce detrimental or beneficial effects to herbaceous plants.

Trees often have canopies large enough to alter the local environment (Olderman, 1991). The magnitude of this effect depends on canopy structure, openness and volume, as well as the tree species. This microenvironment has profound influence on the performance and composition of associated species. Growth of annual plants may be facilitated by higher soil fertility (Garcia-Moya and McKell, 1970) and moisture availability (Dawson, 1993). These factors cause complex interactions between perennial and annual species in microenvironments. Light deprivation and mechanical and chemical effects of litter (Facelli and Pickett, 1991) can also reduce understorey growth. Vegetation strata comprising of a tree canopy and a subcanopy of woody and herbaceous species act as a multi-layered blanket that modifies conditions below it. This affects radiation and precipitation (Ovington, 1965). Increased moisture levels enhance subcanopy vegetation production, but reduce radiance and competition between canopy and subcanopy species suppress production.

In arid and semi arid ecosystems, where variation in spatial and temporal moisture and nutrients are extreme, dominant tree species influence microhabitat conditions and soil properties. Consequently, complex local interactions between vegetation and soil result (Wilson and Agnew, 1992). Small-scale variations in resources influence composition and productivity of annual plants in arid and semi arid regions (Gutierrez and Whitford, 1987). This is particularly so in the understorey of shrubs and trees (West, 1991).

Soils beneath canopy trees are often of a higher nutrient status than those in open grassland (Robertson, 2005). Litterfall and decomposition are some of the important factors influencing soil nutrient status under the canopy. Other factors include aerosols captured by canopy (Virginia, 1986), reduced soil loss, reduced leaching, increased nitrogen supply through nitrogen fixation, increased soil fauna activity and birds and mammals whose excreta adds nutrients. Nyamapfene (1991) has, however, suggested that this effect is due to trees that pump up nutrients from deeper layers of the soil where shallow- rooted plants are unable to reach.

Although herbaceous species composition of savanna ecosystems in general have been studied before (for example Belsky *et al*., 1989, Georgiadis, 1989; Knoop and Walker, 1985; Vetaas, 1992; Scholes and Archer, 1997), little is known about its variation in accordance with tree canopy volume intensity of miombo woody species. This is particularly so among broad-leaved deciduous species. The extent to which *P. curatellifolia* and *B. spiciformis* isolated trees and clumps' differ in understory species composition and soil properties requires detailed investigation. It is highly likely that both tree species have lead to changes in herbaceous floristic composition, patterning, structure and abundance as well as edaphic properties in the canopy zone.

1.2 Research problem

B. spiciformis (Musasa) and *P.curatellifolia (*Muhacha) may alter the nature of herbaceous species composition and patterning. This may lead to a loss of palatable nutritious herbaceous grasses. Such loses in species composition has a possibility of affecting negatively wildlife management in Mukuvisi Woodlands and other parks dominated by the study's focal woody species. Since *B. spiciformis* and *P. curatellifolia* cover expansive areas in the tropical southern Africa savanna biome, they have significant influence on vegetation dynamics. Due to their general structure, which is characterized by spreading boughs and shapely crowns, the two species create localized microclimates that either promote or inhibit the establishment of subcanopy species. The interactive influence of the dominant tree species on sub-canopy vegetation needs to be understood. Thus, most natural resource managers in parks and rangelands located in tropical southern savanna have limited available information to base their natural resource decisions on.

Mukuvisi Woodlands employs habitat manipulation techniques aimed at maintaining artificially high population of giraffe (*Giraffa camelopardalis)* relative to the recreational park's area. The maintenance of canopy cover of all the woody species in the recreational park greatly contributes to the achievement of this aim. There is paucity of information on the influence of *B. spiciformis* and *P. curatellifolia* trees on soils and herbaceous vegetation composition and patterning. The exact floristic composition under the canopy of the study focal tree species is unknown.

1.3 Aim of the study

The overall aim of the present study is to establish the nature and causes of subcanopy vegetation patterning under isolated trees and monospecific tree clumps of *B. spiciformis* and *P. curatellifolia* , and to investigate the influence of the two species on soils.

1.3.1 Specific objectives of the study

a) to determine the nature of subcanopy vegetation patterning under *B. spiciformis* and *P. curatellifolia;*

b) to compare vegetation patterning and structure under the two tree species with that of adjacent open grassland; and

c) to establish major edaphic related determinants of structure and composition of subcanopy vegetation under *B. spiciformis* and *P.curatellifolia*

1.4 Research questions

a) Does *B. spiciformis* and *P.curatellifolia* influence sub canopy vegetation structure and composition?
b) Does *B. spiciformis* and *P. curatellifolia* influence subcanopy soil properties?

1.*5* Null hypotheses of the study

a) *B. spiciformis* and *P.curatellifolia* have no major influence on subcanopy vegetation structure and composition.

b) *B. spiciformis* and *P.curatellifolia* have no influence on subcanopy soils.

1.6 Justification

Although savanna woodlands cover large areas of the southern African continent, and contain almost one- fifth of the world's population, they are probably the least understood of the world's major terrestrial biomes (Huntley and Walker, 1982). Factors governing the balance between trees and herbaceous vegetation are consequently of primary interest. Studies by Walter (1971), McMurtrie and Wolf (1983) and Walker *et al.,* (1981) have failed to consider the relationship between tree canopy and understory herbaceous composition. Thus, the present study proposes to investigate the interactive effects of *B. spiciformis* and *P. curatellifolia* on herbaceous species composition and subcanopy soils.

Holistic ecosystem based natural resource management and minimization of the possible adverse impacts of the competitive/facilitative interaction of trees and grasses are objectives of natural resources managers. Understanding the influence of dominant trees' canopies on understorey vegetation, and establishing the species desirable in the maintenance of habitats and rangelands in semi arid environments (for example, Mukuvisi woodlands) are often a key to achieving rangeland management objectives. Thus, the study focuses on *B. spiciformis* and *P.curatellifolia* as the two species are highly dominant in most parts of southern Africa.

The understanding of herbaceous vegetation pattern, along with its edaphic related causes, is central to understand evolutionary processes such as speciation, as well as ecological processes such as succession, community development and the spread and persistence of species. Reliable research-based information improves planning and decision-making. Availability of new information with regard to woody species' influence on herbaceous layer will increase the ability of ecologists to forecast vegetation changes in wooded savannas. Analysis of the structure of the vegetation is the necessary foundation for the description and definition of grasslands. The basic reason for this choice is the fact that structural data relates to the intrinsic, and some of the most fundamental, characteristics of vegetation.

The study focuses on the understorey microhabitat as an important resource for grazers. Tree canopies tend to ameliorate microclimatic conditions (Kellman, 1979) and alter soil physical and chemical conditions (Charley and West, 1975). This inevitably has an impact on forage quality. Hence the need to understand the floristic composition of the sub canopy zones of the specified woody species. Mukuvisi Woodlands was studied for the following reasons. The Woodland is a protected recreational park. A scientific evaluation of the influence of dominant tree species (for example *B. spiciformis and P. curatellifolia*) is necessary for proper management.

1.7 Study area

1.7.1 Location

Mukuvisi Woodlands lies to the east of Harare at about latitude 17° 50' 35 S and longitude 31° 5' 42 E (Hyde and Western, 2008). The park is made up of two sections, a conservation and wilderness area to the north, and a public access zone to the south. The two sections cover a total area of 275 hectares (Figure 1).

1.7.2 Climate

Mukuvisi Woodlands experiences a tropical savanna climate, with three distinct seasons: a hot dry season from mid-August through October; a hot wet season from November through March; and a warmer dry season from April through early August. Mean annual temperature is in the range 15–20 °C. Warm to hot temperatures range between 26 °C and 35 °C from September to October. The cold dry winter season is from April to August, and has maximum temperatures of 16–20 °C, with occasional nighttime ground frost. Rainfall is highly seasonal, with a marked winter usually lasting from four to seven months, with a mean annual rainfall of 840 mm (Rees *et al.,* 2006).

1.7. 3 Relief, Geology and Soils

Mukuvisi Woodlands lie at a mean altitude of 1440 m above sea level. The Mukuvisi Woodlands are underlain by coarse–grained granite (Baldock *et al*., 1991) which gives rise to coarse-textured sandy soils. The soils are classified at the great group level in the USDA Soil Taxonomy as Ustipsamments (Rees *et al*., 2006).

1.7. 4 Fauna

Mukuvisi Woodlands have a diverse of fauna that consists of mammals and birds. The mammal fauna are zebra (*Equidae equus)*, impala (*Aepycerous melampus*), eland (*Taurotragus oryx)*, giraffe (*Giraffa camelopardalis*), common duiker (*Sylvicapra grimmia*), wildbeest (*Connochaetes taurinus*), bushbuck (*Tragelaphus scriptus*), steenbok (*Raphicerus campestris*) and bush pig (*Potamochoerus larvatus*).

Birds in Mukuvisi Woodlands are highly diverse. Species such as miombo blue-eared starling and greater blue-eared starling are common in the tea garden part of the park. Common birds are the spotted creeper and miombo rock-thrush, although the later is becoming rare. On the causeway over the Mukuvisi River, species like thick-billed weaver, golden weaver, southern red bishop and several species of reed warblers commonly occur. Miombo –double collared sunbird and variable sunbird oftenly occur on either sides of the river. Other species found in the park are woodpeckers (cardinal woodpecker, golden tailed woodpecker, bennett's woodpecker bearded woodpecker), stierling's wren-warbler, spotted creeper, yellow fronted tinkerbird, white breasted cuckooshrike, chinspot batis, summer birds like black cuckooshrike, pennant-winged nightjar, African golden oriole, klaas's cuckoo, African cuckoo and diderick cuckoo. Swallow-tailed bee-eater and copper sunbird are the some of the winter birds of Mukuvisi woodlands.

1.7. 5 Flora

The woodland has low species richness. Monospecific clumps of *B. spiciformis*, *P. curatellifolia* and *Julbernadia globiflora,* as well as isolated trees, predominate. Other common tree species include *Uapaca kirkiana*, *Brachystegia boehmii*, *Monotes glaber*, *Faurea saligna*, *Combretum molle*, *Albizia antunesiana*, *Strychnos spinosa*, *Flacourtia indica,* and *Vangueria infausta*. The woodland incorporates sections of unmodified watercourses (MWA, 1998).

Dominant grass species are *Sporobolus pyramidalis, Hyparrehenia filipendula, Hyparrehenia dissoluta and Heteropogon contortus*. Other species commonly occurring in the park are *Andropogon schirensis, Brachiaria deflexa, Cynodon dactylon, Digitaria milanjiana, Elionurus argentes, Craspedorhachis. rhodesiana, Cymbopogon validus, Eleusine indica, Eragrotis racemosa, E. viscosa, Heteropogon melarnocarpus, Imperata cylindrica, Panicum maximum, Panicum repens, Pogonathria squarrosa, Setaria homonyma, Setaria pumila, Sporobolus stapfianus, Themeda triandra* and *Trachypogon spicatus* (MWA, 1998).

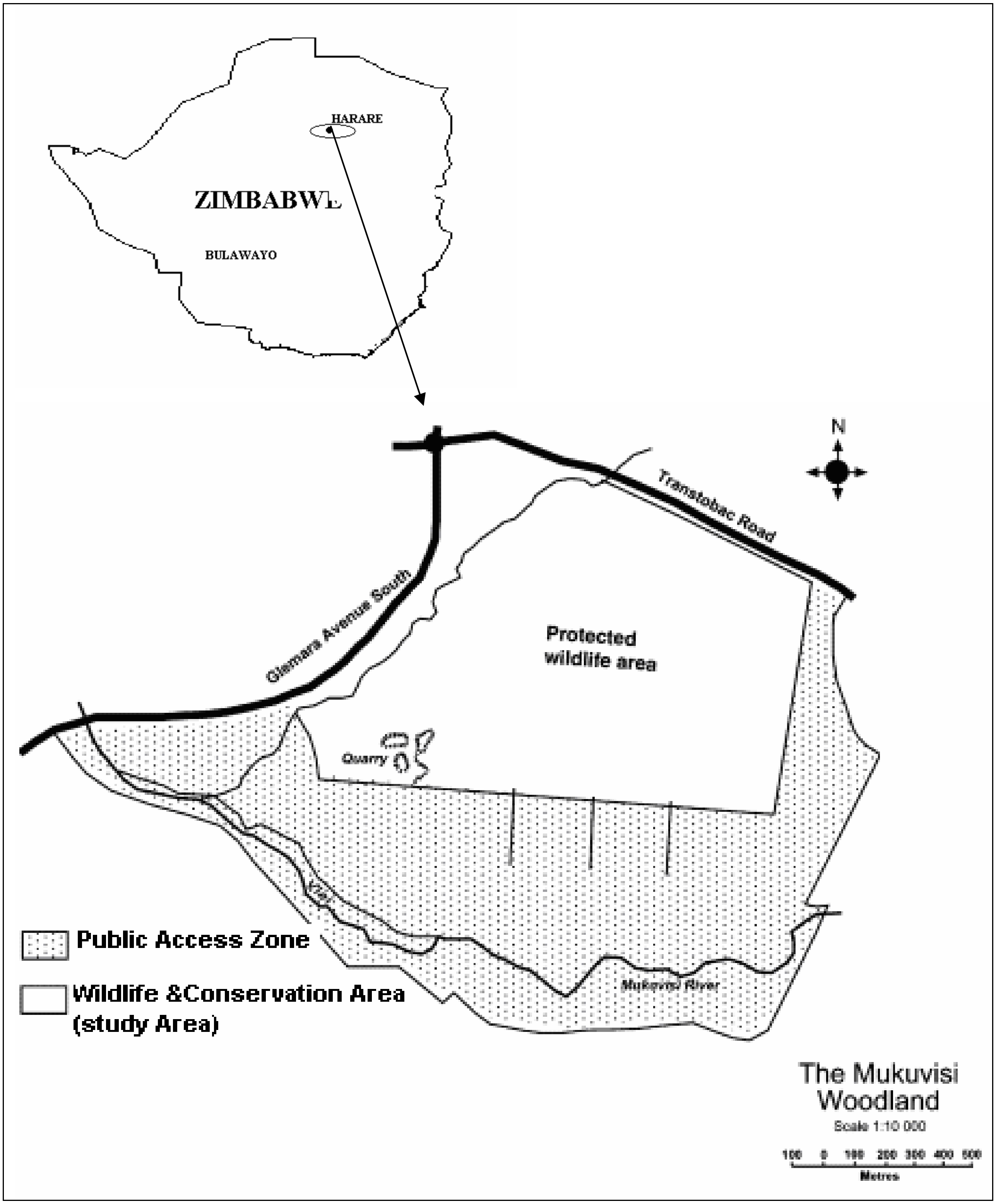

Figure 1. Location and map of Mukuvisi Woodlands

1.7. 6 History of land use

Mukuvisi Woodlands was identified as a potential reserve area in 1910. Official protection was granted in 1977 in terms of short-term 33-year lease. This was further ratified in July 1991, when an agreement was reached with the City of Harare to lease the area to the Mukuvisi Woodland Association (a private voluntary organization), on a 99-year lease. Volunteers have invested time and resources to upgrade the woodlands into a tourist and conservation facility (MWA, 1998). Although the vegetation type constituting Mukuvisi Woodlands is common in the plateau region of the country, this particular area was preserved for aesthetic reason.

Major objective of Mukuvisi Woodlands is the maintenance of the miombo woodlands and other habitats incorporated into its leased area (MWA, 1998). In trying to ensure the provision of the real wilderness, and opportunities to city dwellers to enjoy the inspirational values of nature, the MWA members maintain the ecosystem, species and habitats of its area under optimum possible conditions. Conventional conservation, thus, forms an important and integral part of the MWA's activities.

2.0 LITERATURE REVIEW

2.1 Modification of environment by woody plants

There are several studies on environmental modifications by woody plants in arid and semi-arid systems (Haworth and McPherson, 1995). Facilitative and competitive effects result from environmental modifications. Facilitation occurs where positive interactions occur. Competition of the plants for resources (Scholes and Archer, 1997) results in negative interactions. Vetaas, (1992) reported that the extent of modifications varies in relation to the distance to the plant. Effect of modification decrease as distance increase from the plant, hence a mixed tree-grass community consists of a spatial patchwork of different degrees of competition and facilitation. In addition, interactive nature varies in temporal terms, climatic fluctuations (Western and Praet, 1973) and other disturbing factors such as fire and herbivores (Dublin, Sinclair and McGlade, 1990).

2.1.1 Soil moisture content

It is widely assumed that plant' growth in the Savanna is limited by available moisture due to seasonal nature of rainfall (Scholes and Archer, 1997). Menaut *et al.* (1995) and Skarpe (1992) have agreed to the notion that soil moisture is a key determinant of savanna structure and functioning. Plant productivity is partially limited by soil moisture. Species composition and community structure is constrained by soil moisture.

Soil moisture regime in Zambezi valley downstream of Lake Kariba (Dunham, 1989) influences species composition of grasses. According to van Wigen and Kruger (1985), soil moisture and drainage influence community floristic composition and distribution at Zachariashoek mountain study site, in the Cape Province. McDonald *et al.* (1996) have studied vegetation-environmental relationships in coastal mountains of the fynbos. Findings from this study have showed that soil moisture gradient is the major principal factor. Plant species in the mountain's micro and macro habitats have show a marked response to wet and dry conditions.

Several factors influence subcanopy soil moisture. Litter in the subcanopy area alters physical properties of the surface soil (Tiedemann and Klemmedson, 1973). Resultantly, a reduction in soil temperature and evaporation occurs, which improve infiltration, subsequently increasing the subcanopy moisture content. Rainfall's intensity, duration, frequency and distribution significantly influence soil moisture availability (Haworth and McPherson, 1995). Mordelet and Menaut (1995) reported that tree shading lowers the soil temperatures. Resultantly, there is a reduction in evaporative water loss from the sub canopy area. The effects enhance sub canopy moisture storage, availability, and efficiency of using plant water (Scholes and Archer, 1997).

Through the process of hydraulic lift, deeply rooted trees and shrubs may increase soil moisture to shallow-rooted understorey species (Dawson, 1993). Barnes *et al.* (1998) attributes soil moisture levels to the physical components of the soil. Soil texture substantially influences the available soil moisture. Large surface areas of clay-sized particles combined with its adhesive properties, allow clay to hold more water than sand. Silt loam contains the greatest quantities of plant available moisture because of the favorable distribution of macro and micro pore spaces (Barnes *et al.,* 1998).

However, Amundson, Ali and Belsky (1995) argued that due to different plants' adaptational physiological make-ups, some grass species dominate the sub canopy environments compared to open grassland environment. Through fall and stem flow are the passages of rainfall to the sub canopy environment. These processes are depended on the size, canopy architecture; bark characteristics, leaf area of the tree and wind velocity (Haworth and McPherson, 1995).

Lowered subcanopy radiation by 45-60% (Belsky *et al.,* 1989; Georgiadis, 1989) increase soil moisture due to the resultant reduction in soil temperature and evapo-transpiration. Studies by Shreve (1931), Tiedemann and Klemmedson (1977) observed insignificant difference in soil moisture between open grassland and subcanopy area. The drying effect of winds is the causal factor. Besides that, the interception of rainfall by trees may counteract the effect of canopy shade on soil moisture (Vetaas, 1992).

Woody plants' canopy intercepts rainfall, redistributes the water to the atmosphere by evapo-transpiration, and to the ground by through fall and stem flow (Vetaas, 1992). Thurow, Blackburn and Taylor (1987) reported that interception losses varies from 5 – 50 % of total annual rainfall depending on the type of the tree but generally it is positively correlated to tree size (Pressland 1973). Pressland (1973, 1976) have observed that increasing tree size might decrease through fall and stem flow. During parts of the rainy season in semi arid areas, Belsky *et al.* (1989) have noted that canopy zone soil might appear to be drier than the interspace soil. Canopy interception loss by evaporation is the significant causal factor.

2.1.2 Soil nutrients

Soil nutrient status was found to improve under trees' canopy in several regions from the semi-arid (Garcia-Moya and Mickell, 1970), arid (Charley and West, 1975), neotropical (Kellman, 1979) to South Africa savanna (Radwanski and Wickens, 1967). Deciduous trees enhance pools of soil nutrients (N, P, K, C and cations) (Weltzin and Coughenour, 1990). Soils supporting legumes are nitrogen enriched as compared to non-legume covered soils (Barth and Klemmedson, 1978), hence the notion that soil fertility varies with woody species. Scholes and Archer (1997) have argued that higher carbon and nitrogen densities in sub canopy soils reflect differences in abiotic conditions under and away from trees.

Trees act as nutrient pumps, drawing nutrients laterally beyond the canopy and from deep horizons (Bate, 1981; Virginia, 1986). Accumulated nutrients reach the sub-canopy zone through litter-fall and canopy leaching. This enhances the subcanopy zone's capacity to support specific herbaceous species. Extensively spreading lateral and deep taproots of mature trees and shrubs (Vetaas, 1992) absorb nutrients found in low concentrations throughout the soil profile. The combination of nutrient reallocation, surface root turnover and shedding of leaves act as a nutrient pump (McNaughton, 1983). The effect of leaching nutrients may be insignificant in less dry savanna (Frost *et al.,* 1986). However, nutrient accumulation in the subcanopy area depletes nutrients beyond the subcanopy zone. The concurrent losses from herbaceous patches resulting from heavy grazing (Scholes and Archer, 1997) exacerbate the contrast in soil fertility between subcanopy area and open grassland.

Canopies of rough and tall trees' act as effective traps for atmospheric dust (Szott-Fernandes and Sanchez, 1991). Canopy dust is nutrient rich. During rainstorms, dripping washes off the leaves nutrient rich dust into the subcanopy area enhancing soil fertility. Over long periods, animal droppings increase soil fertility beneath tree canopies (Blackmore, 1990). Birds' nests are a common feature in mature canopy tress and droppings will contribute to the nutrient status of the soil particularly the availability of phosphorus (Vetaas, 1992). However, the activities of the soil micro and macro fauna are important. Soil micro-fauna activities incorporate litter and other organic material into the soil thus improving soil conditions physically and chemically (Frost *et al.,* 1986).

2.1.3 Impacts of shading

Belsky *et al.* (1989) have reported that savanna tree canopy reduces direct and indirect solar radiation reaching shaded sub-canopy area by 25 - 90 %, 45-60%, respectively. Due to the semi-permanent shading effect directly on canopy zone, there is significant reduction in soil and surface ambient temperatures that have an important bearing on evapo-transpiration, thus also affecting plant water status. Studies by Belsky *et al.* (1989), Geogardias (1989), Shreve (1931), Tiedemann and Klemmedson (1977) have shown significant reductions in subcanopy soil temperature in various geographical regions experiencing varying climatic conditions.

Despite the shading effect of tree canopies, savanna grasses under canopy still receive sufficient radiation for relatively high rate of photosynthesis since savannas are located in the sunniest places in the world (Mordelet and Menaut, 1995). Due to the large proportion of the energy that is advected from the surrounding open grasslands and intercanopy areas in the form of heated air, total energy budget in the subcanopy area is less attenuated than the photosynthetically active radiation (PAR). Resultantly, despite shading and soil temperature reductions, transpiration and leaf temperatures may, therefore, remain high in the subcanopy zone (Scholes and Archer, 1997).

Adjacent surrounding areas experience their own microclimatic conditions, which according to Brown (1993) influence their species composition. Surrounding areas fully receive photosynthetically active radiations (PAR) which make them different to subcanopy areas. The absorption of radiation by the plant and soil surfaces in surrounding areas cause changes in the soil and aerial microclimates (Becker *et al.*, 1988, Fetcher *et al.,* 1985). Radiation inevitably influence vegetation development through the quantity and temporal of PAR, through its spectral composition and through its influence on air and soil temperature as well as relative humidity (Brown, 1993).

2.2 Effects of woody plants on herbaceous plants

Woody plants can alter the composition and spatial distribution of grasses in savannas. Ecophysiological or specific characteristics of the tree and grass growth forms, photosynthetic pathway, photosynthetic habit, and resource requirements are significant causal factors (Scholes and Archer, 1997). Other important factors are; availability of resources influenced by the interannual variability in the amount and seasonality of precipitation and topoedaphic properties, extent of selective grazing, browsing or granivory frequency, intensity and extent of disturbances such as fire.

Considering these factors entails that effects ranges from positive - neutral to negative (Scholes and Archer, 1997).

Herbaceous layer species composition under isolated trees is most likely to alter along gradients extending from the bole to the canopy drip line and into the adjoining, inter tree zone (Scholes & Archer, 1997). C_3 grasses and herbaceous dicotyledons dominate subcanopy areas whereas in open grassland beyond the canopy C_4 grasses are dominant (Pieper, 1990). Trees influence herbaceous species individualistically as some grasses are abundant in canopy zones, whereas others flourish at the drip line (Weltzin and Coughenour, 1990). Differences in species composition under and away from savanna trees characterize low rainfall areas (Belsky *et al.*, 1993a).

Reynolds *et al.* (1999) have reported that the magnitude and direction of influence of woody species is highly dependant on their effects on the spatial distribution of soil nutrients and soil moisture availability due to soil infiltration rates. Rates of water loss (Tiedemann and Klemmedson, 1977), the intensity of competition with understorey plants for soil nutrients and water (Belsky, 1994) are causal factors too. Callaway *et al.* (2002) have concluded that canopy-understorey interactions are complex, variable, and highly context dependent.

Ovington (1965) has agued that when canopy is dense few sub canopy plants can survive, but as the canopy opens up, sufficient light penetrates to permit shrub, seedlings, saplings and herbaceous plants to grow. Different tree species, shrubs, saplings, and herbaceous plants grow and develop under different canopy tree species. According to Ovington (1965), shade suppresses the growth of other herbaceous plants not tolerant to shade and eventually they die.

2.3 Influence of woody plant species on ecosystem productivity

The effects of the woody canopy on herbaceous layer composition and dynamics are less well known. Production in treeless grasslands is largely dependent on rainfall (McNaughton, 1983), soil type (Bell, 1982), nutrient availability (Bremen and de Wit, 1983) and grazing intensity (McNaughton, 1985). Trees may compete for water with plants in the herbaceous layer (Knoop and Walker, 1985), and grass production may increase after woody species are removed (Dye and Spear, 1982). Increased irradiance at the grass layer is the causal factor of the latter result. However, nutrient concentration in subcanopy soil of trees and shrubs results from litter decomposition

(Radwanski and Wickens, 1967). This increased soil fertility provides an additional growth stimulant mechanism after woody vegetation clearing.

The woody vegetation of miombo woodlands influences the grass productivity in many ways. They increase structural complexity of simple, single stratum communities by adding taller and longer lived elements, increasing general species diversity by creating and maintaining low-light micro-habitats which are suitable for shade tolerant species in otherwise high light environments (Belsky, 1994). Woody plants also increase spatial heterogeneity of communities by maintaining a constant supply of nutrients below the sub-canopy area, and improve faunal diversity by providing forage and shade for animals requiring browse and protection from full sunlight. Therefore, woody plants contribute to biodiversity, spatial complexity and spatial heterogeneity in miombo woodlands (Belsky, 1994). In areas of low rainfall, moderate soil fertility and low tree densities, woody plant species increase understorey productivity directly under or near tree crowns (Belsky, 1994).

Kellman (1979) observed that dominant trees might facilitate understorey herbaceous growth, and in fact, influence the overall species composition. Since the post Gleason criticism of facilitation by Connell and Slatyer (1977), there was rejection of facilitation as a succession model to explain vegetation dynamics. However, a moderate interpretation of the individualistic concept agrees to the fact that each plant changes the environment to varying degrees (Vetaas, 1992), creating conducive growing localized environment.

In savanna, woody vegetation component has an overall suppression effect on the unit area production of the sub canopy vegetation and herbaceous plants (Barnes, 1992). However, Bosch and Wyk (1970) have argued that there is enhancement of vegetation production directly under the canopy of woody plants. An increase in production of herbaceous plants results from thinning or clearing of trees. Dominant tree' canopy influences forest dynamics by preventing tree regeneration at the seedling stage. Woody canopy structure greatly influences the spatial distribution of herbaceous species. Dense tree canopy cover inhibits growth of some herbaceous plants (Griffiths *et al.,* 2006).

At landscape level, the occurrence of canopy microhabitats in association with other factors such as fire and herbivory, increase community diversity in savanna as compared to open grassland (Belsky, 1994). Through a feedback mechanism caused by trees, resource distribution is uneven. This subsequently results in mosaic vegetation (Vetaas, 1992). Parts of trees and shrubs enrich the subcanopy soil at the expense of nutrient content of the open grassland (Georgiadis, 1989). This explains the improved subcanopy primary production. However, reports of the effects of trees on savanna grasses and soils are inconsistent. Under some circumstances, herbaceous layer productivity is lower under tree canopies than in nearby open grasslands (Dye and Spear, 1982: Walker and Noy-Meir, 1982), whereas in other instances, grassland productivity is higher under tree canopies (Maranga, 1984).

2.4 Disturbance of vegetation community

Due to their clearly defined vertical structure, established trees in grass dominated zones attract perching birds that disseminate seeds of woody species (Archer *et al.,* 1988). Small mammals and insects influence patch dynamics via granivory, burrowing and seedling predation (Scholes and Archer, 1997). Herbivores, both browsers and grazers, and insects (McPherson, 1993) consume and trample highly vulnerable seedlings, small trees and grasses. In some cases, the tree seedlings associated with clumps of unpalatable grass may escape herbivory during this critical stage of their life cycle.

Grazing and browsing intensity are factors that contribute to the herbaceous layer composition. Studies by Belsky *et al.* (1993b) have shown that few differences occur between tree-crown and grassland zones under heavy grazing conditions. Fuhlendorf, Smeins and Taylor (1997) have argued that browsing of trees with low, dense, evergreen canopies can enhance morning and afternoon light levels, facilitate establishment of unique grasses, and increase total herbaceous biomass beneath the tree canopy. Contrary to this, Stuart-Hill and Tainton (1989) have observed that trees stimulated to grow by browsing may suppress herbaceous plants' establishment and growth.

Fires fuelled by high grass biomass affect tree biomass in savanna-wooded grasslands (Kauffman *et al.,* 1994). In contrast, grazing reduces high grass biomass that acts as fuel load, hence the subsequent reduction in fire frequency, intensity and spreading (Savage and Swetnam, 1990). On the other hand, browsing maintains woody plants within the flame zone. Conversely fires keep woody plants browsable. Herbivory, combined with fire have, significant impacts on tree grass mixtures in savanna wooded grasslands (Scholes and Archer, 1997).

Fire may operate more directly to influence tree-grass mixtures and may slow, but not prevent, complete tree domination in savannas where grazing and browsing animals are of little consequence (Hochberg *et al.,* 1994). The fact that such sites persist as savanna rather than forest or woodland may indicate that portions of the landscape do not provide physical or nutritive conditions required for tree establishment.

3.0 MATERIALS AND METHODS

3.1 Study layout

The study focused on isolated and clumped trees of *B. spiciformis* and *P. curatellifolia*. The need to find out how two phylogenetically, morphologically and physiologically different tree species alter their near environments was the basis for the choice of tree species. *B. spiciformis* is common in Mukuvisi Woodlands, and is associated with well-drained soils. It is the dominant woodland tree, which develops heavy spreading boughs and shapely crown. *P. curatellifolia* is a large sclerophyllous species, which grows naturally in open, deciduous woodland especially *brachystegia* woodland, extending to its upper limits and then scattered in upland grassland.

In the present study, isolated trees are individually standing trees, with a minimum distance of 20m from other trees, and having herbaceous under storey. Tree clumps are groups of trees of the same species growing at a site. The number of trees in the clump, projected canopy volume, minimum height per clump and length of perpendicular diameters of the clump were the criteria for choosing tree clumps. In the present study, a stratified random sampling (Mueller-Dombois and Ellenberg, 1974) with three canopy volume classes for isolated trees of each species was used.

Species composition of the herbaceous layer, together with soil fertility, were studied along transects that extended from the trunks of the trees to the surrounding grasslands. This was intended to test whether changes in species composition were correlated with type of tree species, canopy (shading effects), or soil nutrient status.

3.2 Sampling procedures

After a reconnaissance survey of the area, a total of fifteen *B. spiciformis* and fifteen *P. curatellifolia* isolated trees were randomly selected on the basis that they were isolated from neighboring trees. Having recorded two canopy diameters at perpendicular points and total tree height, and calculated tree canopy volumes, trees of each species were grouped into three canopy volume classes: low canopy volume (< 100 m^3, mean dbh 1.15m), medium canopy volume (100 – 300m^3, mean dbh 1.60m) and high canopy volume (>300m^3, mean dbh 2.2m). Table 1 shows canopy volume classes. For the two clumps considered in the study, the mean number of trees was 8 per clump, with a minimum height of 10m, a projected canopy volume of 7900 m^3 per clump and a minimum perpendicular clump diameter of 50m.

Table 1. Replicates for the isolated standing trees in the study

Woody species	Low Canopy Volume (< 100m^3)	Medium Canopy volume (100 – 300 m^3)	High Canopy Volume (> 300 m^3)
B. spiciformis	5	5	5
P. curatellifolia	5	5	5

3.3 Herbaceous species sampling procedures

3.3.1 Herbaceous layer species composition

Three radial line transects were laid from the trunk of each isolated tree at the compass ordinations of 0, 120 and 240 degrees. Each line transect covered a distance double the radius of the crown above. Radial line transects thus extended into the open grassland. Six 1 m^2 (1 x 1 m) quadrants were systematically placed equi-distant along each line transect, the first quadrant (hereafter coded a '1', trunk sampling position) located close to the tree trunk. Subsequent quadrants placement for each transect was at the following distances from the tree trunk: 50 % (hereafter coded a '2', intermediate canopy sampling position), 95 % (hereafter coded a '3', inside canopy edge sampling position), 105% (hereafter coded a '4', outside canopy edge sampling position), 150% (hereafter coded a '5', intermediate grassland sampling position) and 200% (hereafter coded a '6', open grassland sampling position). For all 30 sampled trees, distances between their respective trunk and open grassland quadrants ranged from 8 to 30m.

Under isolated trees, 540 quadrants were included for sampling. Data analysis was based on averaged 180 sampling positions observations. The aerial view of the sampling design under individual tree canopy with quadrants laid along equi-angular transects proportional to radius of crown above transect is shown in Figure 2.

Under each of the two clumps, a distance of 10m was excluded from the periphery. Selected areas were zoned into ten relatively spatially equal zones and ten 1m^2 (1 x 1 m) randomly placed quadrants were sampled for species composition. Assessment of species composition was done at the end of the rainy season (April to May) when species composition was best represented (Walker, 1976) (see Appendix B).

3.3.2 Classification of focal trees using canopy volume

Canopy volume of isolated trees was calculated using the formula:

Tree canopy volume (m^3) = ¼ x CD x D1 x D2

Where CD is the canopy depth

D1 is greatest canopy diameter

D2 is perpendicular canopy diameter to D1

3.3.3 Inclusion criteria for herbaceous plants

All grass species rooted within the quadrant were identified and recorded. Species occurring at the edge of the quadrants were included when part of the rooting system was inside the quadrant. Tufted and rhizomatous grasses were counted as individuals.

3.4 Soil sampling procedures

3.4.1 Soil sampling

Under isolated trees, 180 soil samples were systematically collected in the upper 15 cm depth along the four cardinal points from the tree trunk into the open grassland. Sampling was done along a clockwise direction. The first sample (S1) was collected at the close to tree trunk. The second sample (S2) was collected at the canopy intermediate sampling position. The third sample (S3) was collected some 0.5m inside the canopy edge dripline and fourth sample (S4) was collected some 0.5m outside the canopy edge dripline. The fifth sample (S5) was collected at the grassland intermediate sampling position and sixth sample (S6) at the end of the line transect in the open grassland. Figure 3 shows the aerial view of the systematic soil sampling design.

Ten soil samples were systematically collected under each of the tree clumps, along a 30 m line transect at 3 m intervals. At each sampling point, three soil samples were augured 1m on both sides and at the centre. Subsamples were bulked forming composite samples, which were bagged for later determination of pH, nutrient content (phosphorus-P, potassium-K, and nitrogen-N) and soil moisture content at the Soil Science Analytical Services laboratory, University of Zimbabwe.

3.5 Vegetation variables

3.5.1 Species composition and abundance

Grass species in all sampling quadrants were identified using a field identification guide (Lightfoot, 1998), and those that could not be identified were taken to the National Herbarium for identification.

3.5.2 Diversity of species composition

The diversity of herbaceous plants per sampling position (quadrant) was calculated in terms of the species richness (S), species evenness (E) and Shannon Weiner Index (H').

3.5.3 Herbaceous species density

Density represents the numerical strength of a species in community. It gives the idea of degree of competition (Verma and Agarwal, 1998). Density was calculated using the average number of individual species counted in the six quadrants at different sampling positions (canopy trunk, canopy intermediate, inside canopy dripline, outside canopy dripline, grassland intermediate and open grassland sampling positions) replicated three times for each tree. Formula for density that was used is shown below:

$$\text{Density (plants/ha)} = \text{Number of plants} \times \frac{10{,}000\ \text{m}^2}{\text{Quadrant area (m}^2\text{)}}$$

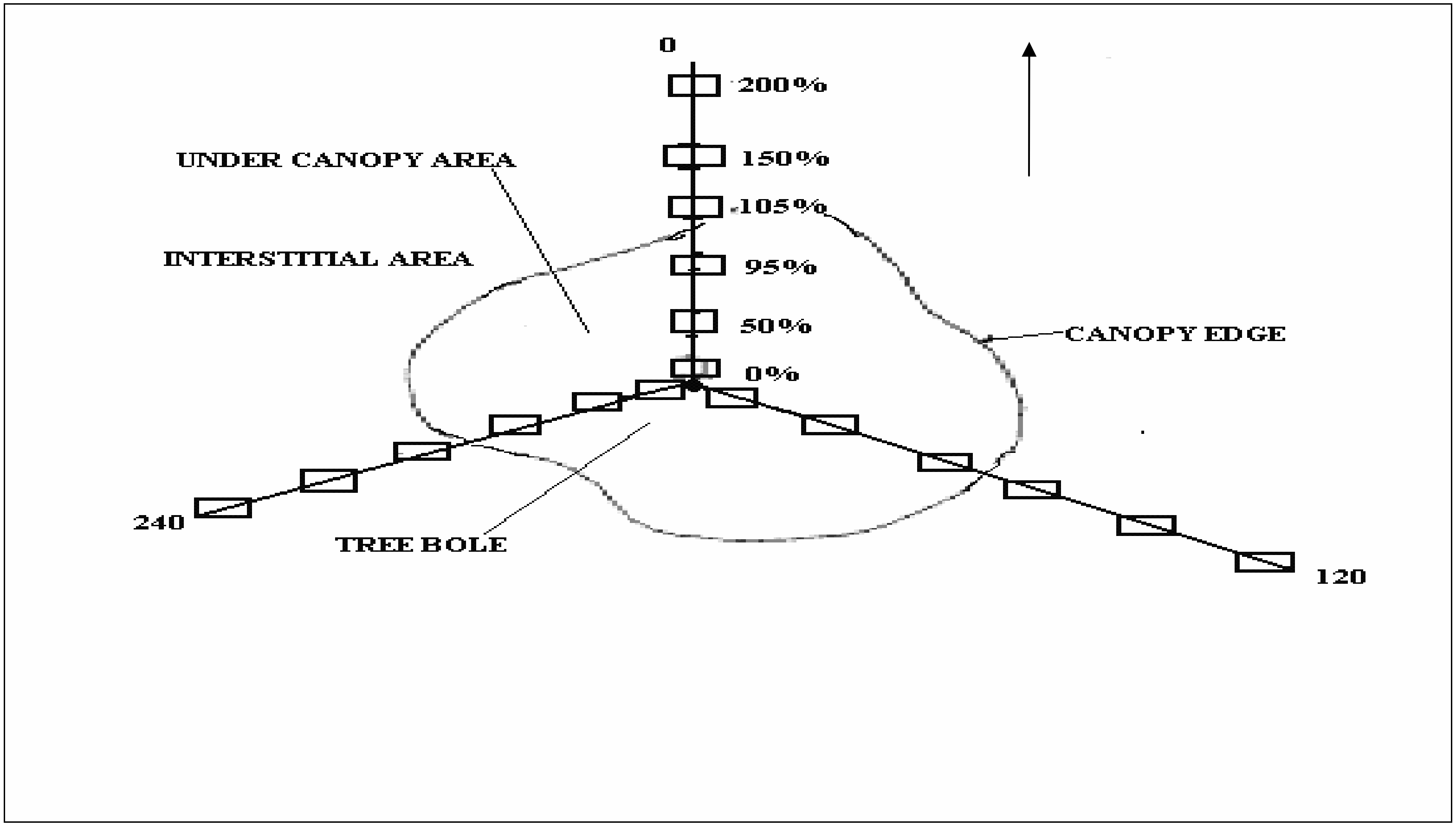

Figure 2. Aerial view of species composition sampling quadrants in canopy zones of isolated trees and adjacent open grassland

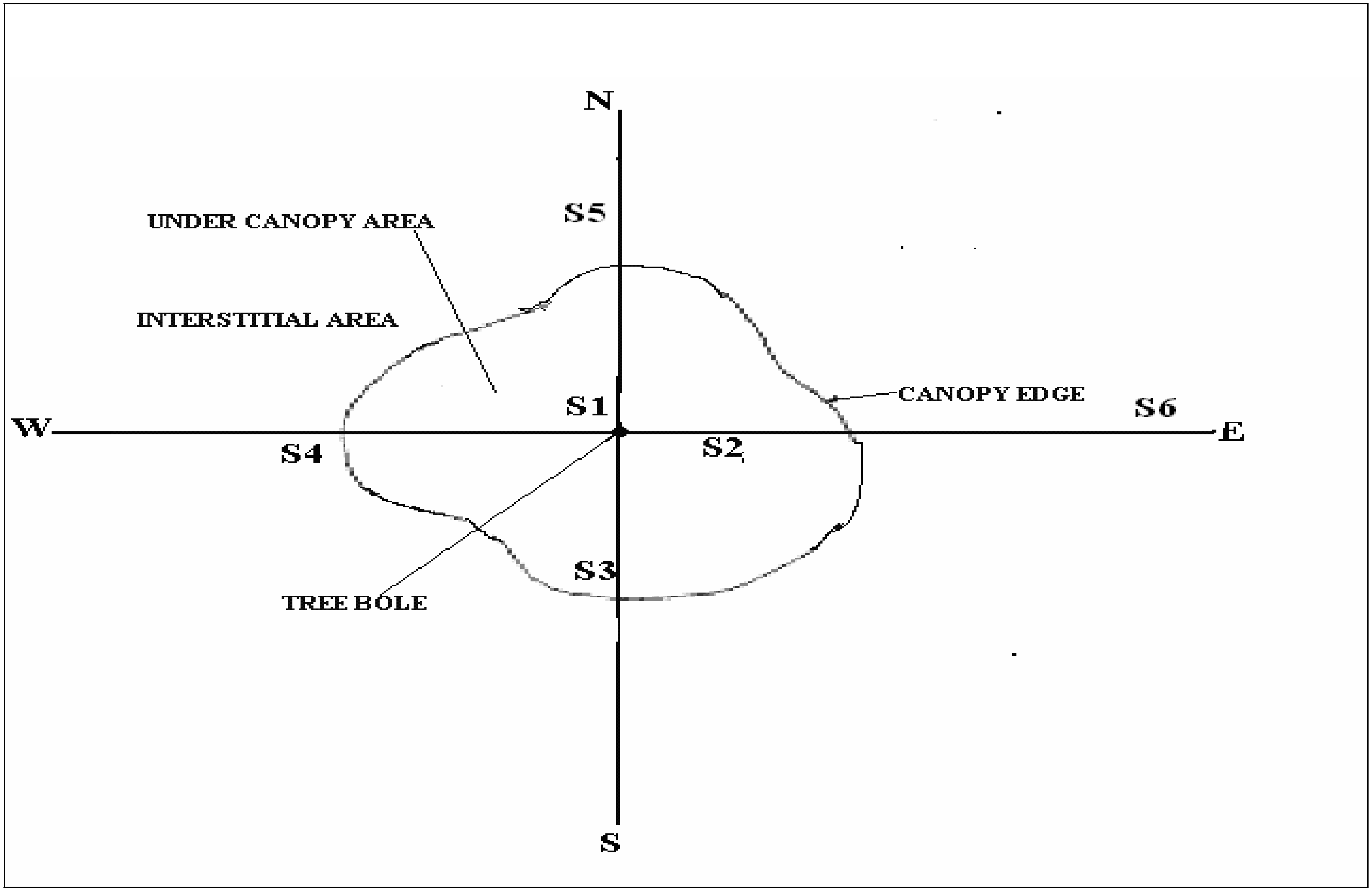

Figure 3. Aerial view of soil sampling locations within and around isolated tree canopy zone

3.7 Data analysis

Variables included for analyses were species composition and abundance, Shannon Weiner Diversity (H'), species richness (S), species evenness (E) and site density of grasses (ha). Soil pH ($CaCl_2$), moisture (*%*), nitrogen-N (ppm), phosphorus-P (ppm) and potassium-K (me *%)* were also included as explanatory variables. Subtracting each value from the mean and dividing by the standard deviation standardized explanatory variables data.

Data on species diversity, species evenness, species richness, site sampling density, pH, soil moisture, potassium, nitrogen and phosphorus levels were tested for normality using the Kolmogorov-Smirnov test in MINITAB Release 13, to determine whether they satisfied ANOVA assumptions (Quinn and Keough, 2002). Descriptive statistics (means and standard errors) were determined using Minitab Release 13 for all variables. Microsoft Excel for Windows was used for the construction of graphs.

A two-way ANOVA using MINITAB Release 13, with woody species-canopy volume class and sampling positions as categorical predictors or factors and vegetation and environmental attributes as dependant variables was performed to test the factors' main and interactive effects on all variables (p-value 0.05 significance level).

Species richness (Krebs, 1999) was determined by counting the total number of different species in each quadrant. Species diversity was determined by calculating the Shannon Weiner Index (H') of diversity (Reynolds and Ludwig, 1988). The formula used was:

$$H' = -\sum pi \ln pi$$

Where *pi* is the proportional abundance of species **i**, LN is the natural logarithm

Evenness was determined using the formula (Ludwig and Reynolds, 1988):

$$E = \frac{H'}{\ln S}$$

Where S is the species richness, H' is the Shannon Weiner Index

Data was further analyzed by ordination techniques to explore patterns, structure and relationships of herbaceous vegetation in response to canopy volume of the two focal woody species. An indirect gradient analysis technique, Principal Component Analysis (PCA) using CANOCO for Windows (Version 4) was used to define both patterns and structure of herbaceous plants (McGarigal *et al.,* 2000) in different canopy volume classes using herbaceous vegetation species as variables.

Canonical Correspondence Analysis (CCA) is a technique that integrates regression and ordination techniques into a method of multivariate direct gradient analysis that is used to detect unimodal relationships between species and explanatory variables (ter Braak and Smilauer, 1998). The aim of canonical ordination is to detect the main pattern in the relations between the species and the observed explanatory variables (ter Braak, 1995).

The relationships can be shown in an ordination diagram by vectors for the explanatory variables, with lengths proportional to their importance in explaining the variation and directions showing their correlation with each axis (Mapaure and McCartney, 2001). Arrows point in the direction of maximum variability of explanatory variables (Velazquez, 1994). The statistical significance of the ordination was tested using an unrestricted Monte-Carlo permutation test (ter Braak, 1995). Both CCA and Monte Carlo test were carried out using the statistical package CANOCO for Windows (Version 4).

4.0 RESULTS

4.1 Herbaceous species composition and abundance

A total of 3986 herbaceous plants were assessed in the 540 sampling quadrants, and some 26 herbaceous species recorded under the isolated trees and in the adjacent grasslands. A total of 235 herbaceous plants were assessed in the 20 sampling quadrants, and some seven (7) herbaceous species recorded under both clumps of trees (Table 2).

Table 2. Herbaceous vegetation sampled in the present study

	Number of sampling units	Number of plants	Number of species
Isolated trees and adjacent grassland	540	3986	26
Clumped trees	20	235	7

Isolated *B. spiciformis* trees falling in the medium canopy category had the highest number of herbaceous species (24). The lowest number of herbaceous species was recorded in *B. spiciformis* sparse canopy category (16). *P. curatellifolia* clumped trees had five herbaceous species, while *B. spiciformis* had six. (Table 3) **(**see Appendix B)

Table 3. Number of herbaceous species per tree species and canopy volume class

	Tree species	
Canopy Volume Class	*B. spiciformis*	*P.curatellifolia*
Sparse	16	18
Medium	24	20
Dense	20	19
Clumped trees	6	5

Herbaceous vegetation under isolated trees' of *B. spiciformis* for the three canopy volume classes was dominated by *C. dactylon*, *P. maximum* and *S. hymonima* which occurred at very low frequencies. Other important species, particularly for dense canopy volume, were *B. deflexa, B. pilosa, S. pallidfusca* and *P. squarrosa*. Under trees falling in the medium canopy volume, *S. pyramidalis* and *H. filipendula* were also found at low frequencies. Under trees falling in the sparse canopy volume, herbaceous species composition apart from the species stated above, *H. dissoluta, P. repens*, *D. milanjiana, H. contortus, E. viscosa, A. schirensis, T. spicatus, I. cylindrica, C. rhodesiana, C. validus, E. argenteus* and *T. triandra* evenly occurred at low frequencies.

Grass species in canopy zone of trees falling in the sparse canopy volume class were also recorded under trees falling in dense and medium classes's sampling positions closer to the dripline (outside and inside canopy edge sites). Other grass species found closer to the dripline inside and outside the canopy zone for *B. spiciformis* trees in descending order of abundance were *H. contortus, P. repens, I. cylindrica, C. rhodesiana, T. spicatus, Stereochlaena cameronni, Sporobolus stapfianus* and *H. melanocarpus*.

The species composition of vegetation under *B. spiciformis*' dense, medium and sparse canopy volumes differed clearly on the sites closer to the tree trunk. Minor differences, however, occurred towards the canopy edge. The species composition of the open grasslands beyond the canopy zones for all the *B. spiciformis* trees were similar. The most common species, in descending order of frequency were *S. pyramidalis, H. filipendula, H. dissoluta, H. contortus.*

Eleusine indica, *S hymonima* and *P. maximum* dominated the herbaceous flora under *P.curatellifolia's* herbaceous vegetation. Other under canopy species of low frequency in the three canopy classes were *S. pumila* and *B. pilosa.* Herbaceous flora under trees in the sparse category was highly diverse. Apart from the above mentioned species, other species recorded under P. *curatellifolia*, included *T. triandra, I cylindrica, T. spicatus, C. Rhodesiana, C. validus, E viscosa, P. repens, A. schirensis, P. squarossa, D. milanjiana* occurred under sparse canopy volume area. The group of species in the sparse canopy zone occurred in the outer site of all *P. curatellifolia* trees regardless of canopy volume class extending less than two meters into the open grassland. Additionally, *S. pyramidalis, H. contortus, H. dissoluta* and *H. filipendula* were found across the canopy dripline. The species composition under *P. curatellifolia*'s dense, medium and sparse classes differed mainly on the areas near the trunk but was nearly homogenous towards the dripline. The species composition beyond the canopy zones of *P.curatellifolia* trees was similar to that under *B. spiciformis* trees.

C. dactylon, P. maximum, and *S. hymonima* dominated species composition under *B. spiciformis* trees clump. Other species that occurred in low abundances were *B. deflexa*, S. *pumila* and *B. pilosa. P.*

curatellifolia trees clump's herbaceous vegetation was dominated by *E. indica*. Co-dominating species at low abundances were *P. maximum, S. hymonima*, *B. pilosa* and *S. pumila.*

Although *S. pumila, S. hymonima* and *P. maximum* occurred under both species, the dominance of *C. dacytlon* and absence of *E. indica* under the *B. spiciformis* clump, and the dominance of *E. indica* and absence of *C. dactylon* under *P. curatellifolia* clump distinguished the herbaceous species composition under the two clumps.

4.2 Comparisons of herbaceous vegetation attributes

4.2.1 Species diversity (H')

Amongst the *B. spiciformis* canopy classes, the medium class had the highest species diversity, followed by the sparse class, with the dense class recording the lowest species diversity. The clump of *B. spiciformis* had the lowest species diversity among the three canopy classes of the species (Table 5). The species diversity under *P. curatellifolia* showed a decreasing trend as canopy volume increases. However, tree clump of *P. curatellifolia* had a higher species diversity compared to the dense canopy volume class from the same tree species (Table 5).

Under both *P. curatellifolia* and *B. spiciformis* isolated trees, the trunk sampling positions had the lowest species diversity. The species diversity gradually increased as the distance from the tree trunk increased up to the outside canopy edge site. Species diversity of the intermediate and open grassland sites were lower compared to inside and outside canopy edge sites (Table 4).

Table 4. Mean herbaceous species diversity (H'), species evenness (E), species richness (S) and density for six sites

	Variable			
Sampling position	**H**	**E**	**S**	**Density**
1	1.214	0.9284	4.07	132222
2	1.373	0.9103	4.87	154000
3	1.617	0.8877	6.30	193333
4	1.727	0.8752	7.17	229111
5	1.572	0.8534	6.43	242555
6	1.566	0.8341	6.63	261111

4.2.1.1 Effects of canopy volume and sampling position on species diversity (H')

Sampling positions significantly influenced the species diversity (H') ($F_{5,\ 144}$=113.72, P<0.001). Similarly, canopy volume classes significantly influenced species diversity ($F_{5,\ 144}$=131.95, P<0.001). Furthermore, sampling positions and canopy volume class highly interacted significantly to affect mean species diversity ($F_{25,\ 144}$=11.08, P<0.001).

4.2.2 Species evenness (E)

The medium canopy volume class of *B. spiciformis* had the highest species evenness, while the sparse class recorded the lowest species evenness. *P. curatellifolia* medium class recorded the highest species evenness, with the dense class recording the lowest (Table 5). Tree clumps of both species recorded the higher species evenness than isolated trees in all canopy volume classes (Table 5). The distribution of herbaceous plants was more even near the trunk for the two tree species and a gradual reduction in species evenness was recorded towards the open grassland under both tree species (Table 4).

4.2.2.1 Effects of canopy volume, sampling site position on species evenness

Sampling position had significant influence ($F_{5,\ 144}$=59.20, P<0.001) on herbaceous species evenness in both tree species. Similarly, canopy volume class significantly influenced ($F_{5,\ 144}$=22.98, P<0.001) species evenness. Furthermore, canopy volume class and sampling position interacted significantly ($F_{25,\ 144}$=4.68, P<0.001) to influence the species evenness under the two tree species.

4.2.3 Species richness (S)

Species richness increased with the reduced canopy volume for the two woody species. Medium and sparse classes for *B. spiciformis* recorded the highest species richness followed by both the medium and the sparse classes for *P. curatellifolia*. *B. spiciformis*' dense recorded the lowest species richness (Table 5). Tree clumps of both species recorded the lowest species richness compared to isolated trees in all canopy volume classes (Table 5). Species richness showed the same pattern along the sampling positions from the tree base into the open grassland as that of species diversity (H') (Table 4).

4.2.3.1 Effects of canopy volume and sampling position on species richness

Like the influence on species diversity and evenness, sampling positions had significant effect on species richness ($F_{5,\ 144}$=105.22, P<0.001). Canopy volume class significantly ($F_{5,\ 144}$=89.92, P<0.001) influenced the species richness under both tree species. The two factors interacted significantly ($F_{25, 144}=9.27$, $P<0.001$) to affect the species richness of the two tree species.

4.2.4 Density per unit area

The density per unit area of herbaceous species under *B. spiciformis* decreased with increasing tree canopy volume. Dense canopy volume class recorded the lowest density per unit area. The highest was recorded under trees falling in the sparse class. A different pattern was shown under *P. curatellifolia.* The medium class had the highest density per unit area, followed by the sparse class, with the dense class recording the lowest density per unit area (Table 5). Herbaceous plants' density per unit area under *B. spiciformis* trees clump was the lowest compared to isolated trees canopy volume classes of the same tree species. The same trend was recorded for *P. curatellifolia* species (Table 5).

Among the six sampling positions, tree trunk sites for both woody species in all canopy volume classes recorded the lowest density per unit area. There was a gradual increase in the herbaceous plants density per unit area as the distance from the tree base increased (Table 4). In all three canopy volume classes under both tree species, open grassland sampling positions had higher density per unit area than canopy zone sampling positions (Figures 4 and 5).

4.2.4.1Effects of canopy volume and sampling position on herbaceous plants density per unit area

Variations in herbaceous density differed significantly at each sampling position ($F_{5, 144}=256.37$, $P<0.001$) under both tree species. Tree canopy volume class significantly influenced ($F_{5, 144}=41.65$, $P<0.001$) herbaceous plants density. Likewise, the two factors significantly affect herbaceous density (($F_{25, 144}=10.64$, $P<0.001$) under both tree species.

Table 5. Herbaceous flora and soil attributes for quadrants under *B. spiciformis* and *P. curatellifolia* tree species relative to canopy volume (Mean ± Standard Deviation, SD)

Species	***B. spiciformis***				***P.curatellifolia***			
	Canopy Volume Class				**Canopy Volume Class**			
Variable	**Dense**	**Medium**	**Sparse**	**Clumps**	**Dense**	**Medium**	**Sparse**	**Clumps**
pH($CaCl_2$)	4.612±0.154	4.877±0.042	4.797±0.039	4.450±0.054	4.770±0.066	4.777±0.067	4.670±0.049	4.4±0.068
K (me %)	0.099±0.008	0.117±0.017	0.097±0.006	0.192±0.013	0.093±0.006	0.118±0.009	0.162±0.020	0.209±0.023
P (*ppm*)	7.467±0.525	7.767±0.529	9.033±0.578	13.000±0.577	7.867±0.567	6.767±0.488	5.933±0.383	6.4±0.499
N (*ppm*)	95.832±4.753	90.467±1.852	92.367±3.144	102.6±5.700	92.333±1.780	92.899±3.532	89.533±10.271	105.4±4.715
MC (%)	0.965±0.072	0.983±0.075	0.521±0.033	1.655±0.171	1.083±0.076	0.718±0.077	0.779±0.052	1.474±0.181
Density per site	165111.200± 13667.970	208777.8± 11444.225	221333.267± 4184.758	76000±5 206.8331	191666.633± 11795.138	215444.433± 9545.866	210000± 5625.594	166000±7630. 3488
H’	1.1907±0.055	1.6737±0.051	1.6421±0.023	1.0567±0.076	1.3347±0.043	1.5918±0.046	1.6358±0.015	1.4049±0.061
E	0.8653±0.010	0.8978±0.007	0.8490±0.0051	0.9588±0.009	0.8793±0.0103	0.9086±0.009	0.8890±0.0048	0.9486±0.001
S	4±0.2689	7±0.3706	7±0.1552	3.1±0 .0233	5±0.2534	6±0.3229	6±0.1065	4.5±0.30732

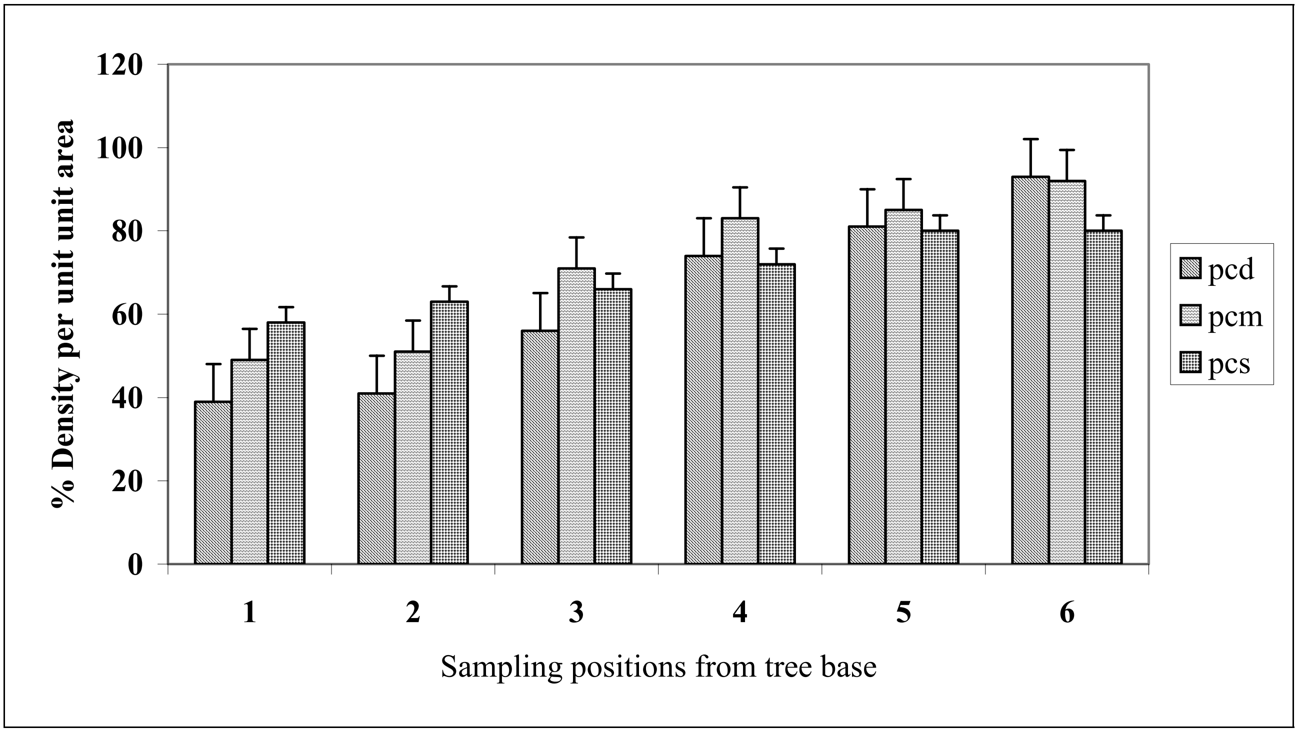

Figure 4. Sampling positions densities (%) for dense, medium and sparse canopy volumes of *P. curatellifolia*

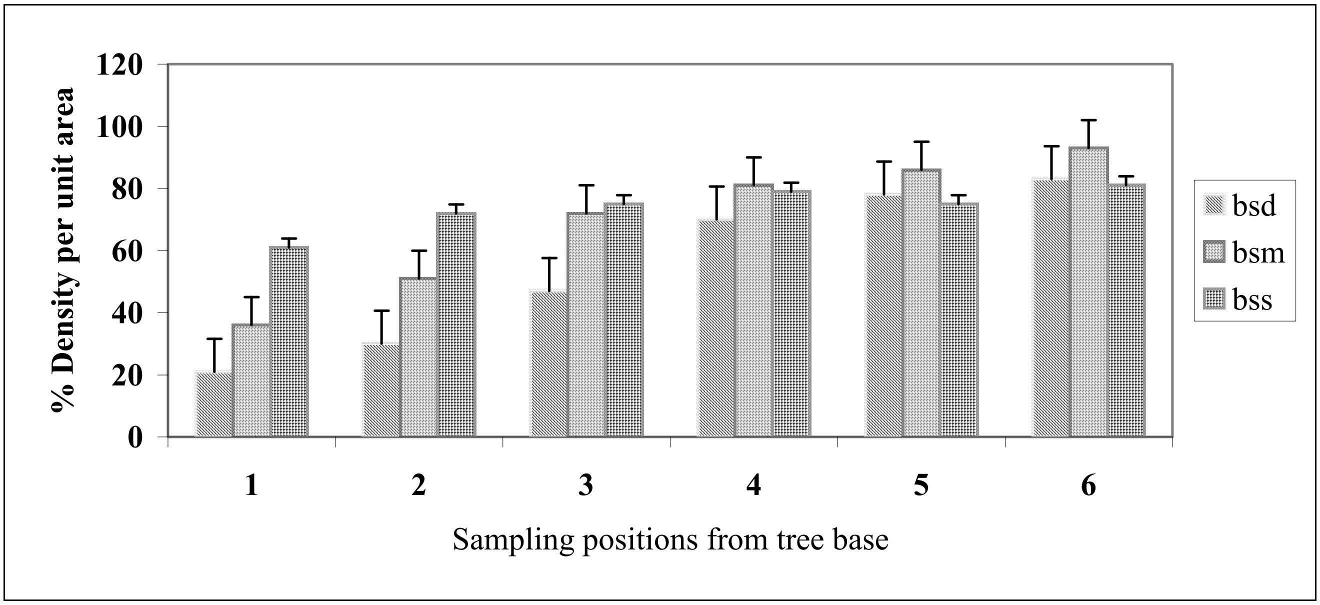

Figure 5. Sampling positions densities (%) for dense, medium and sparse canopy volumes of *B. spiciformis*

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse

bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.3 Comparisons of vegetation attributes between tree clumps

Species diversity (H') and richness (S) varied significantly between *B. spiciformis* and *P. curatellifolia* tree clumps ($F_{1,\ 18}$=12.72, P<0.05; F1$_{,\ 18}$=13.16, P<0.05, respectively). *P. curatellifolia* had higher species diversity and richness (Table 5). In sharp contrast, herbaceous species evenness between the two species' clumps was not different. Significant differences in tree clumps' herbaceous flora density per unit area were recorded between *P. curatellifolia* and *B. spiciformis* ($F_{1,\ 18}$=94.92, P<0.001). Between the two woody species' clumps, *B. spiciformis* had a lower herbaceous flora density per unit area (Table 5).

4.4 Comparisons of soil properties

4.4.1 pH (*$CaCl_2$*)

Both *P. curatellifolia* and *B. spiciformis*' dense canopy volume classes had the highest pH (4.12 and 4.02) in the trunk sampling positions while the lowest pH was recorded for the sparse class volume of *P. curatellifolia* (4.65) followed by sparse *B. spiciformis* (4.54). pH gradually decreased as distance from the canopy base increased. The pH for *B. spiciformis* trees clump was the highest compared to all canopy volume classes of the same species. The same trend was recorded for *P. curatellifolia* species (Table 5). Sampling positions in the open grassland recorded the lowest pH for both trees' different canopy volume classes (Figure 6). *B. spiciformis*' dense volume had the lowest (5.36) followed by *P. curatellifolia*'s dense (5.26) (Table 4).

4.4.1.1Effects of canopy volume and sampling position on pH

Sampling position had a highly significant effect ($F_{5,\ 144}$=16.67, P<0.001) on the pH under both tree species. Similarly, canopy volume class significantly influenced pH ($F_{5,\ 144}$=2.44, P<0.05). Furthermore, these two species interacted significantly to affect pH under both tree species ($F_{25,\ 144}$=2.19, P<0.05

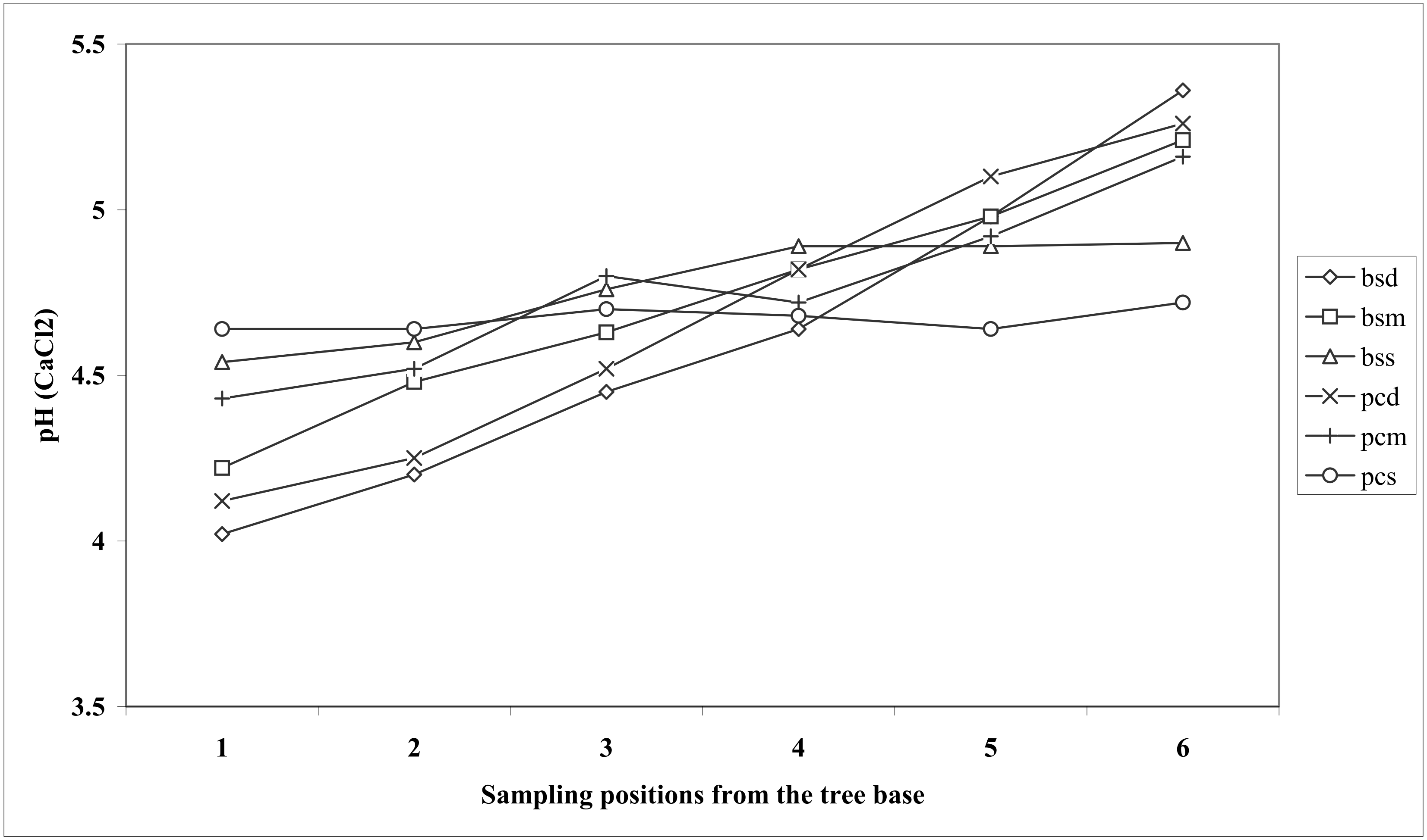

Figure 6. Changes in pH under dense, medium and sparse canopy volumes for the two tree species

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse
bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.4.2 Potassium levels

Potassium concentration was higher at the trunk sampling position for both tree species in all canopy volume classes. *P. curatellifolia*'s dense class recorded the highest (0.252 me %), while the lowest (0.122 me %) at the same sampling position was observed in the *B. spiciformis*' sparse volume (Table 5). The potassium for *B. spiciformis* tree clump was the highest compared all isolated trees canopy volume classes of the same tree species. The same trend was recorded for *P. curatellifolia* species (Table 5). The potassium concentration abruptly decreased from inside canopy zone site to the grassland sites (Figure 7).

4.4.2.1Effects of canopy volume and sampling position on potassium levels

Under both tree species, sampling position significantly affected the potassium levels ($F_{5,\ 144}$=26.31, P<0.001). Similarly, canopy volume class had a highly significant influence on the potassium levels ($F_{5,\ 144}$=8.03, P<0.001) for both tree species. However, sampling position and canopy volume class did not influence mean potassium levels as they interacted insignificantly ($F_{25,\ 144}$=1.57, P>0.05).

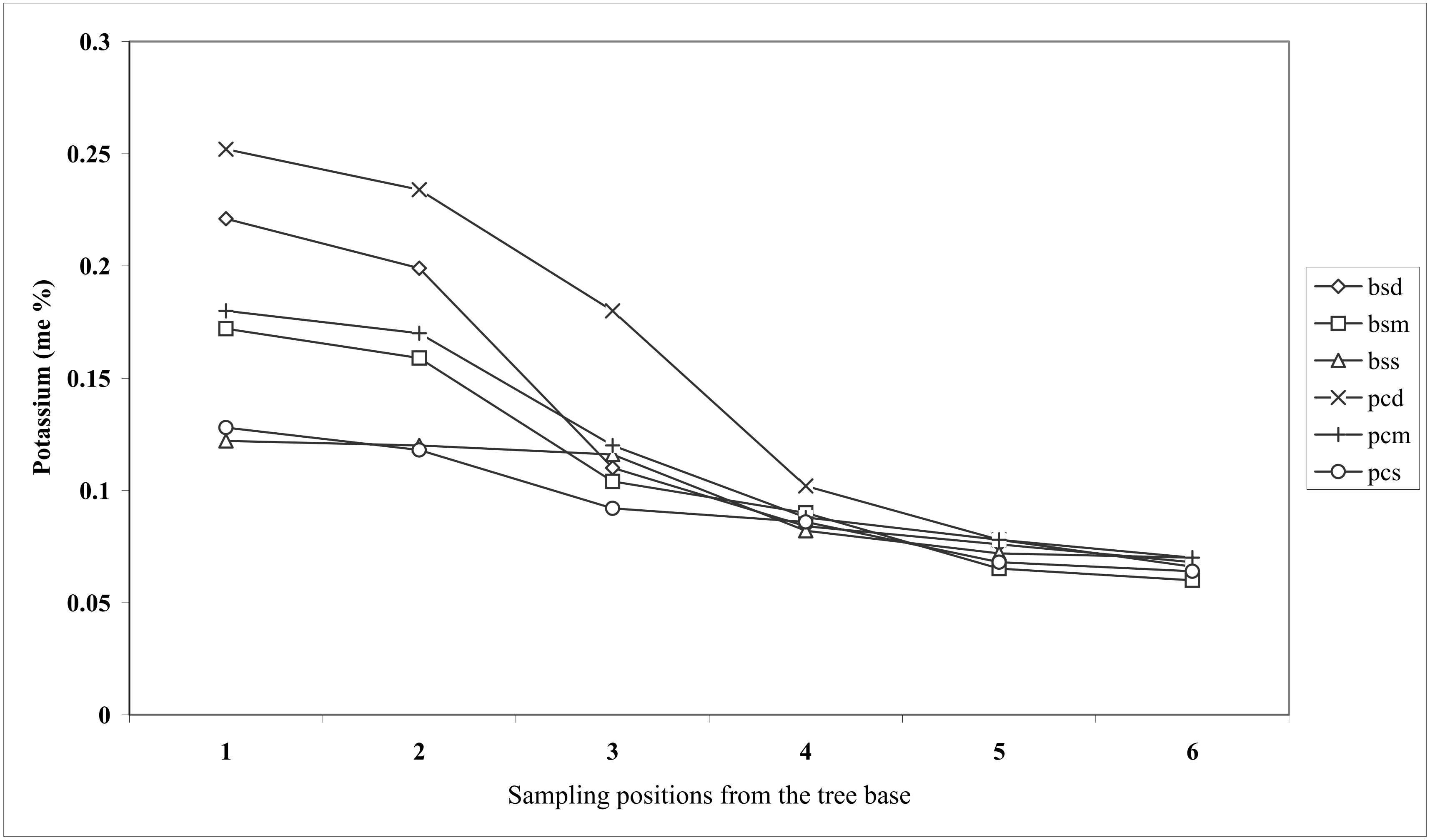

Figure 7. Changes in potassium under dense, medium and sparse canopy volumes for the two tree species

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse
bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.4.3 Phosphorus levels

A similar patterning to that of potassium was observed for phosphorus under both tree species among all the canopy volumes (Table 5). Comparing all the sampling positions, high phosphorus levels were recorded at the trunk sampling position of *B. spiciformis*' dense (12 ppm). *P. curatellifolia*'s sparse recorded the lowest (8.2 ppm) at the trunk sampling position. The phosphorus level for *B. spiciformis* tree clump was the highest compared all isolated trees canopy volume classes of the same tree species. However, *P. curatellifolia* tree clump phosphorus levels were lower as compared to those of dense and medium isolated trees (Table 5). In the open grassland, trees falling in the sparse volumes had nearly the same phosphorus concentration (4.2 ppm). Among all sampling positions, sparse classes' open grassland had the lowest phosphorus levels (Figure 8).

4.4.3.1Effects of canopy volume and sampling position on phosphorus

Phosphorus levels were significantly influenced by sampling position ($F_{5,\ 144}$=31.01, $P<0.001$) under both tree species. Canopy volume class showed significant effects on phosphorus levels ($F_{5,\ 144}$=7.31, $P<0.001$). However, insignificant differences were only found on the combined effect of canopy volume and sampling position on phosphorus levels ($F_{25,\ 144}$=0.24, $P>0.05$).

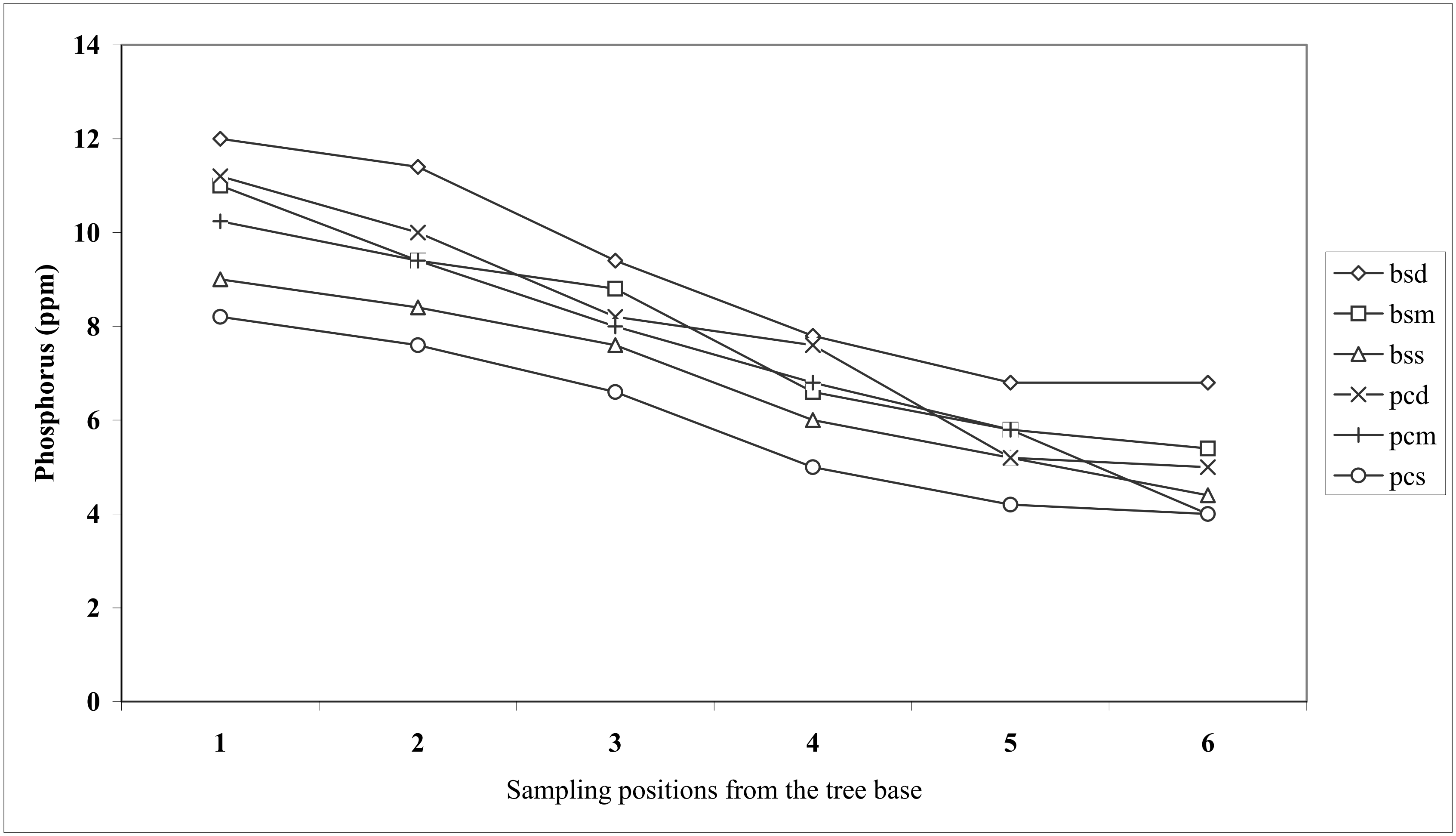

Figure 8. Changes in phosphorus under dense, medium and sparse canopy volumes of the two tree species

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse
bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.4.4 Nitrogen levels

Similar pattern of high nitrogen concentration on all trunk sampling positions under both tree species' different canopy volumes were recorded (Figure 9). The same pattern of higher nitrogen levels under tree clumps compared to dense, medium and sparse isolated trees was recorded for both tree species (Table 5). At the trunk sampling position, *B. spiciformis* and *P. curatellifolia* dense canopy volume classes recorded the highest concentration (110.45 ppm) while trees falling in both sparse volume classes recorded the lowest concentrations (92.23 ppm) (Table 5).

4.4.4.1Effects of canopy volume and sampling position on nitrogen levels

High significant influence on nitrogen levels was shown among the sampling position ($F_{5,\ 144}$=11.17, P<0.001). Like sampling positions, canopy volume class significantly influenced nitrogen levels under both tree species ($F_{5,\ 144}$=2.86, P<0.05). In sharp contrast, insignificant differences were found in the nitrogen levels ($F_{25,\ 144}$=0.87, P>0.05) when sampling position and canopy volume class interacted.

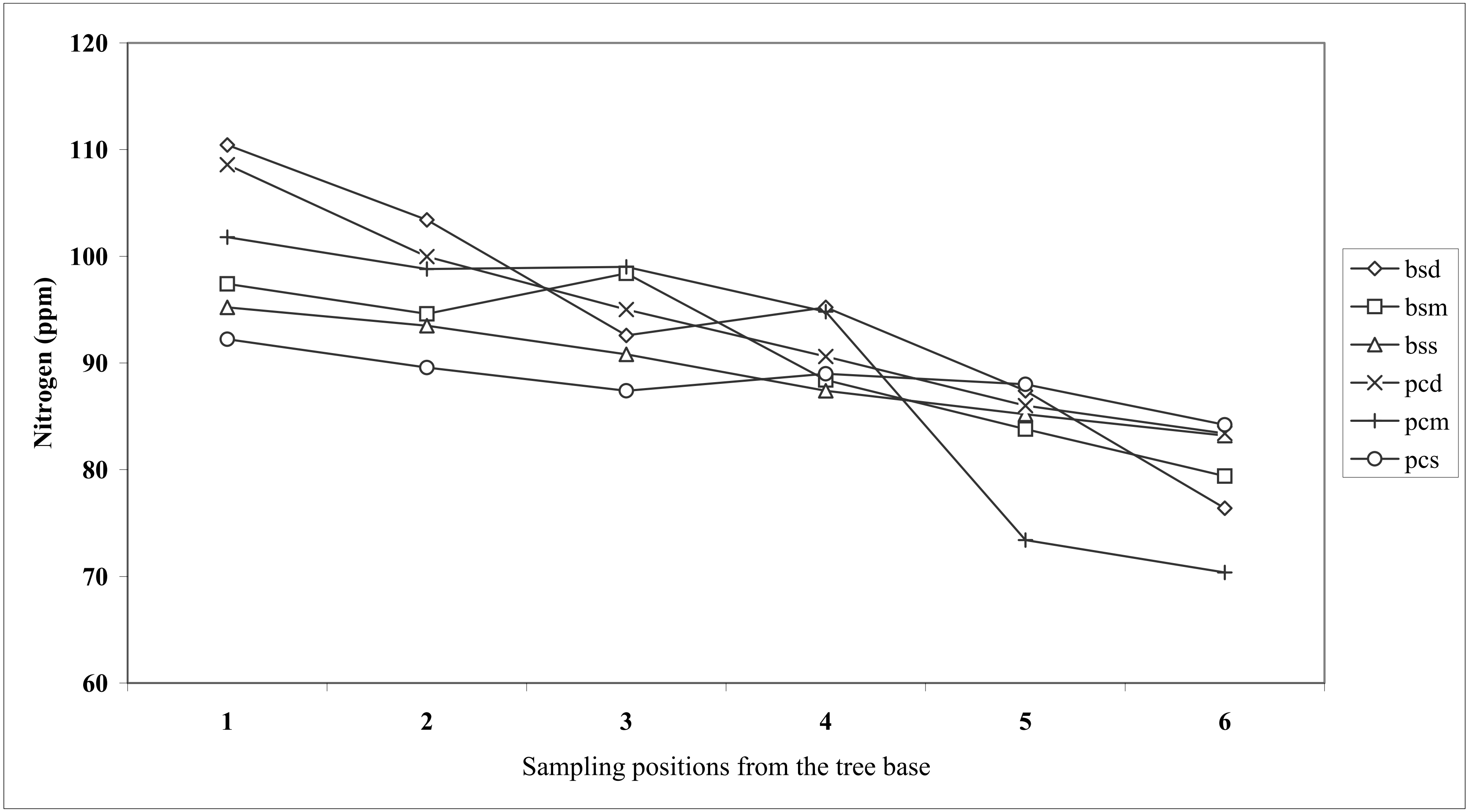

Figure 9. Changes in nitrogen under dense, medium and sparse canopy volumes of the two tree species

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse
bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.4.5 Moisture content levels

A similar pattern of moisture content levels was observed for both woody species' three canopy volume classes. Among all trunk sampling positions, B. *spiciformis* dense trees had the highest (1.39%) moisture content level while B. *spiciformis* sparse trees had the lowest. Moisture levels at intermediate canopy and inside canopy edge sampling positions gradually declined in all canopy volume classes for both woody species (Figure 10). Comparing tree clumps and isolated trees, a similar pattern to that of nitrogen levels was recorded for both tree species (Table 5).

The outside canopy edge sampling position (dripline) had elevated moisture content levels for all canopy volume classes, with the P. *curatellifolia* dense volume class recording the highest (1.6.94 %). Open grassland sampling positions under all canopy volumes recorded the lowest moisture content levels in comparison to other sampling positions. The lowest (0.372%) was in B. *spiciformis* sparse (Table 5).

4.4.5.1Effects canopy volume and sampling positions on moisture content levels

Sampling position had a highly significant effect ($F_{5,\ 144}$=14.15, $P<0.001$) on moisture content levels. Like sampling position, canopy volume class had a significant influence ($F_{5,\ 144}$=14.58, $P<0.001$) on the moisture content levels. Furthermore, sampling position and canopy volume class interacted significantly ($F_{25,\ 144}$=1.67, $P<0.05$) to influence the moisture content levels under both tree species.

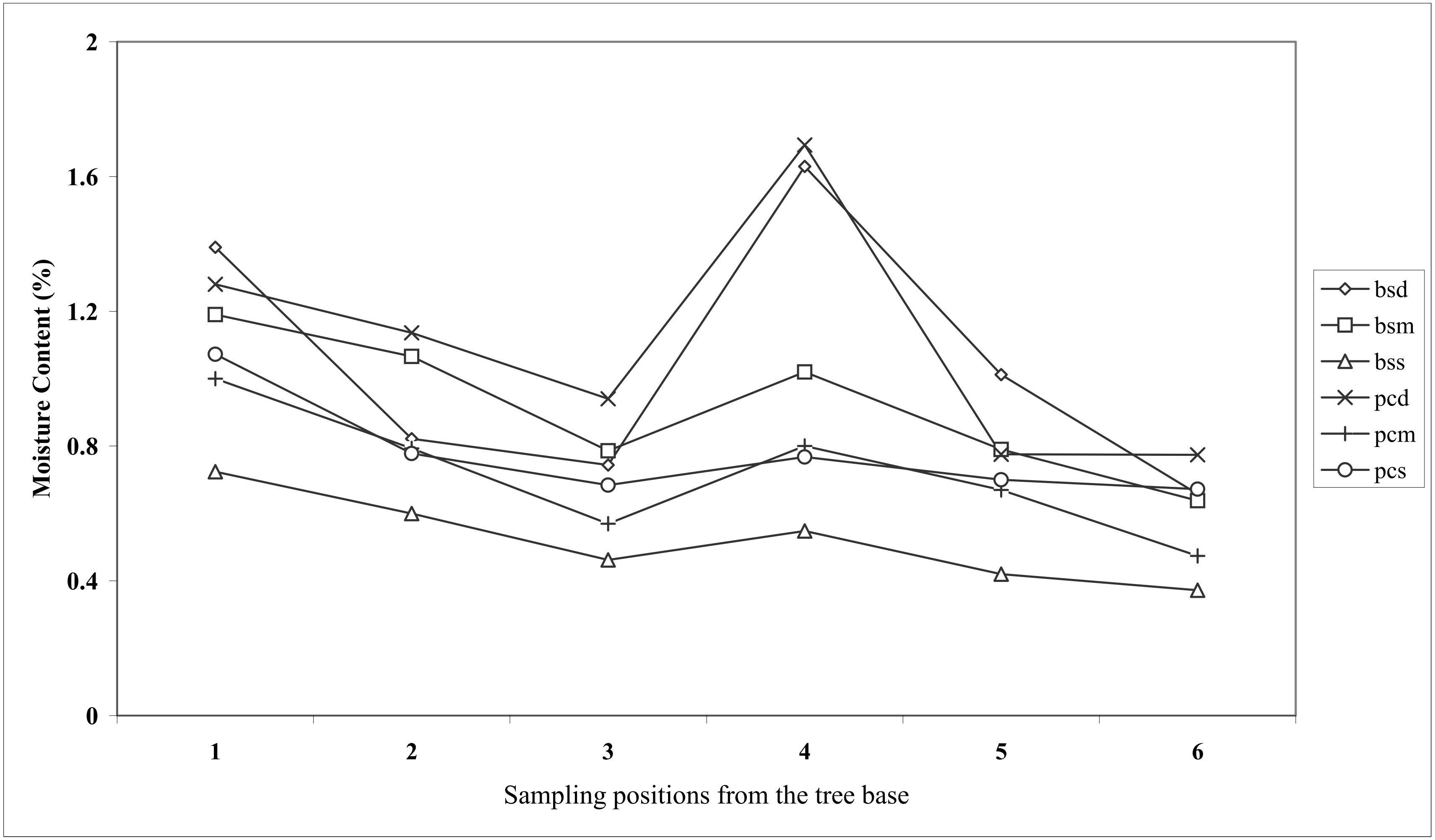

Figure 10. Changes in moisture content under dense, medium and sparse canopy volumes of the two tree species

Note: pcd-*P. curatellifolia* dense; pcm-*P. curatellifolia* medium; pcs-*P. curatellifolia* sparse
bsd-*B. spiciformis* dense; bsm-*B. spiciformis* medium; bss-*B. spiciformis* sparse

4.5 Comparisons of subcanopy soil properties between tree clumps

Potassium levels under *B. spiciformis* clump showed a marked difference as compared to that under *P. curatellifolia* clump. However, phosphorus, pH, nitrogen and moisture content's difference between the two tree clumps were insignificant (Table 5). Under both species' tree clumps, highly significant differences were found in the concentration of phosphorus levels ($F_{1,\ 18}$=74.82, $P<0.001$). However, potassium, pH, nitrogen and moisture content levels insignificantly differed under the two tree species' clumps ($F_{1,\ 18}$=0.40, $P>0.05$; $F_{1,\ 18}$=0.33, $P>0.05$; $F1_{,\ 18}$=0.31, $P>0.05$; $F_{1,\ 18}$=0.53, $P>0.05$) Table 4.6 (see Appendix C (b)).

4.6 Herbaceous vegetation and environment relationships

4.6.1 Isolated trees

CCA output based on species composition and abundance of isolated trees produced an output shown in Table 6. The first four axes of the species–environment plot accounted for 99 % of the total variance (Table 6). The main species-environmental and quadrants – environmental patterns are indicated in biplots of axis one and two (Figures 11 and 12). Axis 1 accounted for 21% of the observed variation in vegetation, whereas Axes 2, 3 and 4 account for 1.6 %, 1.1 % and 0.6 % respectively (Table 6).

The separation of the sampling quadrants and plant species along the first axis was related to pH, nitrogen, and potassium levels. Moisture content, phosphorus and potassium were important in explaining the variation observed. These environmental variables were positively correlated. Along the second axis, the separation was related to potassium levels and moisture content. pH was negatively correlated with the first axis. Soil moisture was negatively correlated with the second axis. Potassium, phosphorus and nitrogen were positively correlated to both axes (Figures 11 and 12). The smaller the angle between the arrow of the variable and the canonical axis the more correlated the variable is with the axis.

The correlation between the plant species and the explanatory variables ranged from 0.195 to 0.542 on all the four axes (Table 6). The measured explanatory variables poorly influence the quadrants and species on the ordination biplots as shown by the relatively low to moderate correlation values. Each of the variables is at least correlated with one of the first two axes on the diagrams. Moisture content is negatively correlated with pH (Figures 11 and 12).

C. dactylon, S. hymonima, *B. deflexa, P. maximum and E. argenteus* are correlated positively with pH but this group of species is negatively correlated moisture content. *S. stapfianus, H. dissoluta, T. triandra, H. contortus, S. pyramidalis, H. fillipendula, I. cylindrical* and *H. melarnocarpus* are positively correlated to nitrogen, phosphorus and potassium while *E. indica, B. pilosa, S. pumila , C. rhodesiana, A. schirensis* and *E. viscosa* are negatively correlated to the stated variables. Moisture content is positively correlated to *D. milanjiana, P. squarossa, S. cameronni, E. racemosa, C. validus, P. repens* and *T. spicatus.*

From the permutation tests, the influence of the variables along the first canonical axis was significant (F=22.730, $P<0.05$) and the overall test for all the canonical axes was significant (F=5.459, $P<0.05$). Potassium, phosphorus, moisture content and pH significantly influenced species composition (F=4.79, $P<0.05$; F=13.65, $P<0.05$; F=3.20, $P<0.05$ and F=5.76, $P<0.05$ respectively). The results of the permutation tests are shown in Appendix C (a). Nitrogen had an insignificant influence on herbaceous floristic composition.

Table 6. Canonical Correspondence Analysis (CCA) summary outputs for isolated trees based on species composition, abundance, and the measured explanatory variables

Axes	1	2	3	4
Eigen values	0.210	0.016	0.011	0.006
Species environment correlations	0.520	0.401	0.420	0.195
Cumulative percentage variance				
Of species data:	11.6	12.5	13.1	13.4
Of species-environment relation:	85.2	91.9	96.6	99.0

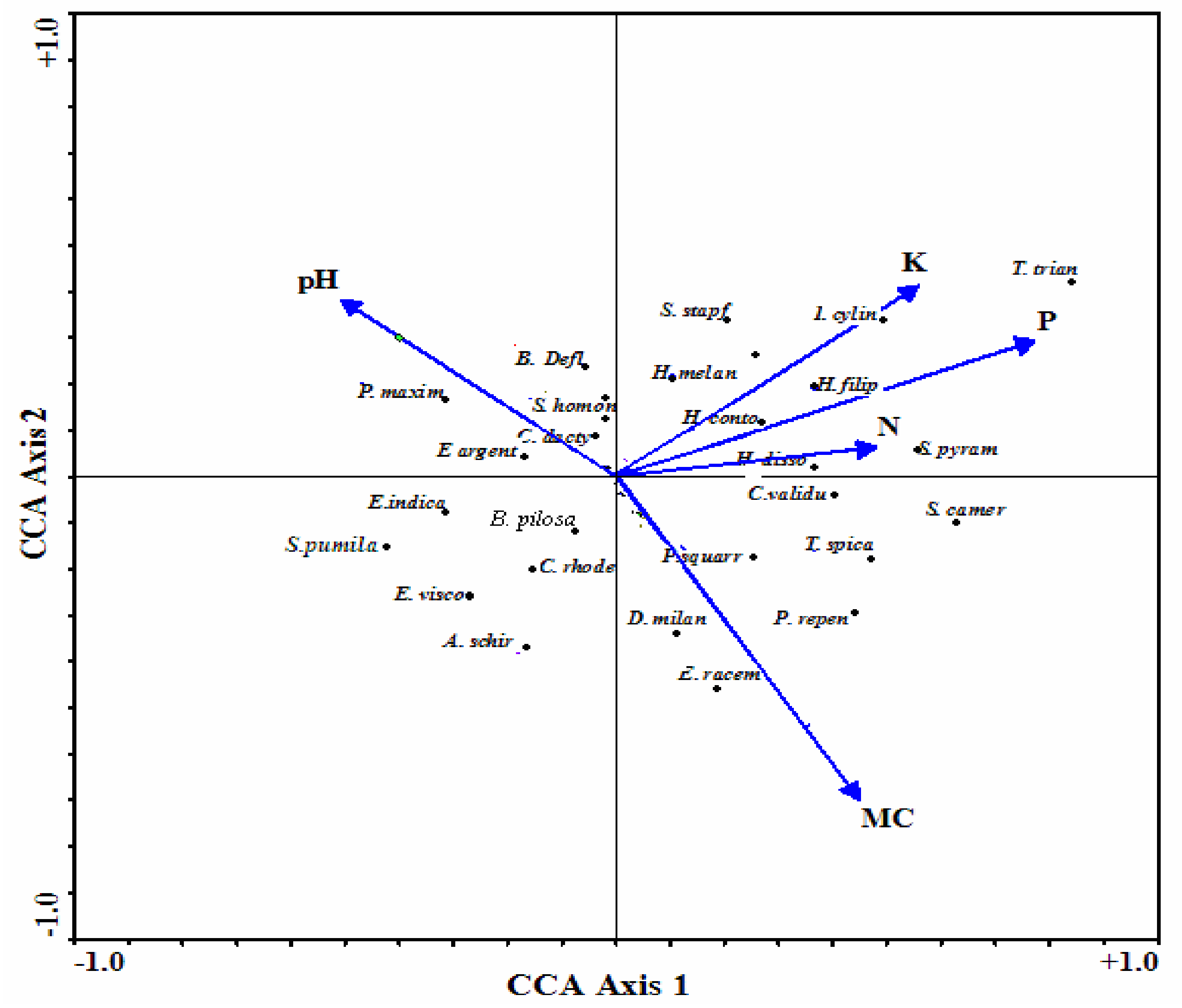

Figure 11. CCA biplot showing the relationship between species and environmental variables under isolated trees

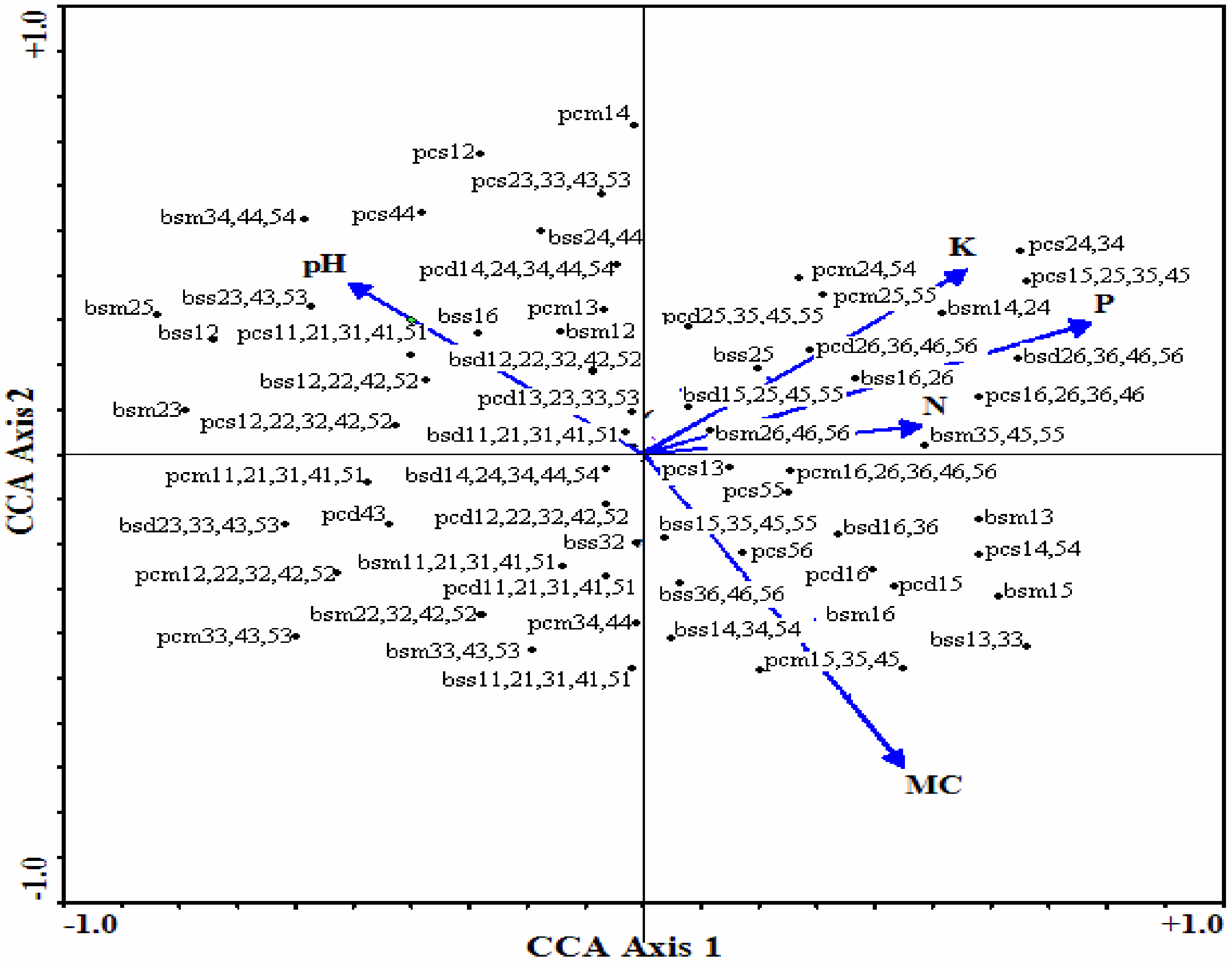

Figure 12. CCA biplot showing the relationship between quadrats and environmental variables under isolated trees

Note: bsm23 refers to; bsm -*B. spiciformis* medium

2- Number of tree replicate

3- Sampling quadrant

4.6.2 Tree clumps

CCA output based on species composition and abundance of tree clumps produced an output shown in Table 7. The first four axes of the species–environment plot accounted for 99.6 % of the total variance (Table 7). The main species and quadrants–environmental patterns are indicated in a triplot of axis one and two (Figure 13). Axis 1 accounted for 29.2% of the observed variation in vegetation, whereas Axes 2, 3 and 4 account for 8.2 %, 4.5 % and 2.4 %, respectively (Table 7).

The separation of the quadrants and species along the first axis was related to phosphorus levels and potassium levels. Phosphorus, moisture content and nitrogen important in explaining the variation observed. Along the second axis, the separation was related to pH, nitrogen levels, and moisture content. Potassium and nitrogen were negatively correlated with the first axis. Soil moisture and pH were negatively correlated with the second axis. Phosphorus is positively correlated to both axes.

Table 7. Canonical Correspondence Analysis (CCA) summary output for tree clumps based on species composition, abundance, and the measured explanatory

Axes	1	2	3	4
Eigen values	0.292	0.082	0.045	0.024
Species environment correlations	0.804	0.687	0.701	0.542
Cumulative percentage variance				
Of species data:	29.7	38.0	42.6	45.1
Of species-environment relation:	65.7	84.1	94.2	99.6

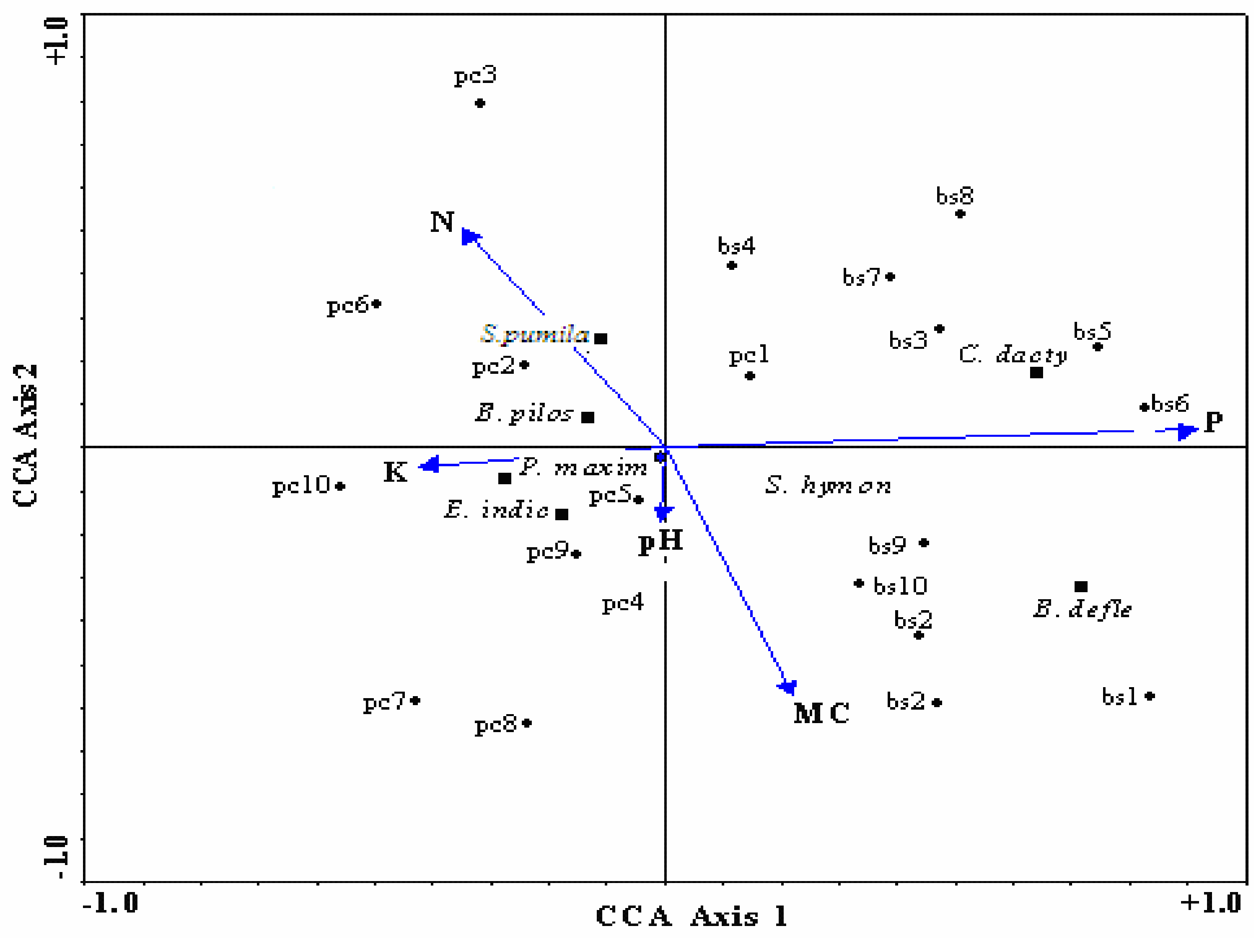

Figure 13. CCA triplot for tree clumps showing the separation of sampling positions, herbaceous species and environmental variables

The correlation between the plant species and the explanatory variables ranged from 0.542 to 0.804 on all the four axes (Table 7). These moderate and relatively high correlation values show that positions of the quadrats and the species on the ordination diagrams are influenced by the explanatory variables measured. Each of the variables is at least correlated with one of the first two axes on the diagrams (Figure 13). Phosphorus is negatively correlated with potassium (Figure 13).

It can be observed from Figure 12 that species such as *C. dactylon, S. hymonima* and *B. deflexa* are correlated positively with phosphorus but this group of species is negatively correlated potassium. *P.maximum, E.indica, S. pumila* and *B. pilosa* are positively correlated to nitrogen and potassium.

From the permutation tests, the influence of the variables along the first canonical axis was significant (F=5.914, P<0.05) and the overall test for all the canonical axes was also significant (F=2.312, P<0.05). The only variable that significantly influenced species composition was phosphorus (F=6.21, P<0.05).

Appendix C (b) shows results of the permutation tests. Soil moisture, nitrogen, pH and potassium had an insignificant influence on herbaceous floristic composition.

4.7 Structure and pattern of herbaceous vegetation

4.7.1 Isolated trees

PCA of 26 herbaceous and adjacent vegetation species, show that Principal Component 1 (PC 1) is accounting for 66.1% of the variance (Table 8). Open grassland species were positively correlated to PC1 with subcanopy shade tolerant species negatively correlated to PC 1. PC 1 therefore defines a gradient from subcanopy zone species to open grassland species (correlations >0.5). PC 2 accounted for 7.2% of the variance (Table 8).

Herbaceous and adjacent grassland species separated into two main groups as shown in Figure 14. The first group is on the right side of Figure 14 and is composed of open grassland species with *S. pyramidalis, H. dissoluta* and *H. fillipendula* being the most important species. Structurally, floristic composition in terms of biomorphological types is composite as there are several different grass species (Figure 14). Stratification of open grassland is bistratal. Field observations evidenced that species such as *S. stapfianus, H. melanocarpus, T. triandra, C. validus, S. cameronni, E. racemosa, and E. viscosa* formed the lower stratum. These grass species had nearly similar heights. *S. pyramidalis, H. dissoluta, H. fillipendula* formed the highest grass stratum in the open grassland. The height of these grass species is moderate (from 50 to 100cm).Field observations showed that cover in the open grassland was dense.

The second group is on the left side of the plot. This group is composed of shade tolerant subcanopy species. *B. pilosa*, *P. maximum* and *E. indica* are the most important herbaceous species (Figure 14). The structure of subcanopy herbaceous layer under both tree species' isolated trees and tree clumps based on composition in terms of biomorphological types is sub-pure. Under *B. spiciformis, C. dactylon* dominated with *B. pilosa, S. hymonima* and *P. maximum* occurring in low abundances. Under *P. curatellifolia, E. indica* dominated with *S. hymonima, S. pumila* and *P. maximum* occurring in low abundances. The description of subcanopy herbaceous layer in terms of stratification, height and cover is unistratal, flat and very sparse respectively.

Table 8. Eigen values and variance accounted for by Principal Components (PC) 1 and 2 for the isolated trees

PCA full data set (180 quadrants)	**PC1**	**PC2**
Eigenvalue	0.661	0.72
Cumulative percentage variance	66.1	73.3
Sum of eigenvalues = 1.000		

Figure 15 is a PCA scatter plot of sample quadrants. Most of subcanopy sampling quadrants formed a single group (B), although some subcanopy sampling quadrants were isolated from this group. These quadrants were associated with shade tolerant herbaceous species (*E .indica, C. dactylon, B. pilosa, S. hymonima, P. maximum).* Quadrats dominated with open grassland species (*S. pyramidalis, H. dissoluta, H. fillipendula, H. contortus, I. cylindrica, S. stapfianus, H. melanocarpus, T. triandra, C. validus, S. cameronni, E. racemosa, and E. viscosa*) formed groups A and C.

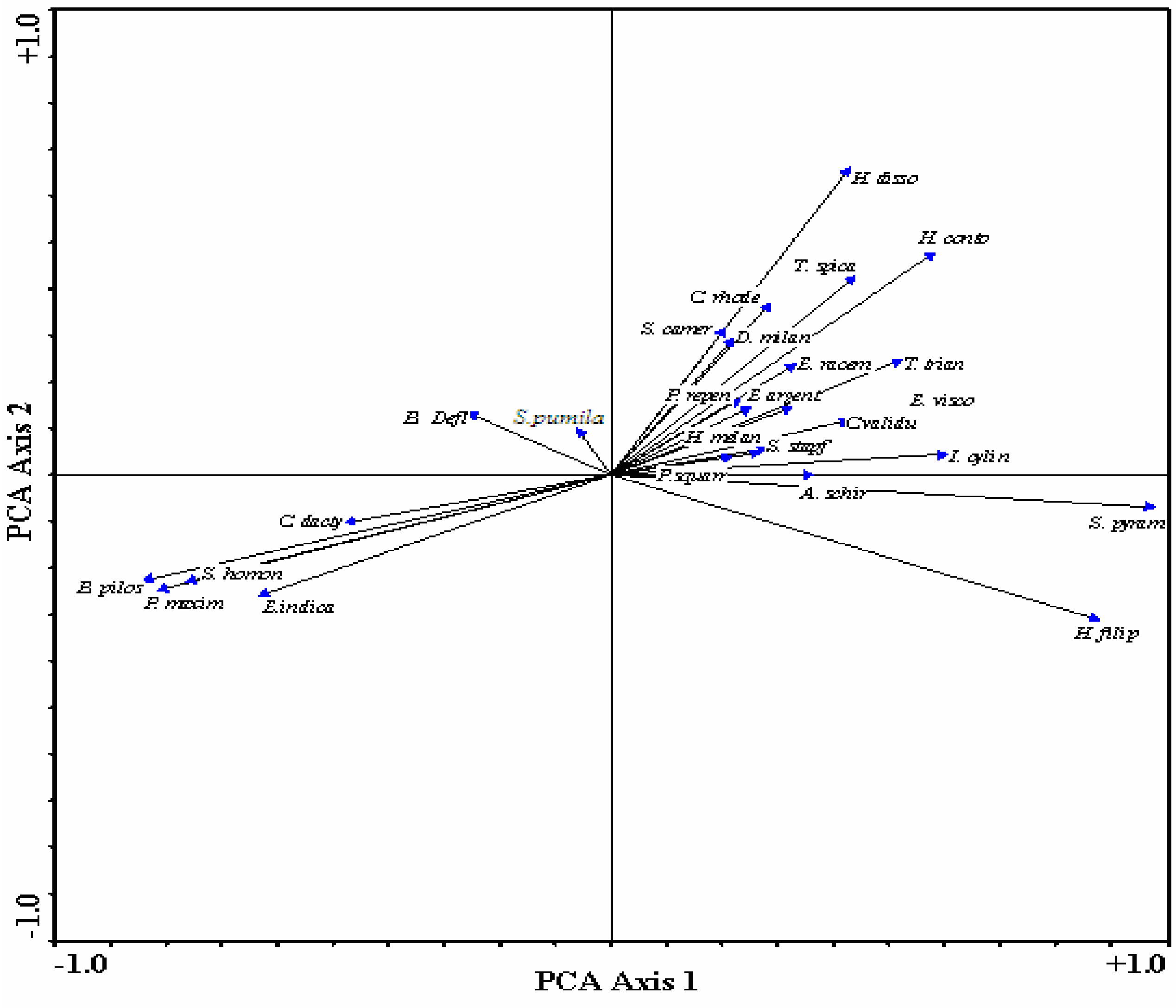

Figure 14. Projections of isolated trees herbaceous vegetation variables on Axes 1 and 2

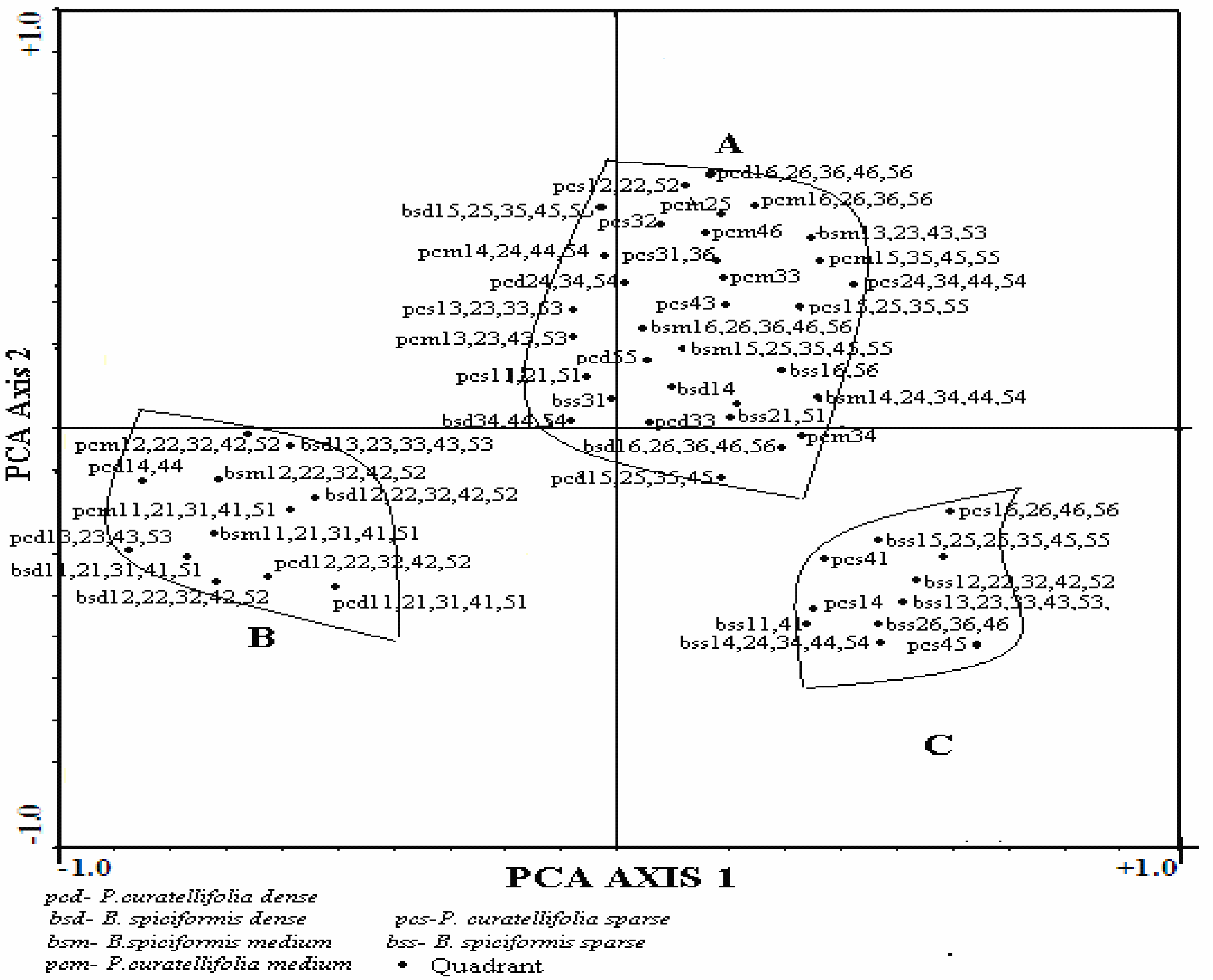

Figure 15. PCA scatter plot of sample quadrants under isolated trees

4.7.2 Tree clumps

PCA for tree clumps results on six herbaceous species show that PC1 accounted for 63.4% of the variance (Table 9). *E. indica, P. maximum* and *B. pilosa* are positively correlated to factor with *C. dactylon* and *B. deflexa* affected by woody species being negatively correlated to PC1 (Figure 16). PC 1 therefore defines a gradient from *S. hymonima, C. dactylon* and *B. deflexa* to *E. indica, P. maximum* and *B. pilosa* (Figure 16). PC 2 accounted for 12.15% of the variance (Table 9). *S. pumila* is highly negatively correlated to PC2.

Table 9. Eigen values and variance accounted by Principal Components (PC) 1 and 2 for the tree clumps

PCA full data set (20 quadrants)	**PC1**	**PC2**
Eigenvalue	0.634	0.121
Cumulative percentage variance	63.4	75.5
Sum of eigenvalues =0.984		

Sampling quadrants with greater abundance of *E. indica*, *B. pilosa*, *P. maximum* and *S. pumila* scored high on PC 1 and were under *P. curatellifolia* tree clump (Figure 16). *E. indica, P. pilosa* and *S. pumila* were the most important herbaceous species under *P. curatellifolia* trees clump. Quadrants associated with *B. deflexa, S. hymonima and C. dactylon* were under *B. spiciformis* trees clump, with *C. dactylon* being the most important herbaceous species (Figure 16).

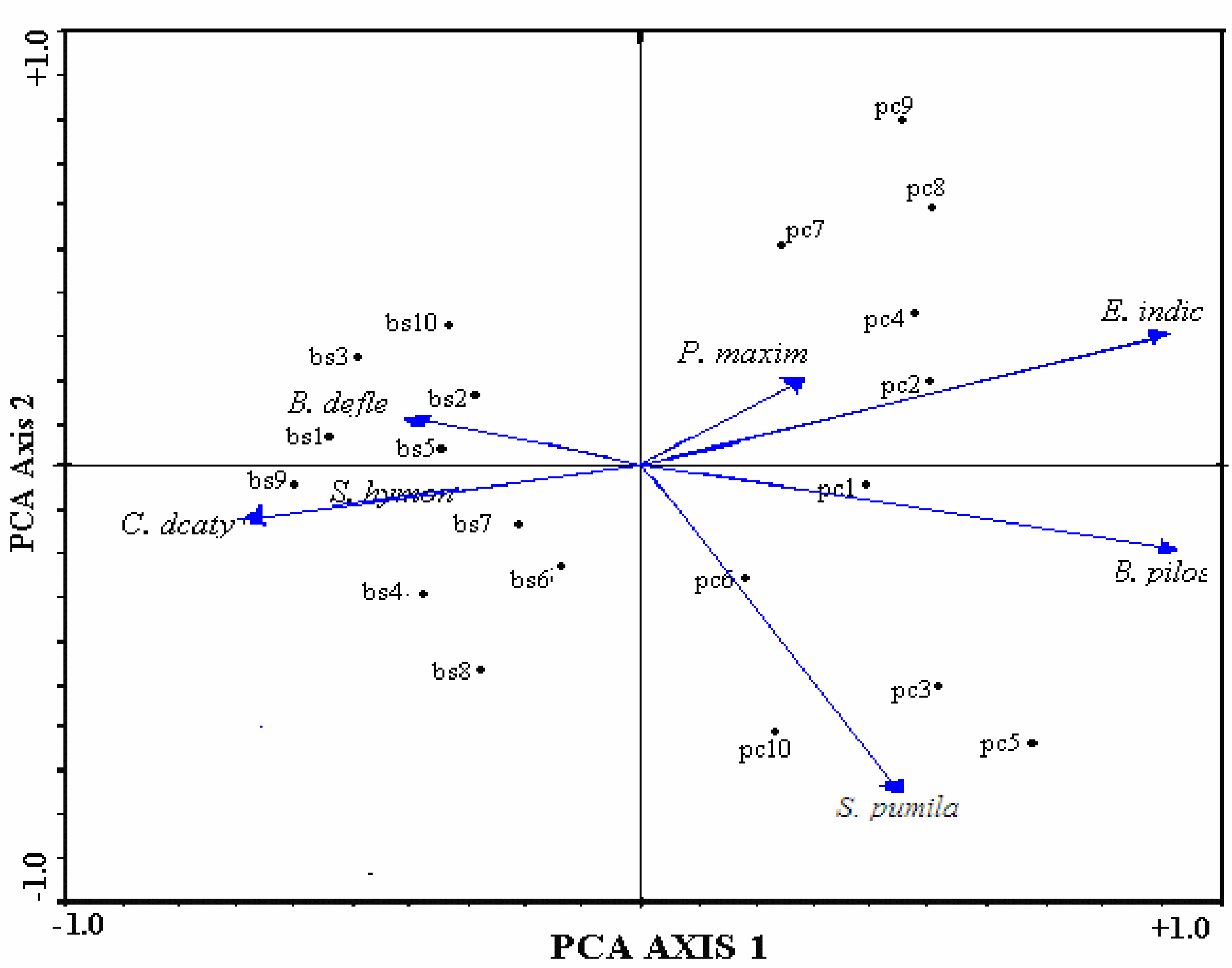

Figure 16. Projections of tree clumps herbaceous vegetation variables and quadrants on Axes 1 and 2

5.0 DISCUSSION AND CONCLUSIONS

5.1 Discussion

5.1.1 Effects of woody species and canopy volume on herbaceous species composition and abundance

Large, isolated trees and tree clumps of *B. spiciformis* and *P. curatellifolia* significantly modified species composition and abundance. It only does so directly within the canopy colony zone. The similarity of environmental effects on these two tree species was most strikingly illustrated in the composition of the vegetation in their canopy zones (Figure 15), which was almost dominated by *C. dactylon* (*B. spiciformis)* and *E.indica* (*P. curatellifolia).* Differences in vegetation along the sampling positions occurred over remarkably short distances (8-30m). The herbaceous layer compositional changes found under large tree canopies in the present study resemble patterns found elsewhere under different tree species (Belsky *et al.,* 1989; Weltzin and Coughenour, 1990; Kennard and Walker, 1973; Charley and West, 1975; Bosch and van Wyk, 1970).

Effects of trees on herbaceous species composition and abundance were concentrated on, but not restricted to tree trunk sites. Herbaceous species were differentially located in relation to canopy size and spatial extent from the tree base. *C. dactylon* and *B. deflexa* dominated subcanopy zones of *B. spiciformis'* isolated trees (Figure 14) and tree clumps (Figure 16). *E. indica* and *B. pilosa* dominated subcanopy areas of *P. curatellifolia'*s isolated trees and tree clumps (Figures 14 and 16). *S. hymonima, P. maximum* and *S. pumila* were subdominant to the dominant herbaceous species. However, *E. indica* did not occur together with *C. dactylon* and *B. deflexa* as it commonly occurred under *P. curatellifolia'* canopy. Scifres *et al.* (1982) reported that at tree scale, herbaceous layer species composition and abundance might change along gradients extending from the tree trunk to the canopy dripline, and into the open grassland. Adjacent open grassland for both tree species had similar compositions as reported in the results.

Woody plants' canopies positively affected *P. maximum, E.indica, C. dactylon, S. hymonima, B. pilosa and S. pumila*. Positively affected herbaceous species maximize their growth, form, and reproduction to the high soil moisture content, pH and soil fertility as well as relatively low temperatures that characterize subcanopy areas. Resultantly, subcanopy herbaceous species' are able to compete efficiently for resources at the expense of their neighbors due to traits allowing highly efficient, plastic growth (Pigliucci, 2001). Under canopy species have different eco-physiological adaptations in order to survive desiccation (Brown, 1977). Field observations suggest that canopy zone preferring grasses had less rigid leaves than such as *H. dissoluta* and *H. filipendula.* This may be attributed to thinner cell walls.

Tropical savannas are characterised by the dominance of C_3 grasses and herbaceous dicots beneath tree canopies while C_4 grasses dominate the open grassland (Pieper, 1990). This observation is in agreement with the results of the present study. C_4 grasses *T. trindra, A. schirensis, P. squarrosa, H. filipendula, H. dissoluta, H. contortus* and *S. pyramidalis* dominated open grassland. Open grassland species require hot tropical conditions, relatively dry, well-drained soils with poor fertility for their growth. Greater cell wall thickness of the C_4 grasses in the open grassland enhances desiccation endurance ability (Brown, 1977).

The differences in herbaceous composition between isolated trees (both *P. curatellifolia* and *B. spiciformis*) and adjacent open grassland may be due to combination of factors. Solar irradiance and fluctuations in temperature and humidity are reduced beneath the canopy of isolated trees relative to open grassland sites (Belsky *et al.,* 1989). Soil fertility is improved (Kellman, 1979; Weltzin and Coughenour, 1990), and soil moisture retention increases (Joffre and Rambal, 1988). Canopy openness regulates the magnitude of all the micro-site conditions. These modified conditions under canopy of isolated trees may enable germination of herbaceous plants, which otherwise could not succeed in the open grassland.

Canopy openness is defined as the proportion of the sky hemisphere that is not obscured by vegetation when viewed from a single point (Brown *et al.,* 2000). It is highly correlated with many aspects of tree microclimate, including total receipts of PAR (Whitmore, 1984), subcanopy soil moisture and temperature. Small, absolute changes in canopy openness produce greater changes in mean irradiance when the forest canopy is almost complete than when the canopy is very open (Brown, 1993). These small changes in mean irradiance greatly affect herbaceous plant growth and survival than open grassland plants.

Differences in canopy openness lead to variations in subcanopy micro-site environmental conditions. In the current study, canopy openness increased with decreasing isolated trees canopy volume. Tree clumps and dense canopy trees categories had the least canopy openness. The level of subcanopy environment modification was mostly reflected under these two categories as variables (pH, P, K, N, soil moisture, E) recorded highest values. Other variables (density, S and H') had lowest values as expected under the same categories where canopy openness was least. Nevertheless, Mordelet and Menaut, (1995) argued that despite the shading effect of tree canopies, savanna grasses under canopy still receive sufficient radiation for relatively high rate of photosynthesis.

Other possible reasons explaining the current study's findings of herbaceous plant species shade against sunlight habitat preferences are tolerance to water stress, soil preferences and less importantly, ability to tolerate herbivory and trampling. Dye and Spear (1982) observed that the association between *P. maximum* and tree canopies is explained by enriched subcanopy soil and increased germination under shade (Sandford *et al*., 1982). Kennard and Walker (1973) noted that seedlings of *P. maximum* and associated herbaceous species have higher survival in the shade than in the open, while the seeds of open grasslands species (*S. pyramidalis* and associated species) germinated poorly in the tree litter under tree canopies (Belsky *et al.,* 1989). These observations are supported by the present study. Scholes and Archer (1997) observed that herbaceous species respond individualistically to tree influences as some plants are ubiquitously distributed beneath and between tree canopies, whereas others may congregate at the drip-line or have clear affinities for one microhabitat or another.

Isolated trees affect their microclimates primarily by intercepting solar radiation (Belsky *et al.,* 1989). On daily and annual basis, canopy shade travels from west to east, and from north to south respectively. Likewise, when rain falls at an angle, the canopy on the leeward side of the tree creates a rain shadow. However, on the windward side of the tree, rainfall is equal to that in the open grassland. In other cases, an increase above ambient rainfall occurs due to the addition of rain dripping from overhead branches. Resultantly, the microclimate associated with isolated trees is locally heterogeneous and extends well behind the borders of the canopy zone. Therefore, microclimates partially influence the abrupt change in species composition at the edge of tree canopies (Belsky *et al.,* 1989).

5.1.2 Impacts of tree canopy on environmental variables

Nitrogen, phosphorus, potassium levels, soil moisture and pH varied significantly between canopy zones of large isolated trees of both *B. spiciformis* and *P. curatellifolia* and the open grassland. These variables decreased with increasing distance from the tree trunk (Figures 10, 9, 8, 7 and 6). This was observed under medium and dense canopy volume trees. Although these variables differed under tree clumps, potassium levels only showed significant differences between the two species.

Compared to open grasslands, subcanopy areas under large, isolated trees recorded higher moisture content levels (Figure 10 and Table 5). Vetaas (1992) reported that tree canopies intercept rainfall and redistribute the water to the ground by through-fall and stem-flow. The amount of water lost by interception depends on the type and architecture of the tree (tree crown size, height, foliage intensity), but generally correlates positively with size of the tree (Pressland, 1973). This is supported by results of the present study which showed higher moisture content under medium and dense canopy volume trees (Table 5). Likewise, tree clumps affected moisture content levels in their colony zones soils.

However, Pressland (1976) argued that increasing tree size may decrease through-fall and stem-flow. This lowers soil moisture levels. This is in contrast with the results of the present study. Moisture content levels were higher under larger tree clumps (Table 5). In tropical semi areas like Mukuvisi Woodlands, rainfall interception by trees may cause a significant loss by evaporation. This leads to aridification of the sub canopy soils compared to the open grasslands during the rainy season (Belsky *et al.,* 1989). However, Specht (1957) argued that the amount of through-fall and stem-flow is depended on the intensity and frequency of the rainfall events as well as wind velocity.

In the current study, the trunk sampling positions of isolated trees recorded the highest moisture levels in the canopy zone (Figure 10). Stem-flow significantly contributed especially when rainfall is of low-intensity (Weltzin and Coughenour, 1990). As rainfall increases, intercepted rainfall exceeds the canopy storage capacity and most of the excess flows down the stem, with some through-fall. Tiedemann and Klemmedson (1973) observed that high litter content in the sub-canopy zone significantly contributed to the high moisture levels. Litter alters the physical properties of the surface soil. Tree litter decomposes more slowly than in-field layer (Joffre and Rambal, 1988). Resultantly, the reduction in soil temperature and evaporation enhance infiltration (Kelly and Walker, 1975), which subsequently improves soil moisture content. This is in agreement with the current study's findings on soil moisture under tree clumps.

The present study results showed that soil moisture content of the outside canopy edge site (dripline) recorded the highest moisture levels (Figure 10). This is explained by the rain dripping effect from the overhead branches to the lower periphery branches. Sampling positions further in the open grassland were drier compared to the dripline site and canopy zone sampling positions (Figure 10). Direct sunlight in the open grassland caused the grassland sites to be drier and the canopy rain shadow effect maintained moisture in the canopy zone, hence the difference between the canopy zone and grassland sampling positions in moisture content (Belsky *et al.,* 1993a).

The present study provides evidence to suggest that isolated trees affected the nutrient concentrations in the savanna grasslands. Results show that soil nitrogen, phosphorus and potassium are similarly elevated in the canopy zone of *B. spiciformis* and *P. curatellifolia* trees compared to the open grasslands (Figures 9, 8 and 7). Likewise, under tree clumps, the variables recorded higher levels. Studies by Belsky *et al.,* (1993a); Weltzin and Coughenour (1990); Aggarwal *et al.,* (1976); Bernhard-Reversat (1982); Isichei and Muoghalu (1992) lended support to the fact that large isolated trees enrich subcanopy soils by nutrients especially close to the trunk.

Nutrient soil enrichment under the two tree species is explained differently. Greater nitrogen, potassium and phosphorus concentrations in shallow soil near tree bole suggested nutrient inputs from the bole and / or a negative effect of shade on soil nutrient source. Leaf fall from the overstory is the most likely nutrient source (Weltzin and Coughenour, 1990). The tree having access to deeper soil moisture, could contribute more litter to the soil than grass alone. Understory grasses would modify their environment with increased litter inputs from both shoots and roots. Additionally, trees transport nutrients from surrounding surface and subsurface soils to their canopy, drop the nutrients in leaf and stem litter.

Bird droppings are major inputs of nutrients under the trees (Belsky *et al.,* 1993a). From field observations, bird droppings covered subcanopy zones under some focal trees. Granivorous birds were active in the study trees and built nests. The persistence of such activities over the lifetime of a tree constitutes a major input of the nutrients. Large mammals also bring nutrients to the trees in their dung, although their contribution may be an insignificant source of nutrient enrichment (Belsky *et al.,* 1993a).

Soil enrichment patterns can also be interpreted based on tree age (Kellman, 1979). Throughout the lifetime of a tree, enrichment of the zone of contact between tree trunk and soil occurs with aerially derived deposits and tree leachate washed off stems and leaves and transported to the ground by stem flow. Soil at the base of the tree, therefore receives rainwater having the highest nutrient concentrations (Kellman, 1979) even though only a small fraction of the total nutrients deposited on the ground are in the stem flow (Escudera *et al.,* 1985).

Bark sloughing is another explanation for enriched canopy soil (Belsky *et al.,* 1993a). Nutrients deposition into the soil occurs when the bark sloughs off trees. Waste products are dropped from termites and other insects that leave on the trunks on the ground. These materials accumulate at the base of the trees, enriching the narrow band of adjacent soil. Reduced soil temperatures under tree canopies would lower decomposition rates (Parton *et al.,* 1987). Capture of precipitation inputs by an increased cation-exchange-capacity in the soil beneath trees and by an increased soil moisture-retention-capacity at the trunk sites result in nutrient accumulation at the tree base (Kellman, 1979). However, in his study, he failed to ascribe the preferential capture of precipitation nutrient inputs beneath savanna trees to an improved soil moisture-retention-capacity.

The current study shows that pH gradually decreased as the distance from the canopy base increased (Figure 6). Sampling positions in the open grassland recorded the lowest pH among all canopy volume classes of both trees species. In comparison with isolated trees trunk sampling positions pH, tree clumps had higher pH. This supports that tree clumps significantly affect the canopy zone. The current study's results are consistent with findings by Isichei and Muoghalu (1992) who reported a significantly higher pH under tree canopies than in the open grassland in the Nigerian savannas.

The higher pH levels under trees may be partly because of organic matter accumulation under them and reduced leaching (Isichei and Muoghalu, 1992). Higher organic matter production by trees causes the accumulation of organic matter. Mineralisation of the organic matter slowly occurs due to reduced temperatures under trees. Canopies are a source of leachates. Nutrient inputs from through-fall and nutrient sequestered by roots from rooting zones to canopies are also sources of nutrients (Isichei and Muoghalu, 1992). Although savanna trees have positive effects on soil nutrient concentration, there paucity information about how this translates into nutrient limitation of the understory vegetation (Campbell *et al.,* 1994; Frost and Edinger, 1991).

5.1.3 Impacts of tree species and canopy on herbaceous species diversity

Species diversity, richness and evenness between the two woody species varied insignificantly. Herbaceous species diversity (H') under *B. spiciformis* varied significantly among the canopy volume classes. The medium class had the highest species diversity, followed by the sparse class, dense class with the tree clumps recording the lowest species diversity. However, *P. curatellifolia* showed a decreasing trend as canopy volume increases on the species diversity (H') (Table 5).

Although *B. spiciformis* and *P. curatellifolia* differ physiologically and morphologically, they had with few exceptions, identical impacts on their subcanopy herbaceous plant diversity. Visual observations suggest that vegetation diversity patterns of other tree species' subcanopy areas in the park (*Acacia species*, *Julbernadia globiflora*) were similar compared to the adjacent open grassland. The results and observations of this current study suggest that the effects of large well-established trees on their canopy zones are partially tree species-specific phenomena, but are common to many tree species.

B. spiciformis' trees clump had the highest species evenness, followed by the medium, dense classes, while the sparse class recorded the lowest species evenness (E). Similarly, *P. curatellifolia* clump of trees had the highest species evenness, followed by the medium, sparse classes, with the dense class recording the lowest. Species richness increased with the decrease of canopy volume intensity for both woody species (Table 5).

Under both tree species, results show a trend of decreasing herbaceous plants diversity with the increase of canopy volume. Differences in the canopy sizes are the causal factors as the magnitude of the influence by the trees found in the different classes varied with respect to tree canopy size. Archer and Scholes (1997) observed that the magnitude of differences in herbaceous plants diversity, richness and evenness under, versus away from, savannas trees vary with tree size and age.

As the tree canopy develops, tree occupation and microhabitat climatic conditions influence soil properties (Archer, 1995). The more time the tree is established, the larger the canopy size, the more the influence of the tree on the subcanopy zone. This results in more apparent negative impacts on the herbaceous plants (Cameron, *et al.,* 1989; Stuart-Hill and Tainton, 1989). This implies that tree clumps and large trees (dense class) compared to small trees (medium, sparse classes) significantly alter microhabitat conditions in their canopy zones. Growth of herbaceous plants was more suppressed under tree clumps and large, isolated trees. This is showed in the present study by low species diversity. When trees are young and small, facilitation may be more important than competition resulting in enhancing herbaceous plants diversity. As trees become larger, competition may overshadow facilitation and adversely affect herbaceous layer diverse production (Archer, 1995).

The increase in species diversity and richness (Table 4) as the distance from the trunk increase up to the dripline sampling position is due to the semi-permanent shading effect directly casted on the canopy zone. Shading reduces light intensities (Kernard and Walker, 1973; Tiedemann and Klemmedson, 1977), soil temperatures (Maranga, 1986) and evaporation from bare soils, litter and standing vegetation. Ovington (1965) agued that when canopy is dense, few subcanopy plants can survive. As the canopy opens up, sufficient light penetrates to permit shrub, seedlings, saplings and herbaceous plants to grow. This is supports the results of the current study. Tree clumps had lower species diversity compared to dense canopy volume at trunk sampling positions (Table 5). The distribution of herbaceous plants was more even at the trunk sampling position and there was a gradual reduction in species evenness towards the open grassland sampling position under both tree species (Table 4).

Low species diversity in the present study in the canopy zone is partially explained by lowered herbaceous production (Belsky, 1994). Wild herbivores sought for tree shade. It is likely that herbivory and trampling disturbs understory soil, hence few species may have the ability to tolerate disturbance (Weltzin and Coughenour, 1997). The canopy dripline sampling positions recorded the highest species richness and diversity compared to trunk and grassland sampling positions (Table 4). This could be attributed to high moisture levels found at the dripline sampling positions and medium disturbance levels by wild animals and tree canopy shade. Aerially derived dust deposits washed off as tree leachate from overhead branches dripping through the periphery lower branches also explain the differences in the species diversity (Vetaas, 1992).

Highest plant diversity occurs at intermediate levels of disturbance (Connell, 1978; Begon *et al.,* 1996). This is the proposal of Intermediate Disturbance Hypothesis (IDH). Findings from the present study are in agreement with the predictions of IDH. The canopy zone under isolated trees and tree clumps is highly disturbed by canopy shade and trampling by wild animals seeking shade, hence the resultant lower species diversity. The grassland site is also relatively highly disturbed by herbivory, fire and trampling by wild animals.

Adjacent surrounding areas experience their own climatic conditions, which according to Brown (1993) influence their species diversity patterns. Unlike canopy zones, surrounding areas are not deprived of PAR. The absorption of radiation by the plant and soil surfaces in surrounding areas cause changes in the soil and aerial microclimates (Becker *et al.*, 1988, Fetcher *et al.,* 1985).

5.1.4 Herbaceous vegetation and environmental relationships

The current study shows strong vegetation-explanatory variable relationships in Mukuvisi Woodlands. Quadrants under isolated trees were grouped into two distinct communities (A and B) (Figure 15) associating with different herbaceous plant species. Canopy shade appeared to be altering species composition and structure both directly and indirectly through the modified soil environment. The direct interception of solar radiation (Georgiadis, 1989), and rainfall (Pressland, 1973) contribute to the modification of soil environment. PC 1 of PCA scatter plot of sample quadrants separates the quadrants along the pH, nitrogen and phosphorus concentrations (Figure 15). The same trend is shown by isolated trees' CCA biplot for quadrants and environmental variables (Figure 12). However, CCA triplot for tree clumps showed that potassium and phosphorus separates sampling quadrants and associated species along the first axis (Figure 13).

Isolated trees' first CCA ordination axis, which was strongly associated with phosphorus, pH and nitrogen, explained much of the variation in species composition in the study area. The CCA biplot for species and environmental variables (Figure 11) shows that separation along the first axis is mainly along the phosphorus, nitrogen and pH gradients. Species such as *H. dissoluta, S. pyramidalis, H. contortus, H. fillipendula, I. Cylindrica, H. melarnocarpus, T. triandra, S. stapfianus, D. milanjiana, P. squarossa, S. cameronni, E. racemosa, C. validus, P. repens and T. spicatus* are associated with low nitrogen and phosphorus levels, low moisture content and more alkaline conditions. This is the reason the associated species are grouping on the right of the ordination diagram (Figures 11 & 14). *E. indica, B. pilosa, S. pumila, C. rhodesiana, A. schirensis*, *E. viscosa, C. dactylon, S. hymonima*, *B. deflexa, P. maximum and E. argenteus* are associated with high nitrogen and phosphorus levels, high moisture content and more acidic conditions are on the left.

CCA ordination diagram for tree clumps (Figure 13) shows that phosphorus levels, nitrogen levels and moisture content explain much of the variation in species composition under tree clumps. Species associated with low phosphorus levels, high potassium levels are on the right side of the ordination diagram, while those associated with low potassium levels, high phosphorus, high nitrogen and low moisture content are on the left side of the ordination diagram.

Sampling quadrants groupings and associated herbaceous species under isolated trees reflect the underlying environmental conditions. These differed with respect to sampling position from the trunk to the open grassland and tree canopy volume. Quadrants under tree clumps were close together with respect to tree species. Vegetation and soils have a close existing relationship that was recognized in some of the early soil classifications (Nyamapfene, 1988). Furthermore, Nyamapfene (1988) documented that vegetation soil relationships can express some very fine differences in edaphic conditions. Much of the variation in herbaceous vegetation composition in Mukuvisi Woodlands is explained mainly by soil pH, and soil moisture and nutrients (N, P, and K).

Plant available moisture and available nutrients are primary determinants of savannas plant communities. Tree species and their canopy shade modify plant available moisture and available nutrients in their canopy zone areas. These factors together with fire and herbivory, determine herbaceous species composition, density and the rates of nutrient and water flow through the system.

Monte-Carlo tests, however, showed that potassium, phosphorus, moisture content and pH significantly influenced vegetation composition in Mukuvisi Woodlands (Appendix C). Nitrogen levels did not show significant contribution. Although nitrogen levels did not contribute significantly in this study, Tinley (1982) found that nitrogen concentrations affect significantly vegetation species composition. According to Scholes and Walker (1993), chemical and physical properties of soil influence plant species composition, morphology and aboveground biomass in semi-arid savannas. Subsequently, the effects of tree canopy shade on the soil properties implicated by the current study are translated into herbaceous species composition and structure.

5.1.5 Impacts of tree canopy on herbaceous vegetation structure

The evidence provided by the present study show that tree canopies negatively affect herbaceous vegetation structure in Mukuvisi Woodlands. Herbaceous plants densities per unit area, species diversity (H', S, E), species composition and abundance were highly significantly different among the canopy volume categories and sampling positions under canopies and in the open grassland. The current study's results showed that values for these variables increased with increasing distance from the tree base towards the open grassland (Table 4, Figures 4 and 5) although the dripline sites recorded relatively higher values.

Vegetation structure in the subcanopy zone and open grassland were different considering densities per unit area, plant species diversity, species composition in terms of biomorphological types and abundance. Stratification, total cover and height of stratums also described structural nature of herbaceous layer in the subcanopy area and open grassland in the current study. The controlling factors for the observed vegetation structure are competition for resources between woody and grass vegetation and disturbance by grazing and fire (Archer and Scholes, 1997).

When trees are young and small, facilitation may be more important than competition, resulting in enhancing herbaceous plants composition, density per unit area, species diversity, species abundance, vertical growth and total cover. However, as trees become larger, competition may overshadow facilitation and adversely affect herbaceous production (Archer, 1995). Tree size/age affect grass composition and production at landscape level of resolution. There is often a strong, negative correlation between tree size and herbaceous cover, species composition, species abundance, species richness and plants density per unit area. Herbaceous diversity and production is low in the subcanopy zones. This is due to competitive effects of trees on grasses. This is in sharp contrast in the open grasslands (Archer, 1995).

Trees and herbaceous layer vertical root distributions influence subcanopy and adjacent grassland vegetation structure. In the subcanopy zones, herbaceous plants' roots are concentrated in shallow 'superficial' soil layers, where their competitive superiority enhances sequestration of topsoil moisture and infiltrating water. Trees have been observed to have some deep roots reaching into subsoil layers where they absorb soil moisture especially when they grow older and larger (Daly *et al.,* 2000). The spatial segregation of woody and herbaceous plants' roots enables minimum competition enhancing coexistence between the two plant forms. Herbaceous layer found under such scenarios are characterised by highly diverse species composition, high numbers of each species, high plants densities per unit area, relatively dense cover as well as even distribution of species. This is in sharp contrast with the findings of the current study.

The use of water resources by *B. spiciformis* and *P. curatellifolia* trees and their herbaceous plants located differently explains the niche separation model (Archer and Scholes, 1997). The fibrous root systems of herbaceous plants intensively exploit a relatively small proportion of the soil profile, whereas woody plants extensively explore a larger volume. (Walter, 1971) suggested that trees may have roots in both topsoil and subsoil, while herbaceous grasses are only rooted in the topsoil. However, high efficiency of the herbaceous plants' roots in sequestering water resources enables a stable equilibrium state.

Furthermore, Mordelet *et al.* (1997) noted that herbaceous and woody perennials used the same water resource. In West African, humid savanna (Menaut, 1979) reported that shallow tree roots competed with herbaceous plants for water resources. Woody plants will not displace grasses, but the proportion of tree roots in the top soil layer has a strong negative influence on the relative abundance of grass (Walker and Noy-Meir, 1982). Sub-pure species composition and diversity, low plants densities per unit area, few numbers of each species per site, flat, unistratal, and very sparse herbaceous cover characterize subcanopy zones where competition of resources is the major controlling factor. This is in agreement with the findings of the current study, hence attributing competition as the major factor between roots of trees (*B. spiciformis and P. curatellifolia*) and their subcanopy vegetation communities for water resources.

The balanced competition model can explain the current study's results on herbaceous vegetation structure (Archer and Scholes, 1997). Woody trees are superior competitors for resources over herbaceous plants. Trees as superior competitors are self-limiting at a biomass insufficient to eliminate herbaceous plants. Under such a scenario where mature trees dominate over grasses, understory herbaceous layer is sparsely covered. According to Archer (1989), this is a stable state condition. Disturbances such as fire and herbivory inhibit such states to attain an equilibrium point (Pellew, 1983) supporting Skarpe (1992)'s proposal that understory vegetation structure is principally shaped by fire and herbivore. Field observations in Mukuvisi woodlands show that fires frequently occur in the park.

5.2 Conclusions

Results of the present study suggest that tree species greatly dictate the patterning and structure of herbaceous vegetation in Mukuvisi Woodlands. The intensity of tree canopy volume was shown in this study as significant factors in altering the herbaceous vegetation composition and abundance of *B. spiciformis* and *P. curatellifolia*. However, impacts of tree canopy volume on the studied trees vary with respect to size of tree. Equal canopy volume categories of *B. spiciformis* and *P. curatellifolia* had similar impacts. Large sized trees with dense canopies had dramatic impacts on the herbaceous plants as they promote low species diversity, low plants densities per unit area with structural changes to herbaceous plants. Medium sized trees result in relatively low species diversity and intermediate structural integrity whereas small sized trees insignificantly influenced the species diversity.

The present study showed that areas in the vicinity of tree trunks had more influence on herbaceous species diversity and abundance than those on the canopy periphery. Distinct patterns of herbaceous species were observed within the subcanopy and the adjacent open grassland. The present study showed a significant interaction of canopy volume and spatial location in structuring herbaceous flora in the Mukuvisi Woodlands. Such interaction seems to affect herbaceous plants differentially on the basis of tree size and distance from the tree base. Species richness in both *B. spiciformis* and *P. curatellifolia* large tree clumps and large sized isolated trees seems to be reduced by canopy impacts. The results of this study show that tree species and tree sizes may have an influence on savanna tree-grass interaction through altering herbaceous species composition, patterns and structure. However, the extent to which this occurs is not deterministic and varies with respect to tree sizes and spatial location in the subcanopy area.

Results of the present study have also revealed that trees influence soil nutrient status of potassium, phosphorus and nitrogen, pH and soil moisture, depending on tree size. Herbaceous vegetation species composition and structure reflect changes in soil properties.

The current study provided strong evidence that large sized trees of B. *spiciformis* and P. *curatellifolia* reduce herbaceous species production and diversity. They also affect other ecosystem processes. Increased woody species density is likely to increase the vulnerability of open grassland species in Mukuvisi Woodlands.

This study was carried out within a single season. The results suggest that a long-term investigation is necessary in order to understand impacts of trees on sub-canopy herbaceous flora. Lack of resources limited the sample size.

REFERENCES

Aggarwal, R.K., Gupta, J.P., Saxena, S.K. and Muthana, K.D. (1976). Studies on soil physico-chemical ecological changes under twelve year old five desert tree species of western Rajasthan. *Indian Forester* 102: 863-872.

Amundson, R.G., Ali., A.R. and Belsky, A.J. (1995). Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. *Journal of Arid Environment* 29: 139– 53.

Archer, S., Scifres, C.J., Bassham, C.R. and Maggio, R. (1988). Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecoogical Monograph* 58: 111– 27.

Archer, S. (1989). Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134: 545– 61.

Archer, S. (1995). Herbivore mediation of grass-woody plant interactions. *Tropical Grasslands* 29: 218– 35.

Baldock, J., Styles, M.T., Kalbskopf, S. and Muchemwa, E. (1991). The geology of the area around Harare greenstone belt and surrounding granitic terrain. *Bulletin* 94. Zimbabwe Geological Survey, Harare

Barnes, D. L. (1992). Management strategies for utilization of Southern Africa savanna.

Barnes, B.V., Zak, D.R., Denton, R.S. and Spur, S.H. (1998). *Forest Ecology*: John Wiley and Sons, Inc. New York

Barth, R.C. and Klemmedson, J.O. (1978). Shrub-induced spatial patterns of dry matter, nitrogen, and organic carbon. *Journal* of *Soil Science Society America* 42: 804– 9.

Bate, G.C. (1981). Nitrogen cycling in savanna ecosystems. In: *Terrestrial nitrogen cycles*. Clark, F.E. and Rosswall, T. (eds) *Ecology Bulletin* 33: 463-475 Stockholm

Becker, P., Rabenold, P.E., Idol, J.R. and Smith, A.P. (1988). Water potential gradients for gaps and slopes in Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* **4:** 173-184

Begon, M., Harper, J.L. and Townsend, C.R. (1996). *Ecology: individuals, populations and communities*. *Blackwell Science* Boston

Bell, R.H.V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. Pp. 193-216 in Huntley, B.J. & Walker, B.H. (eds). *Ecology of Tropical savannas*. Springer-Verlag, Berlin

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients and tree grass competition. *Ecology* 75: 922-932.

Belsky, A.J., Amundson, R.G., Dixbury, J.M., Riha, S.J., Ali, A.R. and Mwonga, S.M. (1989). The effects of trees on their physical, chemical and biological environment in a semi arid savanna in Kenya. *Journal of Applied Ecology* 26: 1005-1024.

Belsky, A.J., Mwonga, S.M., and Duxbury, J.M. (1993b). Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. *Agro forestry Systems* 24: 1– 20.

Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. and Ali, A.R. (1993a). Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* 30: 143– 55.

Bernhard-Reversat, F. (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos* 38: 321–32.

Blackmore, A. C., Mentis, M.T. and Scholes, R. J. (1990). The origin and extent of nutrient enriched patches within nutrient poor savanna in South Africa. *Journal of Biogeography* 7: 463-470.

Bosch, O.J. and van Wyk, J.J.P. (1970). The influence of bushveld trees on the productivity of *Panicum maximum*. *A preliminary report. Proceedings of Grassland Society In Southern Africa* 5: 69-75.

Bremen, H. and de Wit, C.T. (1983). Rangeland productivity and exploitation in the Sahel. *Science* 221: 1341-1347.

Brown, R.W. (1977). Water relations in range plants. In: Sosebee, R.E. (ed). *Rangeland plant physiology*. Society for Range Management, *Range Science Series* 4: 97-140. Denver

Brown, N. (1993). The implications of climate and gap microclimate for seedling growth conditions in Bornean lowland rain forest. *Journal of Tropical Ecology* 9: 153-168.

Brown, N., Jennings, S., Wheeler, P. and Nabe-Nielsen, J. (2000). An improved method for the rapid assessment of forest understory light environments. *Journal of Applied Ecology* 37: 1044-1053.

Callaway, R.M. (2002). Positive interactions among alpine plants increase with stress. *Nature.* 417:844–848.

Cameron, D.M., Rance, S.J., Jones, R.M., Charles-Edwards, D.A. and Barnes, A. (1989). Project STAG: An experimental study in agroforestry. *Australian Journal of Agriculture* 40: 699– 714.

Campbell, B.M., Frost, P., King, J.A., Mawanza, M. and Mhlanga, L. (1994). The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. *Agroforest Systems* 28: 159– 72.

Charley, J. L. and West, N.E. (1975). Plant induced soil chemical patterns in some shrub dominated semi desert ecosystems of Utah. *Journal of Ecology* 63: 945-965.

Connell, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.

Connell, J.H. and Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 3:1119-1144.

Daly, C., Bachelet, D., Lenihan, J.M., Neilson, R., Parton, W. and Ojima. D. (2000). Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications, Ecological Society of America* 10(2): 449-469.

Dawson, T.E. (1993). Hydraulic lift and water use by plants—implications for water balance, performance and plant-plant interactions. *Oecologia* 95: 565– 74.

Dublin, H.T, Sinclair, A.R.E. and McGlade, J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 49: 1147– 64.

Dunham, K. M. (1989). Vegetation-environmental relations of a middle Zambezi flood plain. *Vegetatio* 82: 13-24.

Dye, P.J. and Spear, P.T. (1982). The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. Zimbabwe. *Journal of Agricultural Research* 20**:** 103-118.

Escudero, A., Garcia, B. and Gomex, J.M. (1985). The nutrient cycling in *Quercus rotundifolia* and *Q. pyrenaica* ecosystems of Spain. *Oecologica Plants* 6: 73– 86.

Facelli, J.M. and Pickett, S.T.A. (1991). Plant litter: Light interception and effects on an old-field community. *Ecology* 72: 1024-1031.

Fetcher, N., Oberbauer, S.F. and Strain, B.R. (1985). Vegetation effects in microclimate in lowland tropical forest in Costa Rica. International. *Journal of Biometeorology* 29:145-155.

Frost, P.G., Meanaut, J.C., Walker, B.H., Medina, E. Solbrig, O.T. and Swift, M.J. (1986). Responses of savannas to stress and disturbances. *Biological International. Special* Issues 10.

Frost, W.E. and Edinger, S.B. (1991). Effects of tree canopies on soil characteristics of annual rangeland. *Journal of Range Management* 44: 286– 88.

Fuhlendorf, S.D., Smeins, F.E. & Taylor, C.A. (1997). Browsing and tree size influences on Ashe juniper understory. *Journal of Rangeland Management* 50: 507– 12 .

Garcia-Moya, E. and Mickell, C.M. (1970). Contribution of shrubs to the nitrogen economy of a desert wash plant community. *Ecology* 51: 81-88.

Georgiadis, N.J. (1989). Microhabitat variation in African savanna: effect of woody cover and herbivores in Kenya. *Journal of Tropical Ecology* 5: 93-108

Griffiths, M.E., Lawes, M.J and Tsvuura, Z. (2006). Forest Biodiversity Research Unit. *Journal of South Africa*

Gutierrez, J.L. and Whitford, W. (1987). Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* 68: 2032-2045.

Haworth, K. and McPherson, G.R. (1995). Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. *Journal of Arid. Environment* 31: 153– 70.

Hochberg, M.E., Menaut, J.C. and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the West African savannah. *Journal of Ecology* 82: 217– 26.

Huntley, B.J. and Walker, B.H. (1982). *Ecology of tropical savannas* Spring Verlag New York

Hyde and Western (2008) pp 5

Isichei, A.O. and Muoghalu, J.I. (1992). The effects of tree canopy cover on soil fertility in a Nigerian savanna. *Journal of Tropical Ecology* 8: 329– 38.

Joffre, R. and Rambal, S. (1988). Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecologica. Oecologica Plantarum* 9: 405-422.

Kauffman, J.B., Cummings, D.L. and Ward, D.E. (1994). Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. *Journal of Ecology* 82: 519– 31.

Kellmann, M. (1979). Soil enrichment by neotropical savanna trees. *Journal of Ecology* 67**:** 565-579.

Kelly, R.D. and Walker, B.H. (1975). The effects of different land use on the ecology of a semi-arid region in South-eastern Rhodesia (Zimbabwe). *Journal of Ecology* 64: 553-576.

Kennard, D.G. and Walker, B.H. (1973). Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. Rhodesia. *Journal of Agriculture* 11: 145-153.

Knoop, W.T. and Walker, B.H. (1985). Interaction of woody and herbaceous vegetation in Southern African savanna. *Journal of Ecology* 73:235-253.

Krebs, C.J. (1999). *Ecological Methodology*. 2nd ed. Benjamin Cummings, Menlo Park, California. 620 pp.

Lightfoot, C. (1998). Common Veld Grasses of Zimbabwe. 3rd Edition. Natural Resource Board of Zimbabwe.

Ludwig and Reynolds (1988) pp24

Mapaure, I. and McCartney, M.P. (2001). Vegetation-Environment relationships in a catchment containing a Dambo in Central Zimbabwe. *Bothalia* 31 (1): 135-143.

Maranga, E.K. (1984). Influence of *Acacia tortilis* trees on the distribution of *Panicum maximum* and *Digitaria macroblephara* in South central Kenya. *Unpublished MS Thesis*, Texas A and M University

Maranga, E.K. (1986). An ecological perspective of phytosociology of woody acacia/ herbaceous understory complex. IN: Hansen, R.M., Wole, B. M. and Child, R.D (**eds**). *Proceedings of Conference in Agriculture*. Agricultural Research Center, Egerton College, Njoro, Kenya. April 1986. pp 243-252.

McDonald, D.J., Cowling, R. M. and Boucher, C. (1996). Vegetation-environment relationships on a species rich coastal mountain range in the fynbos biome (South Africa). *Vegetatio* 123: 165-182.

McGarigal (2000), pp25

McMurtrie, R. and Wolf, L. (1983). A model of competition between trees and grass for radiation, water and nutrients. *Botany Annual,* 52: 449-458.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti**,** *Ecological Monographs* 55:259-294.

McNaughton, S.J. (1983) Serengeti grassland ecology. The role of composite environmental factors and contingency in community organization. *Ecological monograph* 53:291-320.

McPherson, G.R. (1993). Effects of herbivory and herb interference on oak establishment in a semi-arid temperate savanna. *Journal of Vegetation Science* 4: 687– 92.

Menaut, J. C. and Ceaser, J. (1979). Structure and production of Lamto savannas. Ivory Coast. *Ecology* 60: 1197-1210.

Menaut, J.C., Lepage, M. and Abaddie, L. (1995). Savannas, woodlands and dry forests in Africa. In: Bullock, S., Mooney, A.H. and Medina, E. (eds) *Seasonally dry Tropical Forests.* Cambridge University Press, Cambridge. 64-82.

Mordelet, P. and Menaut, J-C. (1995). Influence of trees on above-ground production dynamics of grasses in a humid savanna. *Journal of Vegetation. Science* 6**:** 223– 28.

Mordelet, P., Menaut, J.C. and Mariotti, A. (1997). Tree and grass rooting patterns in an African humid savanna. *Journal of Vegetation Science* 8:65-70.

Mueller-Dombois, D. and Ellenberg, H. (1974). *Aims and methods of vegetation ecology*. John Wiley and Sons, New York

Mukuvisi Woodland Association (MWA), (1998). The Mukuvisi Woodland Wildlife and Environment center. *Urban Conservation Programme.* IUCN

Nyamapfene, A. (1988). A note on some Zimbabwean soil-vegetation relationships of important indicator value in soil survey**.** *Kirkia* 13:239-242.

Nyamapfene, K. (1991). *Soils of Zimbabwe.* Harare, Nehanda Publishers.

Olderman, R.A.A. (1991). *Forests. Elements of Silvology*. Springer Verlag, Berlin

Ovington, J.D. (1965). *Woodlands.* The English Press Universities

Parton, W. J., Schimel, D.S., Cole, C.V. and Ojima, D.S. (1987). Analysis of factors controlling soil organic matter in the Great Plains. *Journal of Soil Science Society* 51: 1173-1179.

Pellew, R.A. (1983). The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* 21: 41–74.

Pieper, R.D. (1990). Overstory-understory relationships in pinyon juniper woodlands in New Mexico. *Journal of Range Management* 43: 413– 15.

Pigliucci, M. (2001). *Phenotypic plasticity*. Baltimore, MD: John Hopkins University Press

Pressland, A. J. (1976). Soil moisture redistribution as affected by throughfall and stemflow kin an arid zone shrub community. *Australian Journal of Botany* 24. 641-649.

Pressland, A.J. (1973). Rainfall partitioning by an arid woodland (*Acacia aneura* F. Muell.) in Southwestern Queensland. *Australian Journal of Botany* 21: 235–45.

Quinn, G and Keough, M. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press.

Radwanski, S.A. and Wickens, G.E. (1967). The ecology of *Acacia albida* on mantle soils in Zalingei, Jebbel, Marra. Sudan. *Journal of Applied Ecology* 4: 569-579.

Rees, R.M., Wuta, M., Furley, P.A. and Changsheng Li (2006). Nitrous oxide fluxes from savanna (miombo) woodlands in Zimbabwe

Reynolds J.F., Virginia R.A., Kemp P.R., de Soyza A.G., and Tremmel D.C. (1999). Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monography* 69:69–106.

Reynolds, J.F. and Ludwig, A.J. (1988). *Statistical ecology*. A Primer on methods and computing. John Wiley and Sons. New York

Robertson, J.A. (2005). Grazing ecological condition and biodiversity in riparian river red gum forests in south-eastern Australia. *Proceedings of the Royal Society of Victoria* 117: 85-95.

Sandford, W.W., Usman, S., Obot, E., Isichei, A. O. and Wari, M. (1982). Relationships of woody plants to herbaceous production in Nigeria savanna *Tropical Agriculture* 59: 315-318.

Savage M, Swetnam TW. (1990). Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71**:** 2374– 78.

Scholes, R.G., and Walker, B.H. (1993). An African savanna. *Synthesis of Nylsvley study*. Cambridge University. Cambridge.

Scholes, R.J. and Archer, S.R. (1997). Tree-grasses interactions in savannas. *Annual Review of Ecology and systematics* 28: 517 – 544.

Scifres, C.J., Mutz, J.L., Whitson, R.E. and Drawe, D.L. (1982). Interrelationships of huisache canopy cover with range forage on the coastal prairie. *Journal of Range Management* 35: 558– 62.

Shreve, F. (1931). Physical conditions in sun and shade. Ecology. *Journal of Ecology* 12: 96-104.

Skarpe, C. (1992). Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3: 293– 300.

Specht (1957), pp60

Stuart-Hill, G.C., and Tainton, N.M., (1989). The competitive interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. *Journal Applied Ecology* 26: 285– 98.

Szott, L.T., Fernandes, E.C.M. and Sanchez, P.A. (1991). Soil-plant interactions in agro forestry systems. *Forest Ecology Management* 45: 127– 52.

Ter Braak, C.J.F and **Smilauer** (1998). CANOCO Reference manual and user guide to CANOCO for windows. Software for Canonical Community Ordination (Version 4). Micro Computer Power Ithaca

Ter Braak, C.J.F. (1995). Ordination. In: Jongman, R.H.G., ter Braak, C.J.F., and van Tongeren, O.F.R (1995) *Data analysis in community and landscape ecology*. Cambridge University Press, New York

Thurow, T.L., Blackburn W.H., and Taylor, C.A.J. (1987). Rainfall interception losses by midgrass, shortgrass, and live oak mottes. *Journal of. Range Management* 40: 455– 60**.**

Tiedemann, A.R. and Klemmedson, J.O. (1973). Effect of mesquite on physical and chemical properties of the soil. *Journal of Rangeland Management* 26: 27– 29.

Tiedemann, A.R. and Klemmedson, J.O. (1977). Effect of mesquite trees on vegetation and soils in the desert grassland. *Journal of Rangeland Management* 30**:** 361– 67.

Tinley, K. L. (1982). The influence of soil moisture balance on ecosystem patterns in South Africa. In: Huntley, B. J. and Walker, B.H. (eds) *Ecology of tropical savannas*. pp. 175-191. Springer Verlag Berlin

van Wigen, B.W. and Kruger, F.J. (1985). The physiography and fynbos vegetation communities of the Zachariashoek catchments, south Western Cape, *South African Journal of Botany* 51: 379-399.

Velazquez, A. (1994) Multivariate analysis of vegetation in the volcanos Tlaloc and Pelado, Mexico. *Journal of vegetation science* 5: 263-270.

Verma and Agarwall (1998) pp21

Vetaas, O.R. (1992). Micro sites effects of trees and shrubs in dry savanna. *Journal of vegetation science* 3: 337-344. IAVS; Opulus Printed Uppsala. Printed in Sweden

Virginia, R.A. (1986). Soil development under legume tree canopies. *Forum in Ecology Management* 16: 69-79.

Walker (1976) pp20

Walker, B.H. and Noy-Meir, I. (1982). Aspects of the stability and resilience of savanna ecosystem. *Ecology of tropical savannas* (eds) Huntley, B.J and Walker, B.H. Spring Verlag New York

Walker, B.J. and Noy-Meir, I. (1982). Aspects of stability and resilience of savanna ecosystems. In: *Ecology of Tropical Savannas*, ed. BJ Huntley, BH Walker, pp. 577– 90. Berlin: Springer-Verlag

Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M (1981). Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69: 473-498.

Walter, H. (1971). *Ecology of tropical and sub-tropical vegetation.* Translated by D. Mueller Dombois, Oliver & Boyd Edinburgh

Weltzin, J.F. and Coughenour, M.B. (1990). Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation. Science* 1: 325– 34.

West, N.E. (1991). Nutrient cycling in soils of semi-arid and arid regions. In: *Semi arid land and deserts: Soil resource and Reclamation* (ed) Skujins, J. Pp 295-332. Marcel Dekker Inc., New York.

Western, D. and Praet, C.V. (1973). Cyclical changes in the habitat and climate of an East African ecosystem. *Nature* 241: 104– 6.

Whitmore, T.G. (1984). Gap size and species richness in tropical rainforests. *Biotropica* 16:239.

Wilson, J.E. and Agnew, O.D. (1992). Positive feedback switches in plant communities. *Advances in ecological research* 20: 265-336.

APPENDICES

Appendix A: Sample field data sheets

a) Sample Field Data sheet 1

Tree species…………………… Diameter 1 (D1):…………… Diameter 2 (D2):…..……..

Canopy depth (CD)………….

Canopy Density Class:…………..……………….. Replicate Number:……………………

Canopy Trunk	**Canopy intermediate**	**Inside canopy edge**	**Outside canopy edge**	**Intermediate grassland**	**Grassland**
Transect 1					
Transect 2					
Transect 3					

b) Sample Field Data Sheet 2

Clump Species…………………… ………….

Plot 1	**Plot 2**	**Plot 3**	**Plot 4**	**Plot 5**	**General Comments**
Species No	***Species No***	***Species No***	***Species No***	***Species No***	
Plot 6	**Plot 7**	**Plot 8**	**Plot 9**	**Plot 10**	
Species No	***Species No***	***Species No***	***Species No***	***Species No***	

Appendix B: List of grass species recorded in the quadrats under *B. spiciformis* and *P.curatellifolia* isolated trees and clumped trees in Mukuvisi Woodlands

		B. spiciformis				***P. curatellifolia***			
	Species	**D**	**M**	**S**	**C**	**D**	**M**	**S**	**C**
1	*Andropogon schirensis*	+	±			±	±	±	
2	*Bidens pilosa*	+	±		+	±	±	±	+
3	*Brachiaria deflexa*	+	±		+				
4	*Craspedorhachis rhodesiana*		±	±		±	±	±	
5	*Cymbopogon validus*	+	±	±		±	±	±	
6	*Cynodon dactylon*	+	+		+				
7	*Digitaria milanjiana*		±	±				±	
8	*Elionurus argenteus*		±	±		±	±		
9	*Eleusine indica*					±	±	±	+
10	*Eragritis viscosa*	+	±	±		±	±	±	
11	*Eragrotis racemosa*		±	±		±		±	
12	*Heteropogon melanocarpus*	+	±						
13	*Heteropogon contortous*	+	±	±		±	±	±	
14	*Hyparrhenia fillipendula*	+	±	±		±	±	±	
15	*Hyperthelia dissoluta*	+	±	±		±	±	±	
16	*Imperata cylindrica*	+	±	±		±	±	±	
17	*Panicum repens*	+	±	±			±	±	
18	*Panicum maximum*	+	±		+	±	±		+
19	*Pogonathria squarossa*	+		±			±	±	
20	*Setaria hymonima*	+	±		+	±	±		+
21	*Setaria pumila*	+	+	±	+	±	±	±	+
22	*Sporobolus pyramidalis*	+	±	±		±	±	±	
23	*Sporobolus stapfianus*	+	±			±			
24	*Stereochlaena cameronni*		±				±		
25	*Themeda triandra*	+	±	±		±	±	±	
26	*Trachypogon spicatus*	+	±	±		±	±	±	

Note:
D- Dense
M- Medium
S- Sparse
C-Clumps of trees

Appendix C: Canonical Correspondence Analysis and Permutation Tests

a) Isolated Trees

```
*** Unrestricted permutation ***

 Seeds:  23239   945

 **** Summary of Monte Carlo test ****

 Test of significance of first canonical axis: eigenvalue = 0.210
                                        F-ratio    = 22.730
                                        P-value    = 0.0050

 Test of significance of all canonical axes: Trace      = 0.246
                                        F-ratio    = 5.459
                                        P-value    = 0 .0050

 (199 permutations under reduced model)
No sample-weights specified
 No downweighting of rare species

No. Of active samples: 180
 No. Of passive samples: 0
 No. Of active species: 26

 Total inertia in species data=
 Sum of all eigenvalues of CA = 1.81403

****** Check on influence in covariable/environment data ******
 The following sample(s) have extreme values
 Sample Environmental        Covariable  + Environment space
       Variable Influence   influence     influence

    10     5      5.7x
    20     2     21.6x
    20     4      7.6x
    20                          7.4x
    23     1     27.9x
    23                          8.5x
    32     2     13.7x
    32                          4.8x
    38     1     16.1x
    38                          4.7x
    41     1     35.0x
    41                          9.0x
    44     1     14.9x
    44                          4.6x
    67     4      7.2x
    68     4      5.7x
```

```
   73    3     6.7x
   74    3     5.2x
   94    5     5.1x
  100     5     5.0x
  112     5     6.3x
  121     5     5.7x
  125     4    27.0x
  125                            7.4x
  151     2     5.9x
  175     2     8.9x
  175                            3.3x
  176     2     8.4x
  176                            3.1x
 ****** End of check ******

**** Start of forward selection of variables ****

*** Unrestricted permutation ***

 Seeds:  23239   945
  N     Name Extra fit
 4 N             0.05
 5 MC            0.05
 2 K             0.07
1 pH             0.09
3 P             0.13
P-value 0.0050 (variable   3; F-ratio= 13.65; number of permutations= 199)
P-value 0.0050 (variable   1; F-ratio= 5.76; number of permutations= 199)
P-value 0.0050 (variable   2; F-ratio= 4.79; number of permutations= 199)
P-value 0.0050 (variable   5; F-ratio= 3.20; number of permutations= 199)
P-value 0.6500 (variable   4; F-ratio= 0.68; number of permutations= 199)

*** End of selection ***

   N     name      (weighted) mean         stand. dev.    inflation factor

   1     SPEC AX1              .0000            1.9226
   2     SPEC AX2              .0000            2.4913
   3     SPEC AX3              .0000            2.3823
   4     SPEC AX4              .0000            5.1210
   5     ENVI AX1              .0000            1.0000
   6     ENVI AX2              .0000            1.0000
   7     ENVI AX3              .0000            1.0000
   8     ENVI AX4              .0000            1.0000
   1     pH              -.0661             .9926            1.0373
   2     K                .1479            1.0296            1.1264
   3     P                .1654             .9492            1.1722
   4     N                .0976             .9383            1.1661
```

5	MC	.0779	.9871	1.0580

**** Summary ****

Axes	1	2	3	4
Eigen values	0.210	0.016	0.011	0.006
Species environment correlations	0.520	0.401	0.420	0.195
Cumulative percentage variance				
Of species data:	11.6	12.5	13.1	13.4
Of species-environment relation:	85.2	91.9	96.6	99.0

Sum of all unconstrained eigenvalues	1.814
Sum of all canonical eigenvalues	0.246

b) Tree clumps

```
*** Unrestricted permutation ***
 Seeds:  23239   945

 **** Summary of Monte Carlo test ****

 Test of significance of first canonical axis: eigenvalue   = 0.292
                                               F-ratio     = 5.914
                                               P-value     = 0.0300

 Test of significance of all canonical axes: Trace      = 0 .445
                                               F-ratio     = 2.312
                                               P-value     = 0.0150

 (199 permutations under reduced model)
No sample-weights specified
 No down weighting of rare species

 No. Of active samples: 20
 No. Of passive samples: 0
 No. Of active species: 14

 Total inertia in species data=
 Sum of all eigenvalues of CA = 0.98379


 ****** Check on influence in covariable/environment data ******
 The following sample(s) have extreme values
 Sample Environmental        Covariable  + Environment space
Variable Influence   influence     influence
3                              5            5.0x
11                             2            9.6x
 ****** End of check ******

  **** Start of forward selection of variables ****

 *** Unrestricted permutation ***

Seeds:  23239   945
   N          Name Extra fit
 1 pH           0.02
 5 MC           0.06
 4 N           0.06
  2 K           0 .08
  3 P          0.25


P-value .0050 (variable   3; F-ratio= 6.21; number of permutations= 199)
```

```
P-value .2550 (variable   2; F-ratio= 1.47; number of permutations= 199)
P-value .2100 (variable   5; F-ratio= 1.39; number of permutations= 199)
P-value .5400 (variable   1; F-ratio= 0 .86; number of permutations= 199)
P-value .3150 (variable   4; F-ratio= 1.22; number of permutations= 199)

 *** End of selection ***
   N    name     (weighted) mean        stand. Dev.   inflation factor

   1    SPEC AX1             .0000           1.2436
   2    SPEC AX2             .0000           1.4551
   3    SPEC AX3             .0000           1.4270
   4    SPEC AX4             .0000           1.8446
   5    ENVI AX1             .0000           1.0000
   6    ENVI AX2             .0000           1.0000
   7    ENVI AX3             .0000           1.0000
   8    ENVI AX4             .0000           1.0000
   1    pH          -.0872           .8976           1.3854
   2    K            .0114           .9014           1.1256
   3    P           -.3289           .9044           1.2538
   4    N            .0138           .8291           1.2044
   5    MC          -.0861           .9458           1.2483

**** Summary ****
```

Axes	1	2	3	4
Eigen values	0.292	0.082	0.045	0.024
Species environment correlations	0.804	0.687	0.701	0.542
Cumulative percentage variance				
Of species data:	29.7	38.0	42.6	45.1
Of species-environment relation:	65.7	84.1	94.2	99.6

```
 Sum of all unconstrained eigenvalues                              0 .984
 Sum of all canonical     eigenvalues                              0 .445
[Mon Jul 12 07:01:42 1999] CANOCO call succeeded
```

Appendix D: ANOVA Summaries

a) Two-way ANOVA Summary results on the effects of woody species canopy volume, sampling position, and their interaction under isolated trees.

Design Summary
Number of three level factors: 1 (Canopy volume)
Number of six level factors: 1 (Sampling sites)
Total number of runs (cases, experiments): 180
Number of unique runs (Cases experiments): 180
Number of blocks: 2

Note: * -P< 0.05; **-P<0.001; ***-P<0.0001 and ^{NS}P>0.05

a) ANOVA: Species Diversity (H')

Factor	Df	SS	MS	F	P
1)Sampling position	5	5.15596	1.03119	113.72	0.000**
2)Canopy volume	5	5.98205	1.19641	131.95	0.000**
1x 2	25	2.51217	0.10049	11.08	0.000**
Error	144	1.30572	0.00907		
Total	**179**	**14.95589**			

b) ANOVA: Species evenness

Factor	Df	SS	MS	F	P
1)Sampling position	5	0.184289	0.036858	59.20	0.000**
2)Canopy volume	5	0.071536	0.014307	22.98	0.000**
1x 2	25	0.072886	0.002915	4.68	0.000**
Error	144	0.089661	0.000623		
Total	**179**	**0.418372**			

c) ANOVA: Species richness

Factor	Df	SS	MS	F	P
1)Sampling position	5	210.444	42.089	105.22	0.000**
2)Canopy volume	5	179.844	35.969	89.92	0.000**
1x 2	25	92.689	3.708	9.27	0.000**
Error	144	57.600	0.400		
Total	**179**	540.578			

d) ANOVA: Density

Factor	Df	SS	MS	F	P
1)Sampling position	5	3.937E+11	7.873E+10	256.37	0.000**
2)Canopy volume	5	6.396E+10	1.279E+10	41.65	0.000**
1x 2	25	8.168E+10	3.267E+09	10.64	0.000**
Error	144	4.422E+10	30709955		
Total	**179**	5.835E+11			

e) ANOVA: pH

Factor	**Df**	**SS**	**MS**	**F**	**P**
1)Sampling position	5	4.5689	0.9138	16.67	0.000**
2)Canopy volume	5	0.6696	0.1339	2.44	0.037*
1x 2	25	2.9967	0.1199	2.19	0.002*
Error	144	7.8920	0.0548		
Total	**179**	**16.1273**			

f) NOVA: Potassium

Factor	**Df**	**SS**	**MS**	**F**	**P**
1)Sampling position	5	0.32437	0.06487	26.31	0.000**
2)Canopy volume	5	0.09893	0.01979	8.03	0.000**
1x 2	25	0.09619	0.00388	1.57	0.052^{NS}
Error	144	0.35502	0.00247		
Total	**179**	**0.87522**			

g) ANOVA: Phosphorus

Factor	**Df**	**SS**	**MS**	**F**	**P**
1)Sampling position	5	705.49	141.10	31.01	0.000**
2)Canopy volume	5	166.36	33.27	7.31	0.000**
1x 2	25	27.81	1.11	0.24	1.000^{NS}
Error	144	655.20	4.55		
Total	**179**	**1554.86**			

h) ANOVA: Nitrogen

Factor	**Df**	**SS**	**MS**	**F**	**P**
1)Sampling position	5	7527	1505	11.17	0.000**
2)Canopy volume	5	1925	385	2.86	0.017*
1x 2	25	2941	118	0.87	0.641^{NS}
Error	144	19405	135		
Total	**179**				

i) ANOVA: Moisture content

Factor	**Df**	**SS**	**MS**	**F**	**P**
1)Sampling position	5	6.2818	1.2564	14.15	0.000**
2)Canopy volume	5	6.4700	1.2940	14.58	0.000**
1x 2	25	3.7131	0.1485	1.67	0.032*
Error	144	12.7833	0.0888		
Total	**179**	**29.2482**			

b) One-way ANOVA Summary results on the effects of tree clumps

a) ANOVA: Species diversity (H')

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	0.6059	0.6059	12.72	0.002*
Error	18	0.8572	0.0476		
Total	**19**	**1.4630**			

b) ANOVA: Species evenness

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	0.000527	0.000527	0.72	0.409^{NS}
Error	18	0.013262	0.000737		
Total	**19**	**0.013789**			

c) ANOVA: Species richness

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	9.800	9.800	13.16	0.002*
Error	18	13.400	0.744		
Total	**19**	**23.200**			

d) ANOVA: Density

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	4.050E+10	4.050E+10	94.92	0.000**
Error	18	7.680E+09	426666667		
Total	**19**	**4.818E+10**			

e) ANOVA: pH

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	0.0125	0.0125	0.33	0.574^{NS}
Error	18	0.6850	0.0381		
Total	**19**	**0.6975**			

f) ANOVA: Potassium

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	0.00145	0.00145	0.40	0.534^{NS}
Error	18	0.06485	0.00360		
Total	**19**	**0.06629**			

g) ANOVA: Phosphorus

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	217.80	217.80	74.82	0.000**
Error	18	52.40	2.91		
Total	**19**	**270.20**			

h) ANOVA: Nitrogen

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	39	39	0.31	0.586^{NS}
Error	18	2293	127		
Total	**19**	**2332**			

i) ANOVA: Moisture content

Factor	**Df**	**SS**	**MS**	**F**	**P**
Woody species	1	0.164	0.164	0.53	0.477^{NS}
Error	18	5.594	0.311		
Total	**19**	**5.758**			