CHAPTER 2

LITERATURE REVIEW

2.1 Phytosociological syntheses

2.1.1 Introduction

A phytosociological synthesis can be described as a study of which the main aim is to compile a synthesis of vegetation information based on phytosociological data collected by various researchers at various times in a particular study area. Large vegetation data sets are generally encountered with in phytosociological syntheses, due to the accumulation of information in the form of vegetation relevés. Knowledge on phytosociological syntheses and the treatment of large vegetation data sets are limited in southern Africa. Identification of basic vegetation units still needs attention, lowering general concern of syntheses and vegetation classification on higher ranks.

2.1.2 Previous attempts to treat large vegetation data sets

One of the first attempts to analise large phytosociological data sets in South Africa, was the three-step method proposed by Bredenkamp and Bezuidenhout (1995). Winterbach (1998) also performed this method in a synthesis of *Acacia*-dominated vegetation of the Central Bushveld of South Africa. The three-step method for a phytosociological synthesis of grasslands in South Africa (Bredenkamp & Bezuidenhout 1995) was based on the two-step procedure proposed by Van der Maarel *et al.* (1987).

a) Van der Maarel *et al.* (1987)

The first step of the method of Van der Maarel *et al.* (1987) is preceded by stratification of the data set. Stratification is suggested either by area (in the case of a large and geographically heterogeneous region), or by vegetation type in the case where all plant communities of an area are covered. Cluster analysis is performed on each stratified unit, resulting in basic clusters (first step). These clusters are then summarised by calculating a "synoptic cover abundance value" for each species in each cluster. The resulting clusters are called synrelevés or synclusters. The second step of this approach is to perform cluster analysis and ordination to synclusters resulting from the first step (Van der Maarel *et al.* 1987).

b) Bredenkamp and Bezuidenhout (1995)

The method of Bredenkamp and Bezuidenhout (1995) is an elaboration of the two-step method of Van der Maarel *et al.* (1987) to a three-step approach. The first step also involves stratification of the complete data set under examination by area or project or, where applicable, to vegetation type, followed by a numerical classification and refinement of the resulting clusters. Resulting plant communities are then summarised in a single synoptic table by means of synoptic values calculated for each species in each community. The second step involves numerical classification of all communities in the synoptic table resulted from step 1 as well as refinement procedures in accordance with the Braun-Blanquet approach. According to Bredenkamp and Bezuidenhout (1995) these two steps result in desirable identification of broad vegetation types within the study area. The extra step includes the compilation of phytosociological tables for each identified broad vegetation type as well as the arrangement of comprehensive hierarchy. This step is considered necessary, as plant communities identified from local studies only, are often inadequate to formally describe syntaxa.

Considering the growing need for vegetation classification on a level higher than the association for conservation and land-use purposes, a clear view on methodology of treating large vegetation data sets is needed. An objective evaluation of both methods is presented below.

Advantages

The attempts of Van der Maarel *et al.* (1987) and Bredenkamp and Bezuidenhout (1995) are of great value for holistic views on existing plant communities. Considering limitations within methods used for numerical classification, consolidating fragments of identified plant communities were at the time of these studies the best way to express variation within larger types. New computer tools have however been developed in the meantime, e.g. JUICE (Tichý 2001) to treat large vegetation data sets.

Criticism

The "holistic picture" resulting from studies based on the above methods, is not necessarily truly representative of the vegetation over its distribution range as a type since only fragments of the vegetation may be included in the analysis. Vegetation classification on a small scale, e.g. plant community identification for management purposes on a game farm, cause marginal relevés, that do not fit well into a known plant community. These marginal relevés, which might assist to express a syntaxon on a higher level of classification, are usually forced into plant communities. This manipulation of data creates the overlooking of transition zones or ecotone vegetation identification. Van der Maarel (1990) emphasised the great ecological interest of ecotones and stressed that it deserves more attention in research. Ecotone plant communities are abstract units on paper, although they do exist in the physical environment. Such plant communities need to be classified since they may require a different management approach.

Certain plant communities receive higher rank than deserved during classification of a small study area since it seems, on a small scale, as if they represent a large type. However, looking holistically, they often fade out as plant communities of much lower rank interrupting large vegetation types.

During a synthesis of vegetation classifications, seral communities are easily overlooked. Although seral communities are often of short duration, they might be useful as classified units since rehabilitation projects and other management practices need information on vegetation change and structure over time.

The proposed methods under discussion require well-sampled, well-discussed plant communities for a realistic outcome. In southern Africa, it is most often experienced that areas of great value to vegetation classification are under-sampled or if sampled, data are often not classified or documented. It therefore seems that well-classified and well-documented data are needed for meaningful synoptic clusters to be used in the second step of the analysis. If not, the synrelevés used have little syntaxonomic or synecological value.

2.1.3 The possibility to apply these methods to the Mopaneveld study

Mopaneveld occurs along a distinctive environmental gradient (mostly declining rainfall from East to West): from arid environments (Damaraland, Namibia, Angola), crossing semi-arid areas (Owamboland, Namibia, Caprivi, Namibia, Botswana, southern and western Zimbabwe, southwestern Zambia, north of the Soutpansberg, South Africa) to semi-moist areas (South African Lowveld, northern and eastern Zimbabwe, eastern Zambia, Malawi & Mozambique) (Mapaure 1994). Because of its distribution over environmental extremes, high α-ánd β-diversity is expected. The major constraint in studying Mopaneveld vegetation is the limitations in vegetation studies with adequate phytosociological data over its entire distribution range (Chapter 4). If vegetation classification in the Mopaneveld was adequate, diversity within vegetation patterns would also have been captured, making the discussed methods applicable.

It is however needed to synthesise existing vegetation knowledge and therefore a method is proposed to classify the vegetation of Mopaneveld, with its limitations in available vegetation data. It is important to note that the outcome of the method does not represent a clear picture of Mopaneveld vegetation along its distribution, since many areas of great significance to the classification are undersampled.

2.1.4 New trends in the syntheses of large vegetation data sets

A new computer package, JUICE (Tichý 2001), was recently developed to challenge the international problem of dealing with the classification and analysis of large vegetation data sets. JUICE is an expert system, which comprises analytical methods such as COCKTAIL (Bruelheide 1995, Bruelheide 2000) and TWINSPAN (Hill 1979b). After the analytical phase, synoptic tables can be created in the program using user-defined fidelity measures. The classification results can be exported to WORD, EXCEL, DMAP and IDRISI.

Chytrý *et al.* (in press) proposed a new method for structuring phytosociological synoptic tables in large vegetation data sets and defining diagnostic species using fidelity calculation. According to Chytrý *et al.* (in press), synoptic tables being constructed using the statistical measure of fidelity, have several peculiarities if compared with the traditional synoptic tables widely used in current phytosociological literature. In the traditional synoptic tables, diagnostic value is given to species simply according to frequency difference, as in the case of the Mopaneveld phytosociological synthesis. It is therefore likely for certain species to be labeled as diagnostics within the vegetation type or major plant community of Mopaneveld. Although, with the new proposed method, these species would not necessarily be regarded diagnostic. It is therefore important to note that, although the term "diagnostic species" is used in the description of the major vegetation units within Mopaneveld vegetation (Chapters 5 and 6), it may not express diagnostic (character) species in the true sence of the word. In southern African vegetation studies, little attempts have been made to classify vegetation according to their position in the higher vegetation rank. Therefore, when referring to diagnostic species in the Mopaneveld, it comprises those species most frequently present in that vegetation unit, and based on the present knowledge, they can be used to differentiate between types. The approach of Chytrý *et al.* (in press) attaches diagnostic value only to the species whose diagnostic capacity is valid over many different vegetation types in this wider area.

2.2 Mopaneveld in southern Africa

2.2.1 Definition of Mopaneveld

The identification of a vegetation class where *Colophospermum mopane* is the most conspicuous character species, namely the Commiphoro mollis – Colophospermetea mopani (Winterbach 1998) engendered further analysis on this vegetation class. The proposed Commiphoro mollis – Colophospermetea mopani (class name still to be typified) was identified according to a phytosociological synthesis of the Central Savanna Biome, South Africa. It is speculated that this vegetation class extends along the distribution of the character species, *Colophospermum mopane*. The name Mopaneveld is the suggested common name for this vegetation class. It is derived from a name given to the South African Veld Type, Mopani Veld (Acocks 1953). Acocks (1953) defined a veld type as "a unit of vegetation whose range of variation is small enough to permit the whole of it to have the same farming potentialities". Since the focus of this study does not directly include agricultural potential and because the study area extends across South African borders, the Acocks' proposed Mopani Veld was not considered being used. Low and Rebelo (1998) identified the Vegetation Type which can be described as a vegetation unit representing a coherent array of communities which shares common species (or abundance of species), possesses a similar vegetation structure (vertical profile) and shares the same set of ecological processes. Along the distribution range of *Colophospermum mopane*, vegetation structure and ecological processes vary considerably (Timberlake 1999). Therefore neither the Veld Ttype nor the Vegetation Type is a true reflection of *C. mopane* vegetation in southern Africa. **The Mopaneveld is therefore defined as a vegetation unit where *Colophospermum mopane* generally dominates or co-dominates the woody component**. Although it is apparent that where *C. mopane* occurs it generally forms the sole dominant in the tree layer of a savanna type, Mopaneveld does not necessarily have to be dominated by *Colophospermum mopane*. Data selection criteria (Chapter 4) state amongst others that data should be sampled in areas where *Colophospermum mopane* at least forms a major component of the vegetation. Mopaneveld is however interrupted by vegetation not clearly representative of the Commiphoro mollis – Colophospermetea mopani vegetation class. These units were easily identified as azonal or intrazonal vegetation during analysis (Chapter 4). The remaining vegetation data, after azonal types had been separated and removed, were regarded as representing Mopaneveld, whether the relevé, or combination of relevés contains *Colophospermum mopane* or not. Mopaneveld, as referred to in this study, could only be identified after the first approximation of vegetation analysis. **The definition of Mopaneveld is therefore suggested as a vegetation class where *Colophospermum mopane* forms at least the major component in the woody vegetation on a scale larger than the basic plant community (association)**. Mopaneveld is furthermore often characterised by the typical herbaceous component rather than only by the mere presence of *Colophospermum mop*ane. It is rather a prevalent phenomenon in savanna vegetation that herbaceous species express relations between vegetation units, which in turn exhibit resemblance in vegetation dynamic processes (e.g. O'Connor & Roux 1995; Du Plessis *et al.* 1998). Therefore Mopaneveld does not always have to contain *Colophospermum mopane* in a specific relevé.

2.2.2 The species *Colophospermum mopane*

Colophospermum mopane, often refered to as "mopane", has extensively been reviewed in terms of its biology and ecology (eg. Thompson 1960; Jarman & Thomas 1969; Henning & White 1974; Van Voorthuizen 1976; Scholes 1990; Madams 1990; Choinski & Tuohy 1991; Malan &

Van Wyk 1993; Mapaure 1994; Smit *et al.* 1994; Timberlake 1995; Timberlake 1996; Timberlake 1999; Smit & Rethman 1998a; Smit & Rethman 1998b). These review papers were studied to produce a brief discussion on the species *C. mopane* since this study focuses mainly on the vegetation of Mopaneveld and not on the species itself. The discussion of the species will be in accordance with published reviews from the above-mentioned authors.

2.2.2.1 Taxonomy

Colophospermum mopane (Kirk ex Benth.) Kirk ex J. Léonard is a monotypic genus which belongs to the Detarieae tribe of the sub-family Caesalpinioidae, family Leguminosae or Fabaceae (Lock 1989; Timberlake 1996). The generic name "*Colophospermum*" refers to its seeds and is the Greek for "resinous seed" (Ross 1977). Van Voorthuizen (1976) states that it is derived from the Greek for "seed inhibiting the light". The genus *Colophospermum* was described in 1949 by J. Léonard. *Colophospermum mopane* was previously placed in the genus *Copaifera* L. (*Copaifera mopane* Kirk ex Benth.) along with *Copaifera conjugata* (Bolle) Milne-Redh. (now *Guibourtia conjugata* (Bolle) J. Léonard) and *Copaifera coleosperma* Benth. (now *Guibourtia coleosperma* (Benth.) J. Léonard) (Timberlake 1995). *Colophospermum* is congeneric with the monotypic *Hardwickia*, described from India in 1811 (Breteler *et al.* 1997). Breteler *et al.* (1997) proposed a new combination, namely *Hardwickia mopane*. Supported by various botanists in southern Africa, Smith *et al.* (1998) suggested conserving the name *Colophospermum*, as it is commonly known today. Léonard (1999) responded to the team of researchers (Breteler *et al.* 1997) who proposed to sink *Colophospermum* under *Hardwickia*. According to the author of this montypic genus, *Colophospermum* differs macromorphological more extensively to *Hardwickia* than mentioned by Breteler *et al.* (1997). Léonard (1999) re-established the genus *Colophospermum* with the species *C. mopane* and provided a detailed key in order to distinguish it from the genus *Hardwickia*.

2.2.2.2 General description

The deciduous, leguminous small to medium-sized tree, *Colophospermum mopane* (mopane) constitutes a major component of the main river basins of sub-tropical southern Africa (Werger & Coetzee 1978; White 1983; Madams 1990; Henning & White 1974; Mapaure 1994;

Timberlake 1996). The crown of *C. mopane* is usually erect and narrow, although it often occurs as a low shrub (1–2 m). Leaves are distinctively "butterfly-shaped" (Palgrave 1983; Timberlake 1995; Timberlake 1996; Van Wyk & Van Wyk 1997) consisting of two leathery leaflets (Madams 1990; Timberlake 1995; Van Wyk & Van Wyk 1997). These leaflets are usually open, but in hot, dry conditions they fold together, presumably reducing transpirational water loss (Madams 1990; Timberlake 1995). Leaves fall in the dry season, determined mainly by soil moisture status, wind and exposure (Timberlake 1996). Trees are leafless for approximately five months south of the Zambezi Valley, whilst leafless for only three months (August to October) in the Luangwa Valley, Zambia (White 1983; Madams 1990).

The inconspicuous pale yellowish-green flowers (less than 1.3 cm across) appear in short axillary racemes or sprays (Van Voorthuizen 1976; Van Wyk & Van Wyk 1997) from December to March, after the leaves have developed (Madams 1990; Timberlake 1995; Timberlake 1996). *C. mopane* is wind-pollinated, which is rather an unusual phenomenon in the Caesalpinioidae (Ross 1977). Fruits are thin, kidney-shaped, light brown, papery pods and ripen around May (Van Voorthuizen 1976; Madams 1990; Timberlake 1995; Timberlake 1996; Jordaan & Wessels 1999). Pods are wind-dispersed, indehiscent with numerous scattered resin glands on the surface. Seeds also contain small, sticky, resin glands (Van Voorthuizen 1976; Thompson 1960; Madams 1990; Timberlake 1995). Both the seed and fruit are short-lived which seldom remain viable for more than a year probably because of the thin testa being highly permeable to water (Jordaan & Wessels 1999). Brophy *et al.* (1992) identified significant amounts of essential oils in the leaves, bark and seeds of mopane. Seeds germinate under a wide range of conditions. According to Thompson (1960) seeds of *C. mopane* will germinate on moist, bare soil with only a sparse grass cover. Seedling-survival under these conditions is good, revealing competition with grass species. Seedling-growth increases with increased soil nitrogen and potassium and on soils with less than 7 % moisture (Chionski & Tuohy 1991; Henning & White 1974). Smith (1972) found that seedling growth leads to a reduction in soil pH due to selective uptake of cations.

The bark of *C. mopane* is fibrous, dark grey or brown (Van Voorthuizen 1976) and is strong and tough due to concentric zones of abundant crystalliferous strands with very thin, lignified secondary cell walls (Malan & Van Wyk 1993). It also accommodates secretory ducts or cells, which contain a diversity of secondary compounds. Furthermore, the bark of *C. mopane* is also the habitat of ants (Van Voorthuizen 1976).

Colophospermum mopane is known for extensively utilising moisture in the upper soil horizons (Mapaure 1994) by its shallow, aggressive (30–120 cm deep) root system (Thompson 1960; Madams 1990; Smit & Rethman 1998a). When occurring on deep soil, roots of *C. mopane* are found to penetrate to a depth up to 2 m. A well-developed, vertically growing tap-root is produced during the seedling phase followed by the development of radial roots near the soil surface. At maturity the tap-roots gradually disappear to leave a dense network of roots near the soil surface (Henning & White 1974; Madams 1990; Smit & Rethman 1998a) where soil moisture content and water-holding capacity are optimal. Fine roots (0–1 mm) are concentrated in the top 200 mm of the soil surface and decline linearly with increased soil depth, while coarse roots (100 mm) increase in biomass up to a depth of 400–600 mm, whereafter they also decline (Le Roux *et al.* 1994; Smit *et al.* 1994). Total root biomass in an area covered by dense stands of *Colophospermum mopane*, ranges from 9 760 kg/ha up to 29 790 kg/ha with a mean value of 17 354 kg/ha (Smit & Rethman 1998a). It was also found that root biomass well exceeds leaf biomass (Smit *et al.* 1994; Smit & Rethman 1998a) which consequently implies a high competitive potential with herbaceous plants.

For a long time it was believed that *C. mopane* roots do not nodulate and fix atmospheric nitrogen (Henning & White 1974). In a recent study, bacteria that resemble rhizobia were found to infect roots of *C. mopane* (Jordaan *et al.* 2000). It is however not clear if nitrogen-fixing symbiosis is indeed present. The relation between bacteria and roots of *C. mopane* might be beneficial to tree growth as it seems to induce continuous development of new roots resulting in better mineral uptake (Jordaan *et al.* 2000).

High leaf production of *Colophospermum mopane*, especially in vegetation types dominated by this savanna tree (Dekker & Smit 1996) is of significant value for available browsing material for livestock- or game farmers. It is however not only leaves on the trees that animals feed on, but also fallen leaf litter that provide important food reserves (Owen-Smith *et al.* 1983; Styles & Skinner 1997). In some Mopaneveld plant communities new season leaves *of C. mopane*, often appear as early as September while leaf senescence often starts in June. This long leaf carriage of the dominant tree species of the semi-arid mopane savanna stresses its value as a fodder resource in the Mopaneveld. De la Hunt (1954) already recognised the value of *Colophospermum mopane* as a browser. *C. mopane* leaves have an extremely high feeding value throughout the year, especially during drought conditions and it retains a high feeding value, even when fallen (De la Hunt 1954).

As an adaptation to periodic drought conditions in Mopaneveld systems, *Colophospermum mopane* readily coppices (Henning & White 1974; Timberlake 1996; Timberlake 1999). This property of the species improves fodder production, but is of great concern in the sustainability of the herbaceous layer since higher above-ground biomass reduces grass species production. This also probably enables *C. mopane* to outcompete most other woody species.

Mopane was successfully introduced from Zimbabwe to the arid regions of India in 1963 (Sharma *et al.* 1989). The introduction of *C. mopane* to India was motivated since it was found to grow fast in relation to indigenous trees, tolerates aridity and, according to Sharma *et al.* (1989) improves the fertility of soil. Furthermore it provides good fodder and firewood. Mopane is even found to be effective in sand dune stabilisation (Sharma *et al.* 1989). It however showed poor establishment and survival (Timberlake 1995).

2.2.2.3 Adaptations of *Colophospermum mopane*

Considering its wide distribution, *Colophospermum mopane* has to be adapted to an extreme set of environmental conditions. According to Timberlake (1995) the distribution of *C. mopane* is obviously determined by different ecological factors in different parts of its range. Therefore a continuous range does not exist. Frost incidence and/or minimum temperatures along with minimum annual rainfall may play an important role in the southern and western distribution of *C. mopane*, whilst the higher altitude with an increase in annual rainfall determines its distribution in the north and the east (Werger & Coetzee 1978; Mapaure 1994). In addition to these factors, soil texture was also found to be of influence in the distribution of the species. Henning and White (1974) found *C. mopane* to be highly tolerant of adverse soil conditions, in particular, poor availability of soil water, which explains its wide distribution pattern. It is generally believed that *C. mopane* can tolerate the poorest soil conditions over its distribution range. However, as soon as conditions are more favourable to other woody species, often associated with soil moisture availability, mopane is competed out. Apart from its tolerance towards soil conditions, *Colophospermum mopane* appears to be physiologically adapted to xeric conditions, being able to grow at a matric water potential below -15.2 bar (Henning & White 1974). *C. mopane* is also capable of internal osmotic adjustment. High magnesium levels in the soil tend to favour moisture uptake by *C. mopane* whilst increasing levels of potassium and sodium result in a production decline probably due to increased soil osmotic suction (Timberlake 1995).

2.2.2.4 Uses of *Colophospermum mopane*

Colophospermum mopane is an economically important species to the rural communities of southern African savannas due to its variety of uses.

The long leaf carriage period of *Colophospermum mopane* in the semi-arid areas of its distribution range underlies its value as a fodder resource (Dekker & Smit 1996). Wood is harvested mainly for construction poles and firewood (Timberlake 1995; Chikuni 1996; Madzibane & Potgieter 1999; Van Wyk & Gericke 2000). *Colophospermum mopane* accounts for more than 90 percent of the timber used for living- and storing huts in southern Africa (Van Wyk & Gericke 2000). Mopane is especially popular for its high quality firewood (Timberlake 1995; Chikuni 1996; Van Wyk & Gericke 2000). The remaining ash contains high percentages of phosphorus, calcium and lime, which makes it a suitable fertilizer for small holder farmers (Timberlake 1995; Madzibane & Potgieter 1999). The Herero-speaking people of Namibia use only the wood of *C. mopane* for the sacred fire and for the ceremonial removal of teeth (Van Wyk & Gericke 2000). The inner bark is often used to tie poles together for hut construction (Madzibane & Potgieter 1999; Van Wyk & Gericke 2000). One of the best known uses of the mopane tree is its association with the mopane-worm, an important and popular source of protein for the human diet in rural areas. *Colophospermum mopane* is the major source of food for mopane worms, which are the larvae of the mopane emperor moth (*Imbrasia belina*) (Styles & Skinner 1996; Wiggens 1997; Motshegwe *et al.* 1998; Klok & Chown 1999; Van Wyk & Gericke 2000; Potgieter *et al.* 2001).

C. mopane also has a medicinal value, although of lower significance. Bark decoctions are taken for diarrhoea and stomach pains (Madzibane & Potgieter 1999; Van Wyk & Gericke 2000), constipation is treated by leaf infusions whilst chewed leaves are applied to fresh wounds to stop bleeding. Furthermore, twigs are used as chewing sticks to clean teeth (Van Wyk & Gericke 2000). The Vhavenda in South Africa use mopane roots for gum bleeding, to treat kidney stones and for impotence in a mixture with *Wrightia natalensis*, *Securidaca longipedunculata* and mutshalimela (scientific name unknown) (Madzibane & Potgieter 1999).

2.2.2.5 Management and conservation of the Mopaneveld

Mopaneveld is surely one of southern Africa's most valuable vegetation types. Apart from the different uses of the species, Mopaneveld is commonly associated with specific agricultural practices. Over the last few decades, landowners in the Mopaneveld have switched from livestock farming to game farming. Pressure on the indigenous vegetation due to artificial pasture production has declined consequently. The survival of certain rare animal species, such as the roan antelope, is to a great extent related to successful breeding programmes, which are conducted in conservancies within their natural habitat (Joubert 1976). These usually include Mopaneveld vegetation.

Species cannot necessarily only live in the area to which it is presently confined. It may not have completed its natural migrations and may still be in the process of extending its range (Rattray 1963). Therefore, great concerns have arose involving increasing densities of *Colophospermum mopane* and the resulted decreasing of grass cover, especially in the areas north of the Soutpansberg, South Africa (Donaldson 1979; Smit *et al.* 1994; Smit & Rethman 1998b). Ironically, due to the multiple uses of *Colophospermum mopane* (2.2.2.4) by the growing population of southern Africa and consequently the growing need for natural resources, Mopaneveld in some parts of southern Africa suffers from deterioration and need to be protected. (Anderson & Walker 1974; Lewis 1987; Coe 1991; Ben-Shahar 1996; Bhima & Bredenkamp 1999; Styles & Skinner 1997; Prior & Cutter 1999). These differences between livestock owners and nature conservationists revealed controversy over the management of the Mopaneveld.

Management of Mopaneveld has been reviewed extensively, especially in terms of pasture management. Regarding the conservation of Mopaneveld, the impact of large herbivores (especially the impact of elephants) on the vegetation structure, has received attention. For the scope of this dissertation, no attempt will be made to discuss the different management regimes and conservation attempts. Studies involving the management and/or conservation of Mopaneveld include Rattray (1963), Anderson and Walker (1974), Donaldson (1979), Guy (1981), Lewis (1987), Madams (1990), Lewis (1991), Coe (1991), Coe (1992), O'Connor (1992), O'Connor (1999), Ben-Shahar (1993), Ben-Shahar (1996), Chikuni (1996), Dekker *et al.* (1996), Smit *et al.* (1996), Smit & Rethman (1998), Bhima and Bredenkamp (1999), Bhima and Bredenkamp (in press), Kennedy (2000), and Styles and Skinner (2000).

2.2.3 Review of previous vegetation studies in the Mopaneveld

2.2.3.1 Described communities in the Mopaneveld

A list of most plant communities that have been identified within the southern African Mopaneveld is compiled for future reference (Appendix 1). According to the definition of Mopaneveld all described communities (zonal vegetation) of a certain study are listed and not only those where *Colophospermum mopane* dominates. Although many of the described communities were never published, they are also included in the provided list. The list is however not complete since more vegetation classification studies are presently being undertaken. Listed names of communities are in accordance with the names given by authors. Species names are subjected to change. Where the study was documented in Afrikaans, names were translated into English where applicable.

2.2.3.2 Vegetation types containing Mopaneveld

It is also important to list all vegetation types dominated by *Colophospermum mopane*. Timberlake stated in 1995 that a full list of vegetation types in which *Colophospermum mopane* is found is not available. Appendix 2 represents an attempt to list most of the vegetation types where *C. mo*pane is at least prominent. Vegetation types, as referred to in the provided list, present vegetation mapping units as described in several vegetation maps of countries in southern Africa.

2.2.4 Mopaneveld vegetation

2.2.4.1 Introduction

Covering 54 percent of southern Africa, savanna vegetation is generally characterised by the co-dominance of woody plants and grasses. Small trees or shrubs form an intermediate layer whilst the grass layer may be temporarily absent or replaced by dicotyledonous herbs during periods of drought or disturbance (Scholes 1997). Savannas include plant communities of diverse floristic composition and varying physiognomy from pure grasslands, parklands and low tree and shrub savannas to open deciduous woodlands, thicket and scrub (Cole 1986).

Mopaneveld is an extensive vegetation type (Figure 1) within the savannas of southern Africa, dominated by a well-known, economically and ecologically important tree species, *Colophospermum mopane*. Mopaneveld is abundant in eight different countries in southern Africa covering an area of approximately 550 000 km^2 (Mapaure 1994). The species however ranges further than the distribution of the vegetation type (Timberlake 1999). Individuals of mopane are often well represented outside the vegetation type, where it occurs on termite mounds or on patches where conditions tend to favour its presence (Timberlake 1995; Timberlake 1999). According to Werger and Coetzee (1978), pure stands of *Colophospermum mopane* are often associated with insufficiently drained soils.

2.2.4.2 Physiognomy

The variety of factors influencing the distribution of Mopaneveld vegetation constitutes variance in physiognomical structure over its distribution in southern Africa. However, large areas with locally equal environmental conditions are covered with structurally even and homogenous stands of tree or shrub savanna. In some savanna types gradual floristic and physiognomic changes mark the transition from one type of savanna to another as in the case of Mopaneveld, whilst in others changes are abrupt presenting sharp boundaries (Cole 1986).

C. mopane has four definite growth forms: (i) a tall tree form growing up to 20 m high; (ii) a small to medium sized tree usually from 5–12 m tall (Figure 2a); (iii) a shrubby form up to 6 m tall (Figure 2b), differing from (i) and (ii) in that the bole is not well developed, and (iv) a bushy scrub form usually less than 3 m tall (Figure 2c) (Madams 1990; Timberlake 1995; Timberlake 1996). The closed mopane woodlands (type i) occur in the semi-moist northern parts of its distribution range with trees up to 25 m in height (Werger & Coetzee 1978). This physiognomical structure of Mopaneveld vegetation is often referred to as "cathedral mopane" (Timberlake 1995) and is associated with deeper, less compacted soils, such as alluvium, and higher annual rainfall patterns (Werger & Coetzee 1978; White 1983; Timberlake 1995). The majority of Mopaneveld vegetation is presented with the woodland/savanna tree physiognomical structure (type ii) where it is predominantly found on shallow, sodic, heavier textured solonetzes (Werger & Coetzee 1978; Timberlake 1995). The shrubby, multi-stemmed type (type iv) is associated with heavy clays, often of vertic character (Figure 2c) (Werger & Coetzee 1978; Cole 1986; Van Rooyen & Bredenkamp 1998).

The difference in physiognomy of the species depends upon local environmental conditions, of which soil conditions are usually found to be the most influential. In many parts of Mopaneveld, the physiognomical structure has been modified by fire, herbivory or harvesting, most often leaving dense stands of multi-stemmed shrubs.

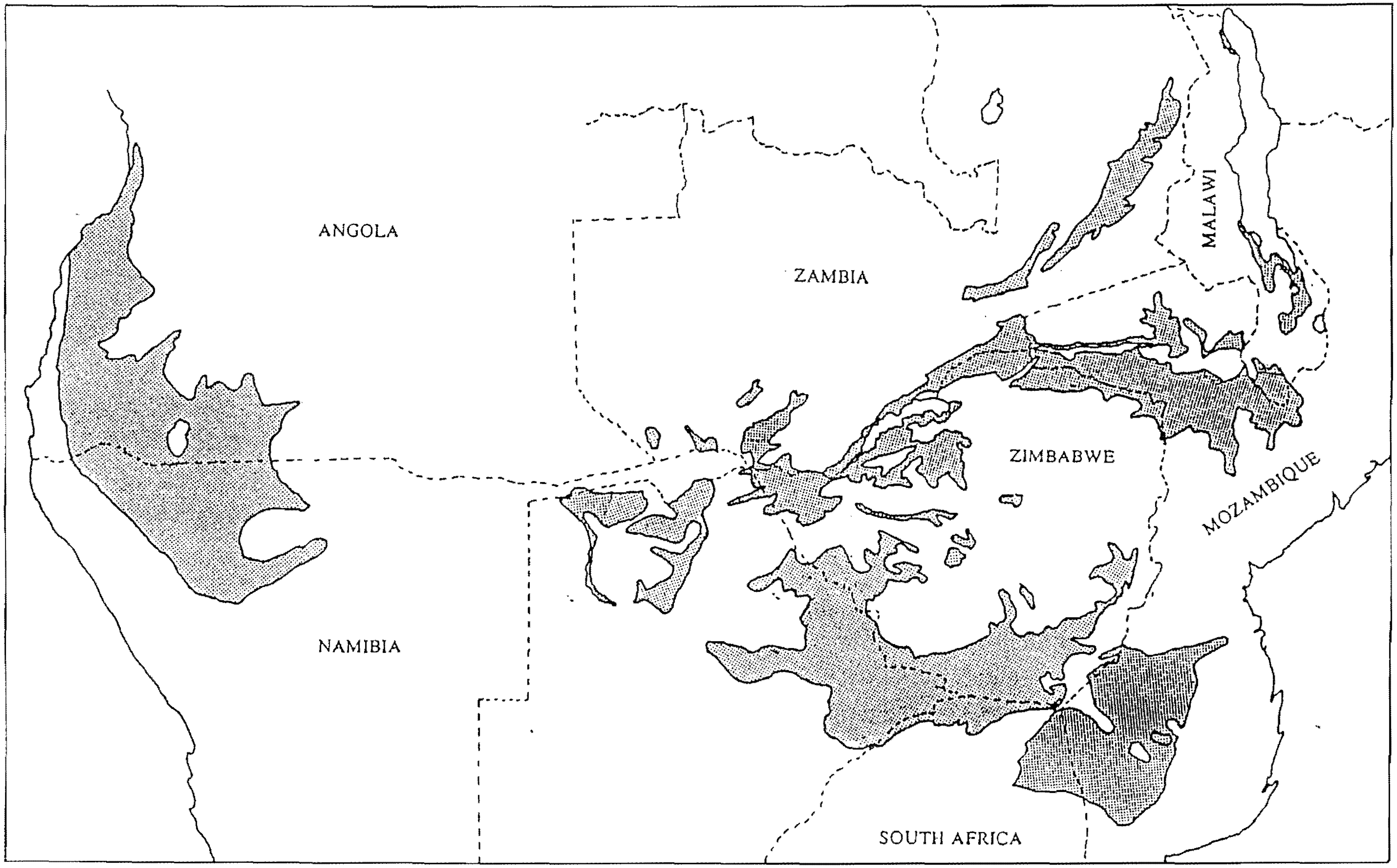

Figure 1 Distribution of Mopaneveld (adapted from Mapaure 1994)

a)

b)

c)

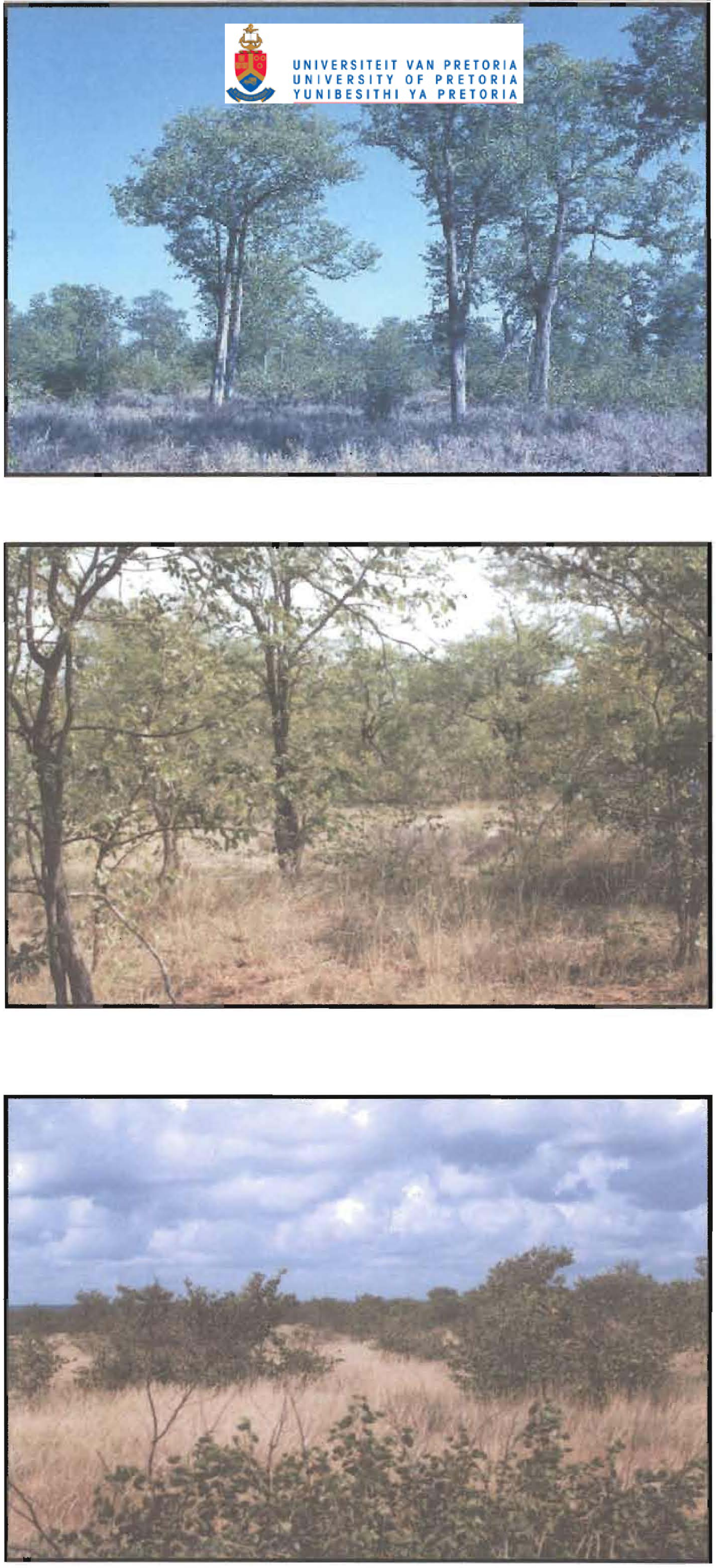

Figure 2 The different growth forms of *Colophospermum mopane*: (a) high trees of 5–12 m in height (b) high mopane shrubs and (c) multi-stemmed bushy shrubs.

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2.2.4.3 Distribution of Mopaneveld

One of the most basic elements of plant ecology is the general study of the various factors influencing the distribution of plants (Rattray 1963; Woodward 1986, Madams 1990). Yet, the causes of particular limits in the distribution of a species, with a few exceptions, are poorly understood (Madams 1990). It is universally believed that plant species occur where environmental conditions favour them (Rattray 1963; Carter & Prince 1988; Dekker & Van Rooyen 1995). The ecological amplitude of a species is mainly set by climatic conditions in the small-scale distribution of a species whilst edaphic, topographic and/or biotic factors play an important part in determining the distribution of species at the larger scale (Woodward 1986).

Colophospermum mopane is certainly one of the most extensive plant species in Africa due to its character to dominate the woody layer of a plant community if conditions are favourable. Considering the vast areas occupied by Mopaneveld in the savannas of southern Africa (Figure 1), factors influencing its distribution are not easily detectable. As already mentioned, the distribution of Mopaneveld generally follows the distribution of *Colophospermum mopane* although the species often occurs as individuals outside the range of *C. mopane*-dominated vegetation (Timberlake *et al.* 1993). Distribution limits of *Colophospermum mopane*, hence Mopaneveld, is obviously determined by different ecological factors over different parts of its range. The distribution of *Colophospermum mopane* is principally influenced by moisture availability expressed through altitude, rainfall and soil texture (Cole 1986; Mapaure 1994). *Colophospermum mopane* generally occupies areas where moisture accumulates at shallow depth. It is therefore often found on impervious bedrock (e.g. granite) overlain by shallow soils or on an impervious layer of transported clay (e.g. riverine silt). Where there is a combination of low rainfall and severe heat, as a result of clay being dispersed by exchangeable sodium, *C. mopane* also occurs (Cole 1986). The shallow rooting system of *Colophospermum mopane* places it in a competitive advantage in areas where conditions lead to the development of a zone of maximum water retention near the surface. Such zones are commonly found in semi-arid savannas due to low rainfall and great heat, which consequently lead to moisture retention near the soil surface.

The general distribution of Mopaneveld is associated with heavier-textured soils in the wide, flat valley bottoms of river valleys such as the Limpopo (Botswana, South Africa, Zimbabwe & Mozambique), Zambezi (Botswana, Zimbabwe, Zambia & Mozambique), Chobe (Botswana), Okavango (Botswana), Cunene (Namibia & Angola), Shire (Malawi) and Luangwa (Zambia & Malawi) (Werger & Coetzee 1978; Cole 1986; Mapaure 1994). *Colophospermum mopane* is profoundly found in the 400 m and 700 m altitudinal range. Following a strongly seasonal summer rainfall regime, it receives between 200 mm and 800 mm annually, coinciding with high temperatures (Mapaure 1994). Low winter temperature is found to be an important distribution determinant to the southernmost distribution of the species. The 5°C isotherm for daily minimum temperatures is thought to coincide largely with the southern distribution boundary of *Colophospermum mopane* (Henning & White 1974; Cole 1986).

Colophospermum mopane is one of several species of the Zambezian Region (White 1983) which penetrates far into the western desert along watercourses. It is however found not to be the dominant woody species in areas receiving less than 300 mm rainfall annually (Timberlake 1995), but rather occurring in the form of bushy trees. *Colophospermum mopane* can tolerate extreme environmental conditions, e.g. surviving on as little as 125 mm rainfall per year in the Kaokoland of Namibia, whilst in the Luangwa Valley in Zambia and central Malawi, it experiences up to 1 000 mm rainfall annually. The majority of plant communities dominated by *Colophospermum mopane* are distributed between the *Brachystegia* - *Isoberlinia* - *Julbernardia* savanna woodlands (miombo) and the *Acacia*-dominated low tree and shrub savanna (Kalahari vegetation). According to Cole (1986) this alternation of different savanna types provides important evidence of the interacting influences of factors and processes affecting the distribution of all categories of savanna and of the plant communities within them.

The distribution of Mopaneveld as well as the vegetation associations and plant communities within, are related not only to the prevailing climatic and edaphic conditions but also to the geomorphological evolution of the landscape, to bedrock geology and to geological events and changes of climate.

The distribution of *C. mopane*-dominated vegetation types has been reviewed by Mapaure (1994) according to vegetation maps from the different hosting countries (e.g. Acocks (1988) for

South Africa, Weare & Yalala (1971) for Botswana, Rattray (1962) for Zimbabwe, Barbosa (1970) for Angola, Giess (1971) for Namibia and Wild & Barbosa (1967) for the Flora Zambesiaca area).

2.2.4.4 Floristic evaluation

According to the floristic map of White (1983) which indicates the main phytochoria of Africa and Madagascar, the Mopaneveld is located within the Sudano-Zambezian Region, or more precisely, its Zambezian domain (Zambezian Regional Centre of Endemism). The Sudano-Zambezian Region comprises vast stretches of woodland, savanna and grassland with occasional dry forests and thickets as well as swampy vegetation (Werger & Coetzee 1978). In the arid regions of Namibia and Angola, Mopaneveld crosses the borders of the Sudano-Zambezian Region into the Karoo-Namib Region (Werger & Coetzee 1978), a region of extensive desert and semi-desert areas. The boundary between the Sudano-Zambezian Region and the adjacent Karoo-Namib Region to the West is however not clear-cut (Werger & Coetzee 1978), explaining the transition of *Colophospermum mopane*-dominated vegetation into the desert Region. White (1983) acknowledges this transition between Zambezian and Karoo-Namib species in his mapping unit 36 (The Zambezian/Kaokoveld-Mossamedes transition in the XIVth phytochoria: Kalahari-Highveld Regional Transition Zone). Mopaneveld of these arid regions is a transition from *Colophospermum mopane* scrub woodland to a Karoo-Namib shrubland (White 1983).

Colophospermum mopane can tolerate extremely dry conditions. In areas where *C. mopane* is subjected to moisture stress, it predominantly occurs along drainage lines (Figure 3). In its western distribution limits, *Colophospermum mopane* occurs as stunted trees (up to 3 m tall) in association with the well-known desert species, *Welwitschia mirabilis* (Figure 4) (White 1983; Werger & Coetzee 1978).

Although *C. mopane* and miombo woodlands are found adjacent to each other over much of its range, they rarely occur together, as their associated floras are dissimilar (White 1983; Timberlake 1995). Vegetation types of alternated dominance of miombo and *C. mopane* are however apparent in the Zambezi Valley (Timberlake & Mapaure 1992; Timberlake *et al.* 1993). Where they occur together, *Colophospermum mopane* is restricted to depositional clay-rich soils in the lower parts of the catena or on termitaria whilst miombo woodlands inhabit the upper parts on lighter-textured soils on rocky outcrops (White 1983; Timberlake & Mapaure 1992; Timberlake *et al.* 1993). Mopaneveld also often shares dominance with *Combretum*-dominated woodlands. In general Mopaneveld possesses fewer species and a poorly-developed grass layer in comparison with miombo and *Combretum* woodlands. The alternation of *Combretum*-dominated vegetation and Mopaneveld vegetation is well-known in South Africa (e.g. Van Rooyen 1981c; Gertenbach 1983; Venter & Gertenbach 1986; Gertenbach 1987) and follows the exact pattern as that of the miombo-mopane association.

Mopaneveld often has a low alpha-diversity due to the almost monospecific stands of *Colophospermum mopane* over much of its distribution range. Beta-diversity is low in comparison to miombo woodlands, and can be altered with infrequent rainfall and grazing events. Variability in rainfall, as well as grazing history in most parts of the Mopaneveld constitutes sporadic responses of especially the herbaceous stratum, which consequently constitute a rapidly changing species composition (O'Connor 1985). Species richness in Mopaneveld is most often dependent on the cover of *Colophospermum mopane*. High cover of *C. mopane* results in low species richness whereas a higher species richness is noted in areas of low *C. mopane* cover (O'Connor 1992). According to Timberlake (1995) Mopaneveld has a low gamma diversity due to typical associated species being similar across much of its range. These typical tree species include *Acacia nigrescens*, *A. nilotica*, *Adansonia digitata*, *Albizia harveyi*, *Balanites* spp., *Combretum apiculatum*, *C. hereroense*, *Commiphora* spp., *Dalbergia melanoxylon*, *Diospyros quiloensis*, *Erythroxylum zambesiacum*, *Kirkia acuminata*, *Sclerocarya birrea*, *Terminalia prunioides*, *T. stuhlmannii* and *Ziziphus mucronata*. Shrubs include *Combretum elaeagnoides*, *Dichrostachys cinerea*, *Gardenia resiniflua*, *Grewia* spp., *Ximenia americana* and species of the family Capparidaceae. The herbaceous layer predominantly contains species of the Acanthaceae. The grass layer is generally poor and often dominated by annuals such as *Aristida*, *Enneapogon* and *Eragrostis* species (Timberlake 1995).

2.2.5 Discussion of Mopaneveld vegetation in the eight hosting countries

Mopaneveld vegetation is discussed according to the eight different countries hosting this extensive savanna type. The vegetation of certain countries is discussed in more detail. These countries contributed to the phytosociological synthesis in terms of adequate, electronic vegetation data and are therefore investigated in more detail. General physiognomy and species composition is discussed in coherence with environmental factors influencing its distribution and general character. The discussion of the vegetation follows species names as published in the literature.

2.2.5.1 Angola

"Angola presents the paradox of possessing one of the richest and most varied, yet least well known wildlife resources in Africa" (Huntley 1974). Although only a drop in the wildlife kingdom of Angola is contributed by Mopaneveld vegetation, it represents the largest expanse of Mopaneveld in southern Africa (112 500 km^2) (Mapaure 1994). It is restricted to the south-western part of the country between Lobito in the north and the Cunene River, bordering Namibia in the south. Angolian Mopaneveld occurs on a variety of soil types mainly derived from granite. Rainfall seems to be the major determinant in its distribution in Angola (Mapaure 1994). The Mopaneveld vegetation represented in Angola continues into the north-western Mopaneveld of Namibia.

Inland from the desert areas along the Atlantic coast, Mopaneveld dominates the savanna on areas where rainfall exceeds 300 mm. In these savanna woodlands Mopaneveld is alternates with *Baikiaea* woodlands which are predominantly located on the Kalahari sands, whereas Mopaneveld inhabits the clayey substrates (Huntley 1974). Further westwards to the Kaokoland (Namibia) and Chela (Angola) escarpments, at an altitude of approximately 250 m, low shrubs of *Colophospermum mopane* together with *Balanites welwitschii* occur predominantly in dry riverbeds under a rainfall of sometimes less than 100 mm annually. Other species associated with 3 m tall *C. mopane* shrubs in these arid-western region, include *Catophractes alexandri*, *Rhigozum virgatum* and *Phaeoptilum spinosum* on dry, often rocky soils (Werger & Coetzee 1978). It is in this region that Mopaneveld crosses the border of the Sudano-Zambezian Region into the Karoo-Namib Region (Werger & Coetzee 1978). On sites with locally more water available, *Spirostachys africana* becomes subdominant or even dominant. Tree species associated with this type include *Pteleopsis diptera*, *Pterocarpus lucens* subsp. *antunesii*, *Commiphora angolensis*, *C. mollis*, *Combretum psidioides*, *C. zeyheri* and several *Acacia* species (Werger & Coetzee 1978).

At the foot of the Chela escarpment (800–1 100 m altitude) and near Ngiva (1 000–1 200 m altitude) mopane woodlands prevail with *Colophospermum mopane* trees varying from 7 m to 15 m in height. Woody species accompanying *C. mopane* include *Terminalia prunioides*, *Commiphora angolensis*, *Combretum oxystachyum*, *Acacia erubescens*, *Balanites angolensis*, *Cordia ovalis*, *Hexalobus monopelatus*, *Croton* spp., *Ximenia caffra*, *Grewia bicolor* and *Euclea* spp. (Werger & Coetzee 1978). In the herbaceous layer species such as *Schmidtia pappophoroides*, *Aristida rhiniochloa*, *A. adscensionis*, *Anthephora pubescens*, *Eragrostis annulata*, *E. porosa*, *E. superba* and *Pegolettia senegalensis* dominate (Werger & Coetzee 1978).

A well-defined mopane shrubland is abundant south of Lubango on predominantly impermeable black clays. This shrubland is associated with several *Acacia* species including *A. kirkii*, *A. nilotica* subsp. *subalata*, *A. hebaclada* subsp. *tristis* and other woody species such as *Flueggea virosa*, *Spirostachys africana*, *Peltophorum africanum* and *Dichrostachys cinerea* (Werger & Coetzee 1978).

2.2.5.2 Botswana

From the Limpopo River in the east to the Makgadikgadi pans in the north as well as surrounding the Okavango swamps, 85 000 km^2 area are covered with mopane woodland and savanna. Its distribution is mainly determined by rainfall, which varies from 400 mm to 600 mm annually (Mapaure 1994). Sands, silts, clay loams and clays support mixed tree and bushland savanna whilst mopane woodlands are associated with fersiallitic soils on uplands and siallitic colluvial soils with impeded drainage in the valleys (Mapaure 1994).

Mopaneveld of Botswana can be subdivided into dry deciduous forest, riparian forest, woodland, thicket, tree or shrub savanna or shrub steppe (Weare & Yalala 1971), therefore hosting most of the physiognomic forms of Mopaneveld. Woody species associated with *Colophospermum mopane* vary in distribution, but generally *Acacia nigrescens*, *Sclerocarya birrea*, *Terminalia prunioides*, *Commiphora mossambicensis*, *Combretum apiculatum*, *C. imberbe*, *Dichrostachys cinerea*, *Maytenus heterophylla* and *Adansonia digitata* are the most prominent ones (Wild & Barbosa 1967; Weare & Yalala 1971; Werger & Coetzee 1978). The grass cover is generally sparse including species such as *Eragrostis lehmanniana*, *E. superba*, *E. rigidior*, *Digitaria eriantha*, *Aristida congesta*, *Brachiaria nigropedata*, *Cenchrus ciliaris* and *Urochloa oligotricha* (Weare & Yalala 1971).

The predominant type in Botswana Mopaneveld is the tree and bush savanna (mopane bushveld) (Weare and Yalala 1971). This broad vegetation type however encompasses several types of *C. mopane* vegetation, that can be differentiated by density and physiognomy of *C. mopane* itself, rather than by differences in its associated species. In the Limpopo River Valley (annual rainfall 400 mm or less), the Mopaneveld is shrubby (maximum 5 m in height) or it occurs as a low treeveld with individuals of *Colophospermum mopane* approximately 8 m tall (Wild & Barbosa 1967; Werger & Coetzee 1978). *Colophospermum mopane* woodlands of lower or even dwarf stature occupy large areas on calcrete in eastern, northern and western Botswana and in the Transvaal Lowveld. A moderately undulating landscape is commonly associated with this tree/shrub savanna. Tree and shrub savanna occurs on reddish and loamy sands underlain by shallow alluvium or colluvium derived from Palapye shales (Timberlake 1980). Species in association include *Terminalia sericea* and *Acacia fleckii*. On more calcareous areas *Tarchonanthus camphoratus*, *Rhigozum brevispinosum* and *Combretum hereroense* are conspicuous. Where it occurs on light sandy soil, *Colophospermum mopane* dominates the woody layer with accompanying trees such as *Terminalia sericea*, *Burkea africana*, *Combretum imberbe* and scattered *Lonchocarpus capassa* and *Commiphora* spp. (Weare & Yalala 1971). A common character of Mopaneveld in Sandveld areas is its varying physiognomy in relation to sand depth. Where alluvium and other "mopane-favouring" soils are close to the surface, density of *C. mopane* is higher whilst *C. mopane* occurs in low densities prevail on a thick cover of sand (Timberlake 1980). A mopane thicket woodland prevails on sandy, impenetrable soils. This low tree savanna is often associated with overgrazing and erosion. Prominent woody species include

Combretum apiculatum, *Acacia erubescens* and scattered individuals of *Terminalia prunioides*, *Acacia mellifera* and *A. tortilis* subsp. *detinens* along smaller watercourses (Weare & Yalala 1971). The Mopaneveld along the Makgadikgadi grassy plains occurs on sands, silt and clays. *Colophospermum mopane* grows as trees in association with *Acacia nigrescens*, *Terminalia prunioides*, *Sclerocarya birrea*, *Combretum imberbe*, *Dichrostachys cinerea* and *Maytenus heterophylla* (Werger & Coetzee 1978). On the silty soils, especially near salt pans such as the Makarikari, a low open mopane bushveld or mixed veld is found with some species of *Acacia* and *Grewia* (3–5 m high) being prominent (Werger & Coetzee 1978).

One of the most interesting Mopaneveld features is located along the Okavango delta (500 mm rainfall annually). *Colophospermum mopane* forms open woodlands over riverine silts in the Okavango delta (Cole 1986). Not only does *Colophospermum mopane* reach heights of over 20 m on these alluvial floodplains, but isolated individuals may also be found on termitaria of the central delta areas (Biggs 1979). A *Colophospermum mopane* woodland and pyrophytic scrub savanna occurs on some of the larger islands within the delta area (Biggs 1979). Woody species associated with these communities include amongst others *Croton megalobotrys*, *Grewia bicolor*, *G. flava*, *G. villosa*, *Commiphora africana* and *Boscia mossambicensis*. Although poorly developed, the following species dominate the herbaceous layer: *Eragrostis curvula*, *Setaria verticillata*, *Aristida stipitata*, *Chloris virgata*, *Achyranthes sicula*, *Tribulus terrestris*, *Sesuvium nyasicum*, *Ruellia patula*, *Acanthosicyos naudinianus*, *Harpagophytum* sp. and *Bidens schimperi* (Biggs 1979).

Further inland of the delta the vegetation is dominated by mopane treeveld in association with *Burkea africana* on shallow east-west valleys. In the Moremi Wildlife Reserve and the Mababe Depression the tall mopane woodlands are interrupted by shrub mopane and a broad-sclerophyll arid bushveld type. Broad orthophyll *Terminalia sericea* bushveld alternates with Mopaneveld in these areas (Werger & Coetzee 1978). Due to impervious clay soils being associated with Mopaneveld, rain pans are common in mopane woodlands. These pans are bordered by microphyllous thorny *Acacia* bushveld (Werger & Coetzee 1978; Biggs 1979) with *Acacia* spp. such as *A. tortilis* and *Albizia harveyi* (Biggs 1979).

Mopaneveld along rivers in Botswana are characterised by a mopane woodland in association with *Acacia nigrescens* in the tree layer and *Grewia flavescens* and *Grewia flava* dominating the shrub layer (Werger & Coetzee 1978). On waterlogged soils *Colophospermum mopane* is alternated by *Acacia xanthophloea* and *Hyphaene petersiana* (Werger & Coetzee 1978).

2.2.5.3 Malawi

The smallest area of Mopaneveld in southern Africa (10 000km^2) is hosted in Malawi where it occurs on altitudes between 450 m and 500 m receiving 800 mm or less rainfall annually (Mapaure 1994). It is these two environmental factors (rainfall and altitude) that is believed to determine the distribution of Mopaneveld in Malawi (Mapaure 1994). Werger and Coetzee (1978) stated that Mopaneveld in Malawi is rarely encountered with and if present, it is not as extensive as in the other hosting countries. Mopaneveld occurs in Liwonde National Park, Lengwe National Park, Majete, Mwabvi and Vwaza Marsh Wildlife Reserves as well as in the mid-Shire Valley in Chingale (Namatunu Forest) in Zomba and Mua-Tsanya Forest Reserve in Dedza (Chikuni 1996). In the mid-Shire Valley, deep soils produce *C. mopane* woodland. In the lower Shire Valley and along the southern shores of Lake Malawi, Mopaneveld is found on compact, alkaline, dark grey sandy clays with free calcium carbonate (Wild & Barbosa 1967; Werger & Coetzee 1978) supporting a tree savanna (Mapaure 1994). This dry deciduous woodland savanna is dominated by *Colophospermum mopane* on deep sandy clay where individuals reach 30–31 m, considerably higher than recorded elsewhere (Dudley 1994). The Malawian Mopaneveld is almost uniform in woody species dominance (Wild & Barbosa 1967). In Liwonde National Park, *Colophospermum mopane* usually forms monotypic stands, although on termite hills *C. mopane* individuals are accompanied by species of *Drypetes*, *Markhamia*, *Cassia*, *Euphorbia*, *Tamarindus*, *Acacia*, *Commiphora*, *Ziziphus*, *Croton*, *Salvadora* and *Dalbergia* (Dudley 1994). The mopane clump savanna is widely distributed in the Liwonde National Park with Mopaneveld restricted to the regularly spaced termite hills. These termite-Mopaneveld communities are surrounded by grassy glades, often seasonally waterlogged (Dudley 1994; Bhima & Bredenkamp in press).

2.2.5.4 Mozambique

The Limpopo, Save and Zambezi rivers, all three being associated with extended Mopaneveld along their valleys, flow through Mozambique to enter the sea. Receiving between 400 mm and 700 mm rainfall annually, the Mopaneveld of Mozambique is principally dominated by woodlands and savanna of which their distribution is thought to be influenced by rainfall (Mapaure 1994). Approximately 98 000 km^2 area is covered by Mopaneveld vegetation in Mozambique (Mapaure 1994). The Save and Limpopo valleys contain calcareous alluvium on which mopane savanna predominates, whilst both mopane woodland and savanna is found in the Zambezi valley, mainly composed of relatively deep, compact, clayey and calcareous soils derived from Karoo formations (Mapaure 1994).

Mopaneveld vegetation in the valleys of the Save- and Limpopo River occurs as a mixed tree and shrub savanna (Werger & Coetzee 1978). Soils are lacustrine, calcareous formations with several alluvial depressions. Rainfall in this region is irregular and less than 400 mm annually, decreasing inland (Wild & Barbosa 1967). The vegetation varies according to variance in soil types, but also according to changes in topography. Generally *Colophospermum mopane* is accompanied by species such as *Ximenia americana*, *Salvadora angustifolia*, *Azima tetracantha*, *Adenium multiflorum*, *Boscia albitrunca*, *Pachypodium saundersii*, *Dombeya kirkii*, *Sanseveria* spp., *Euphorbia* spp., *Maerua edulis* etc. (Werger & Coetzee 1978).

A major contribution to Mopaneveld is located in the Zambezi River valley. Mopaneveld of this valley, stretching from the Caprivi (Namibia) in the West to the Tete district (Mozambique) in the East, consists of almost pure *Colophospermum mopane* woodlands, with scattered *Adansonia digitata* trees. Soils are generally deep, clayey and often contain calcareous material. Annual rainfall measures between 500 mm and 700 mm. Altitude varies from 200 m to 500 m (Werger & Coetzee 1978). A mixed Mopaneveld occurs where the soils are stonier. Species associated with this type include *Commiphora* spp., *Combretum* spp., *Acacia nigrescens*, *Albizia* spp., *Ximenia americana*, *Dalbergia melanoxylon* and several more. The undergrowth is generally sparse and contains species of *Andropogon* and *Setaria* and also *Cenchrus ciliaris* (Werger & Coetzee 1978).

2.2.5.5 Namibia

The distribution of Mopaneveld in Namibia stretches from the Cunene River in the north towards the Ugab in the south and north-eastwards towards Namutoni, as well as occupying patches in the Caprivi strip (Mapaure 1994). Mopaneveld in Namibia covers approximately 77 000 km^2. A variety of soil types accompany the distribution of Mopaneveld in Namibia. Variance in soil type in combination with erratic, variable rainfall patterns probably determine the distribution of Mopaneveld in Namibia (Mapaure 1994).

Colophospermum mopane often makes up a spaced woodland with a shrubby understorey in Namibia. Its southern distribution boundary follows the 5°C isotherm of mean daily minimum temperature for the coldest month, July. This explains why *C. mopane* does not exist either in the eastern part of Owamboland or in the Kavango. Close to its southern boundary, frost damage is frequent. The height of *C. mopane* trees decreases from north to south and west where the weather is cooler and drier. The more alcaline the soil, the poorer the growth of the trees. Soils under *Colophospermum mopane* tend to have poor permeability and high susceptibility to erosion (Erkkilä & Siiskonen 1992).

Colophospermum mopane occupies the arid lands along the Kaokòland escarpment in Namibia and the Chela escarpment in Angola. It is in these arid regions where *Colophospermum mopane* crosses the border of the Sudano-Zambezian Region into the Karoo-Namib region (Werger & Coetzee 1978) (see also 2.2.5.1). Receiving an annual rainfall of 50–100 mm (250 m altitude), the western limits of Namibian Mopaneveld along the Kaokoland escarpment toward the Namib Desert is characterised by a low shrub savanna type. Although still dominating the woody layer, *Colophospermum mopane* is confined to depressions and small riverbeds (Figure 3) (Werger & Coetzee 1978; Giess 1998). Vegetation associated with *Colophospermum mopane* in these arid areas include species such as *Balanites welwitschii*, *Sesamothamnus benguellensis*, *S. guerichii*, *Commiphora* spp. including *Commiphora africana*, *C. angolensis*, *C. anacardiifolia*, *C. crenato-serrata*, *C. discolor*, *C. giessii*, *C. glaucescens*, *C. kraeseliana*, *C. mollis*, *C. multijuga*, *C. pyracanthoides*, *C. tenuipetiolata*, *C. virgata*, *C. wildtii* and many species of the Acanthaceae in the herabceous stratum (Werger & Coetzee 1978; Giess 1998). What is of particular interest, is the occurrence of Mopaneveld on arid lands in the western part of the country, often being associated with the well-known desert species, *Welwitschia mirabilis* (Figure 4).

The Kaokoland lies between the 0–300 mm rainfall isohyets and produces only desert or semi-desert soils and corresponding vegetation. The vegetation of the Kaokoland can be divided into two major components, being arid savanna and desert and sub-desert (Joubert 1971).

In the study of Becker and Jürgens (2000) the vegetation of Kaokoland was examined by analyzing three transects through the study area by means of phytosociological criteria. Although presenting a description of the vegetation of Kaokoland 20 years after the study of Viljoen (1980), the results corresponded to a large extend. For the purpose of an overview of the vegetation of Kaokoland in Namibia, the discussion mainly follows the descriptions by Viljoen (1980).

In the dry, central parts of the Kaokoland escarpment, an open tree savanna predominates on an altitude between 700 m and 1 100 m. Being the dominant woody species for this open savanna, *Colophospermum mopane* reaches a height of 2.5 m (Viljoen 1980). Species accompanying mopane in this savanna type include *Catophractes alexandri*, *Terminalia prunioides*, *Combretum apiculatum*, *Euphorbia damarana*, *Ceraria longipedunculata*, *Commiphora multijuga*, *C. virgata*, *C. africana*, *Maerua schinzii* and *Sesamothamnus guerichii*. The herbaceous stratum is poorly developed with *Schmidtia kalahariensis* being the dominant grass species (Viljoen 1980). In the long, undulating valley of the Hoarusib River, bordered by the Tonnesen- and Girraffen Mountains, a dwarf mopane savanna predominates in association with *Terminalia prunioides* (Viljoen 1980). The annual rainfall of the Hoarusib Valley ranges between 150 mm and 250 mm. Shallow, calcareous, stony soils (Figure 5), interrupted by deep, sandy loamy soils on colluvial and alluvial plains, characterise this arid area (Viljoen 1980). The tree layer is dominated by *Colophospermum mopane* in association with *Terminalia prunioides*. Other species with lesser dominance include *Sesamothamnus guerichii* (Figure 6), *Maerua schinzi*, *Boscia foetida*, *Commiphora pyracanthoides*, *Acacia reficiens*, *A. senegal* var. *rostrata*, *Salvadora persica*, *Petalidium rossmannianum*, *Monechma genistifolia* and *M. arenicola* (Viljoen 1980; Becker & Jürgens 2000). The herbaceous layer is heavily utilised with scattered tussocks of *Schmidtia kalahariensis*, *Enneapogon cenchroides* and *Stipagrostis uniplumis* (Viljoen 1980).

Another open tree savanna, a typical Kaokoland valley Mopaneveld, prevails in the Sesfontein and Warmquelle valleys. This savanna type receives between 72 mm and 164 mm rainfall per year and inhabits calcareous, as well as colluvial and alluvial soils varying in soil moisture content (Viljoen 1980). Trees in this type reach heights of more than 12 m despite the low rainfall patterns (Viljoen 1980). *Acacia tortilis* is in strong association with *Colophospermum mopane* in this valley bushveld. They do occur together, however *Colophospermum mopane* tends to grow denser but lower with scattered individuals of *Maerua schinzii*, whilst *Acacia tortilis* forms an open treeveld with *Salvadora persica* occupying the shrub stratum (Viljoen 1980). Due to over-utilisation no perennial species occur in the herbaceous stratum. Instead, annuals such as *Chloris virgata*, *Setaria verticillata*, *Eragrostis denudata*, *Monelytrum luederitzianum*, *Enneapogon brachystachyus*, *Tribulus* sp. and *Heliotropium ovalifolium* dominate (Viljoen 1980).

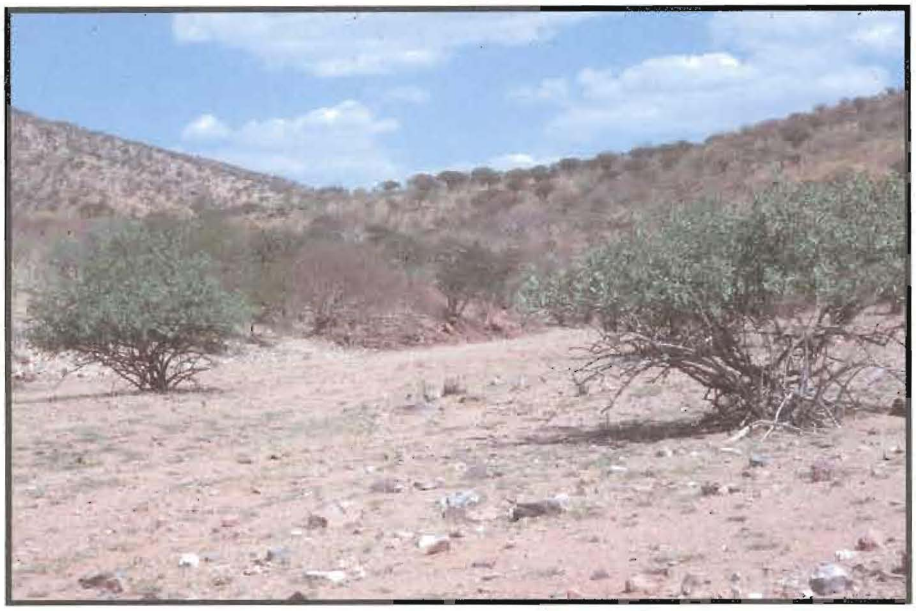

Figure 3 *Colophospermum mopane* often inhabits dry washes in the arid Kaokoland.

Figure 4 One of the most spectacular combinations: *Colophospermum mopane* and *Welwitschia mirabilis* in the Namibian desert.

Figure 5 Shallow, calcareous soils in Namibian Mopaneveld.

Figure 6 *Sesamothamnus guierichii* in a *Colophospermum mopane* community on calcareous soils.

A *Colophospermum mopane – Terminalia prunioides – Combretum apiculatum* tree savanna occurs on an altitude between 850 m and 1 500 m in the undulating, broad valleys of the northeastern Kaokoland (Viljoen 1980). Rainfall figures of this area near 350 mm annually (Viljoen 1980). The vegetation however does not reflect this relatively high rainfall pattern. It is suggested to be ascribed to poor soil moisture availability in the predominant shallow, rocky soils (Viljoen 1980). The most conspicuous tree species of this area include *Colophospermum mopane*, *Terminalia prunioides* and *Combretum apiculatum*. The co-dominance of these species is interrupted by dominance by several *Commiphora* spp. on the mountain slopes and rocky outcrops, whilst on the granitic outcrops *Cissus nymphaeifolia* and *Hexalobus monopetalus* predominate. On the more sandy soils dominance by *Hippocratea africana* and *Pterocarpus lucens* subsp. *antunesii* characterise the vegetation (Viljoen 1980).

From Opuwo and further south the vegetation is also characterised by the co-dominance of *Colophospermum mopane* and *Terminalia prunioides* (Viljoen 1980). On deeper soils however, *Terminalia prunioides* is replaced by *Spirostachys africana* and in the lower-lying valleys of alluvium, *Acacia tortilis* and *Ziziphus mucronata* dominate the tree stratum. On the mountains and hills *Sterculia africana* and several *Commiphora* species predominate. On calcareous plains a dwarf shrubveld occur with the most conspicuous species being *Petalidium rossmannianum* and *Hirpicium gorteroides* (Viljoen 1980).

In the Etosha National Park, Kaokoland vegetation is represented in the western regions of the park on calcrete, rhiolite, andesite and granite of the Damara supergroup (Le Roux *et al.* 1988). Receiving approximately 300 mm rainfall annually, this Kaokoland vegetation type is presented by Mopaneveld type vegetation. On very shallow lithosols on a calcrete substrate *Colophospermum mopane* is accompanied by *Acacia reficiens*, *Terminalia prunioides* in the tree stratum and *Gossypium triphyllum*, *Boscia foetida*, *Monechma genisitifolium*, *Petalidium englerianum* and *Leucosphaera bainesii* in the shrub stratum (Le Roux *et al.* 1988). On sites where aeolian sands cover calcrete boulders, *Sesamothamnus guerichii*, *Catophractes alexandri*, *Otoptera burchellii* and *Mundulea sericea* also become prominent with the herbaceous layer being well-developed and including species such as *Anthephora schinzii*, *Enneapogon desvauxii*, *Stipagrostis hirtigluma* and *Enneapogon cenchroides* (Le Roux *et al.* 1988). Lithosolic soils derived from the andesites are relatively fertile and produce a heterogenic vegetation type on this hilly landscape. The herbaceous stratum is perennial with *Eragrostis nindensis* being very prominent (Le Roux *et al.* 1988).

Mopaneveld vegetation occurring on calcareous substrates in Etosha National Park is furthermore abundant south of the Etosha Pan, extending westwards. Le Roux *et al.* (1988) refers to this vegetation type as Karst woodlands, although it does not represent woodlands in the true sense of the word. Adjoining the sweet grassland, which in turn borders the southern edges of the pan, the vegetation is characterised by the dominance of *Colophospermum mopane* on calcareous lithosols. In some areas *C. mopane* forms homogeneous stands, but generally the woody stratum comprises species such as *Catophractes alexandri*, *Acacia reficiens*, *Acacia mellifera*, *Grewia* spp., *Commiphora pyracanthoides*, *Montinia caryophyllaceae*, *Acacia senegal*, *Boscia foetida*, *B. albitrunca*, *Acacia nebrownii* and *Gossypium triphyllum*. The herbaceous stratum is fairly well developed including species such as *Stipagrostis hochstetteriana*, *Cenchrus ciliaris* and several annual species of *Enneapogon* and *Aristida* (Le Roux *et al.* 1988). On shallower soils *Combretum apiculatum* and *Terminalia prunioides* become more prominent. On areas receiving slightly higher rainfall, although still being Karstveld vegetation, *Colophospermum mopane* and *Terminalia prunioides* are the most prominent trees on boulder calcrete. The soils are very shallow and overlie a calcified dolomite or a low-grade marble. The soils are however fertile and heavy clayey soil often erupts on the surface. *Spirostachys africana* becomes prominent on soils containing higher moisture levels.

Mopaneveld in Namibia is not only restricted to calcareous substrates and alluvium, but also on Kalahari-type sand (Joubert 1971). The dry western sandveld of the Etosha National Park (Le Roux *et al.* 1988) is characterised by shrub Mopaneveld where the sand is shallow and calcretes are exposed. *Leucosphaera bainesii*, *Seddera suffruticosa*, *Rhigozum brevispinosum* and *Commiphora angolensis* are often accompanying mopane in the woody layer whereas *Anthephora pubescens*, *Pogonarthria fleckii* and *Eragrostis dinteri* dominate the grassy layer (Le Roux *et al.* 1988). On deeper Kalahari sand *Terminalia sericea* becomes prominent with *Acacia erioloba*, *Dichrostachys cinerea* and *Croton gratissimus* also present (Le Roux *et al.* 1988).

In small depressions in the Etosha National Park shrub Mopaneveld predominates on loamy soils with a high clay content (Le Roux *et al.* 1988). Species associated with *C. mopane* in this shrub savanna include *Catophractes alexandri*, *Dichrostachys cinerea*, *Leucosphaera bainesii* and *Grewia flava* (Le Roux *et al.* 1988).

Further eastwards from the escarpment, Mopaneveld turns from a predominant shrubland to an open tree savanna in Owamboland of the Cuvelai Delta. Owamboland, a broad plain about 1 100 m above sea level, is located in the northern parts of Namibia. Aeolian Kalahari sands of varying depth cover the area with scattered patches of calcareous concretes. Oshanas, being seasonally flooded water courses, dissect the Cuvelai Delta in Owamboland (Figure 7). This area receives between 350 mm rainfall per year in the southwest, while the northeastern parts receive 550 mm annually. Rainfall patterns are however unpredictable, but generally precipitation peaks in February (Erkkilä & Siiskonen 1992). The western part of Owamboland belongs to Mopaneveld where this extensive vegetation type occurs as interfaces on slightly elevated terraces or sand dunes between the seasonally flooded Oshanas. Due to the availability of water in the semi-arid region of the Cuvelai Delta, the area is densely populated and, at least most of the area is converted to agricultural fields and grazing land (Erkkilä & Siiskonen 1992). Wood harvesting, especially of *C. mopane* is also common along the Oshanas (Figure 8). Trees dominating the vegetation of this area include *Colophospermum mopane*, several species of *Acacia*, *Combretum* and *Commiphora*, *Diospyros mespiliformis*, *Hyphaene petersiana* (Figure 9), *Adansonia digitata* and *Terminalia sericea* (Erkkilä & Siiskonen 1992).

Even more eastwards in the Kavango, *Colophospermum mopane* occurs as scattered individuals but never dominates the woody stratum (Erkkilä & Siiskonen 1992). The three major zonal Mopaneveld vegetation types in the Caprivi (Mendelsohn & Roberts 1997) relate to a large extent the soil types. The Mopaneveld type is restricted to the heavy, poorly-drained clay soils interrupting deep Kalahari sands inhabited by *Baikiaea plurijuga*, *Burkea africana*, *Pterocarpus angolensis*, *Ricinodendron rautanenii* and *Guibourtia coleosperma*. On the light clay soils, *Acacia erioloba*, *Combretum imberbe* and *Acacia nigrescens* are common (Mendelsohn & Roberts 1997). *Colophospermum mopane* occurs as the only large tree in the *C. mopane–Aristida* woodland on heavy clay loams (Mendelsohn & Roberts 1997). Mopane is however accompanied by *Acacia erioloba* and *Albizia harveyi* where the soils are better drained. A mosaic of Mopaneveld and Sandveld often occurs where pockets of Kalahari sands interrupt the "mopane soils" (being heavier-textured clays or clayey loam soils). In this mosaic vegetation type, *C. mopane* occurs with tree species which are usually not associates of mopane, e.g. *Burkea africana*, *Erythrophleum africanum*, *Terminalia sericea* and *Combretum collinum* (Mendelsohn & Roberts 1997).

Figure 7 Oshanas in Owamboland. Mopaneveld occurs on the interfaces within the flooded areas.

Figure 8 Wood harvesting has a pronounce effect on the structure of *Colophospermum mopane* trees in Owamboland, Namibia.

Figure 9 *Hyphaene petersiana* (arrow) is a common associate of *Colophospermum mopane* in Owamboland, Namibia.

2.2.5.6 South Africa

The South African Mopaneveld is distributed along the Limpopo River Valley in the north where it extends towards its affinities in the neighbouring Zimbabwe and Botswana. The Soutpansberg forms the southern distribution limit in the wide, gently undulating landscapes of Limpopo River Valley (Acocks 1988). A broad plain of Mopaneveld extends from the northern border of the Kruger National Park along the eastern end of the Soutpansberg in Venda, to its most southern distribution limit just south of the Olifants River in the Kruger National Park where the annual rainfall is slightly higher (Gertenbach 1987).

Mopaneveld in South Africa covers a total area of 23 00 km^2. Generally it follows areas of altitudes ranging from 400–750 m, rainfall varying between 250 mm and 400 mm annually and high temperatures (15–31°C) (Acocks 1988; Mapaure 1994). Rainfall and altitude seem to influence the distribution of mopane in South Africa, while physiognomy is determined by soil type (Mapaure 1994). Mopaneveld physiognomy is a striking feature in the Mopaneveld of South Africa. Extensive areas of multi-stemmed, shrubby Mopaneveld cover the basaltic plains in the Kruger National Park (Figure 2c) whereas mopane woodlands is associated with soils derived from shale and a mixed mopane treeveld covering granitic and calcareous substrates.

Acocks (1953) did not separate the two distinct physiognomical units of Mopaneveld in South Africa, namely shrubveld and treeveld. Low and Rebelo (1998) distinguished between Mopane Shrubveld and Mopane Bushveld (Van Rooyen & Bredenkamp 1998). Mopane Shrubveld is commonly associated with heavy clayey soils often with vertic or near-vertic properties derived from basalt and gabbro. A stunted, multi-stemmed shrubby growth of fairly dense mopane (1–2 m in height) characterises this type occurring in the broad basaltic plains along the eastern distribution of Mopaneveld in the Kruger National Park (Figure 2c). Individuals of *Combretum imberbe*, *C. hereroense*, *C. apiculatum*, *Sclerocarya birrea*, *Lonchorcapus capassa*, *Acacia nigrescens*, *A. exuvialis*, *Commiphora glandulosa*, *C. africana*, *Grewia bicolor*, *Dalbergia melanoxylon*, *Flueggea virosa*, *Ehretia rigida*, *Maerua parvifolia*, *Dichrostachys cinerea* and *Cissus cornifolia* is commonly associated with this type (Gertenbach 1978; Gertenbach 1983; Van Rooyen & Bredenkamp 1998). Gertenbach (1983) distinguished three variations of mopane shrubveld on basalt and gabbro according to the herbaceous layer. They include the open shrubveld of the *Bothriochloa radicans* variation on Milkwood soils, the mopane shrubveld containing scattered individuals of *Colophospermum mopane* and *Combretum apiculatum* trees of the *Themeda triandra* variation on deeper soils of, either Bonheim, Swartland and Mayo types. The last variation is the *Setaria woodii* (=*S. incrassata*) occurring on concave terrain where soils are very clayey with a vertic character. *Colophospermum mopane* is more sparsely dispersed while species such as *Acacia nigrescens*, *Albizia harveyi* and *Lonchocarpus capassa* become more prominent in the woody stratum (Gertenbach 1983). The herbaceous layer of the mopane shrubveld includes dense stands of *Themeda triandra*, *Setaria incrassata*, *Bothriochloa radicans*, *Panicum coloratum*, and *Digitaria eriantha* (Gertenbach 1978; Van Rooyen & Bredenkamp 1998), whilst others such as *Enneapogon cenchroides*, *Aristida congesta*, *Eragrostis superba*, *Schmidtia pappophoroides*, *Cenchrus ciliaris*, *Urochloa mosambicensis* and *Panicum maximum* occur frequently (Gertenbach 1983).

The mopane shrubveld is however not restricted to the heavy clays derived form basalt and gabbro, but also occurs in the Limpopo River Valley on calcareous soils of an intersected to undulating landscape (Gertenbach 1983; Mapaure 1994). This unique landscape (Gertenbach 1983) is underlain by the Malvernia Formation, which decomposes to give rise to soil with many lime concretions (Gertenbach 1983). The vegetation of this shrub savanna consists of *Colophospermum mopane*, *Maytenus heterophylla*, *Euclea schimperi*, *Grewia bicolor*, *Acacia nigrescens*, *Combretum apiculatum*, *Terminalia prunioides*, *Euclea divinorum*, *Sterculia rogersii*, *Commiphora mollis*, *Zanthoxylum humilis* and *Dalbergia melanoxylon* in the woody layer. Grasses such as *Enneapogon scoparius* and *Aristida congesta* characterise the herbaceous stratum while *Seddera capensis* occurs frequently as a forb (Gertenbach 1983).

Another less common Mopaneveld type is the Olifants River Rugged Veld on metamorphic rock (Gertenbach 1983). The vegetation shows xerophytic characteristics with a field layer being very sparse. *Colophospermum mopane* occurs not as a sole dominant, but the mixed relatively high species diversity open savanna is comprised of individuals of which *Combretum apiculatum*, *C. hereroense*, *Colophospermum mopane*, *Commiphora mollis*, *Commiphora africana*, *Terminalia prunioides*, *Grewia villosa*, *G. bicolor*, *Boscia albitrunca*, *Acacia nigrescens*, *Dalbergia melanoxylon*, *Dichrostachys cinerea* are the most conspicuous (Gertenbach 1983).

Mopane Bushveld (Van Rooyen & Bredenkamp 1998) is commonly associated with deeper soils. Although monotypic stands of *Colophospermum mopane* occur in Mopane Bushveld it is in general more a mixed savanna than the Mopane Shrubveld. In the main river valleys Mopaneveld is more mixed and a striking feature is the scattered individuals of *Adansonia digitata* in the open treeveld (Figure 15) (Acocks 1988).

A familiar Mopaneveld type is the open to closed mopane treeveld savanna in association with *Combretum apiculatum*. This vegetation type is commonly underlain by amphibolite of the Swaziland System, granite and gneiss intersected with dolerite intrusions (Gertenbach 1983). The undulating landscape derived from the Swaziland System constitutes sandy uplands and more clayey bottomlands. *Combretum*-dominated vegetation is confined to the more sandy uplands whilst *Colophospermum mopane* vegetation inhabits the clayey bottomlands. The upland *Combretum*-dominated vegetation includes odd individuals of *Colophospermum mopane* whilst species such as *Combretum apiculatum*, *C. zeyheri*, *Terminalia sericea*, *Albizia harveyi*, *Dalbergia melanoxylon*, *Sclerocarya birrea*, *Cissus cornifolia*, *Acacia exuvialis*, *A. burkei*, *Dichrostachys cinerea*, *Commiphora africana* and *Lannea schweinfurthii* dominate (Gertenbach 1983). In the middle-and footslopes *Colophospermum mopane* occurs in association with *Combretum apiculatum* accompanied by other species including *Ormocarpum trichocarpum*, *Acacia gerrardii*, *A. nigrescens*, *Ozoroa engleri*, *Euclea divinorum*, *Bolusanthus speciosus*, *Combretum hereroense*, *C. imberbe*, *Terminalia prunioides*, *Grewia bicolor*, *Maerua parvifolia* and *Ximenia caffra* in the woody layer (Gertenbach 1983).

The herbaceous layer of both the uplands and bottomlands is well developed with dominant grass species being *Pogonarthria squarrosa*, *Eragrostis rigidior*, *Aristida congesta*, *Digitaria eriantha*, *Panicum maximum*, *Enneapogon cenchroides*, *Heteropogon contortus*, *Schmidtia pappophoroides*, *Bothriochloa radicans*, *Themeda triandra* and *Urochloa mosambicensis* (Gertenbach 1983). Forb species characterising the *Combretum*-mopane type include *Indigofera floribunda*, *Kyphocarpa angustifolia*, *Rhynchosia totta*, *Indigofera bainesii*, *Tephrosia polystachya*, *Ruellia patula*, *Asparagus plumosus*, *Corchorus asplenifolius*, *Seddera capensis*, *Phyllanthus asperulatus*, *Cucumis hirsutus* and *Hibiscus micranthus* (Gertenbach 1983).

Mopaneveld occurring on sands is not to be overlooked. Although it usually does not form the sole dominant of a community in sandveld areas, *Colophospermum mopane* occurs as scattered individuals on, either termitaria, or clayey soils overlain by a shallow sandy sheet (Chapter 6). The Sandveld occurring in the Kruger National Park is derived from, either the Waterberg System, the Phalaborwa Igneous Complex and the Swaziland System. Sandveld derived from the Swaziland System and the Phalaborwa Igneous Complex gives rise to undulating landscapes, generally granitic of origin. The vegetation coincides with the *Combretum*-mopane type associated with granite, although this type is sandier with tree species such as *Peltophorum africanum* and *Pseudolachnostylis maprouneifolia* occurring on heavily leached sandy uplands as a result of a higher rainfall in the area (Gertenbach 1983). The Tsende Sandveld (Gertenbach 1983) is dominated by *Colophospermum mopane*, although not alternated by *Combretum* vegetation according to distinct topography, but *Combretum*-dominated vegetation occurring rather as interrupting strips on sandier plains in the moderately high shrub savanna (Gertenbach 1983). In the northern parts of the Kruger National Park, an ecotone type of Mopaneveld occurs as a border between proper Mopaneveld and Sandveld (Chapter 6). Although conditions do not reflect the typical distribution of *C. mopane* in this area, scattered patches of *C. mopane*-dominated vegetation occurs between deep sandy plains of the Waterberg System, where vegetation is totally atypical of Mopaneveld.

Mopane forests occur in isolated patches of Mopaneveld on deep alluvium (mostly along watercourses) or loamy soils derived from Ecca-shales. The vegetation of these woodlands is mixed with high *Colophospermum mopane* trees (10–15 m in height) and others including *Spirostachys africana*, *Acacia nigrescens*, *Euclea divinorum*, *Grewia bicolor*, *Ximenia americana*, *Maerua parvifolia*, *Zanthoxylum humilis*, *Thilachium africanum*, *Acacia grandicornuta*, *A. tortilis*, *Combretum imberbe*, *C. hereroense*, *Dichrostachys cinerea*, *Boscia albitrunca* and *Dalbergia melanoxylon* (Gertenbach 1983). In the herbaceous layer *Enteropogon macrostachyus*, *Enneapogon cenchroides*, *Chloris roxburghiana*, *Panicum maximum*, *Aristida congesta*, *Digitaria eriantha*, *Bothriochloa radicans* and *Schmidtia pappophoroides* dominate the grassy layer while *Amaranthus thunbergii*, *Hibiscus micranthus*, *Seddera capensis*, *Abutilon fruticosum*, *Crotalaria virgulata*, *Indigofera vicioides* and *Neuracanthus africanus* are conspicuous forbs (Gertenbach 1983). Along drainage lines tall mopane trees in association with tall *Acacia karroo* trees occur with sparse undergrowth, predominantly *Panicum maximum* cover (Acocks 1988). In the Limpopo Valley, a closed canopy of mopane forest occurs with little undergrowth (Acocks 1988). The vegetation is striking, containing, apart from high *C. mopane* which coincides with high temperatures (Fanshawe 1969; Cole 1986; Mapaure 1994). The ability of *C. mopane* to withstand these extreme conditions results in being a good competitor, which explains the almost monotypic stands of the species in parts of the Luangwa Valley. Woody species that are interspersed through the woodland include *Adansonia digitata*, *Combretum elaeagnoides*, *C. obovatum*, *Diospyros quiloensis*, *Holarrhena pubescens*, *Ximenia americana* and *Markhamia obtusifolia*. The undergrowth is sparse with dominant species including *Eragrostis viscosa*, *Andropogon gayanus*, *Aristida adscensionis*, *Chloris virgata*, *Brachiaria eruciformis*, *Echinochloa colona*, *Urochloa mosambicensis*, *Kyllinga alba* and several more (Werger & Coetzee 1978). Mopaneveld in the Luangwa Valley is however also frequently interrupted by patches of *Acacia* savanna and *Combretum-Terminalia sericea* woodland where conditions tend towards lower extremes (Werger & Coetzee 1978). On soils types where a sandy sheet overlays a hard and compact, alkaline sandy loam with a columnar structure, mopane woodlands with trees reaching heights of 25 m is found. A shrub Mopaneveld interrupts this woodland type (Werger & Coetzee 1978; Mapaure 1994).

Mopaneveld in the Zambezi River Valley of the Lake Kariba region differs from the Luangwa and associated valleys. The former is a bit drier, although still receiving more or less 700 mm rainfall per annum.

Termite mound building on the fluvisol-vertisol soils in the Luangwa Valley and the physiognomy of Mopaneveld on these soils depend on the depth and duration of flooding during the rainy season. Slight and temporary, or even absent floods result in the absence of termite mounds with *Balanites* shrubs occurring throughout the woodland. Scattered termite mounds accompanied by species not being able to withstand the floods follow the increase in flood duration and depth. A pure stand of "cathedral" mopane prevails on areas where flood duration and depth went beyond a certain point. Termite mounds are absent from these sites (Fanshawe 1969).

In "The Vegetation of Zambia", Fanshawe (1969) describes two ecotone types involving mopane woodlands. The first, an ecotone of Mopaneveld with miombo woodland, occurs on the colluvial soils of scarp slopes, on basalt soils around Livingstone and on schist ridges in the Gwembe Valley. On basalt around Livingstone, a low, open woodland with a deciduous canopy is characterised by *Colophospermum mopane*, *Acacia nigrescens*, *Adansonia digitata*, *Julbernardia globiflora*, *Kirkia acuminata*, *Peltophorum africanum*, *Pterocarpus lucens* subsp. *antunesii*, *Sclerocarya birrea* and *Sterculia* species (Fanshawe 1969). An ecotone of Mopaneveld with munga woodland occurs on alluvial flats and damboes, Karoo sandstones, alluvial mudstones not being flooded, skeletal mudstones and pebble beds (Fanshawe 1969). The ecotone with munga on sandstone and mudstone is a rich, tall, open deciduous woodland characterised by *Colophospermum mopane*, *Acacia nigrescens* and *Combretum apiculatum*. The understorey is well developed in the shrubby layer where species such as *Acacia nilotica*, *Albizia anthelmintica*, *Boscia matabelensis*, *Combretum elaeagnoides*, *Croton gratissimus*, *Dalbergia melanoxylon*, *Diospyros quiloensis* and *Grewia bicolor* are among the dominants (Fanshawe 1969). Another Mopaneveld-munga ecotone type exists as a broken, low open scrub Mopaneveld accompanied by *Terminalia randii* and *T. stuhlmannii*.

2.2.5.8 Zimbabwe

Zimbabwean Mopaneveld is commonly associated with the Zambezi, Limpopo, Sabi and Shangani valleys with medium size *Colophospermum mopane* trees to tall mopane woodlands (Werger & Coetzee 1978; Mapaure 1994). The distribution of Mopaneveld in Zimbabwe is thought to be determined by rainfall, which ranges between 500 mm and 700 mm annually, and altitude (being approximately 400 m) (Mapaure 1994).

Mopaneveld covers 101 500 km^2 in Zimbabwe (Mapaure 1994) and seems to represent approximately twelve major types. These types can be distinguished according to general physiognomical appearance and species composition, which follow the variance of a combination of factors, of which substrate type, soil depth, altitude and annual rainfall are probably the most important determinants for their distribution (Guy 1975; Timberlake *et al.* 1993; Mapaure 1994). Differences in soils account for the very heterogenous structure of Mopaneveld in Zimbabwe (Guy 1975), and probably in the rest of its distribution range.

Mopaneveld vegetation types in Zimbabwe are discussed according to three major physiognomical structures, which include *Colophospermum mopane* woodlands, tree savannas and shrub savannas. The variance within physiognomical structures is also addressed.

Mopane woodlands

There is great variance in *Colophospermum mopane*-dominated woodlands. They often grade into other woodland types or even into woodland thicket types. It is often difficult to determine where the *Colophospermum mopane* woodland types change to woodland savannas due to the variation in tree density along the valleys of the large rivers dissecting Zimbabwe. In the higher rainfall areas, e.g. in the northern Zambezi Valley in Zimbabwe, Mopaneveld varies between woodland and woodland savanna whereas in the drier south, woodland savanna, tree savanna and tree/bush savanna prevails. As a result of partial clearing for cultivation or cutting for timber, many woodlands have been degraded to more open savanna types (Rattray 1962).

The first *Colophospermum mopane* woodland type is identified as a pure *C. mopane* woodland generally occuring on the valley floors of large rivers dissecting Zimbabwe. In the Zambezi Valley this deciduous woodland occurs as the most extensive vegetation type of the valley floor (Guy 1975). According to Rattray & Wild (1961) this woodland is, as far as tree size and density is concerned, much better developed than those from the Sabi and Limpopo systems. This pure *C. mopane* woodland type occurs on soils which are generally derived from Karoo sediments, particularly mudstone and often sandstone, or old alluvium. These sediments produce deep, well-drained, fertile, sandy clay loam to clay, or often calcareous soils, on which pure stands of *Colophospermum mopane* trees between 10 m and 18 m high predominate (Rattray 1962; Wild & Barbosa 1967; Farrell 1968a; Timberlake & Mapaure 1992; Timberlake *et al.* 1993). Tree species such as *Adansonia digitata*, *Acacia nigrescens*, *Kirkia acuminata*, *Sterculia africana* and several *Commiphora* and *Combretum* species however often interrupt the monotypic appearance of the *Colophospermum mopane* woodland (Rattray & Wild 1961; Wild & Barbosa 1967; Du Toit 1993). On the more sandy soils *C. mopane* trees are typically associated with *Combretum apiculatum*, *C. collinum*, *Diospyros quiloensis*, *Acacia nigrescens*, *Commiphora mollis*, *Erythroxylum zambesiacum*, *Lannea schweinfurthii*, *Schrebera trichoclada*, *Strychnos madagascariensis* and *Xeroderris stuhlmannii* (Timberlake *et al.* 1993). The shrub layer is also better developed on the sandier soils (Timberlake *et al.* 1993). In areas where the *C. mopane* woodlands are tall and well developed with an almost closed canopy, the herb layer is poorly developed with scattered shrubs and a very poor, or even no grass cover is produced (Guy 1975; Timberlake & Mapaure 1992; Timberlake *et al.* 1993). Although not common, *Chloris* *virgata* and species of *Aristida*, *Digitaria*, *Eragrostis* and *Sporobolus* dominate the grass layer (Guy 1975; Timberlake *et al.* 1993). Where the canopy cover is less dense, a good cover of *Andropogon gayanus* occurs (Timberlake & Mapaure 1992). In areas where the canopy is sparser *Acacia nilotica*, *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Diospyros quiloensis*, *Erythroxylum zambesiacum*, *Ximenia americana*, *Gardenia resiniflua*, *Commiphora glandulosa*, *C. africana*, *Vepris zambesiaca*, *Maerua* spp., *Boscia* spp. and *Grewia bicolor* may occur (Timberlake & Mapaure 1992; Du Toit 1993; Timberlake *et al.* 1993). In the Sabi Valley a shrubby *Grewia bicolor* understorey occurs (Rattray 1962).

Occasionally *C. mopane* woodlands occur on old alluvium or colluvium. On these substrates *C. mopane* trees reach heights of 18 m or more and are termed "cathedral mopane". Trees of *Acacia nigrescens*, *A. robusta* subsp. *clavigera*, *Albizia anthelmintica* and *Balanites aegyptiaca* is often associates in this woodland type. This unique woodland type also produces a poorly developed understorey (Timberlake *et al.* 1993).

Although not very common and occuring in small patches, a *Colophospermum mopane* woodland type exists on a gently undulating expanse of sandy terrain along the border of Mozambique in the Zambezi Valley (Du Toit 1993). An open stand of tall, thin *Colophospermum mopane* trees and occasionally accompanied by also tall, scraggly *Combretum apiculatum* trees characterise this type (Du Toit 1993).

Colophospermum mopane often occurs in a woodland type of alternating dominance of *Kirkia acuminata* and *Acacia nigrescens* on shallower lithosols or skeletal soils, mainly derived from basalt (Rattray 1962; Du Toit 1993; Timberlake *et al.* 1993). In this woodland type, *C. mopane* is confined to the slightly deeper soils with *Kirkia acuminata* being predominant on shallow soils and rocky rises (Timberlake *et al.* 1993). *Combretum apiculatum*, *Diospyros quiloensis*, *Erythroxylum zambesiacum*, *Sclerocarya birrea*, *Commiphora mollis*, *C. mossambicensis* and *C. glandulosa* are common associates in the tree layer (Timberlake *et al.* 1993). The shrub layer is well developed with, amongst others, *Carphalea pubescens* and *Dalbergia melanoxylon*, while the grass layer is poorly developed (Timberlake *et al.* 1993). On heavier-textured soils, associated with *C. mopane* dominance, *Terminalia stuhlmannii*, *Combretum hereroense*, *Ximenia americana* and *Commiphora africana* become more important in the woody stratum

(Timberlake *et al.* 1993). *C. mopane* often shares dominance with *Terminalia stuhlmannii* on this undulating, slightly raised terrain. Extensively covered by rounded pebbles, the soils are usually sandy clay loam at medium depths derived from sandstones and siltstones (Timberlake & Mapaure 1992). Species being associated with the *C. mopane* – *T. stuhlmannii* woodland include *Kirkia acuminata*, *Sclerocarya birrea*, *Erythroxylum zambesiacum*, *Commiphora glandulosa*, *C. mossambicensis*, *C. mollis*, *Acacia nilotica*, *A. nigrescens* and *Ximenia americana* (Timberlake & Mapaure 1992; Timberlake *et al.* 1993). On shallower soils, this type is strongly associated with a *C. mopane – Combretum apiculatum* woodland (Timberlake & Mapaure 1992). The latter type includes an open woodland on medium to light textured soils formed from Karoo sandstone. *C. mopane* trees of 6–8 m characterise this type with additional major trees being *Combretum apiculatum* and *Diospyros kirkii*. The *Colophospermum–Diospyros kirkii* open woodland on shallow soils forms a type of its own and represents an open woodland with *C. mopane*, *D. kirkii* and *C. apiculatum* being the major components. The soils are generally shallow, light-textured lithosols with a shallow layer of brown loamy sand to clay loam derived from Karoo sandstone or from basalt (Timberlake *et al.* 1993). On sandier soils miombo elements such *as Pseudolachnostylis maprouneifolia*, *Diplorhynchus condylocarpon* and *Terminalia stenostachya* occasionally occur (Timberlake & Mapaure 1992).

Colophospermum mopane woodlands also occur along fringing rivers or major watercourses. On heavier-textured, fertile soils, a well-developed closed woodland thicket or an open woodland type occurs with trees between 12 m and 20 m high. Conspicuous species in the tree layer include *Colophospermum mopane*, *Diospyros quiloensis*, *Acacia robusta* subsp. *clavigera*, *A. nigrescens*, *Piliostigma thonningii*, *Lonchocarpus capassa*, *Combretum imberbe* and *Lannea schweinfurthii*, whereas *Combretum elaeagnoides*, *C. obovatum*, *C. mossambicense*, *Acacia ataxacantha*, *A. nilotica*, *Friesodielsia obovata* and *Markhamia zanzibarica* are amongst the dominants in the shrub layer. Species such as *Heteropogon melanocarpus* and *Digitaria* spp. define the poorly-developed grass layer (Guy 1975; Timberlake *et al.* 1993; Du Toit 1993).

Although not being a miombo species, *Colophospermum mopane* often interrupts miombo woodlands in northern Zimbabwe expressing ecotone woodlands (Rattray 1962; Farrell 1968b; Timberlake & Mapaure 1992; Du Toit 1993; Timberlake *et al.* 1993). The miombo-mopane association in Zimbabwe coincides with the *Combretum*-mopane association where Mopaneveld tends to inhabit the less sandy, heavier soil types usually on the foothills of an undulating landscape, or in the lower-lying valley floors, whereas miombo and *Combretum*-dominated vegetation (=Combretumveld) are more or less confined to the rocky, sandy soils on the hill crests and middle slopes (Timberlake & Mapaure 1992). Three major miombo-mopane woodland types are recognised in Zimbabwe. The *Brachystegia allenii*–mopane woodland is found at the foot of the Zambezi escarpment on colluvium (Timberlake & Mapaure 1992). The vegetation forms a mosaic with *Colophospermum mopane* being dominant on heavier-textured soils while *Brachystegia allenii* is dominant on coarser-textured soils (Timberlake & Mapaure 1992). The *Brachystegia glaucescens* woodland on hills follows almost the same pattern as the *B. allenii–C. mopane* woodland with *C. mopane* becoming more important towards the heavier-textured, slightly deeper bottomland soils (Timberlake *et al.* 1993). The second type is the *Brachystegia boehmii – Colophospermum mopane* woodland and is associated with heavy, often shallow sandy loam colluvial soils (Rattray 1962; Timberlake & Mapaure 1992; Timberlake *et al.* 1993). The *Brachystegia boehmii–Colophospermum mopane* woodland is open in some areas and closed in others. It can even present a clumped woodland or woodland thicket. The height of the dominant trees varies between 8 m and 16 m (Timberlake *et al.* 1993). Prominent tree species, generally being associated with this type, include *Colophospermum mopane*, *Brachystegia boehmii*, *Julbernardia globiflora* and *Kirkia acuminata*. Timberlake *et al.* (1993) distinguished three subtypes within the *B. boehmii–C. mopane* woodland being separated by species composition following substrate differences. A subtype on Cretaceous and Karoo sandstones represents a woodland to open woodland. A second subtype represents an alternating dominance of *C. mopane*, *B. boehmii*, *Julbernardia globiflora* and *Kirkia acuminata* on paragneiss, gneiss and granite whereas the third subtype is associated with termitaria and rocky outcrops (Timberlake *et al.* 1993). The *Julbernardia globiflora–Colophospermum mopane* woodland (type 3) is commonly associated with shallow, skeletal soils and with rocky, hilly areas derived from Karoo sandstones or associated with large termitaria (Rattray 1962; Du Toit 1993; Timberlake *et al.* 1993). In this woodland type *Julbernardia globiflora* and *Colophospermum mopane* alternate dominance with the miombo element (*J. globiflora* and associates) being confined to the sandier patches on slopes of rocky hills, and *Colophospermum mopane* to the heavier textured soils in the bottomlands (Timberlake *et al.* 1993). Trees accompanying *Julbernardia globiflora* dominance include amongst others *Diplorhynchus condylocarpon*, *Combretum zeyheri*, *Pseudolachnostylis maprouneifolia* and *Burkea africana*.

In the shrub layer *Baphia massaiensis* predominates. The grass layer of this type is generally tall with species such as *Aristida meridionalis*, *Pogonarthria squarrosa*, *Heteropogon melanocarpus* and *Stereochlaena cameronii* (Timberlake *et al.* 1993). Associates of *C. mopane* in the tree layer include *Terminalia stuhlmannii*, *Diospyros quiloensis* and *Terminalia prunioides*. The shrub layer is not well developed, but species such as *Acacia nilotica*, *Mundulea sericea*, *Erythroxylum zambesiacum*, *Boscia mossambicensis* and *B. matabalensis* may occur. In contrast with the *Julbernardia* vegetation, the grass layer of the *C. mopane* type in the bottomlands is not well developed and sparse individuals of *Hyparrhenia* spp., *Loudetia* spp., *Aristida* spp., *Brachiaria* spp. and *Heteropogon melanocarpus* occur (Timberlake *et al.* 1993).

Julbernardia globiflora has in general a wider altitudinal range comparing to the *Brachystegia* species. Pure *Julbernardia globiflora* communities are often found at lower altitudes where climatic conditions are less favourable to *Brachystegia* species. It is under these warm, dry conditions that *Julbernardia* woodlands are associated with *Colophospermum mopane* in ecotone types, as been described above (Rattray 1962). The woodland stature becomes somewhat opened and changes towards a savanna type (Rattray 1962).

Within a miombo type on intercalated sandstone (Du Toit 1993), small patches on deep white sands derived from coarse arkose sandstone represent a *Combretum-Strychnos* woodland in which *Colophospermum mopane* is one of the major components in the tree layer (Du Toit 1993). Other include *Kirkia acuminata*, *Burkea africana*, *Commiphora ugogensis*, *Pteleopsis anisoptera* and *Lonchocarpus bussei* with *Combretum apiculatum* and *Strychnos madagascariensis* being the dominants (Du Toit 1993).

The grass cover of the miombo-mopane associations is in general sparse but on heavy red soils derived from dolerite and epidiorite it is better developed. Perrenial grass species such as *Themeda triandra*, *Heteropogon contortus* and *Setaria sphacelata* tend to dominate on these soil types (Rattray 1962; Timberlake *et al.* 1993).

The Mopaneveld in Zimbabwe also covers semi-arid areas (400–600 mm rainfall annually) in the Limpopo Valley and its larger tributaries. *Colophospermum mopane* woodlands are not as common as in the Zambezi Valley, although large *C. mopane* trees can be found on the deeper alluvium soils along large watercourses (Farrell 1968a; Rogers 1993; Campbell & Du Toit 1994; O'Connor & Campbell 1986).

In Hwange National Park where the Madumabisa mudstones produce sandy clay to clayey soils, *C. mopane* often dominates the tree layer forming an almost uniform woodland type of 8–10 m in height (Rogers 1993). Trees such as *Erythroxylum zambesiacum*, *Acacia nigrescens* and *Diospyros quiloensis* occur as scattered individuals through the gregarious mopane. The understorey is well developed, consisting of *Combretum elaeagnoides*, *Terminalia prunioides*, *Commiphora pyracanthoides*, *C. africana*, *Grewia monticola* and *Vepris zambesiaca* (Rogers 1993). On seasonally inundated areas, *Colophospermum mopane* occurs in a woodland or wooded grassland type in association with woody species such as *Combretum imberbe*, *C. hereroense*, *Lonchocarpus capassa*, *Dichrostachys cinerea*, *Acacia nigrescens*, *Ziziphus mucronata* and *Hyphaene petersiana*.

A *Colophospermum mopane* woodland and mixed shrub woodland occurs on the north bank of the Lundi River on soils of granophytic origin (O'Connor & Campbell 1986). *C. mopane* dominates the tree layer in association with *Adansonia digitata* (O'Connor & Campbell 1986). A *Colophospermum mopane– Markhamia acuminata* (now *M. zanzibarica*) type occurs on the north bank of the Lundi River. Associated species include *Combretum imberbe*, *C. mossambicense*, *Thilachium africanum* and *Vitex* spp. (O'Connor & Campbell 1986). Mopaneveld in the Sabi-Lundi basin occurs on almost all soil types at lower altitudes, being dominant or sub-dominant on alcaline clays (Farrell 1968a). Short thickets or short closed *C. mopane* woodlands occur in the Save Valley on clayey soils derived from granite, gneiss, conglomerate, lava, shale, quartzite, limestone, grits and alluvium (Hin 2000). *Colophospermum mopane* in this region generally dominates the woody layer on flat or slightly rolling topography. The herbaceous layer is generally sparse in the closed woodland whereas a dense herbaceous layer is apparent along drainage lines (Hin 2000).

A mopane woodland on mudstone is found along the watercourses of the Lukosi River and its tributaries in the Hwange National Park (Rogers 1993). The woody component mainly comprises *Diospyros quiloensis*, *Dichrostachys cinerea*, *Combretum mossambicense*, *Terminalia prunioides*, *Erythroxylum zambesiacum*, *Acacia robusta* and *A. ataxacantha* (Rogers 1993).

Mosaic patches of Mopaneveld within other vegetation types are a general phenomenon (e.g. patches of Mopaneveld often interrupt miombo woodlands and woodland thickets on deep sand). Although miombo-type vegetation generally occurs on substrates atypical of Mopaneveld, individuals of *C. mopane* however inhabit the heavier-textured soils. On elevated areas of unconsolidated sand *Colophospermum mopane* occurs as an associate in dry forests and thickets, and not as a sole dominant in the woody component (Timberlake *et al.* 1993). *C. mopane* is however still a major component of the vegetation, therefore being discussed under Mopaneveld vegetation. In contrast to woodlands dominated by *Colophospermum mopane*, these dry forests and thickets contain a well-developed shrub layer, but the grass layer is still of poor condition (Timberlake *et al.* 1993). *C. mopane* occasionally occurs as an associated species in the *Terminalia brachystemma* bushed woodland, the *Combretum* woodland thicket on colluvium and sandstone, the *Combretum collinum* low open woodland on sand, the *Baikiaea* woodland on Kalahari sands and lastly in the *Baikiaea–Acacia* bushed woodland on sand dunes (Timberlake *et al.* 1993). In the *Terminalia brachystemma* bushed woodland on slightly elevated areas of unconsolidated, medium-textured brownish sands, probably remnants of aeolian Kalahari sand, *C. mopane* is amongst the main emergent trees accompanied by *Kirkia acuminata* and *Xeroderris stuhlmannii*. This bushed woodland to wooded bushland is characterised by trees of *Terminalia brachystemma* (6–8 m high) (Timberlake *et al.* 1993). Close to the shores of Lake Kariba the *C. mopane* individuals occasionally occur in a *Combretum* woodland thicket on colluvium and sandstone, usually in association with *Lannea schweinfurthii* (Timberlake *et al.* 1993). In the *Combretum collinum* low open woodland no clear catenary sequence exists, but species such as *C. mopane*, *Combretum apiculatum* and *Lonchocarpus nelsii* seem to occur on patches where the sands are thinner and there is some influence of heavier sub-soils (Timberlake *et al.* 1993). *C. mopane* occasionally occurs on heavier-textured soils in the *Baikiaea* woodlands on Kalahari sand. Patches of atypical miombo interrupt this type by the presence of *C. mopane*, *Combretum apiculatum*, *Boscia albitrunca*, *Grewia flavescens* and *Dichrostachys cinerea* (Timberlake *et al.* 1993). In areas where *C. mopane* occurs as a single species rather than forming pure stands, it is often accompanied by *Kirkia acuminata* and *Acacia nigrescens*.

Colophospermum mopane vegetation on termitaria is certainly a Mopaneveld type that can not be denied. This type is especially associated with Miombo. Deep, well-drained soils are not typical habitat for Mopaneveld, but termitaria within this habitat type provide habitat for

Colophospermum mopane and its associates. Woodland types where *Colophospermum mopane* is confined to termitaria include *Combretum* woodlands in a somewhat sloped landscape on deep, unconsolidated, generally coarse sands derived from Karoo sandstone (Timberlake *et al.* 1993). Termitaria in the *Brachystegia spiciformis–B. boehmii* woodland on deep, redeposited, unconsolidated Kalahari sand, the *Brachystegia boehmii–Pterocapus angolensis* open woodland on unconsolidated, medium to loamy sands derived from Karoo or Chizaira sandstone on a sandstone plateaux, and the *B. boehmii–Julbernardia* woodland on shallow soils, are inhabited by Mopaneveld-type vegetation with *Colophospermum mopane* dominating the tree layer (Timberlake *et al.* 1993).

Tree savanna

South of the Kalahari Sand areas and the main plateau in Zimbabwe, *Colophospermum mopane* woodlands are replaced by open tree savanna vegetation (Wild & Barbosa 1967). Where *C. mopane* is fairly pure and the grass cover is good, perennial grasses include *Eragrostis rigidior*, *Cenchrus ciliaris*, *Schmidtia pappophoroides* and *Urochloa* spp., while annual grasses are represented by *Enneapogon cenchroides*, *Aristida adscensionis*, *Eragrostis viscosa* and *Dactyloctenium aegyptium* (Wild & Barbosa 1967).

One of the most common vegetation types in the Mopaneveld of southern Africa is the *Colophospermum mopane–Combretum apiculatum* mosaic savanna. In Zimbabwe, as in other countries hosting this type, the tree layer is dominated by species of the Combretaceae on sandy rises and dominated by *C. mopane* in the lower areas on heavier soils (Timberlake *et al.* 1993). Trees of 5–10 m high define the open woodland with species such as *Combretum apiculatum*, *C. zeyheri*, *C. collinum*, *Terminalia sericea* and *Lonchocarpus nelsii* being prominent. Scattered large trees of *Sclerocarya birrea* and *Ricinodendron rautanenii* occurs with only a few individuals of *C. mopane* (Timberlake *et al.* 1993). In Hwange National Park, the *C. mopane–Combretum* type is described as one of the more diverse types of the park (Rogers 1993). As in most parts of its distribution, the *C. mopane–Combretum* tree savanna in Hwange National Park is underlain by granitic gneiss producing rocky ground on undulating landscapes of the Basement Complex (Rogers 1993). Several *Combretum* species characterise this type in combination with species such as *Xeroderris stuhlmannii*, *Markhamia acuminata* (=*M.*

zanzibarica), *Commiphora mollis*, *Terminalia randii*, *Cissus cornifolia*, *Dichrostahys cinerea* and *Grewia monticola* (Rogers 1993). Mopaneveld and Combretumveld are not restricted to granitic substrates, but often occur together on basalt. The soils are in general rocky, gravelly clay and sandy clay. *C. mopane* occurs in the tree- and shrublayer in association with, amongst others, *Combretum apiculatum*, *C. hereroense*, *Commiphora pyracanthoides*, *Acacia nigrescens* and *Dalbergia melanoxylon* (Rogers 1993). Where this type approximates Kalahari sand, species such as *Commiphora angolensis*, *Croton gratissimus* and *Bauhinia petersiana* are added to the list, prefering the sandier soils (Rogers 1993).

A second *C. mopane-Combretum* type exists as one being found on very shallow soils overlying basalt (Timberlake & Mapaure 1992). Growing as 6 m high trees, *Combretum apiculatum*, *Acacia senegal* var. *leiorhachis* and *Diplorhynchus condylocarpon* are the most prominent trees for this type whereas *Pterocarpus rotundifolius* subsp. *polyanthus* var. *martinii* and *Colophospermum mopane* occur on deeper soils and *Kirkia acuminata* on the ridges. The grass layer is particularly well developed in this *C. mopane-Combretum* woodland (Timberlake & Mapaure 1992).

C. mopane–Combretum apiculatum associations are especially apparent on granitic substrates, not only in Zimbabwe, but also in the other Mopaneveld-hosting countries (Rattray 1962; Gertenbach 1983; Campbell & Du Toit 1994; Hin 2000). In Zimbabwe this type is a rather mixed dry woodland mosaic ranging from woodland, through open woodland to tree/bush savanna (Rattray 1962; Campbell & Du Toit 1994; Timberlake *et al.* 1993; Hin 2000). Typical species include *Kirkia acuminata*, *Acacia nigrescens*, *A. erubescens*, *Terminalia stuhlmannii*, *Ziziphus mucronata*, *Combretum imberbe*, *C. apiculatum*, *Colophospermum mopane* and *Sclerocarya birrea*. On sandier patches *Peltophorum africanum*, *Afzelia quanzensis* and *Terminalia sericea* occur. The shrub layer is well developed with *Phyllanthus reticulatus* and several *Grewia* species being the dominants, while the grass cover is poor and mainly consists of *Aristida* and *Eragrostis* species and accasionally *Pogonarthria squarrosa* and *Cynodon dactylon* (Rattray 1962; Timberlake *et al.* 1993; Hin 2000). On fine-textured soils derived from greenstone and dolerite, *Colophospermum mopane* forms a major component in the vegetation of a *Combretum apiculatum–Acacia nigrescens* community on mountains and hills (Campbell & Du Toit 1994). Prominent woody species include *Colophospermum mopane*, *Dalbergia* *melanoxylon*, *Combretum adenogonium* and *Julbernardia globiflora*. On sloped terrain, tree species accompanying *C. mopane* include *Julbernardia globiflora*, *Dalbergia melanoxylon*, *Grewia monticola* and *Strychnos madagascariensis* whereas *Ziziphus mucronata* and *Peltophorum africanum* become more important along drainage lines on gneiss (Campbell & Du Toit 1994). In Hwange National Park, a similar type occurs on Basement Complex geology of undulating terrain (Rogers 1993). *Julbernardia globiflora* is also a common associated species, while other prominent tree species include *Combretum apiculatum*, *C. zeyheri*, *Terminalia sericea*, *Diplorhynchus condylocarpon* and *Commiphora mossambicensis* (Rogers 1993). These *Julbernardia globiflora* types resemble miombo vegetation and share dominance with typical miombo species such as *Strychnos madagascariensis*, *Brachystegia boehmii*, *Lannea discolor* and *Pseudolachnostylis maprouneifolia* (Rogers 1993). Another miombo-mopane woodland type occurs on sandy clay soils produced by the Kalahari Group. *Baikiaea plurijuga* and *Colophospermum mopane* are representative of the deep sandy soils and the shallow clayey soils respectively. Other conspicuous species include *Combretum apiculatum*, *Acacia fleckii*, *Boscia albitrunca* and *Terminalia sericea* (Rogers 1993).

On low, elevated, dome-shaped sandstone ridges in Hwange National Park, a *Combretum–Boscia angustifolia* open scrub or thicket occurs (Rogers 1993). *Combretum elaeagnoides*, *C. apiculatum*, *C. celastroides* and *C. collinum* dominate with scattered *Lonchocarpus eriocalyx* trees. *Colophospermum mopane*, although not dominant, is a common species in association with, amongst others, *Diospyros quiloensis*, *Canthium pseudorandii*, *Combretum collinum* and *Boscia angustifolia* (Rogers 1993).

Kalahari sand often produces inter-dune troughs dominated by grassland, but interrupted by clumps of trees, of which *Colophospermum mopane* is one of the major contributors (Rogers 1993). This unique mixed savanna type is associated with calcareous soils and comprises, despite *C. mopane*, many woody species including *Acacia erioloba*, *A. luederitzii*, *A. erubescens*, *Combretum imberbe*, *C. hereroense*, *C. apiculatum*, *Grewia flavescens*, *Boscia albitrunca* and several more (Rogers 1993).

Over most of the tree savanna in the Limpopo Valley and its larger tributaries, trees such as *Sclerocarya birrea*, *Acacia nigrescens*, *Kirkia acuminata*, *Terminalia prunioides*, *Adansonia* *digitata* and species of *Grewia* and *Commiphora* is typically associated with the sloped, stony landscapes (Rattray 1962; Farrell 1968a; Werger & Coetzee 1978; Hin 2000). *Colophospermum mopane* rarely dominates the woody component on steep ridges. Where it occurs, it is often associated with less sandy patches, often along seasonal drainage lines where the terrain is also less sloped (Campbell & Du Toit 1994). In such cases, *C. mopane* is often associated with species such as *Combretum hereroense*, *Euclea divinorum* and *Bolusanthus speciosus* (Campbell & Du Toit 1994). Du Toit (1993) identified a *Kirkia–Colophospermum* ridge vegetation type on crests or steep-sided sandstone ridges. Medium-grained sandy clays evident in shallow soils, underly the vegetation dominated by *Kirkia acuminata* and *Colophospermum mopane* trees. Other conspicuous tree species include *Adansonia digitata*, *Pterocarpus lucens*, *Terminalia prunioides*, *Sterculia africana*, *Diospyros quiloensis*, *Xeroderris stuhlmannii* and *Commiphora karibensis*. The shrub layer is densely dominated by *Combretum elaeagnoides* accompanied by *Combretum apiculatum*, *Acacia ataxacantha*, *A. erubescens*, *Dichrostachys cinerea*, *Gardenia resiniflua* and several more (Du Toit 1993). A *Colophospermum mopane–Commiphora marlothii* mixed woodland or thicket on scree slopes occurs on lithosols of the escarpments of Karoo formations in the Hwange National Park (Rogers 1993). For the purpose of this discussion, this type would rather be regarded as a tree savanna type. *Colophospermum mopane*, *Markhamia zanzibarica*, *Canthium glaucum*, *Combretum elaeagnoides*, *Grewia flavescens* and *Diospyros quiloensis* are the most common woody species (Rogers 1993). The abundance of several *Commiphora* species are characteristic for sloped, rocky areas in Mopaneveld landscapes.

In the Sabi Valley on deep, sandy soils derived from sandstones, a moderate tree savanna to a tree/bush savanna is dominated by *Acacia nigrescens* with other conspicuous woody species being *Colophospermum mopane*, *Sclerocarya birrea* and several *Commiphora* species (Rattray 1962).

Mopaneveld ecotone types occur between Kalahari sands and more clayey soils derived from basalt. These ecotone types are especially apparent in Hwange National Park where *Colophospermum mopane* dominates patches of heavier-textured soils, whereas *Combretum apiculatum*, *C. hereroense*, *C. collinum* and *Acacia nigrescens* inhabit the clayey soils, also derived from basalt, but overlain by a fairly deep strip of Kalahari-type sand (Rogers 1993).

Shrub savanna

On soils derived from basalt, mainly in the southeastern border of Zimbabwe, Mopaneveld occurs as extensive patches of open shrubland or bushveld (Wild & Barbosa 1967; Rattray 1962; Werger & Coetzee 1978; Rogers 1993). In the tree layer, *Acacia* species (e.g. *A. sieberiana*, *A. robusta*, *A. nilotica*) and *Commiphora* species (e.g. *C. africana*, *C. pyracanthoides*) become important (Rattray 1962; Werger & Coetzee 1978; Rogers 1993). Other conspicuous woody species include *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Ximenia americana*, *Grewia monticola* and *G. bicolor* (Rogers 1993). The grass layer is well developed with *Schmidtia pappophoroides*, *Cenchrus ciliaris*, *Enneapogon cenchroides*, *Eragrostis viscosa* and several *Aristida* species being the most conspicuous contributors (Rattray 1962; Werger & Coetzee 1978). Where the soils are heavy and badly drained with compacted base-rich subsoil, *C. mopane* becomes stunted (Farrell 1968b; Werger & Coetzee 1978) and relates the shrubmopaneveld in the Kruger National Park on vertic clays derived from basalt or gabbro. In some areas the stunted *C. mopane* shrubland is associated with almost bare soil. *Craterostigma plantagineum* and *Portulaca hereroensis* are of the only species being able to inhabit these "Sikwakwa", patches (Wild & Barbosa 1967). On the south bank of the Lundi River, a *Colophospermum mopane*–*Spirostachys africana* shrub woodland occurs on black montmorillonitic clay. In this type, stunted individuals of *C. mopane* occur in association with *Salvadora angustifolia* and *Spirostachys africana* (O'Connor & Campbell 1986). On lighter-textured, better-drained soils species such as *Combretum apiculatum*, *Acacia nigrescens* and *Spirostachys africana* interrupt the stunted, monotypic Mopaneveld (Farrell 1968). On gravelly basalt soils near the Sabi River a low Mopaneveld type exists with woodies including *Commiphora mollis*, *Terminalia prunioides*, *Acacia borleae*, *Dichrostachys cinerea* and *Dalbergia melanoxylon* (Farrell 1968a). On basalt-sandstone contact soils *Boscia mossambicensis* and *B. albitrunca* occur in the shrublayer, whereas *Sesamothamnus lugardii* is more or less confined to the sandstone areas and *Catophractes alexandri* particularly dominating the shrublayer on calcrete soils (Rattray 1962; Werger & Coetzee 1978).

On heavy degraded soils near the Chewore mouth, a scrub form of *Colophospermum mopane*, seldom higher than 3 m, is apparent (Guy 1975). On deeper soils near the base of the *ridges C.*

mopane is accompanied by *Adansonia digitata*, *Terminalia prunioides*, *Afzelia quanzensis* and *Gardenia resiniflua*. The grass layer is in general poorly developed (Guy 1975).

2.2.6 Conclusions

From the discussion of Mopaneveld vegetation over its distribution in southern Africa, it is evident that the Mopaneveld is a complex of many vegetation units (plant communities), of which some are related despite their geographical isolation, and others represent distinct, unique communities. With this in mind, it was thought valuable to look holistically at Mopaneveld vegetation by means of a phytosociological synthesis.