The ecology and distribution limits of *Colophospermum mopane* in southern Africa

Reuben J G Sebego[1]

Abstract

Vegetation distribution patterns, especially at species level, have not been accorded serious attention in terms of ecological research in semi-arid areas. In Botswana some wide interest has been shown, especially on investigations toward the biogeography of the species *Colophospermum mopane* because of its abundance, homogeneity and economic importance. Contrasting views on the ecological distribution of this tree species are here cited with a view to incite further research on the topic. The distribution pattern of *C. mopane* is reviewed from various sources ranging from maps, late 19th and early 20th century explorers' notes, dissertations and published papers. In reviewing the literature it is evident that while there is agreement as to the actual spatial distribution of the species, there are still uncertainties regarding the factors behind the distribution pattern. With the goal of finding a methodological approach for ecological research on the inventory, as well as establishing the relationship between the species and its habitat in Botswana, various methods, together with their theoretical underpinnings are reviewed.

Introduction

One of the widely documented topics on vegetation ecology and plant distribution limits in Botswana concerns the species known as *Colophospermum mopane* (J. Kirk ex Benth.) J. Kirk ex J. Leonard, locally known as mopanene (here referred to as mopane). Because of its unique distribution pattern and clearly defined geographical locations as centres of endemism, the species has attracted the attention of many researchers who have since developed theories to explain the causes behind the endemism and distribution patterns and limits. These theories, it can be postulated, signify a move from the more exploratory work of the early 19th century plant geographers to the modem deterministic work of plant ecology. Botanists who have established general agreement between plant distribution and climatic patterns (Koppen 1931; Humboldt 1817; Woodward and Williams 1987) have almost completely described plant distribution patterns on a global scale. It is at regional and local scales such as those describing the distribution of a single species like mopane that further research on species-habitat relationships has to be determined. Scientific efforts aimed at matching plant distribution and other terrestrial features are based on the ecological niche concept, often called the Gause's competitive exclusion principle (Barbour *et al.* 1987). A niche is described as 'a multi-dimensional description of a species resource needs, habitat requirements and environmental tolerances' (Crawley 1986). In the same vein, efforts have been made to develop techniques specifically aimed at describing plant distribution patterns on the basis of environmental variables (Whittaker 1982).

Description of mopane

Colophospermum mopane (which in most instances make up a woodland type called mopane) is a broad-leafed deciduous plant. Mopane is found to exhibit two growth forms, as tree or as a stunted shrub. The stunted shrub are conspicuous when they occur in depressions and large drainage channels as a result of the high water holding capacity of such land forms. There are also reports however that the shrubby appearance of mopane is a result of bush fires (Van Voorthuizen 1976).

[1] Lecturer, Department of Environmental Science, University of Botswana, Gaborone.

Topographic location could be one of the important factors for the distribution of the various life forms. Different life forms could also be a result of alternating generations (age groups) of stands or it could be an effect of physical or chemical soil attributes. Coe (1991) presents an alternative view to the varying life forms. In a study conducted in the Boteti District, results showed that thinning mopane shrubs led to increased diameter and height, implying that growth forms may be density dependent. Mopane is found only in the eastern, northeastern and northern parts of Botswana. An imaginary line (cross-section) drawn from the northeastern tip of Botswana through the east to the east-central parts (Figure 1) displays the characteristic nature of the morphology and structure of mopane. The tallest and largest (in terms of girth diameter) trees are found in the periphery of the Okavango Delta near Maun. Trees in this area exhibit a tall gigantic growth form often reaching 25m in height (Roodt 1992) and have been referred to as 'cathedral mopane' owing to their broad canopies. Stems of fully-grown mopane trees are straight and long, with flaked greyish bark. Younger trees and shrubs normally have darker and smoother barks than in older trees. Leaves of mopane usually appear after the first rains. The younger leaves are glossy and golden in colour, changing to green as they mature. Leaves of mopane are compound, alternate and composed of two symmetrical leaflets characterizing a unique 'butterfly shape' (Figure 2). Mature pods are yellowish brown, compressed, bean shaped and indehiscent (Figure 3). They are produced in large quantities and are often noticeably blown about by wind during the dry season. Inside the pods are reddish, flat, sticky seeds. Mopane seeds germinate readily within 7 days when removed from the pods but several days (up to two weeks) if planted without first removing the pods. They smell of turpentine when crushed and usually appear after the first rains.

Mopane exhibits a shallow rooting system underground (Figure 4). Shallow rooted mopane trees have also been observed in the Moremi Game Reserve where elephants have felled enormous trees. Despite these observations, some long (3m) taproots of mopane seedlings were seen when dug out in a sandveld area north of Palapye. This is in agreement with Henning's (1976) report that the tap root possibly dies back during the later stages of the plant. One striking characteristic of this species is its distinct boundaries displayed both at local and regional scales. The species does not grow naturally in all of the western sandy parts of the country, this means that its western limits are the fringes of the Kalahari except in the area south of Lake Xau Xau. Its southern limit is an abrupt boundary at about 23°S. Locally mopane has been found to be almost a dominant species in most associations as well as being monospecific usually with a low herbaceous cover.

Economic importance of mopane

In a country such as Botswana, where communal agriculture is significant, mopane is economically important to those communities where the species is found. There are three major reasons for its importance. Firstly, it is a browsable species by various types of livestock (cattle and small stock). Goats feed on the green mopane leaves during the wet season as well as dry leaves during the dry season (Powell *et al.* 1996). In the case of cattle, which are mainly grazers, they have been able to survive severe droughts by feeding on the fallen mopane leaves. Macala (1996) reported that green immature mopane leaves contain an average of 15-18% crude protein whilst dry mature leaves contain an average of between 7 and 10% crude protein. This tree is therefore of great importance to the livestock industry. In the past, as during the 1982-87 drought years, the country has gone through severe droughts that had left the rangelands at very low carrying capacities. It is important to note however that most of the estimations for carrying capacity are based on the herbaceous layer (Field 1976). This kind of predetermined procedure neglects the importance of browse in its contribution to usable biomass (Sebego 1993; Ringrose and Matheson 1995; Moleele 1998). This contemporary judgment of carrying capacity should no longer be considered as the standard procedure. Now that it is known that cattle do utilize browse, this important resource should be included in the carrying capacity estimates.

Browsers also enjoy an additional nutritional benefit from mopane leaves. Mopane leaves are also host to the insect *Arytaina mopane*. This insect lays its eggs underneath the leaves covered

Figure 1:
A cross section of the country from west to east along the mopane belt.

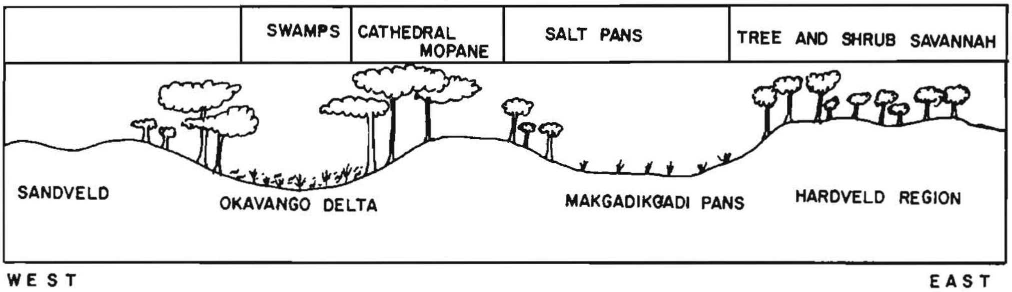


Figure 2: *C. mopane* leaves

Figure 3: *C. Mopane* seed and pod

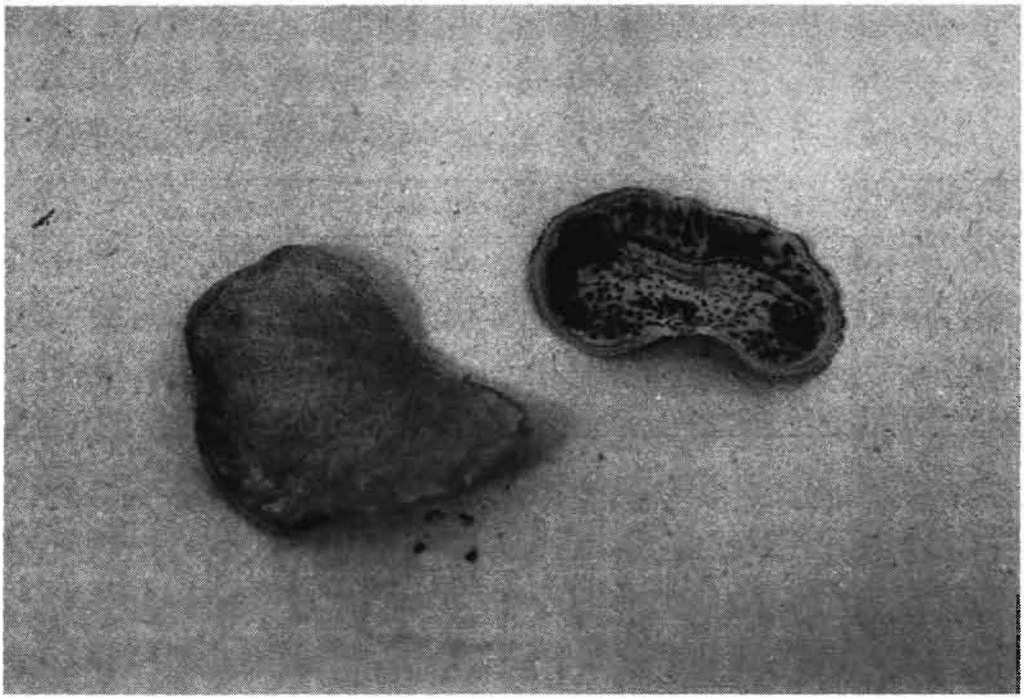


Figure 4: *C. mopane* tree and root system, note the well developed lateral root system exposed by gully erosion

with some waxy secretion that later dries up and becomes scaly. It is by then a palatable food source relished mostly by baboons and monkeys (Roodt 1992). These scales have been reported to be highly nutritious and therefore beneficial to livestock (Sekhwela 1989).

Secondly, the species mopane is a host for the mopane worm (Figure 5). These worms (locally known as phane) hatch from eggs laid by the mopane emperor moth *(Imbrasia befina-Sartumfidae)* on the top surface of the mopane leaves. From hatching to the time when they are adults (before pupating) these worms reside and feed on the mopane leaves, often completely stripping a mature tree by the time they cease to feed. Live adult worms are collected and prepared for consumption. The worms are not killed but their guts (dung and part of the intestines) are squeezed out before they are cooked. Phane is eaten fresh or dried as a snack. This southern African delicacy is served with maize meal or sorghum, as a meat or vegetable substitute. It is a source of income for some informal vendors who often sell it in a dried form. Some farmers have used it for feeding their livestock by incorporating it into bone meal or other feed as a protein supplement.

Lastly, the mopane tree is valued for its useful timber, mainly used for building kraals, as fencing material around homesteads or as roofing rafters. Mopane is resinous and said to be termite-resistant, and as a result structures built from its wood have been found to be still intact after many years. As firewood, mopane heartwood is hard and bums efficiently although with much smoke.

Tietema *et al.* (1991) found that amongst six species used for firewood, mopane was the most preferred because of its slow burning efficiency, which they measured to be 1.42%. In recent years some people have started to cut and sell mopane wood along the major highways, especially between Serule and Francistown and between Nata and Francistown (Figure 6). Piles of wood for sale have recently become a common sight. Even worse are reports that some people may be cutting live trees as the walking distance for collecting dead wood is slowly becoming too great for those in the business. This is something that could be marking the beginning of the road to extinction for the mopane tree or the start of its ecological imbalance.

Rationale of mapping the distribution of mopane

Shortcomings of the methods used in the mapping of vegetation in Botswana are prevalent. Furthermore, some theories rather than research findings have been circulating among the literature for decades now and have almost been considered as factual information. Lastly, it is clear that so far very little has been done in Botswana to study the effects of environmental factors on vegetation distribution.

The focal point of this paper is to review the literature for possible explanations and views on the spatial distribution and geographical limits of mopane. It is also one of my prime objectives to discuss the methods used by previous researchers in mapping the distribution of the species or vegetation. Gaps that need to be filled in this area are also identified. Furthermore, the paper reviews the theories of biogeography, that branch of ecology dealing with plant distribution and the factors that influence it. Such theories are reviewed for the simple reason that they may help explain the distribution pattern of the species that we see today.

Lastly, the paper aims at developing some conclusive recommendations on how to proceed with investigations to determine the habitat of this species and propose some alternative mapping methods.

Explorations on the biogeography of mopane have brought to light some intriguing observations on the incidence of the species. In the southern parts of the country, a number of individual trees have been located in Mochudi and Gaborone, more than 200 km south of the mopane's southern limit. Although all of these are found in residential and public places, it is not clear how they got to grow there, but human dispersal seems most likely to be the cause. In a bid to discern more on the ecological predicament of the mopane species, literature on some of the fundamental ecological theories and plant geography are reviewed.

Models of Plant Distribution

The study of biogeography has and still is being clouded by uncertainty regarding the basis or the formation of plant distribution limits. Two contrasting views regarding the study of biogeography are reviewed. Firstly, there is the theory that vegetation/plant distribution patterns that we find today are a result of past climates. This is termed historical biogeography (Tivy 1993) and it is a theory that is based on geological records. The basis of historical biogeography is that ancient geological events like the Pleistocene glaciations and continental drift have consequently resulted in today's species distribution patterns. The explanation given is that following the last Ice age (during the Quaternary), plant distribution patterns began to form in response to the warming up of the land masses as ice retreated (Archibold 1995). Historical biogeography is in turn divided into two sections: dispersal biogeography; where a species is believed to have originated and radiated outward away from a centre of origin across some existing barriers; and Vicariance biogeography which postulates a common ground between distribution patterns of two unrelated species, sought as a means of proving the hypothesis that vicariated species are so because of the emergence of barriers.

Another school of thought is that plants are responding solely to present day climatic and edaphic factors which is known as ecological biogeography (Rosen 1980). The realm of this model is based upon habitats preferred by individual species and the manner in which many species are extending or detracting their ranges in response to changing environment. The basis of this review is biased towards ecological biogeography. The position taken here is that the characteristic nature of the savannas are a result of a combination of prevailing factors such as climate and land use (e.g. fire) (Goldstein and Samiento 1987; Scholes 1991). It should be understood that these factors, at any given time, force the landscape into a dynamic state. The logical thought is that even if historical biogeography were a major causal phenomenon on the characteristics of the landscape, the latter would still be seen as dynamic. It can be said that ecological biogeography is based on the premise that vegetation distribution is a result of the interaction between organisms/ species and their biophysical environment of either the present or past time scales.

Understandings of specific physiological and morphological properties that govern the reproductive and dispersal abilities become an integral part of elucidating a species distribution pattern. Research has found that the nature of edaphic and climatic factors is dynamic and therefore constantly changing. One of the key elements in vegetation development is the soil. Any biological element, (i.e. plant community) that flourishes in any particular soil unit is there because that soil unit is able to support it. In turn, the development of a particular soil type (unit) is a function of the interactions of parent material, climate, topography and vegetation (litter), reacting with each other over a time scale (Archibold 1995). The biophysical processes like leaching, seepage, erosion and organic matter accumulation consequently derive different soil types (Simmonson 1959).

Biogeographical regions and plant distribution limits

As soon as it was pertinently proved that plants grew in specific patterns and in community associations, ecologists then eagerly found out that the communities or associations were directly correlated to environmental conditions. Similarly, in relating the environmental phenomena to the regional vegetation patterns one thing that comes to people's minds is the ecology of an area; but this is with disregard to some physical geographical barriers such as mountain ranges or large lakes (Crawford 1989). The area where the southern limit of mopane lies is dissected by a series of hill ranges. Other possibilities are that distinct communities could be a result of a limitation in the species' modes of dispersal. Despite the controversies of biogeographical models found in the literature, some common ground can be found. Whether landscape characteristics are a result of present climatic or ecological factors, or responding to environmental and/or climatic changes a long time ago (Barker 1983), one fact remains the same. Three main elements are mentioned in

Figure 5: The mopane worm *(Imbrasia belina)*

Figure 6: A pile of wood displayed for sale on the road side.

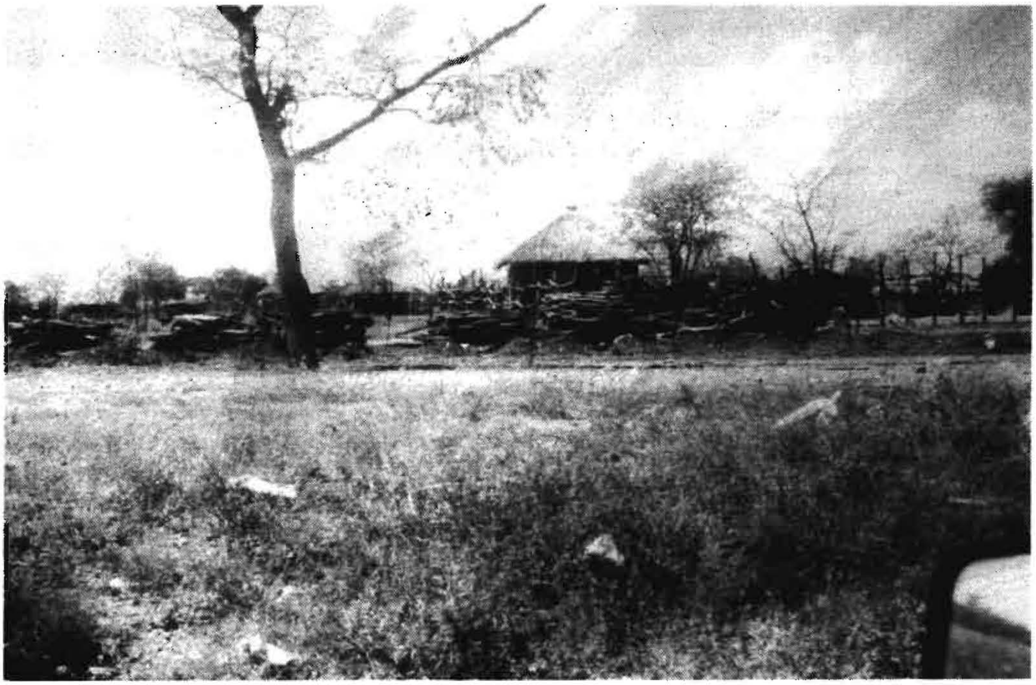
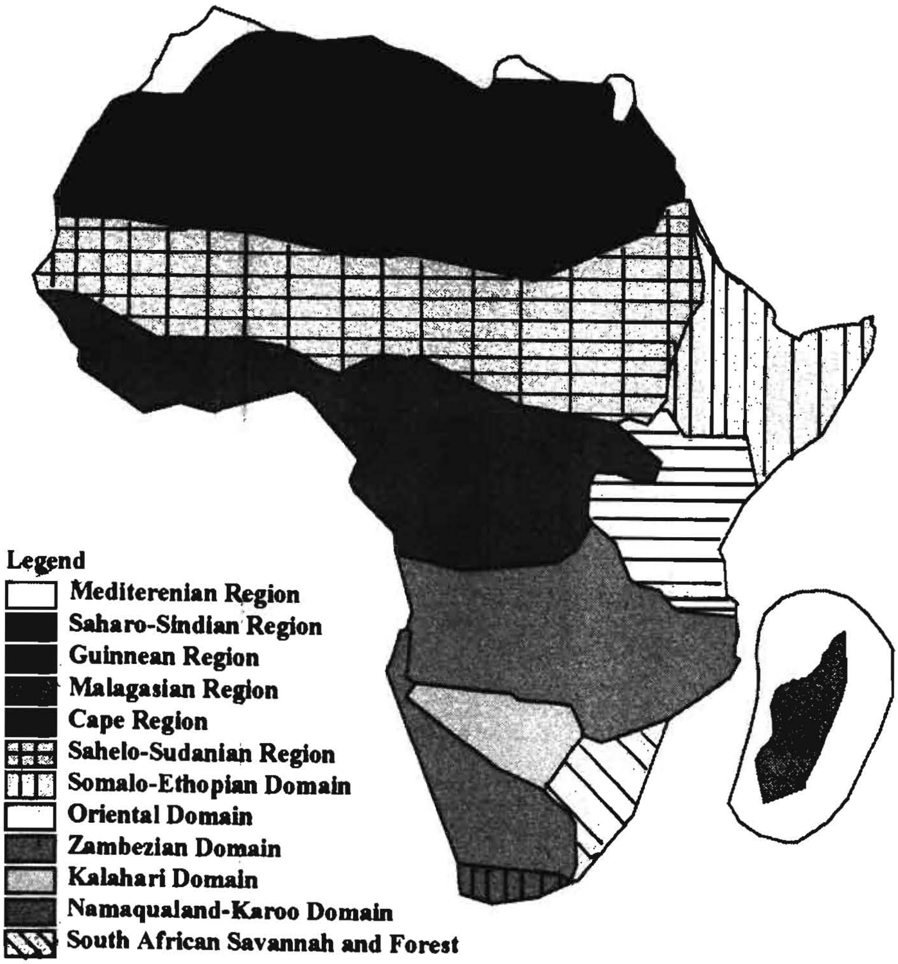


Figure 7: Biogeographical regions in Africa (after Lebrun 1947)



the literature as the major forces behind plant distributions; i.e. irrespective of the exact time when a particular vegetation type may have become established in a particular area. These are identified as the major factors influencing the growth and the spread of plants:

i) **Ecological factors**
These are mainly a combination of land elements acting together to form a unique environment (Huggett 1995). Distribution patterns forming as a result of edaphic factors are mainly responses of plants to the hospitality of an area. Hospitality can be characterised but not limited to factors such as: soil fertility, soil structure and moisture availability. The original parent material determines both soil fertility and soil structure (Scholes 1991), whereas moisture availability is a factor of rainfall, soil structure and topography.

ii) Climatic factors
Many biogeographical regions are said to be attributed to their climatic pattern. The two main elements of climate that form the driving force in vegetation growth and survival are temperature and rainfall.

iii) Anthropogenic factors
Plant distribution patterns may be a result of man's activities. Good examples of such include the old practices of shifting cultivation and bush fires. Campbell and Child (1971) assert that these practices could in fact bring about similar landscape changes as would long term climatic variation. The only difference would be the time frame through which these changes could take place. The impact on vegetation as a result of human practices would in this case be accelerated. A good example is enhanced distribution of mopane in that it is found growing in Gaborone and neighbouring villages clearly as a result of humans as factors of dispersal.

Although correlations between the above named factors (climatic, environmental and anthropogenic) and the present day flora, may have been established, it is often difficult to single out one cause and label it as the real factor behind a certain vegetation type.

Major phytogeographical regions in southern Africa
For southern Africa one recognises the distinguishing regions that are shown in all the phytogeographical maps. The three most recognized regions in the subcontinent are noted as:

- The Cape flora, recognized as a distinctive region by all those who authored a phytogeographical map.
- The Sudano-Zambezian region, sometimes labelled as extending westwards to incorporate parts of the Kalahari (White 1971) even though other authors classify the Kalahari as a transition zone between regions.
- The Kalahari/Karoo-Namib, a distinct region that is also sometimes extended to incorporate the Kalahari or is itself incorporated into the Cape flora.

For the interest of this paper, the geographical area under review falls into the Sudano-Zambezian region or the Zambezian domain as categorized by Mute (1971) and Lebrun (1947) (Figure 7).

Theories of vegetation analysis

Models of plant distribution and development discussed earlier portray an abstraction of vegetation patterns (as influenced by environmental phenomena) at its highest level. At the lower levels (regional and local scales), theories of vegetation analysis have been dominated by two antagonistic models. Firstly, the widely used model of 'classification' labelled as being the brainchild of Clements (1904) (Noy Meir and Van der Maarel 1987). According to the classification model view, vegetation arrangements across the landscape are discontinuous with discrete classes or communities made up of specific species combinations identifiable enough to be called associations. This view has come to be known as the 'community concept' (Tivy 1993). The alternative theory of vegetation analysis, on the contrary, views vegetation patterns as a continuum, often following a specific environmental gradient and certainly dismissing the idea of discrete boundaries or class units. Plant associations on the perspective of the continuum model gradually fade away to form ecotones towards the periphery of their ranges. Accordingly, this theory has come to be known as the 'continuum concept' (Tivy 1993). The continuum concept is closely tied to the study of vegetation communities along a gradient of environmental phenomena- named gradient analysis, after Whitaker (1967) (Whitaker 1982; Noy-Meir and van der Maarel 1987; Roberts 1987).

Existing biogeographical work in Botswana

It is assumed that present contribution to the biogeography of mopane and the mapping methods that are suggested in this paper will be an important addition to the few existing works that are species specific in Botswana. One of the groups that has been relatively well researched and documented is the acacias (Timberlake 1980b). The most recent map showing the distribution of mopane is by De Wit and Becker (1991a). This map was an offshoot of the national soil-mapping project (De Wit and Becker (1991b). Although its accuracy is not questioned at this point, the authors do admit that vegetation data were extracted from areas designated as sample points meant for soil survey purposes. These authors also confess to the possibility of erroneous species identification and grouping, as data was collected and compiled by soil surveyors who had little knowledge of plant taxonomy or ecology.

Acacias have been both physiologically and phytogeographically documented by Timberlake (1980b) in more or less the same fashion as Coates-Palgrave (1983) did for trees of southern Africa. The distribution pattern of this species in the country is clearly shown using excellent illustrations of the physiology of the plants as well as graphic sketches of their distribution limits. For the herbaceous layer Field (1976) gives an account of a nation-wide description of the most 'common' grasses in Botswana. This particular volume combines the physiological characteristics of the grasses, their nutritional value, distribution patterns and their ecological preferences. Similarly, Van Rensburg (1971) has written on the ecology of Botswana, ending his publication with a list of herbs, grasses and trees and their locations.

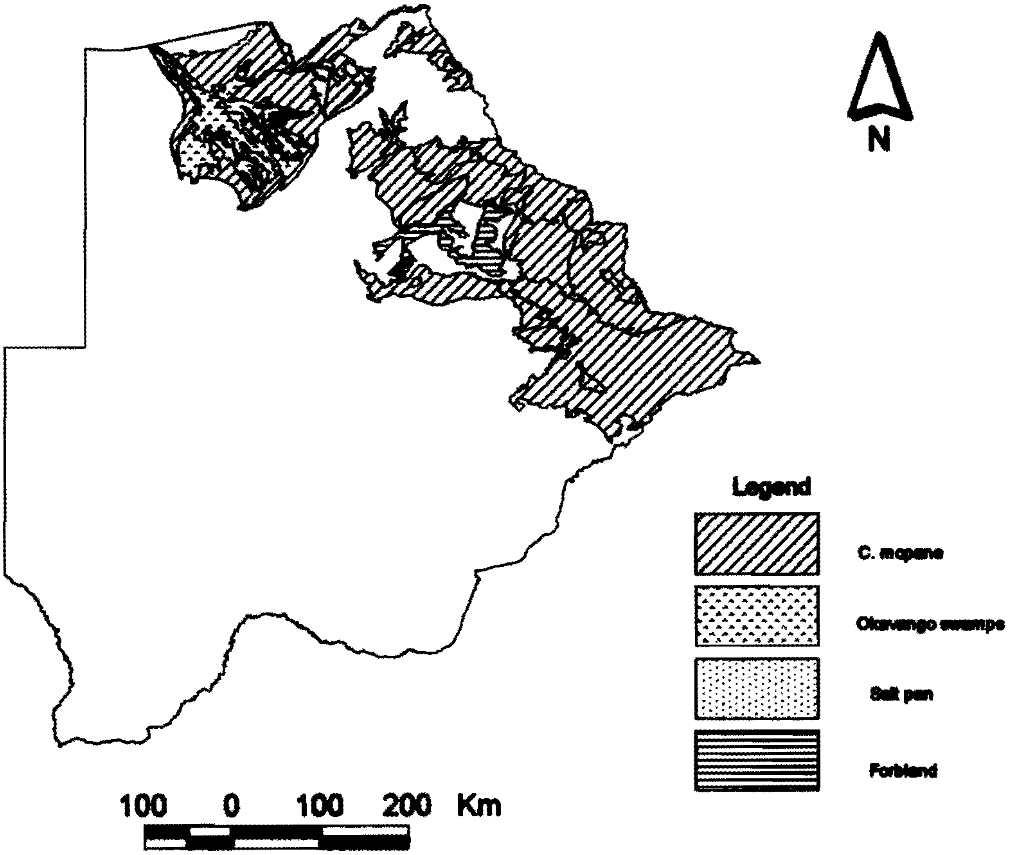
Other contributions on the phytogeography of Botswana include Woollard's (1981) 'A vegetation key to the woody plants of southeast Botswana' and Mott's (1978) 'A key to the flowering plants of Botswana'. Skarpe (1986) investigated ecological variation in the Kalahari Region (Ghanzi) on the basis of soil variation, parent material and moisture availability (based on precipitation). She distinguished three main edaphic factors responsible for the distribution of the different types of vegetation. The Kalahari sand is characterized on the basis of texture (coarse and fine) and colour (white and red). In addition to the sand deposits, very fine white calcareous soils are found on pans. In relating the above land characteristics to vegetation types some specific plant distribution patterns were observed and found to be correlated to soil type and colour. Still in the Kalahari Region Cole and Brown (1976) identified seven major land characteristics as having a strong influence on vegetation associations and communities. The major land characteristics include: the Ghanzi Ridge, a 30 km wide northeast-southwest spine-like outcrop of sedimentary rock that slowly gives way to deep Kalahari sands on both sides of the eastern and western slopes, Kalahari sand plain, deep sand deposits, calcrete outcrops, fossil river valleys, sand ridges, shallow depressions and pans. In reviewing the literature, it is evident that little research has been conducted on the biogeography of the eastern part of the country as compared to the western parts, namely the Kalahari. In addition to this, there has been very little concentrated work to study the biogeography of any single species except in the case of Botswana acacia species (Timberlake 1980b).

Documented evidence for mopane distribution

Some of the earliest publications on plant species distribution in Botswana include those by Pole-Evans (1938) and Miller (1948). In his publication, Pole-Evans (1938) compiled his long journey across the eastern and northern parts of Botswana recording all major vegetation types. He describes the southern limit of the mopane tree as being at about 16 miles (26 km) north of Mahalapye. In addition to the species list along the eastern part of the country, Milfer (1948) describes the various growth forms of the mopane tree and alludes that this species has been reduced to scrub by fire. He also mentions that in some cases, in cleared areas, mopane trees were stunted having coppiced after frost.

To date there exists documentation in the form of maps and inventories of selected resources. Although the maps are small-scale (1:2 000 000), covering the whole country, they show some

Figure 8: Vegetation map of Botswana (distribution area of mopane is highlighted). Source: De Wit and Becker (1990)



class delineations of mopane (Figure 8). Mapping vegetation and other natural resources at such small scale can only be good for reconnaissance purposes. Delineation of boundaries at small scale can only be termed accurate if they can be positioned relative to where they coincide with some distinct landmarks such as river channels or hill ranges. Available maps such as those by Weare and Yalala (1971); De Beer (1962); De Wit and Becker (1991) and their related ancillary data have been produced mainly from conventional methods where aerial photographs and field transects have been used to collect baseline data. Satellite data have rarely been used (De Wit and Becker (1991); Van Heist (1991); Timberlake (1980a); Norwegian Forestry Society (1993)). In the case of the last three authors, Landsat MSS imagery was used. Furthermore, only pre-processed hard copies were obtained, presumably because of the limitations in terms of access to computers at the time. This meant very limited possibilities for data manipulation by the surveyors. For both De Wit and Becker (1991) and Timberlake (1980a), Landsat MSS imagery was used visually to interpret and delineate classes of soil and vegetation respectively. Implications of these investigations are that there were no actual digital classifications of the satellite data.

In her study Van Heist (1991) used Landsat MSS data to determine biomass classes in south-east Botswana. One of her major conclusions was that the spectral as well as the spatial resolution of Landsat MSS were too coarse for a clear-cut determination of woody biomass. Landsat TM,

Figure 9: Map of the distribution of *C. mopane* in southern Africa (after Mapaure 1994)

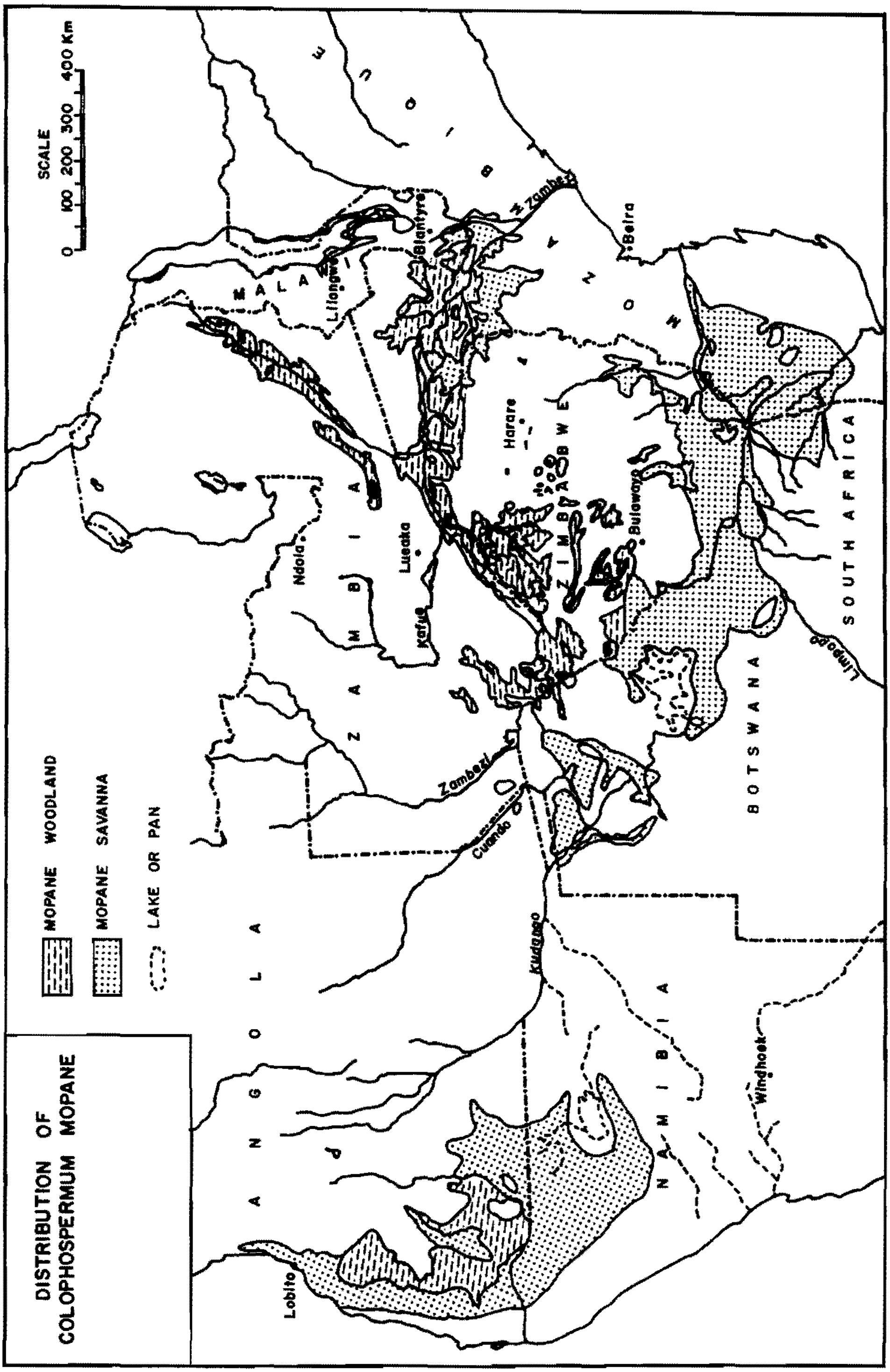
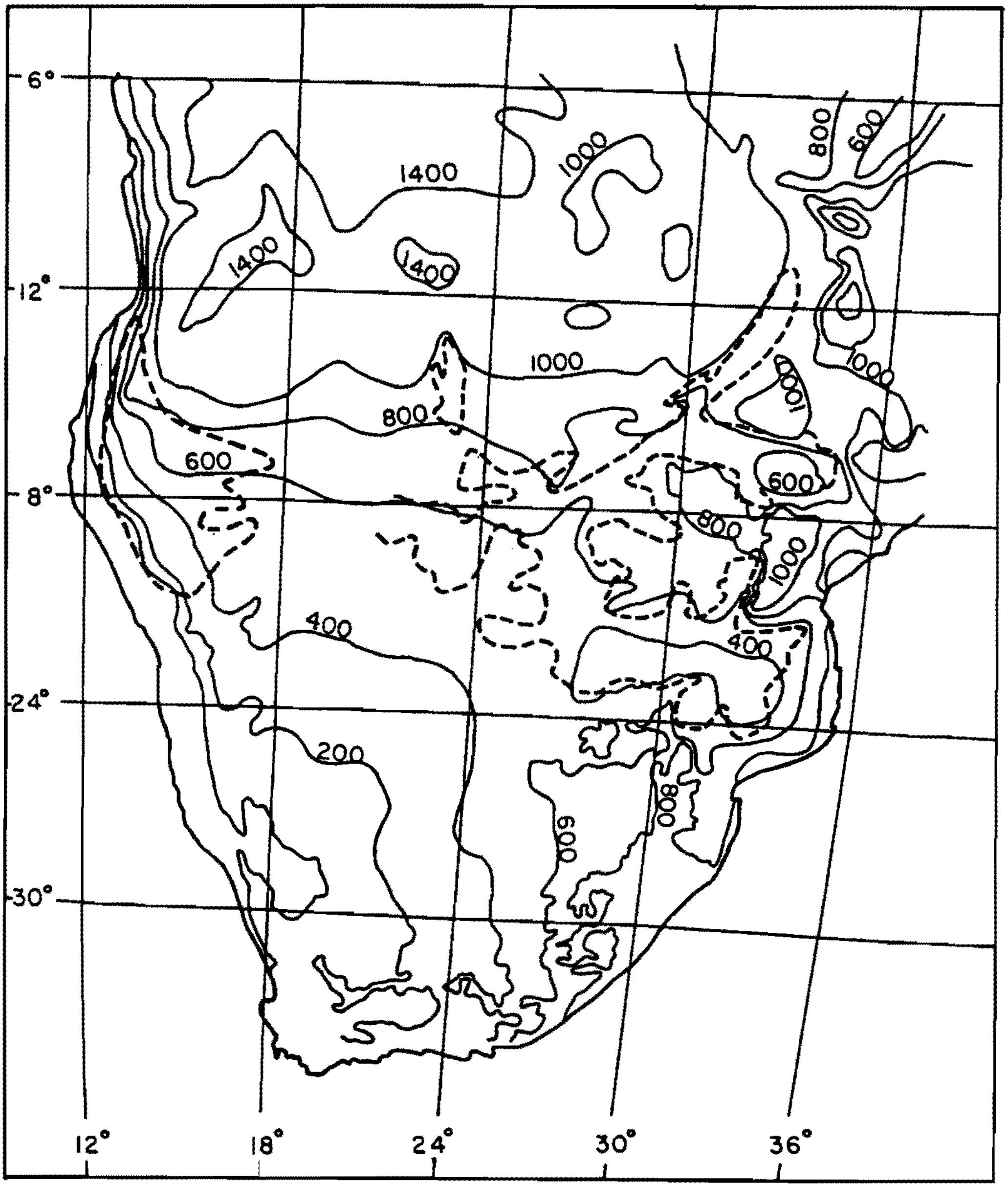


Figure 10: Distribution of *C. mopane* in southern Afrifca in relation to total annual rainfall (after Henning 1976)



with its finer spectral resolution and a smaller (30 x 30 m) spatial resolution could be more suitable for this purpose. The same recommendation was given as a better alternative for the mapping of the forest resources in the Chobe district (Norwergian Forest Society 1993). Ringrose *et al.* (1997) used Landsat TM to map land degradation in the Okavango area and, even though single species mapping was not their main objective, they were able to classify four classes of mopane, amongst other vegetation species.

Distribution pattern

The distribution pattern of mopane is considered at three geographical levels. In this section the species' distribution limits is looked at in its endemic areas in the southern African subcontinent and also at a national level. Eventually, in suggesting experimental designs for subsequent research, the distribution of the species is considered in greater detail, i.e. in a defined study area.

Distribution pattern of mopane in southern Africa

Mopane is a species that is limited only to the subtropical region of southern Africa appearing only within the area between latitude 11° and 24° S and longitude 12° and 36° E (Figure 9). Countries where the species is endemic (west to east) are: northern Namibia, southwest Angola, southeastern Zambia, north, central and eastern Botswana, southern and northeastern Zimbabwe, northeastern South Africa (Northern Province), northern and southern Mozambique and southern Malawi. In as far as the distribution is concerned, the distribution map shows a discontinuous pattern. This is in conformity with the concept of island biogeography (MacArthur and Wilson 1967).

Distribution of mopane in Botswana

The geographical confines of mopane in Botswana appear to have certain ecological preferences. Mopane is evidently restricted to the hardveld portion of the country, being almost totally absent from the sandveld areas of the Kalahari. Countrywide, mopane stretches from the extreme northwest with only some small pockets inside the Okavango Delta, along the edges of the Kalahari sands towards the Makgadikgadi Pans within which the species is completely absent, presumably due to the high salt content. From the periphery of the Makgadikgadi Pans mopane dominates much of the eastern hardveld area stretching as far south as Radisele (23° S) (Figure 8).

Contrasting views on the causes of geographical limits of mopane

The peculiar 'treeline' exhibited by mopane at its southernmost limits has caught the interest of researchers who have worked on this topic and came up with some contrasting views. Research from these investigations seem to be centred on temperature, rainfall and soil distribution with one piece of work Madams (1990) finding no relation between the spread of mopane and any biophysical variable at all.

The theory of frost

It is popularly documented that the well-defined ecotonal boundaries of mopane are largely controlled by the occurrence of frost (Van Voorthuizen 1976; Henning 1976; Timberlake 1980a). There seems to be a rather cyclic cross-referencing between authors on the issue of frost as being the controlling factor for the spread of mopane. Most writers have cited some other earlier writers who themselves have never collected any empirical data to prove their theses. The present author has traced such citations back to 1933 when Obermeijer (1933) wrote in the South African Journal of Science; "Frost, I think, limits their southern distribution" i.e. referring to mopane. The above statement, whether true or not becomes a mere speculation, and is more of a theory or a conceptualised idea than a fact. Contrary to the theory of frost as a controlling factor for the distribution of mopane, Timberlake (1995) reports the occurrence of stands of the species in some severely frost-prone areas near Bulawayo. Such observations warrant further investigations. An analysis of meteorological data by the author on some synoptic stations in Botswana has shown that the southern and central parts of the country (including the area of the southern limits of mopane) are less prone to frost than the northern areas around Francistown. Francistown was calculated to have 7.36% chances of having frost compared to Gaborone and Mahalapye which were calculated to have 6.76% and 5.41% respectively.

Climatic variation

Using a manual overlay method, Henning (1976) matched the map of mopane with rainfall and temperature distribution maps for the southern African sub-region. The result of this overlay is that mopane appears to be restricted to areas of low to moderate rainfall (200-800mm) and that the southern boundary coincides with the 5° C July mean daily minimum isotherm (see also Van Voorthuizen (1976)). In Botswana this isotherm does coincide with the mopane line (Figure 10).

Soil type

A review of the literature on soils supporting mopane woodlands shows that the species is tolerant to a wide range of soils. In general authors involved in research on the biogeography of mopane have cited soils that are characterised by compact, well drained and alkaline properties (Van Rensburg 1968; Timberlake 1995). These characteristics leave out the extreme (antagonistic) edaphic properties as some of the possible limitations for the growth and distribution of the species.

These include soils that are: coarse textured and receiving (sands), water logging and acidic. Of equal importance to plant growth as soil type is nutrient availability. Sodic soils in particular have been widely publicised as contributing to the nourishment of mopane (Cole 1986; Dye and Walker 1980).

Theory of no limiting factors

In his dissertation entitled 'Biogeography of mopane and its distribution limits in eastern Botswana', Madams (1990) found no correlation between vegetation parameters (density and canopy cover) and the chemical properties of soils. The chemical properties here include soil pH cation exchange capacity, available phosphorus, and potential buffering capacity for phosphorus, bulk density and available water capacity. Madams' (1990) conclusions were that mopane is slowly drifting southwards as there is no indication of any factor that limits it to its present location.

Methods used in compiling the pre-existing vegetation maps

In outlining the methods used to map vegetation in Botswana, it is important to note that in the past no particular vegetation type or species was ever targeted. All existing vegetation maps differ in their objectives of mapping a particular species like mopane that is of interest in this particular paper. Brief descriptions of methods are hitherto given mainly for vegetation maps of De Wit and Bekker (1991) and Timberlake (1980a).

The vegetation map of De Wit and Bekker in particular, was constructed under the National Soils Mapping Project. What this means is that the goal of the project was to produce a soils map as well as a soils database for the country. Methods used in the compilation of the map and the database followed the conventions of the Food and Agricultural Organization (FAO). The procedures followed in producing the database are those outlined in the FAO soil map of the world (FAO 1988). Black and white aerial photographs are the main tools that were used to collect baseline data. In utilizing aerial photographs, we are aware that the different soil classes could in fact be a reflection of different shades of vegetation. With this method, vegetation is used as an indicator of soil type through reflectance resulting from tone and texture. It is also known that this is not always true, as vegetation variation does not necessarily coincide with differences in soil variation Westman (1985).

This sounds as if it is a description of procedures followed in mapping soils (which it is) even though the inherent objective is vegetation. True as this may be, the fact is that it was only during field work when notes on the dominant vegetation types and the composite species were recorded at each site. Eventually this data was used towards the production of a vegetation map of the country. Basically, the methods employed in producing both the vegetation and the soils map relied on the use of aerial photography and unclassified hard copies of satellite imagery combined with fieldwork. Ground truthing work as far as vegetation is concerned was mainly recording of species and their associations at certain point locations.

Timberlake (1980a) used Landsat MSS exclusively in defining the vegetation map of south-east Botswana. The methods used involved visual classification of a Landsat MSS image as well as detailed field sampling. Colour composite prints of Landsat images were interpreted on the basis of colour and texture to yield potential vegetation zones. Sample sites were located on delineated classes for field data gathering and confirmation. Vegetation sampling was done at species level for botanical composition of classes for trees, shrubs, grasses and forbs. Field data was analysed using a modified Braun-Blanquet method of vegetation description and analysis.

Limitations of methods

The strengths of any investigation leading to a product such as a national vegetation map is dependent on the method of data collection. In the case of the vegetation map by De Wit and Bekker, it is apparent that point data was used to describe the vegetation classes. This technique assumes homogeneity of vegetation across delineated classes, a potential methodological error that may not depict the true pattern of vegetation across any landscape.

On the methodology adopted by Timberlake (1980a), one could only critique the available tools that were in use at the time, since the methods used for data collection are well established (Braun-Blanquet 1932/51). The colour composite print-outs, used as they are, are limited in highlighting vegetation categories. Automated classification tools that are presently available offer a better solution for vegetation class delineations. It is understandable however that the procedures used could have been the best at the time considering technological developments in image processing systems. The accuracy level of the northern portion covering Palapye and the Tuli Block areas seems to be reasonable, based on the author's experience around the area, This may be attributable to the high number of field observations by the survey team.

Shortcomings of black and white aerial photographs are virtually overcome by the advantages of other tools used in modern remote sensing. In the previous section, mention has been made on the types of data collection techniques used in compiling vegetation maps in Botswana. Mostly, these are well established techniques that have been proved world-wide but, as mentioned above, have their own limitations. Like in any field, limitations are overcome through the development of improved methods which are more precise. In remote sensing we find a good example of improvement of techniques used in data capture coming along with technological development, that is, from field methods to black and white aerial photos, color infrared aerial photographs to digital satellite imagery. In each case advancement meant a number of advantages: greater aerial coverage, speedy automated data collection, cost-effectiveness and improved objectivity. Given the shortcomings of vegetation mapping in Botswana, recommendations are henceforth presented in this paper to try and improve on the quality of data collection and consequently a better output. The recommendations are an effort to find better ways of refining the mapping of the species mopane in this case. It is hoped that with a more refined map of the mopane tree, it would become possible to improve our understanding of the factors that influence its distribution.

Discussion and Conclusions

This review paper has highlighted two main problems regarding plant geography in Botswana with particular reference to mopane. These are the problem of what is meant by distribution and the methods applied in mapping. Working definitions are an essential component in any investigation; species distribution patterns pose a practical problem since 'distribution' can be defined to suit a specific situation. Distribution is scale dependent, for example, one can look at the distribution of a species at community level, or in another situation the same can be considered at the level of an individual plant, or spot occurrence. The definition of distribution patterns is a significant step crucial towards the understanding of the biogeography of plant species.

Techniques used in mapping species distribution, like the distribution, are also scale dependent (Huggett 1995). Mapping techniques therefore depend on the working definitions. Mopane has been mapped at various scales (Weare and Yalala 1971; De Wit and Bekker 1991; Timberlake 1980a). These works resulted in what has locally become known as the 'mopane line', indicating the species' distribution limits. But if one has to switch to a larger scale, the mopane line would be stretched to some 250 km beyond its present position to include trees that have been found to grow in Mochudi, Gaborone and Ramotswa. The latter does have a bearing on the definition because it is now clear that the few mopane trees in the south are some of the early indicators of the anthropological effect on the distribution of mopane.

As this paper is focused on the distribution pattern of mopane, concluding remarks address the problems of understanding the term distribution, methods implied in mapping the distribution and a recommendation of a mapping approach.

Meaning of distribution

Working definitions have to be in place before any investigations on the distribution of mopane can start. Such definitions should indicate the spatial resolution (scale of operation) in order to avert confusion especially that mopane tree plants are found beyond the mopane line.

Recommendation of methods

The fragmented nature of the distribution pattern of mopane, like that of most species in semi-arid regions, pose some difficulty in the various mapping methods to the effect that an interdisciplinary approach to mapping is recommended.

- Spot occurrence of mopane should also be used in defining its distribution. This may seem inappropriate even with large scale mapping, but it does show how far the species has been dispersed. In addition, this method could become appropriate where species are mixed, making it difficult to use other methods.

- Aerial photography remains an important tool in vegetation mapping at large to medium scales. Colour near-infrared photography is recommended for mapping the distribution of mopane. The use of CIR photography could offer the best means of mapping or defining the 'mopane line', first because of the high resolution offered by aerial photography, and secondly, because of the success rate of using CIR air photos for vegetation mapping elsewhere (Stephens 1976).

- At small-medium scales, the distribution pattern of mopane can be captured through the use of satellite imagery. The spatial resolution of satellite images is only good enough for mapping mopane at community level. But even then, because of problems of overlapping signatures and mixed pixels prevalent on semi-arid vegetation types, it is possible that only very dense, pure mopane stands could be mapped with some reasonable level of accuracy as has been found by Ringrose et al. (1997) in the Okavango area.

- Predictive mapping also provides another alternative to vegetation mapping (Franklin 1995). This method would be useful in showing the possible distribution pattern of mopane. The relationship between the spatial distribution pattern of the species and soil type distribution as well as moisture availability make up researchable topics.

References

Archibold, O W (1995) *Ecology of world vegetation* (London: Chapman and Hall).

Barbour, M G, Burk, J H & Pitts, W D (1987) *Terrestrial Plant Ecology* (Reading: The Benjamin/Cummings Publishing Company).

Barker, U (1983) "Towards a biogeography of the Kalahari: Part I and 2", *Botswana Notes and Records* 15: 8 5 -98 (Botswana Society, Gaborone).

Bekker, R P & De Wit P V (1991) *Contribution to the vegetation classification of Botswana* (Ministry of Agriculture/FAO, Gaborone).

Braun-Blanquet, J (1932/51) *Plant Sociology: The study of Plant Communities* (English translation) (New York: McGraw-Hill).

Campbell, A & Child, G (1971) "The impact of man on the environment of Botswana", *Botswana Notes and Records* 3:91-110 (Botswana Society, Gaborone).

Clements, F E (1904) "The development and structure of vegetation", Bot. Survey of Nebraska (University of Nebraska, Lincoln) in: *Relations-between community theory and community analysis in vegetation science some historical perspectives,* Noy-Meir, I. & Van der Miarel, E. (1987) *Vegetatio* 69: 5-15.

Coates-Palgrave, K (1983) *Trees of Southern Africa* (Cape Town: Struik).

Coe, K H (1991) "Effects of thinning on *Colophospermum mopane* in an indigenous woodland setting", *Journal of the Forestry Association of Botswana* 47-57.

Cole, M M (1986) The Savannas: biogeography and geobotany (London: Academic Press).

Cole, M C & Brown, R C (1976) "The vegetation of the Ghanzi area of western Botswana", *Journal of Biogeography* 3: F69-196.

Crawford, R M M (1989) *Studies in plant survival: ecological case histories of plant adaptation to adversity* (Oxford: Blackwell).

Crawley, M J (ed.) (1986) *Plant Ecology* (Oxford: Blackwell Scientific Publications).

De Beer, J S (1962) *Provisional vegetation map of the Bechuanaland Protectorate* (Department of Agriculture, Gaborone).

De Wit, P & Becker, R (1990a) *Vegetation map of the Republic of Botswana* (Ministry of Agriculture, Gaborone).

De Wit, P & Becker, R (1991b) *Contribution to the vegetation classification of Botswana* (Ministry of Agriculture. Gaborone).

Dye, P J & Walker, B H (1980) "Vegetation-environment relations on sodic soils of Zimbabwe Rhodesia", *Journal of Ecology* 68: 589-606.

FAO-UNESCO (1988) FAO-UNESCO *soil map of the world: Revised Legend.* (FAO, Rome).

Field, D I (1976) *A handbook of common grasses in Botswana* (Ministry of Agriculture, Gaborone).

Franklin, J (1995) Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients", *Progress in Physical Geography* 19: 4, 474-99.

Goldstein, G & Sarmiento, G (1987) "Water Relations of Trees and Grasses and their consequences for the structure of Savannah vegetation" in: *Determinants Of Tropical Savannahs* (ed) B H Walker) (Oxford: I.R.L. Press, pp. 13-38).

Henning, A C (1976) *A study of edaphic factors influencing the growth of C. mopane* (Ph.D. Thesis, University of the Wiwatersrand).

Huggett, R J (1995) *Geoecology: an evolutionary approach* (London: Routledge).
Humbodt, A von (1817) "De Distributionae Geographica Plantarum, Paris: Libraria Graeco-latino-Germanica", in: *Biogeography: A study of plants in the Ecosphere.* Tivy, J (1993) (New York: Longman).
Koppen (1918) "Klassification der klimate nach temperature Niederschlag und Jahreslauf" Petermanns. Mitt. 64: 133-203; 243-8. In: *Biogeography: a study of plants in the Ecosphere.* Tivy, J (1993) (New York: Longman).
Lebrun, J (1947) "La vegetation de la plaine alluviale au sud du lac Edouard. Explore". Parc. Nat. Albert. Fasc. 1:-800. Parcs Nat. Congo Belge. Bruxelles, in: *Biogeography and Ecology of southern Africa* (ed) Werger M J A (The Hague: Junk Publishers).
Macala, J P (1996) *"Colophospermum mopane":* A Fodder Tree for Feeding livestock. Proceedings of the First Multi-disciplinary Symposium on Phane, (University of Botswana, Gaborone).
MacArthur, R H & Wilson, E O (1967) *The Theory of Island Biogeography* (Princeton: Princeton, University Press).
Madams, R W (1990) *Biogeography of C. mopane and its distribution limit in eastern Botswana* (Ph.D. Thesis. University of London).
Miller, O B (1948) *Checklist of forest trees and shrubs of the British Empire.* No. 6, Bechuanaland Protectorate (Oxford: Scrivener Press).
Moleele, N M (1998) "Encroacher woody plant browse as feed for cattle. Cattle diet composition for three seasons at Olifants Drift, southeast Botswana", *Journal of Arid Environments* 40: 255-268.
Mott, P J (1978) *Science by investigation: a key to the flowering plants of Botswana* (University of Botswana, Gaborone).
Norwegian Forestry Association (1993) *Chobe Forests inventory and management plan, Final report.* Ministry of Agriculture (Ministry of Agriculture, Gaborone).
Noy-Meir, I & van der Maarel, E (1987) "Relations between community theory and community analysis in vegetation Science some historical perspectives", *Vegetatio* 69: 5-15.
Obermeijer, A A (1933) "Notes on the distribution of Copaifera Mopane Kirk", *South African Journal of Science* XXX 266-269.
Pole-Evans, I B (1938) "A reconnaissance trip through the eastern portion of the Bechuanaland Protectorate and an expedition to Ngamiland". June-July 1937. *Memoir of Botanical Survey of Southern Africa.* No. 21.
Powel, M, Sebego, R & Bonyongo, C (1996) *Inventory and Structural Analysis of Rangelands* (Ministry of Agriculture, Gaborone).
Ringrose, S & Matheson, W (1995) "An update on the use of remotely sensed data for range monitoring in southeast Botswana", *Botswana Notes and Records* 27: 2 5 7-270.
Ringrose S, Vanderpost, C & Matheson, W (1997) "Use of image recessing and GIS techniques to determine the extent and possible causes of land management/fenceline induced degradation problems in the Okavango area, northern Botswana", *International Journal of Remote Rensing* 18: No. 11, 2337-2364.
Roodt, V (I 992) *The Shell field guide to the common trees of the Okavango Delta and Moremi Game Reserve* (Shell Oil, Botswana).
Roberts, D W (1987) "A dynamical systems perspective on vegetation theory", in: *Theory and Models in Vegetation Science* (eds) Prentice, I C, & Van der Maarel, E (1987 Dordrecht: Junk Publishers)
Rosen, B R (1980) "Biogeographic pattenrs: A perceptual overview", in: *Analytical approach to the study of animal and plant distributions* (eds) Myers, A A & Giller, P S (1988) (London)
Rutherford, M C (1983) "Growth rate, Biomass and distribution of selected woody roots in *Burkea africana-Ochna pulchra* Savanna", *Vegetatio* 52: 45-63.
Sebego, R J (1993) *The effects of increased demand for arable land on the quality and quantity of grazing and fuel wood: an example from Ditshukudu Agricultural Extension area-Lentsweletau*

Sub-District of Botswana (Unpublished MSc. Thesis, University of Botswana).
Scholes, R J (1991) "The influence of soil fertility on the ecology of southern African savannas", in: *Savannah Ecology and Management*. (ed) Werner P.A., Ed. *Australian Perspectives and Intercontinental Comparisons* (London: Blackwell).
Sekhwela, M B M (1989) "The nutritive value of mopane bread – mopane insect secretion (maphote or mabote)", *Botswana Notes and Records* 20: 151-153.
Simmonson, R W (1959) "Outline of a generalised theory of soil genesis". *Soil Science Society of America Proceedings* 23: 152-6 in: *Ecology if world vegetation*. Archibold, O W (1995) (London: Chapman and Hall).
Skarpe, C (1986) "Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari", *Vegetatio* 68: 3-18.
Stephens, P R (1976) "Comparison of Colour, Colour Infrared, and Panchromatic Aerial photographs", *Photogrammetric Engineering and Remote Sensing*. Vol. XLII, No. 10, 1976.
Tietema, T, Ditlhogo, M, Tibone, C & Mathalaza, N (1991) "Characteristics of eight firewood species of Botswana", *Biomass and energy* 1: 1, 41-46.
Timberlake, J R (1995) "*Colophospermum Mopane*: Annotated bibliography review", *The Zimbabwe Bulletin of Forestry Research*, No. 11.
Timberlake, J R (1980a) *Vegetation map of southeast Botswana* (Ministry of Agriculture, Gaborone).
Timberlake, J R (1980b) *Handbook of Botswana acacias*. (Ministry of Agriculture, Gaborone).
Tivy, J (1993) *Biogeography*: a study of plants in the Ecosphere (New York: Longman).
Van Heist, M (1991) "Mapping woody biomass classes in southeast Botswana using landsat MSS", *Forestry Association of Botswana*. Gaborone.
Van Rensburg, H J (1971) *Range Ecology in Botswana. Vegetation studies in connection with vegetation/soil correlation and bush encroachment investigations*. FAO Technical Document No. 2, UNDP/SF/359/(BOT. 1), Rome.
Van Voorthuizen, E G (1976) "The mopane tree", *Botswana Notes and Records* 8: 223-230 (Botswana Society, Gaborone).
Weare, P R & Yalala, A (1971) "Provisional vegetation map of Botswana" *Botswana Notes and Records* 3: 131-148 (Botswana Society, Gaborone).
Westman, W E (1985) *Ecology impact assessment, and environmental planning* (New York: John Wiley and Sons).
White, F (1971) "The taxonomic and ecological basis of chorology", *Mit. Bot. Staatssaimml.* Munchen 10:91-112.
Whittaker, R H (1967) "Gradient analysis of vegetation" *Bio. Rev.* 42: 207-264. In: *Theory and Models in Vegetation Science.* Roberts, D W (1987) *Vegetatio* 69: 27-33.
Whittaker, R H (ed.) (1982) *Ordination of Plant communities* (The Hague: Junk Publishers)
Woodward, F I & Williams, B G (1987) "Climate and plant distribution at global and local scales", *Vegetatio* 69: 189-197.
Woollard, J (1981) *A vegetative key to the woody plants of southeastern Botswana.* University College of Botswana, Gaborone.