A STUDY OF EDAPHIC FACTORS INFLUENCING THE GROWTH OF *COLOPHOSPERMUM MOPANE* (KIRK ex BENTH.) KIRK ex J. LEONARD.

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To

Penelope Anne, dearest friend

I, Anthony Charles Henning, do hereby declare that the thesis entitled "A Study of Edaphic Factors Influencing the Growth of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard", has not been submitted in whole or in part to any other University for any degree purposes whatsoever, and that the results contained therein were obtained by my own unaided effort.

A.C. HENNING

Date: 9/5/76

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ABSTRACT

A review of the literature on the growth, distribution and common uses of *Colophospermum mopane* (mopane) is presented, with particular emphasis being given to the controversial and frequently contradictory opinions expressed concerning the role of soil as a limiting factor in the development of this species.

Initially the phytogeographical limits of mopane were investigated in order to provide a wider context within which subsequent field and laboratory studies could be interpreted. The chorological limits of the taxon appeared to be determined by the 1000 mm mean annual rainfall isohyet and the 5°C mean daily minimum isotherm for July. A marked disjunction associated with the 18°S latitudinal line was found to be correlated with low winter temperatures and very probably also, deep Kalahari sands.

Eight sites representative of the known physiognomic diversity of mopane woodland were chosen in Rhodesia, Botswana and South Africa. The correlation between mopane performance (as measured by Σ diameter at breast height times density, over six height classes) and selected physical and chemical properties of the soils was examined using simple linear and step-wise multiple regression analysis. Performance values were highly correlated with total N and $NaHCO_3$-extractable P in the surface soil, percentage moisture in the sub-soil at 0,33 and 15,2 bars matric suction and finally, with exchangeable Mg content in the surface and sub-soil. The importance of magnesium was demonstrated further by the tendency of performance to decline with increases in calcium and sodium relative to this cation.

Based on the evaluation of the field data, experiments were designed to study:

(a) the interaction of nitrogen, phosphate and soil moisture stress on mopane growth;

(b) the interaction of magnesium, potassium and sodium on mopane growth,

under controlled conditions of temperature, light and humidity.

Measurements made on the yield response, water consumption and relative nitrogen content of plants in experiment (a) suggested that mopane was capable of internal osmotic adjustment. Seedlings responded to increased N and P supply on two soils with over 20 per cent water at 0,33 bars matric suction. Fluctuations in the available water supply from 100 to 0 per cent had no effect on yield, evapotranspiration rate or coefficient of water utilization on these soils. On a third soil, with only seven per cent water at 0,33 bars suction, yield and evapotranspiration rate decreased significantly ($P < 0,01$) with increased N and decreasing available water supply. The coefficient of water utilization, however, remained unaffected by rising soil moisture stress. Decline in yield was primarily due to increased soil osmotic suctions associated with increased nitrogen treatment. The growth of mopane declined progressively with increases in osmotic suction from 3 to 8 bars but thereafter remained unaffected till 16 bars at least (32 bars total soil moisture stress).

Stressed plants showed a marked increase in relative nitrogen content and it is suggested that the resistance of this species to severe soil moisture stress might be partly due to the build up of soluble nitrogenous compounds within the cell sap.

Sodium and potassium supplied at the rate of 15 per cent of the C.E.C. caused a significant ($P < 0{,}001$) decline in yield on all three soils. Furthermore, there was a significant positive interaction between K and Na such that the depression in yield was greater when the two salts of K and Na were supplied at the same time. This effect was due to an increase in osmotic suctions in the soil solution (-2–8 bars). Intermediate levels of magnesium partially reversed the detrimental effects of K and Na. This trend could not be explained in terms of an improvement in cation balances within the plant tissue. It appeared therefore that magnesium played a direct role in the water economy of the plant. It is possible that this cation catalyses the metabolic production of organic solutes thereby increasing the osmotic pressure of the cell sap and enhancing the plants ability to withstand moisture stresses.

This study concludes with a brief summary of the main conclusions to emerge from the field and controlled environment work. These conclusions are discussed in terms of the present day chorological limits of mopane. In view of the tolerance of mopane to a wide range of environmental stresses, it is suggested that this species acts as an important buffering element in the maintenance of ecosystem stability within the dry tropics.

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A. INTRODUCTION

Colophospermum mopane (Kirk ex Benth.) Kirk ex J. Leonard, a non-nodulating legume belonging to the sub-family Caesalpinioideae, has been variously referred to as the butterfly tree, the turpentine tree, the balsam tree and Rhodesian ironwood. The more common vernacular names, however, are the Tswana and Venda derivatives "mopane" and "mupini" respectively. In view of the almost international recognition of the specific epithet "mopane", this colloquialism will be used hereafter.*

Mopane may be recognised by its leathery resinous leaves which are made up of two triangular leaflets hinged together by a short midrib. The leaves are thus characteristically shaped like the wings of a butterfly (Plate 1). Morphologically it varies in size from a short coppicing shrub, less than half metre high, to a medium sized tree exceeding twelve metres in height (Plate 2). Occasionally specimens may attain a height of twenty three metres, the rough, deeply fissured trunk exceeding one metre in diameter (De Winter *et al.* 1966). The flowers are small, pale green and borne in tassels; the pods are flat and kidney shaped, and the single seed within is wrinkled and covered by numerous resin secretory glands (Plate 1). According to Palmer and Pitman (1961), these resin glands are an effective dispersal mechanism in that they cause the seed to adhere to the hooves of passing animals.

The distribution of this species is limited to South Central Africa (Wild, 1968). Its trans-continental extension includes representation in Angola, South West Africa, Botswana, Zambia, Malawi, Rhodesia, South Africa and Moçambique (Porter, 1968).

The heartwood of mopane is hard and durable and is used for small articles of furniture, mine props, fence posts and railway sleepers (Pardy, 1953). The wood is very combustible and the ash is said to have a high phosphorus and calcium content (Watt and Breyer-Brandwijk, 1962; van Wyk, 1972a). The leaves are host to a black hairless caterpillar called the mopane worm (*Gonimbrasia belina*). These worms are considered a delicacy amongst rural Africans and are said to have a high protein content.**

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*This species is not without its quota of African romanticism. Livingstone, in his travels noted that the Zambezi inhabitants feared mopane during thunderstorms. "Lightning hates it" they would say, whilst cautioning travellers never to go near the tree (Palmer and Pitman, 1961). It is rumoured that Zambian natives use extracts from mopane bark to treat syphilis (Fanshawe, pers. com.), whilst certain Rhodesian tribes claim that the bark is an effective fish poison (De Winter *et al.*, 1966).

**The mopane worms, with their characteristic white and orange stippled spines, are gutted and then sun dried or roasted before eating. The writer has tasted this "delicacy" and found it to be somewhat leathery with a distinct turpentine flavour.

PLATE 1. Mopane shoot showing "butterfly" leaves and kidney shaped pods containing a single wrinkled seed.

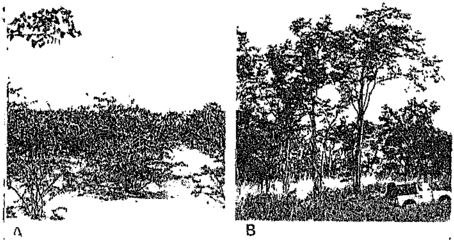


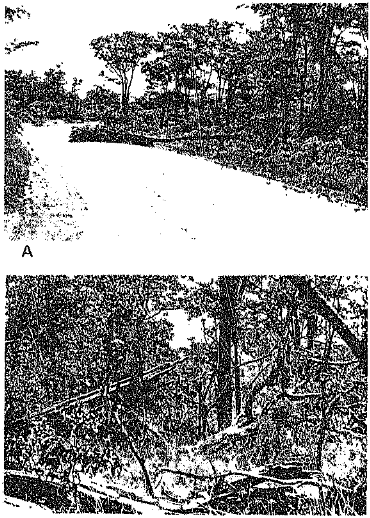
PLATE 2. Stands of shrub (A) and tree (B) mopane *in the Northern Transvaal, occurring* within a few kilometers of one another

Probably the most valuable economic attribute of mopane is its browsing potential. Although this species does not nodulate and fix atmospheric nitrogen (Eyles, 1971) it nevertheless forms a valuable food supplement for cattle in the dry tropics (Lawton, 1967). Even though the leaves and seeds smell strongly of turpentine, milk and meat remain untainted (Watt and Breyer-Brandwijk, 1962). The nutritional value of mopane leaves compares very favourably with a number of dry tropical browse species (Myre and Coutinho, 1966; Lawton, 1967; Du Toit, pers. com.). The shrub and tree forms of this species are browsed by a wide range of wild game, including Elephant (*Loxodonta africana*), Kudu (*Strepsiceros strepsiceros*) and Impala (*Aepyceros melapus*) (Jarman and Thomas, 1969). Elephants will often fell large mopane trees to browse off the soft and succulent apical shoots (Plate 3) (Codd, 1951).

Over much of Africa today, the problem of a protein deficiency in the human diet is becoming more acute. Recently, increased attention has been directed towards the management and utilization of wild animals as a protein source. Talbot *et al.*, (1965) have reviewed the literature on the meat production potential of wild animals in Africa. Much of South Central Africa today is semi-arid woodland savanna of marginal value. Long dry seasons, together with the widespread distribution of tsetse fly, limits the numbers of domestic animals that can survive in these areas (Field, 1968). Wild ungulate populations have selected against these hazards and therefore hold prospects for a sustained protein yield. In many such areas, mopane is the dominant primary producer.

Despite its ability to colonise dry, barren and eroded land, mopane has excited very little research interest. The literature on this species is sparse and very often contradictory. This is to be expected since most of the observations so far have been of a superficial and subjective nature. The environmental factors governing its growth and distribution remain unresolved. In view of the many conflicting ideas on this ecologically important browse plant, a study was made of the influence of selected soil factors on the growth of mopane. Estimates of growth performance were obtained from several diverse sites in *Botswana, Rhodesia and South Africa, and correlated with the chemical properties of* the surface and sub-soils. Hypotheses were deduced from significant correlations and interactions, and then tested by controlled environment studies.

The phytogeographical relationships of mopane were studied at the outset with the view to obtaining a broader interpretation of the more specific studies mentioned above.



A

B

PLATE 3. Mopane trees felled by elephants in the Wankie National Park (A) and Chete Game Reserve (B).

B. REVIEW OF LITERATURE

B.1. Distribution

At the sixth plenary meeting of the "Association pour l'Etude Taxonomique de la Flora de' Afrique Tropicale" (A.E.T.F.A.T.), it was proposed that an atlas of ecologically important plant species in Africa be constructed (White, 1968). Some four hundred plant species were proposed, one of which was mopane. Apart from the chart constructed by Porter (1968), there are no other maps depicting the global (i.e. African) distribution of the species (Fig. 1).

Perhaps the most noticeable feature in Porter's map is the apparent gap in mopane's East-West extension between the 17°E and 21°E meridians. No mopane is depicted between these lines of longitude in the vegetation maps of Angola and South West Africa (Grandvaux Barbosa, 1970; Giess, 1971). These observations are in agreement with floristic studies carried out in the Kovangoland of South West Africa (Volk, 1966).

Other noticeable features on this distribution chart are, firstly, the northerly extension of this species along the low lying Luangwa Valley (Zambia), and secondly, its absence from the highveld regions of Rhodesia. Mopane shows a strong affinity for hot low lying areas (White, 1962) and rarely occurs at altitudes greater than 900 meters (Airy-Shaw, 1947; Porter 1968). Occasionally it may be found growing at higher altitudes (Beatrice, Rhodesia) where unfavourable soil conditions prevent the growth of other species (see Section B.3.). Its southern boundary in the Northern Transvaal coincides almost exactly with the foothills of the Zoutpansberg mountains. The exclusion of this species from higher altitudes is probably due to the combined influences of increased precipitation and lower temperatures (see Section B.2.).

Porter's map was constructed principally from specimen localities obtained from the National Herbarium in Pretoria. In many instances the boundaries depicted on this chart vary significantly from those depicted in current regional vegetation maps (Acocks, 1953; Rattray and Wild, 1961; Wild and Grandvaux Barbosa, 1967; Grandvaux Barbosa, 1970; Giess, 1971; Weare and Yalala, 1971). In view of these discrepancies, the writer has revised Porter's distribution map of mopane, using the regional vegetation maps listed above as a guideline (Fig. 7 — Section D).

B.2. Climatic Factors

According to Thompson (1960), areas receiving less than 450 mm of rainfall per annum may be considered as the most favourable environmental niche of mopane. This

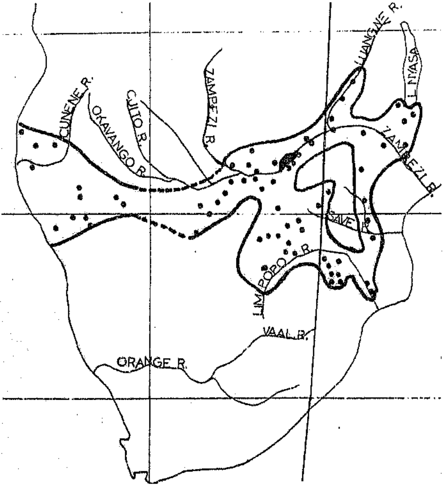


FIG. 1. Distribution of *Colophospermum mopane* (Porter, 1968).

figure is in close agreement with the values reported by Child (1968) and West (1969). Mopane can survive in areas receiving as little as 200 mm p.a., but is excluded from areas receiving over 800 mm p.a. (Porter, 1968). In the Kaokoveld (South West Africa), shrub mopane survives in *areas receiving less than 125 mm p.a. (Owen-Smith, 1970; Clinning,* pers. com.). Presumably mopane is precluded from higher rainfall zones through competition from species more adapted to wetter environments.

Mopane is able to grow in areas experiencing high summer temperatures. At meteorological stations along the Zambezi valley, for example, mean maximum temperatures often exceed 36°C during the months of October and November (Climatological Summaries, 1963) (Appendix 1). Low winter temperatures, on the other hand, appear to be an important factor restricting the southern extension of this species. The southern boundary of mopane's distribution shows a close correlation with the July mean daily minimum isotherm of 10°C (Porter, 1968). Although tolerant of light frosts (Thompson, 1960; West, 1969) this species is susceptible to severe frost conditions (Child, 1968; van der Schijff, 1969). In many areas the coppicing growth habit of mopane has been attributed to frost damage (Tinley, 1966; Joubert, 1971). The writer is of the opinion that this coppicing response may be due to a release of apical bud dominance after severe frost damage (Leopold, 1964).

B.3. Edaphic Factors

It would appear from the literature that mopane has a wide ecological amplitude and is thus capable of surviving on a variety of soil types. Mopane is often associated with shallow, compacted, clayey and strongly alkaline soils that are poorly drained (Henkel, 1930; Ellis, 1950; Vincent and Thomas, 1961; Hudson, 1970; Louw, 1970). Occasionally it may be found on deep, well drained, slightly acid soils, where high temperatures and low rainfall restrict the downward movement of water to a shallow depth. Along the southern banks of the Kafue River (Zambia) it occurs on hard, compacted, greyish black clay soils that are generally covered by a wash of sand at the surface (van Rensburg, 1968). In the Sabi-Lundi and Gokwe districts of Rhodesia, shrub mopane grows on alkaline, heavy clay soils, but attains woodland status on lighter, better drained soils (Farrell, 1968a; 1968b). In South West Africa, however, this species generally occurs on shallow, sandy alkaline soils (Joubert, 1971) or sandy well drained soils, and appears to avoid heavy clay conditions (Volk, 1966).

Observations in the Kruger National Park (South Africa) indicate that mopane does not grow on poorly drained impermeable soils. Waterlogging during the rainy season is normally associated with species such as *Combretum imberbe, Combretum hereroense* and *Acacia xanthophloea* but never with mopane (van der Schijff, 1969). The intolerance of this species to waterlogged conditions has also been reported by Rattray and Wild (1955), Thompson (1960), West (1969) and Child (pers. com.).

This species frequently grows on shallow stony soils (Miller, 1938; Wild, 1953; Wild, 1955), and does not encroach upon very deep sands of the Kalahari type (Boughey, 1963; van der Schijff, 1969; van Wyk, 1972a; Attwell, pers. com.). A study of the soil maps of Rhodesia and Zambia (Trapnell *et al.*, 1948; Thompson *et al.*, 1960; Thompson. 1965) would seem to indicate that mopane occurs predominantly on skeletal, lime accumulating, shallow to moderately shallow loamy sands over sandy loams, or sandy loams over sandy clay loams. Staples and Murray (1951), however, contend that where mopane occurs particularly in the hotter and drier regions, the soils will be completely different from the types depicted in current soil maps. "Mopane soils are characterised by a fairly light, neutral or slightly acid top soil overlying a compacted heavy alkaline subsoil. These areas are unsuitable for general crops, but are suitable for grazing particularly if mopane is stumped out."

The viewpoint that mopane is responsible for a radical change in soil properties (from that normally expected under a given set of soil forming factors) is also shared by Ellis (1950) and Hudson (1970). Both these authors are of the opinion that soils under mopane gradually develop a high exchangeable sodium content, which inevitably results in a reduction in permeability and an increased susceptibility to erosion. As examples, Ellis cites the soils at Umgusa and Beatrice (Rhodesia) where sodium is the dominant exchangeable cation (> 50% of total exchangeable cations). It should be noted, however, that both these areas occur on the Rhodesian highveld, beyond the normal altitudinal limits of this species. Field trials carried out by Thompson (1960) indicate that mopane seedlings are able to grow under sodium influenced conditions, albeit at a reduced growth rate. Tolerance to high exchangeable sodium might well enable this species to colonise unfavourable soils (e.g. Umgusa and Beatrice) in the absence of competition from other less tolerant species. Beyond its normal distribution limits, mopane is a reliable indicator of unfavourable soil conditions (Wild, pers. com.) and for this reason it is generally and sometimes erroneously associated with infertile soils (Vincent and Thomas, 1961).

Grass cover under mopane woodland is generally sparse and discontinuous (Henkel, 1930; Miller, 1938; Bawden and Stobbs, 1963; Myre and Coutinho, 1966; Weare and Yalala, 1971). In the southern lowveld of Rhodesia, however, mopane soils support a fairly dense substratum of perennial and annual grasses (West, 1967), whilst in the Moremi (Botswana) this species is often associated with a dense grassland understorey (Tinley, 1966). According to van der Schijff (1969), the grass cover under mopane does not differ significantly from that under other woodland types.

Presence or absence of an adequate grass cover has often been used as a subjective assessment of fertility status in mopane soils (Ellis, 1950; Bawden and Stobbs, 1963; Hudson, 1970). Ellis attributes the sparse grass cover under mopane to the adverse conditions associated with high sodium saturation, together with competition for essential nutrients and moisture. Mopane roots seldom penetrate to a depth greater than four feet (Thompson, 1960) and the dense mat of fine roots produced near the surface coincides with the zone of maximum soil moisture penetration (Ellis, 1950). Subjective assessment of soil fertility based on grass cover should be regarded with some reservation, since in numerous instances the ground storey vegetation appears subject to other influences (see Section B.4.).

B.4. Biotic Factors

According to Thompson (1960) the sparse grass cover under mopane woodland may be attributed to competition. Conversely, seedlings of the species will not compete favourably in dense grassland areas. In addition to competition for nutrients and moisture (Ellis, 1950), light may also be an important limiting resource. When mopane trees are felled by elephants, increased light penetration through the canopy enables a dense sward of grass to develop (Tinley, 1966). Competition with indigenous grasses, and not soils and climate directly, is said to preclude the establishment of mopane on the highveld region of Rhodesia (Thompson, 1960).

Numerous authors, however, are of the opinion that sparse grass cover under mopane is primarily the result of overgrazing by game and cattle (Rattray and Wild, 1955; Mitchell, 1961; West, 1967; Child, 1968; Farrell, 1968a; Weare and Yalala, 1971). Mopane seedling survival is also significantly reduced through browsing by a variety of game including Impala, Kudu, Warthog and Baboon (Jarman and Thomas, 1969). Severe browsing pressure may induce the coppicing growth habit of this species (Boughey, 1963).

Fire is yet another factor that should not be excluded in the assessment of mopane's competitive ability. Severe bush fires often result in complete destruction of the aerial components of this species. Recovery is rapid, however, in the form of a multi-stemmed coppicing shrub which develops from the protected underground parts (Seagrief and Drummond, 1958; Boughey, 1963; Tinley, 1966; Joubert, 1971). The vigour of perennial grassland is generally reduced by indiscriminate burning and overgrazing, thereby favouring invasion and colonisation by fire tolerant woody species such as mopane (Child, 1968). Coppicing, induced by fire contributes to the aggressive competitiveness of this species and thus favours its permanent encroachment on perennial grasslands (Mitchell, 1961; Tinley, 1966; Brynard, 1964). This encroachment is enhanced by drought conditions (van Wyk, 1972b), especially on shallow, gritty lithosolic soils (Austen, 1972).

C. MATERIALS AND METHODS

C.1. Phytogeographical Studies

Vegetation maps of the countries in which mopane occurs were photographically reduced to a scale of 1:10,000,000. The distribution limits of mopane were then traced off these reduced copies and reproduced on a single 1:10 000 000 ground chart of Africa. The collated distribution map of this species is presented to a scale of 1:15 000 000 (Fig. 7, Section D). The sources referred to for this construction are as follows:

(a)	1:1 500 000,	Veg. map of South Africa	(Acocks, 1953)
(b)	1:2 500.000,	Veg. map of the Federation of Rhodesia and Nyassaland	(Rattray and Wild, 1961)
(c)	1:2 500.000,	Veg. map of the Flora Zambesiaca area	(Wild and Grandvaux Barbosa 1967)
(d)	1:2,500.000,	Carta Fitogeografica de Angola	(Grandvaux Barbosa, 1970)
(e)	1:3 000 000,	Veg. map of Botswana	(Weare and Yalala, 1971)
(f)	1:3,000 000,	Preliminary veg. map of South West Africa	(Giess, 1971)

Likewise, a 1:10 000 000 map of the various geological formations under mopane veld was drawn (Fig. 10, Section D). The sources referred to for this construction are as follows:

(a)	1:2 000 000,	Carte Geologique de'l Angola	(Mouta and O'Donnel, 1933)
(b)	1:2 500 000,	Prov. geological map of Fed. of Rhodesia and Nyasaland	(Fed. Govt. Printer, Salisbury, 1961)
(c)	1:1 000,000,	Geological map of South West Africa	(Martin, 1963)
(d)	1:2 000 000,	Carte Geologica Provincia de Mocambique	(Oberholzer, 1968)
(e)	1:2 000.000,	Prov. geological map of Botswana	(Boocock, 1968)
(f)	1:1.000.000,	Geological map of the Republic of South Africa	(Coertze *et al.*, 1970)

The Climatological Atlas of Africa (Jackson, 1961) was studied and synoptic charts were made. These showed close correlation with the distribution limits of mopane (Fig. 8 and 9, Section D).

C.2. Field Techniques

C.2.1. Techniques available for the assessment of plant performance

The term "plant performance" describes somewhat loosely, the abundance of a particular species as reflected by its density, ground coverage or yield per unit area. Many techniques have been devised for assessing the performance of plant species in the field (Phillips, 1959; Brown, 1963). When one penetrates to the core of any of these methods, one finds that plant performance is measured and assessed by one or more of four criteria: frequency of occurrence, number of individuals per unit area, area covered by base or canopy, or weight (Brown, 1963). Frequency alone affords valuable information on floristic composition and distribution (Brown, 1963), but is subject to numerous limitations in the quantitative assessment of dominance or performance within a plant community (Penfound, 1945; Kershaw, 1973). Weight measurement, obtained by destructive sampling, offers the most direct and accurate means of vegetation assessment and is widely used in pasture management and forestry. Its application in the analysis of indigenous woodland vegetation is limited, however, particularly in protected areas where destructive sampling is prohibited. The remaining parameters, density and cover, offer an accurate and absolute measure of performance (Brown, 1963; Kershaw, 1973).

More recently, dimensional analysis has been used as a non-destructive means of estimating the weight of plants (biomass) in stands of woody species (Poole, 1974). Allometric regressions of diameter on the weight of different tree components have shown that this parameter (diameter) may be used to give reliable estimates of tree weight (Kittredge, 1944; Nomoto, 1964; Loomis *et al.*, 1966; Whittaker and Woodwell, 1968). According to Newbould (1967) diameter at breast height (D.B.H.) may be used for biomass estimation in stands of varied age and physiognomic type. The product of diameter squared and height (D^2H) is also significantly correlated with tree weight and is widely used in dimensional analysis (Newbould, 1967; Nihlgard, 1972).

The choice of sampling technique to use in any particular study is governed by the objectives in mind and by the nature of the vegetation being analysed. Quadrats are favoured by numerous workers because of their versatility and adaptability to a variety of vegetation types (Phillips, 1959; Brown, 1963). The line intercept method of Canfield (1941) has been widely used and is a rapid and accurate means of assessing cover over wide stretches of grassland. This method is easily adapted to the measurement of woodland vegetation, cover being determined as the percentage of the total length of line covered by the canopies of bushes and trees.

In phytosociological studies much attention has been devoted to ways and means of determining the most suitable quadrat size for sampling various vegetation types. According to Hopkins (1957) and Greig-Smith (1957) minimal area as determined by species-area curves can never be more than a gross approximation, and subjective judgement is often necessary in assessment of quadrat size. Some authors are of the opinion that quadrat size is of little relevance when quantitative measurements such as density and canopy cover are made (Penfound, 1945; Ashby, 1969).

Undoubtedly quadrat size (as determined by variance-area curves) is of prime importance in pattern analysis (Poole, 1974), but in stands composed of randomly distributed individuals, this criterion is immaterial except from the standpoint of convenience (Kershaw, 1973). Most plant populations do, however, exhibit groupings of individuals and since it is usually difficult to predetermine the scale of this pattern, quadrat size has to be chosen quite arbitrarily (Kershaw, 1973). According to Scheepers (pers. com.) and Morris (pers. com.) ten metre square quadrats are more than adequate for sampling in the various South African savanna woodland types.

C.2.2. Sample site selection

Field studies were carried out at eight localities in Botswana, Rhodesia and South Africa. The purpose of these studies was to obtain some estimate of growth performance in the field and to relate this to selected physio-chemical properties of the soils. Sites were selected to include the full range of mopane growth habit from dwarf coppice to the tall tree form (Plate 4). The soils at these localities overlie a variety of geological formations and with the exception of sites 1 and 2, mopane is almost exclusively the dominant woody vegetation element. The characteristics of each sample site have been summarised in table form (Table 1).

C.2.3 Sampling procedure

In each of the mopane populations listed in Table 1, a 240 metre square sample site was selected (area 57 600 m^2, 5,76 hectares). Each site was sub-divided into four 120 metre square replicate sub-plots in which a number of 10 metre square quadrats were distributed at random (Fig. 2). The sides of each replicate were treated as axes of length (12 units) and co-ordinates for quadrat location were then selected from random number tables (Rayner, 1967). The co-ordinates thus selected were located using metre tapes and a prismatic compass, using the lower left hand corner as the origin of the quadrat. Stratified random sampling of this nature was used to obtain an even distribution of quadrats throughout each sample site.

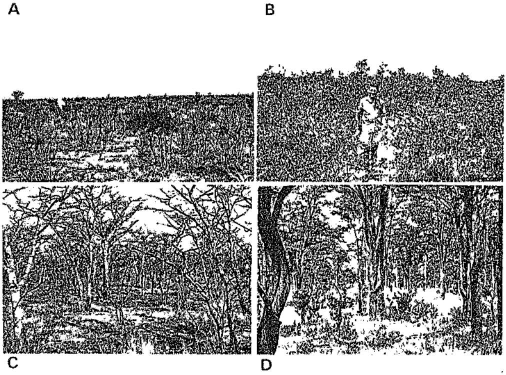


PLATE 4. Diversity of growth habit encountered in this study:
(A) Site 4, short coppice mopane (< 2m)-Orapa, Botswana.
(B) Site 6, shrub mopane (1–3m)- Bubi River, Rnodesia.
(C) Site 5, small tree mopane, (4–8m) - Orapa, Botswana.
(D) Site 7, tall tree mopane (> 8m) - Wankie, Rhodesia.

TABLE 1 – Vegetation characteristics and soil parent materials of eight sites representative of mopane woodland types in southern Africa.

Site No.	Location	Underlying parent material	Description of vegetation
1	Chete Game Park, N.W. Rhodesia (17^oS, 28^oE)	sandstone	Dominant *Combretum spp.*, mopane sub-dominant, height 4–7m
2.	Chete Game Park	sandstone	Dominant *Combretum spp.*, mopane sparse, height 4–10m
3.	Tzaneen, N.E. Transvaal (24^oS, 30^oE)	Archaean granites, gneiss	Shrub mopane, height 1–3m; tree mopane, height 6–8m
4	Orapa, S. of Makgadikgadi Pan, Botswana (21^oS, 26^oE)	Kalahari sand over calcrete and basalt	Shrub mopane, height 0,5–1m
5	Orapa, Botswana	Kalahari sand over calcrete and basalt	Small tree mopane, height 4–6m
6	Bubi River, S. Rhodesia ($21,5^oS$, $30,5^oE$)	paragneiss	Tall shrub mopane, height 2–3m
7	Wankie, N.W. Rhodesia ($18,5^oS$, 26^oE)	paragneiss	Tall tree mopane, height 10–12m
8	Wankie, N.W. Rhodesia	sandstone	Tall tree mopane, height 8–10m

Individuals were grouped into height classes of two metre intervals and the following parameters were then measured.

(a) Diameter at breast height (D.B.H.) – expressed in metres. For coppice and shrub plants basal diameter was used as an estimate for (D.B.H.).

(b) Density – expressed as no. of individuals per 100 sq. metres.

(c) Canopy cover – expressed as a percentage intercept along three 10 metre lines in each quadrat (Fig. 3).

An "individual" was taken to mean any stem or coppice of stems that could reasonably be assumed to have a common root stock.

Five auger samples were collected from the surface (0–10cm) and sub-soil (20–30cm) in each quadrat (Fig. 3). These sub-samples were combined in equal quantities and thoroughly mixed to obtain a representative sample of the surface and sub-soil for each replicate. The soils were air dried in the field and stored in plastic bags for subsequent chemical analysis. This method of sampling was used in the hopes of compromising the requirements for adequate coverage of the soil with subsequent costs and time involved in lab‹ atory analyses (Petersen and Calvin, 1965). Soil pits w.re dug at each sample site, :rof descriptions made, and samples collected in tins so that moisture determinations cou‹ made.

C.2.4. Sampling intensity

Sample size (n) was chosen by calculating the standard deviation (s) of the mean density, aiming to detect differences between any two sample means ($\bar{x}$) drawn from the whole population that were greater than 15% at a confidence limit of 95 per cent or $p < 0{,}05$. A detection limit of 10% ($p < 0{,}05$) would have necessitated a disproportionately higher increase in sampling rate, as may be shown by the formula:

$$n = \left[\frac{2s}{0{,}15\bar{x}}\right]^2 \qquad \text{(Gregory, 1969)}$$

Trial values of (n) were selected; mean density and standard deviation values determined, and (n) then estimated from the above equation. Details of mean density, standard deviation and quadrat frequency for each site are given in Table 2.

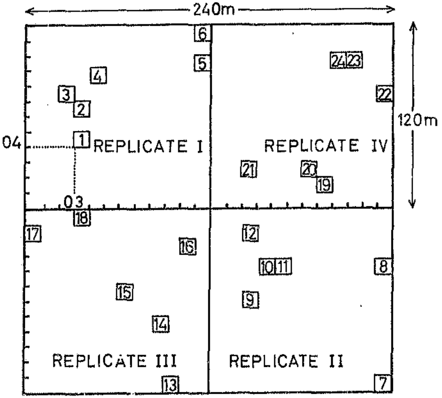


FIG. 2. Plan diagram of sample site I (Chete Game Park, N.W. Rhodesia) illustrating the stratified random sampling procedure used. (Scale 1cm:20m).

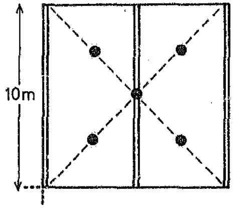


FIG. 3. Layout of 10 metre square quadrat showing intercept lines (----) and soil sampling points (•).

TABLE 2 – Determination of quadrat frequency and sampling precision for each sample site.

Sample site	1	2	3	4	5	6	7	8
Mean density ($\bar{x}$)	6,87	0,71	32,70	21,85	13,56	45,50	6,16	8,50
Sample standard deviation (s)	7,62	1,07	11,10	5,38	3,01	11,76	1,45	2,20
Estimated minimum no. of *quadrats (n)*	*219*	*378*	*20*	*11*	*9*	*12*	*10*	*12*
Final quadrat no.	24	24	20	12	12	15	15	14
S.E. of the mean	1,56	0,22	2,47	1,54	0,86	3,02	0,37	0,60
Precision $\frac{S.E..100}{\bar{x}}$ %	22,7	31,0	7,6	7,1	6,3	6,7	6,0	7,1

It was immediately obvious that the values of (n) required to satisfy the original premise for sites 1 and 2 were impractical. The high variation in density values obtained for these two sample sites may be attributed to the heterogeneity of floristic composition and spatial distribution within the two samples. Moreover, site 2 was composed mainly of *Combretum sp.* and contained relatively few mopane individuals. Consequently zero density values for mopane were recorded in a number of quadrats. Ultimately 24 quadrats were located at each of these sites, this number constituting a 4% coverage of the total area and being the largest sample that time would permit.

C.2.5. Treatment of vegetation data

The mean density of mopane in each height class was calculated and by summing these values over all height classes, the mean density for each sample site was determined. The percentage canopy cover at each site was calculated in a similar manner. On regression analysis, however, no significant correlations were obtained between these parameters and the chemical properties of the soils (see Section C.3.).

The poor correlations obtained between canopy cover and soil factors may have been due to errors inherent in the measurement of this parameter. The open nature of the canopy prevented an accurate assessment of cover, particularly of individuals exceeding four metres in height. Moreover, this error was exaggerated at sites four and five, both of which were sampled during the winter months after leaf-fall had occurred.

The lack of correlation between density and soil properties is not surprising, in view of the varied physiognomic types encountered at each site. Performance, as estimated by density, was highest in the stands of coppice mopane and lowest in populations of the tall tree form, despite the greater trunk diameter and taller stature of the latter. It was thus reasoned that the density values of the taller height classes should be weighted by some factor which varied proportionately with height, before legitimate inter-stand comparisons of performance could be made.

Accordingly, the mean D.B.H. (m) of mopane individuals encountered in this study, was calculated for each height class. As mentioned previously (Section C.2.1.), diameter measurements have proved useful in the biomass estimation of stands. Furthermore, mean diameters of mopane were found to increase curvilinearly with height (Fig. 4). By summing the product of D.B.H. times density over all height classes, a *performance value* (No. of individuals/metre) was estimated for mopane at each site. Regression analysis revealed a number of significant correlations, and these were explored further under controlled environment conditions.

C.3. Soil Analysis

The composite samples obtained from the field were first lightly ground in a pestle and mortar to break any stable aggregates (Piper, 1944; Beckwith, 1964). The samples were sieved (< 2mm) and chemical analyses then performed in duplicate on the fine earth.

C.3.1. pH

pH was measured in 0,01M $CaCl_2$ according to the method of Peech (1965), using a soil to liquid ratio of 1:2 (White, 1969).

C.3.2. Cation exchange capacity (C.E.C.)

C.E.C. was measured according to the $CaCl_2$ equilibration procedure adapted from Tucker and Emerson (1969).

A 20g sample was equilibrated with 200mls of 0,1M $CaCl_2$ for one hour and then centrifuged at 3500 r.p.m. to bring the soil out of suspension. The equilibration procedure was repeated three times using fresh 0,1M $CaCl_2$ on each occasion. The advantages of using $CaCl_2$ over NaOAc and NH_4OAc (Chapman, 1965), may be summarised as follows:

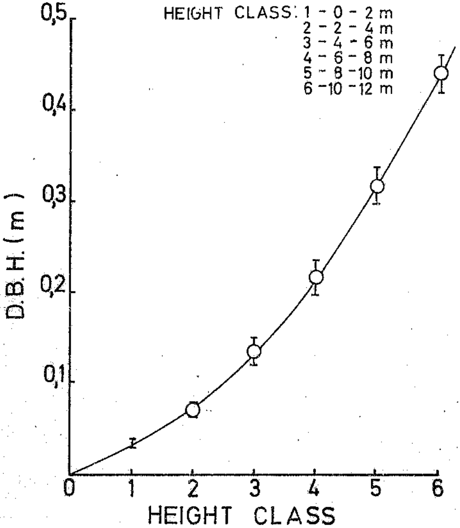


FIG. 4. The relation between D.B.H.(m) and Height Class. Vertical bars (I) indicate S.E. of mean D.B.H.

(a) Calcium is generally the dominant exchangeable cation in the soil.

(b) Calcium is an efficient displacer of other cations and is not readily displaced from interlayer sites.

(c) It may be used for both acid and calcareous soils and is easily analysed by a variety of methods.

After equilibration the entrained $CaCl_2$ solution was removed with 100mls of isopropyl alcohol. Washing with alcohol was justified since there was very little positive charge per gram of clay (at pH of 7 and above), which might have led to internal charge compensation on expansion of the double layer (Sumner, 1963). The qualitative ammonium oxalate test (Chapman, 1965) showed that the last few mls of isopropyl alcohol contained negligible amounts of calcium.

Adsorbed calcium was displaced by leaching with 450mls of 1N NH_4NO_3 in 60% ethanol. For calcareous soils (pH 7,4 in 0,01M $CaCl_2$), NH_4NO_3 buffered to pH 8,5 was used to minimise solution of $CaCO_3$. The filtered leachate was made up to 500mls and the concentration of calcium (ppm) determined by atomic absorption spectrophotometry.

Standards (0–10ppm) and test solutions contained equal amounts of 1N NH_4NO_3 to eliminate any extraneous effect this compound might have had on the readings obtained. 0,2% strontium (as $SrCl_2$ w/v) was used as a "releasing agent" to eliminate the formation of stable calcium compounds (e.g. $CaAl_2O_4$) in the flame (Rich, 1965; Isaac and Kerber, 1971). The results obtained for C.E.C. were expressed as meq.Ca^{++} /100g soil.

C.3.3. Total exchangeable cations (T.E.C.)

T.E.C. was determined by the NH_4Cl displacement technique of Tucker and Emerson (1968).

A 25g sample of soil was first leached with 100mls of 60% ethanol to remove all soluble salts. No traces of calcium could be detected in the last few drops of alcohol. The exchangeable cations were then displaced by leaching with 450 mls of 1N NH_4Cl in 60% ethanol (pH7 – 0,01M $CaCl_2$). For calcareous soils (pH 7,4 – 0,01M $CaCl_2$) 1N NH_4Cl buffered to pH 8,5 was used. The leachate was made up to 500mls and the concentration (ppm) of Ca, Mg, K and Na then determined using the SP.90 atomic absorption spectrophotometer. Calcium and magnesium were determined by absorption, in the presence of 0,2% strontium, whilst potassium and sodium were estimated by emission. The results obtained were expressed as meq per 100g soil.

C.3.4. **Total nitrogen**

Total nitrogen (including NO_3–N) was determined by the macro-Kjeldahl method of Bremner (1965). By using "Quick-fit" apparatus (Plate 5), the quantitative transfer step between digestion and distillation was eliminated. Bumping during distillation was reduced to a minimum by adding three grams of granulated zinc to the digest (Vogel, 1961). The NH_3-nitrogen released on addition of 10N NaOH was distilled into 50mls of 2% (w/v) H_3BO_3 and then determined by titration with standard 0,05N H_2SO_4(1 ml ≡,7 mg NH_3–N). A mixed methylene blue-methyl red indicator (McKenzie and Wallerce, 1954) modified by Coe (pers. com.) was used to determine the end point of the titration. Equal quantities of methylene blue (,1% w/v) and methyl red.(,1% w/v in 99mls abs. alcohol + 1 ml 0,1N NaOH) were mixed and one ml then used for each titration. The end point was marked by a colour change from green to blue to purple. Recovery rates in excess of 98% were obtained when the efficiency of distillation was tested according to the procedure of Vogel (1961). Blank determinations were performed regularly and taken into consideration when calculating the nitrogen concentration of the soil digest.

C.3.5. "Available" phosphorus

Available phosphorus was determined by the sodium bicarbonate extraction procedure of Olsen *et al.*, (1954). In calcareous, alkaline or neutral soils containing calcium phosphate, this extractant (,5M $NaHCO_3$; pH 8,5) decreases the concentration of calcium in solution by causing precipitation of Ca as $CaCO_3$; as a result, the concentration of P in solution increases (Olsen and Dean, 1965). In acid soils, the high pH of this extractant liberates phosphorus from sparingly soluble compounds such as variscite and strengite, should these be present (Olsen and Dean, 1965).

Phosphorus was determined spectrophotometrically by measuring the intensity (absorbance at 882 nm. with 4 cm pathlength cells) of the molybdenum blue colour developed on reduction of phosphomolybdate by ascorbic acid (John, 1970). A correction was applied to the normality of H_2SO_4 used in John's reagent, in order to neutralise excess $NaHCO_3$ contained in a 5ml aliquot of extract. The ascorbic acid procedure was used in preference to stannous chloride (Olsen and Dean, 1965), because of its relative insensitivity to temperature, time and concentration of reductant (John, 1970). Reagent blanks were determined regularly and the phosphorus concentration in the soil was expressed in parts per million (ppm).

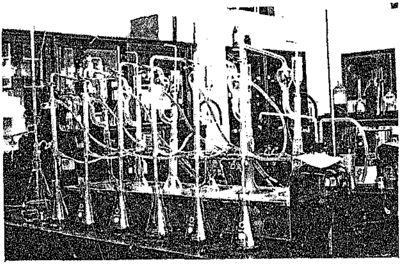


PLATE 5. Quick-fit apparatus used for the macro-Kjeldahl determination of nitrogen.

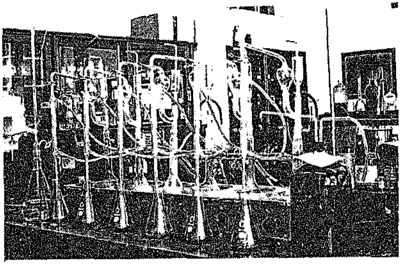


PLATE 5. *Quick-fit apparatus used for the macro-Kjeldahl determination of nitrogen.*

C.3.6. Potential buffering capacity for phosphorus (P.B.C.)

P.B.C. has been defined as the ability of a soil to maintain the concentration of phosphorus in the soil solution (intensity factor-I), on addition of phosphorus to or its removal from that soil. P.B.C. is thus dependent on the amount of phosphorus held by the solid phase (quantity factor-Q) and may be determined by measuring the slope of a curve relating quantity and intensity factors (Beckett and White, 1964).

$$\text{Thus P.B.C.} = \frac{(\Delta Q)}{(\Delta I)} I' - I''$$

where (Δ Q) *is the amount of phosphate taken* up or released by the soil over a given range of concentration (I' –I'').

P.B.C. measurements were made according to the procedure outlined by White and Haydock (1968). Soils from each replicate were bulked to obtain composite samples of the surface soil and sub-soil at each site. 2g sub-samples were shaken for one hour in 100mls of 0,01M $CaCl_2$ containing graded amounts of $Ca(H_2PO_4)_2$. The equilibration rates and soil to solution ratio used in this method were based on earlier studies by White (1964), White and Beckett (1964) and White (1966).

The suspension pH was measured prior to centrifuging at 3500 r.p.m. and the phosphorus concentration in the clear supernatant then determined using the ascorbic acid procedure (John, 1970). Graphs were then constructed of net gai or loss of phosphate *per gram of soil, against the final phosphate concentration in solution. The slope of the* resultant Q/I relationship was used to define P.B.C. (Fig. 5).

$$\text{Thus P.B.C. (L/g)} = \pm \frac{(\Delta P)}{(\Delta I)} \text{Ieq} - \text{Imax}$$

Where $\pm\Delta$P equals the net gain or loss of phosphate over phosphate concentrations in solution (Δ I), *from the equilibrium* phosphate concentration (Ieq – obtained by interpolation) to the phosphate concentration at which maximum yield is attained (Imax). A value of 2,2 µM was chosen for (Imax) based on yield responses of Siratro pastures to variations in the soil phosphate concentration (White and Haydock, 1968).

C.3.7. Bulk density

The significance of soil bulk density in creating favourable conditions for root penetration and growth is discussed by Daubenmire (1964) and Russell (1973).

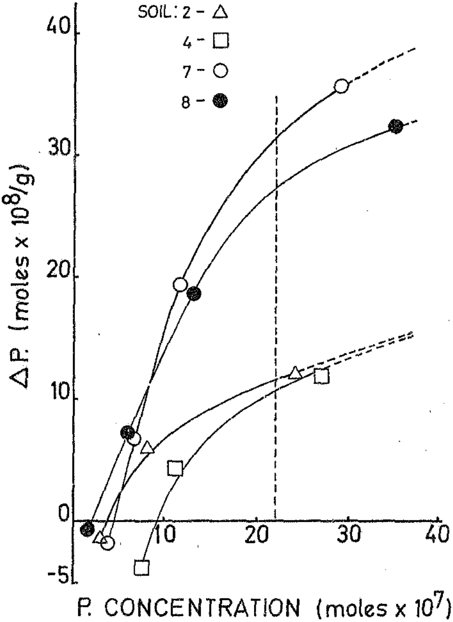


FIG. 5. $^{Q}/_{I}$ *plots for some* selected surface soils to illustrate the determination of P.B.C.
P.B.C. = $(\Delta P / \Delta I)_{Ieq.-Imax.}$

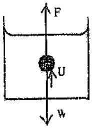
A number of oven dry clods representative of the various horizons were selected *from profile samples taken at each site. The clods were weighed and then immersed in a* 1:50 v/v rubber-benzene solution (Abrol and Palta, 1968). This coating procedure was repeated three times allowing for a five minute drying interval between each immersion. various horizons were selected

The rubber coated aggregates were carefully supported in a fine nylon hair net and then suspended in a beaker of deionised water placed on a Mettler top pan balance. The volume of each clod was determined directly by measuring the weight of the submerged clod, which was regarded as a floating body. Thus, from the adjacent diagram it may be seen that at equilibrium:

W = F + U

∴ U = W–F

= weight of body *suspended* in water (recorded by balance)



But U (upthrust)

= weight of water displaced (Archimedes principle)

= vol. of water displaced

= vol. of suspended body

This method proved more convenient for large clods (2–3cm diam.) than the procedure advocated by Abrol and Palta (1968). Meanvalues for A and B horizons over all soil pits at each site were calculated, thus giving a representative bulk density value (g/cm^3) for the surface and sub-soils.

C.3.8. Available water capacity (A.W.C.)

Available water has been defined as the amount of water held between moisture con*tents at field capacity (F.C.) and at the permanent wilting point (P.W.P.). It was originally* suggested (Veihmeyer and Hendrickson, 1949) that all this water was equally available to the plant for growth. Wadleigh and Ayres (1945), however, showed that availability, as measured by the growth response of the plant, declined as the percentage water tended towards P.W.P.. However, the original postulate is reasonably valid for light textured soils, wherein most of the available water is held at moisture tensions close to those corresponding to F.C. (at least < 1 bar) (Russell, 1973).

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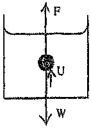
$W = F + U$

$\therefore U = W - F$

= weight of body *suspended* in water (recorded by balance)



But U (upthrust)

= weight of water displaced (Archimedes principle)

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= vol. of suspended body

This method proved more convenient for large clods (2–3cm diam.) than the procedure advocated by Abrol and Palta (1968). Meanvalues for A and B horizons over all soil pits at each site were calculated, thus giving a representative bulk density value (g/cm^3) for the surface and sub-soils.

C.3.8. Available water capacity (A.W.C.)

Available water has been defined as the amount of water held between moisture contents at field capacity (F.C.) and at the permanent wilting point (P.W.P.). It was originally suggested (Vollmeyer and Hendrickson, 1949) that all this water was equally available to the plant for growth. Wadleigh and Ayres (1945), however, showed that availability, as measured by the growth response of the plant, declined as the percentage water tended towards P.W.P.. However, the original postulate is reasonably valid for light textured soils, wherein most of the available water is held at moisture tensions close to those corresponding to F.C. (at least < 1 bar) (Russell, 1973).

The assessment of A.W.C. of a soil depends on the accurate measurement of F.C. and P.W.P. (*Salter and Haworth, 1961a.*) . *Direct methods, such as sampling after irrigation* and after wilting of indicator plants, offer the most accurate and consistent results (Veihmeyer and Hendrickson, 1949; Salter and Haworth, 1961b), but have the disadvantage of being both tedious and time consuming.

Determination of the 0,33 and 15,2 bar % as approximations of F.C. and P.W.P. respectively overcome this problem at the expense of accuracy. Pretreatment of samples (drying, sieving etc.) often influences moisture retention properties of soil (Richards and Fireman, 1943). In addition, the use of a single pressure (0,33 bar) precludes the accurate measurement of F.C., since the percentage water at F.C. is held at different pressures for different soils (Jamison, 1956).

Composite sub-soil samples were prepared for each sample site. Air dry specimens (< 2mm) were wetted for six hours with an excess of water (Richards, 1949) and then brought to equilibrium with the pressure membrane apparatus of Coleman and Marsh (1961). The samples were housed in gauze based perspex containers (~ 4,5cm diam. x 2,5cm ht.) and packed to within 15% of the mean bulk density values obtained for each sample site. Dialysis tubing was used as membrane material and was backed against a porous bronze disc of grade A porosity. The membrane was kept moist throughout the equilibration period to ensure against excessive gas leakage and consequent drying out of the sample. Commercial nitrogen was used to obtain the required tensions and leakage across the membrane was less than 3% over a 24 hour period. F.C. and P.W.P. were obtained by interpolation from percentage moisture versus time curves (Fig. 6). In addition, moisture retention curves (0,33 to 15,2 bars) were constructed for selected sample sites.

C.4. Controlled Environment Studies

Based on the evaluation of the field data and soil analysis, experiments were designed to study:

(a) the interaction of nitrogen, phosphate and soil moisture stress on mopane growth, and,

(b) the interaction of magnesium, potassium and sodium on mopane growth

under controlled conditions of temperature, light and humidity (Plate 6). Soils from sites 2, 4 and 6, which provided the full range of mopane performance in the field, were selected

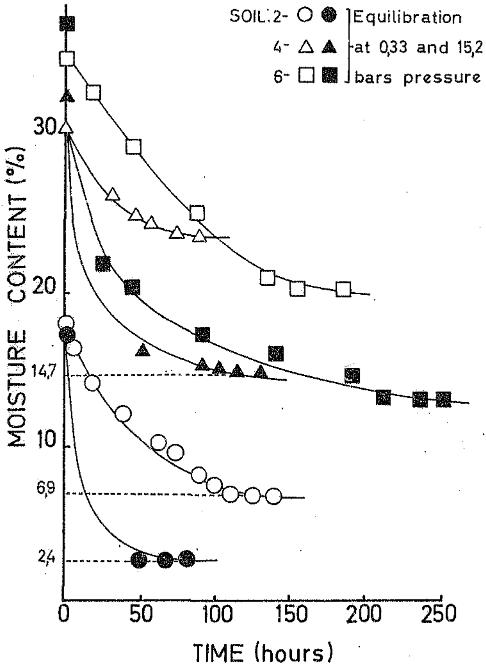


FIG. 6. Equilibration curves for some selected soils to illustrate the determination of moisture contents at 0,33 and 15,2 bars matric suction.

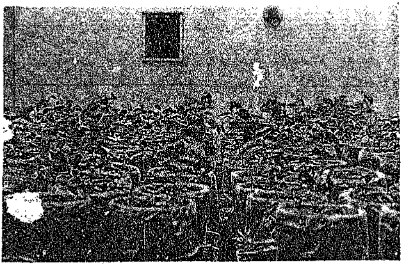


PLATE 6. Mopane seedlings grown under controlled environment conditions.

for the above experiments. Approximately 250kg soil was taken from each site by collecting randomly located samples (~ 10 kg) to a depth of 20cm (Andrew and Fergus, 1964).

C.4.1. Experimental design

(a) Nitrogen, phosphate and soil moisture stress

A factorial combination of three levels of N, two levels of P and three moisture regimes was imposed, with two replications in time, on mopane grown in soil from sites 2, 4 and 6. A grid pattern of randomization was used and all pots were re-randomized at weekly intervals to eliminate positional effects on the yield responses obtained (Haydock, 1964).

Nitrogen was applied as NH_4NO_3 in solution at the rates of 0, 0,29g/pot (56 kg/ha) and 0,86g/pot (160 kg/ha); phosphorus as KH_2PO_4, mixed through the soil at the rates of 0 and 0,45g/pot (56 kg/ha). These standard agricultural applications were scaled down to g/pot by using a conversion factor for a pot of 15,2cm diameter at soil level (Andrew and Fergus, 1964). Soil moisture levels, initially at a value corresponding to 0,33 bars, were allowed to fall to approximately 90%, 40% and 0% of the "available water" (defined as the amount of water held between tensions of 0,33 and 15,2 bars), before being restored to the original value. These moisture treatments were applied from the fourteenth day, when the seedlings were well established.

The pots were weighed daily to measure evapotranspiration. Deionised water was applied when necessary, according to the change in moist soil weights; a correction was made for the increase in fresh plant weight, determined from weekly harvests of plants grown in a series of control pots under optimum conditions of N, P and moisture. Evapotranspiration rate was computed by linear regression analysis, in g H_2O lost per day, and the coefficient of water utilization expressed as g H_2O lost per gram dry weight per day.

After harvesting and drying, nitrogen content in the plant tissues was determined by semimicro-Kjeldahl procedure. Samples of tissues were wet ashed in concentrated HNO_3, $HClO_4$ and H_2SO_4, and the phosphorus concentration measured using the molybdovanadate method of Kitson and Mellon (Jackson, 1958) (Section C.4.3.).

(b) Magnesium, potassium and sodium interactions

A factorial combination of three levels of Mg, two levels of K and two levels of Na was imposed, with three replications, on mopane grown in soil from sites 2, 4 and 6.

Chemical analyses were performed on the bulked sample from each site (Table 3); the various treatment levels were then applied, commencing from the natural levels of exchangeable Mg, K and Na, expressed as a percentage of the C.E.C. for each soil. The aim was to achieve approximately the same percentage saturation of any one cation for each soil (see Table 4). It was unavoidable in the attainment of a suitable range of individual cation levels, that total cation saturations greater than 100% were attained at the higher treatments.

Magnesium as $MgSO_4.7H_2O$, potassium as KCl and sodium as NaCl, were mixed through the soil at the rates specified in Table 4. The sulphate supplied under optimum magnesium treatment, was "balanced out" in pots receiving intermediate or zero levels of magnesium, by adding graded amounts of 0,1N H_2SO_4 to the soil during the pre-planting equilibration period. Phosphate as H_3PO_4 and nitrogen as NH_4NO_3, were applied in solution at the rates of 0,32 and 0,29g/pot respectively.

The soils were watered to field capacity and stored at 20°C for two months (Martin *et al.*, 1953; Andrew and Fergus, 1964). During the equilibration period the pots were weighed regularly and brought to 0,33 bars tension with deionised water.

During the growing period, a grid pattern of randomization was adopted and all pots were re-randomized at weekly intervals. The soils were watered to field capacity on every alternate day; a correction was made for increment in fresh weight, using the data obtained from the control pots of the previous experiment. After harvesting and drying, tissue samples were wet ashed and the cation contents determined by absorption and emission spectrophotometry (Section C.4.3.).

C.4.2. Plant growth techniques

Mopane seeds were removed from their pods and then soaked in aerated water for twelve hours. The pre-imbibed seeds were sown on the surface of pots containing the equivalent of 2,5Kg air dry soil. The pots were lined with disposable polythene bags to facilitate the removal of roots from the soil during harvesting (Hewitt, 1966).

The seeds and soil surface were covered by a 2,5cm layer of black "alkathene" granules to reduce evaporative losses and to exclude light during the preliminary stages of root growth (Hewitt, 1966). A single application of a modified Long Ashton nutrient solution (Hewitt, 1966), excluding the nutrients under study, was applied to each pot before sowing (Appendix 2). The seedlings were thinned on the tenth day for uniformity and vigour, to four individuals per pot (Hewitt, 1966).

TABLE 3 – Chemical properties of soils from sites 2, 4 *and 6.*

Site	Exchangeable Cations (meq %) (means of 6 with S.E.)						Cation Saturation (% of C.E.C.)				
	pH	Ca	Mg	K	Na	C.E.C.	Ca	Mg	K	Na	Total
2	5,5 (± 0,0)	2,05 (±0,19)	0,42 (±0,02)	0,25 (±0,02)	0,18 (±0,03)	4,43 (±0,08)	46	9	6	4	64
4	7,2 (±0,0)	12,48 (±0,23)	1,97 (±0,03)	1,01 (±[illegible]05)	0,24 (±0,02)	21,06 (±0,63)	5[illegible]	9	5	1	74
6	6,4 (±0,0)	9,93 (±0,24)	3,75 (±0,05)	0,97 (±0,06)	0,21 (±0,01)	18,19 (±0,70)	55	21	5	1	82

TABLE 4 – Treatment levels of magnesium, potassium *and sodium* applied to soils from sites 2, 4 and 6

	SOIL 2							SOIL 4							SOIL 6						
	Magnesium			Potassium		Sodium		Magnesium			Potassium		Sodium		Magnesium			Potassium		Sodium	
	Mg_0	Mg_1	Mg_2	K_0	K_1	Na_0	Na_1	Mg_0	Mg_1	Mg_2	K_0	K_1	Na_0	Na_1	Mg_0	Mg_1	Mg_2	K_0	K_1	Na_0	Na_1
Estimated *Saturation* of C.E.C. (%)	9	22	32	6	22	4	21	9	22	32	5	15	1	15	21	26	36	5	15	1	15
Amount of cation added (g/2,5 Kg soil)	0	0,169	0,304	0	0,705	0	0,431	0	0,810	1,453	0	2,100	0	1,677	0	0,297	0,850	0	[illegible],716	0	1,447
Amount of cation added (meq/100g soil)	0	0,556	1,000	0	0,721	0	0,750	0	2,665	4,780	0	2,148	0	2,918	0	0,977	2,769	0	1,756	0	2,518
Cation content at commencement of experiment (meq %)	0,417	0,973	1,417	0,253	0,974	0,180	0,930	1,970	4,635	6,750	1,014	3,162	0,242	[illegible]	3,752	4,729	6,521	0,973	2,729	0,207	2,725

The plants were grown under a 14 hour photoperiod (at approximately 12 k lux). Air temperatures varied from 30°C in the light to 18°C in the dark, with a relative humidity in the range 60–65%. Temperature and humidity settings were based on mean values, obtained from a number of meteorological stations situated within the distribution limits of mopane (Climatological Statistics, 1954; Climatological Summaries, 1963).

After 60 days, shoots and roots of the plants were harvested, the roots being removed from the soil by washing. Dry weights were measured after drying the plants in a forced draught oven at 80–90°C for 48 hours. The dangers of driving off volatile nitrogenous compounds at higher drying temperatures is discussed by Bryan *et al.*, (1964).

C.4.3. Chemical analysis of plant tissues

Roots and shoots were ground in a "Wiley" mill to pass a 0,5mm sieve. According to Piper (1944), finely ground tissues (< 0,5mm) renders a more homogeneous sample, especially when small quantities (± 1–2g) are used for individual chemical determinations. The samples were stored in airtight specimen tubes and the contents were thoroughly mixed and re-dried before an aliquot was withdrawn for analysis (Hegarty, 1964).

(a) Semimicro-Kjeldahl determination of nitrogen

Nitrogen content was determined on 200mg samples using a semimicro-Kjeldahl digestion technique (Humphries, 1956), modified to include nitrate nitrogen (Bremner, 1965). Ammonia was distilled into 35ml of 2% w/v H_3BO_3 using the steam distillation apparatus of Markham (1942). NH_3-N was determined by titration with standard 0,01N H_2SO_4 (1 ml N/100 H_2SO_4 ≡ 0,14mg NH_3 – N) using a mixed methylene blue-methyl red indicator (Section C.3.4.). Recovery rates varied between 95–99%; blank determinations were performed regularly and allowed for when the nitrogen content of the digest was calculated.

(b) Tri-acid digestion for the determination of phosphate and cations

Aliquots of plant tissue (± 500mg) were wet ashed in HNO_3–$HClO_4$–H_2SO_4 mixture (Piper, 1944; Humphries, 1956) and made up to volume with deionised water. The Kjeldahl digestion flasks were calibrated to 125mls beforehand, using mercury of SG 13,54 at 22,5°C.

A 25ml aliquot of digest was transferred to a 50ml volumetric flask and reacted with molybdate-vanadate solution (Jackson, 1958). Phosphorus was detetermined after two hours by absorption at 480nm, using phosphate standards in the range 0,8–8,0ppm.

For cation determinations (Ca, Mg, K, Na) a 2ml aliquot of digest together with 10mls of 0,02% $SrCl_2$ were transferred to 100ml volumetric flasks, made to volume with deionised water and determined by absorption and emission spectrophotometry. Lower concentrations of "releasing agent" were used so as not to exceed the solubility product of $SrSO_4$ and thus cause precipitation of this compound in the standard and test solutions (Vogel, 1961).

C.5. Statistical Methods

The correlation between performance and the chemical properties of the surface and sub-soils was examined using simple linear and stepwise multiple regression analysis (Freese, 1967; Bishop, 1969). Factor interactions in the controlled environment experiments were examined using analysis of variance (Bishop, 1969).

C.5.1. Simple linear regression

Simple linear regression analysis was performed by IBM 3600 computer programmed to calculate the following values for each data set:

(a) the regression coefficients a and b defined by the regression equation ($y = a + bx$)

(b) the general means of the data ($\bar{x}, \bar{y}$)

(c) the correlation coefficient (r)

Data on time versus cumulative water loss (Section C.4.–N, P and soil moisture interactions) was also subject to simple linear regression analysis, the regression coefficient b giving the rate of evaporation from each pot.

C.5.2. Stepwise multiple regression analysis

Stepwise multiple regression analysis was performed by the computer programmed to calculate the following values:

(a) the regression sum of squares

(b) cumulative regression sum of squares for the introduction of successive factors, singly

(c) multiple correlation coefficient (R)

(d) coefficient of determination (R^2)

(e) cumulative coefficient of determination for each new factor introduced

(f) F-value, for analysis of variance

(g) regression coefficients a and b

The percentage variation accounted for by regression of performance of any soil factor, or combination of soil factors, was calculated using the formula:

$$1 - \frac{(n-1)}{(n-p-1)} \times (1 - R^2) \times 100$$

where n = no. of observations per problem; p = no. of coefficients in the multiple regression equation and R^2 = coefficient of determination.

C.5.3. Analysis of variance

Analysis of variance was performed by the computer programmed to calculate the following values:

(a) Sum of squares, degrees of freedom, and mean squares for each source of variation recognised
(c) Factor means for each treatment and block
(c) Grand mean

Variance ratios were tested for significance against standard F tables. L.S.D. values were calculated using the formula:

$$t_{(P<0,05)} \sqrt{\frac{2 \text{ error variance}}{n}}$$

where n = number in the mean.

D. RESULTS AND DISCUSSION

D.1. Phytogeographical Relationships

D.1.1. Distribution of mopane

A map of the approximate limits of distribution of mopane is given in Figure 7. As mentioned previously (Section C.1.) this chart was collated from a number of regional vegetation maps. Possible inaccuracies in these maps will therefore be reflected in Figure 7. Kerfoot, Attwell and Mitchell (pers. com.), for example, contend that mopane extends further north along the Luangwa valley than actually depicted by Wild and Grandvaux Barbosa (1967). Prospectors in the Tête district of Moçambique claim that the published vegetation map of this area is inaccurate. These views are, however, lacking in direct evidence and must therefore be regarded with some reservation.

The distribution chart presented here varies considerably from that given by Porter (1968) (compare Fig. 1 and 7). Noticeable differences are:

(a) Mopane does not extend to the Atlantic coasts of South West Africa and Angola.

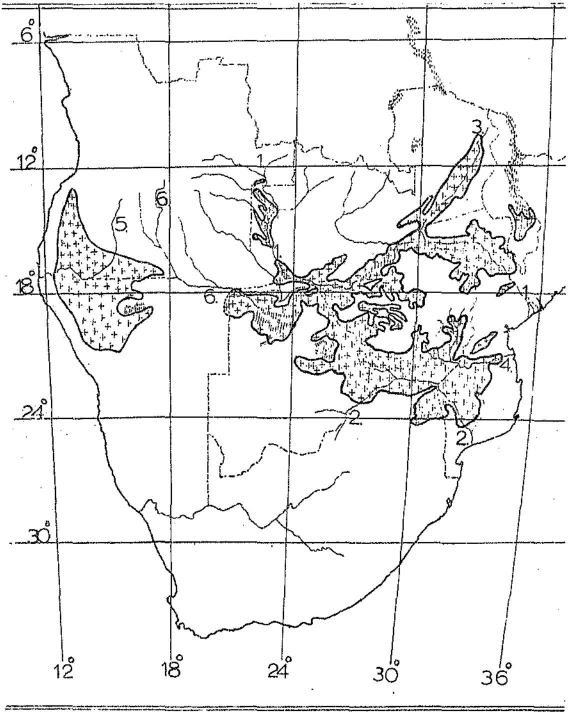
(b) Fairly large stands of mopane occur in the N.W. corner of Zambia along the upper reaches of the Zambezi valley (River system 1 – Fig. 7).

(c) The latitudinal extension of this species through Malawi and Moçambique is broken and discontinuous.

The appar... distribution along the Okavango river system between South West Africa a... d its absence from the highveld of Rhodesia and the Transvaal are reflec... aps.

D.1.2. Climate

The southern limit of this species may be set by low winter temperatures. Isotherms for the July mean daily minimum temperature, shown in Figure 8, indicate that mopane does not extend far beyond the 5°C line. Low winter temperatures may also explain its discontinuous distribution along the Okavango river system (cf. Figs. 7 and 8). There would seem to be no correlation between the southern boundary of this species and the 10°C isotherm, as suggested by Porter (1968). The intolerance of mopane to low temperatures has been discussed in Section B.2.



MAJOR RIVER SYSTEMS: 1. Zambezi 2. Limpopo 3. Luangwa
4. Save 5. Cunene 6. Okavango
Lakes + pans

FIG. 7. Distribution of *Colophospermum mopane* – collated from the regional vegetation maps of Acocks (1953), Rattray and Wild (1961), Wild and Grandvaux Barbosa (1967), Porter (1968), Grandvaux Barbosa (1970), Weare and Yalala (1971) and Giess (1971).

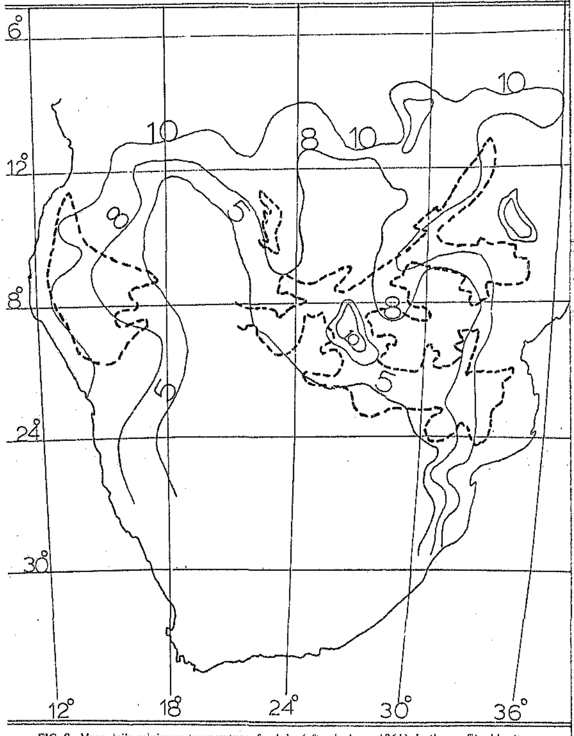


FIG. 8. Mean daily minimum temperatures for July, (after Jackson, 1961). Isotherms fitted by the author; the broken line indicates the approximate limits of mopane, simplified from Fl[illegible].

As well as a temperature limitation to growth, mopane appears to be restricted to regions of low to moderate rainfall (Section B.2.). It is noteworthy that the northern and eastern limits of its distribution appear to be set by the 1000mm. isohyet of mean annual rainfall (Fig. 9). The bulk of its distribution, however, occurs within the range 200–800mm. Rainfall values below and above these limits may prevent the extension of mopane to the Atlantic coast, and onto the highveld regions of the hinterland, respectively. It has been suggested by Thompson (1960) that mopane is excluded from higher rainfall zones through competition from species more suited to wetter conditions.

It is possible that phytoclimatic studies of this nature, at the regional or sub-regional level, could reveal further interesting relationships between climatic parameters and the distribution of this species.

D.1.3. Geology and soils

Mopane grows on soils overlying a wide variety of parent materials, notably; sandstone, dolomitic limestone, granite, paragneiss and sediments derived from various depositional processes (Fig. 10). The major soil types associated with these geological formations have been extracted from the mapping units of the 1:5,000.000 soil map of Africa (D'Hoore, 1964) and are presented below.

(a) *Non-differentiated skeletal soils with poorly developed structure (lithosols):*

These occur on dolomite (S.W. Africa), granite and paragneiss (S. Rhodesia, N. Transvaal, Zambia) and sandstone (N. Rhodesia, Zambia), and are indicative of steep slopes, sporadic rainfall and sparse vegetation, all of which are conducive to erosion. They often occur on calcareous or ferruginous deposits.

(b) *Brown soils of arid and semi-arid tropical regions:*

These soils are common on Kalahari sand in areas where the annual rainfall rarely exceeds 500mm (S. of 18° parallel; cf. Fig. 9 and 10), but may also occur on other superficial deposits (S. Moçambique) and in association with lithosols on dolomite (S.W. Africa) and granite (N. Transvaal, S. Rhodesia, S. Zambia). They are zonal soils and are characterized by calcium carbonate accumulation at depth. The organic matter content is low ($< 1\%$) but well distributed throughout the profile. Cation exchange capacities are ~ 15 meq/100g and cation saturation ranges from 60–80 per cent.

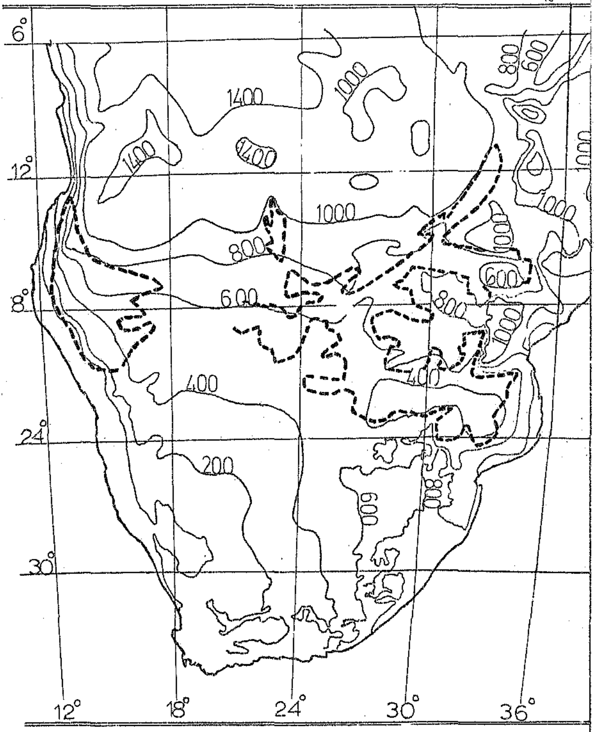


FIG. 9. Mean annual rainfall for South Central Africa (after Jackson, 1961). The broken line indicates the approximate limits of mopane, simplified from Figure 7.

(c) *Ferruginous tropical soils on sandy parent materials:*

These are generally found between the 500–1200mm isohyets, and are common on Kalahari sands north of the 18° line of latitude, and on schists and granite (S.W. Africa). They also occur in association with brown soils on superficial deposits (S. Moçambique), and in association with lithosols on sandstone (N. Rhodesia, Zambia). These soils generally have well-developed ferric oxide concretions at depth.

Cation exchange capacities range from 4–20 meq/100g and cation saturation is usually greater than 40 per cent.

(d) *Ferrallitic soils on loose sandy sediments:*

These soils occur on Kalahari sand (N.W. Rhodesia, N.W. Zambia), and in association with lithosols and ferruginous tropical soils on sandstone (N. Rhodesia, Zambia). They are characterized by a sandy layer several metres thick and showing only slight differentiation down the profile. Cation exchange capacity and percentage saturation are lower than those of ferruginous tropical soils.

(e) *Halomorphic soils:*

This group is generally comprised of solonetz, saline and alkaline soils. Halomorphic soils are common on alluvial and lacustrine deposits of recent origin (Zambezi R. – N.W. Zambia, Okavango Swamps and Makgadikgadi Pan – Botswana). They also occur in association with lithosols, ferruginous and ferrallitic soils, on sandstone (N. Rhodesia, Zambia).

The more temperate highveld regions of Rhodesia and the Transvaal are associated with non-differentiated ferrisols, humic ferrallitic soils and ferruginous soils derived from acidic igneous rocks. Mopane is generally absent from these regions and occurs only in isolated areas with a salt-affected overburden (Beatrice district – Rhodesia). According to Thompson (*pers. com.*) the high salt content of the Beatrice soils creates a condition of physiological dryness, which is not conducive to the colonisation and establishment of most Rhodesian highveld species (see Section B.3.).

Further mention should be made of the discontinuity in mopane distribution along the eighteenth parallel. D'Hoore (1964) depicts the overburden in this area as being brown soils on loose sediments which grade into ferruginous tropical soils further northwards. According to Shantz and Marbut (1923), however, the northern extremities of the brown soils unit are associated with very deep, sandy conditions. Some idea of the depths involved may be gauged from Mountain (1968) who reports that the Kalahari sands east of Etosha (S.W. Africa) often exceed 240m in thickness.

Large tracts of the north eastern and south eastern Kalahari have also been described as deep, porous and structureless semi-desert sands (Bawden and Stobbs, 1963; Blair Rains and McKay, 1968). These soils have a slightly acid reaction and are extremely low in exchangeable cations, organic matter and total nitrogen content (Blair Rains and McKay 1968). Mopane is conspicuously absent from these areas.

More recently, surveys carried out by De Beers Mining Group in the Central Kalahari (S. of Makgadikgadi Pan – Botswana) indicate that wherever this species occurs on Kalahari sand it is invariably associated with calcrete deposits at or near the surface (Plate 7, cf. Table 1). This observation is in keeping with the common view point that mopane is most frequently associated with shallow soils (Section B.3.).

In conclusion, the salient environmental features pertaining to mopane's distribution may be summarised as follows:

(a) The southern extension of this species coincides with the July mean daily minimum isotherm of 5°C. The discontinuity in its distribution along the 18° line of latitude, may in part be explained by its intolerance of low winter temperatures.

(b) The northern and eastern distribution limits of mopane appear to be set by the 1000mm mean annual rainfall isohyet. The bulk of its distribution occurs within the range 200–800mm.

(c) Deep Kalahari sands which are reportedly low in exchangeable cations and total nitrogen content are not conducive to mopane growth, even in areas with a favourable climatic regime (compare Figs. 8, 9, 10). This observation is in agreement with the viewpoints of Boughey (1963), van der Schijff (1969), van Wyk (1972a), Attwell (pers. com.), Walker (pers. com.) and Wild (pers. com.).

Futher attention will be given to the phytogeography of mopane after the field and controlled environment studies have been reported and discussed.

It is felt that certain observations to emerge from these studies may in part, shed more light on its present day distribution pattern.

PLATE 7. Calcrete deposits occurring in South Central Botswana. Note the relatively shallow overburden of Kalahari sand.

D.2. Soil. Studies

D.2.1. Profile characteristics

Pits were excavated tangentially to the stems of mopane individuals so that root and soil features could be studied simultaneously. Detailed profile descriptions were made using the terminology advocated by Clark and Beckett (1971), and are presented in Appendix 3. A sample of the range of profile types and root growth habits encountered is shown in Plates 8 and 9.

All the pits examined were relatively shallow and seldom exceeded 100cm in depth. At sites 1 and 4 the soils exhibited lithosolic characteristics (cf. Millar *et al.*, 1965), showing very little profile development and consisting of shallow weakly developed sands over loamy sands or sands over silty clay loams (Profiles 1, 2, 7 and 8) (Plate 8A). At site 2 (Profiles 3 and 4) the soil consisted of weakly developed sands over sandy loams and showed some degree of resemblance to the ferruginous tropical soils described by D'Hoore (1964). Soils from the remaining sites consisted predominantly of moderately developed sandy loams over sandy clay loams, and showed a marked compaction in the subsoil. (Plate 8B to 8D). There was also a variable accumulation of lime at depth, a feature common to the brown tropical soils described by D'Hoore (1964).

Soil properties such as percentage moisture, bulk density, pH, C.E.C., and total cation saturation showed fairly consistent increases with increase in depth down the profile (Appendix 3). Moisture levels were low throughout the soil (3–12%), a feature not uncommon in the semi-arid savanna regions of South Central Africa. Even in the rainy season, moisture levels below the permanent wilting percentage may persist for as long as five weeks at a time (Walker, pers. com.).

Bulk density values ranged from ~ 1,5g/cm^3 in the loose surface soils to ~ 1,9g/cm^3 in the more compacted subsoils. Total cation saturation values were high (60–95%) and in all cases calcium was the dominant exchangeable cation. Noticeably, sodium contributed least to the total exchangeable cation content, and rarely exceeded 5% saturation in the lower horizons.

D.2.2. Physio-chemical properties of surface and subsoils

(a) pH, C.E.C., and T.E.C.

Mean values of pH, cation exchange capacity and exchangeable cations for surface and sub-soils at each site are given in Table 5. The percentage saturation of exchangeable cations ($E.C./C.E.C. \times \frac{100}{1}$) is presented in Table 6.

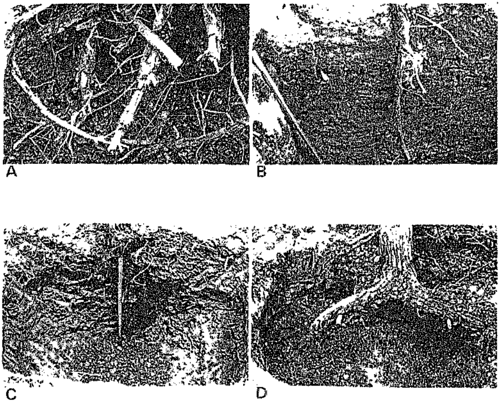


PLATE 8. Profile characteristics and root growth habit of mopane:

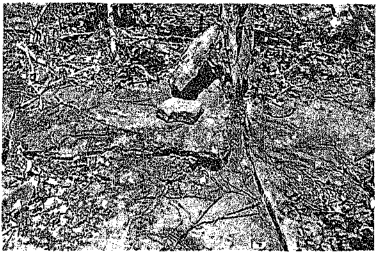
(A) Profile 7, Site 4. – Shallow soils (~ 50cm) of weakly developed structure, showing numerous adventitious roots derived from a coppice form of mopane.

(B) Profile 5, Site 3. – Sandy clay loam of moderately developed structure, showing the tap root system of a shrub mopane. Note the increasing abundance of $CaCO_3$ concretions with depth (~80cm).

(C) Profile 11, Site 7 – Moderately developed sandy clay loam showing the tap root development of a tall tree form of mopane. Soil very compact at depth (80–110cm) and tap root diverted to grow laterally.

(D) Profile 13, Site 8. – Shallow (~ 70 cm) moderately developed sandy clay loam, showing the lateral root development of a tall tree mopane. Note the absence of a tap root.

A



B

PLATE 9. Root growth habit of mopane:

(A) Site 3. Tall tree form of mopane with a well-developed lateral root system. No tap r-ot evident.

(B) Site 1. Shrub mopane growing on exposed parent material (sandstone) and exploiting cracks and crevices for root growth.

pH values ranged from an acid reaction at site 2 (5,44 at 0–10cm; 4,40 at 20–30cm) to slightly alkaline conditions at site 4 (7,20 at 0–10 cm; 7,48 at 20–30cm).

C.E.C. was lowest at site 2, varying from 3,37 meq % in the surface soil to 3,48 meq % in the sub-soil. In contrast, the C.E.C. at site 5 ranged from 18,63 meq % in the surface soil to 23,90 meq % in the sub-soil. These values are consistent with those quoted by D'Hoore (1964) and Thompson (1965) for a variety of dry tropical soil types (Section D.1.3.)

Exchangeable cations followed closely the trends exhibited by C.E.C. Except for the sub-soil at site 2, calcium was the dominant exchangeable cation, generally followed by magnesium, potassium and sodium in order of decreasing abundance. This sequence is common for most soil types (Millar, Turk and Foth, 1965), although in leached acid soils (site 2) and alkali soils, calcium is more often than not exceeded by exchangeable magnesium and sodium respectively (Russell, 1973).

Calcium frequently exceeded 50% saturation (Table 6); at site 4, for example, calcium levels in the sub-soil were 8;20 and 80 fold higher than exchangeable Mg, K and Na respectively. Exchangeable magnesium ranged from 0,30 meq % (8,6 % saturation) in the sub-soil at site 2 to 4,27 meq % (17,9 % saturation) in the sub-soil at site 5. Mg levels were thus well above the 0,2–0,4 meq % limits below which fertilizer application becomes necessary to promote crop growth (Russell,1973).

Exchangeable potassium levels were low at sites 1, 2 and 3 (0,12–0,39 meq %); moderate at sites 4 and 6 (0,59–0,81 meq %), and moderate to high at sites 5, 7 and 8 (0,83–1,43 meq %). This assessment was based on the broad limits set by Blair Rains and McK[illegible] (1968) during recent land resource surveys in Botswana. Levels of exchangeable K sufficient for crop growth are seldom given in the literature, probably because its availability to plants is governed by numerous criteria (cf. Truog, 1961; Townsend, 1973; Russell, 1973). For example the transfer of this cation into the exchangeable pool is largely dependent upon the activity ratio of the K^+ ion ($aK^+ : \sqrt{aCa^{++} + Mg^{++}}$) in the soil solution (Russell 1973). Furthermore, the growth response to this cation is considerably influenced by the N, P and Ca status of the soil (Albrecht, 1943; Baver, 1943; Cullinan and Batjer, 1943). The potassium supply of a soil may be adequate for crops grown under low N and P, but becomes inadequate if the levels of these nutritients are increased (Cullinan and B[illegible]r, 1943; Russell, 1973).

The exchangeable Na content at most sites was generally in the range 0,03–0,30 meq%. In the sub-soil at site 1 sodium attained a level of 0,61 meq % (8,6% saturation). These values

TABLE 5 pH, cation exchange capacity and total exchangeable cations for surface and sub-soils from each sample site. (The values given are the means of four replicates together with S.E.'s).

Site	Depth (cm)	pH	C.E.C. (meq %)	Exchangeable cations (meq %)				
				Ca	Mg	K	Na	Total
1	0–10	5,87± 0,32	5,47± 0,14	2,33±0,38	1,08± 0,24	0,17±0,03	0,21±0,06	3,79±0,14
	20–30	5,97± 0,67	7,08± 1,53	2,94± 0,04	1,81± 0,62	0,16± 0,03	0,61±0,18	5,53± 2,02
2	0–10	5,44 ±0,04	3,37 ±0,26	0,91 ±0,04	0,40 ±0,02	0,12 ±0,01	0,03 ±0,01	1,46 ±0,06
	20–30	4,40±0,09	3,48 ±0,03	0,21 ±0,04	0,30 ±0,07	0,13 ±0,01	0,06 ±0,04	0,70 ±0,10
3	0–10	5,32±0,07	11,98 ±0,85	5,68 ±0,56	2,63 ±0,13	0,39 ±0,03	0,15 ±0,02	8,85 ±0,64
	20–30	5,33 ±0,31	17,73 ±1,62	7,00 ±1,01	3,52 ±0,30	0,13 ±0,01	0,29 ±0,07	10,94 ±1,11
4	0–10	7,20 ±0,05	20,53 ±1,19	11,95 ±0,98	2,07 ±0,26	0,81 ±0,01	0,19±0,02	15,02±1,32
	20–30	7,48±0,06	18,65 ±2,75	12,78 ±1,64	1,64 ±0,28	0,65 ±0,05	0,16±0,03	15,23 ±1,97
5	0–10	6,98±0,10	18,63 ±0,45	11,93 ±0,86	3,39 ±0,29	0,95 ±0,03	0,19 ±0,01	16,46 ±0,79
	20–30	7,24 ±0,09	23,90 ±1,02	15,05 ±0,82	4,27 ±0,35	0,92 ±0,05	0,21 ±0,01	20,45±0,45
6	0–10	6,18±0,06	14,67 ±1,83	6,30 ±0,88	2,85 ±0,37	0,73 ±0,09	0,07 ±0,02	9,95 ±1,30
	20–30	6,64±0,15	18,38±1,81	8,25 ±1,07	3,86 ±0,47	0,59 ±0,05	0,17 ±0,04	12,87 ±1,05
7	0–10	6,84 ±0,18	12,80 ±1,56	6,68 ±1,23	1,29 ±0,19	0,83 ±0,14	0,08 ±0,01	8,88 ±1,52
	20–30	7,15±0,15	18,05 ±2,14	9,30±1,74	2,07±0,08	1,43 ±0,09	0,10 ±0,01	12,90 ±1,81
8	0–10	6,77±0,25	13,30±2,27	6,90 ±1,71	1,40±0,22	0,84 ±0,15	0,05 ±0,01	9,19 ±2,08
	20–30	6,88±0,30	17,91 ±2,52	10,28 ±2,23	2,30 ±0,34	1,16 ±0,08	0,27 ±0,14	14,01 ±2,70

TABLE 6 Cation saturation values for surface and sub-soils from each sample site. (Calculated from replicate means given in Table [illegible]

Site	Depth (cm)	Cation saturation (% of C.E.C.)				
		Ca	Mg	K	Na	Total
1	0–10	42,6	19,7	3,1	3,8	69,3
	20–30	41,5	25,6	2,3	8,6	78,1
2	0–10	27,0	11,9	3,6	0,9	43,3
	20–30	6,0	8,6	3,7	1,7	20,1
3	0–10	47,4	22,0	3,3	1,3	73,9
	20–30	39,5	19,9	0,7	1,6	61,7
4	0–10	58,2	10,1	4,0	0,9	73,2
	20–30	68,5	8,8	3,5	0,9	81,7
5	0–10	64,0	18,2	5,1	1,0	88,4
	20–30	63,0	17,9	3,9	0,9	85,6
6	0–10	42,9	19,4	5,0	0,5	67,8
	20–30	44,9	21,0	3,2	0,9	70,0
7	0–10	52,2	10,1	6,5	0,6	69,4
	20–30	51,5	11,5	7,9	0,6	71,5
8	0–10	51,9	10,5	6,3	0,4	69,1
	20–30	57,4	12,8	6,5	1,5	78,2

were considered more than adequate for growth, particularly since there appeared to be no potassium deficiency in the soils studied. A sodium requiring crop such as sugar-beet, for example, only responds to fertilizer treatment if the soil contains less than 0,05 meq/100g of readily exchangeable sodium (Russell 1973). It is noteworthy that the sodium content at all sites fell well below the 15% saturation limit set for alkali soils by the U.S. Salinity Laboratory Staff (1954). It is difficult to reconcile this observation with the conclusions of Ellis (1950) and Hudson (1970) namely, that mopane is best adapted to sodium influenced soils (Section B.3.).

(b) **Total N, available P and P.B.C.**

Mean values of total nitrogen, available phosphorus and phosphorus buffering capacity are given in Table 7.

Percentage N was low at all sites (compare Blair Rains and McKay 1968) and ranged from 0,032% in the sub-soil at site 2, to 0,088% in the surface soil at site 3. According to Lawton (1955), the total nitrogen for most mineral soils (1–5% organic matter) falls within the range 0,05–0,25%.

$NaHCO_3$ extractable phosphorus ranged from 0,25 ppm in the subsoil at site 4 to 7,56 ppm in the surface soil at site 6. These values were high by comparison with those quoted by Blair Rains and McKay (1968) for the Northern State Lands of Botswana, but nevertheless well below the 20 ppm limit suggested by Olsen *et al.* (1954) for crop sufficiency.

P.B.C. values generally exceeded 1 L/g, although lower values were obtained for the surface soils at sites 2 (0,63L/g) and 4 (0,85 L/g), and for the sub-soil at site 5 (0,89 L/g). A value of 3,40 L/g was obtained for the sub-soil at site 3. The buffering capacities of 42 West Australian soils (measured as $\Delta Q/\Delta I$; Imax = 0,2 μg/ml) were found to range from 0–5 L/g (Barrow 1967).

(c) **Bulk density; F.C., P.W.P. and "available" water**

Details of bulk density, moisture content at 0,33 bar and 15,2 bar matric suction and available water are given in Table 8.

Bulk density readings were high and often exceeded 1,8g/cm^3 in the sub-soils. According to Russell (1973) the roots of most herbaceous and semi-woody plants rarely penetrate a light textured soil if its bulk density exceeds 1,7–1,8g/cm^3, or a heavy textured soil if its bulk density exceeds 1,5–1,6 g/cm^3. The author is of the opinion that

TABLE 7 Total nitrogen, "available" phosphorus and potential buffering capacity for phosphorus for surface and sub-soils from each sample site.

Site	Depth (cm)	Total N (%)	Available P (ppm)	Buffering capacity for P (L/g)
1	0–10	0,066 ± 0,003	3,31 ± 0,09	1,10
	20–30	0,040 ± 0,005	1,13 ± 0,36	1,36
2	0–10	0,050 ± 0,002	2,94 ± 0,56	0,63
	20–30	0,032 ± 0,002	2,63 ± 0,82	1,02
3	0–10	0,088 ± 0,003	4,00 ± 0,18	1,48
	20–30	0,075 ± 0,004	3,56 ± 1,22	3,40
4	0–10	0,066 ± 0,005	1,81 ± 0,49	0,85
	20–30	0,056 ± 0,002	0,25 ± 0,10	1,14
5	0–10	0,060 ± 0,003	6,19 ± 0,57	1,05
	20–30	0,057 ± 0,002	3,88 ± 0,94	0,89
6	0–10	0,058 ± 0,004	7,56 ± 1,28	1,00
	20–30	0,047 ± 0,001	0,72 ± 0,17	1,83
7	0–10	0,077 ± 0,005	2,19 ± 1,04	1,72
	20–30	0,063 ± 0,008	3,50 ± 0,97	1,75
8	0–10	0,062 ± 0,006	3,19 ± 1,43	1,30
	20–30	0,061 ± 0,005	3,13 ± 0,24	1,40

TABLE 8 Bulk density, moisture content at 0,33 bar and 15,2 bar matric suction, and available water content for soils from each sample site.

Site	Depth (cm)	Bulk density (g/cm^3)	Moisture content at 0,33 bar (%)	Moisture content at 15,2 bar (%)	A.W.C. (%)
1	0–10	1,60	–	–	–
	20–30	1,91	9,5	6,1	3,4
2	0–10	1,77	–	–	–
	20–30	1,81	6,9	2,4	4,5
3	0–10	1,65	–	–	–
	20–30	1,36	20,5	10,6	9,9
4	0–10	1,53	–	–	–
	20–30	1,56	24,0	14,7	9,3
5	0–10	1,71	–	–	–
	20–30	1,86	25,8	13,7	12,1
6	0–10	1,61	–	–	–
	20–30	1,62	20,6	13,7	6,9
7	0–10	1,65	–	–	–
	20–30	1,91	17,2	11,8	5,4
8	0–10	1,79	–	–	–
	20–30	1,85	19,9	10,6	9,3

the high bulk densities exhibited by mopane soils is due to partial cementation of subsoil horizons by calcium carbonate. This situation is most prevalent in arid and semi-arid regions subject to alternate periods of intense wetting and dehydration (Barshad, 1955). Of course, the shallow rooting behaviour of mopane may also be a contributory factor towards subsoil compaction (Section D.2.4.).

Available water content of the soils was relatively low, ranging from 3,4% at site 1 to 12,1% at site 5 (6,5% to 22,4%, by vol.). Soil surveys in England and Wales showed available water contents (% vol.) ranging from 8–16% for loamy sands, and 12–40% for clay loams, silty clay loams and sandy clay loams. Higher textural classes (clays – silty clays) had lower available water contents (12–24%) than loams, mainly because P.W.P. increased as the soil texture became finer (Russell 1973). Certainly the relatively high P.W.P. at sites 3–8 (predominantly sandy clay loams) restricted the amount of water available to mopane. The concept of available water should be regarded with some reservation, however, since drought resistant species are often capable of extracting water at soil moisture contents well below P.W.P. as determined by 15,2 bars suction (Levitt, 1972).

D.2.3. Root growth habit of mopane

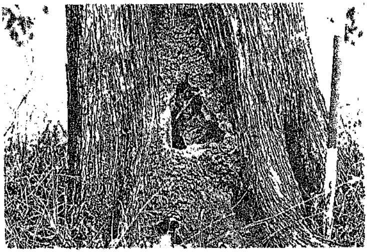
Observations from the field and controlled environment studies indicate that mopane seedlings initially give rise to a well developed tap root system which grows vertically downwards. This rooting habit persists in some individuals (Plate 8), but more often than not the tap root disappears altogether leaving a system of shallow lateral roots (Plate 8 and 9). It is the latter rooting behaviour that is most frequently described for mopane (Ellis, 1950; Thompson, 1960).

Mopane trees with no tap root nearly always show signs of termite attack (Plate 10). Although the two phenomena may be purely coincidental, the author is of th[illegible] [illegible]n that termite attack follows directly on tap root senescence. Senescing tap r[illegible] [illegible]uld be very susceptible to termite action and would also expose the dead heartwood of the stem trunk to further attack.

Possible reasons for tap root disappearance, and the characteristic rooting behaviour of mopane generally, are given in Section D.2.4.

D.2.4. Discussion of results

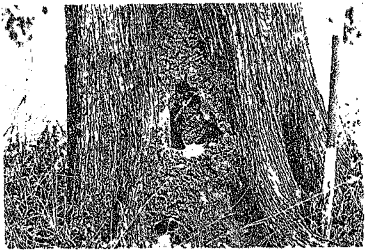
The main characteristics of mopane soils, as assessed from observations at eight different sites distributed throughout southern Africa, may be summarised as follows:



A

B

PLATE 10. Termite damage sustained by mopane individuals in the Chete Game Park (Site 2).



A

B

PLATE 10. Termite damage sustained by mopane individuals in the Chete Game Park (Site 2).

(a) They consisted predominantly of shallow to moderately shallow, lime accumulating sands over loamy sands or sandy loams over sandy clay loams, and often exhibit a marked degree of compaction in the subsoil.

(b) Total cation saturations ranged from 20% at site 2 to 88% at site 5. Calcium was generally the dominant exchangeable cation followed by magnesium, potassium and sodium, in order of decreasing abundance Compaction in the subsoil could not be attributed to the influence of sodium since the levels of this cation rarely exceeded 1,5% saturation of the exchange complex.

(c) Apart from the particularly high levels of exchangeable calcium, the overall nutrient status compared very favourably with that of most other semi-arid tropical soils (cf. D'Hoore, 1964; Blair Rains and McKay, 1968). Nitrogen and phosphorus levels, however, were low by agricultural standards.

(d) Available water contents were low and bulk densities were high, the result being that the soils developed an extremely hard consistency during dry periods.

Broadly speaking, therefore, the soils examined in this study had much in common with the dry tropical soil units described by D'Hoore (1964) (compare Sections D.1.3. and D.2.), and also with a variety of soil types described for Rhodesia (Trapnell *et al.*, 1948; Thompson *et al.*, 1960; Thompson, 1965). This suggests that climate and geology are the main factors governing soil formation under mopane woodland.

The author believes that many of the adverse soil conditions reportedly associated with mopane (infertility, high sodium levels and compaction), *are not a direct consequence of* its presence at all, but merely reflect the wide ecological amplitude and resultant competitive advantage which this species has over other xerophytic plants. Its association with sodium influenced soils outside its normal distribution range serves to illustrate this point (Section B.3.). No doubt this opinion will be hotly disputed by those who subscribe to the views of Ellis (1950), Staples and Murray (1951) and Hudson (1970).

It is possible that the shallow rooting habit of mopane contributes to compaction in the subsoil. The absence of root activity at depth would tend to restrict those biological processes which govern aggregate formation and hence increase porosity and reduce compaction (cf. Russell, 1973). The author subscribes to the view that compaction under mopane soils is primarily caused by cementation processes operative under arid and semi arid climates (cf. Barshad, 1955) (see Section D.2.2.).

There is little doubt that mopane's shallow lateral root system offers this species a strong competitive advantage, particularly in areas of low P/E ratio where moisture penetration is often restricted to a shallow depth (Kerfoot, 1963; Savory, 1963; Levitt, 1972). Its shallow rooting behaviour may also help to explain its apparent absence from deep Kalahari sands, where water tables are often at great depths, and where the loose surface soils exhibit poor moisture retention properties and offer inadequate mechanical stability.

What is puzzling is why the tap roots of many mopane individuals atrophy after a certain period of time. This phenomenon would appear to have very little adaptive significance, particularly in shallow to moderately shallow soils which should become saturated throughout the profile after cloud bursts in the dry tropics (cf Climatological Summaries, 1963). Increased rooting depth in these soils would obviously enable the plants to withstand longer periods between profile recharge, (cf. Pearson, 1974).

It is possible that tap root disappearance is associated with the observed tendency towards compaction in the lower horizons. Compacted soils are associated with conditions of reduced porosity and soil aeration (Taylor, 1974) and as such are prone to waterlogging. Despite the controversies regarding mopane and waterlogging (Section B.3), it seems more than likely that compacted mopane soils occasionally become inundated during intensive cloud bursts in the dry tropics, albeit for relatively short periods of time. This situation would be prolonged at depth and could cause tap root degeneration. The adverse effects of waterlogging on root development are discussed at length by Merkle (1955), Kerfoot (1963), Russell (1973) and Stolzy (1974). The view has been expressed that mopane individuals with senescent tap roots become susceptible to termite attack (Section D.2.3.).

The above hypothesis is in keeping with the suggestion that mopane adapts to a wide range of adverse soil conditions, and is not a prima facie cause of such conditions. The author's views are, however, only conjectural and emphasize the need for more detailed studies along the mopane belt of southern Africa.

D.3. Relation of Mopane Performance to Soil Factors

The relation of performance value to various soil factors was studied using linear regression analysis, the main aim being to detect any factors which might limit mopane growth in the soils under study. The use of linear regression analysis was considered adequate for this purpose since growth responses to limiting factors (i.e. limiting to growth either through deficiency or excess) are approximately linear between certain limits (cf. Russell, 1973).

Freese (1967, rns of the dangers in ascribing more meaning to fitted regressions than is actually warrented. A linear regression, for example, does not show that the line fitted gives the best possible description of the data (a curved line might be better), nor does it mean that the true mathematical relationship between the variables has been found. With ind, experiments were subsequently designed to test the validity of hypotheses c ialysis of the field data (Section C.4., D.5.). This strategy was prompted further onsideration that performance value was assumed to be a reliable index of mopane biomass, without prior verification involving destructive sampling.

2.3.1. Performance value of mopane at each site

The mean density (no. of individuals/100 sq. m) at each site is given in Table 9. A breakdown of the data from which these values are derived is presented in Appendix 4. To enable inter site comparisons of growth performance, D.B.H (Table 10) was applied as a multiplicative correction factor to the density values given in Table 9 (see Section C.2.5.). The performance values (no. of indiv./m) thus obtained are given in Table 11.

There was a 16-fold range in mopane performance values, the lowest being 0,11 indiv./m at site 2 and the highest 1,77 indiv./m at site 6. An intermediate performance value of 0,83 indiv./m was obtained at site 4. Mopane "biomass" assessed in this manner was significantly correlated with a number of soil factors (Section D.3.2.).

D.3.2. Simple linear regression analysis

Correlation coefficients obtained on regression of performance value against various soil factors are presented in Table 12. Mopane performance was significantly correlated with the following soil parameters (cf. Table 12):

Total N	–	at 20–30cm	($r = + 0{,}69$, $P < 0{,}05$);
Available P	–	at 0–10cm	($r = + 0{,}59$, $P < 0{,}10$);
P.B.C.	–	at 20–30cm	($r = + 0{,}61$, $P < 0{,}10$);
% H_2O (0,33 bar)	–	at 20–30cm	($r = + 0{,}72$, $P < 0{,}05$);
% H_2O (15,2 bar)	–	at 20–30cm	($r = + 0{,}75$, $P < 0{,}02$);
Ex. Mg	–	at 0–10cm	($r = + 0{,}78$, $P < 0{,}02$);
Ex. Mg	–	at 20–30cm	($r = + 0{,}85$, $P < 0{,}01$) and
T.E.C.	–	at 20–30cm	($r = + 0{,}63$, $P < 0{,}10$).

Regression lines of performance value on total N (subsoil) and percentage H_2O at 0,33 bar and 15,2 bar (subsoil), are given in Figure 11; and of performance value on exchangeable Mg in both surface and subsoil, in Figure 12.

TABLE 9 The mean density of mopar[illegible]ch sample site.

Ht. class	Mean density (no. of indiv./100 sq.m)						Total
	1	2	3	4	5	6	
Site 1	5,18	0,83	0,25	0,38	0,23	–	6,87
Site 2	0,21	0,17	0,08	0,04	0,17	0,04	0,71
Site 3	21,05	11,15	0,25	0,20	0,05	–	32,70
Site 4	20,10	1,75	–	–	–	–	21,85
Site 5	4,40	3,83	5,00	0,33	–	–	13,56
Site 6	40,40	5,10	–	–	–	–	45,50
Site 7	1,93	1,00	0,13	0,73	1,70	0,67	6,16
Site 8	4,40	0,80	0,40	1,40	1,40	0,10	8,50

TABLE 10 The mean D.B.H. (m) of mopane in each height class, averaged over all sites.

Ht. class	1	2	3	4	5	6
No. in sample (n)	28	40	22	43	51	18
Mean D.B.H. ($\bar{x}$)	0,035	0,070	0,135	0,215	0,315	0,440
S.E. $\bar{x}$	±0,003	±0,006	±0,014	±0,019	±0,019	±0,021

TABLE 11 Performance values (D.B.H. x density) of mopane at each sample site.

Ht. class	Performance (no. of indiv. / m)						Total
	1	2	3	4	5	6	
Site 1	0,181	0,058	0,034	0,082	0,073	–	0,428
Site 2	0,007	0,012	0,012	0,009	0,054	0,018	0,112
Site 3	0,737	0,781	0,034	0,043	0,016	–	1,611
Site 4	0,704	0,123	–	–	–	–	0,827
Site 5	0,154	0,268	0,675	0,071	–	–	1,168
Site 6	1,414	0,357	–	–	–	–	1,771
Site 7	0,068	0,070	0,018	0,157	0,536	0,295	1,144
Site 8	0,154	0,056	0,054	[illegible]01	0,441	0,044	1,050

TABLE 12 Correlation coefficients obtained on regression of performance value against the measured physical and chemical properties of the soils from sites 1 to 8.

Soil Factors		Correlation coefficient (r)	
		0–10cm	20–30cm
Total N	(%)	+ 0,496	+ 0,690**
Available P	(ppm)	+ 0,586*	+ 0,136
Buffering capacity for P	(l/g)	+ 0,517	+ 0,612*
Bulk density	(g/cm^3)	– 0,211	– 0,078
Moisture content	(%)		
at 0,33 bar		–	+ 0,715**
at 15,2 bar		–	+ 0,745***
"Available" water	(%)	–	+ 0,532
pH		+ 0,133	+ 0,393
Exchangeable cations	(meq.%)		
Ca		+ 0,437	+ 0,567
Mg		+ 0,781***	+ 0,853****
K		+ 0,557	+ 0,291
Na		– 0,006	– 0,127
T.E.C.		+ 0,537	+ 0,632*
Cation saturation	(% of C.E.C.)		
Ca		+ 0,436	+ 0,446
Mg		+ 0,416	+ 0,334
K		+ 0,351	+ 0,072
Na		– 0,422	– 0,467
T.E.C.		+ 0,565	+ 0,443

Significance rating: * (P< 0,01); **(P < 0,05); ***(P < 0,02); ****(P < 0,01)

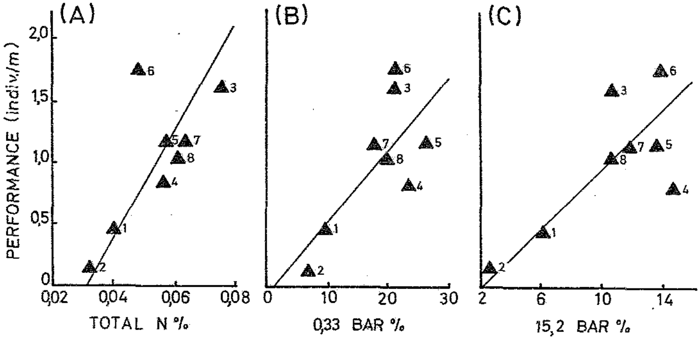


FIG. 11. Regression of performance value on: (A) Total N %, in sub-soil – (r = + 0,69; P < 0,05);
(B) % H_2O at 0,33 bar, in sub-soil – (r = + 0,72; P < 0,05);
(C) % H_2O at 15,2 bar, in sub-soil – (r = + 0,75; P < 0,02).

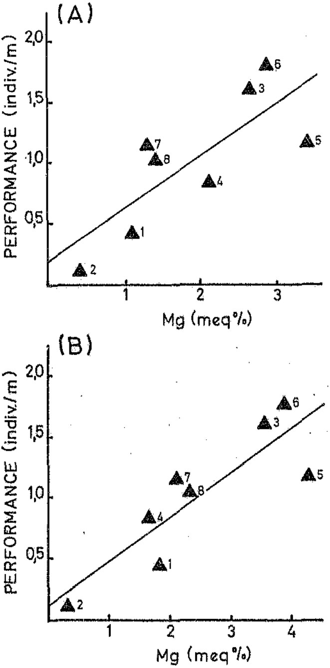


FIG. 12. Regression of performance value on:
(A) Ex. Mg. (meq %) in the surface soil ($r = + 0{,}78$; $P < 0{,}02$);
(B) Ex. Mg (meq %) in the sub-soil ($r = + 0{,}85$; $P < 0{,}01$)

Performance also seemed to be directly related to the quantities of available calcium and potassium (Table 12), although high levels of the former cation were slightly detrimental to growth (Figure 13). The phenomenon of growth restriction by deficiency or excess of any particular factor is a manifestation of "Shelford's Law of Tolerance" (Odum, 1959).*

The adverse effects of high levels of exchangeable Ca may have been due to an imbalance in the supply of calcium and magnesium (Fig. 14), since the plants responded so markedly to magnesium. It may be seen from Figure 14, however, that sites 1 and 2 had low performance values despite having apparently favourable Ca:Mg ratios in the surface and subsoil. Because of this the regression of performance value on Ca:Mg ratio yielded very poor correlation coefficients ($r = -0{,}007$ for surface soil, $r = +0{,}121$ for subsoil). Nevertheless, this did not exclude the possibility of mopane being sensitive to imbalances in Ca and Mg particularly since soils 1 and 2 were deficient in most nutrients (Tables 5–7), all of which could have contributed towards the low performance values at these two sites.

By way of example, Key *et al.* (1962) found that soybeans did not respond to favourable Ca:Mg ratios in soils of low C.E.C. (< 3 meq %), and attributed this to cation deficiency overriding the influence of Ca:Mg ratio. Similarly Vlamis (1949) found that lettuce and barley grown in serpentine soil did not respond to N, P and K fertilizers, unless Ca levels in the soil exceeded a certain critical minimum. The observations of these two authors serve to illustrate "Liebigs Law of the Minimum" (Odum, 1959).** This law implies that if several factors limit the growth of a species, then favourable levels of any one factor (in this case Ca:Mg ratio in soils 1 and 2) would be ineffectual in stimulating its growth (cf. Russell, 1973).

Sodium appeared to be detrimental to growth, particularly at the levels found in the subsoil ($r = -0{,}127$; cf. Table 12 and 5). This effect was more apparent when sodium in the subsoil was measured relative to the $\sqrt{Ca + Mg}$ ($r = -0{,}457$), or to C.E.C. ($r = -0{,}467$) or to T.E.C. ($r = -0{,}755$; $P < 0{,}02$). These observations prompted a closer look at the effect of

*Shelford's "law" of tolerance: *The presence and success of an organism depends upon the* completeness of a complex of conditions. Absence or failure of an organism can be controlled by the qualititative or quantititative deficiency or excess with respect to any one of several factors which may approach the limits of tolerance for that organism.

**Liebig's "law" of the minimum: To occur and thrive in a given situation, an organism must have essential materials which are necessary for growth and reproduction ..... The essential material available in amounts most closely approaching the critical minimum needed, will tend to be the limiting one.

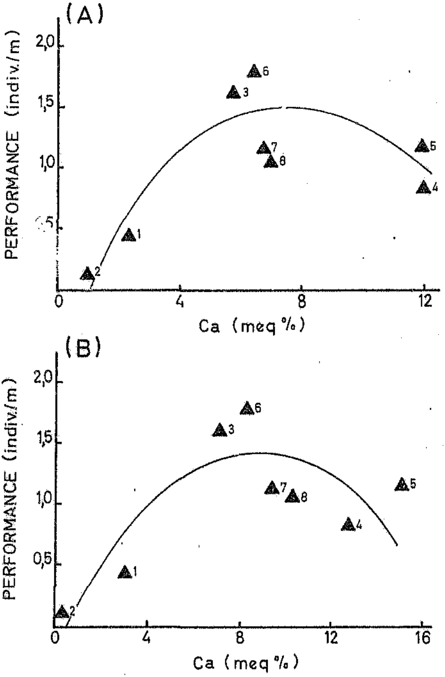


FIG. 13. Effect of exchangeable calcium (meq %) in the surface (A) and subsoil (B) on performance value.

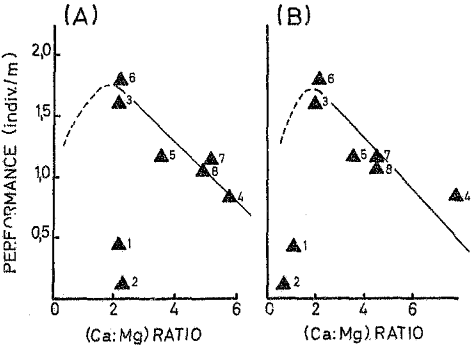


FIG. 14. The effect of Ca:Mg ratio in the surface (*A*) and subsoil (*B*) on performance value.

sodium when measured relative to other soil cations individually. Performance value was found to be strikingly correlated with increase in Mg:Na ratio in both the surface and subsoil ($r = +0,835$; $P < 0,01$ for surface soil; $r = +0,762$; $P < 0,02$ for subsoil). This suggested that increased Mg levels in particular were able to overcome the detrimental effects of sodium. Regression lines of performance value on Na:T.E.C. ratio in the subsoil and Mg:Na ratio in the surface and subsoil are given in Figures 15 and 16, respectively.

D.3.3. Multiple regression analysis

Data obtained from the regression of performance value on various soil factor combinations simultaneously, are given in Appendix 5. Analyses accounting for a significant portion of the variation in performance value were summarised from Appendix 5 and are presented in Table 13.

Thus phosphorus and nitrogen (0–10 cm), and phosphorus, nitrogen and potassium (0–10cm) accounted for 67,9% and 82,5% respectively of the variation in mopane performance. Magnesium and sodium in the surface and sub-soil accounted for 63,7% (0–10cm) and 68,4% (20–30cm) of the variation in performance. The latter values, however, did not differ substantially from those obtained on regression against magnesium singly (54,5%-surface soil; 68,4%-sub-soil).

Similarly Mg:Na and Mg:K ratios in the surface soil accounted for 69,8% ($P < 0,05$) of the variation in mopane performance, as opposed to a value of 62,5% ($P < 0,05$) obtained with Mg:Na ratio singly. In the subsoil, however, the introduction of Mg:K ratio into the regression of performance value on Mg:Na ratio, caused the percentage variation accounted for to increase appreciably from 51,0% ($P < 0,05$) to 72,6% ($P < 0,05$).

From the above analyses it appeared that mopane growth was strongly influenced by N, P, K, and cation ratio interactions in the soil. In particular, the significance attached to soil magnesium on simple linear regression analysis was augmented by the multiple regression of performance value on magnesium ratios in the soil.

D.3.4. Discussion of results

(a) Nitrogen, phosphorus and soil moisture

In section D.2.2. (b), it was pointed out that nitrogen and phosphorus levels in the soil were well below the limits suggested for crop sufficiency. It was not surprising therefore, that mopane performance was positively correlated with total N (20–30cm, Fig. 11 A),

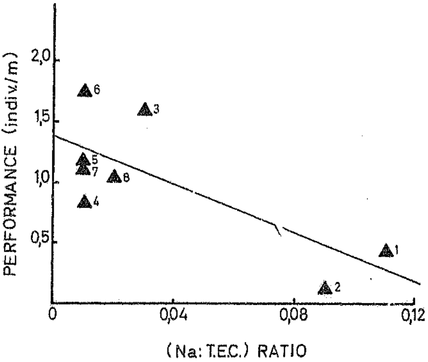


FIG. 15. Regression of performance value on Na:TEC ratio in the subsoil ($r = -0{,}76$; $P < 0{,}02$).

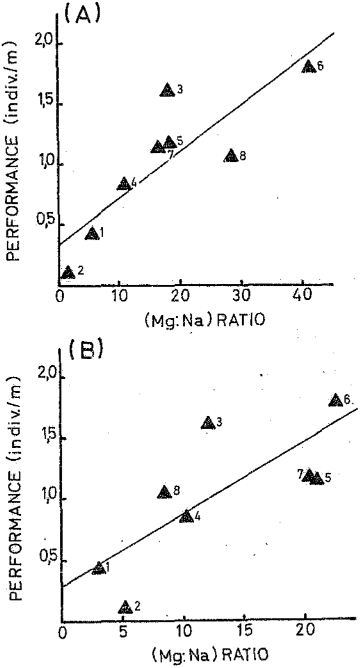


FIG. 16. Regression of performance value on:
(A) Mg: Na ratio in the surface soil ($r = +0,84$; $P < 0,01$).
(B) Mg: Na ratio in the subsoil ($r = +0,76$; $P < 0,02$).

TABLE 13 Stepwise multiple regression of performance value on the measured chemical and physical properties of soils from sites 1 to 8. (Simplified from data presented in Appendix 5).

Step	Soil Factor	Depth (cm)	R	% variation accounted for	F-value
1	P.	0–10	0,586	23,3	3,138
2	P; N.	"	0,856	67,9	8,438*
1	P.	0–10	0,586	23,3	3,138
2	P; N.	"	0,856	67,9	8,438*
3	P; N; K.	"	0,928	82,5	12,026*
1	Mg.	0–10	0,781	54,5	9,392*
2	Mg; Na.	"	0,836	63,7	7,167*
1	Mg.	20–30	0,853	68,1	15,971**
2	Mg; Na.	"	0,858	68,4	8,560*
1	Mg/Na.	0–10	0,835	62,5	12,696*
2	Mg/Na; Mg/K.	"	0,865	69,8	9,087*
1	Mg/Na.	20–30	0,762	51,0	8,302*
2	Mg/Na; Mg/K.	"	0,879	72,6	10,287*
3	Mg/Na; Mg/K; Mg/Ca.	"	0,902	76,6	8,653*

Significance rating: *(P < 0,05); **(P < 0,01) available P (0–10cm, Table 12), P.B.C. (20–30cm, Table 12), and that nitrogen and phosphorus (0–10cm) accounted for 67,9% of the variation in performance value (Table 13).

Mopane performance was also significantly correlated with moisture content at 0,33 bar and 15,2 bar matric suction (Fig. 11 B + C), but bore no significant relationship to the "available" water content of the soil (Table 12). This suggested firstly, that the overall water holding capacity of the soil, as defined by the amount held at 0,33 bars, was of greater significance to mopane than "available" water content as such, and secondly, that this species was capable of extracting soil water at tensions corresponding to the P.W.P. (15,2 bars, nominal P.W.P.).

The above interpretation casts some doubt on the contentions of Hendrickson and Veihmeyer (1945), and others, that P.W.P. is a soil constant indicating the lower limit of water availability for all plants. Indeed, Slatyer (1957a, 1957b) puts forward the thesis, subsequently acknowledged by Levitt (1972), that P.W.P. is essentially dependent upon the osmotic potential of the cell sap in the plant under study. The argument is advanced that irreversible loss of turgidity (permanent wilting), can only occur when the water potential of the plant and total soil moisture stress tend towards equilibrium. In an enlightening review, Slatyer (1957b) explains how standard laboratory procedure for the determination of P.W.P. (cf. Veihmeyer and Hendrickson, 1949; Salter and Haworth, 1961b) may cause plants to adjust osmotically, such that xerophytic species become induced to wilt at tensions more typical of mesophytic plants. Only when groups of plants exhibit similar osmotic characteristics, does it become possible to associate a single value for the P.W.P. with wilting phenomena of plants within any one group.

In view of the above correlations a factorial experiment was designed to test yield responses of mopane to applications of nitrogen and phosphorus, and to variations in soil moisture stress. The suggestion that this species was capable of extracting water at tensions corresponding to the P.W.P., prompted a study of its water utilization pattern under conditions of varying soil moisture stress. Details of experimental procedure have been reported in Section C.4., and results are presented in Section D.4.

(b) Soil cations

Mopane performance was significantly correlated with exchangeable magnesium, the values of which ranged from 0,30 to 4,27 meq % (Fig. 12). These corresponded to magnesium saturations from 8 to 26% of the C.E.C.

Bear and Toth (1948) found magnesium saturations of 10% to be optimum for alfalfa when grown in soil where 65% and 5% of the exchange complex was occupied by calcium and potassium respectively. Citrus seedlings grown in Hanford sandy loam (C.E.C. = 11–17 meq%) were found to be insensitive to Mg-saturations in the range 6–28% (Martin and Page, 1969). Higher saturation levels of this cation caused a marked decline in citrus yield, unless compensatory levels of calcium were also made available to the plants. Martin and Page (1969) interpreted this observation as a degree of calcium-magnesium antagonism.

Calcium at high levels appeared to be detrimental to the growth of mopane (Fig. 13). This may have been due to a calcium-magnesium antagonism since performance decreased appreciably with increase in Ca:Mg ratio (Fig. 14). Ca: Mg ratios in the field ranged from approximately 2 to 6 with the higher performance values occurring at a value of 2:1 in both the surface and sub-soil. Key *et al.* (1962) found that soybeans and corn, grown in soil and sand resin culture (C.E.C. = 3, 9 and 27 meq %), were unaffected by Ca:Mg ratios in the range 50:1 to 1:1. Yield always declined, however, when exchangeable magnesium exceeded exchangeable calcium (Ca:Mg < 1). Variations in the Ca:Mg ratio from 1:4 to 32:1 had no effect on the yield of alfalfa plants, despite corresponding decreases in plant magnesium from 95 to 20 meq% (Hunter 1949). In the absence of added sodium, sudan grass was found to grow best at ratios of 2:1; in the presence of sodium (15% of C.E.C.) the optimum ratio rose to 11:1. Joffe and Zimmerman (1944) interpreted these observations as a magnesium and sodium antagonism to calcium uptake.

The apparent intolerance displayed by mopane towards sodium (Tables 12 + 13; see Section D.3.2.) was surprising, particularly since the level of this cation seldom exceeded 1,5% saturation of the exchange complex (Table 6). Significant correlations obtained on regression of performance value against Na:T.E.C. ratio (Fig. 15) and Mg:Na ratio (Fig. 16), suggested that this species was sensitive to imbalances between sodium and other soil cations, particularly magnesium. Bower and Wadleigh (1948), using a mixture of sand and synthetic resin, found that bean plants were sensitive to exchangeable sodium percentages exceeding 15% of the C.E.C. Rhodes grass and garden beet were found to be tolerant of much higher sodium levels (~ 75%). In all the test plants, applications of sodium caused corresponding decreases in the calcium, magnesium and potassium contents of the shoots as well as a marked decrease in the potassium content of the roots. Martin *et al.* (1953) found that increases in exchangeable sodium percentage from 4–28% caused a progressive decline in the yield of citrus seedlings. Increased sodium uptake by the citrus plants was assoc' .ted with a corresponding decrease in leaf calcium. Leaf magnesium on the other hand, only became appreciably reduced at 28% exchangeable sodium.

soil individually (Table 14). There were no significant interactions between N, P and available water supply on the total yield of mopane grown in pots. Phosphate increased the yield on all three soils, and nitrogen the yield on soils 4 and 6, but the effects were not significant. The effect of nitrogen on shoot growth in soil 6 was significant ($P < 0,05$) but a concomitant decline in root growth rendered the effect on total yield non-significant.

A striking feature was the significant ($P < 0,01$) decrease in yield with increasing N supply and moisture stress on soil 2. Repeated fluctuations in the available water supply from 100 to 0 per cent had no significant effect on growth in soils 4 and 6. The decreasing yields on soil 2 with increased N and moisture stress were accompanied by a significant ($P < 0,01$) decrease in evapotranspiration rate from the soil-plant system (Table 15). Evaporation from the soil alone, measured in control pots, was never greater than 10g H_2O per day, under the most favourable soil moisture conditions. Evapotranspiration rates from soils 4 and 6 were unaffected by N, P and fluctuating water supply.

In spite of large decreases in yield and water consumption with increasing N and soil moisture stress on soil 2, the coefficient of water utilization remained unchanged (Table 16). Phosphate treatment on soil 2 caused a significant ($P < 0,05$) decrease in the coefficient of water utilization, whilst on soil 6 values increased significantly ($P < 0,01$) with rising soil moisture stress. However, apart from these two significant trends, the changes in rates of evapotranspiration and growth were mutually compensatory so that the coefficient of water utilization was relatively independent of soil type and the imposed treatments.

The above observations suggest a capacity for internal osmotic adjustment (Slatyer, 1957a; Wilson *et al.*, 1970; Levitt, 1972; Russell, 1973) by mopane, especially when viewed in the light of the moisture retention properties of the three soils used (Fig. 17). Most of the available water was held at suctions less than 6 bars on soils 4 and 6, and at suctions below 1 bar on soil 2. Clearly, plants subjected to the most unfavourable watering treatment absorbed water against a wider range of increasing soil moisture suction, before reaching the 15,2 bar percentage. In the absence of an osmotic adjustment mechanism therefore, one would have expected a marked decrease in evapotranspiration rate together with an even greater decrease in yield, thus leading to an overall increase in the coefficient of water utilization on all three soils under the most unfavourable watering treatment (Section D.4.3.).

The absence of an effect of extreme variation in available water supply on mopane growth on soils 4 and 6, suggested that the detrimental effects of increased N level and rising soil moisture stress in soil 2, may have been due to excessive osmotic concentrations of the soil solution. Soil 2 contained only 6,9% water at 0,33 bars and had an extremely low range of "available" water, most of which was held at suctions less than 1 bar soil individually (Table 14). There were no significant interactions between N, P and available water supply on the total yield of mopane grown in pots. Phosphate increased the yield on all three soils, and nitrogen the yield on soils 4 and 6, but the effects were not significant. The effect of nitrogen on shoot growth in soil 6 was significant ($P < 0{,}05$) but a concomitant decline in root growth rendered the effect on total yield non-significant.

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TABLE 14 The effect of nitrogen, phosphate and fluctuating available water supply on the dry weight yield (shoots plus roots) of mopane

Soil 2

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g dry weight (means of 12)	kg/ha+	g dry weight (means of 12)	kg/ha	g dry weight (means of 18)
100↔90	2,65	0	2,63	0	2,14
100↔40	2,24	56	2,30	56	2,33
100↔0	1,82	168	1,78	–	–
Level of significance for F test++	**		**		n.s.
L.S.D. ($P < 0,05$)	0,46		0,46		0,38
Interactions			–		

Soil 4

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g dry weight (means of 12)	kg/ha	g dry weight (means of 12)	kg/ha	g dry weight (means of 18)
100↔90	4,01	0	4,00	0	4,21
100↔40	4,20	56	4,30	56	4,24
100↔0	4,47	168	4,41	–	–
Level of significance for F test++	n.s.		n.s.		n.s.
L.S.D. ($P < 0,05$)	0,57		0,57		0,46
Interactions			–		

Soil 6

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g dry weight (means of 12)	kg/ha	g dry weight (means of 12)	kg/ha	g dry weight (means of 18)
100↔90	5,21	0	4,94	0	5,05
100↔40	5,17	56	5,39	56	5,39
100↔0	5,27	168	5,32	–	–
Level of significance for F test++	n.s.		n.s.		n.s.
L.S.D. ($P < 0,05$)	0,62		0,62		0,50
Interactions			–		

+ Approximate equivalent per hectare of the element applied in g per pot; ++ n.s. not significant; * significant for $P < 0,05$; ** significant for $P < 0,01$.

TABLE 15 The effect of nitrogen, phosphate and fluctuating available water supply on the evapotranspiration rate (g water/day) of mopane

Soil 2

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 18)
100↔90	21,1	0	21,4	0	17,1
100↔40	17,2	56	18,3	56	18,0
100↔0	14,5	168	13,1	–	–
Level of significance for F test+	**		**		n.s.
L.S.D. ($P < 0,05$)	3,3		3,3		2,7
Interactions			–		

Soil 4

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 18)
100↔90	38,4	0	39,6	0	41,1
100↔40	42,4	56	42,2	56	41,78
100↔0	43,4	168	42,5	–	–
Level of significance for F test+	n.s.		n.s.		n.s.
L.S.D. ($P < 0,05$)	4,9		4,9		4,0
Interactions			–		

Soil 6

Effect of water stress		Effect of N		Effect of P	
% available H_2O	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 12)	kg/ha	g H_2O day^{-1} (means of 18)
100↔90	43,5	0	45,0	0	45,3
100↔40	46,3	56	47,4	56	45,9
100↔0	47,1	168	44,4	–	–
Level of significance for F test+	n.s.		n.s.		n.s.
L.S.D. ($P < 0,05$)	4,9		4,9		4,0
Interactions			–		

+ See Table 14.

TABLE 16 The effect of nitrogen, phosphate and fluctuating available water supply on the coefficient of water utilization (g water/g dry weight/day) by mopane.

Soil 2

Effect of water stress: % available H_2O	g H_2O/g plant day^{-1} (means of 12)	Effect of N: kg/ha	g H_2O/g plant day^{-1} (means of 12)	Effect of P: kg/ha	g H_2O/g plant day^{-1} (means of 18)
100↔90	10,1	0	10,6	0	11,4
100↔40	10,6	56	10,8	56	9,4
100↔0	10,5	168	10,0	–	–
Level of Significance for F test+	n.s.		n.s.		*
L.S.D. (P < 0,05)	1,9		1,9		1,6
Interactions			–		

Soil 4

Effect of water stress: % available H_2O	g H_2O/g plant day^{-1} (means of 12)	Effect of N: kg/ha	g H_2O/g plant day^{-1} (means of 12)	Effect of P: kg/ha	g H_2O/g plant day^{-1} (means of 18)
100↔90	10,0	0	10,2	0	10,0
100↔40	10,4	56	10,2	56	10,2
100↔0	9,9	168	9,9	–	–
Level of Significance for F test+	n.s.		n.s.		n.s.
L.S.D. (P < 0,05)	0,6		0,6		0,6
Interactions			–		

Soil 6

Effect of water stress: % available H_2O	g H_2O/g plant day^{-1} (means of 12)	Effect of N: kg/ha	g H_2O/g plant day^{-1} (means of 12)	Effect of P: kg/ha	g H_2O/g plant day^{-1} (means of 18)
100↔90	8,5	0	9,2	0	9,1
100↔40	9,0	56	8,8	56	8,8
100↔0	9,4	168	8,9	–	–
Level of Significance for F test+	**		n.s.		n.s.
L.S.D. (P < 0,05)	0,4		0,4		0,3
Interactions			–		

+ See Table 14.

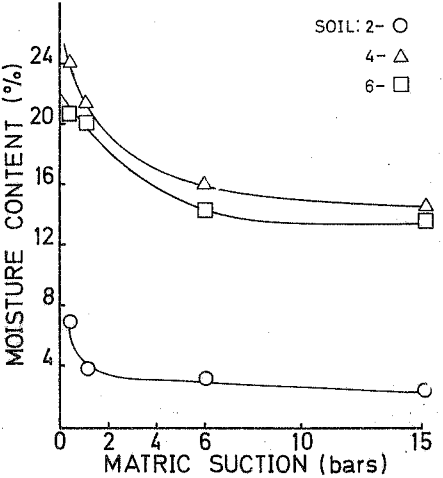


FIG. 17. Moisture retention curves between the matric suctions of 0,33 and 15,2 bars, for soils 2, 4 and 6.

(Fig. 17). Accordingly, soil solution concentrations were calculated for each soil, taking into account the salts added in the basal nutrient solution and the nitrogen treatments, at two extreme moisture regimes:

(a) at 0,33 bars matric suction, and (b) at 15,2 bars matric suction.

Osmotic suction was calculated from the approximate formula:

$$\pi = RTC$$

where C is the molar concentration of the soil solution. Total plant yields, averaged over replicates and phosphate levels, are plotted against π in Figure 18. Clearly, on soils 4 and 6, increased N-levels over the two extreme watering regimes caused only minor fluctuations in osmotic suction of between 0,3 and 3,0 bars (up to 18,2 bars T.S.M.S.). Yield was not markedly affected, indicating that mopane could tolerate total soil moisture stress of up to 18,2 bars in these heavier textured soils without any apparent ill effects. On soil 2 osmotic suctions were never less than 3 bars and increased up to 6 bars with increased nitrogen applications at 0,33 bars matric suction (6,33 bars T.S.M.S.). Although yield was significantly ($P < 0,05$) depressed within this range of osmotic suctions, the coefficient of water utilization remained constant (Table 16). This pointed to an osmotic adjustment mechanism within the plant which enabled it to maintain a favourable water potential gradient between the cell sap and the soil solution. Evidence presented later (Section D.4.2. and D.4.3.), suggests that such a mechanism might involve an increase in osmotically active solutes within the cell sap, possibly through an increase in amino-acids and sugars relative to proteins and other carbohydrates respectively. After such an adjustment, increased osmotic suction had no further effect on yield and plants were able to tolerate total soil moisture stresses reaching 31,2 bars (15,2 + 16 bars) for limited periods.

D.4.2. Chemical analysis of plant tissue

(a) Relative nitrogen content of shoots

The mean relative nitrogen content of mopane shoots grown under factorial combinations of N, P and soil moisture stress is given in Appendix 9, and a summary of the main treatment effects is presented in Table 17. The mean relative nitrogen content of plants grown on the three soils differed markedly, being 1,76% for soil 2, 1,05% for soil 4 and 1,21% for soil 6. In all three soils the nitrogen concentration in the shoots increased significantly ($P < 0,01$) with increase in N level.

Phosphorus significantly ($P < 0,01$) enhanced the uptake of nitrogen by plants grown on soil 4 and showed variable interactions with nitrogen in soils 2 ($P < 0,05$) and 6

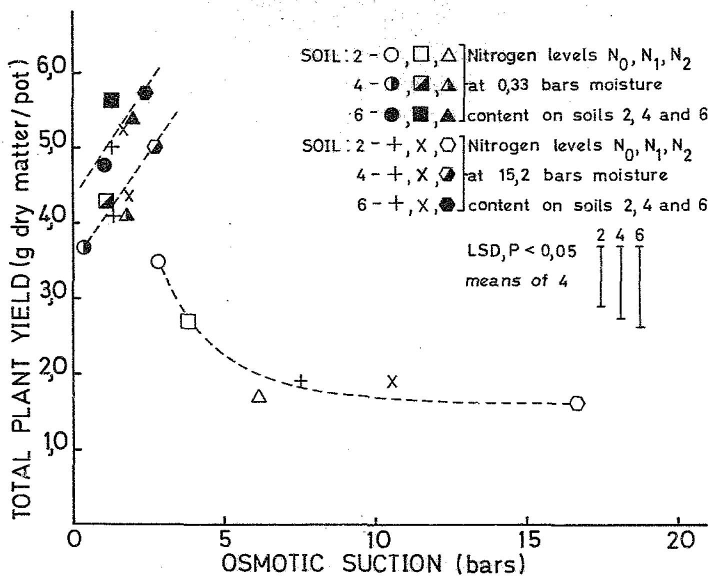


FIG. 18. The relation between total yield of mopane and osmotic suction for soils 2, 4 and 6.

TABLE 17 The effect of nitrogen, phosphate and fluctuating available water supply on the relative nitrogen content (%) of mopane shoots

Soil 2						Soil 4						Soil 6					
Effect of water stress		Effect of N		Effect of P		Effect of water stress		Effect of N		Effect of P		Effect of water stress		Effect of N		Effect of P	
% available H_2O	% N content (means of 12)	kg/ha	% N content (means of 12)	kg/ha	% N content (means of 18)	% available H_2O	% N content (means of 12)	kg/ha	% N content (means of 12)	kg/ha	% N content (means of 18)	% available H_2O	% N content (means of 12)	kg/ha	% N content (means of 12)	kg/ha	% N content (means of 18)
100↔90	1,68	0	1,48	0	1,76	100↔90	1,02	0	0,86	0	1,00	100↔90	1,23	0	0,88	0	1,21
100↔40	1,71	56	1,61	56	1,75	100↔40	1,05	56	1,08	56	1,10	100↔40	1,20	56	1,31	56	1,21
100↔0	1,87	168	2,18	–	–	100↔0	1,08	168	1,20	–	–	100↔0	1,18	168	1,43	–	–
Level of significance for F test[+]	n.s.		**		n.s.		n.s.		**		**		*		**		n.s.
L.S.D. ($P < 0{,}05$)	0,17		0,17		0,14		0,07		0,07		0,06		0,04		0,04		0,03
Interactions			N x P–*					–						N x P–**			

+ See Table 14

($P < 0{,}01$). Moisture stress had a variable effect on the nitrogen accumulation in plants grown on the three soils. On soil 6, for example, percentage N decreased significantly ($P < 0{,}05$) with rising soil moisture stress, whilst on soils 2 and 4 a positive but non significant response was obtained.

The ability of plants grown on soil 2 to accumulate significant ($P < 0{,}01$) amounts of nitrogen at moisture stresses and N levels unfavourable to growth (cf. Tables 14 and 17), prompted a closer look at the relation between relative nitrogen content and rising osmotic suction. Percentage nitrogen values, averaged over replicates and phosphate levels, are plotted against π at 15,2 bars matric suction in Figure 19. Clearly, the relative nitrogen content of plants increased significantly ($P < 0{,}05$) with rising osmotic suctions between 1,3 and 16,5 bars. The possible role of nitrogen in the osmoregulation of the cell sap is discussed in Section D.5.3.

(b) Relative phosphorus content of shoots

The mean relative phosphorus content of plants grown under factorial combinations of N, P and soil moisture stress is given in Appendix 10, and a summary of the main treatment effects is presented in Table 18. The mean relative phosphorus content of plants grown on soils 2 and 6 was 0,24% and 0,23% respectively, whilst a considerably lower value of 0,15% was obtained for plants grown on soil 4. On all three soils the percentage phosphorus increased significantly ($P < 0{,}01$) with increase in phosphate level.

On soil 6, the uptake of phosphorus increased significantly ($P < 0{,}01$) with increased N level and decreased significantly ($P < 0{,}01$) with rising soil moisture stress. Significant interactions were obtained between moisture stress and phosphorus on soils 2 ($P < 0{,}01$) and 6 ($P < 0{,}05$); between moisture stress and nitrogen on soil 2 ($P < 0{,}05$) and between nitrogen and phosphorus on soil 6 ($P < 0{,}01$).

D.4.3. Discussion of results

The yield response of mopane to N and P was not as marked as might have been expected from the field data (Section D.2.2.(b); D.3.4.(a)) particularly in soils 4 and 6, where the range of available water was sufficient to prevent the development of harmful osmotic effects. The lack of a significant response cannot be attributed to a possible unavailability of N and P (cf. Birch, 1958; Russell, 1973), since the accumulation of both these nutrients in the shoots responded strikingly to increased N and P level respectively.

Russell (1973) points out that when yield responses are appreciably less than expected, then other factors limiting yield are generally present. For example Vlamis (1949) found that

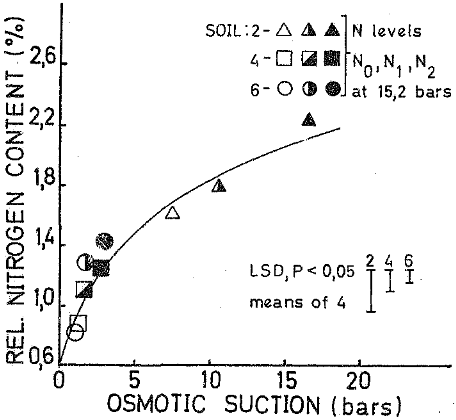


FIG. 19. The relation between relative nitrogen content of mopane shoots and osmotic suction for soils 2, 4 and 6.

TABLE 18 The effect of nitrogen, phosphate and fluctuating available water supply on the relative phosphorus content (%) of mopane shoots.

	Soil 2					Soil 4						Soil 6					
Effect of water stress		Effect of N		Effect of P		Effect of water stress		Effect of N		Effect of P		Effect of water stress		Effect of N		Effect of P	
% available H_2O	% P content (means of 12)	kg/ha	% P content (means of 12)	kg/ha	% P content (means of 18)	% available H_2O	% P content (means of 12)	kg/ha	% P content (means of 12)	kg/ha	% P content (means of 18)	% available H_2O	% P content (means of 12)	kg/ha	% P content (means of 12)	kg/ha	% P content (means of 18)
100↔90	0,23	0	0,23	0	0,20	100↔90	0,15	0	0,15	0	0,12	100↔90	0,26	0	0,20	0	0,21
100↔40	0,24	56	0,22	56	0,27	100↔40	0,14	56	0,14	56	0,14	100↔40	0,22	56	0,23	56	0,24
100↔0	0,24	168	0,25	–	–	100↔0	0,15	168	0,15	–	–	100↔0	0,22	168	0,25	–	–
Level of significance for F test +	n.s.		n.s.		**		n.s.		n.s.		**		**		**		**
L.S.D. (P <0,05)	0,03		0,03		0,03		0,03		0,02		0,02		0,01		0,01		0,01
Interactions	Moisture x Nitrogen * Moisture x Phosphorus **											Nitrogen x Phosphorus ** Moisture x Phosphorus *					

+ See Table 14.

lettuce and barley did not respond to N, P and K fertilizers unless calcium in the soil exceeded a certain critical minimum (see Section D.3.2.). Even though standard nutrient solution (Appendix 2) was applied to all three soils before commencement of the experiment, this did not exclude the possibility of some nutrients remaining unavailable to mopane. Perhaps certain essential nutrients were rendered unavailable during the alternate wetting and drying of the soil (cf. Wadleigh and Richards, 1961). The observed disparity between N and P uptake and yield response, suggested a reduced rate of utilization of these nutrients in fundamental growth processes such as DNA, RNA and protein synthesis. Reduced metabolic efficiency may be induced by a wide variety of nutrients when in short supply. In a review article Steinberg (1961) concludes that inadequate supplies of nutrients such as Ca, Mg, K, S and B lead to an accumulation of amino acids over protein and reducing sugars over carbohydrate. In support of the above argument is the observation that soil 6, which had the most favourable nutrient status as assessed by performance value, afforded the best yield response to increased N and P level (Table 14).

The stimulatory effect of N and P level on the relative nitrogen and phosphorus content respectively was consistent on all three soils. The remaining treatment effects, however, differed markedly from soil to soil, as did the various treatment interactions (Tables 17 and 18). It is difficult to ascribe physiological, or ecological significance to these varied effects, particularly in the absence of meaningful yield responses. The interactions reported in Tables 17 and 18 were thoroughly investigated but no meaningful interpretations could be gleaned from the data. In experiments of this nature it is often difficult to distinguish between interactions that occur in the soil and those that occur in the plant (cf. Hiatt and Leggett, 1974).

The response of mopane to soil moisture stress was not that expected of a drought senstitive species. For example, Wadleigh and Ayres (1945) found a continuous decrease in the growth of red kidney beans with increase in soil moisture stress from 1 to 10 atm. Furthermore, the effects of increasing severity of soil moisture stress, whether due to a reduced supply of available water, or due to increasing osmotic suction, were comparable. The results obtained from this experiment (Fig. 18), suggested that mopane growth was unaffected by fluctuating osmotic suctions up to 3 bars at least (and total soil moisture tensions up to 18 bars) on the two soils of higher available water content (sites 4 and 6). On the soil of very low field capacity and available water content (site 2), however, growth was reduced by the consistently high osmotic suctions (3–6 bars) imposed by increased nitrogen levels. At the higher osmotic suctions (6–16 bars), internal osmotic adjustment appeared to have occurred and yield values remained unchanged. With such an adjustment transpiration rate was reduced, but the coefficient of water utilization was maintained at a value applicable to unstressed plants (Table 15 and 16).

On soils 4 and 6 transpiration rate was unaffected by drying the soil to 15,2 bars matric suction. Slatyer (1957b) found that the transpiration rate of tomato, privet and cotton plants declined progressively with rising soil moisture stress. Continued transpiration was still observed although at considerably reduced rates, at total soil moisture tensions corresponding to permanent wilting of the leaves (20, 38 and 48 atm. for tomato, privet and cotton respectively). A measure of mopane's drought resistance may be gauged from the fact that no symptoms of wilting were detected, even in plants grown on soil 2, where total soil moisture stresses sometimes exceeded 30 bars under the most unfavourable watering regime. Unfortunately the total soil moisture stress equivalent to permanent wilting of mopane leaves was not determined in this experiment. Nevertheless, observations made on mopane grown in pots lend support to the hypothesis that the 15,2 bar % does not set the lower limit of water availability for this species (Section D.3.4(a)).

Nitrogen was implicated in the ability of mopane to ensure a sustained water supply on soil 2, where total soil moisture stresses fluctuated above 18 bars with alternate wetting and drying of the soil. Plants subjected to water stress generally show a decline in RNA, protein and polysaccharide content, and a concomitant build up of amino acids and reducing sugars. (Singh and Alderfer, 1966; Kramer, 1969; Levitt 1972). Assuming this phenomenon to hold true for mopane, then the significant accumulation of N in response to rising osmotic suction (Fig. 19), must have caused a substantial increment in the concentration of osmotically active solutes (sugars and amino acids) in the cell sap of the plants subjected to severe soil moisture stress. This observation, therefore, favours the hypothesis that mopane's drought resistance mechanism is essentially one of osmotic adjustment through solute accumulation.

Levitt (1972) broadly classifies xerophytic plants into either a drought-avoiding or drought-tolerating category. Drought avoiders are characterised by the ability to maintain a high water potential, either through the restriction of transpiration (the water savers), or by being able to locate sufficient water at depth to maintain a high transpiration rate (the water spenders). Likewise, drought tolerating plants may be divided into two categories; the dehydration avoiders and the dehydration tolerators. Plants belonging to the former category are able to avoid dehydration by maintaining an equilibrium between plant and environmental water potential. This is generally achieved by osmotic adjustment through solute accumulation. The dehydration tolerators, on the other hand, are capable of almost complete dehydration without sustaining structural or metabolic damage.

The daily water requirement of mopane (~ 10g/g dry wt./day) places it outside the category of water saving species (cf. Millar *et. al.*, 1965; Kramer, 1969; Slavik, 1974).

Equally, the observed tendency of this species to shed its leaves during extended periods of drought, excludes it from belonging to the class of dehydration tolerators. Thus it would seem that mopane is either a drought avoiding water spender, or a drought tolerant dehydration avoider.

The results obtained in this experiment suggest that the drought resistance mechanism of mopane is primarily one of dehydration avoidance by osmotic adjustment. Observations made in this study (Section D.2.3.) and by other workers (Miller, 1938; Wild, 1953; Wild, 1955; Thompson, 1960; Porter, 1968; and others) indicate that mopane is not inherently a deep rooting species. Water spenders generally have deep root systems, and rely on water reserves at or near the water table to ensure a high water potential and sustained transpiration output. In the absence of readily utilizable reserves, water spenders exhibit a linear decline in transpiration rate after a set period of time, and usually at soil water potentials in the range −6 to −12 bars (Levitt, 1972).

In addition to being shallow rooted, mopane is reportedly associated with alkaline, calcareous or sodium rich soils (Henkel, 1930; Ellis, 1950; Hudson, 1970; Louw, 1970; and others), where osmotic suctions may be expected to rise sharply on depletion of the available water supply (cf. Russell, 1973). One would not expect a species to colonise such soils unless it was capable of utilizing the high salt content to counteract the detrimental effects of rising osmotic suction.

The adaptive significance of mopane's resistance to soil moisture stress is discussed further in Section E. Unfortunately, the existence of an efficient osmotic adjustment mechanism within this species is based solely on circumstantial evidence. Conclusions drawn from this hypothesis are therefore only tentative, and must await the outcome of more detailed studies designed to monitor changes in plant and soil water potential with time (cf. Levitt 1972). With recent technical advances in the measurement of plant and soil water potential it is now possible to conduct this type of study in the field. The pressure bomb technique of Scholander *et. al.* (1965) offers a rapid and fairly reliable means of assessing plant water potential (cf. Slatyer, 1967; Kramer, 1969), whilst the temperature insensitive thermocouple-psychrometer developed by Rawlins and Dalton (1967) may be used for obtaining field recordings of soil water potential. More recently, readings on plant water potential have been obtained using an adaptation of the latter technique (Slavik, 1974).

D.5. Controlled Environment Studies – Mg, K and Na Interactions

D.5.1. Yield

The mean yield responses of mopane to factorial combinations of Mg, K and Na are given in Appendix 11. The main treatment effects were best reflected in the analysis of whole plant yields (roots and shoots). A summary of the results is presented in Table 19.

Mean yields on the three soils differed appreciably being 2,03g on soil 2, 5,17g on soil 4 and 4,61g on soil 6. Overall, magnesium increased the yield on all three soils but the effect was only significant ($P < 0,001$) on soil 2. Surprisingly, potassium had a detrimental effect on the growth of mopane on all three soils ($P < 0,001$ for soils 2 and 6; $P < 0,05$ for soil 4). Increased sodium level was also associated with a significant ($P < 0,001$) decline in yield on all three soils.

The above effects are illustrated in Figure 20 where yields are plotted against increased magnesium level in the presence and absence of added potassium and/or sodium. By itself, magnesium stimulated growth on soil 2 but caused a decline in yield on soils 4 and 6. However, plants grown on the two latter soils did respond positively to intermediate levels of magnesium in the presence of sodium or potassium (cf.. Fig. 20 and Plate 11).

Sodium and potassium interacted significantly ($P < 0,05$) on soils 2 and 6. The nature of this interaction may be gauged from Figure 20 where clearly, the reduction in yield with Na and K supplied individually was greater than the effect on yield of supplying the two elements together. A similar trend was apparent on soil 4, but failed to attain significance at the 95% confidence limit. The above interaction is illustrated further in Figure 21 where yield values averaged over replicates and magnesium levels are plotted against the sodium content of the soil.

The observed effects of Mg, K and Na on yield gave rise to a number of distinct possibilities. For example, the detrimental effects of K and Na treatment may have been due to the creation of cation imbalances within the plants, or alternatively, to the imposition of unfavourable osmotic stresses in the soil. Tissue analyses were therefore performed in an attempt to clarify the above observations.

D.5.2. Chemical analysis of plant tissue

The relative cation content (Ca, Mg, K and Na) of mopane grown under factorial combinations of Mg, K and Na is given in Appendix 12 and 13. A summary of the main treatment effects on the relative content of individual cations is given in Tables 20 to 23 and the effects on total relative cation content (Σ Ca, Mg, K, Na meq %) in Table 24.

(a) Relative calcium content

The mean relative calcium content of plants grown on the three soils was 39,5 meq % for soil 2, 75,8 meq % for soil 4 and 68,0 meq % for soil 6 (Table 20). Increase in magnesium

TABLE 19 The effect of magnesium, potassium and sodium on the dry weight yield (roots plus shoots) of mopane

	Soil 2						Soil 4						Soil 6					
	Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na	
	meq %	g dry weight (means of 12)	meq %	g dry weight (means of 18)	meq %	g dry weight (means of 18)	meq %	g dry weight (means of 12)	meq %	g dry weight (means of 18)	meq %	g dry weight (means of 18)	meq %	g dry weight (means of 12)	meq %	g dry weight (means of 18)	meq %	g dry weight (means of 18)
	0	1,67	0	2,46	0	2,49	0	4,57	0	5,77	0	6,46	0	4,24	0	5,74	0	6,48
	0,56	1,95	0,72	1,61	0,75	1,56	2,67	5,76	2,15	4,57	2,92	3,87	0,98	5,02	1,76	3,41	2,52	2,73
	1,00	2,49	–	–	–	–	4,78	5,18	–	–	–	–	2,77	4,57	–	–	–	–
Level of significance for F test +		***		***		***		n.s.		*		***		n.s.		***		***
L.S.D. (P < 0,05)		0,40		0,32		0,32		1,14		0,93		0,93		0,67		0,55		0,55
Interactions	K x Na*												K x Na*					

+ n.s. not significant; * significant for P < 0,05; ** significant for P < 0,01; *** significant for P < 0,001.

Note: Only the treatment levels for each cation are given above. The initial levels of each cation in the soil may be obtained from Table 3 (Section C.4.1.)

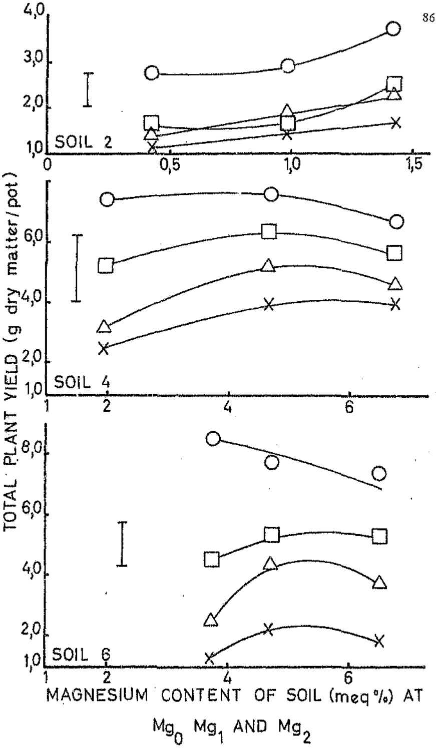
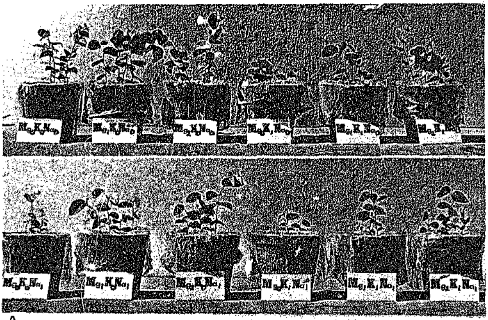
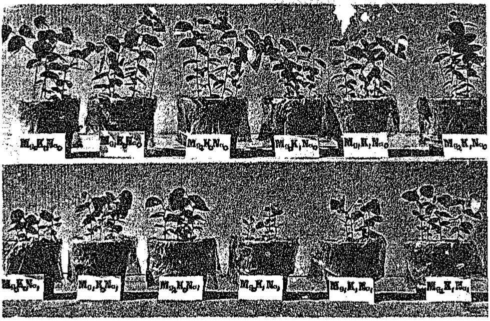


FIG. 20. Effect of magnesium on the yield of mopane in the presence and absence of added potassium or sodium. Vertical bars (I) indicate – L.S.D. values ($P < 0,05$, means of 3).

Legend o—o *Effect of Mg at (K_0Na_0)* △—△ *Effect of Mg at (K_0Na_1)*
□—□ Effect of Mg at (K_1Na_0) x—x Effect of Mg at (K_1Na_1)



A



B

PLATE 11. The effect of factorial combinations of Mg, K and Na on the growth of mopane in soils 2(A) and 6(B).

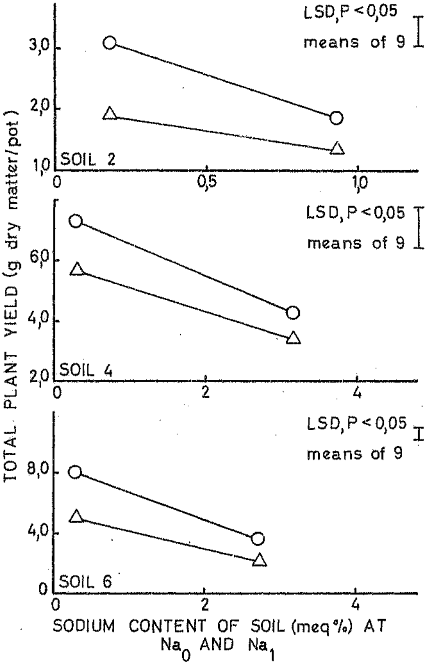


FIG. 21. The effect of sodium on yield in the presence and absence of added potassium

Legend O—O Effect of Na at K_0

△—△ Effect of Na at K_1

TABLE 20 The effect of magnesium, potassium and sodium on the relative calcium content (roots plus shoots) of mopane

Soil 2						Soil 4						Soil 6					
Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na	
meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)
0	41,56	0	45,71	0	40,30	0	86,1		74,91	0	71,30	0	73,23	0	65,66	0	66,81
0,56	40,81	0,72	33,29	0,75	38,70	2,67	74,55	2,15	76,71	2,92	80,32	0,98	67,33	1,76	70,31	2,52	69,16
1,00	36,12	–	–	–	–	4,78	66,69	–	–	–	–	2,77	63,39	–	–	–	–
Level of signifance for F test+	*		***		n.s.		***		n.s.		**		**		*		n.s.
L.S.D. (P < 0,05)	4,20		3,73		3,73		7,25		5,92		5,92		4,48		3,66		3,66
Interactions						K x Na*						K x Na***					

+ See Table 19.

level was associated with a significant decrease in calcium concentration within the plant tissue ($P < 0,05$ for soil 2; $P < 0,001$ for soil 4 and $P < 0,01$ for soil 6). Potassium caused a significant ($P < 0,001$) decrease in the relative Ca content of plants grown on soil 2. On soils 4 and 6 a positive response to K was obtained, but this effect was only significant ($P < 0,05$) on the latter soil. The effect of sodium was similar to that of potassium, but significance ($P < 0,01$) was only attained on soil 4. The significant negative interactions between Na and K on soils 4 ($P < 0,05$) and 6 ($P < 0,001$) are illustrated in Figure 22. Clearly, the increase in relative calcium content of plants was greater for Na and K individually than when supplied together.

(b) Relative magnesium content

The mean relative magnesium content of mopane did not vary markedly, being 24,01, 20, 79 and 24,01 meq % for soils 2, 4 and 6 respectively (Table 21). The accumulation of magnesium on all three soils increased significantly ($P < 0,001$ for soils 2 and 4; $P < 0,05$ for soil 6) with increased magnesium level. Potassium significantly enhanced the uptake of magnesium on soils 4 ($P < 0,05$) and 6 ($P < 0,01$), whilst on soil 2 a slightly negative response was obtained. Sodium also enhanced the accumulation of magnesium, causing a significant increase in the relative magnesium content of plants grown on all three soils ($P < 0,001$ for soils 2 and 6; $P < 0,01$ for soil 4). There were no significant interactions between Mg, K and Na on the relative magnesium content of mopane grown in pots.

(c) Relative potassium content

The mean relative potassium content of mopane was 73,66 meq % on soil 2, 64,04 meq % on soil 4 and 69,35 meq % on soil 6 (Table 22). Increased potassium levels caused a significant ($P < 0,001$) increase in the accumulation of potassium on all three soils. Sodium decreased the relative potassium content of plants grown on soil 2, whilst on soils 4 and 6 a positive but non-significant response was obtained. Magnesium treatment decreased the level of potassium on all three soils, but this effect was only significant ($P < 0,05$) in plants grown on soil 4. There was also a significant ($P < 0,05$) interaction between K and Na on the relative potassium content of mopane grown on soil 4. Relative potassium values, averaged over replicates and magnesium levels and plotted against the sodium content of the soil, showed this interaction to be positive (Fig. 23). Clearly the increase in relative potassium content was greater for Na and K supplied together than for each cation supplied individually.

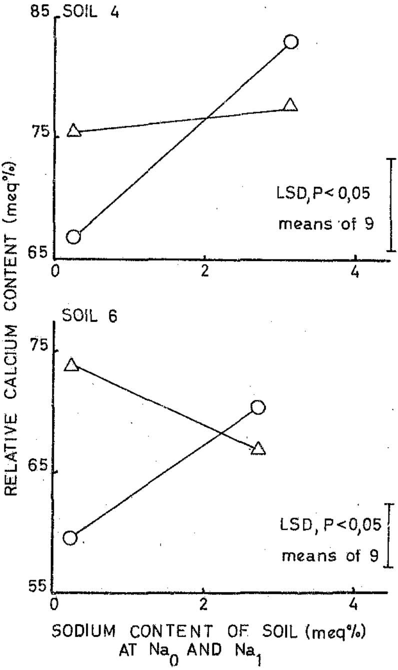


FIG. 22. The effect of sodium on the relative calcium content in the presence and absence of added potassium.

Legend O—O Effect of sodium at K_0

△—△ Effect of sodium at K_1

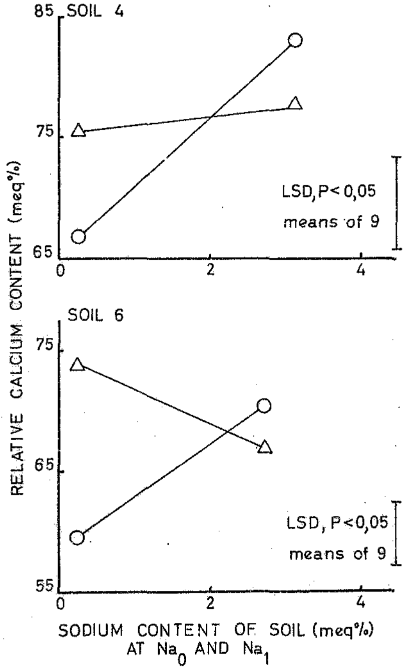


FIG. 22. The effect of sodium on the relative calcium content in the presence and absence of added potassium.

Legend O—O Effect of sodium at K_0

△—△ Effect of sodium at K_1

TABLE 21 The effect of magnesium, potassium and sodium on the relative magnesium content (roots plus shoots) of mopane

Soil 2						*Soil 4*						*Soil 6*					
Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na	
meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)
0	18,74	0	24,95	0	22,02	0	17,03	0	19,87	0	19,63	0	23,18	0	21,61	0	20,59
0,56	25,24	0,72	23,06	0,75	26,00	2,67	20,63	2,15	21,71	2,92	21,95	0,98	22,17	1,76	26,40	2,52	27,43
1,00	28,04	–	–	–	–	4,78	24,72	–	–	–	–	2,77	26,67	–	–	–	–
Level of significance for F test+			n.s.		***		***		*		**		*		**		***
L.S.D. (P < 0,05)	2,46		2,01		2,01		2,06		1,68		1,68		3,32		2,71		2,71
Interactions																	

+ See Table 19.

TABLE 22 The effect of magnesium, potassium and sodium in the relative potassium content (roots plus shoots) of mopane

Soil 2						Soil 4						Soil 6					
Effect of Mg		*Effect of K*		*Effect of Na*		*Effect of Mg*		*Effect of K*		*Effect of Na*		*Effect of Mg*		*Effect of K*		*Effect of Na*	
meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)
0	77,50	0	59,91	0	79,27	0	64,22	0	59,81	0	62,73	0	68,44	0	65,26	0	68,35
0,56	76,74	0,72	87,40	0,75	68,05	2,67	64,03	2,15	66,26	2,92	63,34	0,98	70,26	1,76	73,39	2,52	70,30
1,00	66,74	–	–	–	–	4,78	60,85	–	–	–	–	2,77	69,28	–	–	–	–
Level of significance for F test[+]	n.s.		***		*		*		***		n.s.		n.s.		***		n.s.
L.S.D. (P < 0,05)	11,23		8,35		8,35		2,90		2,37		2,37		3,33		2,72		2,72
Interactions						K x Na*											

+ See Table 19.

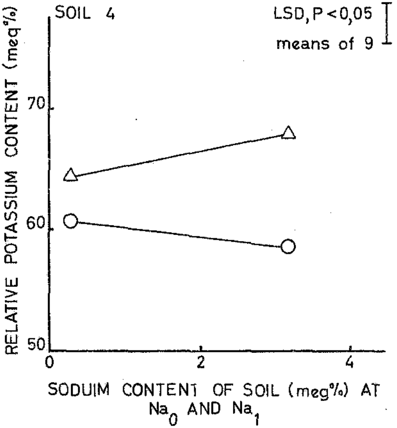


FIG. 23. The effect of sodium on the relative potas·ium content in the presence and absence of added potassium.

Legend O—O Effect of sodium at K_0

△—△ Effect of sodium at K_1

(d) **Relative sodium content**

Mopane on all three soils accumulated very little sodium. Mean values for relative sodium content were 7,8 meq % on soil 2, 4,20 meq % on soil 4, and 10, 11 meq % in soil 6 (Table 23). Sodium treatment enhanced the accumulation of sodium by plants in all three soils ($P < 0{,}01$ for soil 2; $P < 0{,}001$ for soils 4 and 6). Potassium also enhanced sodium accumulation on all the soils but the effects were not significant. Magnesium on the other hand decreased the relative sodium content of plants, but this effect was only significant ($P < 0{,}05$) on soil 4. There were no significant interactions between Mg, K and Na on the relative sodium content of mopane grown in pots.

(e) **Total relative cation content (Σ Ca, Mg K Na meq %)**

The mean total relative cation content of mopane was 144,9 meq % on soil 2, 163,85 meq % on soil 4 and 171,4 meq % on soil 6 (Table 24). Magnesium treatment caused an overall decline in total cation accumulation, this effect being significant ($P < 0{,}001$) on soil 4. Potassium caused an appreciable increase in total cation accumulation on all three soils ($P < 0{,}01$ for soils 2 and 4, $P < 0{,}001$ for soil 6). This was also true for sodium treatment on soils 4 and 6 ($P < 0{,}001$), whilst on soil 2 a slight negative response was obtained. The above responses clearly reflect the main effects of Mg, K and Na treatment on the relative content of individual cations (compare Table, 20 to 23 with Table 24). There were no interactions between Mg, K and Na on the total relative cation content of mopane grown in pots.

'as immediately apparent from the results reported that the detrimental effects ı and potassium could not be explained in terms of these two r t nts causing ation imbalances within the plant tissue. For example, both Na. a K caused appreciable increases in the relative magnesium content of plants grown on all ... soils (Table 21). Thus the favourable effects of Mg-treatment were not due to increased levels of this cation overcoming a K–Na antagonism to magnesium uptake. Antagonistic effects attributable to sodium and potassium did nevertheless occur. For example, on soil 2 sodium inhibited potassium uptake (Table 22) and potassium inhibited calcium accumulation. Further, a limited degree of K–Na antagonism could possibly be inferred from the interaction of these two nutrients on yield (Fig. 21) and from the observation that sodium treatment reduced the total amount of potassium (meq) accumulated by plants on all three soils. However, these trends and interactions did not account for the strikingly detrimental effects of sodium and potassium on yield.

It seemed possib e therefore, that the main effect of these two monovalent cations was to cause a build up of unfavourable osmotic suctions in the soil solution. This view was prompted further by the observation that both sodium and potassium caused a marked

TABLE 23 The effect of magnesium, potassium and sodium on the relative sodium content (roots plus shoots) of mopane.

Soil 2						Soil 4						Soil 6					
Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na	
meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)
0	11,01	0	6,47	0	4,72	0	5,29	0	4,09	0	2,14	0	12,68	0	9,12	0	6,79
0,56	5,98	0,72	9,[illegible]0	0,75	10,86	2,67	3,62	2,15	4,31	2,92	6,24	0,98	9,04	1,76	11,09	2,52	13,42
1,00	6,39	–	–	–	–	4,78	7,0	–	–	–	–	2,77	8,61	–	–	–	–
Level of significance for F test+ n.s.			n.s.		**		*		n.s.		***		n.s.		n.s.		***
L.S.D. (P < 0,05) 5,47			4,46		4,45		1,50		1,22		1,22		4,55		3,72		3,72
Interactions																	

+ See Table 19.

TABLE 24 The effect of magnesium, potassium and sodium on the total relative cation content (roots plus shoots) of mopane.

Soil 2						Soil 4						Soil 6					
Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na		Effect of Mg		Effect of K		Effect of Na	
meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)	meq %	meq % (means of 12)	meq %	meq % (means of 18)	meq %	meq % (means of 18)
0	148,80	0	137,05	0	146,29	0	172,80	0	158,67	0	155,80	0	177,53	0	161,67	0	162,54
0,56	148,76	0,72	152,83	0,75	143,59	2,67	162,82	2,15	169,03	2,92	171,90	0,98	168,82	1,76	181,26	2,52	180,33
1,00	137,25	–	–	–	–	4,78	155,95	–	–	–	–	2,77	167,95	–	–	–	–
Level of significance for F test+	n.s.		**		n.s.		***		**		***		n.s.		***		***
L.S.D. (P < 0,05)	12,50		10,21		10,21		8,06		6,58		6,58		11,80		9,64		9,64
Interactions																	

+ See Table 19.

increase in the total relative cation content of the plant tissue (Table 24). Evidence has already been produced for mopane possessing an osmotic adjustment mechanism, and the importance of organic solute accumulation (amino acids and sugars) in such a mechanism was outlined (Section D.4.3.).

Accordingly, soil solution concentrations at the 0,33 bar percentage were calculated for each soil, taking into account the ammonium nitrate added in the basal nutrient solution, the "balanced out" levels of sulphate (see Section C.4.1.(b)) and the amounts of chloride anion accompanying sodium and potassium treatments. The contributions of Mg^+, K^+ and Na^+ to osmotic suction were not taken into consideration since it was not possible to estimate the soil solution concentrations of these cations for each treatment. The osmotic values given here are therefore an underestimation of those which actually prevailed at commencement of the experiment. The contribution of sodium and potassium ions to osmotic suction must have been fairly substantial, particularly in those pots where cation saturation exceeded 100 per cent (Table 4 – Section C.4.1.(b)).

Total plant yields and total relative cation content, averaged over replicates and magnesium levels, are plotted against osmotic suction in Figure 24 (π = RTC ; see Section D.4.1.). Clearly, an increase in osmotic suction from ~ 2–9 bars with increased application of sodium and/or potassium was associated with a marked curvi-linear decrease in yield on all three soils (Fig. 24A). This trend was identical to that obtained in a previous experiment (Fig. 18) when increased N levels caused the osmotic suction on soil 2 to rise above 3 bars. Decline in yield was accompanied by a marked increase in the relative cation content of the plant tissue. (Fig.24 B). With the exception of plants grown on soil 2 (where salt uptake was limited by low T.E.C. and C.E.C.) the cation content curves appeared to be mirror images of the yield curves. This suggested that increase in relative cation content was due mainly to a concentration effect brought about by reduction in yield at the higher osmotic suctions. A specific mechanism for the pumping of solutes into the plant to create higher osmotic pressures of the cell sap would therefore seem to be highly improbable.

D.5.3. Discussion of results

The most striking features to emerge from this experiment were:

(a) the adverse effects of both sodium and potassium on yield (Fig. 20; Plate 11);

(b) the relatively low levels of sodium accumulated by mopane (Table 23);

(c) the favourable effects of increased levels of sodium and potassium on the relative content of magnesium (Table 21), and finally,

(d) the ability of intermediate levels of magnesium to partially reverse the detrimental effects of sodium and potassium on yield (Fig. 20).

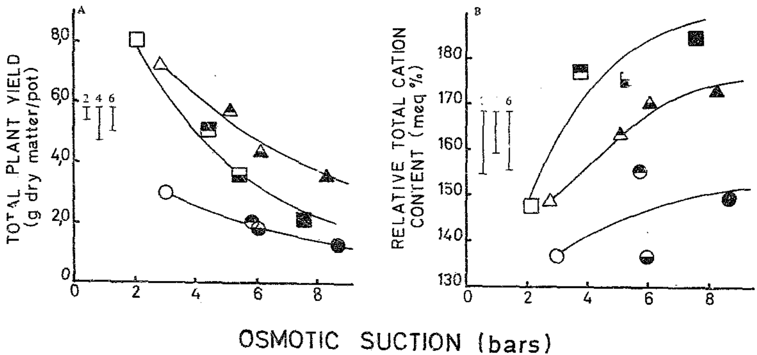


FIG. 24. The relation between total yield (A), relative total cation content (B) and osmotic suction for soils 2,4 and 6. Vertical bars indicate L.S.D. values (P < 0,05, means of 9)

Legend — Soil 2 – ○ ◓ ◒ ● } Nutrient levels
4 – △ ▲ ▲ ▲ } (Na_0K_0) (Na_0K_1) (Na_1K_0) (Na_1K_1)
6 – □ ▤ ▤ ■ } at 0.33 bars matric suction.

The detrimental effects of Na and K were primarily due to unfavourable osmotic suctions which developed in the soil solution. Osmotic suctions between ~ 3 and 8 bars resulted in a marked curvi-linear decrease in yield on all three soils (Fig. 24A). This response was strikingly similar to that obtained on soil 2 when increased levels of nitrogen at 0,33 bars moisture content caused osmotic suctions in the soil solution to exceed 3 bars (Fig. 18). The slight tendency towards levelling off of yield-decline at suctions exceeding 8 bars could be interpreted as further evidence for an osmotic adjustment mechanism in this species. It should be remembered that the osmotic suction values given in Figure 24, and in particular, those values representing maximum treatment levels of Na and K (K_1 Na_1), are more than likely an underestimation of the suctions which actually prevailed in the soil solution (See Section D.5.2.). Had the contribution of cations to osmotic suction been taken into consideration then the tendency towards levelling off of yield response would undoubtedly have been more pronounced (in that higher suctions would have been achieved). Measurements on the total relative cation content indicated that soil solutes were not specifically pumped into the plant to counter the detrimental effects of soil moisture stress (Fig. 24B). The possiblity of the osmotic adjustment process occurring through a change in metabolism to produce an accumulation of organic solutes is discussed at a later stage.

For a species which reportedly colonises soils of high exchangeable sodium content (Ellis, 1950) mopane accumulated surprisingly little of this cation. By way of contrast Bower and Wadleigh (1948) found that sodium-sensitive bean plants were able to accumulate up to 100 meq % Na when this cation was supplied at a rate of 15% of the C.E.C.. Rains and Epstein (1967a) (1967b) and Epstein *et al.* (1969) offer a convincing theory for the almost universal presence of K^+ over Na^+ ions in plant cells. Their work on excised barley roots led them to conclude that there were two distinct uptake mechanisms in plants. The first mechanism (Mechanism I) was operative at low external concentrations (0,002 - 0,2mM) and had a much higher affinity for K^+ than Na^+ ions. The second mechanism (Mechanism II) operated at higher concentrations (,2 - 50 mM) and possessed more or less equal affinity for both sodium and potassium. Since both mechanisms are thought to be functional at concentrations exceeding 2mM plants must invariably accumulate more potassium than sodium. Mechanisms I and II of alkali cation transport have become widely accepted today, the only proviso being that workers now think that absorption through mechanism II is essentially a passive process involving diffusion and Donnan phenomena (Hiatt and Leggett, 1974; Mengel, 1974).

The low levels of Na accumulated by mopane would seem to suggest that this cation is only absorbed passively, possibly through a system similar to that of mechanism II of alkali cation transport. In recent years, however, much attention has been given to evidence of an active sodium extrusion mechanism in higher plants (Pitman and Saddler, 1967; Pierce and Higinbotham, 1970; Mengel, 1974). The possiblity of such a mechanism accounting for the low Na status in mopane cannot be excluded, although no convincing evidence could be obtained from the data in this regard. Unfortunately factorial experiments do not lend themselves to conclusive predictions on the precise nature of uptake mechanisms operative in plants (cf. Hiatt and Leggett, 1974). Moreover, Elzam and Hodges (1967) warn of the hazards of applying results with one or more plants to all species. Furthermore, care should be taken in extrapolating the findings of excised root studies to whole plant behaviour (White, 1973).

Contrary to expectation, sodium and potassium treatment regularly increased the relative magnesium content of the plant tissue. Bower and Wadleigh (1948) for example, found that sodium treatment (15% of C.E.C.) was associated with a decline in yield and a concomitant decline in relative calcium, magnesium and potassium content. Potassium and sodium treatment is frequently associated with a decline in calcium and magnesium accumulation (Cooper and Carman, 1942; Wallace *et al.*, 1948; Lunt and Nelson, 1949; Martin *et al.*, 1953; Omar and El-Kobbia, 1966; Russell, 1973).

There did appear to be a certain degree of ionic antagonism involving Na and K on all three soils. For example, sodium inhibited potassium uptake and potassium inhibited calcium accumulation in plants grown on soil 2 (Tables 22 and 20). Also, the interactions obtained between potassium and sodium on yield (Fig. 21) and on calcium accumulation (Fig. 22) were suggestive of a limited degree of K–Na antagonism on soils 4 and 6. It is possible that these competitive interactions prevailed as a result of soil solution concentrations approaching the range at which Mechanism II of alkali cation transport is operative (see above). Alternatively, these interactions could be a manifestation of the concept of "cation equivalency" i.e. that there is a limit to the total internal concentration of cations which a plant can tolerate (cf. Russell, 1973; Hiatt and Leggett, 1974). In support of this suggestion it may be noted that the healthiest plants on all three soils seemed to be those associated with the lowest total cation concentration (compare Tables 19 and 24).

A third interpretation may be accorded to the interaction between K and Na on the dry weight yield of mopane (Fig. 21). It is possible that the greater osmotic suctions in the soil solution when K and Na were supplied together induced an increased capacity for osmotic adjustment of the cell sap. With such an adjustment yield was not depressed as much as might have been expected if the effects of K and Na were additive.

The yield response of mopane grown in pots reaffirmed the importance of magnesium to this species. On soil 2 which had low levels of exchangeable magnesium (Tables 3 and 5; cf. Bould, 1963; Russell, 1973) this cation caused a significant increase in yield under all factorial combinations of Mg, K and Na (Table 19, Fig. 20). On soils 4 and 6, however, magnesium only improved the yield of plants subjected to potassium and sodium treatment. On all three soils increased Mg levels were associated with significant increases in relative magnesium content and a concomitant decline in relative calcium, potassium and sodium content. With the possible exception of relative calcium content, this trend appeared to be a dilution effect brought about by the stimulatory effect of magnesium on growth. The significant ($P < 0,05 - P < 0,001$) decline in relative calcium content on all three soils was suggestive of a marked degree of competition between magnesium and calcium. On soil 6 in particular, the relative and total calcium content decreased significantly with magnesium treatment. This observation is consistent with excised root work on other species (cf. Hiatt and Leggett, 1974).

It is doubtful whether the observed yield responses to magnesium on soils 4 and 6 could be explained in terms of an improvement in cation balances within the soil-plant system. The application of magnesium to soil 4, for example, caused the Ca:Mg ratio to change from 6,33 (Mg_0) to a more favourable value of 1,85 at Mg_2 (see Section D.3.4(b)). This change, however, had an adverse effect on mopane grown in pots (Fig. 20). The fact that magnesium was only beneficial to plants grown under conditions of osmotic stress (i.e. plants receiving K and Na treatments), suggested that this cation played a role in the osmo-regulatory system of mopane. Magnesium is of universal importance in enzyme systems which catalyse group transfer (e.g. PO_4) and is of prime importance in organic acid production (Hewitt, 1963; Nason and McElroy, 1963). A magnesium catalysed production of organic solutes would benefit the plants by increasing cell sap concentration and thereby countering the detrimental effects of rising soil moisture stress.

Although the concentration of soil cations in the plant tissue increased markedly with rising osmotic stress (soils 4 and 6, Fig. 24B) these levels were nevertheless within the range expected for mesophytic species (cf. Bower and Wadleigh, 1948). A metabolic contribution towards increased cell sap concentration appeared therefore to be highly probable, since mopane was able to tolerate soil moisture stresses inimical to mesophytic plants. It is possible that unfavourable moisture stresses in the soil solution trigger off a Mg-catalysed production of organic solutes. This suggestion is in keeping with the view developed in the previous experiment where it was argued that the osmotic adjustment mechanism involved a shift in equilibrium between protein and non-protein nitrogen (Section D.4.3.).

The fact that the highest treatment levels of magnesium (Mg_2) were detrimental to growth may have been due to internal salt concentrations exceeding the cation equivalency optimum for this species.

In the light of the above results, it would seem that the role of magnesium in improving growth performance in the field (Fig. 12), lies mainly in its ability to partially reverse the detrimental effects of osmotic stresses imposed by soil moisture deficit. The relationship of performance value to various cation ratios in the soil (Fig. 14 and 16) cannot be reconciled in terms of impeded magnesium uptake or specific membrane effects as was previously suggested (Section D.3.4(b)). The ability of this species to adjust to osmotic stresses, together with its ability to maintain a low Na status, may account for its reported occurrence on sodium influenced soils (Ellis, 1950; Hudson, 1970). Clearly this species would enjoy a competitive advantage on such soils, which, apart from having sodium as a potentially detrimental ion, usually have poor structure and unfavourable moisture characteristics. Further research involving, for example a study of Michaelis-Menton type absorption kinetics (cf. Fried and Broeshart, 1967) and organic solute equilibria under conditions of osmotic stress must obviously be forthcoming before the above views can be verified.

E. CONCLUDING DISCUSSION

The main conclusions of this study have been summarised from preceding discussions and are itemized below. Future and perhaps more intensive investigations along the mopane belt of southern Africa may well modify existing concepts, and it is hoped that this preliminary study will stimulate renewed interest in one of the most ecologically important taxa south of the equator.

(a) Mopane is generally confined to areas of low to moderate rainfall (200–800mm p.a.) and is intolerant of severe frosts. The northern and southern boundaries of this species appear to be determined by the 1000mm mean annual rainfall isohyet and the 5°C July mean daily minimum isotherm, respectively (Section D.1.2). Its intolerance of low winter temperatures in particular, may well account for disjunction in its distribution noted along the 18° line of latitude (Fig. 7).

(b) The distribution range of mopane extends over a wide variety of geological formations and soil types (Section D.1.3; Fig. 10). It is nevertheless conspicuously absent from areas with an overburden of deep Kalahari sand. Observations made on a regional basis also suggest that mopane is intolerant of deep sandy soils (Boughey, 1963; van der Schijff, 1969; van Wyk,. 1972a; Walker, pers. com.). It is possible therefore, that the discontinuity in the distribution of mopane along the 18°S line of latitude coincides with sandy soils too deep for its effective colonisation and establishment. According to Mountain (1968) the Kalahari sands east of Etosha (S.W. Africa) often exceed 240m in thickness.

(c) Observations made at eight different sample sites in southern Africa suggest that mopane is essentially a shallow rooted species, growing predominantly on shallow to moderately shallow, lime-accumulating sands over loamy sands or sandy loams over sandy clay loams (Section D.2.4; Appendix 3). This conclusion is in accordance with the views of Miller (1938), Trapnell *et al.* (1948), Wild (1953)(1955), Thompson (1960)(1965) and Thompson *et al.* (1960). The shallow rooting habit of mopane may be one of the criteria responsible for its intolerance of deep sandy soils. Apart from affording very little mechanical stability, these soils also exhibit poor moisture retention properties at or near the surface.

(d) Measurements made on the growth of mopane in the field (as assessed by performance value) and in pots under controlled environment conditions suggest that this species is capable of growth at matric suctions exceeding 15,2 bars (cf. sections D.3.4. and D.4.3.). Indeed mopane seedlings grown in pots were capable of withstanding total soil moisture stresses up to at least 32 bars without showing visible signs of temporary wilting. This observation supports the view of Slatyer (1957a; 1957b) that the P.W.P. (as given by the soil water content at 15,2 bars matric suction) is not a soil constant defining the lower limit of water availability for all plants.

(e) Although the dry weight yield of mopane declined appreciably with rising osmotic suctions within the range ~ 3 to 8 bars, it nevertheless maintained a constant growth rate at suctions exceeding 8 bars (up to 15 bars at least) (Fig. 18). This, together with the fact that stressed plants maintained a constant coefficient of water utilization (Table 16), indicated a capacity for internal osmotic adjustment. The significantly higher relative nitrogen content of stressed plants (Fig. 19) suggested that this mechanism may involve an increase in osmotically active nitrogenous compounds within the cell sap. An inevitable consequence of such an adjustment would be a reduction in growth because of a shift in equilibrium between protein and non-protein nitrogen. Nevertheless this shift in metabolism could have strong survival and competitive advantages. Clearly one would not expect mopane to colonise saline or salt accumulating soils (cf. Hudson, 1970) unless it had an effective mechanism for ensuring a sustained water supply, particularly in times of drought when soil osmotic suctions might be expected to increase sharply (Russell, 1973 p.751).

(f) Growth performance in the field was appreciably reduced in soils with low levels of nitrogen and phosphorus (Fig. 11) and in soils of low C.E.C. and T.E.C. content (e.g. Soils 1 and 2; cf. Tables 5 and 11). In particular, mopane showed a striking dependence on exchangeable magnesium content and on the ratio of this cation to other soil nutrients, notably calcium and sodium (Fig. 12, 14 and 16). Exchangeable sodium and optimum levels of exchangeable calcium, on the other hand, appeared to be detrimental to growth (Fig. 13 and 15). The importance of magnesium was demonstrated further under controlled environment conditions. Intermediate levels of this cation partially reversed the detrimental effects of osmotic stress induced by sodium and potassium supplied at 15% of the C.E.C. (Fig. 20 + 24; Section D.5.3.). The response of performance value to increased magnesium ratios in the field appeared therefore, to be the result of a Mg-induced improvement in water uptake rather than an improvement in the status of this cation relative to other cations in the plant tissue. Magnesium may well play a role in the osmotic adjustment mechanism of mopane, by catalysing the formation of organic nitrogenous compounds and thereby increasing the osmotic pressure of the cell sap (cf. Section D.4.3. and D.5.3.). In this context it is tempting to suggest that the intolerance of mopane to deep sandy soils stems amongst other things from an inadequate supply of magnesium (cf. Blair Rains and McKay, 1968) and a consequent inability to adjust to drought conditions.

(g) Mopane seedlings grown in pots maintained a low sodium status inspite of this cation being supplied at a rate of 15% of the C.E.C. (Table 23). This observation, together with that of the plant's ability to withstand severe soil moisture stresses may well account for its reported occurrence on soils with a high sodium content (Ellis, 1950; Staples and Murray, 1951; Hudson, 1970). Implicit in this statement is the viewpoint expressed in Section D.2.4., that mopane is not a prima facie cause of soil infertility as is popularly believed. Rather its occurrence on such soils reflects its wide ecological amplitude and adaptability to adverse soil conditions. Many of the conflicting opinions held on this species could be reconciled if viewed in the light of the above conclusion (Section B.3.).

Finally, mention should be made of the possible role of this species in the maintenance of ecosystems in the dry tropics of southern Africa. Current thinking, suggests that ecosystem integrity in such areas depends largely on the presence of certain plant species which possess a high level of tolerance of a wide spectrum of environmental stresses (Walker, pers. com.). Although the removal of these species may result in a flush of increased productivity by less resistant plant groups, the long term outcome is inevitably one of regression towards barren and eroded land. The factors responsible for this decline in ecosystem vigour are as yet not fully understood. Mopane may well fit into the "key species" category outlined above. Apart from being resistant to a wide range of unfavourable soil conditions, it possesses a remarkable ability for recovery from fire, light frost and overbrowsing (Section B.2. and B.4.). Its recovery invariably takes the form of an extremely competitive coppicing shrub which effectively excludes the colonisation of less competitive plant species. The latter illustration should not be interpreted as underscoring its role in the ecosystem since coppice mopane is an inevitable consequence of mismanagement (e.g. indiscriminate burning and overgrazing). The resistance of mopane to a wide spectrum of environmental stresses together with its importance as a source of browse for wild animals, suggests that this species plays an indispensible role in the functioning of ecosystems in the dry tropics.

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APPENDICES

APPENDIX 1 Mean maximum temperatures (°C) for three stations along the Zambezi Valley. Northern Rhodesia (Climatological Summaries, 1963).

Month	Binga 17,38°S, 27,20°E Alt. = 617m	Chirundu 16,00°S, 28,54°E Alt. = 395m	Kariba Gorge 16,31°S, 28,46°E Alt. = 604m
July	26,8	28,4	28,4
August	29,7	31,4	31,1
September	33,4	34,6	34,2
October	36,2	37,5	36,8
November	33,5	35,6	35,5
December	32,6	32,5	32,4
January	31,1	31,6	31,8
February	30,3	31,2	31,0
March	31,8	32,0	32,4
April	32,2	32,3	32,7
May	30,6	30,9	30,7
June	27,4	28,2	28,3
Year	31,3	32,2	32,1

APPENDIX 2 Standard nutrient solution used in controlled environment studies

Application per pot	Stock solutions (M) or (g)/litre	Dilution procedure
2,8mM. $CaCl_2.H_2O$	0,4M	350ml aliquots of
2,8mM. $MgSO_4.7H_2O$	0,4M	each stock solution
1,4mM. K_2SO_4	0,2M	were combined in a
20mg. Fe-E.D.T.A.	4,0g	5L volumetric flask
70mg. $MnCl_2.4H_2O$	10,0g	and made to volume.
7mg. $ZnSO_4.7H_2O$	1,0g	100mls of bulk
3,5mg. $CuSO_4.5H_2O$	0,5g	solution yielded
3,5mg. H_3B0_3	0,5g	the required
1,4mg. $Na_2\ MoO_4.2H_2O$	0,2g	nutrient levels
		per pot.

APPENDIX 3. Profile descriptions for soil pits dug at each sample site (cf. Clark and Beckett,1971).

Profile 1 Sample site 1. Pit 46cm deep at base of mopane tree (8m).

0–15 cm Horizon 1. Light grey sand, self-coloured, structureless and loose. *Several very large woody lateral roots, no tap root. Merges into horizon 2.*

15–46cm Horizon 2. Light brown loamy sand, self-coloured and loose. Very weakly developed structure – small crumbs with soft consistency when dry. Several very large woody lateral roots with numerous fibrous secondary roots. *Occasional boulders, becoming increasingly stony with depth.*

46cm Horizon 3. Slightly darker, very stony, decomposing rock – (sandstone)

Profile 2 Sample site 1. Pit 46cm deep, at foot of scrub mopane (lm)

0–15cm Horizon 1. Light grey sand, self-coloured, structureless and loose. One large tap root, with many fibrous secondary roots developing at 12cm; merges into horizon 2.

15–46cm Horizon 2. Light reddish brown loamy sand, self-coloured, loose. Very weakly developed structure – small and medium crumbs; with soft consistency when dry. Few reddish concretions and numerous small rounded stones which increase in size and number down the profile. Large tap root, no secondary roots.

46 cm Darker, decomposing horizon 3. Predominantly large stones and rock. *Large tap root penetrates into decomposing parent material* (Sandstone).

Analytical data for profiles 1 and 2

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq.%)	Exchangeable cations(meq %) Ca	Mg	K	Na	Saturation (%)
1	0–15	6,75	1,68	6,75	8,25	2,20	2,80	0,96	0,79	81,8
	15–46	8,18	1,90	8,18	8,16	3,90	2,80	0,58	0,47	95,0
2	0–15	5,86	1,62	5,86	6,28	2,48	1,10	0,29	0,45	68,8
	15–46	7,95	1,92	7,95	8,38	3,90	1,60	0,48	0,62	78,8

APPENDIX 3 (continued)

Profile 3 *Sample site 2.* Pit 61cm deep, at foot of scrub mopane (1m).

0–10cm Horizon 1. Light grey sand, self-coloured, structureless and loose.

10–20cm Horizon 2. Light brown sand, self-coloured, structureless and loose. Large tap root with large, strong, woody secondary roots at 20cm.

20–61cm Horizon 3. Clearly defined. Reddish brown sandy loam, self-coloured and friable. Weakly developed structure – large crumbs with soft consistency when dry. Large, free growing, woody tap root with fine *fibrous secondary roots.*

61cm Horizon 4. Very stony with occasional boulders. Stones coated with red and black dust, probably iron and manganese staining. Difficult to penetrate with pick. Tap root penetrates into decomposing sandstone.

Profile 4. Sample site 2. Pit 53cm deep, at base of tall scrub mopane (3m).

0–10cm Horizon 1. Light brown sand, self-coloured, structureless and loose Single, large, free growing, woody and strong tap root.

10–22cm Horizon 2. Clearly defined. Reddish brown sandy loam, self-coloured and friable. Weakly developed structure – large crumbs and occasion*al small nuts* with soft consistency when dry. Large free growing woody tap root with well developed secondary roots at 15–53cm depth.

53cm Darker decomposing horizon 3. Very stony and gravelly. Tap root twisted and distorted.

Analytical data for profiles 3 and 4.

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq %)	Exchangeable cations (meq %) Ca	Mg	K	Na	Saturation (%)
3	0–15	5,69	1,76	5,69	3,50	2,60	0,24	0,18	0,04	87,4
	15–60	5,41	1,83	5,41	4,04	2,38	0,34	0,26	0,04	74,8
4	0–10	6,53	1,72	6,53	5,84	2,53	0,74	0,32	0,04	62,2
	10–50	7,50	1,80	7,50	6,05	3,40	0,91	0,93	0,06	87,8

APPENDIX 3 (continued)

Profile 3 Sample site 2. Pit 61cm deep, at foot of scrub mopane (1m).

0–10cm Horizon 1. Light grey sand, self-coloured, structureless and loose.

10–20cm Horizon 2. Light brown sand, self-coloured, structureless and loose. Large tap root with large, strong, woody secondary roots at 20cm.

20–61cm Horizon 3. Clearly defined. Reddish brown sandy loam, self-coloured and friable. Weakly developed structure – large crumbs with soft consistency when dry. Large, free growing, woody tap root with fine *fibrous secondary roots.*

61cm Horizon 4. Very stony with occasional boulders. Stones coated with red and black dust, probably iron and manganese staining. Difficult to penetrate *with pick. Tap root penetrates into decomposing sandstone.*

Profile 4. Sample site 2. Pit 53cm deep, at base of tall scrub mopane (3m).

0–10cm Horizon 1. Light brown sand, self-coloured, structureless and loose Single, large, free growing, woody and strong tap root.

10–22cm Horizon 2. Clearly defined. Reddish brown sandy loam, self-coloured and friable. Weakly developed structure – large crumbs and occasional small nuts with soft consistency when dry. Large free growing woody tap root with well developed secondary roots at 15–53cm depth.

53cm Darker decomposing horizon 3. Very stony and gravelly. Tap root twisted and distorted.

Analytical data for profiles 3 and 4.

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm³)	pH	C.E.C. (meq %)	Exchangeable cations (meq %) Ca	Mg	K	Na	Saturation (%)
3	0–15	5,69	1,76	5,69	3,50	2,60	0,24	0,18	0,04	87,4
	15–60	5,41	1,83	5,41	4,04	2,38	0,34	0,26	0,04	74,8
4	0–10	6,53	1,72	6,53	5,84	2,53	0,74	0,32	0,04	62,2
	10–50	7,50	1,80	7,50	6,05	3,40	0,91	0,93	0,06	87,8

APPENDIX 3 (continued)

Profile 5 Sample site 3. Pit 100cm deep, at foot of scrub mopane (3m).

0–2cm Horizon 1. Light grey sand, self-coloured, structureless and loose.

2–12 cm Horizon 2. Greyish sandy loam, self-coloured and friable. Moderately developed structure – medium nutty with slightly hard consistency when dry. *Large tap root, woody, free growing, with large well developed secondary roots starting at 12 cm.* Merges with horizon 3.

12–100cm Horizon 3. Greyish brown sandy clay loam, speckled with numerous white flecks, and fairly compact. Moderately developed with small rounded and angular clods, hard consistency when dry. Horizon scored by numerous, thin vertical cracks. White concretions ($CaCO_3$) become evident at 80cm. *Large tap root, woody, free growing and strong; secondary* roots becoming more fibrous with depth. Tap root ends abruptly at 80cm.

100cm White impenetrable crust, probably calcrete.

Profile 6. Sample site 3. Pit 40cm deep, base of large mopane tree (10m).

0–2cm (Same as profile 5).

2–10cm *(Same as profile 5).* Numerous very large lateral roots, woody, free growing and strong; no tap root; trunk hollow.

12–40cm (Same as profile 5). Large lateral roots traverse profile pit, making further digging difficult.

Analytical data for profiles 5 and 6.

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq %)	Exchangeable cations (meq %) Ca	Mg	K	Na	Saturation (%)
5	0–10	4,40	1,68	5,0	16,90	6,87	3,56	0,50	0,21	65,9
	40–60	*9,90*	*1,99*	*6,2*	28,75	10,78	8,72	0,67	2,38	78,4
6	0–10	2,41	1,61	5,9	16,00	6,39	2,63	0,97	0,38	64,8
	30–40	8,60	1,93	7,1	23,25	11,78	9,41	0,82	0,38	96,3

APPENDIX 3 (continued)

Profile 7 Sample site 4. Pit 46cm deep, at foot of scrub mopane (3,5m).

0–5cm Horizon 1. Light grey sand, self-coloured, structureless and loose. Merging into horizon 2.

5–46cm Horizon 2. Greyish brown silty clay loam. Weakly developed and friable with large crumbs, soft to slightly hard consistency when dry. Many hard and rounded white concretions ($CaCO_3$) increasing in number and size down the profile. Numerous large, woody lateral roots and a dense network of fine fibrous roots; no tap root.

46cm Impenetrable calcareous crust. One or two fibrous roots entering calcrete.

Profile 8 Sample site 4. Pit 60cm deep, at foot of coppicing scrub mopane (1m).

0–10cm Horizon 1. Greyish sand, self-coloured, structureless and loose. Merging into horizon 2.

10–50cm Horizon 2. Greyish brown silty clay loam, self-coloured and friable. Weakly developed structure – large crumbs with soft consistency when dry. Numerous white concretions. Soil becomes slightly more compact with depth.

50–60cm Horizon 3. Little soil surrounding numerous large rounded white concretions. Many medium, strong fibrous roots.

60cm Solid calcrete with few large woody lateral roots.

Analytical data for profiles 7 and 8

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq %)	Exchangeable cations (meq %) Ca	Mg	K	Na	Saturation (%)
7	20–30	5,32	1,52	7,3	17,50	11,78	1,18	1,23	0,17	82,1
	45	5,26	1,62	7,4	18,38	12,78	1,32	1,41	0,30	[illegible]
8	10–20	3,15	1,54	7,2	19,38	12,18	1,15	1,69	0,17	78,4
	40–50	4,64	1,54	7,3	20,25	13,57	1,12	1,28	0,17	79,7

APPENDIX 3 (continued)

Profile 9 Sample site 5. Pit 100 cm deep, at base of scrub mopane .(0,25 m).

0–8cm Horizon 1. Greyish sand,self coloured, structureless and loose.

8–70cm Horizon 2. Sharply defined. Darkish brown sandy clay loam, self-coloured and compact. Moderately developed structure – large nutty peds with a hard consistency when dry. Large woody and strong tap root with fibrous secondary roots coming off at intervals. Merges into horizon 3.

80–100cm Horizon 3. Similar to horizon 2, except for presence of numerous white speckles. Tap root becomes twisted and distorted and terminates at 90cm. Holes in this horizon, probably caused by termite activity.

100cm Impenetrable calcrete.

Profile 10. Sample site 6. Pit 59cm deep, at base of coppice mopane .(1,5m)..

0–5cm Horizon 1. Light brown loamy sand,self-coloured, structureless and loose. Merging into horizon 2.

5–50cm Horizon 2. Dark brown sandy clay loam, self-coloured and very compact. Moderately developed with small rounded and angular clods. Few medium and large clods with a hard consistency when dry. Coppicing stems have a common woody and strong tap root stock which terminates at 50cm. Numerous fibrous secondary roots.

Analytical data for profiles 9 and 10.

Profile	Depth	Moisture	Bulk density	pH	C.E.C.	Exchangeable cations (meq %)				Saturation
	(cm)	(%)	(g/cm³)		(meq %)	Ca	Mg	K	Na	(%)
9	0–8	3,36	1,71	6,1	23,00	13,57	4,93	1,54	0,13	87,7
	40–50	5,59	1,86	7,2	22,15	14,07	5,58	1,13	0,66	96,8
	80–90	8,54	1,86	7,6	28,00	18,47	6,25	1,78	1,39	99,6
10	0–5	7,28	1,61	6,4	26,88	12,38	5,53	1,82	0,21	74,2
	40- 50	12,78	1,62	7,3	29,40	17,37	7,73	1,48	0,38	91,7

APPENDIX 3 (continued)

Profile 11 Sample site 7. Pit 110cm deep, at base of mopane tree (8m).

0–10cm *Horizon 1. Light brown sandy loam, self-coloured and friable.* Medium crumbs with soft consistency when dry. Merges into horizon 2.

10–110cm Horizon 2. Light reddish brown sandy clay loam, speckled with numerous white flecks. Compact, becoming very compact at 80cm. Moderately developed structure – rounded and angular medium clods and few large clods with hard to very hard consistency when dry. Large, woody, strong tap root traverses this horizon, becoming twisted and distorted at 110cms. Root diverted to grow laterally at this depth. Many fibrous secondary roots at 10–20cm depth. Few large strong secondary roots develop from tap root at various depths along profile.

110cm Very hard and compact, profile not dug to parent material.

Profile 12 Sample site 7. Pit 100cm deep, at base of mopane tree (6m).
Similar characteristics to profile 11. Similar rooting habit. Numerous fibrous secondary roots developed from tap root between 10–20cm. Thick strong secondary roots developed further down. Tap root bends horizontally at 100cm and stops abruptly.

Analytical data for profiles 11 and 12.

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq %)	Exchangeable cations (meq %)				Saturation (%)
						Ca	Mg	K	Na	
11	0–10	2,56	1,65	5,9	11,13	4,29	1,38	0,97	0,61	65,1
	60–70	6,28	1,85	6,2	12,00	6,19	2,04	1,32	0,17	81,0
	100–110	4,16	1,97	7,2	15,00	9,38	1,81	1,20	0,30	84,6
12	0–10	4,33	1,64	6,4	11,50	5,69	1,45	1,13	0,09	72,7
	50–60	5,98	1,97	6,8	13,00	7,39	1,81	1,46	0,09	82,7
	90–100	5,05	–	7,3	15,50	9,98	1,65	1,32	0,21	84,9

APPENDIX 3 (continued)

Profile 13 Sample site 8. Pit 70cm deep, at base of mopane tree (8m).

0–5cm Horizon 1. Greyish sandy loam, self-coloured and friable merging into horizon 2.

5–50cm Horizon 2. Sandy clay loam, speckled with numerous white concretions and fairly compact. Moderately developed structure – medium nutty peds with slightly hard consistency when dry. Large porous crumbs with soft consistency also present. No tap root, and stem trunk hollow. Very large, woody and strong lateral roots spread out horizontally, immediately below the surface of the soil. Large strong secondary roots arise from the lateral roots.

50–70cm. Horizon 3. Decomposing parent material (sandstone). Predominantly large stones and occasional boulders. Large white calcareous concretions also present.

Analytical data for profile 13

Profile	Depth (cm)	Moisture (%)	Bulk density (g/cm^3)	pH	C.E.C. (meq %)	Exchangeable cations (meq %) Ca	Mg	K	Na	Saturation (%)
13	0- 10	7,29	1,66	7,3	26,00	18,86	1,48	1,87	0,21	86,20
	20–30	7,85	1.66	7,4	26,20	18,86	0,79	1,05	0,21	79,80
	60–70	8,61	–	7,3	28,00	19,00	0,80	1,10	0,21	75,40

APPENDIX 4 The replicate mean density (no. of individuals/100 sq.m) of mopane for *each height class*

		Ht. Class					
Site 1	Rep.	1	2	3	4	5	6
	I	0,50	–	–	0,20	0,30	–
	II	6,20	0,50	0,50	0,70	0,30	–
	III	9,50	1,00	–	0,30	0,30	–
	IV	4,50	1,80	0,50	0,30	–	–
	Mean	5,18	0,83	0,25	0,38	0,23	–

		Ht. Class					
Site 2	Rep.	1	2	3	4	5	6
	I	0,17	–	–	–	–	–
	II	–	–	–	–	0,33	–
	III	0,33	0,17	0,33	0,17	0,33	0,17
	IV	0,33	0,50	–	–	–	–
	Mean	0,21	0,17	0,08	0,04	0,17	0,04

		Ht. Class					
Site 3	Rep.	1	2	3	4	5	6
	I	23,00	8,60	–	–	–	–
	II	21,00	13,80	0,60	–	–	–
	III	29,60	13,20	–	0,20	0,20	–
	IV	10,60	9,00	0,40	0,60	–	–
	Mean	21,05	11,15	0,25	0,20	0,05	–

		Ht. Class					
Site 4	Rep.	1	2	3	4	5	6
	I	23,00	1,67	–	–	–	–
	II	19,00	0,33	–	–	–	–
	III	23,70	0,67	–	–	–	–
	IV	14,70	4,33	–	–	–	–
	Mean	20,10	1,75	–	–	–	–

APPENDIX 4 (continued)

Site 5

Rep.	Ht. Class 1	2	3	4	5	6
I	4,00	5,00	4,70	–	–	–
II	5,30	4,30	4,00	1,00	–	–
III	4,00	4,00	5,30	0,30	–	–
IV	4,30	2,30	6,00	–	–	–
Mean	4,40	3,83	5,00	0,33	–	–

Site 6

Rep.	Ht. Class 1	2	3	4	5	6
I	58,00	3,70	–	–	–	–
II	33,30	3,50	–	–	–	–
III	46,80	4,00	–	–	–	–
IV	28,00	9,00	–	–	–	–
Mean	40,40	5,10	–	–	–	–

Site 7

Rep.	Ht. Class 1	2	3	4	5	6
I	–	1,00	–	1,25	3,00	0,25
II	3,00	0,50	0,25	–	1,25	1,50
III	2,00	0,50	–	0,50	1,75	0,75
IV	3,00	2,33	0,33	1,33	0,33	–
Mean	1,93	1,00	0,13	0,73	1,70	0,67

Site 8

Rep.	Ht. Class 1	2	3	4	5	6
I	2,67	2,30	–	1,70	1,30	–
II	5,00	–	1,30	0,70	1,30	0,30
III	5,25	0,50	0,25	1,00	2,00	0,30
IV	4,25	0,50	–	2,00	1,00	–
Mean	4,40	0,80	0,40	1,40	1,40	0,10

APPENDIX 5 Stepwise multiple regression of performance value on the chemical and physical properties of soils from each sample site

Step	Soil Factors	Depth (cm)	R-value	% variation accounted for	F-value
1	P.	0–10	0,586	23,3	3,138
2	P; N.	"	0,856	67,9	8,438*
3	P; N; PBC.	"	0,840	63,2	5,011
1	N.	20–30	0,690	39,0	5,466
2	N; PBC.	"	0,668	33,5	2,761
3	N; PBC; P.	"	0,620	23,0	1,698
1	P.	0–10	0,586	23,3	3,138
2	P; N.	"	0,856	67,9	8,434*
3	P; N; K.	"	0,928	82,5	12,026*
4	P; N; K; Ca.	"	0,923	80,2	8,099
1	N.	20–30	0,690	39,0	5,466
2	N; P.	"	0,664	32,9	2,716
3	N; P; Ca.	"	0,587	18,1	1,515
4	N; P; Ca; K.	"	0,426	9,2	0,854
1	FC.	20–30	0,715	42,9	6,269*
2	FC; N.	"	0,719	42,0	3,533
3	FC; N; Av.H_2O.	"	0,714	38,6	2,469
4	FC; N; Av.H_2O; P.	"	0,628	19,3	1,415

Significance rating – * ($P < 0,05$)
** ($P < 0,01$)

APPENDIX 5 (continued)

Step	Soil Factors	Depth (cm)	R-value	% variation accounted for	F-value
1	PWP.	20–30	0,745	48,2	7,501*
2	PWP; Bulk den.	"	0,754	48,2	4,266
3	PWP; Bulk den.; FC.	"	0,696	35,6	2,291
4	PWP; Bd· FC; Av.H_2O.	"	–	–	–
1	Mg.	0–10	0,781	54,5	9,392*
2	Mg; Na.	"	0,836	63,7	7,167*
3	Mg; Na; Ca.	"	0,805	56,2	3,976
4	Mg; Na; Ca; K.	"	0,820	56,4	3,251
1	Mg.	20–30	0,853	68,1	15,971**
2	Mg; Na .	"	0,858	68,4	8,560*
3	Mg; Na; Ca.	"	0,830	61,2	4,671
4	Mg; Na; Ca; K.	"	0,795	51,0	2,822
1	Mg/Na.	0–10	0,835	62,5	12,696*
2	$\frac{Mg}{Na}$; $\frac{Mg}{K}$.	"	0,865	69,8	9,087*
3	$\frac{Mg}{Na}$; $\frac{Mg}{K}$; $\frac{Mg}{Ca}$.	"	0,855	66,4	5,593
4	$\frac{Mg}{Na}$; $\frac{Mg}{K}$; $\frac{Mg}{Ca}$; $\frac{Mg}{TEC}$.	"	0,823	57,1	3,316
1	Mg/Na.	20–30	0,762	51,0	8,302*
2	$\frac{Mg}{Na}$; $\frac{Mg}{K}$.	"	0,879	72,6	10,287*
3	$\frac{Mg}{Na}$; $\frac{Mg}{K}$; $\frac{Mg}{Ca}$.	"	0,902	76,6	8,653*
4	$\frac{Mg}{Na}$; $\frac{Mg}{K}$; $\frac{Mg}{Ca}$; $\frac{Mg}{TEC}$.	"	0,879	69,7	5,015

Significance rating * ($P < 0,05$)
** ($P < 0,01$)

APPENDIX 6 Mean dry weight yield (gms) of mopane under factorial combinations of nitrogen (N_0–N_2), phosphorus (P_0–P_1) and rising soil moisture stress (M_0–M_2)

The numerical values attached to each treatment level are as follows

N_0– 0Kg/ha	P_0– 0 Kg/ha	M_0–100↔90
N_1– 56 "	P_1–56 "	M_1–100↔40
N_2–168 "		M_2–100↔ 0

Soil 2

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Shoots	P_0	3,20	2,23	1,44	2,02	2,05	1,57	1,27	1,[illegible]	1,00
	P_1	2,87	1,89	1,71	2,53	1,86	1,56	1,72	[illegible]	1,74
Roots	P_0	0,43	0,46	0,26	0,42	0,36	0,40	0,23	0,29	0,22
	P_1	0,52	0,38	0,44	0,40	0,30	0,33	0,30	0,41	0,29
Whole plants	P_0	3,63	2,69	1,69	2,44	2,41	1,96	1,50	1,74	1,21
	P_1	3,39	2,27	2,15	2,93	2,16	1,88	2,01	2,19	2,02

APPENDIX 6 (continued)

Soil 4

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Shoots	P_0	2,95	3,67	2,99	4,11	3,66	3,11	3,27	3,41	4,17
	P_1	2,99	3,34	3,70	3,16	3,30	4,09	3,54	3,26	4,30
Roots	P_0	0,70	0,92	0,63	0,77	0,73	0,54	0,58	0,86	0,80
	P_1	0,66	0,67	0,81	0,57	0,74	0,84	0,71	0,69	0,82
Whole	P_0	3,64	4,59	3,62	4,87	4,38	3,65	3,93	4,27	4,96
plants	P_1	3 65	4,01	4,51	3,73	4,04	4,95	4,24	3,95	5,12

Soil 6

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Shoots	P_0	3,67	4,09	3,72	4,27	4,18	4,05	4,22	4,00	4,66
	P_1	3,65	3,78	3,91	5,08	4,58	4,55	4,74	4,48	4,86
Roots	P_0	1,02	1,35	1,09	0,77	1,04	0,85	0,79	0,85	0,85
	P_1	1,11	1,08	1,23	1,17	0,90	0,92	0,83	0,73	1,00
Whole	P_0	4,69	5,26	4,81	5,03	5,22	4,90	5,00	4,85	5,50
plants	P_1	4,76	4,85	5,14	6,25	5,48	5,47	5,56	5,21	5,83

APPENDIX 7 Mean evapotranspiration rates (g H_2O/day) of mopane under factorial combinations of nitrogen (N_0–N_2), phosphorus (P_0–P_1) and rising soil moisture stress (M_0–M_2)

Numerical values attached to each treatment level are given in Appendix 6.

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Soil 2	P_0	23,53	21,47	15,75	17,01	18,10	18,11	14,64	13,26	12,32
	P_1	30,79	19,13	17,79	24,11	18,79	13,76	16,30	12,63	9,45
Soil 4	P_0	33,95	47,49	36,01	43,53	44,52	38,19	37,87	38,51	49,48
	P_1	34,56	42,02	43,50	36,39	43,08	47,59	41,85	39,10	45,58
Soil 6	P_0	41,00	48,51	47,51	44,36	45,48	45,49	42,10	42,29	50,95
	P_1	40,00	45,52	47,45	47,80	49,28	52,25	45,81	46,48	38,84

APPENDIX 8 Mean coefficients of water utilization (g H_2O/g dry wt./day) of mopane under factorial combinations of nitrogen (N_0–N_2), phosphorus (P_0–P_1) and rising soil moisture stress (M_0–M_2)

Numerical values attached to each treatment level are given in Appendix 6.

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Soil 2	P_0	11,02	10,77	11,03	11,37	12,86	9,33	9,67	13,67	12,57
	P_1	9,06	10,37	10,66	9,56	8,81	12,70	9,73	7,46	6,67
Soil 4	P_0	9,63	10,81	10,20	9,21	10,44	10,46	10,31	9,13	10,03
	P_1	9,66	10,88	9,86	10,61	10,71	10,03	10,55	10,23	9,09
Soil 6	P_0	8,89	8,97	9,90	8,84	8,72	9,38	8,67	8,97	9,43
	P_1	8,49	9,38	9,38	7,69	8,97	9,54	8,30	8,91	9,00

APPENDIX 9 Mean relative nitrogen content (%) of mopane shoots under factorial combinations of nitrogen (N_0–N_2), phosphorus (P_0–P_1) and rising soil moisture stress (M_0–M_2)

Numerical values attached to each treatment level are given in Appendix 6

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Soil 2	P_0	1,30	1,40	1,54	1,45	1,50	1,69	2,56	2,11	2,29
	P_1	1,45	1,53	1,66	1,50	1,65	1,88	1,82	2,11	2,19
Soil 4	P_0	0,88	0,83	0,88	0,94	1,05	1,07	1,10	1,11	1,16
	P_1	0,92	0,81	0,88	1,05	1,23	1,14	1,21	1,30	1,35
Soil 6	P_0	0,97	0,85	0,85	1,37	1,33	1,33	1,40	1,41	1,37
	P_1	0,87	0,85	0,88	1,30	1,30	1,25	1,47	1,48	1,45

APPENDIX 10 Mean re[illegible]e phosphorus content (%) of mopane shoots under factorial combina[illegible]s of nitrogen (N_0–N_2), phosphorus (P_0–P_1) and rising soil mois[illegible]e stress (M_0–M_2)

Numerical values attached to each treatment level are given in Appendix 6.

		N_0			N_1			N_2		
		M_0	M_1	M_2	M_0	M_1	M_2	M_0	M_1	M_2
Soil 2	P_0	0,20	0,19	0,19	0,16	0,17	0,20	0,29	0,18	0,24
	P_1	0,25	0,28	0,32	0,21	0,30	0,30	0,28	0,35	0,18
Soil 4	P_0	0,13	0,11	0,16	0,11	0,12	0,13	0,12	0,12	0,12
	P_1	0,17	0,15	0,17	0,16	0,17	0,16	0,20	0,19	0,17
Soil 6	P_0	0,18	0,16	0,18	0,23	0,22	0,22	0,26	0,24	0,24
	P_1	0,23	0,23	0,21	0,27	0,24	0,22	0,28	0,24	0,25

APPENDIX 11 Mean dry weight yield (gms) of mopane under factorial combinations of magnesium (Mg_0–Mg_2), potassium (K_0–K_1) and sodium (Na_0–Na_1). The numerical values (meq %) attached to each treatment level were summarised from Table 4 and are given for soils 2, 4 and 6 individually.

Soil 2

Mg_0–0 meq % K_0–0 meq % Na_0–0 meq %
Mg_1–0,56 " K_1–0,72 ". Na_1–0,75 "
Mg_2–1,00 "

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Shoots	Na_0	2,20	1,26	2,35	1,29	3,02	1,96
	Na_1	1,03	0,74	1,50	1,06	1,83	1,27
Roots	Na_0	0,51	0,34	0,54	0,39	0,65	0,43
	Na_1	0,34	0,26	0,34	0,33	0,48	0,32
Whole plants	Na_0	2,70	1,60	2,89	1,67	3,67	2,39
	Na_1	1,37	1,00	1,84	1,39	2,30	1,59

APPENDIX 11 (continued)

Soil 4

Mg_0–0 meq % | K_0–0 meq % | Na_0–0 meq %
Mg_1–2,67 " | K_1–2,15 " | Na_1–2,92 "
Mg_2–4,78 "

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Shoots	Na_0	5,91	4,30	6,22	5,15	5,07	4,51
	Na_1	2,48	2,12	4,27	2,55	3,68	3,21
Roots	Na_0	1,57	0,89	1,38	1,12	1,64	1,02
	Na_1	0,60	0,41	0,94	0,71	0,85	0,73
Whole plants	Na_0	7,48	5,19	7,60	6,27	6,71	5,52
	Na_1	3,08	2,52	5,20	3,93	4,53	3,94

Soil 6.

Mg_0–0 meq % | K_0–0 meq % | Na_0–0 meq %
Mg_1–0,98 " | K_1–1,76 " | Na_1–2,52 "
Mg_2–2,77 "

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Shoots	Na_0	6,66	3,61	5,90	4,35	5,60	4,32
	Na_1	1,92	1,10	3,76	2,05	3,15	1,56
Roots	Na_0	2,04	0,89	1,78	1,03	1,74	0,87
	Na_1	0,48	0,27	0,72	0,38	0,60	0,42
Whole plants	Na_0	8,69	4,50	7,80	5,38	7,34	5,19
	Na_1	2,40	1,36	4,48	2,41	3,75	1,98

APPENDIX 12. Mean relative cation content (meq %) of mopane under factorial combinations of magnesium (Mg_0–Mg_2), potassium (K_0–K_1) and sodium (Na_0–Na_1).

Numerical values attached to each treatment level are given in Appendix 11 or Table 4.

Soil 2

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Calcium	Na_0	49,21	37,01	48,40	34,44	43,64	29,12
	Na_1	46,42	33,60	46,19	34,21	40,40	31,35
Magnesium	Na_0	17,43	15,14	22,69	23,48	26,78	26,59
	Na_1	24,22	18,18	28,21	26,59	30,39	28,39
Potassium	Na_0	67,14	96,85	66,36	97,34	60,62	87,32
	Na_1	55,40	90,61	56,64	86,60	53,33	65,70
Sodium	Na_0	1,97	10,80	1,36	4,97	3,70	5,53
	Na_1	15,89	15,35	7,84	9,74	8,09	8,22

APPENDIX 12 (continued)

Soil 4

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Calcium	Na_0	83,16	85,61	64,33	74,44	53,47	66,80
	Na_1	90,10	85,90	80,37	79,05	78,04	68,44
Magnesium	Na_0	13,78	16,32	19,66	21,27	21,17	25,58
	Na_1	18,49	19,55	19,21	22,38	26,93	25,18
Potassium	Na_0	60,37	67,02	63,68	65,58	58,28	61,44
	Na_1	59,82	69,71	59,60	67,25	57,10	66,58
Sodium	Na_0	1,99	2,62	2,06	1,74	3,20	1,25
	Na_1	6,86	9,69	5,03	5,67	5,39	4,94

Soil 6

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Calcium	Na_0	66,02	83,46	60,88	75,97	52,36	62,14
	Na_1	73,31	70,15	68,25	64,22	73,16	65,91
Magnesium	Na_0	16,80	22,15	19,60	23,45	19,78	23,77
	Na_1	24,04	29,74	22,77	24,87	28,68	34,45
Potassium	Na_0	61,92	70,68	63,72	76,51	64,35	72,77
	Na_1	67,36	73,82	67,80	73,01	66,27	73,55
Sodium	Na_0	6,02	6,69	6,99	8,01	7,14	5,90
	Na_1	14,81	23,18	9,91	11,24	9,83	11,56

APPENDIX 13 Mean total relative cation content (meq %) of mopane under factorial combinations of magnesium (Mg_0–Mg_1), potassium (K_0–K_1) and sodium (Na_0–Na_1).

Numerical values attached to each treatment level are given in Appendix 11 or Table 4.

		Mg_0		Mg_1		Mg_2	
		K_0	K_1	K_0	K_1	K_0	K_1
Soil 2	Na_0	135,75	159,80	138,81	160,23	134,73	148,41
	Na_1	141,92	157,74	138,87	157,14	132,21	133,66
Soil 4	Na_0	159,30	171,57	149,73	163,03	136,12	155,07
	Na_1	175,27	185,05	164,16	174,35	167,47	165,13
Soil 6	Na_0	150,76	182,98	149,19	183,94	143,80	164,58
	Na_1	179,52	196,88	168,82	173,33	177,94	168,81

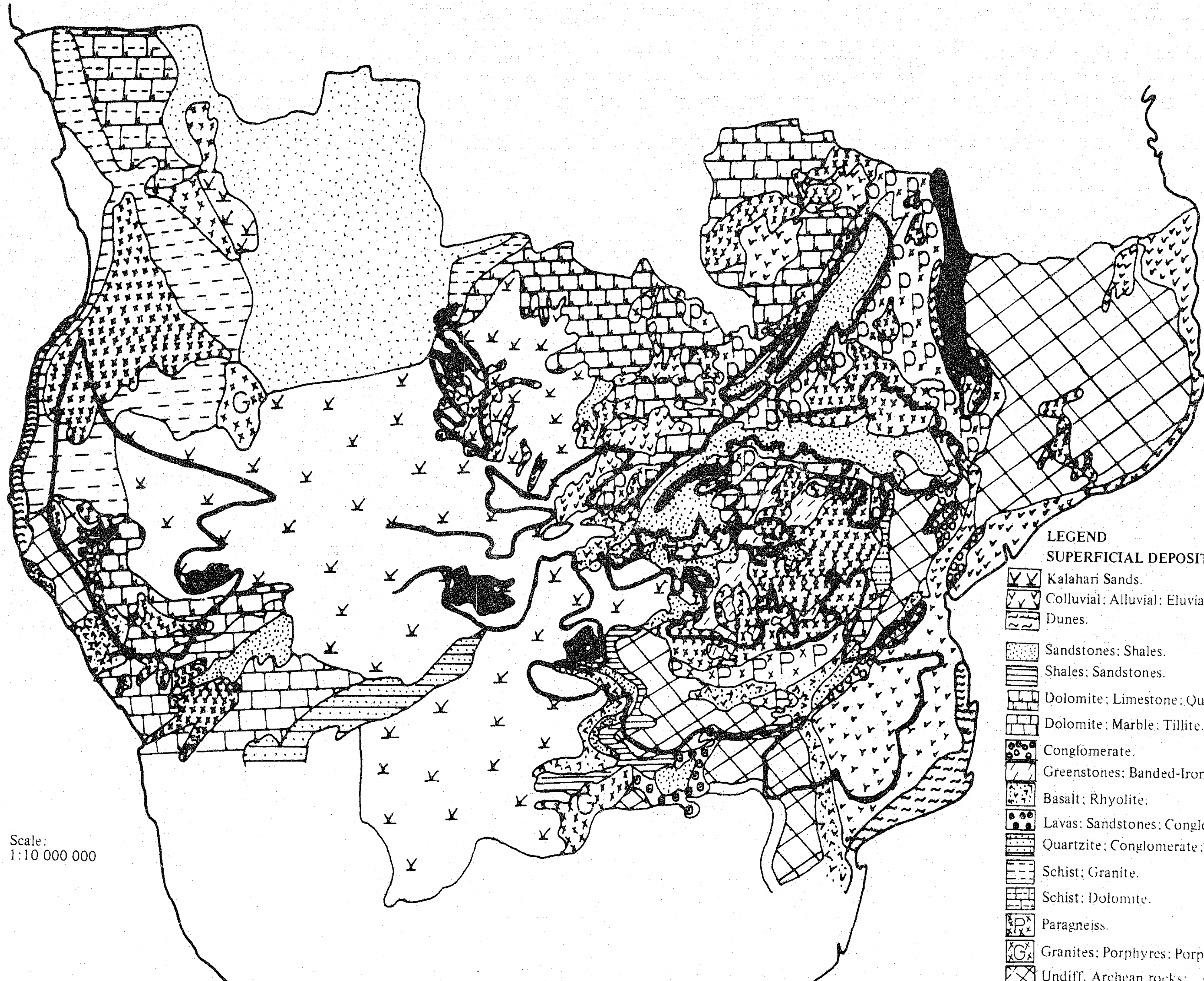

FIG. 10. Geological map of South Central Africa -- collated from the regional geological maps of Mouta and O'Donnel (1933). Fed. Govt. Printer, Salisbury (1961), Martin (1963), Oberholzer (1968), Boocock (1968) and Coertze *et al.* (1970). The thickened line indicates the approximate limits of mopane, simplified from Figure 7.

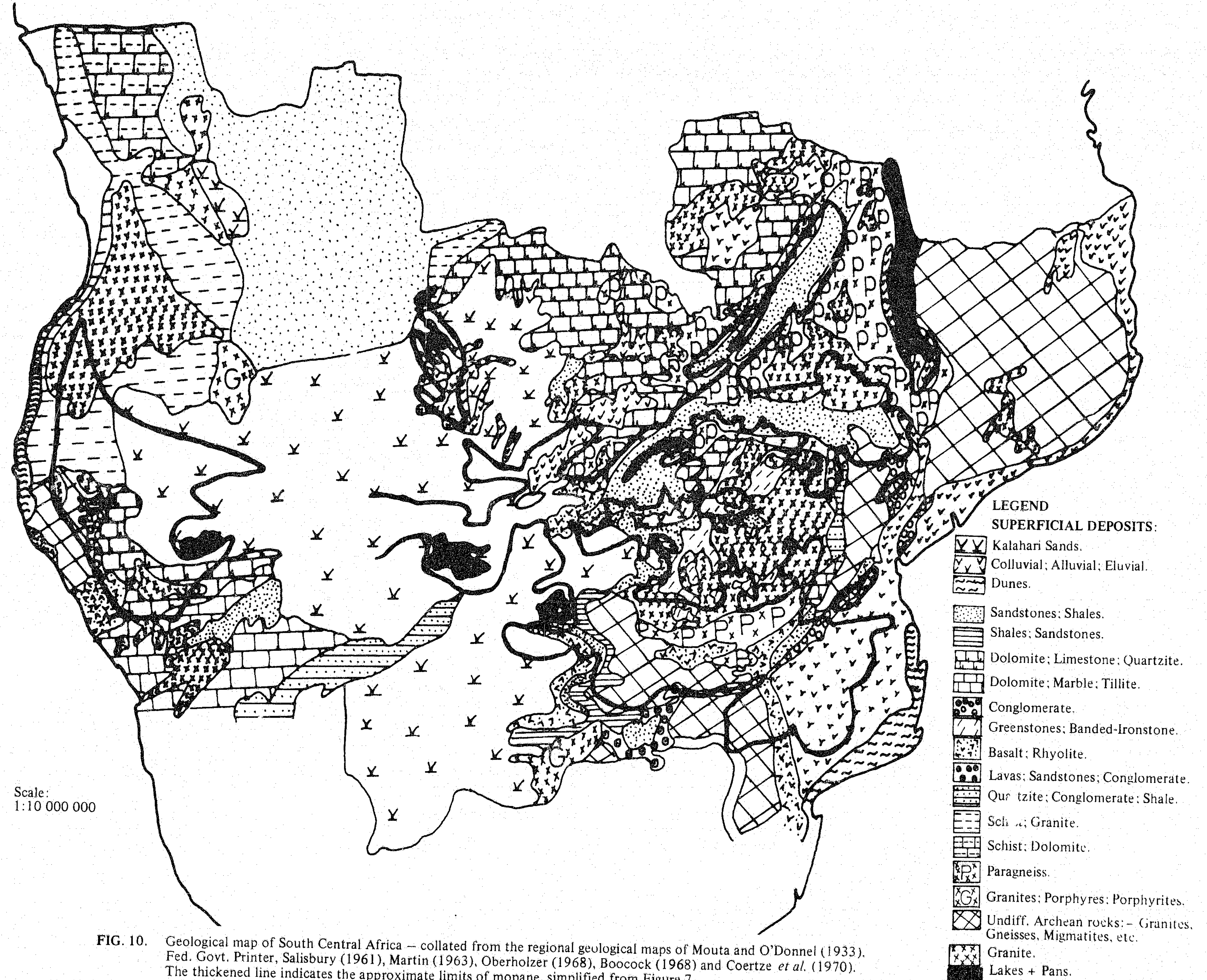

FIG. 10. Geological map of South Central Africa – collated from the regional geological maps of Mouta and O'Donnel (1933), Fed. Govt. Printer, Salisbury (1961), Martin (1963), Oberholzer (1968), Boocock (1968) and Coertze *et al.* (1970). The thickened line indicates the approximate limits of mopane, simplified from Figure 7.