AGE DETERMINATION OF *ACACIA ERIOLOBA* IN THE KALAHARI GEMSBOK NATIONAL PARK

by

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ABSTRACT

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High quality wood core samples were collected from individual *Acacia erioloba* trees of unknown age by means of an effective non-destructive method of sampling.

The equipment used is a definite improvement over conventional, hand-turned borers and other described powered equipment. Cores were smooth, not burned and large enough to study more than one radius.

In the majority of samples examined, seasonal changes were reflected in the wood anatomy as bands of marginal parenchyma on the polished surfaces of discs or cores. Estimated carbon age was determined by means of ^{14}C analysis for all samples. There was a strong correlation between growth-ring count and estimated carbon age.

A correlation was also found between age and stem circumference although age based on stem circumference overestimated age.

Age structure of the *Acacia erioloba* population in the interior dune area and northen Nossob Riverbed was subsequently determined.

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CHAPTER 1

INTRODUCTION

Research in the arid areas has always been hampered by these regions' inaccessibility and harsh environmental conditions. The southern Kalahari is no exception and only limited and usually broadscale information is available on the biotic component and dynamics of the region. Basic and applied research on a number of aspects regarding the functioning and management of the ecosystem is therefore needed (Van Rooyen *et al.* 1996).

For a more complete understanding of the population dynamics of tropical trees, and consequently their sustained management, information on their age and growth rates are required (Gourlay & Grime 1994). It is obvious that before any attempts can be made to identify climatic conditions that relate to successful regeneration, it is necessary to develop a technique for dating the tree. One of the possible techniques of age determination is the counting of annual growth rings in wood samples. In the tropics and sub-tropics growth periodicity may however not be clearly limited to a particular season, so that it is necessary first to ascertain whether any anatomical structures delimit annual periods.

In order to date any tree by means of dendrochronology it is essential to assume that one growth-ring can be equated with one year's growth. Tree growth-rings are widely applied in ecological studies for determining tree ages, for investigating changes in growth rates and elucidating their causes. Age measurements are usually used to determine the age-class distribution of a tree population from which inferences on the dynamics of that population can be drawn (Fritts & Swetnam 1989).

Quantitative analyses of tree rings also gives information on the frequency of droughts and floods beyond the limited period of hydrological records. Tree rings are the most geographically widespread entity that can provide actual year-to-year dating of current and prehistoric environmental changes (Jacoby & Wagner 1993).

The relationship between ring counts and age is likely to be unique to a particular geographical area on the basis of climate. Even within one area, there is a high degree of variability in the relationship. This suggests that site characteristics may be important (e.g. moisture holding capacity of the soil; browsing pressure) and necessitates that sampling be done over a wide range of sites and ages (Martin & Moss 1997).

The Kalahari Gemsbok National Park is most suitable for vegetation studies as it is representative of the entire southern Kalahari duneveld and the vegetation, being protected from the over-utilization common in the adjacent farming areas, is in good condition (Lubbinge 1998).

The vegetation of the Kalahari Gemsbok National Park is both unique and sensitive. *Acacia erioloba* plays a pivotal role as keystone species in this environment and is of special ecological importance (Milton & Dean 1995). To manage the Kalahari Gemsbok National Park in a sustain-able manner it is therefore of vital importance to study this keystone species to obtain as much information as possible.

Preliminary data (Van Rooyen *et al.* 1996) showed that a large proportion of the northern Nossob Riverbed in the Kalahari Gemsbok National Park exhibits an unhealthy *Acacia erioloba* population structure in that there is a poor survival of seedlings and an almost complete absence of juvenile plants. This recruitment failure leads to a decline in isolated mature trees, which may result in a change in the population structure of *Acacia erioloba* (Jeltsch *et al.* 1996) as well as their function in the ecosystem (Milton & Dean 1995). A decline in scattered mature trees may have serious implications for species diversity in the southern Kalahari (Milton & Dean 1995).

Should a tree ring analysis of the wood of *Acacia erioloba* be possible, this would allow more precise quantification of plant growth rates and population age structure in relation to soils, disturbance, succession and climate than has been previously possible for this species.

The objectives of this study were therefore to:
✦ investigate whether a wood anatomical feature, that has been shown to delimit annual periods in some African *Acacia* species, can be used to determine age in *Acacia erioloba*;

- ✦ determine whether growth-ring counts correlate with actual age as determined by carbon dating in *Acacia erioloba*;
- ✦ relate age and growth rate to stem circumference data;
- ✦ relate age and growth rate to meteorological data available for sites;
- ✦ develop age-size relations for *Acacia erioloba* on the basis of ring counts and carbon dated ages;
- ✦ analyse the age structure of the dominant species, i.e. *Acacia erioloba* in an attempt to infer both past and future states of the population; and
- ✦ make recommendations for future sustained management of the *Acacia erioloba* population.

CHAPTER 2

STUDY AREA

2.1   LOCATION

The study was conducted in the Kalahari Gemsbok National Park, one of Africa's last unspoilt wilderness areas. Unlike the neighbouring Namib desert, the Kalahari Gemsbok National Park is not a true desert but belongs to the Savanna Biome and is quite densely covered with grasses, shrubs and trees (Leistner 1967). It is an arid, open landscape with the southern part mainly open shrub savanna and the northern part open woodland or tree savanna (Bothma & De Graaff 1973). The Kalahari Gemsbok National Park covers approximately 9 600 km² and is situated in the south-western corner of the Kalahari Desert between 24°15'S and 26°30'S and 20°00'E and 20°45'E (Figure 2.1). The altitude varies from 870 m at Twee Rivieren in the south to 1 080 m at Unie End in the north.

The river systems of the Kalahari Gemsbok National Park are the life blood of the ecosystem. The Nossob and Auob rivers both originate in the Auas mountains in Namibia and join at Twee Rivieren. Although covering only about 4% of the total area of the park, it sustains most of the animal life in terms of palatable grazing, potable water and habitat diversity (Van Rooyen *et al.* 1996). Tourist routes are mainly restricted to the riverine areas. The reason for this is twofold: from the perspective of the tourism industry these are the areas where wildlife is to be seen in abundance and from a conservation point of view, restricted access to the sand dunes is essential for the conservation of this unique and sensitive ecological system (Van Rooyen *et al.* 1996).
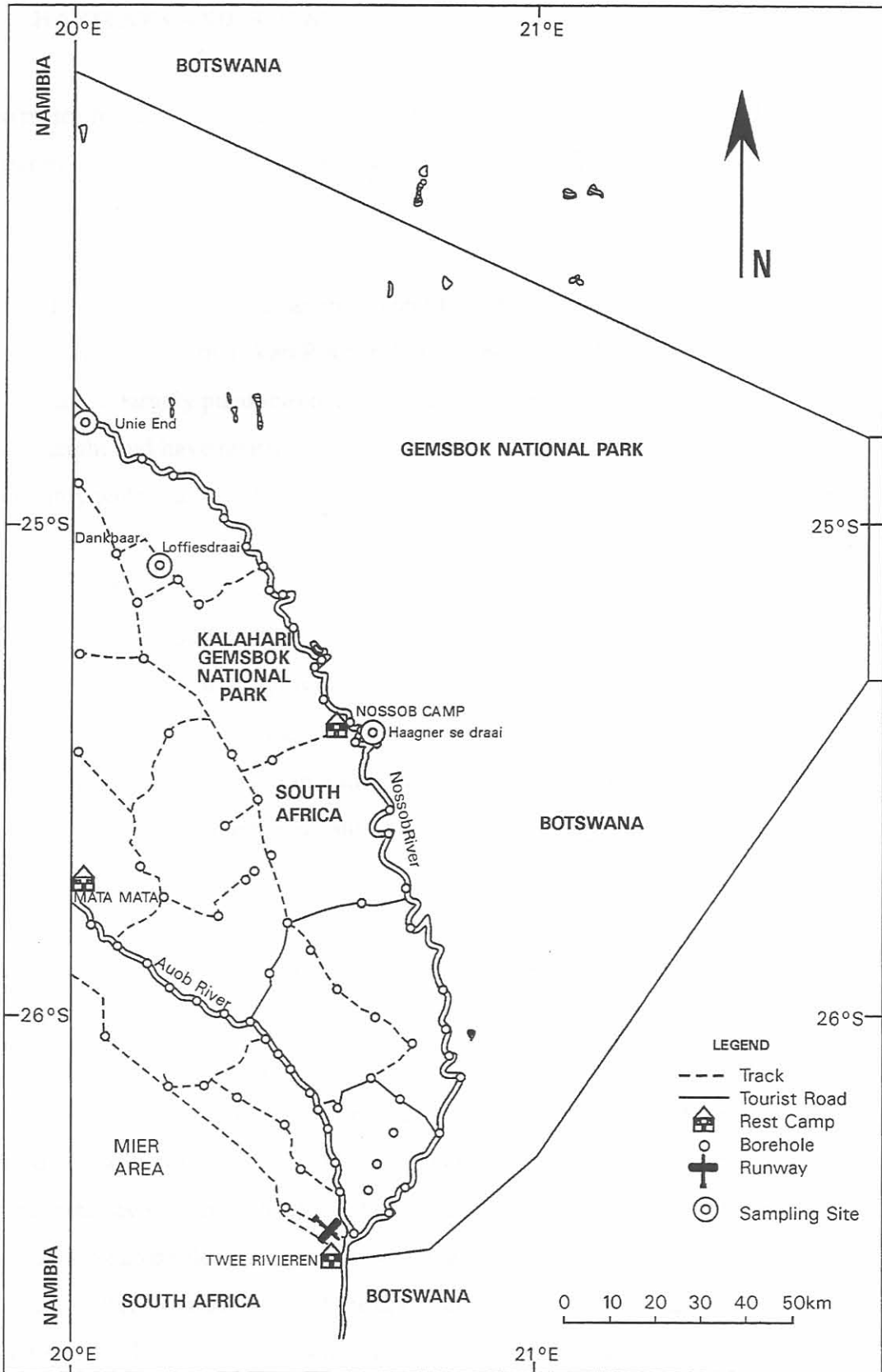
Figure 2.1 **The Kalahari Gemsbok National Park and the location of the sampling sites** (after Bothma *et al*. 1993).

2.2   HABITATS AND SOILS

Three major habitat types can be distinguished in the southern Kalahari, and these correspond to differences in soil types: (a) dunes and undulating sand flats; (b) dry riverbeds; and (c) pans (Van Rooyen 1984).

The Kalahari sands are of aeolian origin and form the parent materials of the red Hutton and yellow Clovelly soil forms (Van Rooyen 1984). Aeolian sand covers over 95% of the southern Kalahari and is largely piled into northwest- to southeast-running dunes. These dunes average 10 m in height and have relatively flat tops, often up to 9 m wide. The dunes are separated by considerably wider valleys (Werger 1978). The dunes that run parallel to each other consist of red or pink sand. Red sands are by far the commonest, the colour being due to a coating of ferric oxide around the particles. Only where the valleys between the dunes are so deep that the underlying calcrete stratum nears the surface, or in the vicinity of dry riverbeds and pans, does the sand have a paler colour. This can be due to mixing with calcrete particles, or to a mixture of red and white sand. No distinct horizons can be distinguished in these sandy soils. The sands, both red and pink, are also poor in nutrients. In the deep dune valleys the pink sands are some-what richer in water-soluble calcium due to the calcrete layer being near the surface (Van Rooyen 1984).

The soils of the dry riverbeds are either silty, rocky or sandy. Silty or clayey soils cover the actual riverbeds. The soils of the riverbeds are compact, poorly drained and rich in nutrients. There are, however, considerable differences in ionic composition of the soils of the different rivers of the southern Kalahari. This probably related to the different areas of origin of these rivers. Rocky soils commonly occur on the banks of the dry riverbeds where these cut deep into thick calcrete layers. The calcrete surface is usually weathered and there are frequent small pockets and fissures filled with gravelly white sand. Belts of fairly shallow white sand typically occur on the slightly raised sides of the dry riverbeds, between the calcrete banks and the silty central riverbed. These soils of washed sand with compact underlying substrates possess a higher nutrient content than the pink and red sand (Werger 1978).

Pan soils consist either of white (washed) sand when the pans are shallow, rocky soils when the calcrete layer crops out, or most typically, clays or sandy clays. The latter soils are rich in mine-rals, particularly Na, K, and Mg ions, and have a high pH. Extensive pan-like areas occur in the slightly higher-lying portions of dry riverbeds where they are isolated from the river course by a raised, compact calcareous sand formation. These areas are therefore not influenced by the rare flood waters. This pan-like alluvium consists of sandy loam soils with a fairly high mineral con-tent (Figure 2.2) (Werger 1978).
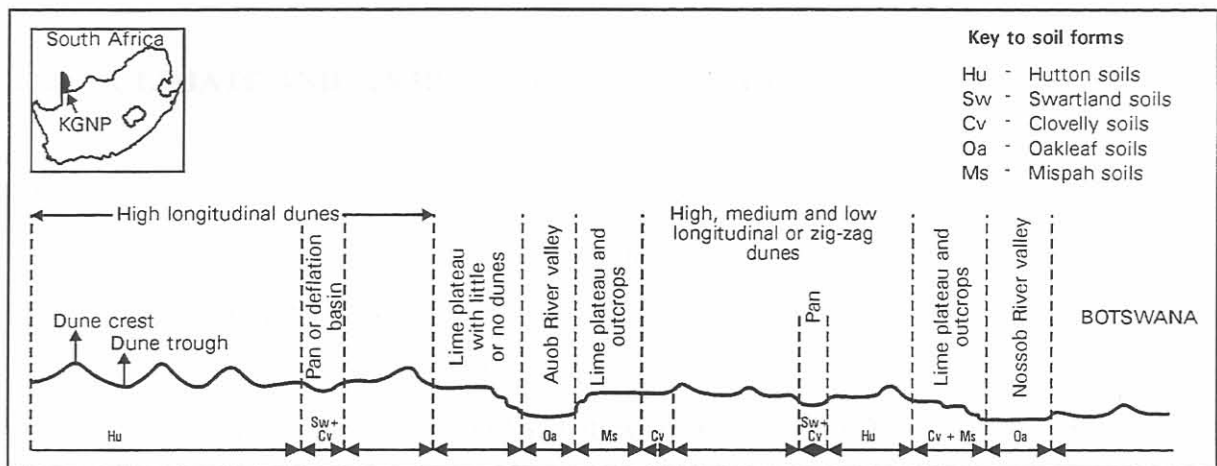
Figure 2.2   Locality and schematic cross section from west to east of the Kalahari Gemsbok National Park showing the relationship between landform and soils (after Van Rooyen 1984).

Alluvial soils along the Nossob River are loamy and alkaline (pH 7-9). The fine, sandy soils of the surrounding dunes are acid to neutral (pH 5-7) with a low conductivity. Total nitrogen and available phosphorus are generally low in all soils of the Kalahari Gemsbok National Park but higher in alluvial than dune soils (Van Rooyen 1984).

The soils of arid to semi-arid regions are, as a rule, well supplied with most of the essential plant nutrients. Such soils suffer little loss of solubilised nutrient compounds through leaching. In contrast to this, the sandy soils of the Hutton and Clovelly forms in the Kalahari Gemsbok National Park are inherently infertile. Hutton soil form is extremely deficient in available phos-phate. The series of both soil forms have clay contents of less than 6% and are correspondingly poor in exchangeable cations. Potassium and magnesium availability is low to medium. It can

thus be stated that these soils are in general free from soluble salts and especially exchangeable Na^+ and sodium salts as far as the major plant nutrients are concerned. Total nitrogen, which is mainly contained in the organic matter fraction, is generally low in all the soils of the Kalahari Gemsbok National Park (Van Rooyen 1984). It remains uncertain how the large *Acacia erioloba* trees are able to absorb sufficient phosphate from the extremely P-deficient Hutton soil form in the Kalahari. The higher phosphate and water levels in the alluvial soils of the Auob and Nossob Rivers may account for the large *Acacia erioloba* trees in these riverbeds (Van Rooyen 1984).

2.3   CLIMATE AND ITS RELATIONSHIP TO THE VEGETATION

The climate of the Kalahari Gemsbok National Park may be described as arid to semi-arid. The mean annual rainfall ranges from 200-250 mm and is unreliable and irregular. The rainy season usually extends from November to April with fifty percent of the precipitation occurring in mid to late summer (January to March). The rainfall can vary from less than a 100 mm up to more than 700 mm per annum. The rainfall statistics since 1975 at different sites in the Kalahari Gemsbok National Park are summarized in Figures 2.3 to 2.4 and Tables 2.1 to 2.2.
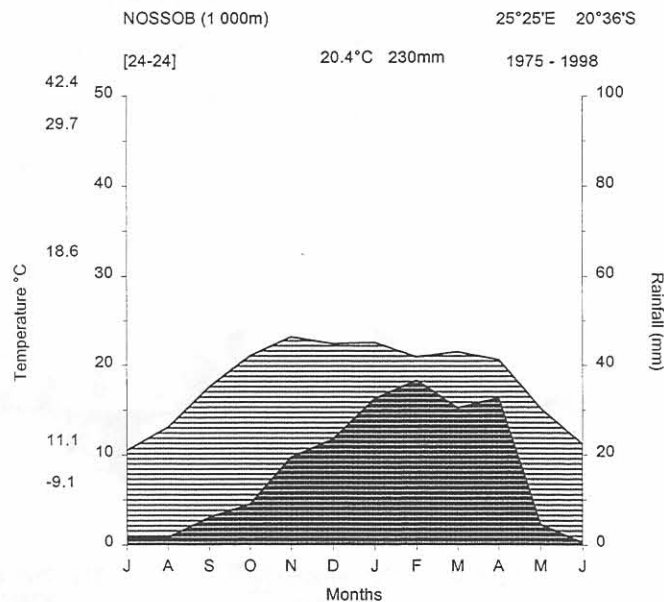
Figure 2.3 Climate diagram for Nossob Camp in the Kalahari Gemsbok National Park
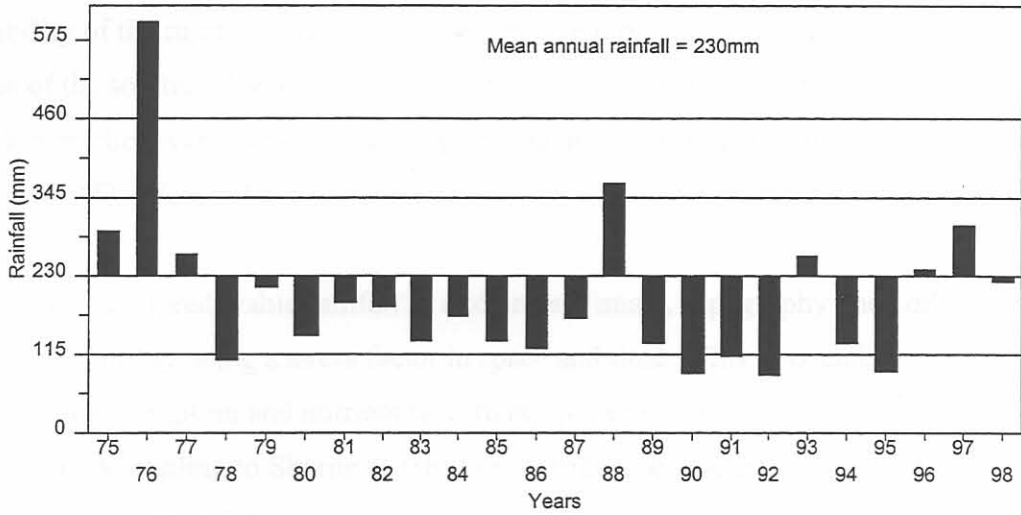
Figure 2.4 Rainfall deviation from the long-term average for Nossob Camp in the Kalahari Gemsbok National Park (1975-1998) (Weather Bureau 1998).

Dyer and Tyson (1977) analysed the long-term rainfall cycles for the summer rainfall region of southern Africa and estimated future extended wet and dry spells. It was suggested that the periods 1972-1981 and 1991-2000 would experience above normal rainfall and the period 1981-1990 would be drier than normal (Figure 2.5). According to Figure 2.4 it is obvious that except for 1976, 1988 and 1997, which experienced above mean annual rainfall, the Kalahari Gemsbok National Park experienced very dry years since 1978. The timing and amount of seasonal rainfall and the existence of relatively long-term wet and dry rainfall periods play a major role in the dynamics of the vegetation and should be incorporated in management strategies for the Kalahari Gemsbok National Park.
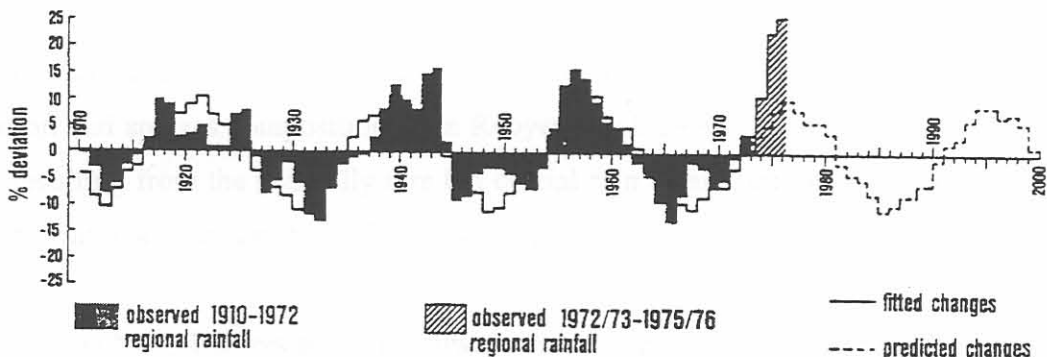
Figure 2.5 Observed, calculated and predicted regional rainfall changes (after Dyer & Tyson 1977).

A feature that is of great significance to the vegetation of the Kalahari is the variability and unreliability of the rainfall (Leistner 1967). Climate induced variations in the vegetation composition of the southern Kalahari is a result of seasonal variation (short-term and mostly phenological), periodical variations over a few years (medium-term) and long-term changes (Leistner & Werger 1973; Werger 1978).

Due to low and unpredictable rainfall in arid areas climate, topography and soils contribute to resource availability being a stress factor in space and time. This also leads to the processes of production, consumption and nutrient flow to be sporadic and difficult to predict (Crawford & Gosz 1982). According to Skarpe (1986) the coefficient of variation in rainfall between years in the Kalahari Gemsbok National Park is more than 80%.

Sala and Lauenroth (1982) hypothesised that short-term rainfall is an important and significant resource for ecosystems in semi-arid areas. An ecologically significant shower is one that changes the water status of the environment of a plant for a longer period, this is necessary for survival. Light showers regularly activate those processes related to nutrient cycles close to the soil surface which are controlled by water availability.

Rainfall in the southern Kalahari has a marked influence on the presence or dominance of annual species. Early summer rains promote growth of perennial grass species while late summer rains are beneficial to the woody component. Summer annuals are also different from the winter annuals (Leistner 1967). During drought periods annuals are virtually absent, while during particularly wet seasons numerous species, which are normally rare, will occur in great profusion (Van Rooyen et al. 1984).

The existence of long wet and dry periods therefore play a major role in the dynamics of the vegetation and species composition (Van Rooyen et al. 1990). The effect of competition for water, resulting from the generally rare but crucial rain events, on the dynamics of semi-arid savannas was also emphasized by Jeltsch et al. (1996).

The Auob and Nossob rivers are almost always dry and only flow during years of above average rains. The floods that occur play an important role in that they sustain the relatively low water-table of the rivers and ensure that the riverbed is not blocked by dune sand (Leistner 1967).

Table 2.1   Rainfall data (mm) for Nossob Camp for the period April 1975 to December 1998

Month	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	AVE
Jan	n/a	197.5	42.4	9.2	33.7	17.3	0.8	12.9	11.9	2.2	29.7	7.4	9.3	55.8	4.2	0.3	55.3	1.7	0	49	0	59.7	91.5	89.1	32.54
Feb	n/a	124.2	76.8	41.2	52.8	40	33.7	20.3	9.9	1.9	13.9	9.9	85.5	65.3	92	3	0	5	48.5	55.5	0	42.5	24	34	36.66
Mar	n/a	181.6	34.1	41.8	0.1	39.1	57	4	13.6	21.8	29.9	11.7	2.5	30.3	8.9	4.3	4.5	63	43.5	24.5	18.5	0	85.5	12.5	30.53
Apr	212	39.7	68.8	8.5	27.1	8.3	0	25.2	17.7	82.6	1.3	9.1	5.7	95.4	27.1	49.4	0	5.8	65.5	0	0	28.5	0	8	32.74
May	7.2	15.9	3.5	0	16.1	0	0	7.2	9	9.1	0	0	0	0	0.8	0	0	0	0	0	3	15	23	0	4.58
Jun	0	1.6	0	0.2	0.2	0	2.2	0	1.6	0	0	6.1	0	0	0	0	0	0	0	0	0	0	0	0	0.50
Jul	0.2	0	0	0.1	2	0	0	8	0	0	0	3.7	0.2	0	0	0	0	0	0	0	0	26	0	0	1.68
Aug	0	0.2	4.1	1.5	3.3	6	24.7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1.70
Sep	0.1	32.4	2.2	0.1	0	7.3	1.2	7.3	0.5	0	0	0.4	1.7	0	0	0	0	0	0	1	4.3	23	56	10	6.15
Oct	4.7	6.7	6.2	0.2	16.1	1.4	8.1	31.2	4.7	20.9	5	8.4	6.5	6.5	0	0	0	6.8	32	0	0	0	11	41.5	9.08
Nov	36.4	0	13	0	29.1	1.5	41.4	40.8	31.1	32.3	5.5	65.6	46.4	20.5	0.3	24	2.9	3.4	22	4	40	9.5	0	0	19.57
Dec	36	2.5	11.4	4	32.9	24.3	23.3	28.1	34.2	0	51.9	3.4	10.8	93.2	0	7.2	51.7	0	47.6	0	26	36.2	14	26.3	23.54
Total	296.6	602.3	262.5	106.8	213.4	145.2	192.4	185	134.2	170.8	137.2	125.7	168.6	367	133.3	88.2	114.4	85.7	260.1	134	91.8	240.4	305	221.4	199.25

Table 2.2   Total rainfall (mm) per year for Unie End for the period 1981 to 1998

1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
57.2	n/a	n/a	178.2	132.4	128.4	113.9	565.3	279.9	245	315.6	33.2	283.8	171.9	85	100.5	256.5	91

Table 2.3 Mean monthly maximum temperature (°C) for Nossob Camp for the period April 1975 to December 1998

Month	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	AVE
Jan	n/a	30.2	35.9	34.8	34.3	36.1	n/a	36.5	37.3	37.1	36.3	36.8	37.5	35.9	33.2	37.5	34.1	38.5	36.6	33	39.6	34.1	32.9	34.7	26.27
Feb	n/a	30	n/a	32.6	33.4	34.4	n/a	36.4	36.4	37.4	34.7	35	34.1	32.9	29.8	34.4	n/a	37.2	33	n/a	n/a	34.4	35.1	36.9	25.75
Mar	n/a	29.4	n/a	32.6	33.4	31.8	n/a	33.2	34.1	33.7	32.1	33	34.3	32.8	33	33.7	n/a	34.7	33.4	35	33.4	34.6	30.9	35.1	27.68
Apr	28.6	29.4	28.8	27.5	31.4	29.5	29.4	26.7	30.8	28	28.8	30.7	32	28.1	28.7	28.5	30	31.8	27.9	30.8	30.1	29.6	27.3	33.1	29.48
May	24.7	24.5	25.1	26.6	25.2	26.4	24.9	26.6	23.7	24.1	25.6	28.5	28.6	n/a	28.1	24.9	27.7	26.6	26.4	27.7	25.5	25.7	24.3	26.7	24.92
Jun	24	21.7	23.8	21.6	21.9	22.6	21.7	22	23	21.9	23.8	22.8	22.1	21.4	22.1	22.7	22.2	n/a	22.9	22	22.7	24.1	22.9	25.5	21.73
Jul	22.8	22.2	23.4	23.6	21.5	22.9	23	20.4	22.5	22.6	23	22.5	21.9	23.4	22.9	23.1	22.4	n/a	24.3	n/a	22.4	19.4	23.5	23.3	20.71
Aug	24.7	24.1	25	25.6	25	25.4	22	26	24	26.4	27.4	24.8	24.3	26.7	26.9	26.5	25.4	n/a	25.6	26.4	25.8	n/a	27.1	25.4	23.35
Sep	31.1	29.6	28.8	27	28.2	n/a	26.6	30.3	30.4	29.9	29	28.4	26	28.8	29.5	29	28.5	29.8	32.3	31.6	30.4	n/a	30.4	29.1	26.86
Oct	31.3	30.2	33.2	30.8	31.7	n/a	29.5	30.7	31.6	31.4	33.2	31	32.5	31.2	31.4	32.3	32.9	32.7	34.4	31.9	30.4	n/a	32.6	31.8	29.11
Nov	32.6	33.1	35.7	35.3	34.2	n/a	34.9	34.3	32.7	33.4	33.7	32.3	34.9	33.9	34.5	36.5	34.8	34	32.7	34.5	34.1	n/a	34	34.3	31.27
Dec	33.1	n/a	35.6	35.8	36.1	n/a	36.7	33.7	33.8	35.5	33.9	37.8	36	33.9	37.8	34.8	33.6	37.3	36.6	n/a	n/a	n/a	36.4	35.3	28.07
Y-AVE	21.08	25.37	24.61	29.48	29.69	19.09	20.73	29.73	30.03	30.12	30.13	30.30	30.35	27.42	29.83	30.33	24.30	25.22	30.51	22.74	24.53	16.83	29.78	30.93	26.27

Table 2.4 Mean monthly minimum temperature (°C) for Nossob Camp for the period April 1975 to December 1998

Month	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	AVE
Jan	n/a	18.90	19.60	19.40	19.30	19.00	20.70	18.80	21.70	18.80	21.30	20.80	19.10	20.20	18.60	19.00	18.80	19.20	19.10	17.80	21.70	20.00	19.90	19.60	18.80
Feb	n/a	17.20	19.80	19.10	21.10	20.10	20.10	21.00	17.70	20.30	21.00	17.90	22.30	19.20	16.80	17.00	n/a	19.20	19.40	n/a	n/a	18.60	18.00	20.70	16.10
Mar	n/a	15.60	15.40	17.70	14.00	18.60	15.50	17.40	17.30	18.90	16.60	16.70	17.80	17.30	14.10	17.70	n/a	16.50	17.60	14.50	18.70	16.70	16.30	17.70	15.36
Apr	10.30	11.20	14.00	11.80	13.70	9.70	12.10	11.60	13.90	12.70	10.80	12.40	13.70	12.40	9.30	12.40	9.00	13.00	10.90	10.30	11.80	12.60	7.10	14.60	11.72
May	3.30	6.60	3.60	5.50	7.30	5.00	6.40	6.00	5.80	6.90	6.30	7.70	7.90	n/a	6.70	3.80	n/a	3.90	2.80	3.30	7.80	10.50	7.00	5.30	5.39
Jun	1.80	0.60	0.90	-1.30	3.20	1.70	0.20	2.80	1.90	1.90	-0.20	3.30	0.50	-0.30	-1.40	0.60	-0.40	-0.20	-2.40	-2.00	0.70	1.70	1.70	1.40	0.70
Jul	0.20	-3.10	-0.70	3.40	2.10	2.10	1.20	1.60	1.30	0.50	0.00	1.20	0.20	-1.70	-2.00	-1.50	-1.60	-0.70	1.70	n/a	-0.80	-0.40	1.10	3.30	0.31
Aug	1.30	-0.50	2.70	2.10	4.60	5.50	2.40	3.20	1.10	3.30	5.10	3.20	0.90	2.30	2.80	3.40	0.40	2.30	3.10	1.80	3.40	2.80	3.60	7.10	2.83
Sep	7.70	6.50	6.80	7.20	7.80	6.80	6.80	11.20	8.90	7.90	8.00	9.20	7.30	5.90	4.90	14.40	7.20	8.70	7.30	7.40	11.20	7.10	10.70	9.80	8.20
Oct	9.50	12.50	13.30	8.40	13.00	13.30	10.60	14.70	13.70	14.60	16.10	14.60	14.00	11.40	10.20	18.70	13.20	11.70	17.60	9.00	10.30	13.50	14.40	14.40	13.03
Nov	15.80	12.20	14.70	16.60	16.40	13.20	16.60	14.80	15.80	n/a	16.40	16.60	19.20	16.80	14.40	19.20	16.70	14.70	15.30	14.50	17.70	15.20	13.90	15.50	15.09
Dec	18.40	16.90	17.80	18.00	18.60	18.20	19.20	17.40	19.30	16.60	17.70	20.20	19.60	19.40	18.50	17.50	18.80	18.20	17.30	n/a	n/a	17.80	18.30	19.10	16.78
AVE	5.69	9.55	10.66	10.66	11.76	11.10	10.98	11.71	11.53	10.20	11.59	11.98	11.88	10.24	9.41	11.85	6.84	10.54	10.81	6.38	16.86	11.34	11.00	12.37	10.36

Large temperature fluctuations, both on a daily and seasonal basis, are also characteristic of the climate. Mean maximum and minimum temperatures are 37.4°C and 19.5°C in January and 22.2°C and 1.2°C in July (Tables 2.3 and 2.4). Temperatures reach extreme values with winter lows reaching -9.1°C and summer highs of up to 42.4°C (Figure 2.3) (Weather Bureau 1998).

The most common winds, which are northwesterly with accompanying dust (sand) storms, occur during September to November. During winter southwesterly winds can bring cold weather for short periods. Frost is common in winter (Van Rooyen 1984).

Phenologically the annual cycle in the Kalahari lacks a clear demarcation into four calender seasons, instead, it essentially has only two seasons (summer and winter), linked by transitional periods (Leistner 1967).

2.4   VEGETATION

Names of plants from the literature discussed below conform to the nomenclature of Arnold and De Wet (1993).

The vegetation of the southern Kalahari is described by Acocks (1953, 1988), Leistner and Werger (1973) and Leistner (1979). Twelve plant communities were distinguished and described in detail by Leistner and Werger (1973). Each of these communities is floristically clearly distinct and is correlated with specific habitat conditions. The different plant communities of the southern Kalahari are grouped by Werger (1978) according to the four main habitats namely communities on sand, calcrete, pans and riverbeds.

The vegetation structure of the Kalahari is described by Leistner (1979) as 'savanna or "bushveld", and grassland with interspersed tall shrubs and/or trees'. The dunes and sandy flats are largely covered by an open shrub or tree savanna, sparse dwarf shrub formations occur on calcrete outcrops, while riverbeds and pans support open grass communities.

Bothma and De Graaff (1973) recognized six major habitat categories in the Kalahari Gemsbok National Park viz. (1) the riverbeds of the Auob and the Nossob, (2) pans, (3) tree savanna,

(4) dunes with tree- or shrub-covered crests, (5) dunes superficially devoid of trees and shrubs and (6) flat, open grassy plains (Figure 2.6). Within these categories some smaller subdivisions occur in different localities. Only two of the major habitat categories are applicable to the sampling sites and will be discussed in more detail:

(1)   The riverbeds

Nossob riverbed

The Nossob riverbed varies considerably in width. It tends to form a relatively narrow channel (100-500 m across), flanked with steep limestone banks in the south, changing to a wide, shallow, sandy bed up to one kilometre and more in width in the north. The latter is typical of the area from Nossob Camp northwards to Unie End. From the Nossob Camp to Unie End the vegetation in the riverbed has a savanna appearance with large *Acacia erioloba* trees in a grassland dominated by *Panicum coloratum* and *Eragrostis bicolor*. The banks have no calcrete outcrops and are dominated by *Stipagrostis obtusa*, mixed in some areas with *Rhigozum trichotomum*. The transition area between the riverbed and the sandveld interior is covered by grasses such as *Schmidtia kalihariensis, Stipagrostis ciliata, Eragrostis lehmanniana*, and by the shrubs *Rhigozum trichotomum* and *Monechma genistifolium* (= *Monechma australe*) and by the dominant tree, *Acacia erioloba*. The river dunes of the northern Nossob are characterized by denser stands of shrubs and trees.

(2)   Tree savanna

A tree savanna typically develops in Kalahari areas with an annual rainfall exceeding 250 mm (Leistner 1967). In the Kalahari Gemsbok National Park tree savanna is found in the area adjacent to the Nossob and Auob Rivers and in the immediate proximity of Dankbaar and Loffiesdraai in the far north (Figure 2.6).

The vicinity of Dankbaar consists of scattered irregular dunes interspersed with long, wide valleys or flats. In the valleys the dominant tree is *Acacia erioloba*. On the dune slopes and crests specimens of *Boscia albitrunca* are encountered, with a fair scattering of trees and shrubs such as *Rhus tenuinervis, Terminalia sericea, Albizia anthelmintica* and *Grewia retinervis*. Also present are *Acacia mellifera, Grewia flava* and *Lycium bosciifolium*. The area between the dunes is

grassland consisting of *Eragrostis lehmanniana*, *Stipagrostis uniplumis* var. *uniplumis*, *Centropodia glauca* (= *Asthenatherum glaucum*) and *Stipagrostis amabilis*.

Previously the Thorny and Shrubby Kalahari Dune Bushveld were classified by Acocks (1953, 1988) as one vegetation type, i.e. Kalahari Thornveld [A16] (Low & Rebelo 1998). According to the new classification and vegetation map of South Africa (Low & Rebelo 1998) the Thorny Kalahari Dune Bushveld occurs on deep sand in the Kalahari Gemsbok National Park at more or less 1 000 m altitude. The area is characterised by parallel dunes with dune valleys (streets). This bushveld vegetation type is encountered on aeolian sandy to loamy sand, underlain by calcrete. It is characterised by sparsely scattered trees, mainly *Acacia erioloba*, including a few individuals of *Acacia luederitzii* and *Boscia albitrunca*. *Terminalia sericea* is conspicuous on some dune crests. The shrub layer is poorly developed and individuals of *Lycium bosciifolium*, *Grewia retinervis* and *Rhus tenuinervis* occur widely scattered. Depending on the amount of rainfall, the grass layer is moderately developed. Grasses such as *Eragrostis lehmanniana* and *Schmidtia kalihariensis* are conspicuous in the dune valleys and *Stipagrostis amabilis* is abundant on the dunes. This vegetation type is almost totally contained within the Kalahari Gemsbok National Park.

The Shrubby Kalahari Dune Bushveld covers most of the Kalahari Gemsbok National Park. The landscape comprises of gently undulating dunes with pans scattered throughout this vegetation type at an altitude between 1 000 m and 1 100 m. This shrubby bushveld is encountered on deep aeolian sandy soils underlain by calcrete. The area is characterised by scattered shrubs of mainly *Acacia haematoxylon* including a few individuals of *Acacia erioloba* and *Boscia albitrunca*. The shrub layer is poorly developed and individuals of *Grewia retinervis* and *Rhus tenuinervis* occur widely scattered. The grass layer is well developed and resembles a grassland. Grasses such as *Stipagrostis amabilis*, *Eragrostis lehmanniana*, *Aristida meridionalis* and *Centropodia glauca* are conspicuous on these plains.
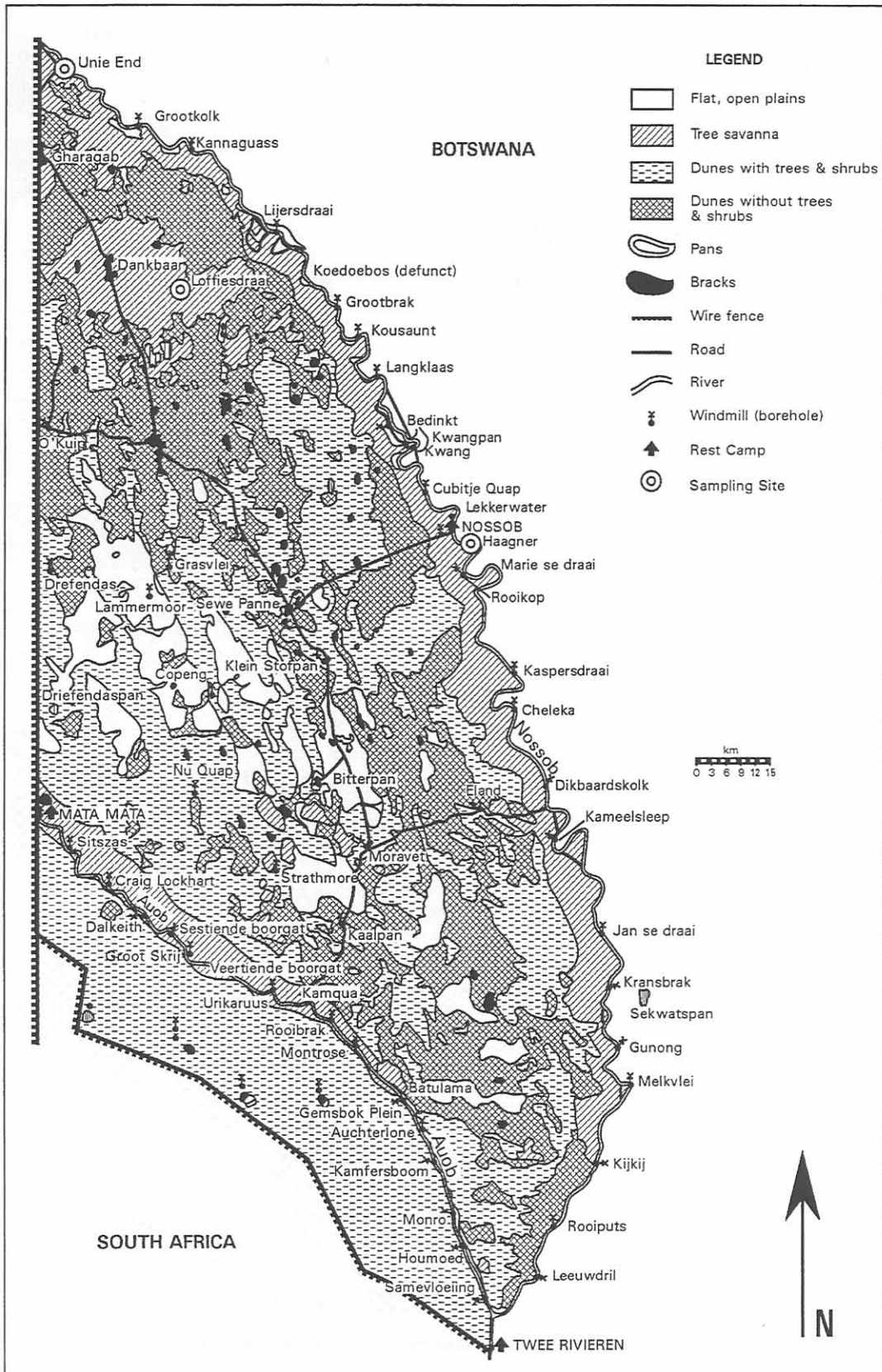
Figure 2.6   Habitat map of the Kalahari Gemsbok National Park (after Bothma & De Graaff 1973).
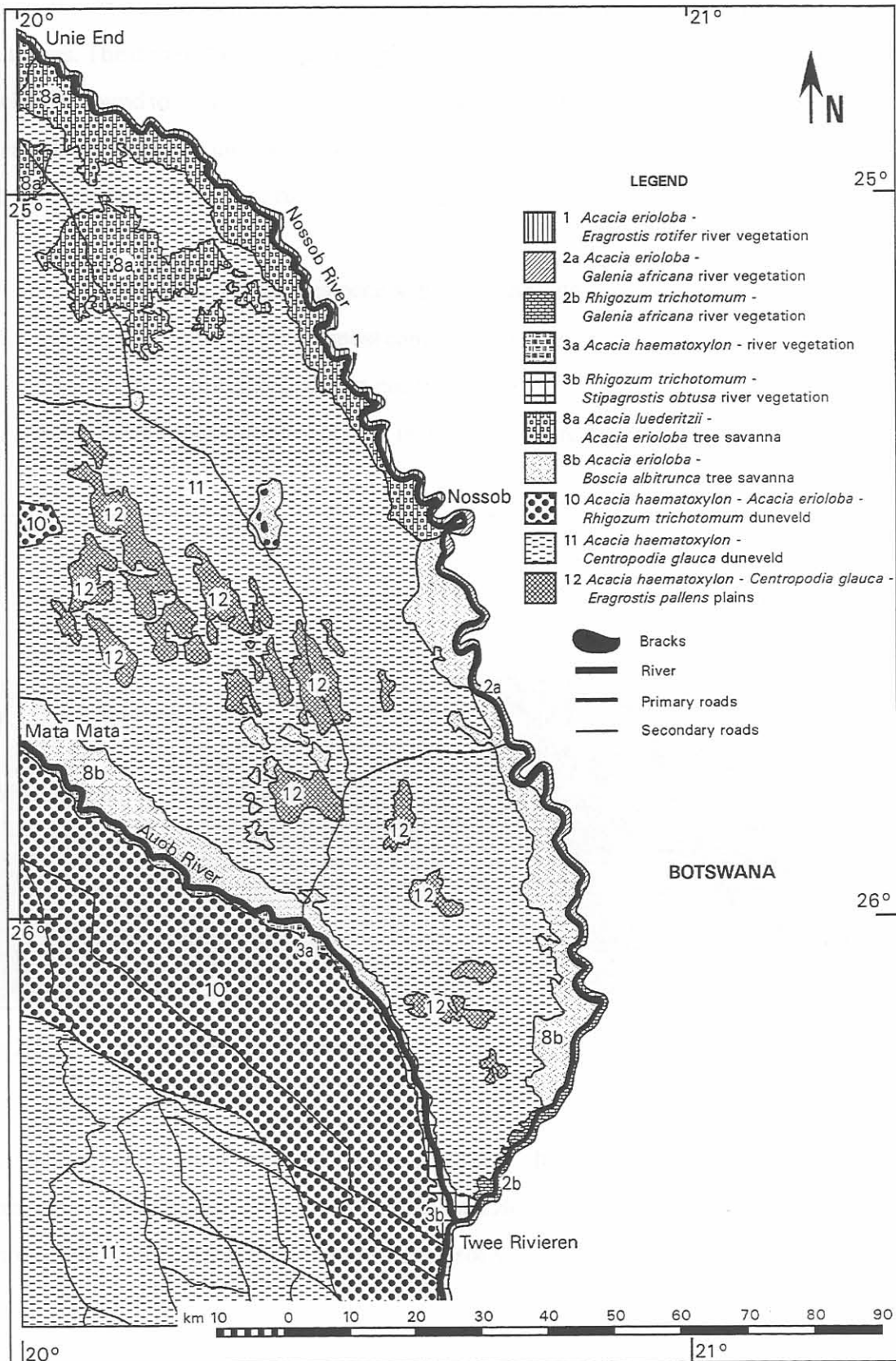
Figure 2.7   Vegetation types of the Kalahari Gemsbok National Park (after Lubbinge 1998).

Lubbinge (1998) subdivided the vegetation of the southern Kalahari duneveld into 33 plant communities. The duneveld consists of 17 plant communities and the rivers and pans of 16. The duneveld was found to be more species rich than the rivers and pans, but the rivers and pans have a higher species diversity/unit area than the duneveld. In the Kalahari Gemsbok National Park 10 of these vegetation types are represented (Figure 2.7).

The greatest diversity of communities occurs in those habitats where competition apparently is least. These habitats are also by far the most common and extensive ones in the southern Kalahari and are all savanna communities. In the northern parts of the park, a tree savanna of which *Acacia erioloba* is the most prominent tree, is present (Figure 2.8).

Figure 2.8 *Acacia erioloba*, **the dominant tree in the tree savanna in the northern parts of the Kalahari Gemsbok National Park.**

Huge *Acacia erioloba* trees are a distinctive feature of the riverine areas. In the central and southern parts of the Kalahari Gemsbok National Park *Acacia haematoxylon* becomes dominant and Karoo flora elements increase on the shallow soils.

CHAPTER 3

ACACIA ERIOLOBA IN THE
KALAHARI GEMSBOK NATIONAL PARK

3.1   NATURAL DISTRIBUTION

As useful pioneers, species of the genus *Acacia* are unrivalled by any other group of trees and shrubs in the combined importance of their distribution throughout the seasonally dry to arid regions of the African continent, their varied ecologies, their ability to colonize and rehabilitate degraded sites and fix sand dunes, and their relatively fast growth. They are commonly found throughout the continent and are of great ecological and socio-economic importance (Barnes & Fagg 1995).

Acacia erioloba is largely restricted in its natural occurrence to the Kalahari sand formations of the north-western and central side of southern Africa where it is often the only tree of any size and forms a conspicuous feature of the landscape (Figure 3.1) (Ross 1979; Barnes *et al.* 1997).

In the drier parts of its range, the tree establishes itself in rare periods of rainfall when the seed germinates, after passing through the digestive tract of a herbivore, and uses the transient surface moisture to send a taproot deep down to permanent water supply after which it is independent of annual rainfall and can live for hundreds of years. In these situations *Acacia erioloba* is often the only tree in the environment, whereas in the better watered parts, it is a component of savanna woodland communities (Barnes *et al.* 1997).

3.2   CHARACTERISTICS OF THE SPECIES

Acacia erioloba's habit varies from a small, very spiny shrub barely 2 m high, to a tree up to 16 m in height with a wide, spreading crown. The bark is grey to blackish-brown, rough, fissured often flaking off when old. Stipules are spinescent, with strongly developed spines up

20

to 60 cm in length. Leaves have 2 to 5 pairs of pinnae and the flowers are bright golden-yellow balls. The fruit is an indehiscent, thickened, comparatively short pod densely covered with grey velvety hairs (Palgrave 1977).

A detailed botanical description of *Acacia erioloba* is given by Barnes *et al.* (1997).

It has been recorded that *Acacia erioloba* has a deep root system. Timberlake (1980) recorded roots found at 46 metres deep in a borehole in Namibia. As a result of the deep root system, fluctuations in annual rainfall are buffered by the permanent access to ground water. Some of the water that is drawn from the depths is released into the surface soil enabling its shallow feeder roots to dissolve and absorb the accumulated nutrients. This water may also benefit the shrubs and annuals under its canopy (Milton & Dean 1999).
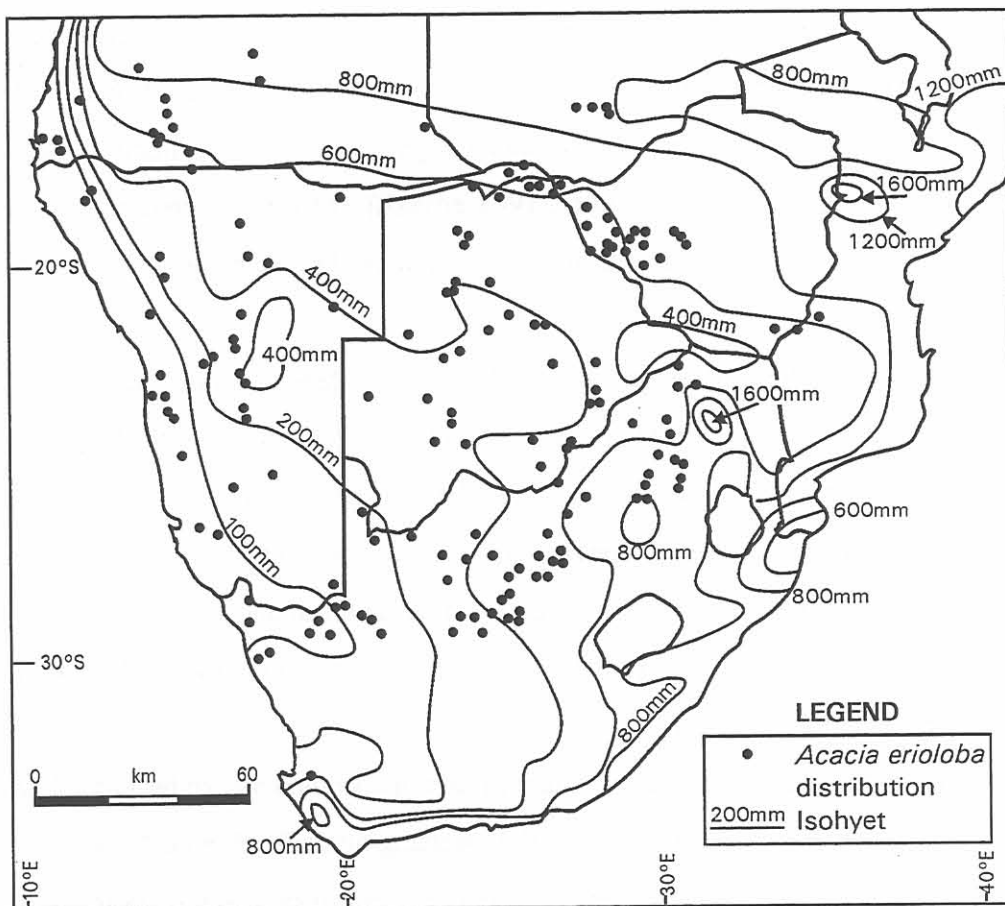
Figure 3.1 Distribution of *Acacia erioloba* (after Barnes *et al.* 1997).

Fluctuations in rainfall do not affect flower production. It is probably because of this that pod production is high and consistent from year to year compared to most other *Acacia* species. *Acacia erioloba* is insect pollinated (Barnes *et al.* 1997).

The highly variable rainfall and seasonality in the south-western range of *Acacia erioloba* apparently leads to episodic recruitment. Size-class distributions of *Acacia erioloba* populations indicate that seedlings germinate and survive more abundantly in high than in low rainfall years (Hoffman *et al.* 1995) and seedlings and saplings suffer high mortality rates in dry years (Van Rooyen *et al.* 1984, 1990; Theron *et al.* 1985).

Recruitment is spatially as well as temporally variable (Skarpe 1991). The presence of large quantities of scarified seed, or even germinated seedlings, does not necessarily guarantee survival. Other factors in the environment, such as rainfall distribution, grass competition and sizes of predatory insect and rodent populations, have to be favourable and coincide with the presence of scarified seed for successful stand establishment. Young *Acacia erioloba* trees tend to be closely spaced, while old trees are widely and randomly spaced. The spatial distribution has been attributed to competition and fire (Skarpe 1991), and can be simulated by spatially explicit models that include physical and biotic factors (Jeltsch *et al.* 1996).

In the Kalahari savanna, dense stands of small trees do not perform the same function as large, scattered trees (Milton & Dean 1995). Scholes and Walker (1993) suggest that episodic mortality of mature trees, through various agents of disturbance (fire, herbivory, drought, frost, lightning, wind and wood harvesting) prevent the trees from reaching the upper limit of density imposed by intertree competition, and thus maintain coexistence of trees and grass in savannas. This view is supported by the savanna model of Jeltsch *et al.* (1996). The simulation results also indicated that the scattered distribution of trees which is typical of a number of semi-arid savannas is probably not caused by the combination of inter and intraspecific competition for soil water or large-scale disturbances by fire and grazing. Jeltsch *et al.* (1996) hypothesised that the isolated distribution pattern of the trees is predetermined by other factors, e.g. small-scale heterogeneities in grass density, soil water or nutrient distribution. Trees in certain localities therefore have a better chance for establishment and survival. Another possible effect of small-scale hetero-

geneities is the local accumulation of tree seeds, which increases the establishment probabilities in these sites. Possible processes that leads to local tree seed accumulation in savannas range from rare but important floods (Ward & Breen 1983) to seed dispersal in herbivore dung (Leistner 1961; Hoffman *et al.* 1989).

Lightning fires occur only rarely, especially after years of above average rainfall and it is particularly the *Acacia erioloba* communities in the rivers that are damaged. Large fires can sweep through the Kalahari and burn down large *Acacia erioloba* trees. The occurrence and influence of fire on the vegetation of the Kalahari are also discussed by Van der Walt (1974,1975), Skarpe (1980), Van der Walt and Le Riche (1984) and Van Rooyen *et al.* (1996). In November 1976 the Nossob River valley was damaged by a fire originating from the interior duneveld (Van Rooyen *et al.* 1996). The influence of fires on spatial distribution is evident in the Nossob River valley. Numerous dead trees in the Nossob River valley bear testimony of the influence of fire (Figure 3.2). In the sites monitored by Van der Walt and Le Riche (1984), nearly 33% of the trees were destroyed while approximately 50% suffered from different intensities of burning. During November to December 1994, fires occurred in the central dune areas of the Kalahari Gemsbok National Park and affected approximately 35% of the total area of the park.

Mature trees do show some fire resistance, except where large social weaver nests occur in the crown and where a high percentage of dead material or rat nests increase fuel loads. When these are set alight by a fire they burn with such intense heat that the tree can be de-limbed or even completely destroyed. This apparently happened on large scale after the 1974 and 1976 rainy seasons when there were severe lightning fires. These fires were set off in the dense grass cover (*Setaria verticillata* and *Schmidtia kalihariensis*) that developed after the rain. There was a high correlation between tree size and death due to fire (Van der Walt & Le Riche 1984; Van Rooyen *et al.* 1996).
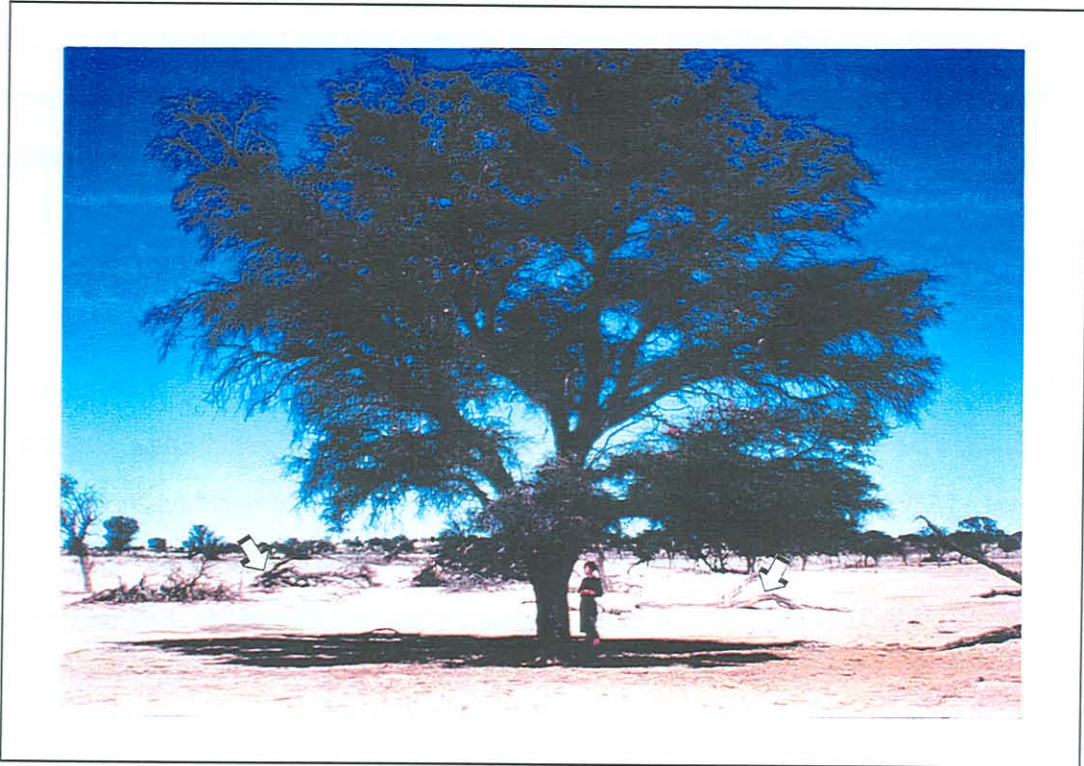
Figure 3.2 Numerous dead trees in the Nossob River valley bear testimony of fire damage.

3.3   CLIMATIC REQUIREMENTS

Where the annual rainfall is less than 250 mm, *Acacia erioloba* probably depends upon its extraordinary capacity to root to great depths to gain access to ground water supply. In these areas the presence of *Acacia erioloba* is said to indicate underground water (Timberlake 1980).

Acacia erioloba tolerates extremes of temperature in the desert region and it is soil rather than freezing conditions that provide the constraints to its distribution. It can probably withstand temperatures as low as -15°C to -20°C although flowerbuds may be damaged by less extreme temperatures (Barnes *et al.* 1997).

The ability of *Acacia* species to tolerate drought and adverse soil conditions, notably salinity and alkalinity, and their successful adaptation to herbivore pressure, are major reasons for their dominant position in the woody vegetation of arid and semi-arid areas (Fagg & Stewart 1994).

Although it was pointed out that mature *Acacia* trees have the ability to tolerate drought, Van Rooyen *et al.* (1984) pointed out that seedlings and saplings of *Acacia erioloba* in the Kalahari are sensitive to drought.

3.4   SOIL REQUIREMENTS

Throughout its range, *Acacia erioloba* is invariably confined to the wind-blown sandy soils on the Kalahari sand sheet. It reaches its best development on the deep alluvial soils in the valleys, drainage lines and riverbeds (Leistner 1967; Barnes *et al.* 1997; Acocks 1988). *Acacia erioloba* communities serve as indicators of deep Hutton soil form and are confined to soils generally deeper than 1 m. Although the sandy nature of the soil allows for maximum absorption of rain water, their water holding capacity is low (Van Rooyen & Burger 1974).

3.5   GROWTH PATTERNS

Acacia erioloba grows very slow for the first four or five years although it develops a deep root system during this period. After this the tree can grow quite rapidly and attain a stem diameter at ankle height in the region of 300 mm and a height of about 7 m after another 15 to 20 years (Barnes *et al.* 1997). On sandy soils saplings reach a height of up to 1 m in their first year.

The following is a diagrammatic representation of the life cycle of an *Acacia erioloba* tree as depicted by Milton and Dean (1999):
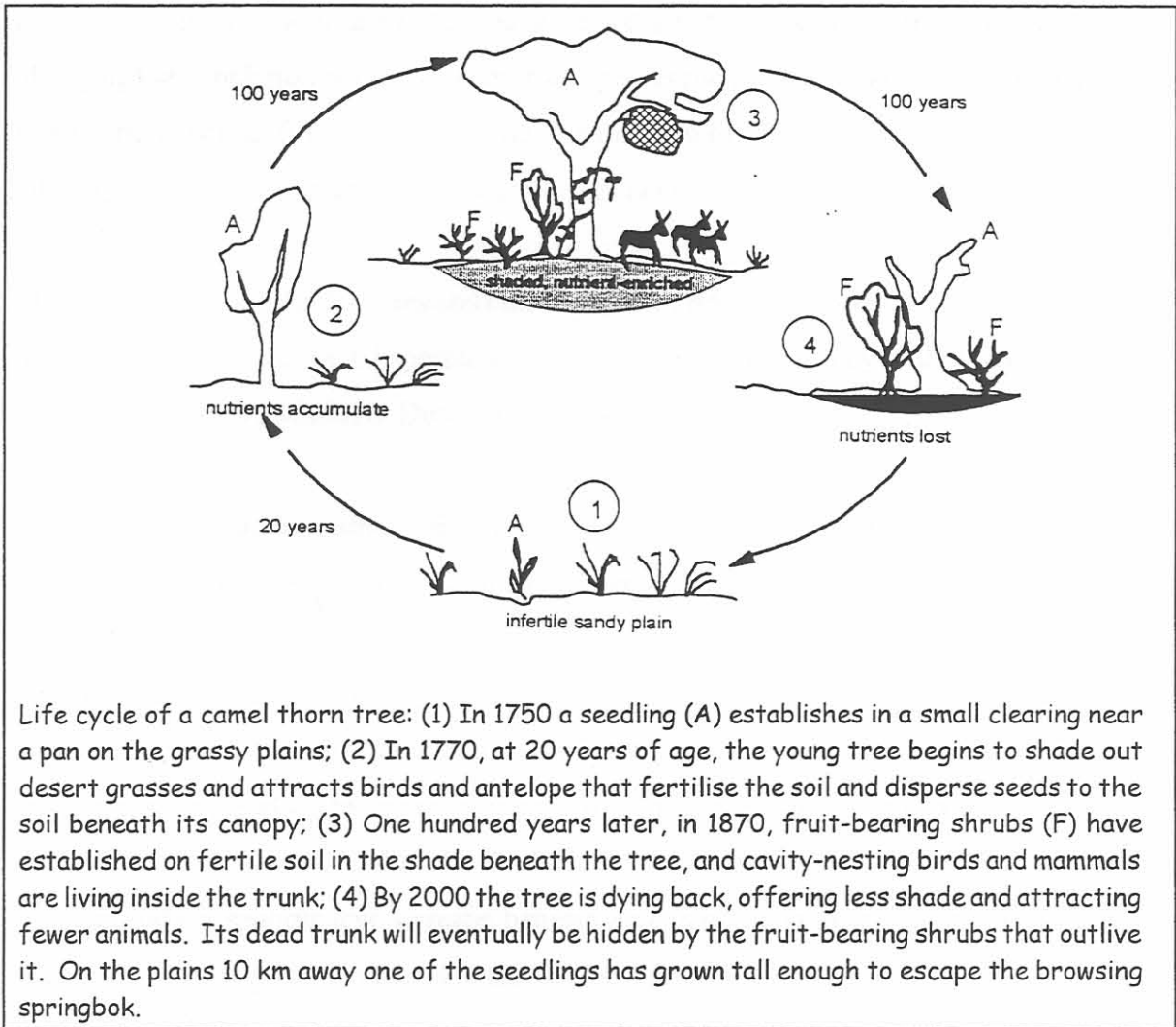
Life cycle of a camel thorn tree: (1) In 1750 a seedling (A) establishes in a small clearing near a pan on the grassy plains; (2) In 1770, at 20 years of age, the young tree begins to shade out desert grasses and attracts birds and antelope that fertilise the soil and disperse seeds to the soil beneath its canopy; (3) One hundred years later, in 1870, fruit-bearing shrubs (F) have established on fertile soil in the shade beneath the tree, and cavity-nesting birds and mammals are living inside the trunk; (4) By 2000 the tree is dying back, offering less shade and attracting fewer animals. Its dead trunk will eventually be hidden by the fruit-bearing shrubs that outlive it. On the plains 10 km away one of the seedlings has grown tall enough to escape the browsing springbok.

Figure 3.3 Life cycle of an *Acacia erioloba* tree (after Milton & Dean 1999).

3.6   ECOLOGICAL IMPORTANCE

Acacia erioloba is regarded as a keystone species in the Kalahari because it facilitates the processes (e.g. seed dispersal, site modification) which maintain heterogeneity and species diversity. Keystone species are defined as those species upon which many other plant and animal species depend (Milton & Dean 1995; Jeltsch *et al.* 1996).

The character of the Kalahari ecosystem depends on spatial heterogeneity (nutrient-rich, shaded islands) which increases biotic diversity in an otherwise exposed and oligotrophic system. The role of *Acacia erioloba* in generating patchiness depends on the structure of its population. By

role of *Acacia erioloba* in generating patchiness depends on the structure of its population. By changing the population structure of keystone species such as *Acacia erioloba* through management action such as fire and overgrazing, the function of the species in the ecosystem can be altered, indirectly influencing pattern and diversity (Barnes *et al.* 1997).

Many fleshy-fruited shrubs, trees and climbers grow under the canopies of old *Acacia erioloba* trees, where they have been dispersed to nutrient-rich, shaded sites by birds and jackals (Figure 3.3) (Leistner 1967; Milton & Dean 1995; 1999).

The life cycles of many animals, birds and insects are intimately bound up with *Acacia erioloba* wherever it occurs. The most extreme instances are in the most arid areas where the trees provide the primary, if not the only, source of food and shelter as evidenced by the tracks of large animals, e.g. the gemsbok, *Oryx gazelle* (Smithers 1983). Use of *Acacia erioloba* trees by birds and sheltering antelope and other animals, concentrates nutrients and disturbs the soils beneath the tree canopy, leading to the development of distinctive plant assemblages under the trees (Figure 3.3) (Leistner 1967; Milton & Dean 1995; 1999). Milton and Dean (1995) found carbon, nitrogen and phosphorus levels greater beneath *Acacia erioloba* trees than in soils from matrix vegetation in their study conducted in the Nossob River valley. Although these trees may bring nutrients from deep soil layers and distribute it on the surface in the form of litter, much of the nutrient enrichment of soils under the trees is probably the result of animal activity.

Of the many birds that are associated with *Acacia erioloba* the most conspicuous are two species of weavers that build large nests in the crowns of the trees. The sociable weaver, *Philetairus socius*, occurs in the west of the species' range and builds huge nests that make the tree vulnerable to fire. The white-browed sparrow weaver, *Plocapasser mahali*, occurs throughout the range of *Acacia erioloba* and builds smaller but numerous grass nests on the south-western side of trees that are over 3 m high.

Large *Acacia erioloba* trees also provide essential perches for large raptors, owls and vultures and cover for hunting leopards (Bothma & Le Riche 1984) (Figure 3.4).

Figure 3.4 Leopard (*Panthera pardus*) in an *Acacia erioloba* tree.

Although *Acacia erioloba* does not appear to nodulate, there is evidence that it draws nitrogen from deep ground water. It cycles nutrients from great depths and this provides conditions for the growth of nutritious grass species under and near its canopy. The trees and their associated herb and grass assemblages are often the only support for animal life in these environments (Barnes & Fagg 1995).

The relationship between *Acacia erioloba* and termites is clearly important for both insect and tree, but is not yet understood. Young trees are periodically encased in the earthworks when the termites remove dead bark, but they rarely damage the tree. It is possible that termite activity may play some role in what appears to be the allelopathic effect of *Acacia erioloba* (Milton & Dean 1995). In the literature studied no indication is given of any role played by termites in seed dispersal or scarification of seeds.

CHAPTER 4

LITERATURE REVIEW ON DENDROCHRONOLOGY

4.1   DENDROCHRONOLOGY AND ITS APPLICATION TO TROPICAL TREES

Dendrochronology can be defined as the science of dating annual growth layers (rings) in woody plants and the use of the information they contain to manage the plants and the environment (Fritts 1971).

Dendrochronology is based on the biological principle that a tree grows both apically and radially each growing season; the radial increase being visible as a distinct ring on a transverse section of certain trees (Curtis *et al.* 1979). It is well known that the age of a tree which produces annual growth-rings can be estimated by counting the rings present in a portion of the stem as close to the ground as possible (Fritts 1976).

The science of dendrochronology has centred around the strong tendency of coniferous trees in temperate areas to produce an identifiable layer of wood each year (Jacoby & Wagner 1993). However, in the tropics, sub-tropics and semi-arid regions, only an annual period of cambium dormancy, such as would be incurred by an extended dry season, would result in a similar growth pattern (Jacoby & Wagner 1993). The major difficulty in applying dendrochronological techniques to tropical areas has been in ascertaining if growth-rings are formed annually (Ogden 1981).

The ability to develop growth layers is determined by the genetic constitution of the particular species and is found in trees of both temperate and tropical zones. A growth layer is usually a product of one season's growth, but various environmental conditions may induce the formation of more than one growth layer in one season (Esau 1977).

Dendrochronologists are concerned with patterns of variability in tree ring width measurements, their correlation from tree to tree, site to site or their relationships to environmental influences, particularly climate (Ogden 1981). Moreover, a correlation of patterns of wide and narrow rings between trees can be used to establish the year in which the rings were formed. Such dating of rings is possible due to the fact that tree growth, in terms of changes in ring widths, is often affected by variations in climate (Fritts 1976; Curtis *et al*. 1979).

Stokes and Smiley (1968), as quoted in Curtis *et al*. (1979), pointed out that four conditions are imperative for a dendrochronological study:

- It is essential that only one ring be laid down per growing season.
- There must be one environmental factor which is dominant in limiting growth.
- The limiting factor must vary in intensity from year to year.
- The limiting factor must be uniformly effective over a large geographical area so that samples from different areas may be cross-dated.

The most suitable trees for dendrochronological studies are those growing in somewhat stressed environments or environments with significant seasonal variations, for example high altitude or semi-desert conditions. In these environments narrow rings occur as a result of slow growth. Any variation in moisture or temperature is reflected in the tree ring sequences, producing alternating wide and narrow ring-width patterns. In contrast, particularly in the tropics, the absence of seasons and of extremes in rainfall and temperature are largely responsible for poorly defined tree rings.

According to Wyant and Reid (1992), even though rings might be missing or poorly demarcated, dendrochronological techniques provide an improvement over size measurements for determining tree ages.

4.2   DENDROCHRONOLOGICAL POTENTIAL OF ANGIOSPERMS

The secondary vascular tissues in a tree are produced during the second major stage of plant development, in which an increase in thickness results from lateral additions of new tissues to

the axial parts of the plant. This results from the activity of the vascular cambium (Figure 4.1). Successive growth layers are formed. Each growth layer may be a product of one season's growth, but various environmental conditions may induce the formation of more than one growth layer in one season (Esau 1977, Fahn 1982).
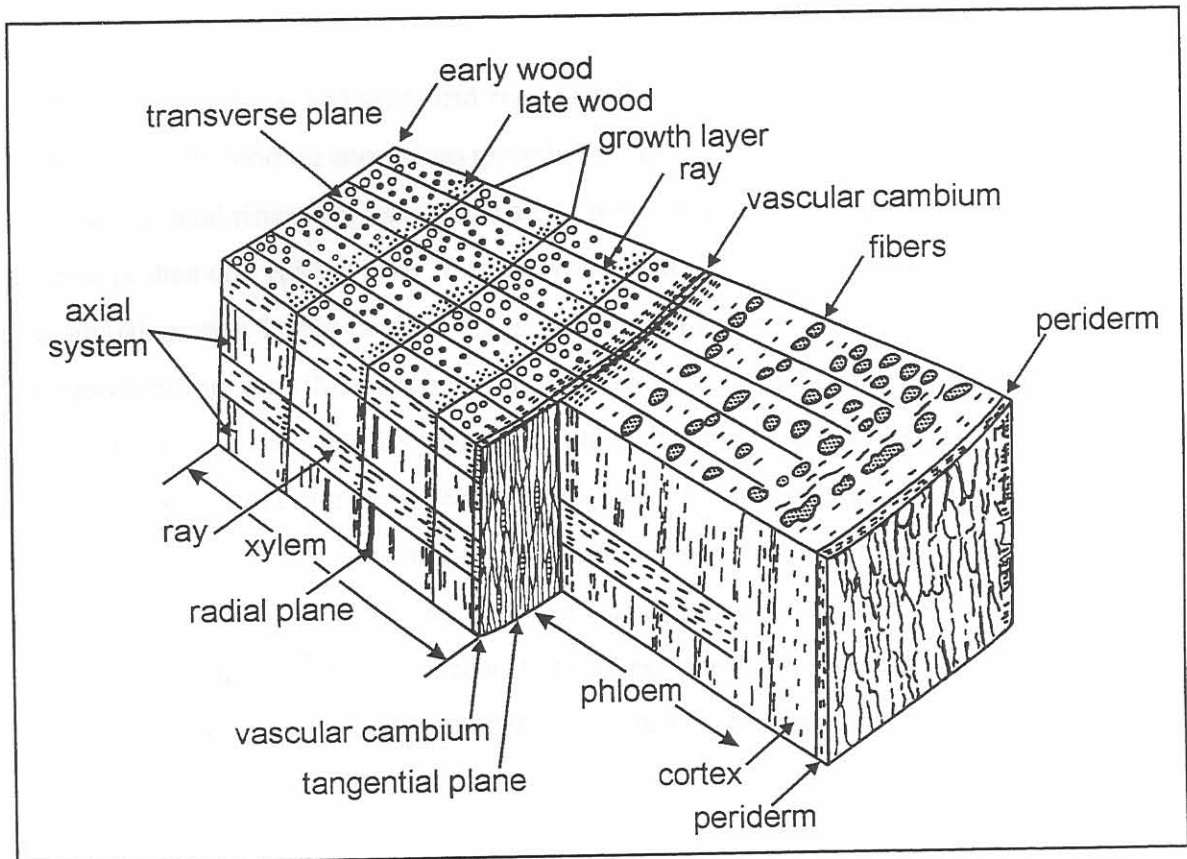
Figure 4.1 Block diagram illustrating basic features of secondary vascular tissues and their spatial relation to one another and to vascular cambium and periderm (after Esau 1977).

When conspicuous layering is present each growth layer is divisible into early and late wood (Figure 4.1). Early wood is the distinct inner component of a growth-ring, formed during the first part of the growing season whereas late wood constitutes the distinct outer component of the growth-ring. The early wood is less dense than the late wood because wider cells with thinner walls predominate in the early wood and narrower cells with thicker walls in the late wood (Esau 1977; Fahn 1982). The late wood forms a distinct boundary in a growth-ring because of its sharp contrast to the early wood of the following season, but the change from early wood to late wood of the same growth layer is more or less gradual. The earlier increments of secondary xylem

become nonfunctional in conduction and storage. The relative amounts of the non-functioning wood, the heartwood, vary in different species and are also affected by environmental conditions. The heartwood is the non-living and commonly darker-coloured wood at the centre of the tree, which can be distinguished from the outer living part of the trunk, the light-coloured sapwood (Esau 1977; Fahn 1982).

In tropical, sub-tropical and semi-arid regions the majority of trees are angiosperms. Angiosperms frequently produce anomalous growth patterns and rings which, for the most part, are not necessarily annual rings. For example, a stress period may occur during a growing season and cause more than one growth layer to form within that year. These growth features are termed intra-annual growth bands or false rings (Fritts 1976). Alternatively, when conditions are extremely limiting, growth cannot occur and no ring is produced. Locally absent or missing rings may occur during excessively dry years with little or no growth. Certain regions of the cambium may not divide at all giving the appearance of a missing ring (Fritts 1976; Lilly 1977; Curtis *et al*. 1979; Gourlay 1995). False rings are dark late wood- type bands in light early wood which give the appearance of an extra ring. The exact cause of false rings is not known, but may be related to sudden abnormal weather conditions, insect infestations, disease or some other factor temporarily halting growth (Curtis *et al*. 1979). Dating may be complicated due to the occurrence of missing and/or false rings.

Lilly (1977) noted that, unlike gymnosperms where a ring margin is clearly demarcated by a change in density, angiosperm ring margins can be delimited in various ways which are not equally distinct. In gymnosperms we find only two unfavourable growth features (false and missing rings), whereas in angiosperms there are five features which reduce the clarity of ring margins. Angiosperm wood is composed of a large variety of cell elements arranged in different ways and a standard angiosperm ring structure does not exist. Instead numerous combinations of cell types give rise to an infinite number of ring-structures.

Angiosperm ring-structures

The following five ring features can occur in any number of combinations (Lilly 1977):

- **Boundary/marginal parenchyma**

Certain species produce longitudinal parenchyma strands either at the end or the beginning of a growth season and are referred to as boundary or marginal parenchyma. The fineness of marginal parenchyma can be a disadvantage when it is blurred or hidden by dense paratracheal parenchyma. It is advantageous if marginal parenchyma is the only form of parenchyma present.

- **Ring porosity**

Ring porosity is the only form of angiosperm growth structure in which early wood and late wood are as well defined as in the gymnosperm growth-ring and where there is a similar marked change in density. It is due to this similarity that dendrochronologists have used ring-porous woods in preference to any other dicotyledonous wood structure. Lilly's (1977) survey of 115 species indigenous to South Africa indicated only one indigenous ring-porous tree i.e. *Celtis africana*.

- **Dense late wood lines**

Angiosperm growth-rings mostly consist of early wood with a fine late wood margin; unlike gymnosperm rings which are made up of two distinct sections. As the change in density is minimal, a sharp contrast is not produced between rings.

- **Semi-ring-porous structures**

It is generally agreed that a ring-porous structure consists of early wood pores which are both larger and more numerous than late wood pores and consequently form a well defined ring. Various gradations of ring-porous structure exist, four of which are specific enough to indicate a ring-structure:

  - tangential pore alignment;
  - diminution in pore size;
  - reduction in pore numbers; and
  - concentric zone devoid of pores.

- **Growth-related variations in parenchyma patterns**

Certain woods display variations in their distribution of longitudinal parenchyma. Only metatracheal and confluent parenchyma tend to be strongly modified as the growing season advances.

The marked changes in parenchyma distribution which indicate the positions of ring margins are:

- concentrations of metatracheal parenchyma;
- coalescence of confluent bands; and
- concentric zones free of parenchyma.

Generally, the clarity of ring margins outlined by variations in parenchyma distribution is highly variable. Frequently, only the approximate positions of ring boundaries are indicated. For this reason changes in parenchyma arrangement cannot be relied on as sole indicators of ring margins, although it is valuable as an additional feature which aids in highlighting and delimiting rings (Lilly 1977).

Only two of the five basic types of angiosperm growth-rings mentioned above are commonly recognised as ring-structures; these are ring porosity and an increase in wood fibre density. Of these only the former has been used in American and European dendrochronological studies. It can therefore not be taken for granted that the remaining four types of ring margins reliably delimit seasonal growth increments. The seasonality of these different forms of ring-structure within particular trees must first be determined before correlation between ring width and various environmental controls can be made (Lilly 1977).

The appearance of a particular type of angiosperm ring-structure does not automatically ensure that the wood is suitable for dendrochronological purposes. The manner in which the favourable and unfavourable anatomical features of angiosperm xylem interact must be taken into account when assessing the dendrochronological potential of a particular hardwood species (Lilly 1977).

Lilly (1977) devised a rating system taking into account all favourable and unfavourable characteristics in order to evaluate the ring-structures of indigenous woods. The criteria chosen for the rating system are listed in descending order of dendrochronological suitability (Table 4.1). These features contribute either positively or negatively to the clarity of the ring margins and have been rated accordingly. The summation of these positive and negative values equals the final dendrochronological rating (DR) (Table 4.1). The system ultimately determines which trees have a structural combination suitable for dendrochronological purposes.

Table 4.1   Criteria used in rating dendrochronological potential of indigenous South African plant species (after Lilly 1977)

Criterion Rating	Criteria
7	Slow growth rate (6-14 rings per cm)
6	Boundary parenchyma
5	Ring porosity
4	Denser late wood fibres
3	Semi-ring-porous structures
2	Growth-related variations in parenchyma patterns
1	Evidence of a ring-structure
0	Diffuse porosity
-1	Sapwood/heartwood differentiation
-2	Banded parenchyma
-3	False or disjointed rings
-4	Missing or discontinuous rings
-5	Indistinct boundaries
-6	Fast growth rate (3 rings per cm)
-7	Macroscopically deceptive ring pattern

Depending on the dendrochronological rating (DR) of a species it can then be divided into the following three categories:

(a) promising species: $DR > 5$;

(b) possible species: $0 \leq DR \leq 5$;

(c) rejected species: $DR < 0$.

Most indigenous angiosperms are hardwood species that impede coring (the standard method of collecting wood samples). They also have extremely complicated ring structures and many have no discernable structures at all. Lilly (1977) suggests that among South African angiosperms only *Albizia forbesii, Burkea africana, Clutia abyssinica, Ekebergia capensis, Fagara davyi, Rhus pyroides* and *Vepris undulata* show a sufficiently high dendrochronological potential to warrant further study.

Evaluating the dendrochronological potential of ring structures

According to Lilly (1977), wood anatomists do not always recognise boundary parenchyma as a ring-structure. Boundary parenchyma is frequently blurred or hidden by dense paratracheal parenchyma, especially if it is confluent or banded. Obviously it is advantageous if marginal parenchyma is the only form of parenchyma present. The fineness of marginal parenchyma can however be a disadvantage as the bands are not easily recognised when the ring structure is complex.

While a single layer of radially compressed fibres does create a definite boundary between rings, thicker-walled cells tend to produce a gradual transition between increments, which becomes increasingly apparent with higher magnification.

The following difficulties are faced in dendrochronological studies where identification and counting of marginal parenchyma bands (growth-rings) are used:

- confusion with other wood parenchyma (Détienne 1989; Gourlay & Kanowski 1991; Gourlay & Barnes 1994; Martin & Moss 1997);
- inability to be certain of the presence of a growth-ring where it can not be traced around the circumference (Jacoby 1989; Worbes 1989; Gourlay & Kanowski 1991; Gourlay & Barnes 1994);
- detecting rings where they are very narrow (Mariaux 1981; Détienne 1989);
- identifying rings near the cambium (Mariaux 1981);
- identifying rings near the pith (Fahn et al. 1981; Gourlay 1995);
- merging or dividing rings (Gourlay & Kanowski 1991; Martin & Moss 1997);
- different numbers on different radii (Mariaux 1981);
- false rings (Curtis et al. 1979; Fahn et al. 1981; Détienne 1989; Gourlay 1995);
- incomplete, discontinuous rings (Fahn et al. 1981; Ogden 1981; Gourlay & Kanowski 1991);
- dark heartwood and other changes in wood colouration (Gourlay & Kanowski 1991; Martin & Moss 1997);
- missing rings (Curtis et al. 1979; Détienne 1989; Wyant & Reid 1992; Gourlay 1995);

- variation in ring width (Worbes 1989); and
- rings with ill-defined boundaries (Ogden 1981).

## 4.3 DENDROCHRONOLOGICAL POTENTIAL OF INDIGENOUS AFRICAN TREES

The estimation of tree ages in southern Africa and in tropical, sub-tropical and semi-arid areas in general, has been problematic due to the lack of distinct growing seasons and corresponding climatic extremes. The lack of distinct ring boundaries and the frequency of anomalous growth patterns have hindered the science of dendrochronology in southern Africa. Little information is therefore available on growth-ring characteristics in indigenous trees.

Although dendrochronology is not a common practise in South Africa, attempts to introduce tree ring analysis have been made in neighbouring countries (Curtis *et al.* 1979). The earliest dendro-climatic investigations were carried out in Namibia by Walter (1940) who analysed the ring widths of *Acacia erioloba*. Although Walter could not identify growth-rings with certainty, he found that ring-width correlated positively with rainfall (Walter 1940).

In the wood of *Acacia erioloba*, ring margins are demarcated by strands of disjointed boundary parenchyma which are poorly defined. The distinctness of ring boundaries is further reduced by wide aliform-confluent parenchyma (Figure 4.2). This probably explains why Walter (1940) could not identify the growth-rings with certainty.

In investigations carried out by Guy (1969) in Zimbabwe on *Adansonia digitata*, no correlation was found between ring width and rainfall, although it was suggested that *Adansonia digitata* does offer some evidence that annual rings are produced.

In a preliminary dendrochronological study of seven indigenous species in Zimbabwe, Storry (1975) found five of the species i.e., *Rapanea melanophloeos, Macaranga capensis, Maesa lanceolata, Hypericum revolutum* and *Acacia abyssinica* unsuitable for normal dating techniques because no recognisable growth patterns could be distinguished in the sample cores. Storry (1975) also recorded the difficulty of obtaining suitable cores.
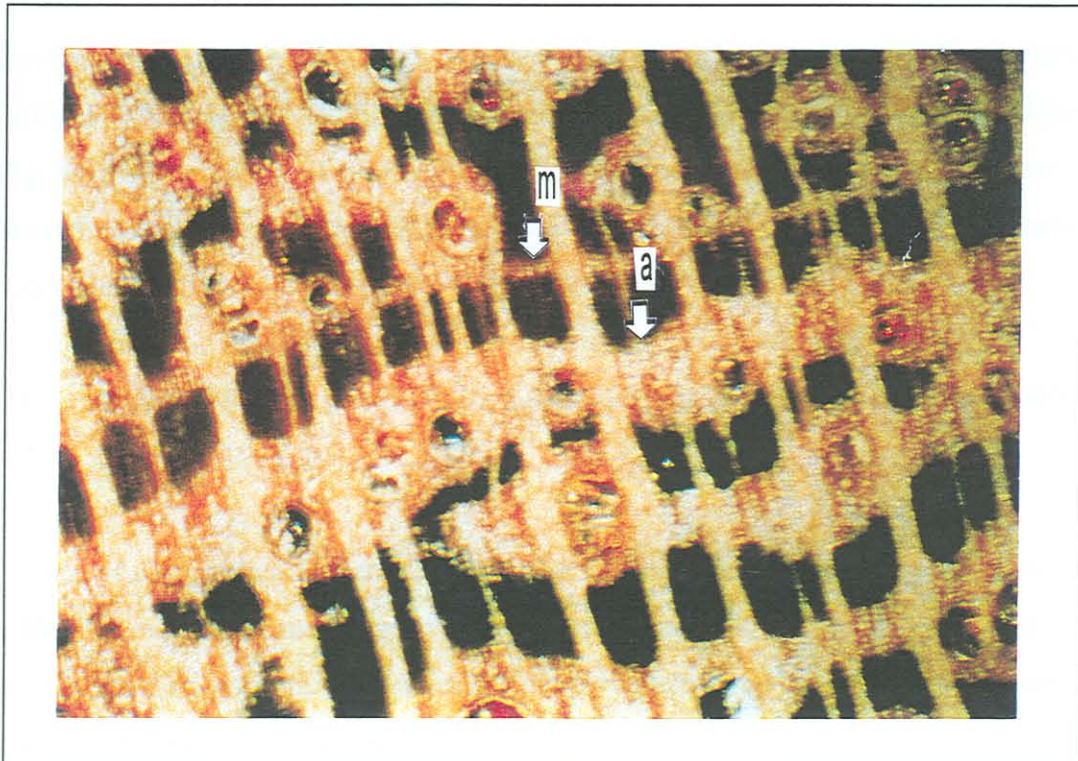
Figure 4.2 Wide aliform-confluent (a) parenchyma and thin marginal (m) parenchyma visible in a transverse section of a sanded disc of *Acacia erioloba* from the Kalahari Gemsbok National Park (4x magnification).

According to Lilly (1977) macroscopic and microscopic characteristics of the wood anatomy of a very limited number of southern African trees were described in early publications. However a comprehensive microscopic identification key which describes transverse, radial and tangential surfaces of 136 of South Africa's most important indigenous trees was subsequently compiled by Kromhout (1975). Unfortunately, although the occurrence of distinctive rings is mentioned, Kromhout gives no definite information on the appearance of ring-structures. A survey by Lilly (1977) to determine the dendrochronological potential of 108 South African tree species, is probably the most extensive on African tree species. Lilly (1977) concluded that indigenous tree species in South Africa are not as well suited to dendrochronological studies as their European and North American counterparts. Lilly's work was followed by a study of the wood anatomy of 37 *Acacia* spp. by Robbertse *et al*. (1980).

Tree ring research in southern Africa appears to have been hampered by a lack of suitable species (Lilly 1977; Curtis *et al*. 1979). Problems encountered include indistinct ring boundaries, severe ring wedging and short life spans (Norton 1990). The occurrence of clearly defined boundary parenchyma in a few hardwood species however does indicate their possible successful application in dendrochronological work.

4.4 ANATOMICAL FEATURES USEFUL IN DEFINING GROWTH ZONES IN *ACACIA* SPECIES

The specific anatomical characters responsible for delineating growth-rings vary greatly between different tree species, and the growth zone is often incomplete when traced around the circumference of a disc. Anatomical features that clearly denote annual growth-rings in temperate trees, such as ring-porous wood and pronounced cell-wall thickness and dimensional changes, are uncommon in tropical species. Tropical woods are typically diffuse in their anatomical structure and exhibit predominantly parenchyma (Gourlay 1992).

4.4.1 MARGINAL PARENCHYMA

Several forms of parenchyma occur in *Acacia* species. The two main forms of banded parenchyma are apotracheal bands, which are independent of the vessels, and paratracheal bands which are associated with the vessels. Both forms can complicate the determination of growth-rings by producing light coloured concentric bands that give the appearance, to the inexperienced observer, of regular growth-rings. Irregular convoluted paratracheal bands, much broader than the marginal parenchyma, often obscure the much finer marginal parenchyma bands (Figure 4.3) (Gourlay 1995).

It is generally accepted by botanists that marginal parenchyma is either initial or terminal; that is, it occurs at the beginning or the end of a growth-ring (Lilly 1977). Parenchyma formation and reduced vessel size appear to correspond with slow growth, which can arise through a variety of environmental stresses (Ogden 1981).
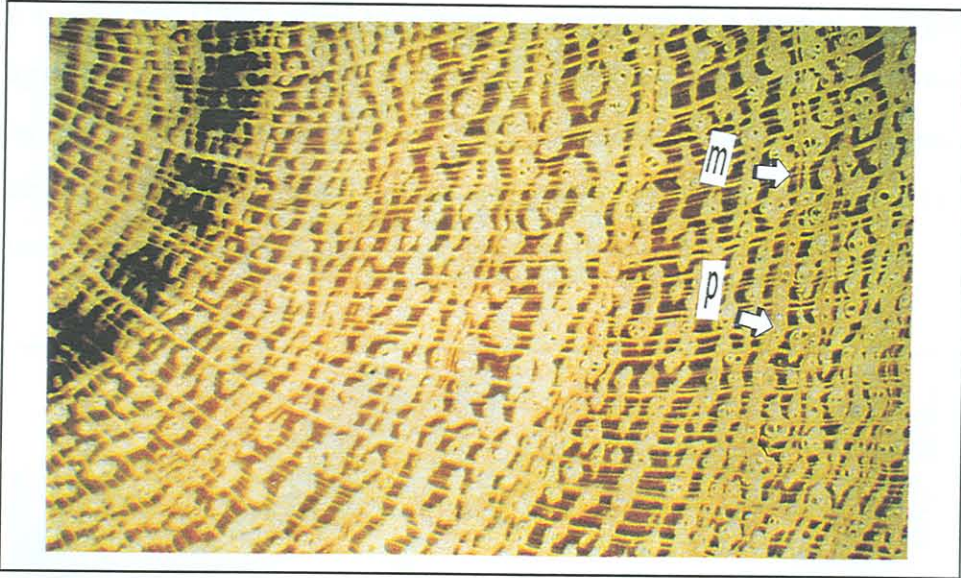
Figure 4.3 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park showing marginal (m) parenchyma bands obscured by broader, convoluted paratracheal (p) bands.

According to Mariaux (1975), as quoted in Gourlay (1995), the paratracheal bands produce patterns of decreasing and increasing frequencies at a growth-ring boundary where the feature positively assists in identifying the growth-ring zone (Figure 4.4).
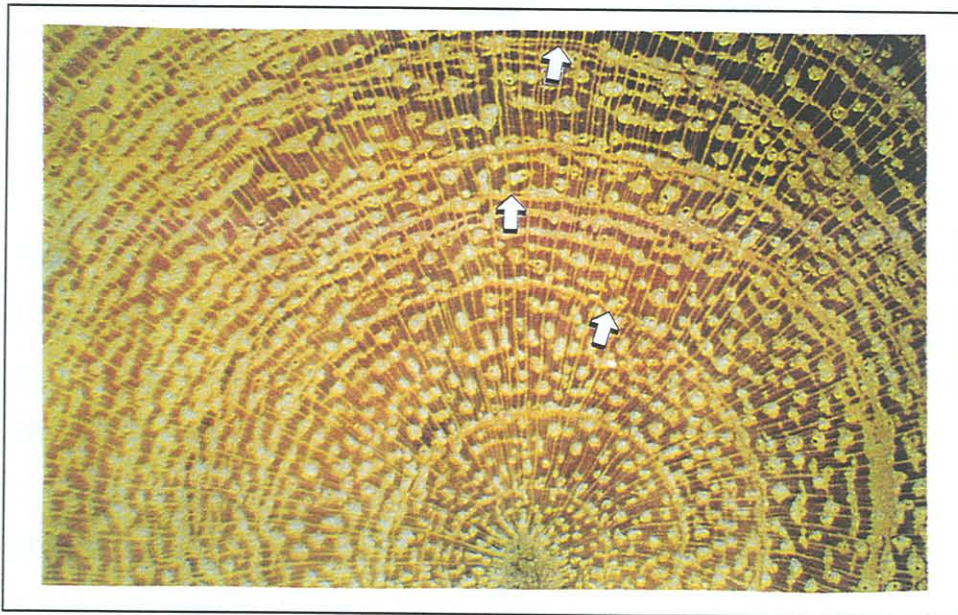

Figure 4.4 Growth-ring boundaries (arrows) clearly visible on a transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park (1x magnification).

The IAWA Committee (1989) refers to marginal parenchyma as a form of axial parenchyma produced by some tree species in bands (a more or less continuous layer of variable width) at the beginning or end of a growth season. Gourlay (1995) describes these bands as commonly composed of less than five rows of parenchyma cells (Figure 4.5) forming a continuous layer visible on the transverse surface as a fine light-coloured band (Figure 4.6).
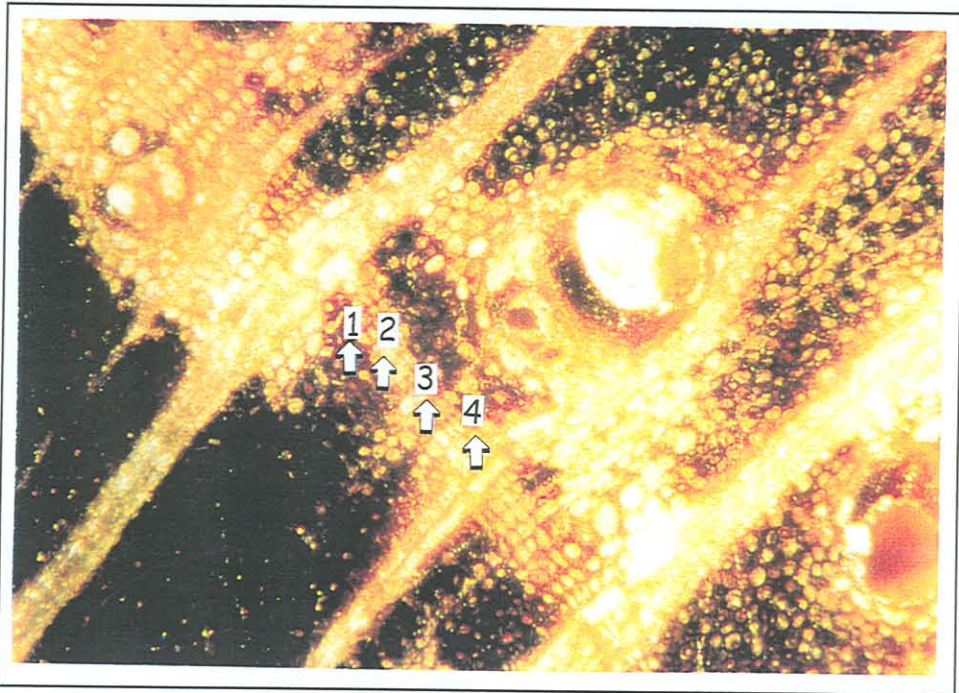
Figure 4.5 Transverse section of marginal parenchyma composed of 4-5 rows of cells (arrow) of a sample of *Acacia erioloba* from the Kalahari Gemsbok National Park (10x magnification).

Worbes (1989) recorded that particular ring types are dominant in certain families. The growth zones of all Fabaceae are for example separated by marginal parenchyma bands. In many trees of the family Fabaceae these bands of continuous marginal parenchyma are filled with amorphous substances or crystals.

Gourlay and Kanowski (1991) examined the growth-rings of six African *Acacia* species. Rings were apparent in most species as narrow bands of marginal parenchyma filled with long crystal chains. The marginal parenchyma bands are extremely difficult to detect due to the presence of aliform-confluent parenchyma, a feature common to most *Acacia* species. The broad bands often mask the finer marginal bands (Figure 4.3). A further complication sometimes arises in the form

of merging and or partial rings. They also found that in *Acacia erioloba* marginal parenchyma bands were quite clear with small concentrations of crystals in the marginal parenchyma.
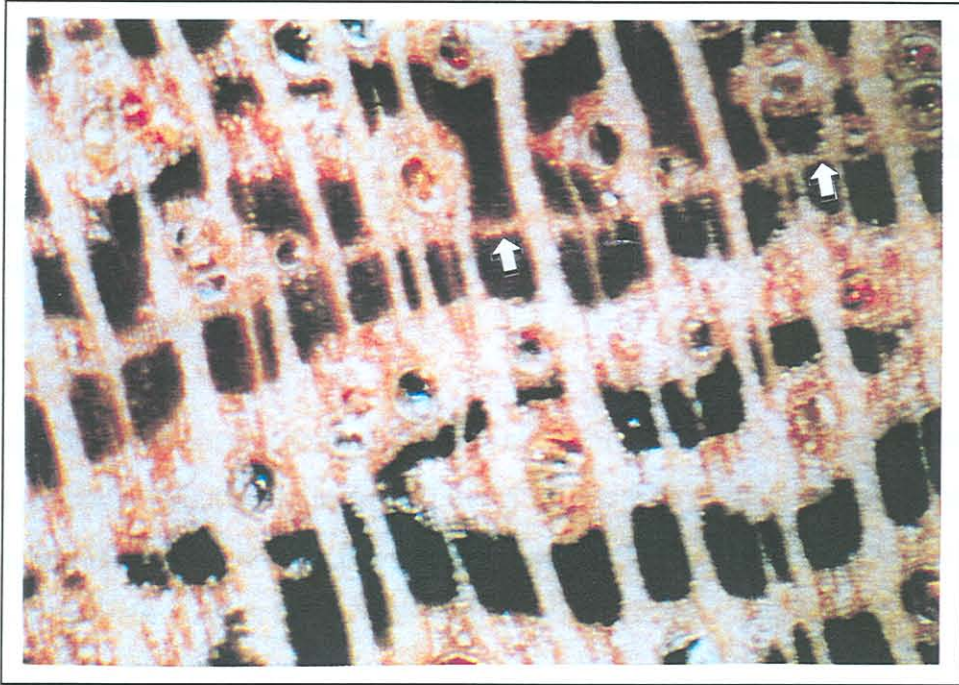
Figure 4.6 **Marginal parenchyma visible as a fine light-coloured band (arrows) in a transverse view of *Acacia erioloba* from the Kalahari Gemsbok National Park (4x magnification).**

A wide variety of anatomical features define the resulting growth-ring, including early wood/ late wood transitions, bands of marginal parenchyma, alternating patterns of parenchyma and fibres and ring porous structures (Worbes 1989). Détienne (1989) remarks that well-marked boundaries of annual growth-rings are those delimited by marginal bands of parenchyma. These bands are easy to detect in species having mostly paratracheal or apotracheal parenchyma in short bands.

Mariaux (1975), as quoted in Gourlay (1995), suggested that in *Acacia radiana* the real limits of growth are indicated by a very fine line of parenchyma (Figure 4.6), comprised of very flat cells which appear among the fibres where the line rejoins the paratracheal parenchyma. He found it necessary to follow the broad bands of parenchyma to assure himself that a fine line was not associated with them. The number of rings found in most trees was less than that commonly assumed for such trees in an arid environment.

Research by Wyant and Reid (1992) on *Acacia tortilis* in Turkana District, Kenya, demonstrated a significant (r = 0.90) linear relationship between ring count and known tree age. However, they did not identify the anatomical features responsible for this band or qualify its dependence on water by correlating the ring widths with rainfall. They suggested that there is a good possibility that ages of tropical trees can be determined by ring counts in ecosystems with a strongly seasonal, unimodal rainfall pattern. Even though rings may not form every year, the frequency of missing rings may be related to drought frequencies. They found approximately one missing ring for every 3-4 years of growth. This corresponded with the frequency of annual drought, as confirmed by climatic records.

Gourlay (1995) counted rings from individuals of a number of *Acacia* species of known planting date and generally found their number to be slightly less than or equal to the known age in areas with a unimodal rainfall pattern. For trees from areas of bimodal rainfall the number of rings corresponded to the number of peaks in local rainfall records.

On examining *Acacia karroo* it was established that the marginal parenchyma bands were laid down at the beginning of the dry season when wood production ceases (Gourlay 1992). This was also stressed by Ogden (1981), who pointed out that these bands could be formed during times of stress.

Kromhout (1975) described the parenchyma in 13 South African *Acacia* species, including *Acacia erioloba,* as mainly paratracheal and with an indication of marginal parenchyma.

Lilly (1977) gave *Acacia erioloba* a dendrochronological rating of 0 (see Table 4.1). She identified the following tree ring characteristics: boundary parenchyma (6), evidence of a ring structure (1), diffuse porosity (0), banded parenchyma (-2) and indistinct boundaries (-5). She concluded that *Acacia erioloba* could be of possible use in dendrochronological studies.

Robbertse *et al.* (1980) reported growth-rings, consisting of flattened marginal parenchyma or thick-walled fibres present in most species of the sub-genus *Aculeiferum* and a few species of the subgenus *Acacia*. They found banded parenchyma and growth-rings in *Acacia erioloba*.

4.4.2 CRYSTALLIFEROUS CHAINS IN PARENCHYMA

The presence of calcium oxalate crystals in woody tissue is quite common, and their size, quantity and distribution may be used in wood anatomical identification and classification (Chattaway 1956; IAWA Committee 1989; Gourlay & Grime 1994). Crystals in African *Acacia* species have been documented by several authors (Chattaway 1956; Kromhout 1975, Robbertse *et al.* 1980; Fahn *et al.* 1981; Gourlay & Grime 1994).

In African *Acacia* species where samples did not display clear bands of marginal parenchyma, it was possible to define rings by taking radial sections of the complete radius and identifying the crystalliferous chains. In a dendrochronological study of several African *Acacia* species, Crystals are more numerous in arid zone species and occur at the termination of growth periods in some species (Fahn *et al.* 1981; Gourlay & Grime 1994). These crystals proved to be of great value in establishing the presence of a growth-ring in samples where clear bands of marginal parenchyma are not displayed (Gourlay & Grime 1994). By means of a scanning proton microprobe the crystals were subsequently identified as calcium oxalate (CaC_2O_4). The presence of crystals is apparently associated with certain plant families. In the Cactaceae and Chenopodiaceae, the content can reach more than 10% of the dry weight of the wood (Fahn *et al.* 1981).

Prior and Cutler (1992) suggested that the presence of oxygen-bearing calcium oxalate crystals in Zimbabwean *Acacia karroo*, *Acacia tortilis*, *Colophospermum mopane* and *Combretum apiculatum* is a key factor in wood quality and has an important influence on the fire retardant properties in these species as it acts as a flame retardant and promotes a glowing combustion. Calcium oxalate (CaC_2O_4) crystals are formed when tree roots absorb salt-rich water from the soil. The tree removes any excess calcium ions, which combine with oxalic acid, a constituent of cell sap, to produce insoluble calcium oxalate. The calcium oxalate is then stored as large prismatic crystals in many parts of the plant. The presence of calcium oxalate crystals also makes tropical trees less palatable to termites.

John (1990), as quoted by Gourlay (1995), found that, in *Acacia nilotica* subsp. *kraussiana* from Swaziland, growth-rings were sometimes indistinct, although usually marked by a band of marginal parenchyma. The late wood was frequently rich in crystalliferous cells. She also found that

the chemical composition or the physical structure of fibre walls often changed abruptly at growth-ring boundaries. The quantity of crystals appeared to increase in the late wood and also in samples from sites with a high level of exchangeable calcium. However, crystal numbers per unit area varied even on some sites with similar soil types and with the same levels of calcium and magnesium in the soil. The only observable difference in these sites appeared to be water availability. She also noted that the crystals increased in quantity with the dryness of the site. At sites where the crystals were more numerous, growth-rings were more clearly defined.

4.5 RELATIONSHIP BETWEEN WOOD ANATOMY AND CLIMATIC VARIABLES

A primary cause of annual ring variations in trees is climate. If the climate is consistent over large enough areas, trees will cross-date over distances from tens to hundreds of kilometres (Jacoby & Wagner 1993). A problem in studying environmental effects on growth is that the relative importance of an environmental factor can change during the growing season (Kramer & Kozlowski 1979). Conditions preceding the growing season sometimes have a greater influence on ring width than conditions during the growing season. The relative effects of these factors on growth vary with latitude, altitude and environmental factors at the site. Climatic factors are sometimes directly related to the growth and at other times are inversely related to growth. Statistical methods are employed for ascertaining these differences in the climatic response of trees from different sites (Fritts 1971; Kramer & Kozlowski 1979).

An abrupt change in the environment does not alter growth similarly in all trees of the same species in a stand. This may be the result of differences among trees in exposure, crown size, depth of rooting, inherent growth characteristics, and other causes, including micro-environmental heterogeneity (Kramer & Kozlowski 1979).

Numerous studies applying dendrochronological techniques to temperate species suggest that wood anatomy provides a lasting and reasonably accurate record of trees' reaction to the environment (Schweingruber 1988). The reaction mechanisms in trees are very complicated (Figure 4.7). Chain reactions are set up between the influencing environmental factors and the parts of the tree which react to these influences (Fritts 1971).

Figure 4.7   **Physiological model illustrating how low precipitation and high temperature during the growing season (season of cambial activity) may cause a ring to be narrow for conifers growing on semi-arid and warm sites** (after Fritts 1971).

Physiological processes initiated by a change in the environment eventually become directly measurable as a growth change or evident in the variation of such features as tree ring width. Growth-rings can therefore be used to investigate relationships between tree growth and climate by comparing annual variations in ring width with annual variations in the climate of the area of study (Fritts 1976). Schweingruber (1988) agrees that the growth-rings of trees are of ecological significance because of the periodicity of their formation. Growth-rings can therefore be related to age.

Although periodic cambial growth in tropical trees is genetically determined, it can be influenced by climate. While the phenological patterns of shoot development are linked to periodicity of cambial activity, the exogenous influences, other than temperature, are only likely to affect the cambium directly. Of all the climatic factors, temperature plays the major role in regulating the cambial activity and phenological events. In desert conditions however, the amount of water in the soil becomes the limiting factor (Mushove *et al.* 1995).

In general rainfall is the dominant factor in determining growth in arid regions (Fahn *et al.* 1981; Mushove *et al.* 1995). Ring formation in *Acacia* species is closely associated with changes in water availability (Gourlay 1995). In their study of African *Acacia* spp., Gourlay and Kanowski (1991) found that in samples originating from climatic zones with a single wet season, the number of marginal parenchyma bands approximated the age of the tree. In samples originating from bimodal climatic zones, the number of marginal bands were more or less twice the age of the tree. Ring widths correlated highly with total annual rainfall (Gourlay 1995).

Mushove *et al.* (1995) examined wood samples of *Colophospermum mopane* and *Combretum apiculatum* from four sites for growth increments. Increments were small and sometimes difficult to discern, so measurements were made to the nearest 0,1 mm. In contrast to the studies on *Acacia* spp., it was shown that rainfall and its corresponding interactions with site and species were of no significance in explaining differences in tree ring widths.

Gourlay and Kanowski (1991) stress that the development of ecological understanding and sustainable management practises for the natural tropical forests depend partly, on reliable means of estimating the age and growth rate of trees, but are quick to point out how difficult the identification of growth-rings in certain tropical species can be. Others working on the wood anatomy of tropical trees also agree that it can be difficult to establish whether all visible growth-rings in tropical trees correspond to annual increments (Lilly 1977; Ogden 1981; Van Daalen *et al.* 1992).

The primary problem in tropical tree ring analysis is the frequent lack of well-defined cyclical growth-rings. Absence of seasonality (which induces dormancy and associated anatomical change) is the main reason for this problem. Temperatures are relatively uniform throughout the year and the daily temperature fluctuations often exceed the annual fluctuations. There is no annual cold season to induce dormancy in the trees (Fritts 1976).

Boundaries of annual growth-rings are always formed during the longest dry season and clearly express the rhythm of cambial activity. The appearance and nature of these growth-rings vary according to genera rather than types of climate (Détienne 1989).

The widths of growth-rings in woody plants can serve as natural records of climate when they vary as a function of some limiting factor. In arid and semi-arid regions, ring widths have been shown to vary directly with the intensity and duration of drought. In mature trees on arid sites a growth layer may have approximately the same average width throughout the main stem except in the uppermost, exposed portions of the tree where it is often narrower (Fritts 1971).

In cases where rings are not formed every year, the frequency of missing rings may be related to drought frequencies. Extensive cross-dating should account for missing rings (Fritts 1971).

Tree rings are the most geographically widespread entity that can provide actual year-to-year-dating of current and prehistoric environmental changes (Jacoby & Wagner 1993).

4.6   ALTERNATIVE METHODS OF DETERMINING AGE

4.6.1   STEM DIAMETER AND HEIGHT

In most studies of forest tree dynamics it is common practise to age a sample of the trees studied. Using the resultant age-diameter relationship, the ages of the remaining trees are then estimated based on their diameters. There are, however, some serious limitations associated with this approach. Because of the considerable uncertainties involved in determining the age of individual trees, an unavoidable error is built into the age-diameter model. The magnitude of this error is usually unknown (Norton & Ogden 1990).

In many cases age and diameter are not closely related. This arises largely because competition among trees causes marked differences in growth rates and is often best seen in even-aged stands where a wide variation in diameters can be found. Clearly there are very real limitations in the use of size class data to determine age structures. Even if the relationship between age and diameter is statistically significant, as it often is, it may still be misleading to predict age from diameter because of the large variance in age for any diameter class (Norton & Ogden 1990).

Phenological observations may be very helpful in denoting species and locations where a definite cessation of growth would be likely to produce an anatomical feature marking dormancy and

restart of radial growth. Some phenological studies include recordings of diameter growth, although diameter changes often respond to hydration and dehydration rather than cell division. Hydration and dehydration can occur on a daily and seasonal basis and such variations must be considered in diameter growth studies (Jacoby 1989).

Early work on diameter measurement and anatomical studies is reviewed by Mariaux (1981) and Fahn *et al.* (1981).

Nicholson (1965), as quoted by Ogden (1981), stressed that in natural forest stands radial growth increments vary greatly between individuals within species and size classes. He reasoned that a more reliable estimate of age might be obtained by averaging only the fastest growing individuals in a size class in proportion to their representation in the size class above.

In their study of *Acacia tortilis* in South Turkana, Kenya, Wyant and Reid (1992) found that although the correlation between basal stem diameter and known age is high, stem diameter may be useful only for predicting the age of young trees. After about 10 years the scatter around the regression line becomes large.

These difficulties clearly highlight the need for careful sampling and sample analysis in age determinations. Where possible the utilization of cross-dating techniques will greatly increase the accuracy of the age estimates. These will assist in obtaining more accurate information on the ecology and dynamics of forest trees (Fritts 1971; Norton & Ogden 1990).

4.6.2 RADIOCARBON DATING

During an international workshop entitled "Age and growth rate of tropical trees: New directions for research", Stuiver *et al.* (1981) proposed the use of radiocarbon to establish age and growth rates in tropical trees.

There are three isotopes of carbon which occur in nature: two stable isotopes, ^{12}C and ^{13}C and the unstable or radioactive isotope ^{14}C. The latter is produced in the atmosphere by cosmic rays and,

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after oxidation, is mixed with the carbon dioxide in the air. Through photosynthesis this isotope mixture is incorporated into living plants and, subsequently through consumption into the bodies of animals (Vogel 1969). The organic compounds in living organisms thus acquire a defined relative concentration of radioactive ^{14}C. The ^{14}C level of the carbon in such compounds will then slowly decrease by radioactive decay with a half-life of 5730 years. This forms the basis of the radiocarbon dating technique. By measuring the ^{14}C level in such material the age can be calculated. The statistical uncertainty of the age is normally ±50 years or in the case of high-precision dating ±20 years can be achieved.

Initially it was assumed that the cosmic ray flux and therefore the ^{14}C level in the atmosphere had remained constant in the past. It was found, however, that fluctuations did occur through time and adjustments need to be made to the radiocarbon ages to arrive at the historical date (De Vries 1958). For trees older than 350 years this calibration is usually straight forward, but in the period between 1650 and 1955 relatively large variations did occur and a precise date cannot be given. In the ageing of a tree calibrated dates can, however, be obtained by analysing two or three samples at increasing radial depth through the trunk (Talma & Vogel 1993). The calibration curve for this time-period is shown in Figure 4.8.
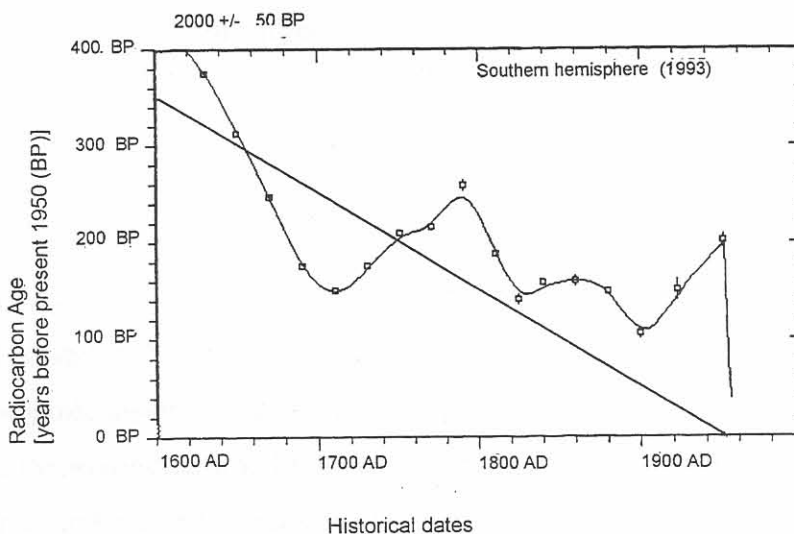
Figure 4.8 Calibration curve for ^{14}C age in years before present (BP) 1950 for the southern hemisphere. (The diagonal line gives the expected correlation between historical dates and ^{14}C age in the case of a 1:1 correlation. The curved line shows the actual calibration curve for the period 1600 AD to 1950 AD).

In the second half of the 20th century the situation changed completely. The atmospheric nuclear weapon tests conducted between 1954 and 1962 drastically increased the ^{14}C content of the environment. The effect of this artificial ^{14}C on the carbon dioxide in the air is shown in Figure 4.9. In the southern hemisphere the level reached a value of 65% above normal in 1965 and has subsequently gradually decreased to about 10% above normal in 1998 (Vogel 1971; Vogel *pers. comm.* 1998[1]). Using this curve for calibration, material in this time range can be dated to ±1 year (Figure 4.9).
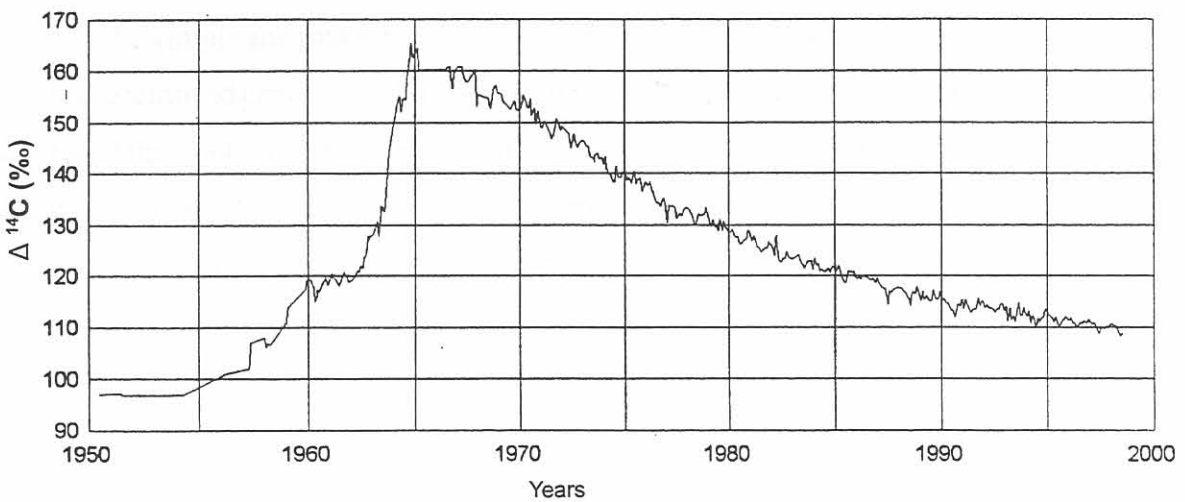
Figure 4.9 ^{14}C content of atmospheric carbon dioxide in recent years, expressed in per mille above normal, extended (after Vogel 1971).

Owing to the variations in the atmospheric ^{14}C level briefly outlined above, radiocarbon dating of plant material may involve considerable effort. In determining the age of a tree the first step would be to date the inner annual growth-rings of the trunk (Vogel 1971; Ogden 1981). If the age lies between 130 and 230 years, two or three further samples along the radius would indicate which of the possible historical dates actually apply to the core. With sufficient measurements one can locate the individual wood sample on the ^{14}C curve for recent decades. One can also place the samples in time and interpolate or extrapolate for ages of other portions on the same radius of the sample. If one assumes a relatively uniform, or at least predictable, growth rate

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[1] Vogel, J.C. Quaternary Dating Research Unit, Division of Water, Environment and Forestry Technology, CSIR, Pretoria, South Africa

through time, the age of the tree can be estimated. ^{14}C measurements are expensive and it is possible to estimate growth rates by using only two samples of the same radial dimension (Jacoby 1989). Lacking this, other considerations may be used to arrive at the "most probable" age for the specimen.

With the dating of wood there arises a further complication in that the sample may contain organic matter that is younger than the annual rings themselves. During the formation of the heartwood, organic substances that are up to 20 years younger than the annual rings are deposited in the cells. If this organic carbon derives from after 1957 this would significantly increase the ^{14}C level of the sample and make it appear younger. As a rule all organics that are soluble in acid and alkali are removed prior to analysis (AAA method), but this may not be adequate in all cases. The degree of this contamination depends on the species and is not yet well known. The problem can be overcome by preparing pure cellulose from the sample, since this carbon definitely dates to a single year (Van Daalen *et al.* 1992; Kromer & Becker 1995).

Archaeologists have always favoured wood as material for radiocarbon measurement. In theory at least the carbon in each annual ring in wood largely represents the production of photosynthesis for that year. Some material is transported in wood rays from the phloem to older wood where it contributes to the formation of heartwood. There may be some synthesis of cellulose in the formation of tyloses in the heartwood formation zone in some genera (e.g. *Quercus* species), but most of the material transported to the heartwoods is in the form of tannins, gums and resins. Most radiocarbon studies of wood employ some form of extraction to remove tannins and resins. Although the ^{14}C activity of each annual ring may thus be specific to the year of formation, problems do occur, as in the case of dendrochronology where missing rings and decayed sapwood must be taken into account.

Radioactive isotopes can be used in many ways to help determine growth rates in trees lacking annual or seasonal growth-rings (Jacoby 1989).

The major disadvantages of the ^{14}C dating technique are the high cost and the time needed for analysis (4 months). It does, however, provide a reliable method for dating tropical trees where rings are often missing or false.

4.6.3   CAMBIAL WOUNDING OR DYE-INJECTION

One of the safest, but most time consuming ways of dating wood is marking by mechanical wounding (Mariaux 1976, as quoted in Worbes 1989) or poisoning of the cambium. The tree is then felled after some years and the number of rings can be compared with the time difference between marking and felling (Détienne 1989; Worbes 1989).

The marking of growth layers by scarring or dye-injection permits precise determination of seasonal changes in radial growth. Periodic sampling of the outermost layers also preserves a record of cambial activity. Subsequent anatomical analysis of samples from either procedure can reveal the sequence of radial growth during a year or preferably years (Jacoby 1989).

Shiokura (1989) describes a method whereby four nails are driven into a tree in a zigzag pattern, one every 3 months (Figure 4.10), at breast height. One year after the first nail was inserted the trees are felled and the amount of wood (barrier zone) formed subsequent to nailing is measured in an area about 1 centimetre above or below the site where the nails were driven in. Due to the distinctness of the cambial response to nailing this method appears to be a simple and effective method for measuring radial increment in tropical trees.
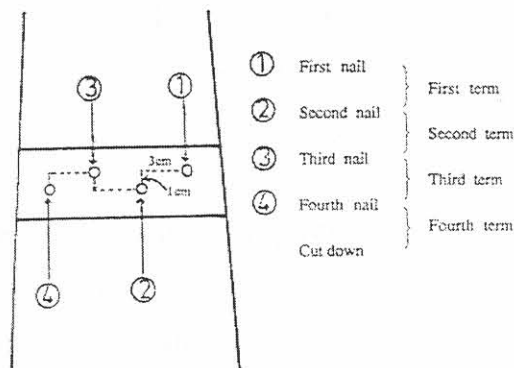
Figure 4.10 Arrangement of nailed locations (after Shiokura 1989).

Results from a periodic wounding study performed by Gourlay and Grime (1994) on *Acacia* species indicated that the marginal parenchyma/crystalliferous band was produced at the onset of the dry season and, therefore, the tree did not produce wood during the dry winter period.

4.6.4 XYLEM VESSEL DIMENSIONS

Carlquist (1977) found that xylem vessel diameter decreased with decreasing water supply and suggested that a correlation exists between xylem anatomy and habitat (see also Zimmerman *et al.* 1971; Baas *et al.* 1983). February (1993) investigated the above using *Protea caffra* and *Combretum apiculatum*, and while he did find a relationship to rainfall, he could find no relationship to temperature in either of these species.

Gillespie *et al.* (1998), in a preliminary investigation of xylem vessel diameter and area as a tool for tree ring identification and age determination in *Breonadia salicina*, found patterns of radial vessel diameter across tree rings related to each other. A climatic variable can also be related to this same pattern of xylem vessel diameter thereby making it possible to estimate tree age. Radial vessel diameter was found to be the most sensitive to annual rainfall but there was no correlation between mean annual temperature and vessel diameter.

4.6.5 DENSITOMETRY

Densitometry as it pertains to tree ring analysis is the measurement of variations in wood density on an intra-annual and annual basis (Jacoby 1989). According to Jacoby (1989) densitometry has not yet proven to be very useful in species other than conifers and further efforts are needed to evaluate this method with regard to tropical trees. Gourlay (1995) also pointed out that the relatively high density wood of *Acacia* species (> 1.0 g/cm^3), and the presence of gum, contribute to the lack of growth-ring definition by densitometric analyses.

4.6.6 PHENOLOGY

There have been more phenological studies of tropical trees than tree ring studies. These phenological studies are encouraging in that many of them document definite seasonality of growth changes. Seasonal flowering, fruiting, flushing, and leaf fall all indicate a rhythm that could be accompanied by radial growth cycles. In the transitions between the phases of the cycles there may be identifiable changes in the anatomy of the radial growth (Jacoby 1989). The phenological observations may be very helpful in denoting species and locations where a definite cessation of growth would be likely to produce an anatomical feature marking dormancy and restart of radial growth. Some of the phenological studies include recordings of diameter growth, although diameter changes may often be responses to hydration and dehydration rather than cell division (Reich & Borchert 1984).

CHAPTER 5

AGE STRUCTURE OF *ACACIA ERIOLOBA* POPULATION

5.1   INTRODUCTION

Trees are an integral component of African savannas. The function of savanna trees may how-
ever vary greatly with their population structure, density and distribution, which are controlled
by either weather patterns or management actions (Jeltsch *et al.* 1996). According to Skarpe
(1991), the structure and function of arid and semi-arid savannas are largely governed by soil
moisture, soil nutrients, fire and herbivory.

Preliminary data (Van Rooyen *et al.* 1996) on the size structure of the *Acacia erioloba* trees in
the northern Nossob Riverbed in the Kalahari Gemsbok National Park show a poor survival of
seedlings and an almost complete absence of juvenile plants. This recruitment failure is presently
resulting in the decline in isolated mature trees, which may result in a change in the population
structure of the species (Jeltsch *et al.* 1996).

Since the age, size, condition and density of *Acacia erioloba* trees in a population may influence
the function of the species in the ecosystem (Milton & Dean 1995, 1999), any decline in scattered
mature trees may have serious implications for species diversity in the southern Kalahari.

The population structure of *Acacia erioloba* in the Kalahari Gemsbok National Park has been
based on size-structure derived from size-class data, i.e. stem circumference and height. In order
to have a more complete understanding of the population dynamics and their sustained
management it is however essential to determine accurate age-structure (Gourlay 1995; Martin
& Moss 1997).

The objective of this study was therefore to develop age-size relationships for *Acacia erioloba*
on the basis of ring counts and carbon dating. Such relationships enable determination of the
age-class distribution of the population and consequently the dating of successful regeneration
events, which can then be related to records of climate.

5.2   MATERIALS AND METHODS

5.2.1   COLLECTION SITES FOR WOOD SAMPLES

Wood samples were collected in the vicinity of Loffiesdraai, which is representative of the interior duneveld habitat, Unie End, which is representative of the northern Nossob Riverbed, as well as in the southern Nossob Riverbed at Haagner's draai.

According to the vegetation map of Lubbinge (1998) the different localities where the surveys were conducted are representative of the following plant communities (Figure 2.6):

Loffiesdraai (25°05'S, 20°11'E) :   *Acacia luederitzii-Acacia erioloba* tree savanna (8a)

Unie End (24°48'S, 20°07'E) :   *Acacia erioloba-Eragrostis rotifer* river vegetation (1)

Haagner's draai (20°36'S, 25°25'E) : *Acacia erioloba-Eragrostis rotifer* river vegetation (1)

5.2.2   SAMPLING AND SAMPLE PREPARATION

Twenty-five samples were collected from selected *Acacia erioloba* trees of unknown age in ten stem circumference classes at the three different sites (Table 5.1).

Table 5.1   Distribution of samples of different stem circumference classes at three different sites in the Kalahari Gemsbok National Park [LD = Loffiesdraai; UE = Unie End]

Stem circum- ference classes (cm)	Total	Duneveld (Loffiesdraai)	Nossob River (Unie End)	Nossob River (Haagner's draai)
0-20	4	LD 6, LD 8	UE 16, UE 17	
> 20-40	4	LD 3, LD 4	UE 15, UE 23	
> 40-60	3	LD 2, LD 5	UE 21	
> 60-80	4	LD 1, LD 7	UE 22, UE 18	
> 80-100	2	LD 9, LD 10		
> 100-120	2		UE 19	UE 24
> 120-140	2	LD 12		UE 25
> 140-160	1	LD 11		
> 160-180	2	LD 13, LD 14		
> 180-200	1		UE 20	

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For dendrochronological studies as well as carbon dating, large core samples (> 50 mm in diameter) are needed that include all growth-rings from pith to cambium. Because of the importance of individual trees in this semi-arid region, a non-destructive method of sampling was developed (Steenkamp *et al.* 1999). In a number of cases it was unfortunately necessary to fell juvenile trees. Cores were taken at a height of 0.5 m, while discs were cut using a chain saw.

The wood of *Acacia erioloba* is dense and very hard and can therefore not be sampled with conventional hand-driven increment corers (Gourlay 1995). According to Kromhout (1975) the density of *Acacia erioloba* is 1.07 g/cm³.

Small-diameter samples pose a difficulty in obtaining enough material from the pith and adjacent growth-rings, which are essential for carbon dating. Because of the frequent eccentricity of the pith it is necessary to use a drill bit with a large diameter (Echols & Mergen 1955; Brown 1958; Sulc 1967).

Taking the requirements for increment borers suggested by Echols (1969) into account and noting the problems experienced by earlier researchers (Stonecypher & Cech 1960; Nicholls & Santer 1961; Forest Biology Subcommittee 1963; Johansen 1987; Lussier, *pers. comm.* 1998[1]) a drill bit was then designed to fit a commercially available electric drill.

An electric drill fitted with a 2-speed gearbox and powered by a generator was used. A core drill bit, fitted with tungsten tips, was designed to fit the electric drill. The drill bit used was 100 mm in diameter and 350 mm long. The tungsten tips were attached to the outside of the cylinder to ensure that the core could be removed easily (Figure 2: Steenkamp *et al.* 1999).

The electric drill was fitted on a lightweight pipe stand with wheels for easy mobility and was powered by a portable generator. Conventionally this drill is used for extracting cores for soil sampling, and drills in a vertical position. The stand was set up in a horizontal position and secured in position by steel droppers (Figure 1: Steenkamp *et al.* 1999).

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[1] Lussier, J.M. 1998. Chercheur scientifique, Centre de forestrie des Laurentides, Service Canadien de Forêts Canada (JMLussier @ exchange.cfl.forestry.ca)

Once revolving, the bit was slowly driven into the tree by simply applying pressure to the handle. The drill bit was water cooled while drilling at a low speed, 450 rpm, to prevent burning and compression of the core. The bit was frequently reversed out of the tree by hand, using the handle which regulates the depth of the drill. Because of this action it was possible to cool the drill bit and to remove bark and sawdust that tended to clog the drill bit.

The increment borer could easily be driven completely through a tree in cases where the shank was longer than the tree diameter, thereby extracting a core from bark to bark. Trees with a stem diameter of more than 350 mm were carefully measured and then drilled from both sides of the trunk. The holes that remained after sampling were plugged with wooden dowels to lessen insect and fungal attack.

The time required for the operation varied according to tree size, but on average was in the order of one hour for a core of 100×350 mm.

Stem circumference was measured at a height of 0.5 m using a measuring tape. Tree height, stem diameter, crown diameter and location were also recorded (Table 5.2).

In the laboratory a belt sander was used to smooth the surfaces, starting with a coarse grit (60 grain) and working down to 80 grain. An orbital sander was then used to smooth it down from 100 grain to the finest available (1 200 grain) (Figure 5.1). This procedure had to be followed meticulously, because if sanded down too soon with a fine grain, scratches remained. The final polishing ensured that fine scratches could not be confused with marginal parenchyma.

Accentuation of rings using a variety of stains, oils and polishes was attempted, but without any success.

Table 5.2 Details of *Acacia erioloba* trees sampled in this study

Tree number	Locality	Stem circum-ference (cm)	Stem diameter (cm)	Height (m)	Crown diameter (m)
LD 1	Duneveld	79	25.0	5.5	4.0
LD 2	Duneveld	43	14.0	3.8	2.2
LD 3	Duneveld	29	9.0	3.0	2.6
LD 4	Duneveld	35	11.0	4.0	2.0
LD 5	Duneveld	52	16.5	5.1	3.0
LD 6	Duneveld	14	4.5	2.2	1.3
LD 7	Duneveld	78	24.8	7.5	4.0
LD 8	Duneveld	20	6.4	2.6	2.0
LD 9	Duneveld	98	31.0	7.5	4.5
LD 10	Duneveld	97	31.0	8.5	5.0
LD 11	Duneveld	147	47.0	9.0	8.5
LD 12	Duneveld	130	41.0	8.0	9.0
LD 13	Duneveld	170	54.0	7.0	9.0
LD 14	Duneveld	170	54.0	7.0	9.5
UE 15	Nossob Riverbed	22	7.0	2.0	1.5
UE 16	Nossob Riverbed	8	2.5	1.3	1.3
UE 17	Nossob Riverbed	12	3.8	1.8	1.3
UE 18	Nossob Riverbed	64	20.4	5.5	4.0
UE 19	Nossob Riverbed	118	37.5	6.5	6.0
UE 20	Nossob Riverbed	200	64.0	11.5	11.0
UE 21	Nossob Riverbed	50	16.0	6.0	2.5
UE 22	Nossob Riverbed	69	22.0	6.5	3.5
UE 23	Nossob Riverbed	28	9.0	2.2	2.1
UE 24	Nossob Riverbed	118	37.5	7.0	7.0
UE 25	Nossob Riverbed	134	42.6	8.5	9.0

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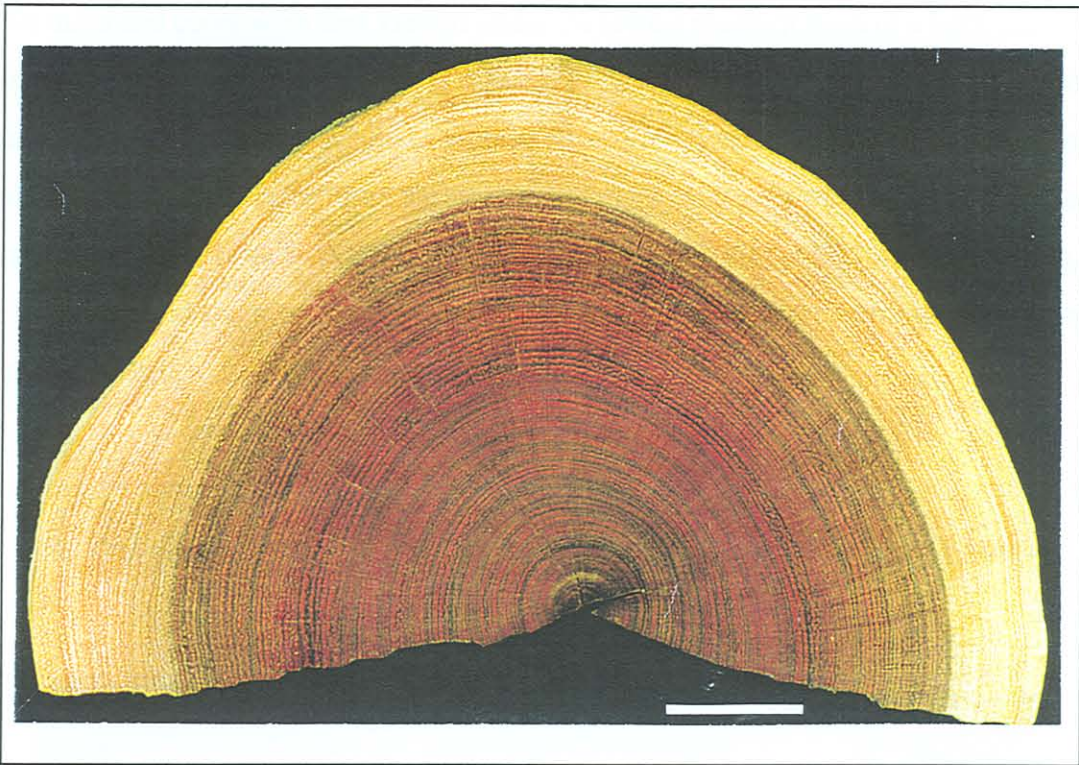
Figure 5.1 Sanded, polished disc of *Acacia erioloba* [Scale bar = 20 mm].

5.2.3 ANATOMICAL STUDY

The lack of distinct ring boundaries and the frequency of anomalous growth patterns in African indigenous trees are discussed in detail in Section 4.3. In the wood of *Acacia erioloba* the growth zones are separated by marginal parenchyma bands (Gourlay 1995).

The term 'marginal parenchyma' is used throughout this work in accordance with the IAWA List of Microscopic Features for Hardwood identification (IAWA Committee 1989) *viz*.: parenchyma bands that form a more or less continuous layer of variable width at the margins of a growth-ring or which are irregularly zonate. Marginal parenchyma is a form of axial parenchyma produced by some trees at the end or beginning of a growth season. These bands are commonly composed of less than five rows of parenchyma cells, forming a continuous layer visible on the transverse surface as a fine light-coloured band. This feature can often delimit growth in tropical woods as it may appear more clearly defined than vessel boundaries or other anatomical features used to describe growth-rings (Gourlay 1992).

Sample discs and cores were first viewed under the lowest magnification of a light microscope. Unfortunately only small sections could be viewed and it was difficult to trace the marginal rings around the disc. The cores and discs were then viewed under a dissection microscope (4× magnification). In the case of discs the marginal parenchyma rings were identified on the three best radii through the least disturbed sectors and then marked (Figure 5.2). Where possible, rings were traced around the disc to check for continuity. The final ring count was determined by taking an average of the counts on the radii.

Because of the size of the cores (100 mm in diameter) it was also possible to mark the rings on more than one radius. An average ring count was also determined for each core sample.
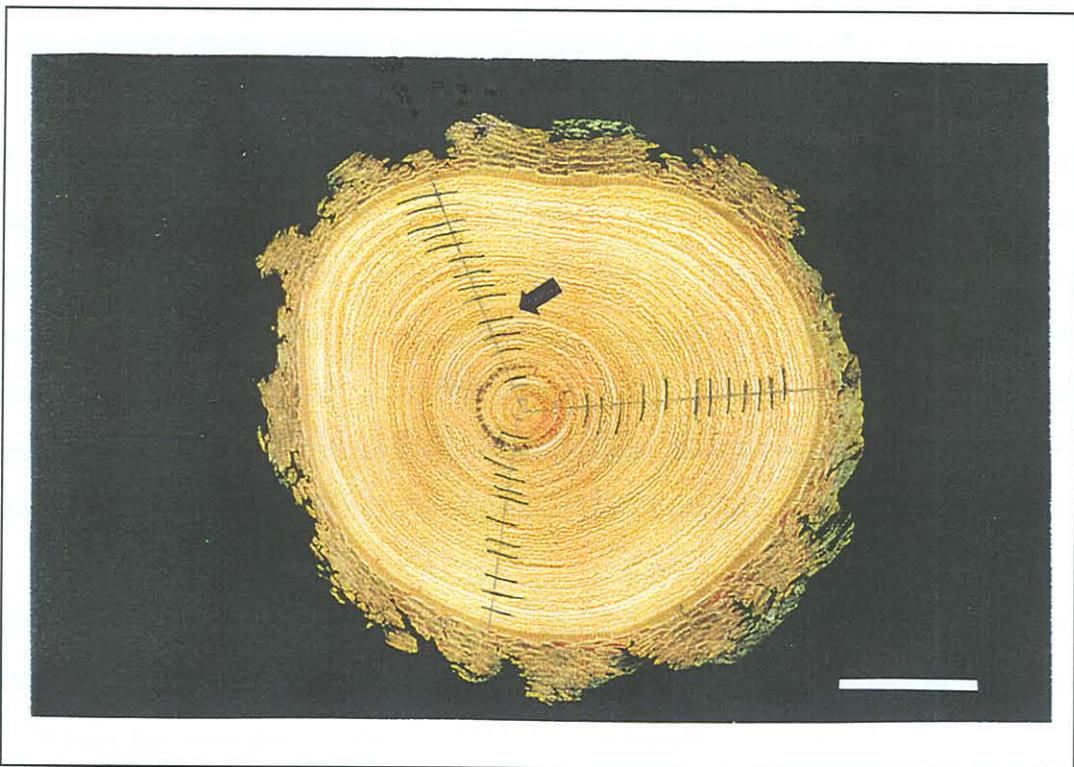
Figure 5.2 Marginal parenchyma bands (arrow) marked on different radii of an *Acacia erioloba* disc from the duneveld (LD 3; stem circumference = 29 cm; tree height = 3 m; ring count = 15; estimated age by carbon dating = 20 years) [Scale bar = 20 mm].

In samples where it was difficult to determine the number of marginal rings, due to missing rings or samples with a rotten core, growth zones were measured and growth rates per mm calculated.

If one assumes a relatively uniform, or at least predictable, growth rate through time, the age of the tree can be estimated.

5.2.4   CARBON DATING

The ^{14}C dating was done in the Quaternary Dating Research Unit of the Division Water, Environment and Forest Technology of the Council for Science and Industrial Research (CSIR) in Pretoria.

About 25 g of wood is needed for a ^{14}C analysis. To determine when the tree started growing, a segment is removed from the inner core (0-25 mm) on the radius of the tree. The wood is then chopped to matchstick size and vigorously treated with dilute acid and alkali, to remove the soluble organics (AAA method) before combustion to carbon dioxide (Vogel *et al.* 1995).

Pure cellulose was also prepared from some of the samples by initial extraction with benzene and ethanol, and oxidation with sodium hypochlorite and acetic acid to remove the extractable organics before combustion. The radiocarbon content of the resulting carbon dioxide was measured in high precision proportional counters used for radiocarbon dating. The results were corrected for variations in the initial isotope ratio of the carbon. The ^{14}C content was expressed as percentage of modern carbon (PMC). Dates are reported in conventional radiocarbon years, before 1955, using a half-life of 5568 years for ^{14}C (Vogel, J.C. & Fuls, A. *pers. comm.* 1999[2]).

Initially the centre of each disc or core was sampled for analysis. Within the age range of the trees sampled the ^{14}C analysis usually produced two or more possible dates (Figures 4.8 and 4.9). Where the core dated to before 1955 the age became indistinct. In these cases a second sample was processed from a point between the core and the bark. The age was then estimated by extrapolation, assuming a linear growth rate. It was then determined which of the possible historical dates actually applied to the core. With sufficient measurements the individual wood sample can be located on the ^{14}C calibration curve (Figure 4.9) for recent decades. Ring counts and carbon dates were compared (Table 5.3 and Figure 5.6).

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[2]   Vogel, J.C. & Fuls, A. Quaternary Dating Research Unit, Division of Water, Environment and Forestry Technology, CSIR, Pretoria, South Africa

5.2.5 POPULATION STRUCTURE

The population structure of several prominent tree species have been monitored in the interior duneveld and Nossob River areas of the Kalahari Gemsbok National Park since 1978 (Van Rooyen *et al*. 1996).

Stem circumference and height were measured for a number of *Acacia erioloba* trees in the northern Nossob Riverbed (Unie End to Kannaguass) [n = 311] and in the vicinity of Loffiesdraai (duneveld) [n = 494].

The influence of watering points in the duneveld and the Nossob Riverbed on the population structure of *Acacia erioloba*, was also investigated. Therefore not only climate-influenced changes were monitored, but also the influence of grazing although of relatively low intensity. The first surveys were carried out before or soon after the establishment of the watering points and could therefore be used as control surveys (Van Rooyen *et al*. 1996).

5.2.6 METEOROLOGICAL DATA

Reliable meteorological data, consisting of monthly and annual rainfall records were obtained for the area where trees were sampled (Tables 2.1 and 2.2). Monthly temperature data were also obtained for the area (Tables 2.3 and 2.4) (Weather Bureau 1998).

The availability of meteorological data enabled comparison of the age structure and estimated annual growth rates with meteorological parameters.

5.3   RESULTS AND DISCUSSION

5.3.1 SAMPLING OF WOOD CORES

Jacoby (1989) points out that in semi-arid regions each individual tree has a relatively great value and therefore should not be felled. *Acacia erioloba* is also classified as a keystone species in the Kalahari Gemsbok National Park (Milton & Dean 1995). It was therefore necessary to develop a non-destructive sampling method for trees with a diameter of > 200 mm in diameter.

Core sampling in indigenous hardwood species is not a common practice and the difficulties of sampling and examining hard, dark and gum-filled species has been discussed in numerous research projects (Curtis *et al.* 1979; Jacoby 1989; Ogden 1981; Gourlay 1995). However, through this research a unique and effective non-destructive method of sampling was developed, whereby high quality material suitable for carbon dating and dendrochronological studies, can be obtained without permanently damaging trees. The problems inherent to the use of cores i.e. small size and the inability to locate the pith of the tree during coring, were solved by taking large increment cores (100×350 mm). The quality of the cores taken, was excellent. Samples were smooth, not burned and outer rings did not "corkscrew" (Figure 3: Steenkamp *et al.* 1999). This could be attributed to the fact that the drill bit used in this research could be water cooled and drilled at a low speed, thus preventing burning and compression of the cores. The fact that the bit could be reversed frequently also contributed to high quality samples.

Although it was pointed out (Gourlay & Kanowski 1991; Gourlay 1995) that a whole-tree disc is preferable to a sample taken from an increment core, the cores taken during this study proved to be large enough to examine more than one radius.

The equipment used is a definite improvement over conventional, hand-turned borers and other described powered equipment (Steenkamp *et al.* 1999). It can readily be used where a large number of cores must be taken from hardwood species in a fairly accessible area. The equipment used in this study can also be adapted to suit specific sampling needs.

5.3.2 GROWTH-RINGS

The specific anatomical characteristics responsible for delineating growth-rings can vary greatly between species and the growth zone will often be incomplete when traced around the circumference of the disc (Gourlay 1992). Several wood anatomical features have been used in attempts to identify growth periods in tropical trees that do not have a visible and detectable ring pattern related to any cyclic event. Those anatomical features that have been considered include maximum vessel diameter, the frequency of occurrence of vessels of two sizes, narrow vessels with a higher average vessel wall thickness and shorter vessel length, terminal parenchyma, dense thick-walled latewood fibres, semi-ring porous vessel arrangements, growth-related variations

in the parenchyma and variations in cell length (Lilly 1977; Baas *et al.* 1983). Walker *et al.* (1986) in their study of six indigenous tree species found that features which, superficially, appear to delineate growth-rings were either discontinuous or rows of fibres laid down in response to stress. They, therefore, had to base their analysis of population structure and dynamics on tree size.

In a study conducted by Wyant and Reid (1992) in the South Turkana district of Kenya, a fine band of white cells was identified in the xylem as indicators of ring boundaries in *Acacia tortilis*. However, while these authors demonstrated a significant ($r = 0.90$) linear relationship between ring count and known tree age, they did not identify the anatomical features responsible for this band.

Worbes (1989) pointed out that the growth zones of all Fabaceae were separated by marginal parenchyma bands, even though in several species additional structural zonation was also present. Few authors have found a relationship between seasonal climatic parameters and anatomical variation in the wood of African *Acacia* species (Gourlay 1995; Mariaux 1981; Wyant & Reid 1992).

Wood anatomical studies of *Acacia erioloba* however revealed the presence of marginal parenchyma and distinct heartwood (Kromhout 1975; Robbertse *et al.* 1980; Gourlay 1992).

In the majority of samples examined in this study, seasonal changes were reflected in the wood anatomy as bands of marginal parenchyma on the polished surfaces of discs or cores. As earlier work has shown, however, these narrow bands are not always clearly defined around the whole circumference of the disc. Bands of marginal parenchyma, often only a few cells wide (Figure 5.3), were identified.

The marginal parenchyma bands can usually be distinguished from the frequent intra-seasonal banded parenchyma by their fineness, by more irregular spacing between the broader bands and by evenness of appearance in contrast to the more irregular, wavy, confluent bands (Figure 5.4). These bands were extremely difficult to detect due to the presence of much broader bands of

aliform-confluent parenchyma, a feature which is common in most *Acacia* spp. The broad bands often mask the finer marginal bands (Figure 5.3), and sometimes completely obscure them. A further complication in the form of merging and/or partial rings and the presence in several samples of dense, dark heartwood, often filled with gum deposits (Figure 5.5) was experienced. This demanded diligent study of the growth zone around the circumference.
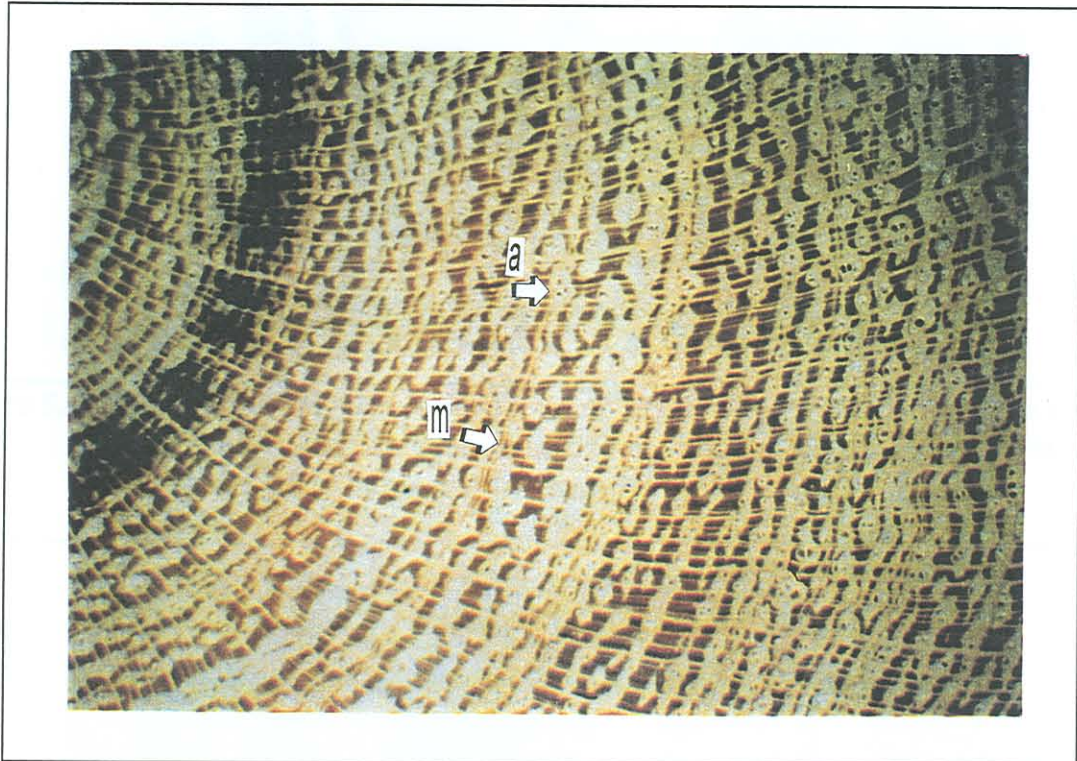
Figure 5.3 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing the fine marginal parenchyma (m) partially obscured by the broader aliform-confluent parenchyma (a).
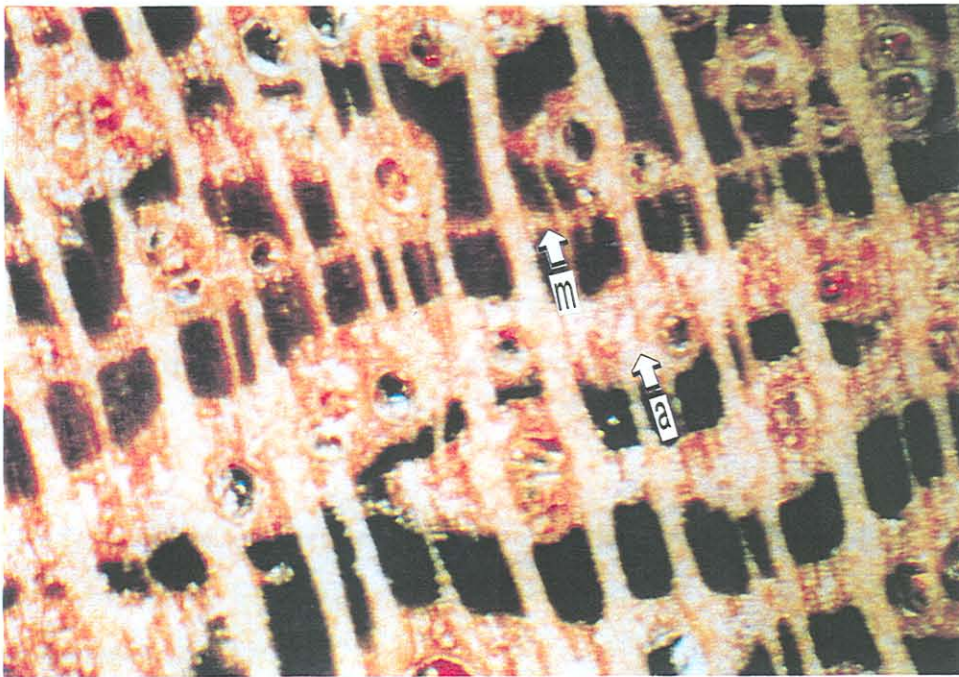
Figure 5.4 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing fine marginal parenchyma (m) clear of the aliform-confluent parenchyma (a).
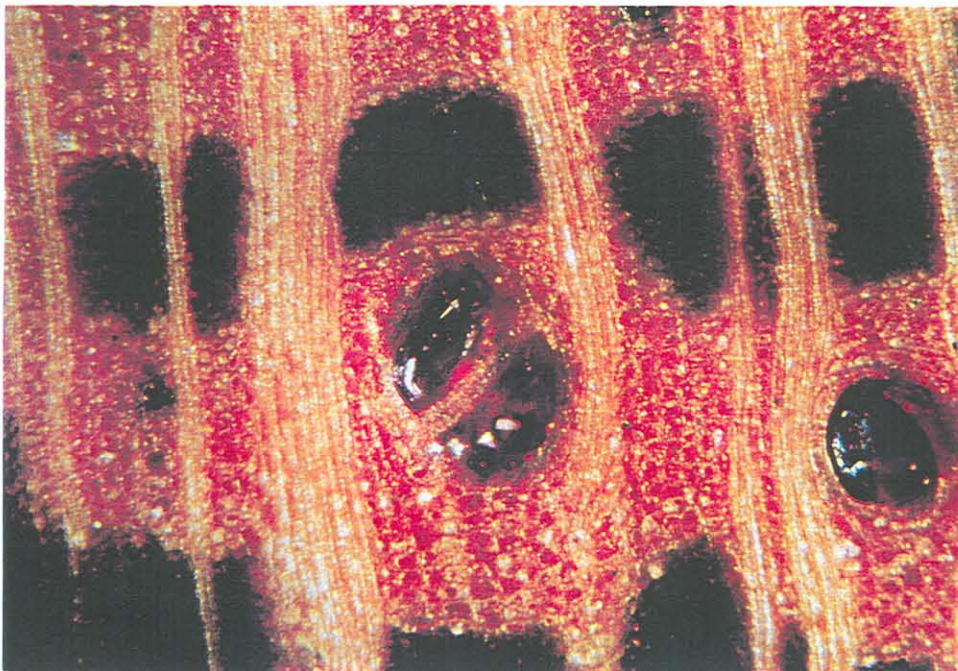
Figure 5.5 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing dense, dark heartwood, filled with gum deposits (10 x magnification).

5.3.3 CARBON DATING

All samples examined were of trees of unknown age. Table 5.3 was compiled to display sample details, ring counts, carbon dates and growth rates estimated by means of visible marginal parenchyma bands and/or carbon dates.

Ring count was plotted against carbon age 1 and carbon age 2 (Figure 5.6). Carbon age 1 refers to estimated age of tree in years by carbon dating whereas carbon age 2 refers to possible age by carbon dating.

It is evident from Figure 5.6 that there was a stronger relationship between ring count and carbon age 1 than carbon age 2. Carbon age 1 is thus the preferable age to use in further data analysis. This is demonstrated in Figure 5.7.

The carbon age referred to further throughout this discussion will therefore be carbon age 1.
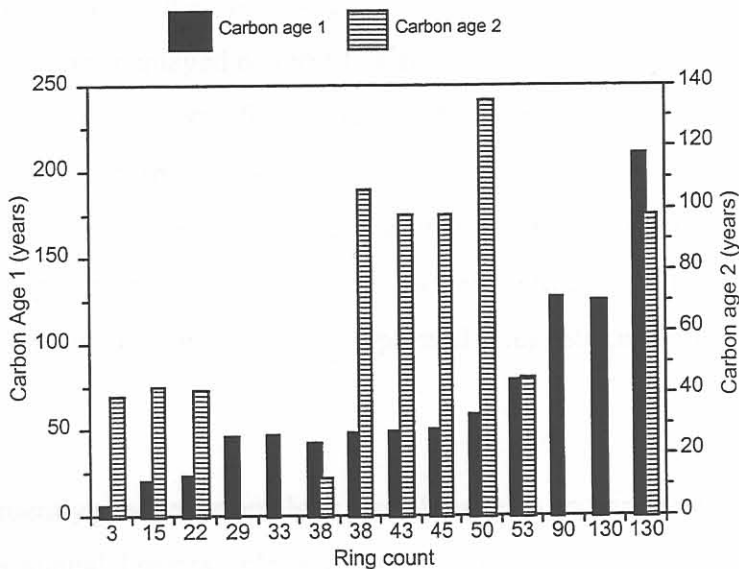
Figure 5.6 Relationship between ring count and estimated carbon age 1 and 2 for *Acacia erioloba*.

A regression of the samples, forced through the origin, exhibited a high correlation ($r^2 = 0.96$) between ring count and estimated age by radiocarbon dating (Figure 5.7).
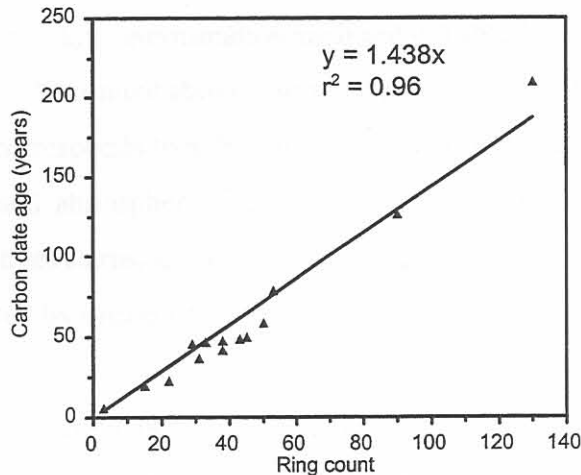
Figure 5.7 **Relationship between estimated age by carbon dating and ring count for *Acacia erioloba*.**

The age as estimated by marginal parenchyma ring counts was however on average 23% lower than the estimated age determined by carbon dating. This can be attributed to the number of missing rings and/or cores damaged by termite action or rotten heartwood. The estimated number of missing rings is one in every five years. With all dendrochronological-based research, there is always a risk of incorrect measurements or counts due to false and missing rings. This is particularly so in areas of severe drought stress, which can induce erratic growth in the cambium, causing multiple growth-rings in the same season, and preventing a complete sheath of xylem forming in the lower stems of old or suppressed trees (Stokes & Smiley 1986; Wyant & Reid 1992).

Angiosperms frequently produce anomalous growth patterns and rings which, for the most part, are not necessarily annual. For example, a stress period may occur during a growing season and cause more than one growth layer to form within that year. Alternatively, when conditions are extremely limiting, growth cannot occur and no ring is produced. Certain regions of the cambium may not divide at all giving the appearance of a missing ring (Fritts 1976; Lilly 1977; Curtis *et al.* 1979; Walter *et al.* 1986).

It was also difficult to detect the first few rings. It is likely that the more erratic growth pattern observed in the first three or four rings reflects the juvenile years of growth of the cambium, rather than the influence of climate.

The results of the radiocarbon age determination are listed in Table 5.3. Six of the samples where the centre was dated, had a ^{14}C content above normal, that is, elevated ^{14}C levels. On the conventional ^{14}C age scale this corresponds to a "negative" age. However, when this derived age was corrected for the increased atmospheric ^{14}C levels resulting from nuclear weapon tests, it becomes evident that the trees started growing after 1955 (Table 5.3). The ages of these samples can, therefore, be estimated by means of Figure 4.9.

For sample LD 14 (stem circumference = 170 cm; radius = 18.0 cm; height = 7.0 m) a ^{14}C content of 97.4% was determined. The radiocarbon age in radiocarbon years before present (BP) 1950 gives a value of 180 BP±50 (Figure 5.8). If this is projected on the historical scale, five historical dates are possible i.e. 1689, 1733, 1813, 1939 and 1955. The 1σ range will therefore be: 1674-1775, 1799-1888 and 1915-1952 while the 2σ range will be 1660-1953. If the calibration curve is examined (Figure 5.8), both the earlier dates (>1800) and later dates (i.e. 1939 and 1951) can be ignored based on the stem circumference (170 cm), in comparison to other samples studied. The most probable date is 1813. It can, therefore, be assumed that the sample is 185 years old. Since the wood is very porous, the estimated extrapolation to the core is 15 years. The age of sample LD14 was therefore calculated at 200 years (Figure 5.8).

The plot of the derived ^{14}C results against the ring count would usually clearly indicate which of the possible dates was preferred (Figure 5.6). Ring counts could be used effectively to eliminate possible age where more than one date was obtained (Figure 5.6).

Table 5.3 Estimated age of *Acacia erioloba* samples by carbon dating and ring counts

Sample number	Radius (cm)	Stem circumference (cm)	Location of sample for carbon analysis (cm) from outside	^{14}C content pmc	Average radial growth rate (cm/year)	Estimated age of tree (years)	Also possible age (years)	Ring count	Comments
LD1	11.25	79	11.25-8.75	98.6±0.3	0.23	50	98	45	
LD2	6.00	43	6.0-5.0	100.2±0.6	0.12	47		33[#]	Missing rings scarred tissue
LD3	3.50	29	3.5-2.5	126.0±0.6	0.17	20[†]	42	15	
LD4	4.50	35	4.5-3.5	133.0±0.6	0.20	23[†]	41	22	
LD5	7.25	52	7.25-6.25	100.8±0.3	0.16	46		29	
LD6	1.70	14	1.7-0.7	119.1±0.7	0.08	18[†]	37		
LD7	11.25	78	11.25-10.25	118.4±0.3	0.27	42	12	27+11[#]	Missing rings
LD8	2.50	20	2.5-1.5	123.7±0.7	0.12	21[†]	42		
LD9	14.50	98	14.5-12.5 / 3.5-2.5	99.7±0.3 / 98.5±0.3	0.07	210[*]	98	130+[#]	Decayed core
LD10	13.75	97	10.5-9.5	98.8±0.3	0.23	59	135	37+13[#]	Decayed core missing rings
LD11	21.50+ 2.6	147	18.0-17.0 / 6.2-4.8	99.3±0.3 / 100.3±0.6	0.19	125[*]	117+13[#]		Decayed core missing rings
LD12	15.0	130	15.0-14.0	99.8±0.6	0.15	100	45		
LD14	18.0	170	18.0-17.0 / 17.0-16.0 / 6.4-4.9	97.4±0.3 / 97.8±0.6 / 106.5±0.6	0.14	127[*]	200	90[#]	Very porous, decayed
UE16	0.8	8	0.8-0	113.0±0.6	0.13	6[†]	39	3	
UE20	31.0	200	31.0-28.0 / 10.1-9.5	99.7±0.3 / 109.0±0.5	0.25	45 126[*]			Very porous
UE21	7.5	50	7.5-4.5 / 7.5-4.5	98.3±0.3 / 99.5±0.3	0.15	49	98	43	
UE22	8.0	69	8.0-7.0	99.1±0.5	0.17	48	106	38	
UE24	13.75	118	13.75-11.75 / 8.0-6.7	99.5±0.3 / 101.4±0.3	0.17	79	45	53+	
UE25	19.0	134	19.0-17.0	157.3±0.3	0.51	37[†]	31	31	

[#]   *Not all rings could be counted and the age is extrapolated assuming linear growth estimated from the counted rings.*

[†]   *These specimens show post nuclear ^{14}C and are accurate to ±2 years. The ages of the rest are much less precise.*

[*]   *The age is based on extrapolation assuming linear growth.*
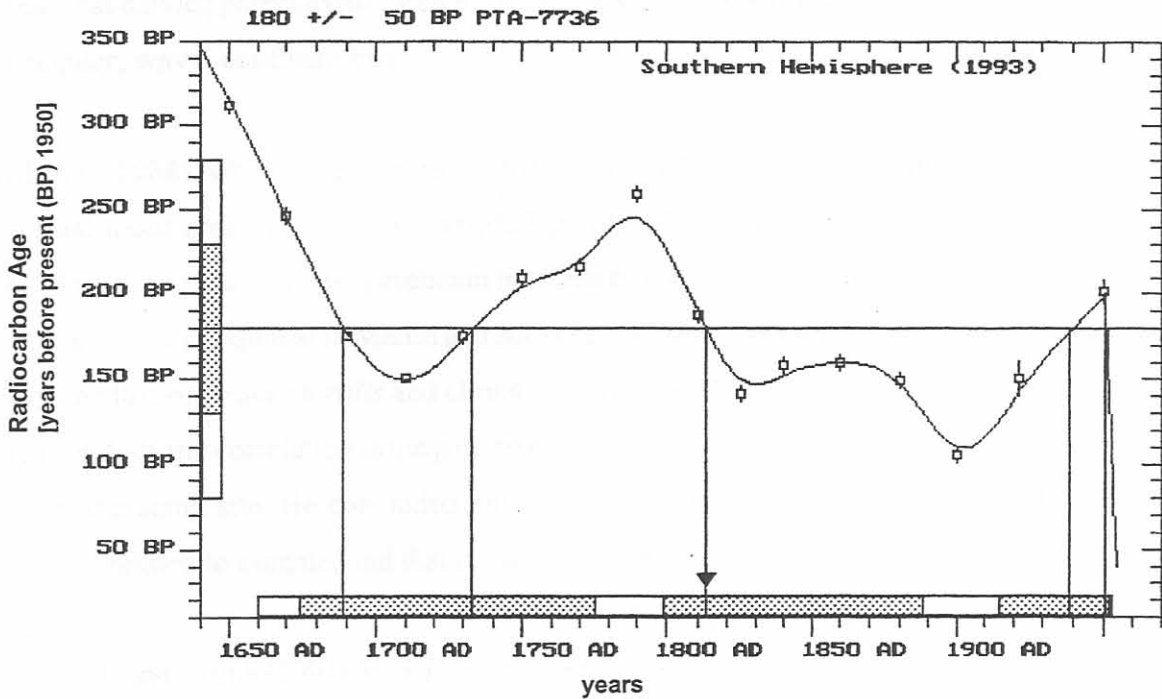
Figure 5.8 Determination of age of Sample LD 14 using the ^{14}C curve. Possible age (arrow).

Mean annual radial growth rates were estimated on the basis of the growth-rings identified for all samples for which a complete ring count was possible. The mean annual radial growth rates for samples were calculated at 2 mm/year corresponding to an annual diameter increment of 4 mm/year. The mean annual rainfall for this study area is 230 mm. Growth rate estimates resulting from this study, indicated that at the sites examined, the average growth rate was slower than that previously reported for *Acacia* spp. growing in arid and semi-arid conditions.

The African *Acacia* trees studied by Gourlay (1995) were of known age and generally selected from areas less likely to be damaged by animal or human agents. The mean annual ring width across all *Acacia* spp. and sites examined by Gourlay were between 6 and 7 mm radial growth per year, corresponding to an annual diameter increment of 12-14 mm.

The results of this investigation into the problem of determining the age of semi-arid trees suggest that the marginal parenchyma bands can indicate seasonal growth patterns in *Acacia erioloba*. The marginal parenchyma bands can usually be distinguished from the frequent intra-

seasonal banded parenchyma by their fineness and evenness in appearance in contrast to the more irregular, wavy, confluent bands.

Milton (1988), who studied *Acacia tortilis* in South Africa, found a strong correlation between annual basal area increment and rainfall (r = 0.999). Mariaux (1975), as quoted by Gourlay (1995), found only a weak correlation between ring widths in *Acacia tortilis* and annual rainfall. Martin (1995) as quoted in Martin and Moss (1997), attempted to find a relationship between the ring-widths of *Acacia tortilis* and climatic data in the Marsabit District, Kenya, but was unable to establish any correlation in the pattern or sequence of ring-widths between trees of similar age from the same site. He concluded that growth-limiting factors were highly variable and not simply related to climate, and that browsing was likely to be particularly significant.

Gourlay and Grime (1994) used the presence of calcium oxalate crystals in marginal parenchyma as an indicator of ring boundaries in their study of African *Acacia* species of known age. John (1990), as quoted in Gourlay (1995), used crystalliferous chains to indicate growth. The only other study that appears to have found crystalliferous chains in the marginal parenchyma and successfully compared this anatomical feature in *Acacia* spp. with climatic data, is that of Walter (1940). He reported a good correlation between growth rate measurements and precipitation for *Acacia erioloba* and on the basis of this data, suggested there were long-term (10-20 years) climatic cycles.

This study has enabled the determination of age and subsequent growth rates for *Acacia erioloba* trees in the Kalahari Gemsbok National Park by identifying seasonal growth changes in the wood anatomy and correlating ring counts with carbon date age. This can be expressed and related to environmental and climatic factors.

The results depicted in Table 5.3 show the following with regard to the ages of the trees sampled:
- samples with a radius of < 5 cm give an average age of 20 years;
- all trees sampled are younger than 250 years;
- the oldest tree sampled (210 years) is LD 9 with a radius of 14.5 cm;

- there is not a significant difference in age between trees sampled at Loffiesdraai (dune area) in comparison to trees sampled at Unie End (northern Nossob Riverbed) with approximately the same stem circumference;

- the only exception is UE 25 with a radius of 19 cm which gives an estimated age of 37 years.

Although more sophisticated future dendrochronological studies may provide more accurate ages for older trees, it can be concluded that in fact many *Acacia* spp. are probably far younger than commonly believed.

5.3.4 POPULATION STRUCTURE

The distribution of size classes of *Acacia erioloba* in the duneveld shows the reverse J-shaped curve characteristic of viable populations (Barbour *et al.* 1987) (Figure 5.9). However, the *Acacia erioloba* population in the northern Nossob Riverbed in the Kalahari Gemsbok National Park shows poor recruitment and also an increase in mortality of adult trees (Figures 5.10 and 5.14). (Vegetation types according to Lubbinge (1998) of the different sites are given in brackets.)
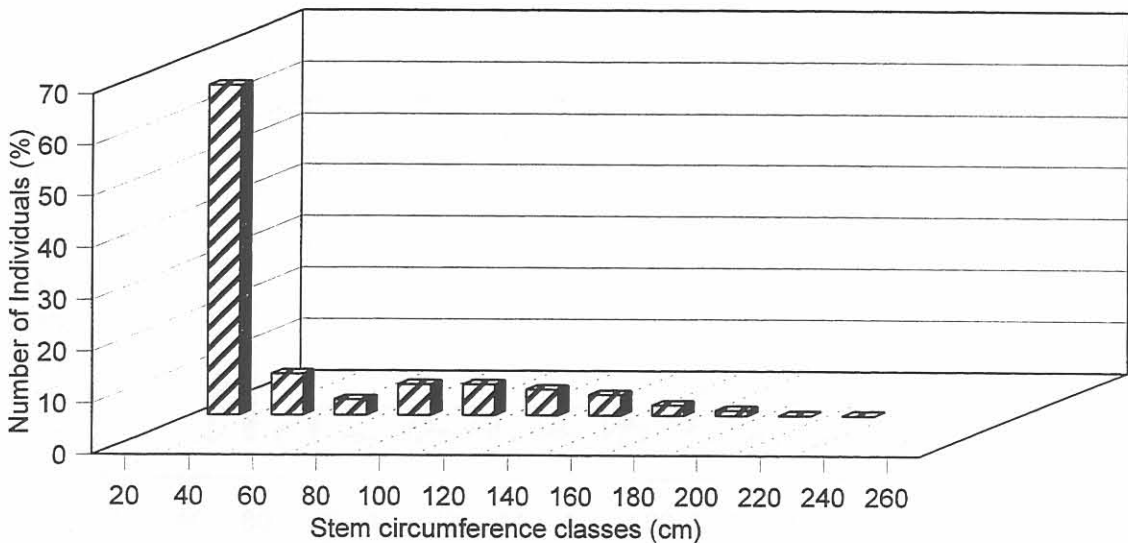
Figure 5.9   Size structure of *Acacia erioloba* based on stem circumference classes in the interior dune area of the Kalahari Gemsbok National Park (8a) [n = 494 individuals].
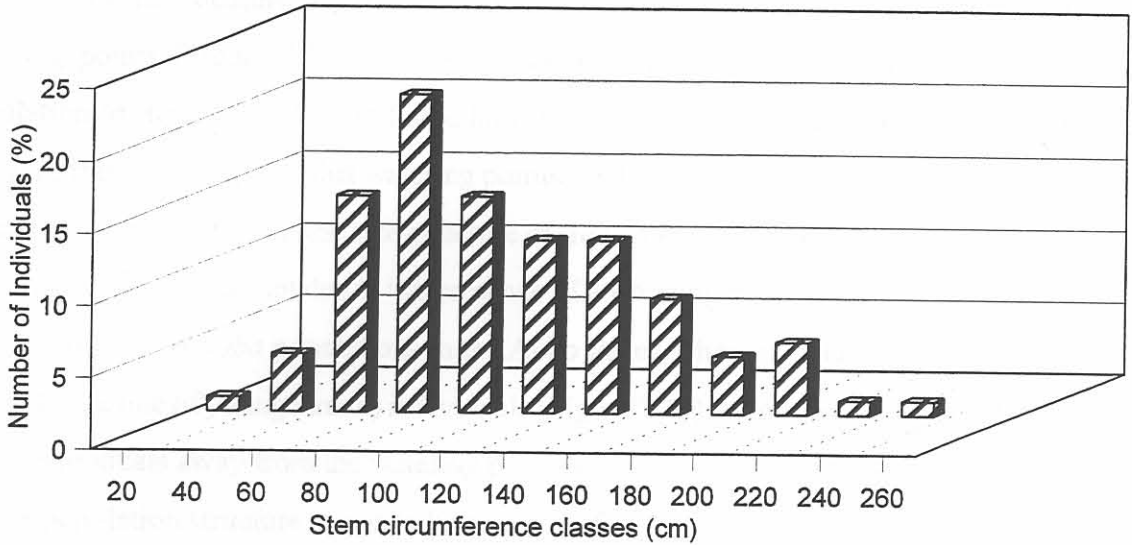
Figure 5.10   Size structure of *Acacia erioloba* based on stem circumference in the
northern Nossob Riverbed of the Kalahari Gemsbok National Park (1)
[n = 311].

At water [n = 247]   Away from water [n = 421]
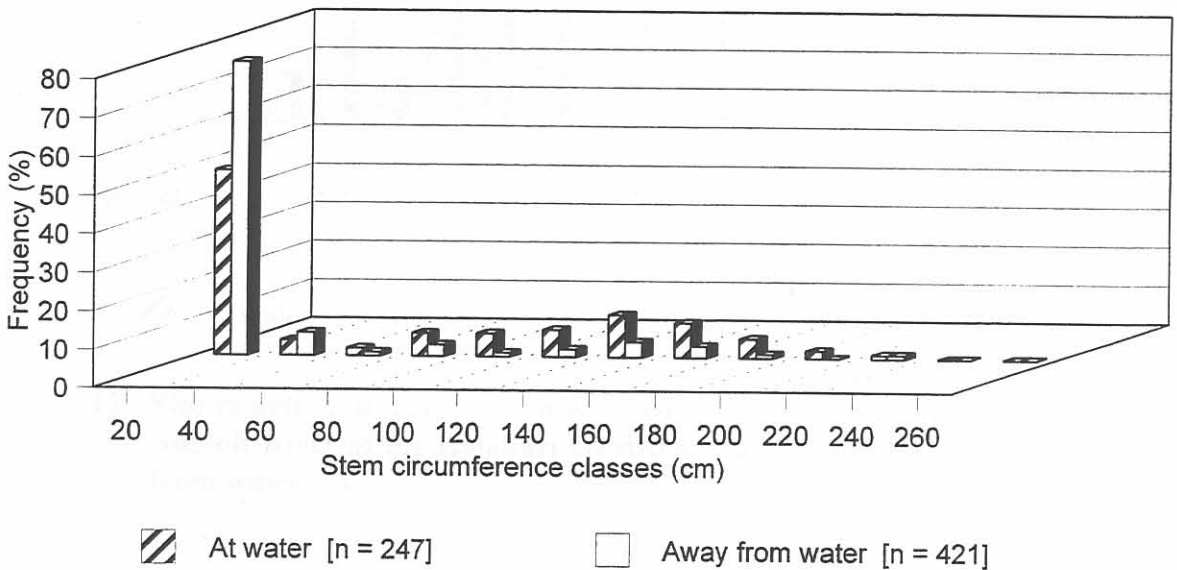
Figure 5.11   Size structure of *Acacia erioloba* based on stem circumference classes at
Gharagab in the interior dune area of the Kalahari Gemsbok National Park,
at and 3 km away from water (8a).

In the duneveld a healthy population of *Acacia erioloba* exists both at and 3 km away from watering points (Figure 5.11). In the Nossob Riverbed, however, a non-viable/unhealthy population of *Acacia erioloba* is found both at and 5 km away from watering points (Figure 5.12). It, therefore, appears that watering points (and their associated perceived higher grazing pressure) have no effect on the size structure of *Acacia erioloba* and that the decrease in young (small) individuals was not due to the presence of a watering point. This was, however, not the case for *Acacia erioloba* populations in the Auob River, where populations at a watering point showed a decline of young (small) individuals (Figure 5.13) as opposed to the high frequency of small individuals away from the watering point (Figure 5.13). Thus the influence of browsing on tree population structure seems to be area specific.
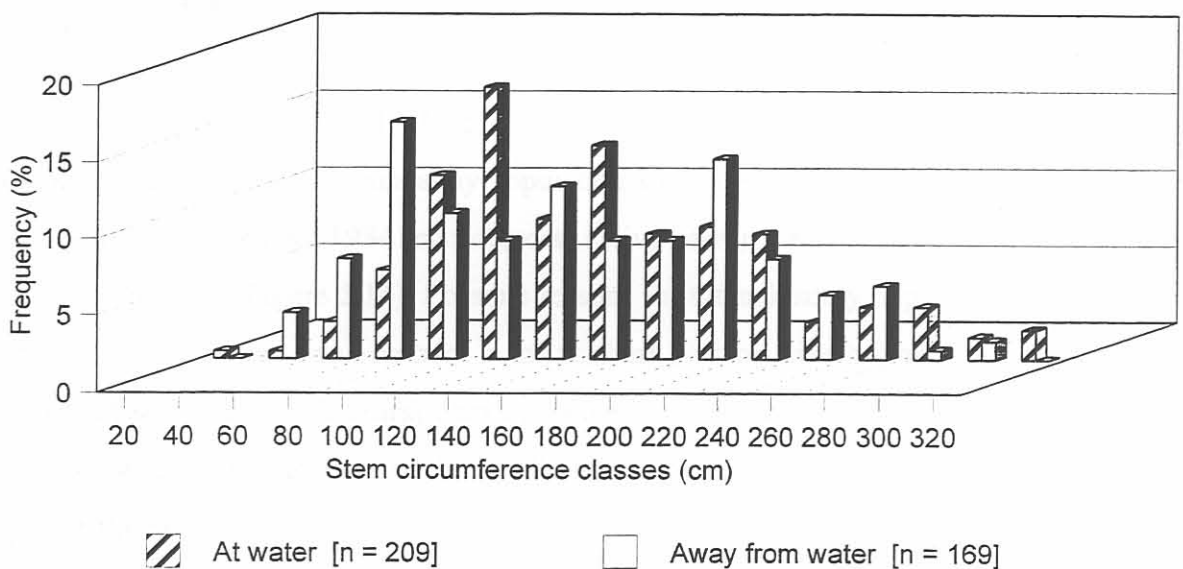
Figure 5.12 Size structure of *Acacia erioloba* based on stem circumference classes in the Nossob River of the Kalahari Gemsbok National Park, at and 5 km away from water (1).
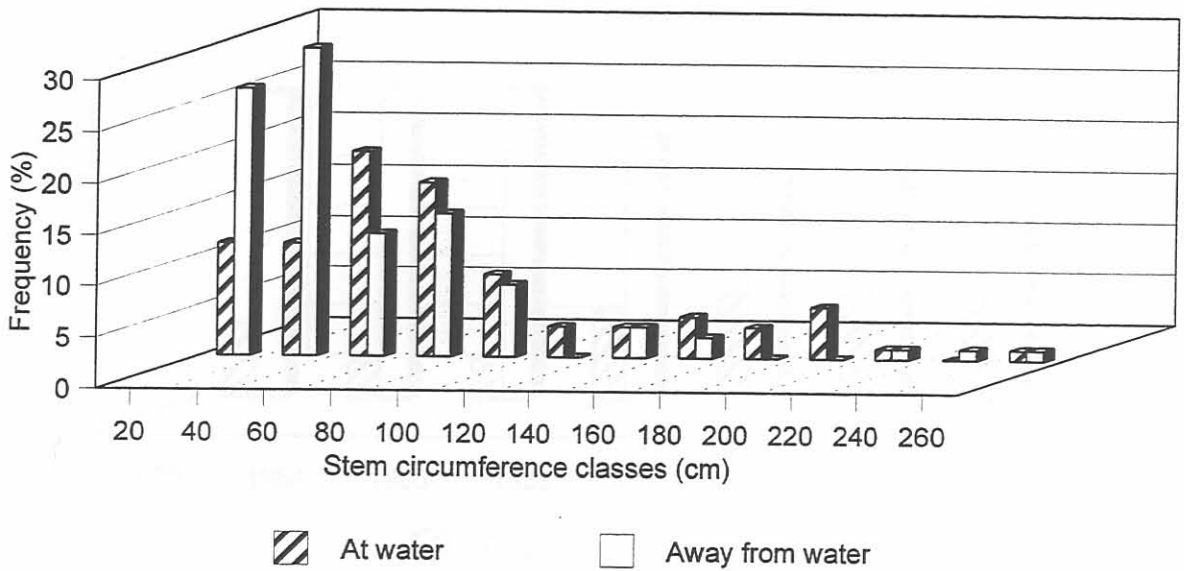
Figure 5.13 Size structure of *Acacia erioloba* based on stem circumference classes in the Auob River of the Kalahari Gemsbok National Park, at and away from water (3a).

It is therefore evident that only the population structure of *Acacia erioloba* in the northern Nossob Riverbed shows an unhealthy population structure. An increase in density of dead *Acacia erioloba* trees since 1984 and a decrease in live trees in the northern Nossob Riverbed has also been recorded (Figure 5.14). Possible reasons for the unhealthy population structure and increase in dead *Acacia erioloba* trees in the northern Nossob Riverbed are:

■ lack of successive (2-3 years) above-average rainfall years (Figure 2.4) and/or a lack of floods which influences survival of seedlings. (Above average rainfall years preceded 1978. With the exception of 1988, 1993, 1996 and 1997 all the subsequent years had below average rainfall.)

■ lack of a seed bank due to high parasitism or failure to establish.
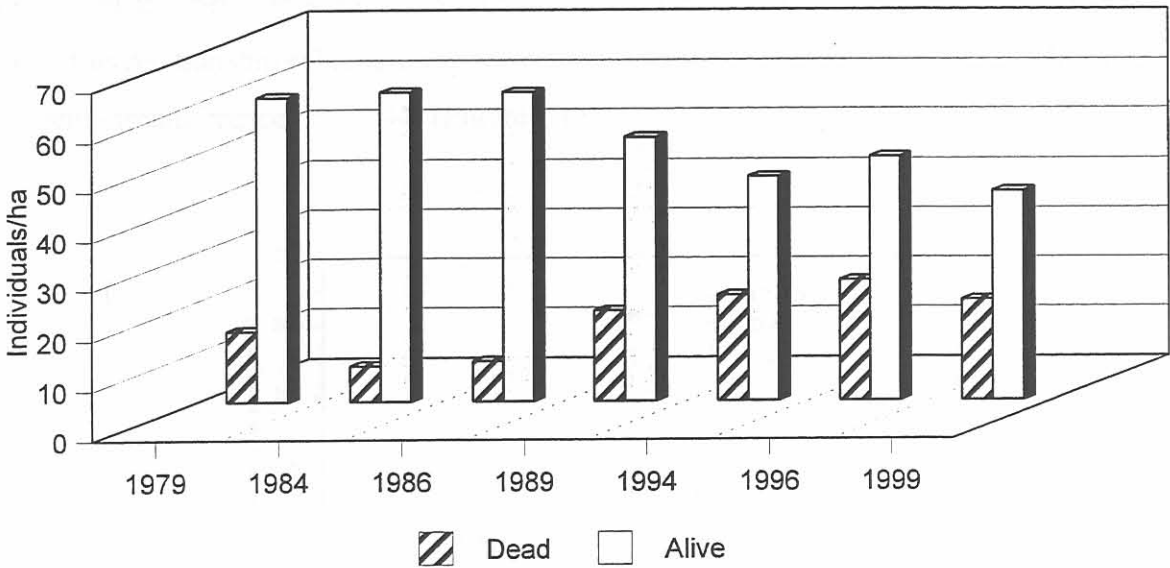
Figure 5.14 Number of individuals/ha of dead and alive *Acacia erioloba* in the northern Nossob River of the Kalahari Gemsbok National Park (1).

Seed predation, germination and establishment are especially sensitive to environmental variations and mortality rates during these stages are much higher than during adult stages (Brubaker 1986). It was pointed out by Hoffman *et al.* (1995) that the size-class distribution of *Acacia erioloba* populations indicate that seedlings germinate and survive more abundantly in high than in low rainfall years. This was confirmed by Van Rooyen *et al.* (1984;1990) and Theron *et al.* (1985) when they found that seedlings and saplings of *Acacia erioloba* suffer high mortality rates in dry years. Accumulation of tree seeds at a specific site increases the establishment probabilities. Ward and Breen (1983) indicated that one of the possible processes that leads to accumulation of tree seeds is rare, but important floods. As was pointed out above average rainfall preceded 1978 and although there were a few exceptions, all subsequent years had below average rainfall (Figure 2.4) with the last flood being recorded in 1963.

Observations have shown that African *Acacia* seedlings fail to establish under the canopy of established individuals, regardless of species (Smith & Goodman 1986). This failure can be due to high predation by bruchid weevils and tree rats (Milton & Dean 1999) as well as low levels of irradiation (Smith & Goodman 1986).

The relationship between stem circumference and carbon date age was also determined. A regression of this relationship exhibits a low correlation between estimated age by radiocarbon dating and stem circumference ($r^2 = 0.44$) (Figure 5.15).
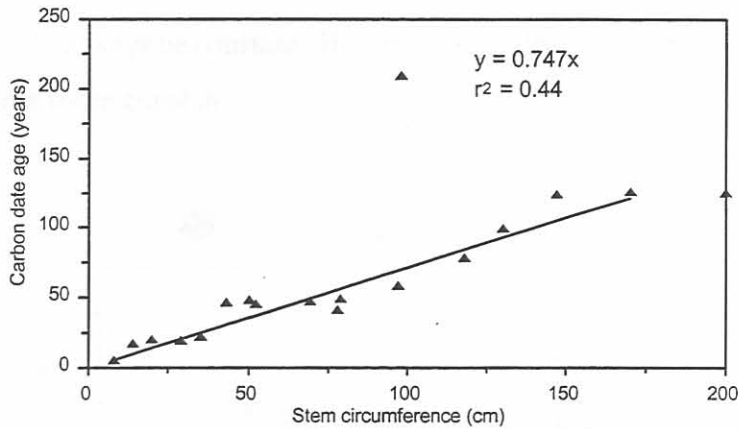
Figure 5.15 The relationship between stem circumference and estimated age of *Acacia erioloba* by radiocarbon dating.

If the outliers (Figure 5.15) are disregarded the regression (Figure 5.16) exhibits a much better relationship ($r^2 = 0.93$). Due to this high correlation the size-classes can be used as age-classes. However, it is suggested that a larger number of samples in the bigger size classes (> 120 cm) are needed to confirm this relationship in older trees.
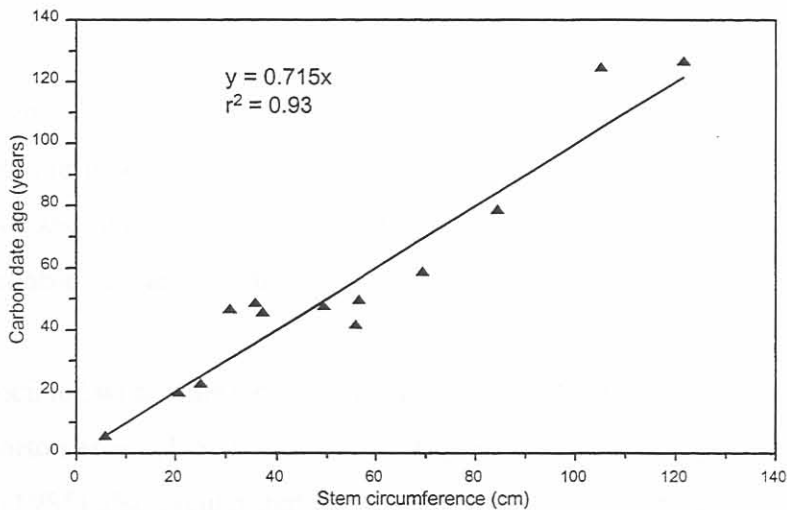
Figure 5.16 The relationship between stem circumference and estimated age of *Acacia erioloba* by radiocarbon dating.

Taking samples from trees is both time consuming and expensive. Field agents, therefore, often use the stem circumference and height measurements of trees to determine size and consequently age structure of a population.

In Figure 5.17 it is clear that there is a relationship between stem circumference and height although it appears not to always be constant. However, as the tree gets older (> 50) this relation-ship appears to become more constant.
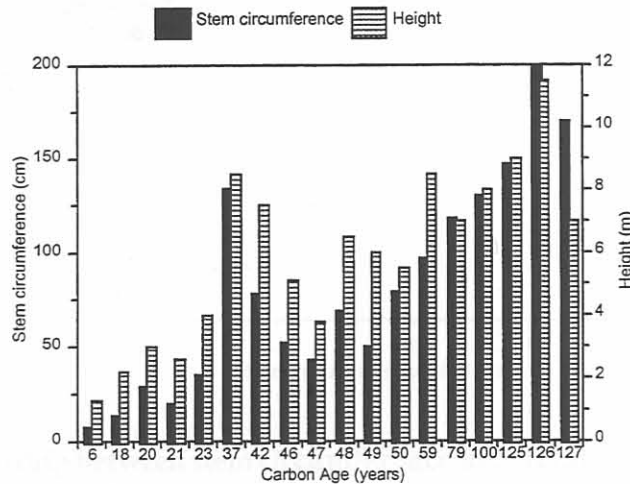
Figure 5.17 Relationship between stem circumference, height and carbon date age for *Acacia erioloba* in the Kalahari Gemsbok National Park.

This data was re-analysed as stem circumference/height ratio. The relationship between stem circumference/height ratio and carbon date age was then determined (Figure 5.18). A regression of the line ($r^2 = 0,66$) reflects the inconsistency of the data as depicted in Figure 5.17. Although stem circumference and height can be used to determine a population's age structure, it would however not be reliable. It can nevertheless serve as a good indication.

The problems associated with using stem diameter to predict age are discussed by Jacoby (1981); Ogden (1981); Norton *et al.* (1987); Norton and Ogden (1990); and Wyant and Reid (1992). Lieberman *et al.* (1985) also argued that the tendency for the growth rates of trees in natural conditions to show high inter-tree variation does mean that the precision of any estimate of the age-size relationship is likely to be low (Wyant & Reid 1992). In their study of *Acacia tortilis*

in South Turkana, Kenya, Wyant and Reid (1992) found that although the correlation between basal stem diameter and known age is high, size may be useful only for predicting the age of young trees. After about 10 years the scatter around the regression line becomes large. In this study the age-size (stem circumference/height ratio) relationship shows a correlation of $r^2 = 0.66$ (Figure 5.18). This is higher than the $r^2 = 0.44$ (Figure 5.15) but lower than the corrected data ($r^2 = 0.93$) (Figure 5.16).
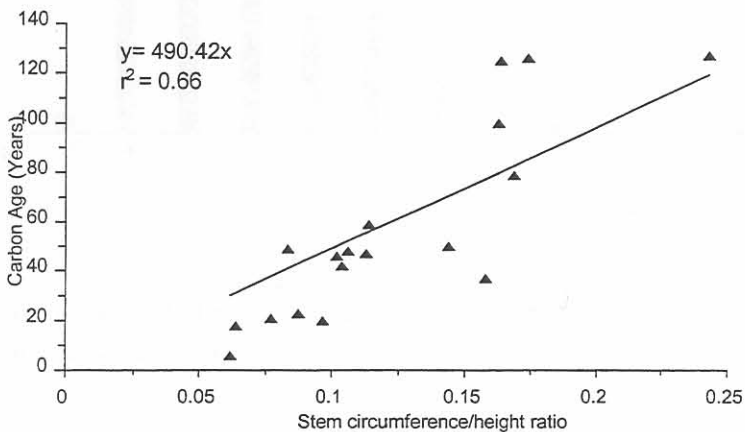
Figure 5.18 Relationship between stem circumference/height ratio and carbon age in years of _Acacia erioloba_.

If the regression line y = 490.42x is applied to available stem circumference and height data for the interior dune area and the northern Nossob Riverbed, the age structure of these population can be determined (Figures 5.19 and 5.20).

It is clear from Figure 5.19 that this population no longer has the typical reverse J-shaped age structure of a viable population, but the population peaked at 60-80 years with 35% of the population falling in this age class.

In Figure 5.20 the structure is similar, but the peak is at a younger stage. 65% of the population is 80 years or younger and 50% of these trees are between 60-80 years. Due to the lack of clima-tic data before 1975 it is impossible to speculate as to the reasons for this unusual population structure.
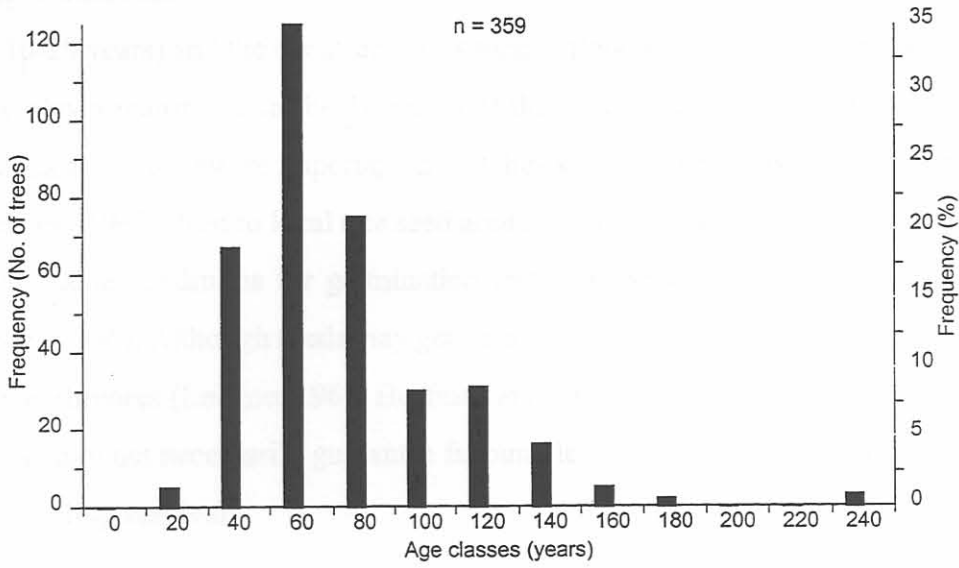
Figure 5.19 Age structure of *Acacia erioloba* using the calculated regression line in the interior dune area.
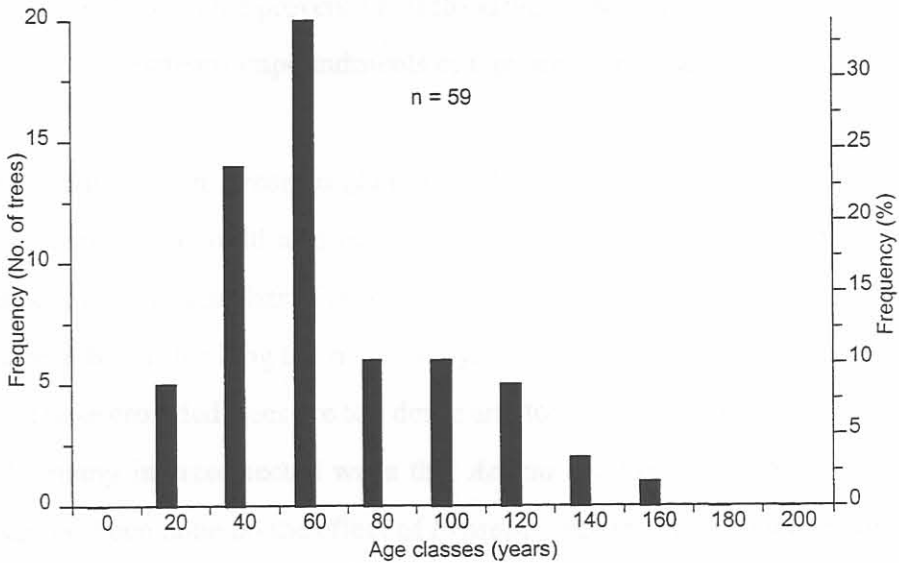
Figure 5.20 Age structure of *Acacia erioloba* using the calculated regression line in the northern Nossob Riverbed.

The timing and amount of seasonal rainfall, the existence of relatively long-term rainfall/drought cycles (± 10-20 years) and the occurrence of sporadic flooding of the Auob and Nossob Rivers, apparently play a major role in the dynamics of the vegetation (Van Rooyen *et al.* 1996). Although floods are rare they are important in that they sustain the relatively low watertable of the rivers (Leistner 1967), lead to local tree seed accumulations (Ward & Breen 1983; Jeltsch *et al.* 1996), favourable conditions for germination and increase establishment probabilities (Van Rooyen *et al.* 1996). Although seeds may germinate as a result of other factors such as ingestion of pods by herbivores (Leistner 1967; Hoffman *et al.* 1989; Barnes *et al.* 1997; Milton & Dean 1999), these may not necessarily guarantee favourable moisture conditions after seed dispersal to ensure seedling survival.

Floods occurred in the Nossob River during 1934 and for the last time in 1963, whereas the Auob River floods about once every 11 years. This corresponds to approximately 70 and 40 years ago respectively, which may have caused the high number of individuals observed in the age classes three and four (40 to 80 years). The large *Acacia erioloba* trees in the Nossob Riverbed depend on a source of underground water (Barnes *et al.* 1997; Milton & Dean 1999). When this source is diminished either through the prevention of flood waters from reaching the Kalahari Gemsbok National Park or by upstream impoundments or tapping of artesian water, the big trees die.

The severe invasion of alien, *Prosopis glandulosa* trees in the upper reaches of the Nossob River in Namibia (Figure 5.21) could also have disastrous effects on the long-term ecology of the riverine ecosystems of the Kalahari Gemsbok National Park. Thickets of *Prosopis* trees develop from seeds spread by cattle along the river valleys and displace the indigenous plants (Milton & Dean 1999). These crowded trees are too dense and too small to function as a key resource for wildlife in the many interconnected ways that *Acacia erioloba* does (Milton & Dean 1999). Little research has been done on the effect of *Prosopis* spp. invasion on water consumption and *Acacia erioloba* populations.

A preliminary study carried out in the Molopo River in the Kalahari however indicates that *Prosopis* spp.'s water consumption probably leads to the death of mature *Acacia erioloba* trees by decreasing the available water supply. The wood of mature *Prosopis* samples contain 31%

water. The amount of ground water used by the *Prosopis* trees has not yet been determined (Woodborne *pers. comm.* 1999[2]).
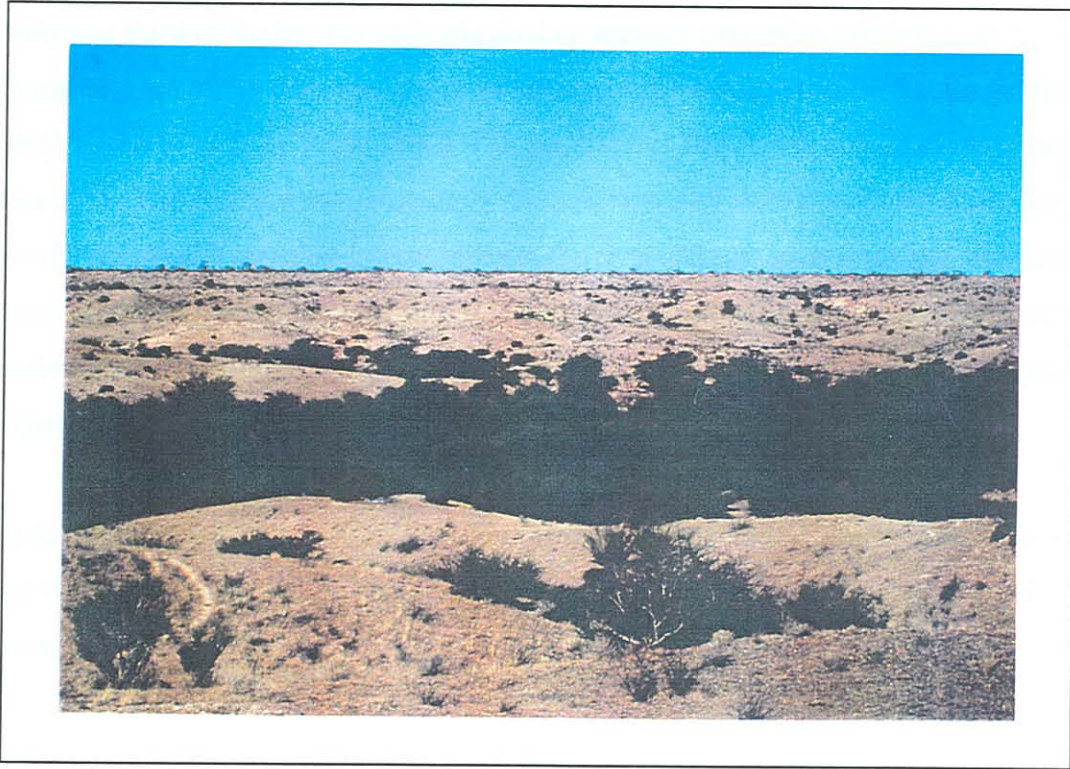
Figure 5.21 Invasion of the upper reaches of the Nossob River in Namibia by *Prosopis* trees.

Fires are less common in semi-arid and arid than in mesic savannas, but are regarded as important since they generally occur after very good rain seasons. This is, however, also the critical period for tree seedling establishment (Jeltsch *et al.* 1996). In the Kalahari Gemsbok National Park fire is not applied as a management tool. The motives for formulating a fire policy as described by Trollope (1981) do not apply to these areas. In general, abnormal thickening of shrubs and accumulation of organic material do not occur in this ecosystem. When rainfall is high for consecutive years, fuel loads may build up which increases the fire frequency for several years following the wet cycle.

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[2] Woodborne, S. Quaternary Dating Research Unit, Division of Water, Environment and Forestry Technology, CSIR, Pretoria, South Africa

Fires have been recorded during 1934, 1968, 1974/5 and 1994/5. Exceptionally high rainfall was also experienced during the same periods. The effect of a single fire in 1976 on the survival of an *Acacia erioloba* community in the dry Nossob River valley was monitored at 3 sites. Approximately one third of the trees in each site died on account of the fire, while almost 50% suffered varying degrees of fire damage. The most extensive fire damage occurred amongst fully grown trees (Van der Walt & Le Riche 1984). This implies that the *Acacia erioloba* communities in the rivers of the Kalahari are not particularly fire resistant. The most significant effect that fire may have on the *Acacia erioloba* communities in the river valleys, apart from high mortality, would be the alteration of the age structure of the population. The control of fires should therefore receive high priority considering the aesthetic and ecological importance of the *Acacia erioloba* community.

The decrease in the frequency or even possible cessation of the flooding regime may justify the need to control fires within the Nossob River valley during periods of successful seedling survival of *Acacia erioloba*.

In the duneveld areas as well as in the Auob River valley of the Kalahari Gemsbok National Park, the *Acacia erioloba* community exhibits a favourable age-structure that allows for recruitment of older trees, whereas a large proportion of the northern Nossob is characterised by an age structure skewed towards mature trees (Figures 5.10, 5.12 and 5.14). This is suggested to be as a result of drought and previous fires that have destroyed tree seedlings, which are susceptible to grass fires (Jeltsch *et al.* 1996). Thus consecutive recruitment failures due to drought and fires may impoverish the river valley community of a favourable age-structure and hence lead to population decline.

Acacia erioloba seedlings germinate and survive more abundantly in high than low rainfall years with highly variable rainfall quantity and seasonality leading to episodic recruitment (Barnes *et al.* 1997). In addition, recruitment is also spatially and temporarily variable. Although rainfall is erratic, it very much follows the pattern as predicted in that a wet cycle is experienced every 10-20 years (Figure 2.4). Rainfall, therefore, cannot be the only factor attributing to seedling survival. Survival of seedlings is dependent on numerous environmental factors, such as rainfall amount and distribution, grass competition and population levels of predatory insects and rodents

(Jeltsch *et al.* 1996; Barnes *et al.* 1997). These factors need to be favourable and coincide with the presence of scarified seeds for successful stand establishment of seedlings. Although seedlings may be well established in their first year, this does not guarantee survival during the following three to four critical years of growth (Barnes *et al.* 1997), while a single veld-fire may cause serious damage to younger seedling generations.

Although above average rainfall was experienced during 1975, 1976, 1988, 1993 and 1997 it is not sufficient to sustain the survival of seedlings after germination. Establishment probabilities in specific sites are increased by local accumulation of tree seeds. One of the processes that leads to accumulation is rare, but important, floods; the last flood being recorded in 1963. If large trees die, the possibility of seed accumulation through the dispersal in herbivore dung also decreases.

It is suggested that although prevention of flood waters is seen as one of the major factors influencing recruitment, it is important to look at the population levels of predatory insects and rodents in the northern Nossob as a possible cause for low survival of seedlings. Another factor which could contribute to low recruitment figures as well as the increase in the death of older trees, is diseases.

CHAPTER 6

CONCLUSION AND RECOMMENDATIONS

The character of the Kalahari ecosystem depends on spatial heterogeneity which increases biotic diversity. *Acacia erioloba* is considered a keystone species in the Kalahari and therefore create spatial heterogeneity, prevent single species dominance and supply a critically limiting resource or service (Milton & Dean 1995). The functions performed by a keystone species may be modified by its population structure, density and distribution.

Preliminary data on the size structure of the *Acacia erioloba* population in the northern Nossob Riverbed of the Kalahari Gemsbok National Park showed a poor survival of seedlings and an almost complete absence of juvenile plants (Van Rooyen *et al.* 1996). This recruitment failure is presently resulting in the decline in isolated mature trees, which may result in a change in the population structure of the species.

The generation of patchiness, a keystone function, can only be performed by large trees, and a change in the population structure of *Acacia erioloba* could therefore also alter its role in the ecosystem. From a management view point it is therefore important to recognize *Acacia erioloba* as a keystone species and to be aware of the functions it performs. It became essential to determine the accurate age-structure in order to have a more complete understanding of the population dynamics and the sustained management of *Acacia erioloba*.

Core sampling in indigenous hardwood species is not a common practice and the difficulties of both sampling and examining species has been discussed in numerous research reports. However, through this research a unique and effective non-destructive method of sampling was developed, whereby high quality cores suitable for carbon dating and dendrochronological studies can be obtained without permanently damaging trees.

In indigenous species it is often found that features which appear to delineate growth-rings are either discontinuous or rows of fibres laid down in response to stress. This necessitates the analysis of population structure and dynamics to be based on tree sizes.

The results of this investigation into the problem of determining the age of semi-arid trees suggest that the marginal parenchyma bands can indicate seasonal growth patterns in *Acacia erioloba*. The marginal parenchyma bands can usually be distinguished from the frequent intraseasonal banded parenchyma by their fineness and evenness in appearance in contrast to the more irregular, wavy, confluent bands.

Carbon dating of samples was done at the Quaternary Dating Research Unit of the Division Water, Environment and Forest Technology of the CSIR in Pretoria. Estimated carbon date age was determined by making use of calibration curves. Ring counts and carbon date ages were compared and exhibited a high correlation ($r^2 = 0.96$).

A correlation was also found between stem circumference/height and carbon date age ($r^2 = 0.66$). This was used successfully to estimate population structure from data that has already been collected. It is recommended that more samples be collected and analysed in order to improve the regression. Estimated age based on stem circumference overestimate age.

By identifying seasonal growth changes in the wood anatomy and correlating ring counts with carbon date age, age and subsequent growth rates for *Acacia erioloba* in the Kalahari Gemsbok National Park were determined. Mean annual radial growth rates were calculated at 2mm/year which indicated that the average growth rate was slower than that previously reported for *Acacia* spp. growing in arid and semi-arid conditions.

Although more sophisticated dendrochronological based research may provide more accurate ages for older trees, it has been the conclusion of this study that in fact many *Acacia* spp. are probably far younger than believed.

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Further work in this field to cast light on the relationship between growth rate and meteorological data should include cambial marking techniques which do not require felling of trees. Periodic marks with pins or nails (Wolter 1968; Shiokura 1989) or with vertical knife cuts permit collection of wood samples without cutting down the tree. The time of the year when the marginal parenchyma bands are produced can then be identified precisely. This has potential for trees of any age or size, provided it is conducted over sufficient years to allow for variation in an area with highly erratic rainfall.

It is suggested that although the cessation of flood waters is seen as one of the major factors influencing the decline of juvenile plants a comprehensive study needs to be undertaken. This research should take into account possible:

- decrease in insect populations responsible for pollinating *Acacia erioloba*;
- increase in predatory insects and rodents;
- impact of increased grazing during drought periods; and
- diseases and fungal infections of mature trees.

SUMMARY

AGE DETERMINATION OF *ACACIA ERIOLOBA* IN THE
KALAHARI GEMSBOK NATIONAL PARK

by

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Magister Scientiae

Trees are an integral component of African savannas. The function of savanna trees may however vary greatly with their population structure, density and distribution. The structure and function of arid and semi-arid savannas are largely governed by soil moisture, soil nutrients, fire and herbivory. To manage and sustainably utilize the trees in semi-arid regions an understanding of their population dynamics is needed. In this regard knowledge of their age and growth rates is essential.

Acacia erioloba plays a pivotal role as keystone species in this environment and is of special ecological importance. To manage the Kalahari Gemsbok National Park in a sustainable manner it is therefore of vital importance to study this important species.

Population structure of *Acacia erioloba* in the Kalahari Gemsbok National Park has been based on size-structure derived from size-class data i.e. stem circumference and height. In order to have a more complete understanding of the population dynamics and their sustained management accurate age-structure is needed. The aim of this study was therefore to develop age-size relationships for *Acacia erioloba* on the basis of ring-counts and carbon dating. Such relationships enable determination of the age-class distribution of the population and consequently the dating of successful regeneration events.

An effective non-destructive sampling method was developed and high quality cores were obtained. Cores were used to determine age by means of carbon dating and anatomical investigation. Seasonal growth changes were reflected in the wood anatomy as bands of marginal parenchyma on the polished surfaces of discs or cores. A strong relationship was found between ring count and estimated carbon age which enabled the determination of age and subsequent growth rates for *Acacia erioloba* in the Kalahari Gemsbok National Park. Age-size relationships for *Acacia erioloba* on the basis of ring-counts and carbon dating lead to the analysis of age-structure for the population of *Acacia erioloba* in the interior dune area and the northern Nossob Riverbed.

Successive above-average rainfall and the occurrence of sporadic flooding play a major role in the dynamics of the vegetation. Floods are rare but they are important in that they sustain the relatively low watertable, lead to tree seed accumulations and favourable conditions for germination and establishment.

OPSOMMING

OUDERDOMSBEPALING VAN *ACACIA ERIOLOBA*

IN DIE KALAHARI GEMSBOK NASIONALE PARK

deur

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Bome is 'n integrale komponent van Afrika savannas. Die rol wat bome in savannas speel, verskil grootliks as gevolg van die populasie struktuur, digtheid en verspreiding van die bome. Die struktuur en funksie van ariede en semi-ariede savannas word grootliks bepaal deur die beskikbaarheid van grondvog, die beskikbaarheid van voedingstowwe, vure en beweiding. Ten einde bome in ariede en semi-ariede streke volhoubaar te bestuur, is dit nodig om die populasie dinamika daarvan te verstaan. In die verband is kennis rakende die ouderdom en groeitempo van die bome noodsaaklik.

Acacia erioloba speel 'n sleutelrol in die savanna omgewing en is van besondere ekologiese belang. Ten einde die Kalahari Gemsbok Nasionale Park op 'n volhoubare wyse te bestuur is dit gevolglik noodsaaklik om hierdie belangrike spesie te bestudeer.

Die populasie struktuur van *Acacia erioloba* in die Kalahari Gemsbok Nasionale Park is tot dusver beskryf in terme van die grootte van die bome en afgelei van grootte-klas data, dit wil sê stamomtrek en hoogte. Ten einde 'n vollediger begrip van die populasie dinamika en die volhoubare bestuur daarvan te verkry, is dit noodsaaklik om betroubare data rakende die ouderdom van die bome te bekom. Die doel van hierdie navorsing was derhalwe om die ouderdomstruktuur van *Acacia erioloba* te bepaal gebaseer op die tel van jaarringe en koolstofdatering.

Hierdie verwantskap stel ons in staat om die ouderdomklas verspreiding van die populasie akkuraat vas te stel en gevolglik om die voorwaardes vir regenerasie te beskryf.

'n Effektiewe metode om eksemplare van 'n hoë gehalte vir ouderdomsbepaling te neem sonder om die bome permanent te beskadig, is ontwikkel. Ouderdomme is bepaal deur gebruik te maak van koolstofdatering en 'n anatomiese studie. Seisoenale veranderinge in die groei is gereflekteer in die houtanatomie as marginale parenchiem ringe op die oppervlak van gepoleerde skywe en boorsels. 'n Duidelike verband is gevind tussen die jaarringe en die koolstof gedateerde ouderdom wat dit moontlik gemaak het om die ouderdom en groeitempo van *Acacia erioloba* in die Kalahari Gemsbok Nasionale Park akkuraat te bepaal. Die bepaling van die ouderdomgrootte verwantskap van *Acacia erioloba* gebaseer op jaarringe en koolstofdatering het gelei tot die ana-lise van die ouderdomstruktuur van die populasies in die binneveld en noordelike Nossob rivier-bed.

Opeenvolgende bogemiddelde reënval en die voorkoms van sporadiese vloede speel 'n belangrike rol in die dinamika van die plantegroei. Vloede is skaars maar belangrik in die sin dat dit die relatiewe lae watertafel onderhou, lei tot saadakkumulasie en gunstige toestande vir ontkieming en vestiging.

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APPENDIX A

A non-destructive sampling method for dendrochronology in hardwood species

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ABSTRACT

Core sampling in indigenous hardwood species is not a common practise. A field method was developed to obtain a large enough sample without permanently damaging the trees. A Milwaukee Dymo 2,3 kW electric drill fitted with a 2-speed gearbox and powered by a generator was used. A core drill bit (100 mm x 350 mm) fitted with tungsten tips was designed to fit the electric drill. Core samples of mature trees of unknown age were collected according to height and diameter classes in the Kalahari Gemsbok National Park. This non-destructive method was found to be suitable for collecting large core samples of hardwood species.

INTRODUCTION

Acacia erioloba is classified as a keystone species in the Kalahari (Dean and Milton, 1995). A keystone species being defined as one upon which a diversity of other plant and animal species depend.

In a study to determine the population structure of *Acacia erioloba* in the Kalahari Gemsbok National Park it became essential to determine the exact age of the trees. For dendrochronological studies as well as carbon dating, large samples are needed that include all growth-rings from pith to cambium. However, because of the importance of individual trees in this semi-arid region a non-destructive method of sampling had to be developed.

EARLIER ATTEMPTS AT CORE SAMPLING AND RELATED PROBLEMS

Generations of foresters used the increment borer developed by the German forester, Pressler, to obtain samples from living trees, mainly to determine age and to study growth rates at different ages (Sulc, 1967). The Pressler borer, however, was designed to be used on softwoods and the core obtained is too small for a detailed study of wood characteristics. The process is also rather slow and the position of the pith difficult to locate (Echols and Mergen, 1955; Brown, 1958; Sulc, 1967).

Early attempts at mechanization of large increment borers were only partially successful. All of these power sources were rather massive and, therefore, difficult to transport (Stonecypher and Cech, 1960; Nicholls and Santer, 1961; Forest Biology Subcommittee 1963; Echols, 1969).

Furthermore both the electric drills and the gasoline engines turned the borers too fast and caused "burning" of the cutting edges. Moreover the electric drills and the gasoline engines used, were usually not reversible and could not be used to turn the increment borers out of trees (Echols, 1969). The diameter of the cores obtained by this method was small and subject to degradation by temperature and compression due to increasing frictional forces (Nicholls and Santer, 1961; Sulc, 1967).

Johansen (1987) describes a power system used on pine trees which is much more portable, comfortable and produces smooth cores. Unfortunately it has not been used to extract cores from hardwood species.

Many manufacturers of increment borers do not recommend using borers with electric drills, since the borer may break due to the high friction and torque (Lussier, pers. com. 1998).

REQUIREMENTS FOR CORE SAMPLING

The wood of *A. erioloba* is dense and very hard and can therefore not be sampled with conventional hand-driven increment corers (Gourlay; 1995). According to Kromhout (1975) the density of *Acacia erioloba* is 1,07 g/cm³.

In studies carried out on African *Acacia* species it was not unusual for the tempered steel borer to break due to excessive torque (Gourlay 1995). The researcher may, therefore, miss or fail to reach the pith in some cases. In such cases the length of missing core and number of missing growth-rings has to be estimated.

Small-diameter samples pose a difficulty in obtaining material from the pith and adjacent growth-rings, which are essential for carbon dating. Because of the frequent eccentricity of the pith it is necessary to use a drill bit with a large diameter.

Taking the requirements for increment borers suggested by Echols (1969) into account and noting the problems experienced by earlier researchers a drill bit was then designed to fit a commercially available electric drill.

MATERIALS AND METHOD

The method adopted may be of interest to other researchers and is therefore described in some detail.

In the present study a Milwaukee Dymo 2,3 kW electric drill was fitted with a 2-speed gearbox and powered by a generator.

A core drill bit, fitted with tungsten tips, was designed to fit the electric drill. The drill bit used was 100 mm in diameter and 350 mm long. The tungsten tips were attached to the outside of the cylinder to ensure that the core could be removed easily (Figure 2).
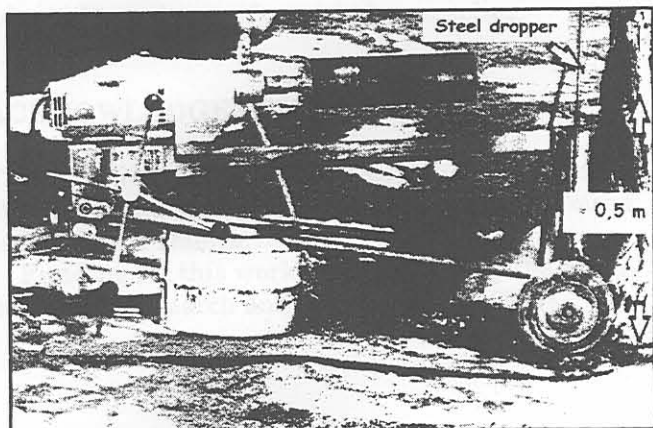

FIGURE 1. Equipment used in sampling Acacia erioloba.

The electric drill was fitted on a lightweight pipe stand with wheels for easy mobility and was powered by a portable generator. Conventionally this drill is used for extracting cores for soil sampling , and drills in a vertical position. The stand was set up in a horizontal position and secured in position by steel droppers (Figure 1).
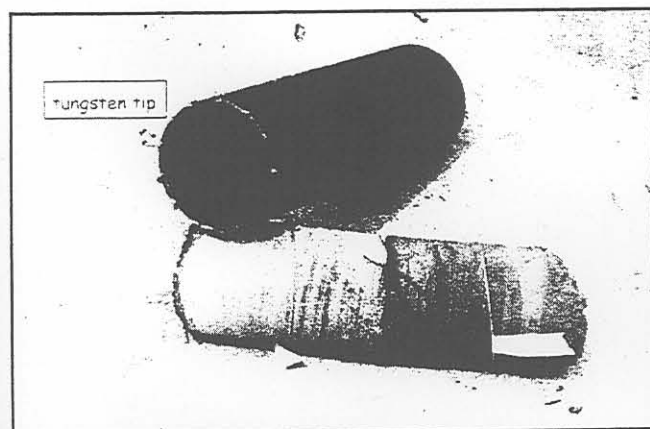

FIGURE 2. Customised drill bit and core sample.

Samples of mature trees of unknown age were collected according to height and diameter classes in both the Nossob River and duneveld areas of the Kalahari Gemsbok National Park. Samples were collected at a height of .0,5 m above the ground (Figure 2) .

Once revolving, the bit was slowly driven into the tree by simply applying pressure to the handle. The drill bit was water cooled while drilling at a low speed, 450 rpm, to prevent burning and compression of the core.

The bit was frequently reversed out of the tree by hand, using the handle which regulates the depth of the drill. Because of this feature it was possible to remove bark and sawdust that tended to clog the drill bit.

The increment borer could easily be driven completely through a tree in cases where the shank was longer than the tree diameter, thereby extracting a core from bark to bark. Trees with a stem diameter of more than 350 mm were carefully measured and then drilled from both sides of the trunk.

The holes that remained after sampling were plugged with wooden dowels to lessen insect and fungal attack.

The time required for the operation varied according to tree size, but on average was in the order of one hour for a core of 100 x 350 mm.

RESULTS AND DISCUSSION

The quality of the cores taken by making use of the described method, was excellent. Samples were large enough to include both the pith and adjacent growth-rings. Samples were smooth, not burned and outer rings did not "corkscrew" (Figure 3).
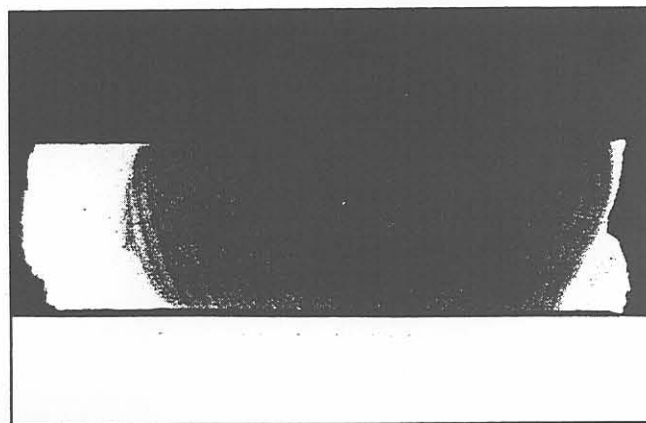

FIGURE 3. Core sample

Trees with a large diameter had to be carefully measured and then drilled from both sides of the trunk. This was problematic and in future studies longer drill bits should be used in order to extract cores from bark to bark in large trees. For trees with a smaller circumference bits with a smaller diameter can be used.

The drill bit used in this research can be water cooled and drills at a low speed therefore preventing burning and compression of the cores. The fact that the bit could be reversed frequently also contributes to high quality samples.

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CONCLUSION

The equipment used is a definite improvement over conventional, hand-turned borers and other described powered equipment and can readily be used where a large number of cores must be taken from hardwood species in a fairly accessible area.

Using this method of sampling enabled the researcher to obtain high quality material suitable for carbon dating and dendrochronological studies without permanently damaging the trees.

The equipment used in this research can also be adapted to suit specific needs for sampling.

ACKNOWLEDGEMENTS

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