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 however 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 circumference 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	

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

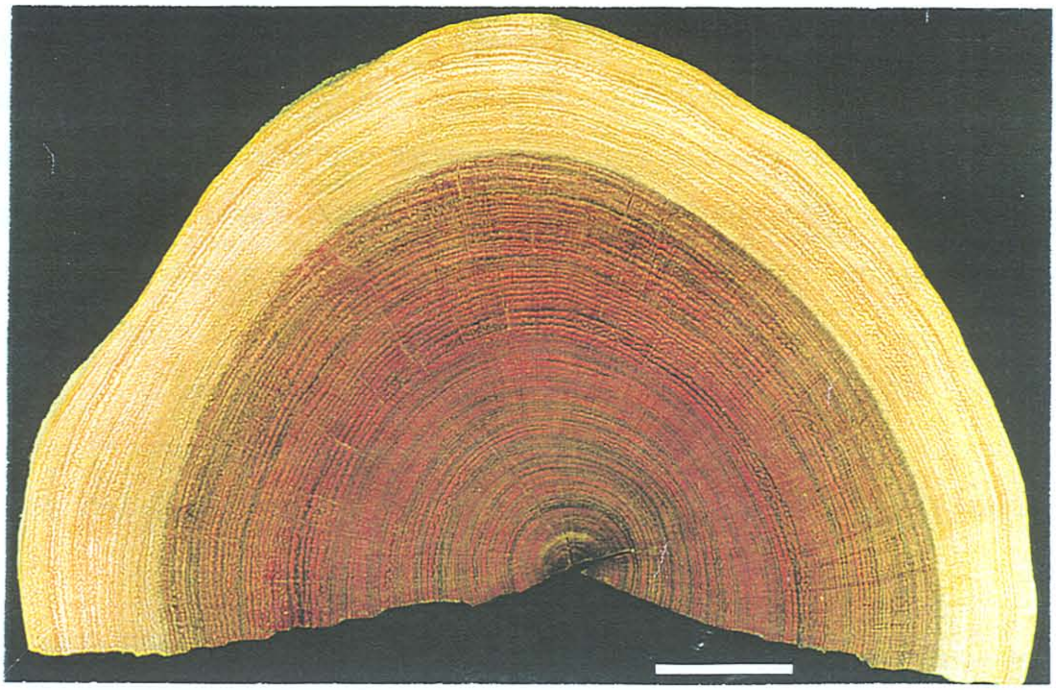

Figure 5.1 Sanded, polished disc of *Acacia erioloba* [Scale bar = 20 mm].

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.

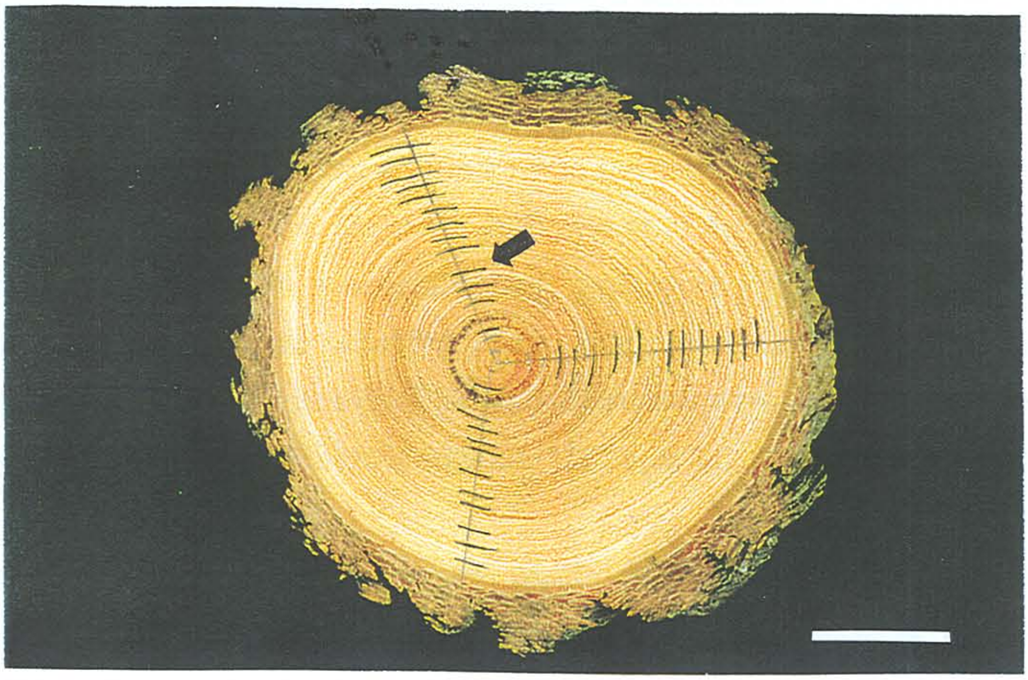

Figure 5.2 Marginal parenchyma bands (arrow) marked on different radii of an *Acacia erioloba* disc from the duneveld (LD 3; stem circumference = 29 cm; tree height = 3 m; ring count = 15; estimated age by carbon dating = 20 years) [Scale bar = 20 mm].

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.

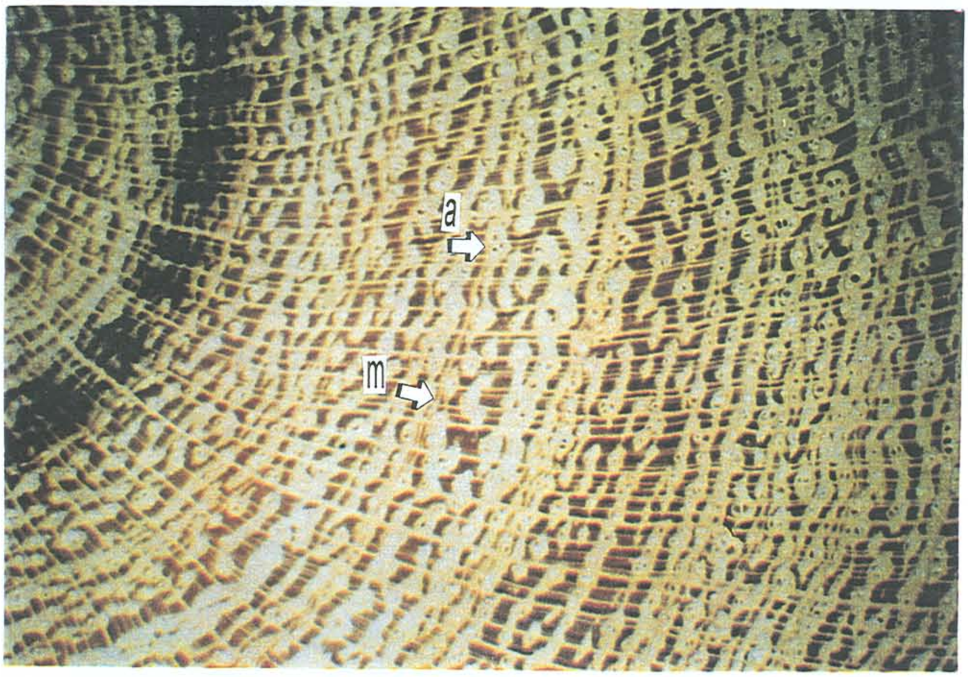

Figure 5.3 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing the fine marginal parenchyma (m) partially obscured by the broader aliform-confluent parenchyma (a).

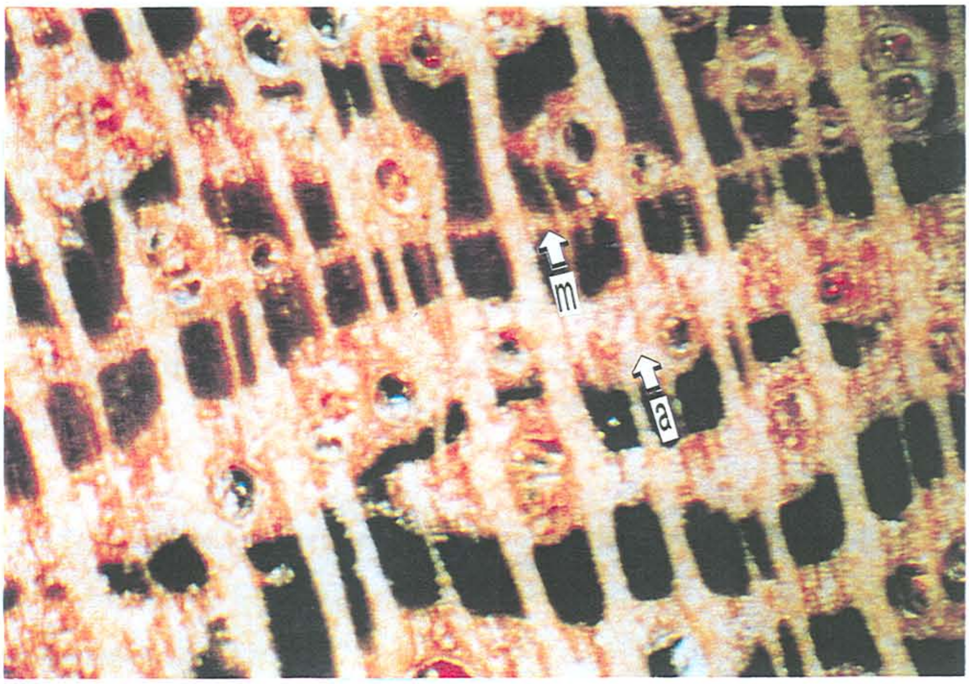

Figure 5.4 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing fine marginal parenchyma (m) clear of the aliform-confluent parenchyma (a).

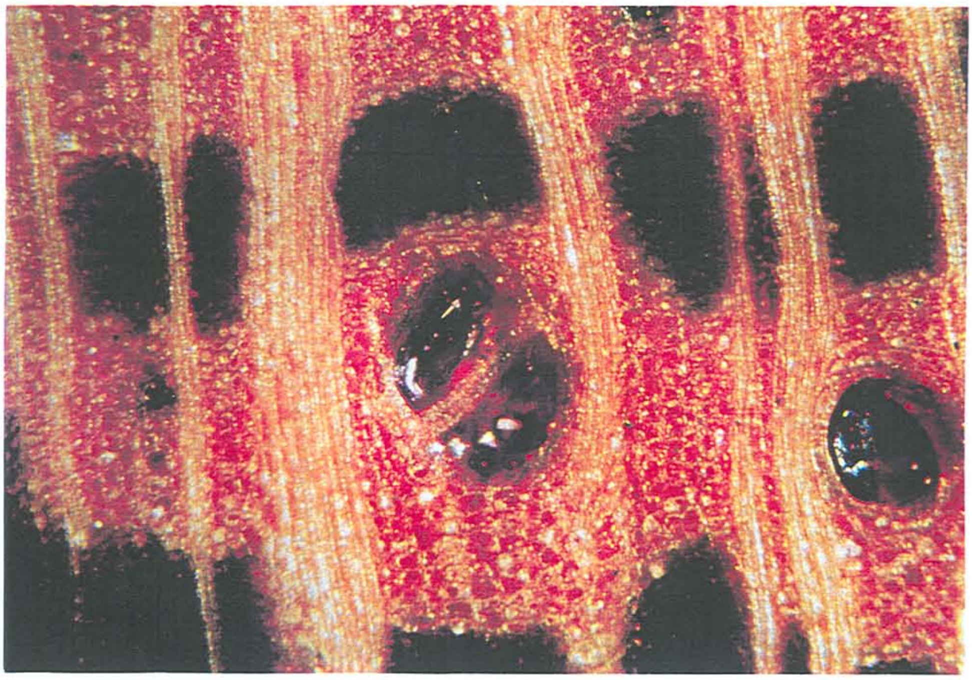

Figure 5.5 Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park, showing dense, dark heartwood, filled with gum deposits (10 x magnification).

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.

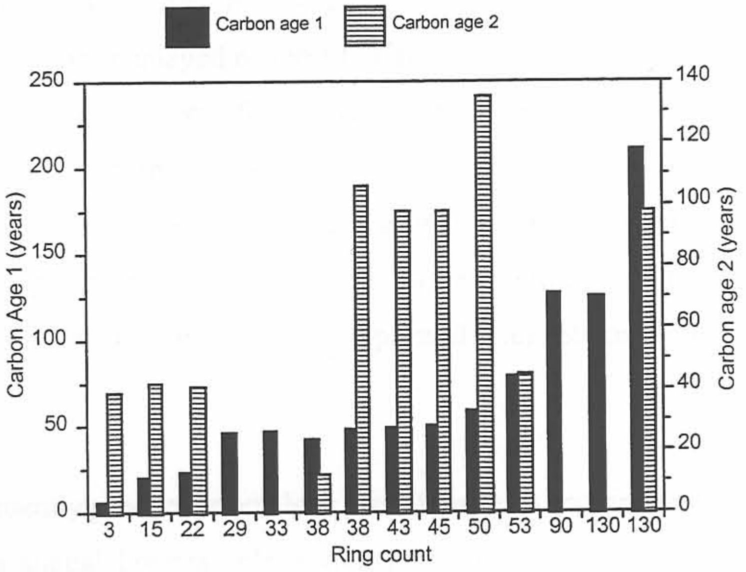

Figure 5.6 Relationship between ring count and estimated carbon age 1 and 2 for *Acacia erioloba*.

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).

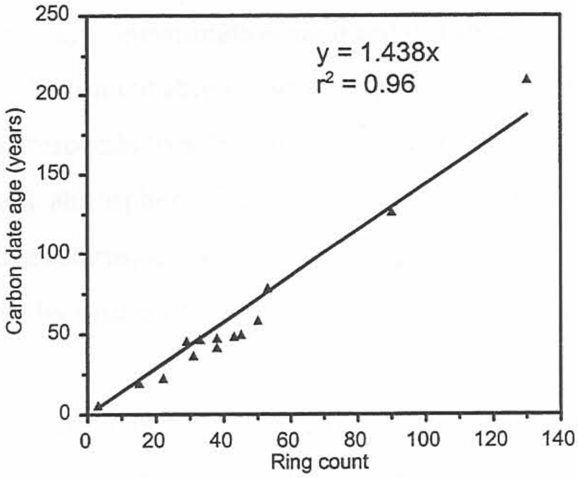

Figure 5.7 Relationship between estimated age by carbon dating and ring count for *Acacia erioloba*.

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.*

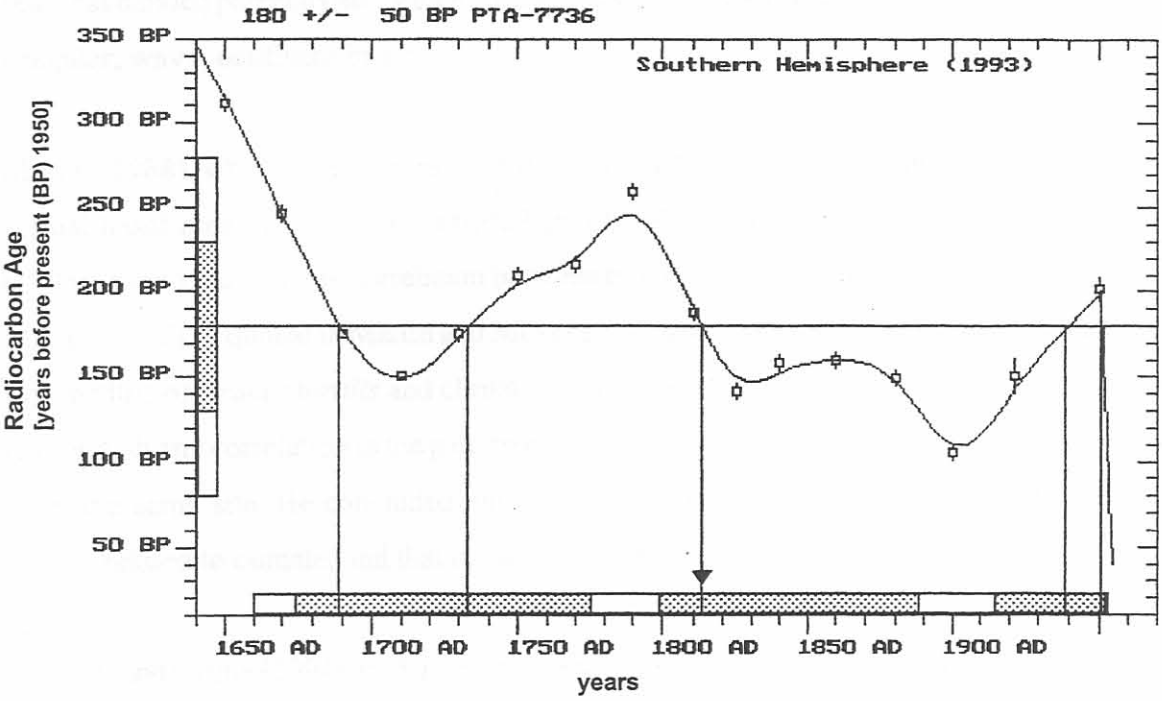

Figure 5.8 Determination of age of Sample LD 14 using the ^{14}C curve. Possible age (arrow).

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.)

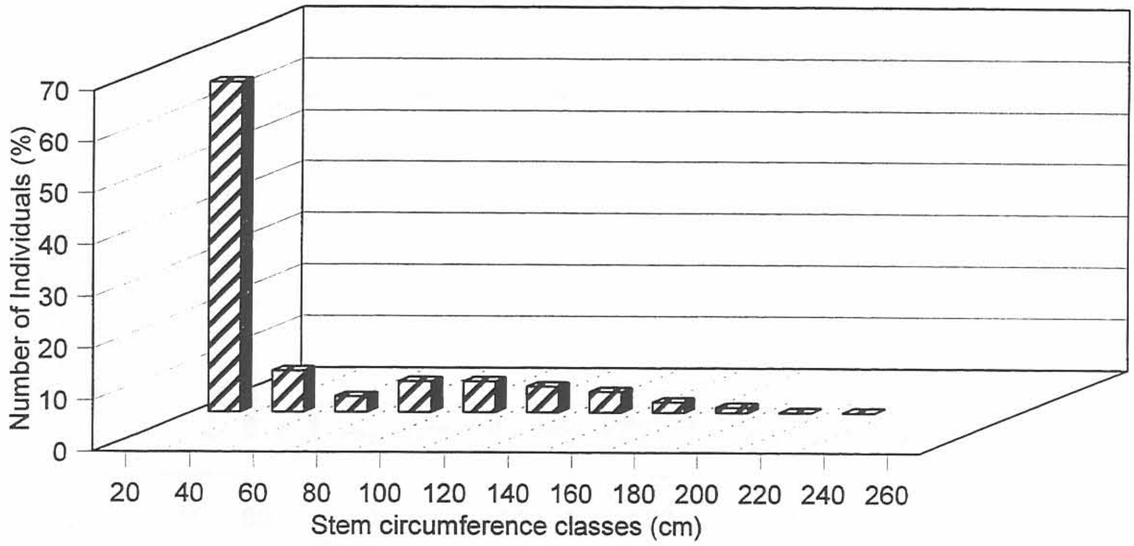

Figure 5.9 **Size structure of *Acacia erioloba* based on stem circumference classes in the interior dune area of the Kalahari Gemsbok National Park (8a) [n = 494 individuals].**

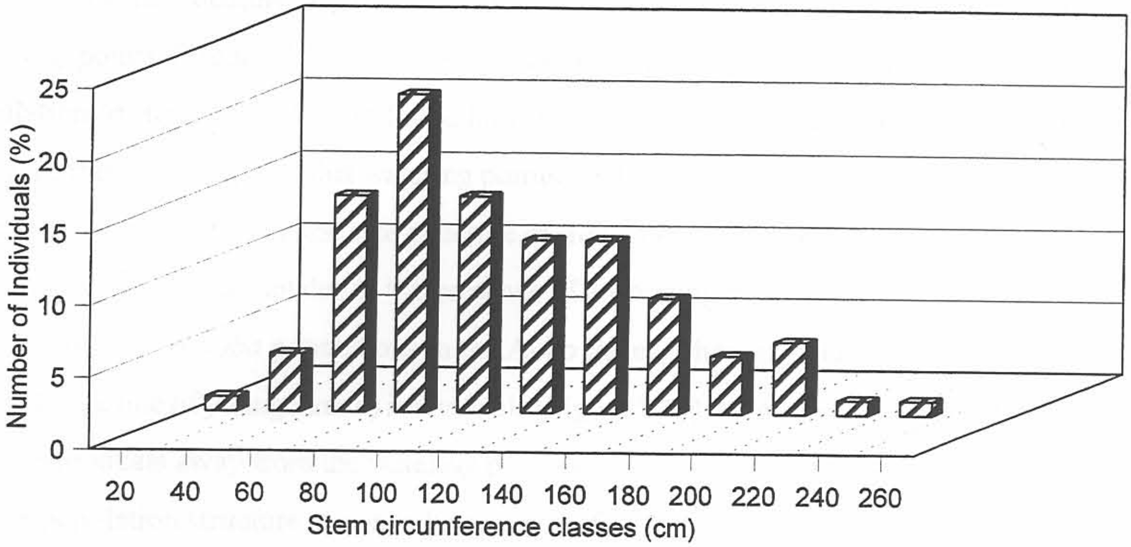

Figure 5.10 Size structure of *Acacia erioloba* based on stem circumference in the northern Nossob Riverbed of the Kalahari Gemsbok National Park (1) [n = 311].

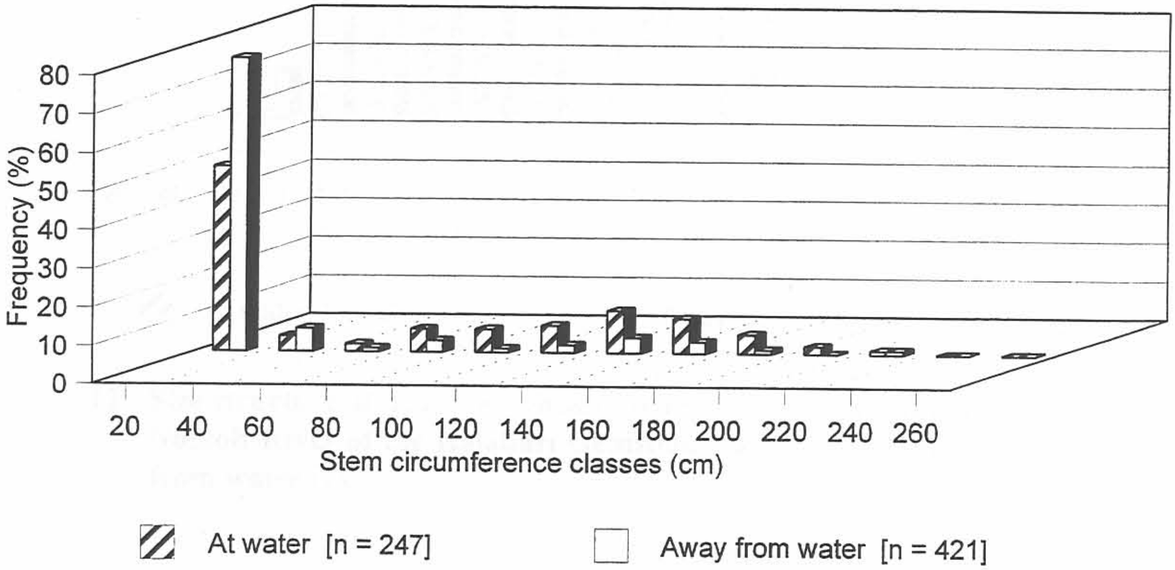

Figure 5.11 Size structure of *Acacia erioloba* based on stem circumference classes at Gharagab in the interior dune area of the Kalahari Gemsbok National Park, at and 3 km away from water (8a).

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.

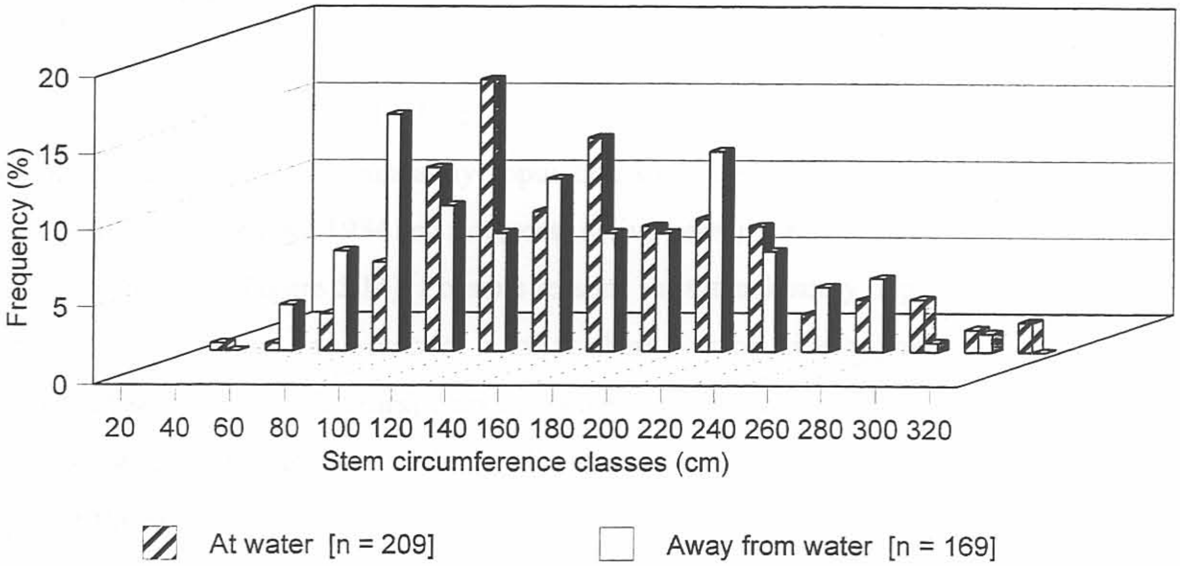

Figure 5.12 **Size structure of *Acacia erioloba* based on stem circumference classes in the Nossob River of the Kalahari Gemsbok National Park, at and 5 km away from water (1).**

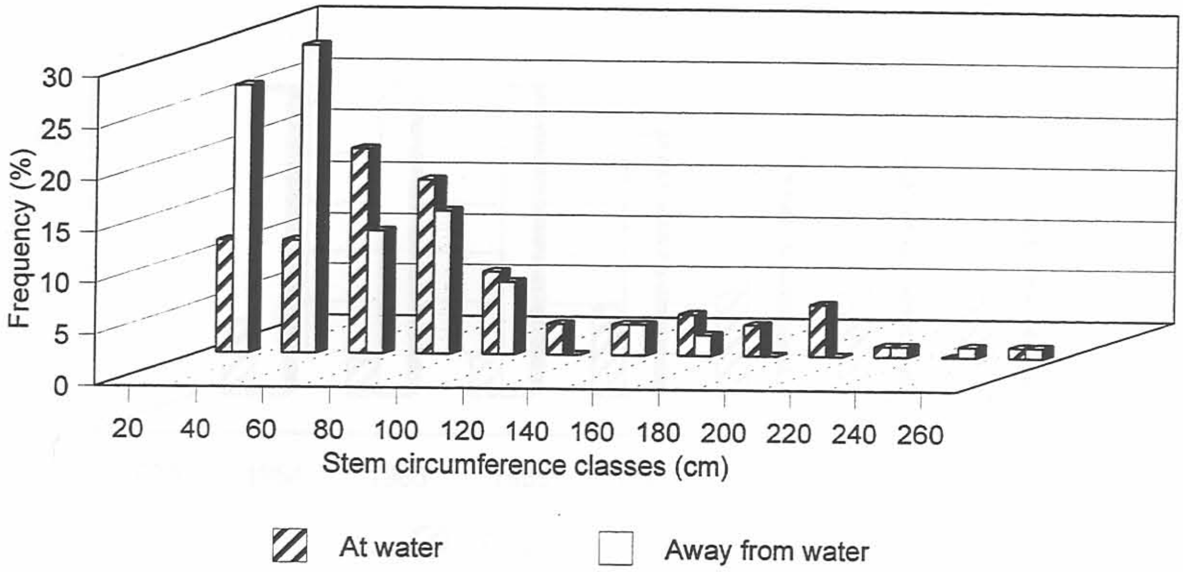

Figure 5.13 **Size structure of *Acacia erioloba* based on stem circumference classes in the Auob River of the Kalahari Gemsbok National Park, at and away from water (3a).**

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.

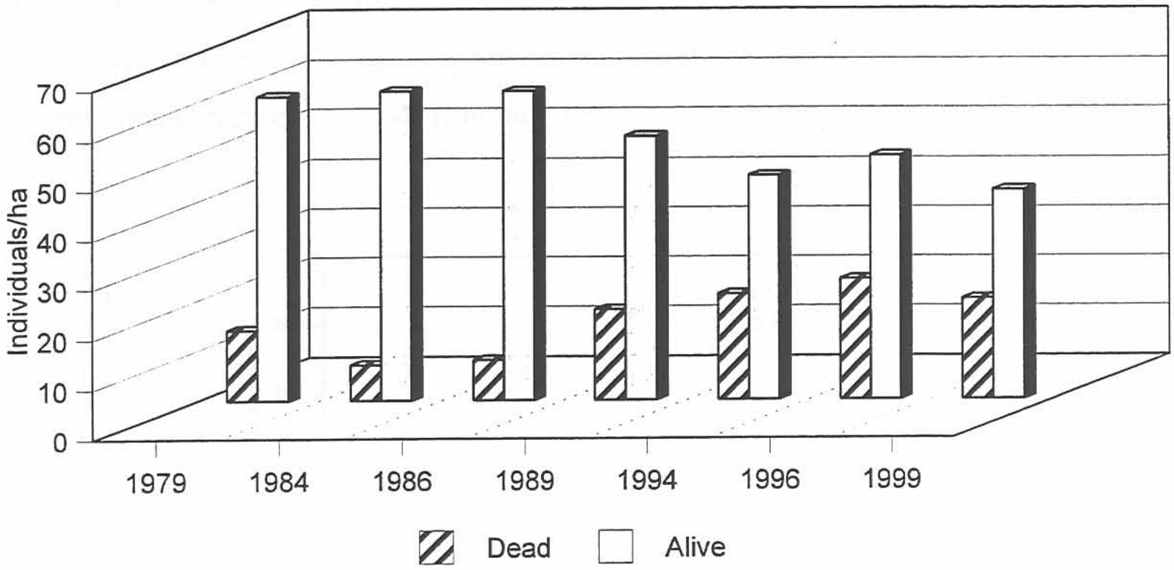

Figure 5.14 Number of individuals/ha of dead and alive *Acacia erioloba* in the northern Nossob River of the Kalahari Gemsbok National Park (1).

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).

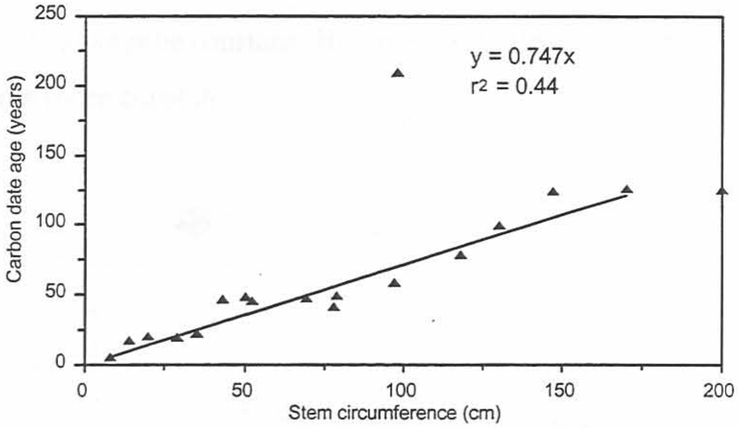

Figure 5.15 The relationship between stem circumference and estimated age of *Acacia erioloba* by radiocarbon dating.

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.

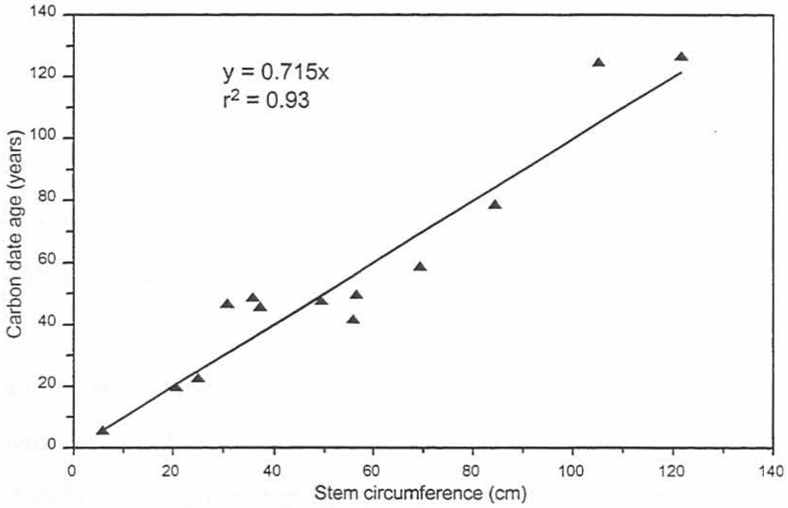

Figure 5.16 The relationship between stem circumference and estimated age of *Acacia erioloba* by radiocarbon dating.

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 relationship appears to become more constant.

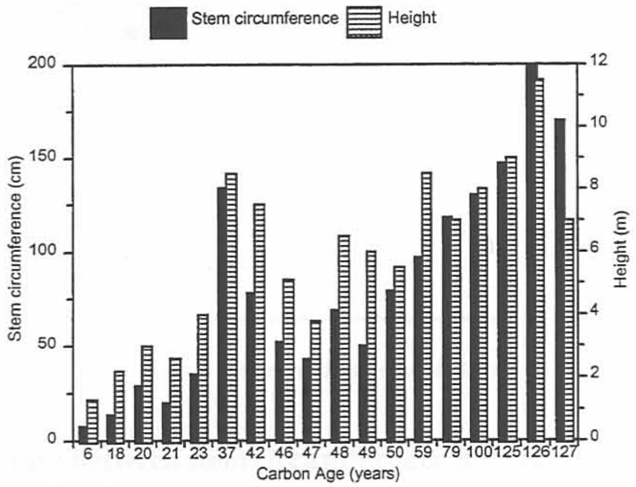

Figure 5.17 Relationship between stem circumference, height and carbon date age for *Acacia erioloba* in the Kalahari Gemsbok National Park.

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).

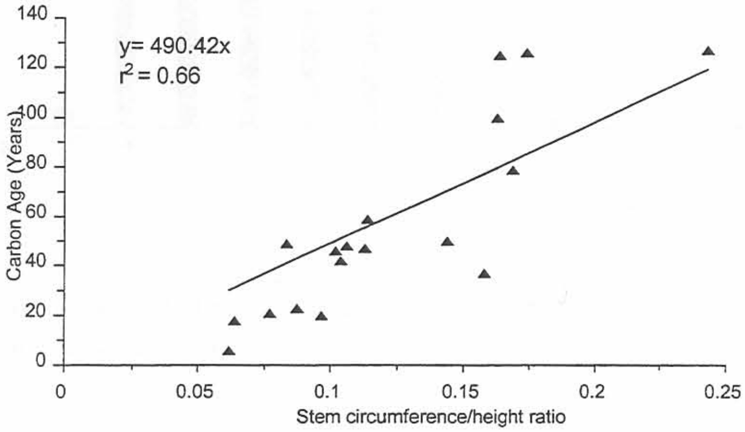

Figure 5.18 Relationship between stem circumference/height ratio and carbon age in years of *Acacia erioloba*.

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 climatic data before 1975 it is impossible to speculate as to the reasons for this unusual population structure.

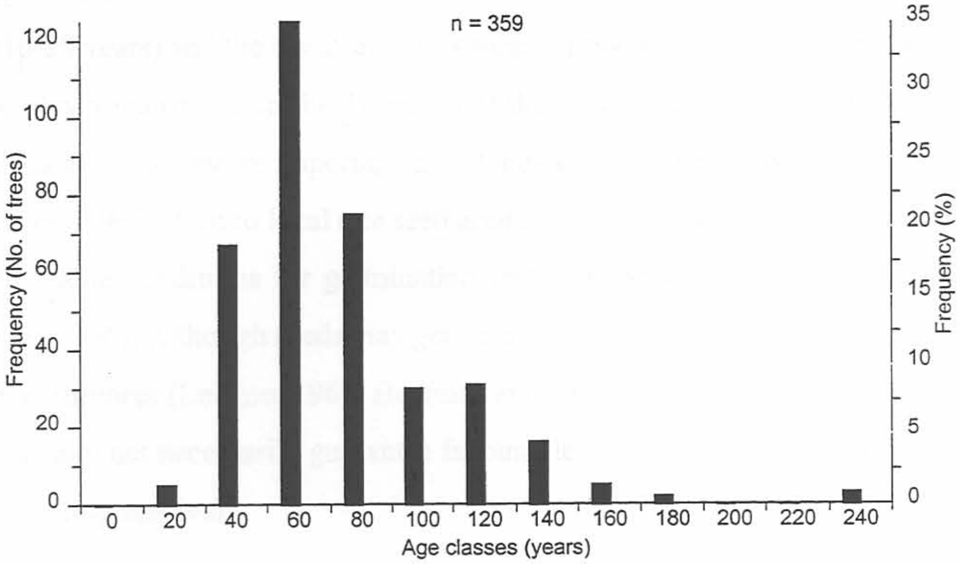

Figure 5.19 Age structure of *Acacia erioloba* using the calculated regression line in the interior dune area.

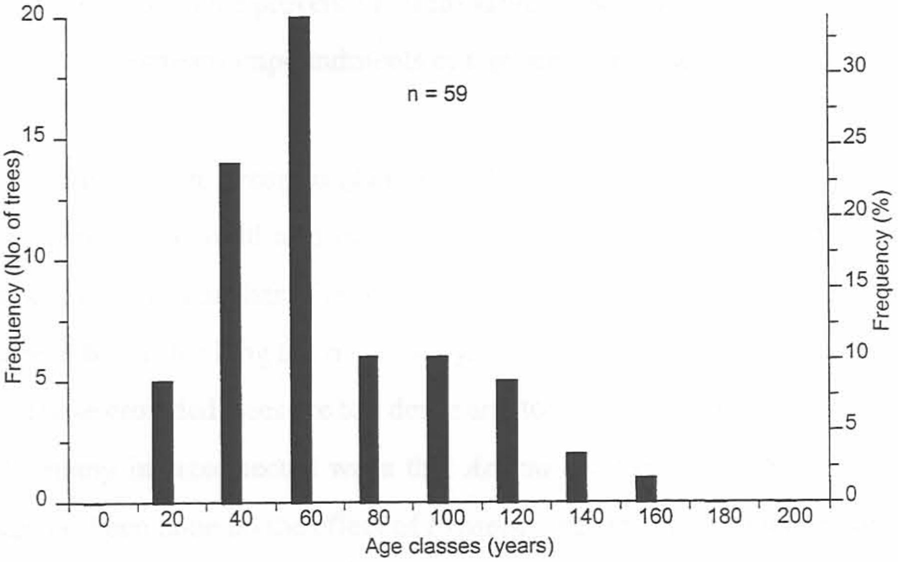

Figure 5.20 Age structure of *Acacia erioloba* using the calculated regression line in the northern Nossob Riverbed.

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]).

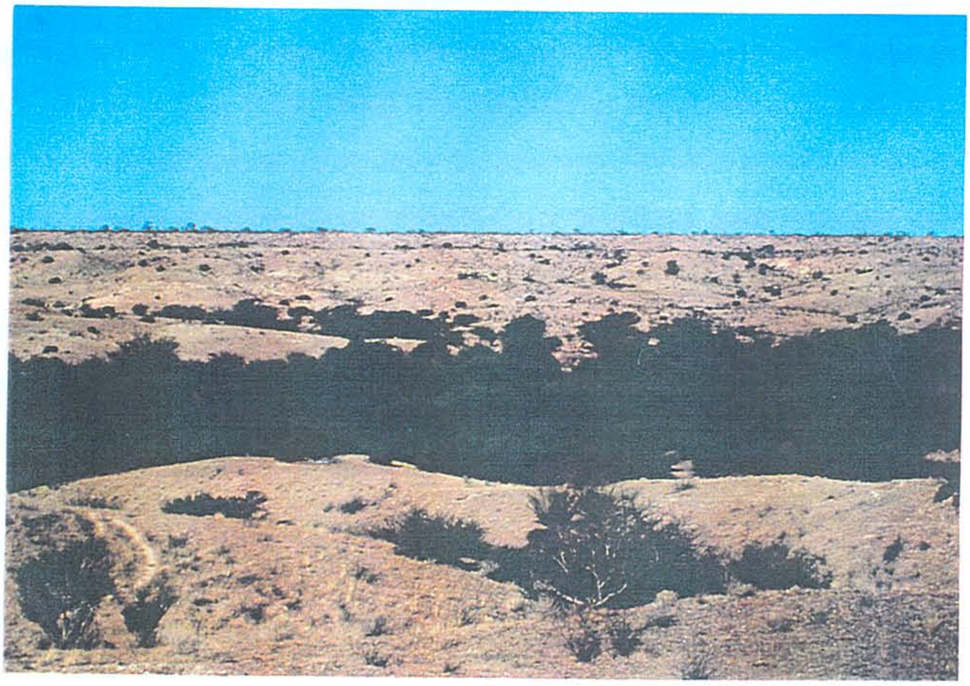

Figure 5.21 Invasion of the upper reaches of the Nossob River in Namibia by *Prosopis* trees.

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.