

PALYNOLOGICAL AND PALAEOBOTANICAL STUDIES IN THE  
SOUTHERN CAPE

BY  
ANTON SCHOLTZ

Thesis presented in partial fulfilment of the requirements for the degree of Master of Arts at the  
University of Stellenbosch



November 1986

## ACKNOWLEDGEMENTS

Some of the work done for this thesis was funded within a CSIR-CSP project, Pleistocene and Holocene climates in the Fynbos Biome (1979-83), granted to H.J. Deacon, Department of Archaeology, University of Stellenbosch.

I should like to thank the following: Hilary Deacon for his interest in developing palaeobotanical research and for allowing me to study the charcoal assemblages from Boomplaas Cave; Fred Kruger for some substantial criticism; Vicki Lautenbach for her support; Gustav Scholtz for his help in programming and running the computer and other devices; Anne Thackeray for checking punctuation and language and general editorial comments; and Madelon Tusenius for her interest and enthusiasm.

## C O N T E N T S

	Page
ACKNOWLEDGEMENTS .....	ii
LIST OF FIGURES .....	vi
LIST OF TABLES .....	xi
I GENERAL INTRODUCTION .....	1
REFERENCES .....	13
II POLLEN ANALYSIS OF THE NORGGA PEAT, GEORGE DISTRICT, SOUTHERN CAPE .....	14
ABSTRACT .....	14
INTRODUCTION .....	16
PREVIOUS RESEARCH ON THE HISTORY OF THE KNYSNA FORESTS .....	20
LOCATION AND DESCRIPTION OF THE SITE .....	21
MATERIALS AND METHODS .....	26
DATING .....	34
FACTOR ANALYSIS .....	35
RESULTS: ZONATION OF THE POLLEN DIAGRAMS AND THEIR INTERPRETATION .....	42
DISCUSSION .....	49
REFERENCES .....	64

III	ANALYSIS OF THE RELATIVE ABUNDANCE OF IDENTIFIED WOOD MORPHOLOGICAL TYPES PRESERVED AS CHARCOAL ASSEMBLAGES FROM BOOMPLAAS CAVE, CANGO VALLEY, SOUTHERN CAPE .....	70
	ABSTRACT .....	70
	INTRODUCTION .....	71
	THE SITE .....	71
	MATERIALS AND METHODS .....	72
	DESCRIPTION OF MORPHOLOGICAL TYPES .....	76
	RESULTS AND INTERPRETATION .....	91
	DISCUSSION .....	98
	REFERENCES .....	104
IV	ECOLOGICALLY DIAGNOSTIC XYLEM ANALYSIS:	
	THEORY AND METHODOLOGY .....	107
	ABSTRACT .....	107
	INTRODUCTION .....	109
	INTEGRATED AND COMPARATIVE PLANT ECOPHYSIOLOGICAL/ANATOMICAL STUDIES .....	110
	BASIC PROBLEMS AND GENERAL CONSIDERATIONS .....	114
	METHODOLOGY .....	118
	THE DIAGNOSTIC VALUE OF VARIABLES .....	133
	EDXA AND TAXONOMIC/ECOLOGICAL WOOD ANATOMY .....	140
	EDXA AND EXPERIMENTAL BOTANY .....	156
	EDXA AND DENDROCLIMATOLOGY: CONTRASTING TWO APPROACHES TO THE DIAGNOSIS OF PAST CLIMATES FROM WOOD ANATOMY .....	160
	REFERENCES .....	165

V	APPLICATION OF THE EDXA-APPROACH IN ANALYSIS OF CHARCOAL ASSEMBLAGES FROM BOOMPLAAS CAVE	178
	ABSTRACT .....	178
	INTRODUCTION .....	179
	MATERIAL AND METHODS .....	180
	RESULTS AND INTERPRETATION .....	191
	CONCLUSIONS .....	216
	REFERENCES .....	223
VII	MINIMUM PIECE DIAMETER ANALYSIS (MPDA) AND THE TAPHONOMY OF CHARCOAL ASSEMBLAGES	225
	ABSTRACT .....	226
	INTRODUCTION .....	227
	THE TAPHONOMY OF CHARCOAL ASSEMBLAGES	231
	METHODS .....	244
	INTERPRETING MPDA DATA .....	248
	PREDICTING MPD DISTRIBUTIONS .....	251
	THE APPLICATION OF MINIMUM PIECE DIAMETER ANALYSIS TO CHARCOAL ASSEMBLAGES FROM BOOMPLAAS CAVE .....	255
	CONCLUSIONS .....	275
	REFERENCES .....	276

## LIST OF FIGURES

## Chapter I

1.1	Location map .....	2
1.2	Summary of climatic change in the southern Cape during the last ca 60 000 years .....	6
1.3	EDXA data for morphological type 11 ( <u>Rhus</u> ) from sites in the southern and northeastern Cape and for the Holocene time period .....	9

## Chapter II

2.1	Location and rainfall map for the George area .....	17
2.2	Map of soil types in the vicinity of the Norga Peat site .....	23
2.3	Perspective on and section through the Norga Peat .....	25
2.4	Pollen diagram for location 1 .....	29
2.5	Pollen diagram for location 2 .....	30
2.6	Graphs of a summary statistic .....	39
2.7	Correlating temperature curves for the late Holocene with the SSF1 curve ...	47

## Chapter III

3.1	Plan and section of Boomplaas Cave ..	73
3.2	Relative abundances of morphological types in the nine assemblages .....	77

3.3	Transverse sections of selected morphological types	
3.3.1	Type 1 <u>Acacia karroo</u> (mature wood) ..	79
3.3.2	Type 1 <u>Acacia karroo</u> (twig-sized branch)	79
3.3.3	Type 2 <u>Nymania capensis</u> .....	79
3.3.4	Type 3 <u>Passerina</u> .....	80
3.3.5	Type 4 <u>Buddleia salviifolia</u> .....	80
3.3.6	Type 5 <u>Protea nitida</u> (mature wood).....	80
3.3.7	Type 5 <u>Protea nitida</u> (twig-sized branch)	82
3.3.8	Type 6 <u>Rhus undulata</u> .....	82
3.3.9	Type 7 <u>Buddleia glomerata</u> .....	82
3.3.10	Type 8 <u>Maytenus/Pterocelastrus</u> .....	83
3.3.11	Type 9 <u>Tarchonanthus/Brachylaena/Chrysanthemoides</u> .....	83
3.3.12	Type 10 <u>Euclea/Diospyros</u> .....	83
3.3.13	Type 11 <u>Rhus</u> spp. ....	85
3.3.14	Type 11 <u>Rhus</u> spp. ....	85
3.3.15	Type 12 <u>Olea/Dodonea</u> .....	85
3.3.16	Type 12 <u>Olea/Dodonea</u> .....	87
3.3.17	Type 13 <u>Protea/Leucadendron</u> .....	87
3.3.18	Type 13 <u>Protea/Leucadendron</u> .....	87
3.3.19	Type 14 <u>Salix mucronata</u> .....	88
3.3.20	Type 14 <u>Salix mucronata</u> .....	88
3.3.21	Type 15 <u>Rhamnus</u> .....	88
3.3.22	Type 16 <u>Elytropanpus/Stoebe</u> .....	90
3.3.23	Type 16 <u>Senecio/Metalasia</u> .....	90
3.3.24	Type 17 <u>Helichrysum</u> .....	90
3.3.25	Type 18 <u>Euryops</u> (subtype 1) .....	92

3.3.26	Type 18 <u>Euryops</u> (subtype 2) .....	92
3.3.27	Type 20 <u>Erica</u> .....	92

## Chapter IV

4.1	EDXA analysis of four areas of xylem tissue .....	123
4.2	Examples of RELV:vess and RELV:relv graphs .....	134
4.3	Schematic illustration of how mean vessel diameter for a florule relates to provenance on an ecoclimatic gradient .....	150

## Chapter V

5.1	MPD (estimated branch minimum diameter) size class distributions for assemblages from Boomplaas Cave ...	182
5.2	EDXA analysis of four areas of xylem tissue .....	185
5.3	Mean values per assemblage for a selected set of EDXA variables .....	188
5.4	The RELV:vess and RELV:relv-type graphs	189
5.5	RELV:vess and RELV:relv distributions for nine assemblages from Boomplaas Cave .....	190
5.6	EDXA analysis. Morphological type 12	196
5.7	EDXA analysis. Morphological type 7	198
5.8	EDXA analysis. Morphological type 20	200
5.9	EDXA analysis. Morphological types 11	



	& 6 .....	206
5.10	EDXA analysis. Morphological types 1 & 10 .....	209
5.11	Summarising the EDXA analysis of assemblages from Boomplaas Cave in terms of the variables RELV and VULM .....	220
5.12	Distribution of values for individual pieces of MT12 ( <u>Olea/Dodonea</u> ) .....	221
Chapter VI		
6.1	Predicted charcoal production for three burning patterns .....	252
6.2	Results of three small fire charcoal production experiments .....	256
6.3	Excavations at Boomplaas Cave; plan and section .....	258
6.4	MPD (estimated branch minimum diameter) size class distributions for assemblages from Boomplaas Cave (by size class) .....	260
6.5	MPD (estimated branch minimum diameter) size class distributions for assemblages from Boomplaas Cave (by assemblage) .....	261
6.6	A. Mean MPD values graphed against kindling:non-kindling ratios .....	264
	B. Kindling:non-kindling ratios .....	
	C. Mean MPD values .....	
6.7	Examples of MPD size class distributions for individual morphological types per assemblage .....	265
6.8	Relative abundances of morphological types in the nine assemblages .....	270

## LIST OF TABLES

## Chapter I

1.1	Summary of charcoal analytical data from sites in the southern and north- eastern Cape .....	8
-----	--	---

## Chapter II

2.1	The ecological significance of the taxa recorded in the Norga pollen diagrams	32
2.2	Scores for factors 1 and 2 of a factor analysis .....	36
2.3	Summary of the evidence for climatic change in the southern Cape .....	55

## Chapter III

3.1	Summary of the archaeological record for Boomplaas Cave .....	93
-----	--	----

## Chapter IV

4.1	Variables produced by program EDXA2 ..	121
4.2	Computer prompts and examples of four sets of inputs .....	122
4.3	Reported correlations between wood anatomical and ecoclimatic variables	135
4.4	Ecoclimatic variables which most powerfully determine plant life forms	144

## Chapter V

5.1	Computer prompts and examples of four sets of inputs .....	184
5.2	List of wood anatomical variables and their suggested ecoclimatic significance	192

5.3	A summary and comparison of the results obtained through EDXA and MTRAA-type analyses .....	194
5.4	Correlations between palaeoclimatic inferences drawn from other lines of evidence .....	217
Chapter VI		
6.1	Chi-square table .....	262
6.2	Summary of the archaeological record for Boomplaas Cave .....	268

## C H A P T E R O N E

### GENERAL INTRODUCTION

This thesis consists of five separate studies (Chapters 2-6), each presented in the form of a self contained research paper. Chapter 2 deals with the analysis of palynomorph (pollen and spore) assemblages, while Chapters 3 to 6 deal with the analysis of charcoal assemblages.

The pollen record preserved in the 3 m deep Norga Peat, located on the coastal platform west of the town of George (Fig.1.1), was analysed using measures of relative abundance of identified pollen types and by measures of pollen concentration. Evidence for three climatic phases in the last 4 000 years was obtained. In the earliest phase 4000 - 2500 B.P. conditions were favourable for the spread of forest, the climate was equable and adequate rain was received in summer. From 2500 - 1800 B.P. the climate was less favourable and west of George, forest vegetation only survived in protected and relatively well watered kloofs and lower mountain slopes. The climate then ameliorated and since 1800 B.P. conditions have been similar to the present. However, the present day climate is not as favourable for forest vegetation as was the climate during the Holocene climatic optimum before 2500 B.P.

The Cango Valley lies 75 km north of the Norga site, inland of the town of Oudtshoorn and below the Swartberg

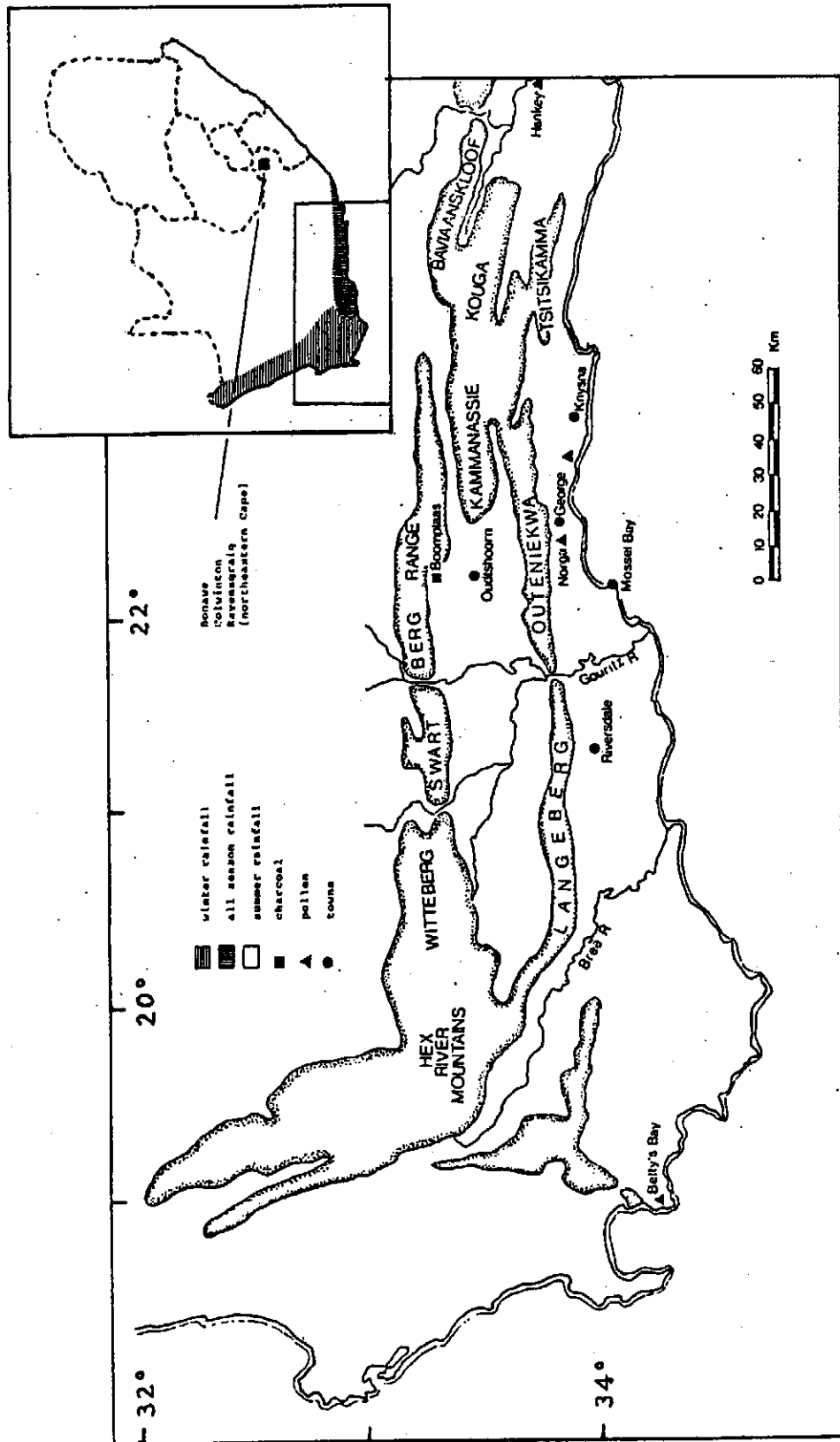


Fig.1.1 Location map for the sites mentioned in the text

Mountains. Boomplaas Cave is located on a low limestone ridge in this valley, about 4 km west of the famous Cango Caves (Fig.1.1). The cave was excavated during the 1970s by the Department of Archaeology, University of Stellenbosch, and contained five metres of deposit. A series of radiocarbon determinations provides reliable dating control over the age of the sediments and the base of the deposit is estimated to date to ca 80 000 B.P. Charcoal was regularly recovered during the excavations and the studies presented in Chapters 3, 5 and 6 are concerned with the analysis of charcoal assemblages from the cave sequence.

Charcoal is amongst the commonest biological remains recovered from archaeological excavations. In the past it has been used mostly as material for radiocarbon dating and, less often, the wood preserved as charcoal has been identified and the history of woody vegetation in an area reconstructed using changes in the relative abundance of identified types of wood as data. The term "charcoal analysis" has usually been used to describe a study of this nature (Deacon et al 1983; Tussenius 1986). As other approaches to studying charcoal assemblages also make use of identifications, this may be regarded as the basic form of charcoal analysis. For various reasons however, the author became convinced that charcoal assemblages potentially contained more information, both concerning past climates and human behaviour, than is

recoverable by this type of analysis. The general aim of the three studies presented in Chapters 4 to 6 was to explore and develop new ways to analyse this category of archaeological material. The exploratory nature of these studies should therefore be appreciated.

The type of study reported in Chapter 3 has been termed Morphological Type Relative Abundance Analysis (MTRA). This is to indicate that the identifications of fossil charcoal referred in the first instance to artificial morphological types, rather than taxa. In this sense the data reported in Chapter 3 are different from those produced in an earlier study of the charcoal assemblages from Boomplaas Cave, briefly reported by Deacon et al (1983). However, the two approaches produce very similar data and the differences between them should not be emphasised.

Chapter 4 describes an approach to the quantitative analysis of wood anatomy which has been termed Ecologically Diagnostic Xylem Analysis (EDXA). The approach is computer based and is designed to measure a wide range of those functionally significant wood anatomical variables which are visible in the transverse section of wood. Apart from describing the procedures for taking measurements and the computer package itself, the topics dealt with in this chapter include: problems concerning the comparability of data, i.e. of method; problems concerning the integral nature of xylem tissue; the functional

significance of wood anatomical variables and indices and the relationship between EDXA and dendroclimatology.

Chapter 5 applies the methods described in the previous chapter to the analysis of charcoal assemblages from Boomplaas Cave, Cango Valley. The results of EDXA analysis of areas of xylem tissue from nine charcoal assemblages are reported. The analysis was done using the units of the total assemblage (florule) and various morphological types (species). The evidence produced by the two forms of analysis was mostly complementary and allowed a relatively confident and detailed account of the climate at nine periods during the last ca 60 000 years. The palaeoclimatic inferences made on the basis of the EDXA data are correlated with the inferences produced by the MTRA-type analysis and from analyses of the macro and microfauna.

Fig.1.2 summarises the evidence produced in Chapters 2, 4 and 5 concerning the history of vegetation and climates in the southern Cape during the last 60 000 years. The most dramatic event recorded by the analyses of charcoal assemblages from Boomplaas Cave is the amelioration of climate which occurred after the Last Glacial Maximum (LGM) between 17 and 14 000 B.P.. In the period preceding 17 000 B.P. woody vegetation in the valley consisted mostly of small composite shrubs and the climate was cold and dry. After 14 000 B.P. the climate was such that a range of trees and large shrubs could



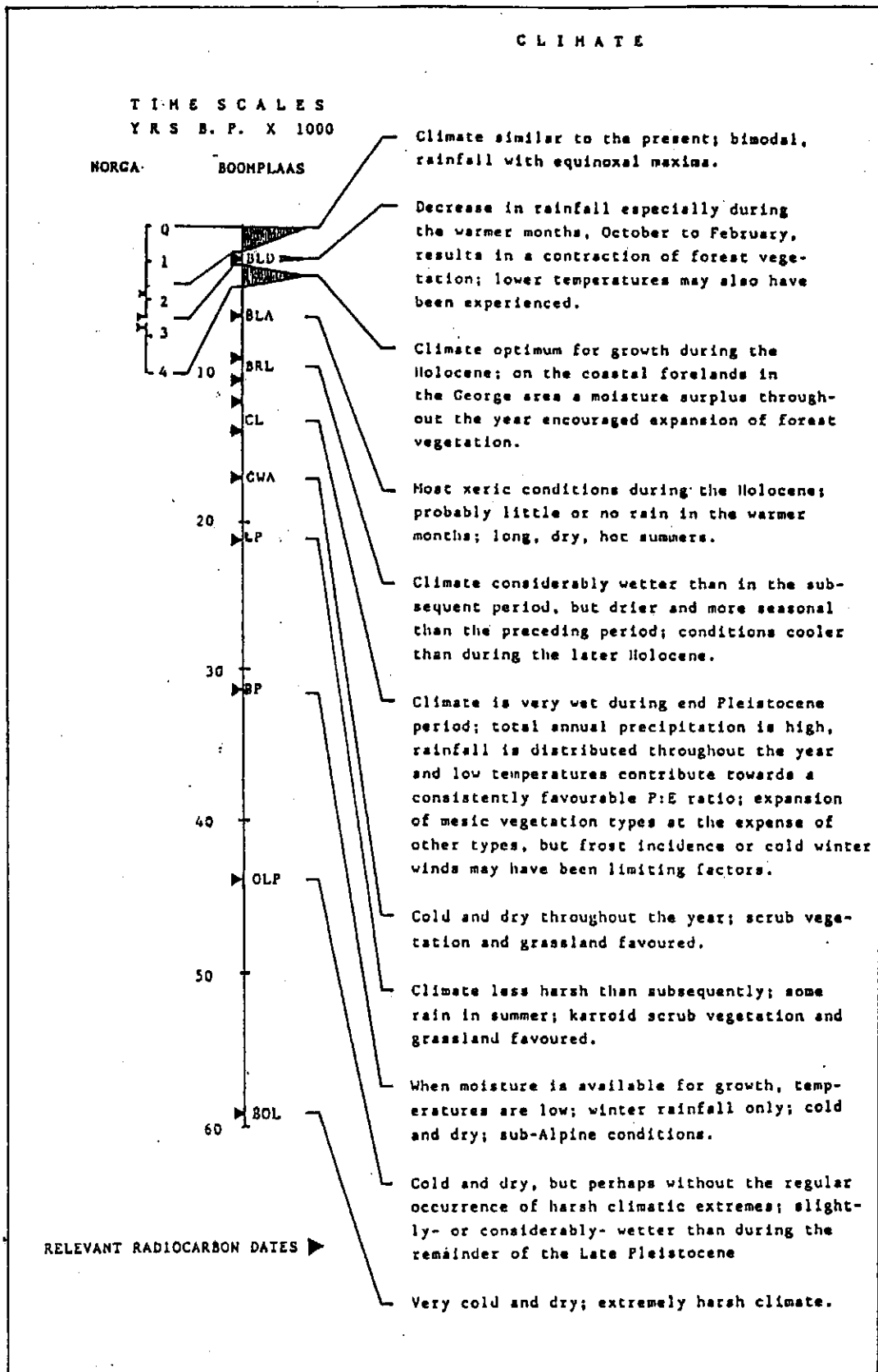


Fig.1.2 Summary of climatic change in the southern Cape during the last ca 60 000 years

grow in the valley. These included species of Olea, Rhus, Euclea and Acacia. Xylem analysis indicates that the period between 14 000 and 12 000 B.P. was in fact the most mesic period experienced after the post LGM amelioration of climates. The most prominent event recorded in the Holocene time period is the recent expansion of Acacia karroo.

No attempt is made in Chapters 3 and 5 to correlate the palaeoclimatic inferences made on the basis of these charcoal studies with the evidence produced by the study of material from other sites in the region. Therefore, at this point in the general introduction some correlations are noted. Table 1.1 summarises and correlates the evidence for palaeoclimates during the Holocene and end Pleistocene time period obtained via charcoal analysis from sites in the northeastern (Tusenius 1986) and southern Cape (this study). The evidence correlates well and, in particular, both studies have produced evidence for a moist late Pleistocene and a dry mid Holocene period.

Fig.1.3 is based on EDXA analysis (Chapter 4) of pieces of wood identified as that of the genus Rhus from charcoal assemblages from the Bonawe Cave site, northeastern Cape (Tusenius 1986) and Boomplaas Cave, southern Cape (Fig.1.1). The figure correlates changes in the variables RELV (relative conductivity) and VULN (vulnerability) with values for the SSF1 index from the Horga study. It is suggested in Chapter 2 that this index measures a xeric/mesic gradient. It is also argued

Table 1.1 Climatic trends recorded by forms of charcoal analysis from sites in the southern and north-eastern Cape (after Tussenius 1986)

Years BP	RAVENS CRAIG	COLWINTON	BONAWE	BOOMPLAAS
1000	Layer 1 *	2 *		* BLD
2000	Layer 2	Probably moister. <u>Cliffortia</u> dominant in the charcoal, very little <u>Euryops</u> .		Dominance of <u>Acacia karroo</u> . EDXA - BLA not as wet as CL, not as dry as BLA.
3000	Layers 3 - 1 Relatively moister. Increases in abundance of <u>Leucosidea</u> , <u>Cliffortia</u> and <u>Passerina</u> .		Layers 3a, 2 ** 1b *	
4000			Layers 3b, 3a, 2, 1b Increase in the diversity of woody taxa.	
5000		Relatively drier. <u>Euryops</u> abundant.	Moister conditions - EDXA.	
6000				* BLD
7000			Low diversity of taxa. Predominantly <u>Olea</u> and <u>Rhus</u> . Relatively drier - EDXA.	* BLA Thicket taxa still predominant. EDXA suggests BLA = driest period of Holocene. Somewhat in conflict with microfauna - driest period at about 9 000 BP.
8000			* Layer 3c	
9000				
10 000	Layer 5 *, Layer 4			* BRL
11 000	Relatively moister. High % of <u>Leucosidea</u> . Relatively drier (possibly warmer). Very high frequencies of <u>Euryops</u> .			Thicket taxa ( <u>Maytenus/Pterocelastrus</u> , <u>Euclea/Diospyros</u> ) become common. Trend to warmer and drier conditions. EDXA - drier than CL, not as dry as BLA.
12 000				
13 000				Appearance of woodland taxa ( <u>Olea</u> , <u>Rhus</u> ) suggests relatively moister conditions. EDXA - wettest conditions of the last 14 000 years.
14 000				* CL

\* = C14 dates

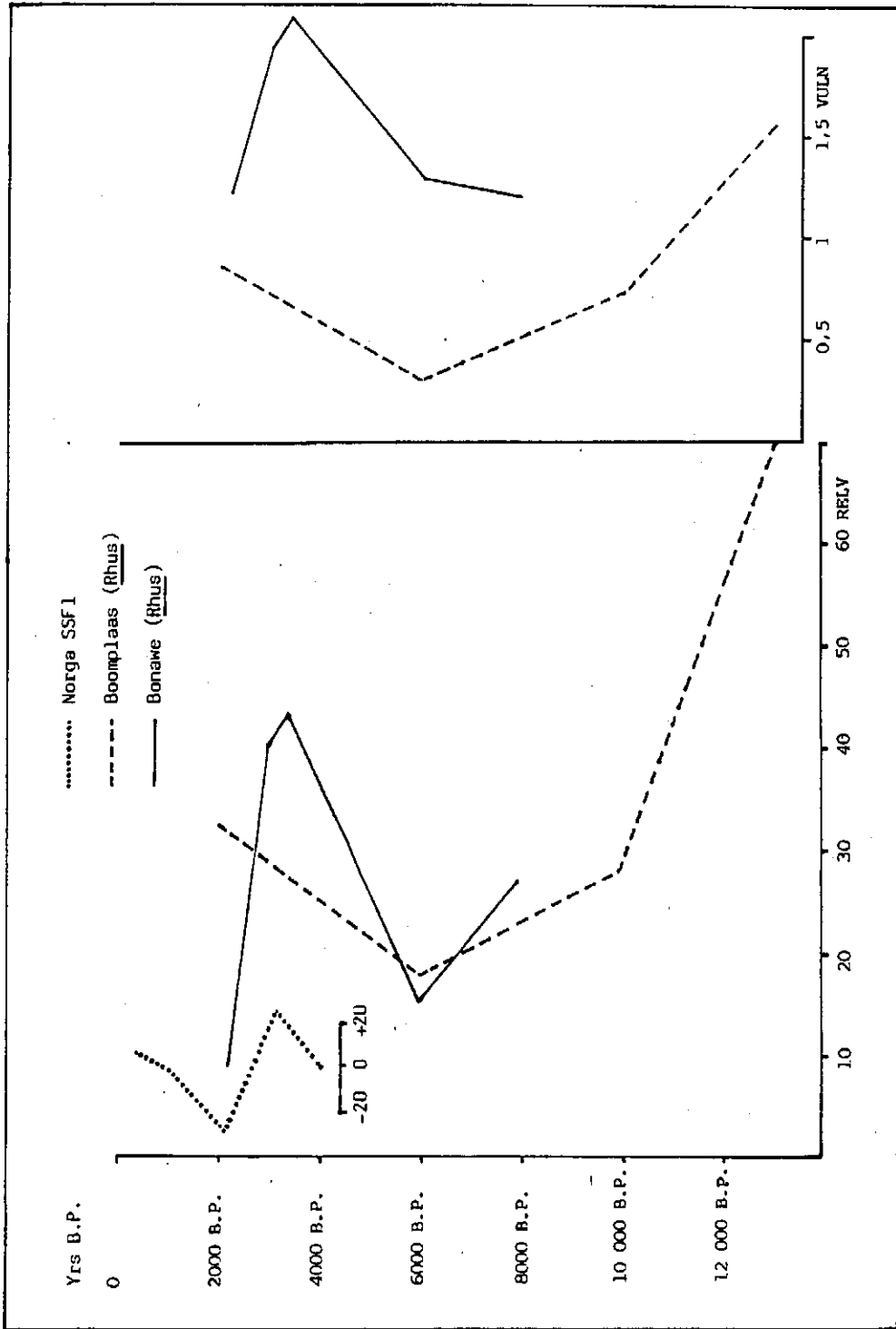


Fig.1.3 EDXA data for morphological type 11(Rhus) for assemblages from Boomplaas Cave (southern Cape) and Bonawe (northeastern Cape)



in Chapter 2 that the decline in forest vegetation recorded between 2500 and 1700 B.P. could be ascribed to a decline in summer rainfall. The steep decline in the values for RELV and VULN recorded at exactly the same time in the northeastern Cape, a summer rainfall area, is strong supporting evidence for this suggestion. The indication that vegetation in the Congo Valley was not as strongly affected may provide an additional measure of the scale of this change, but cannot really be evaluated since evidence for the preceding more mesic period is apparently not preserved in the Boomplaas sequence (Fig.1.3). The possible implications of this observation are discussed below.

Fig.1.3 also shows that, as could be expected, vegetation in the Congo Valley, southern Cape has always been more drought adapted at equivalent times in the Holocene than vegetation in the northeastern Cape (VULN, Fig.1.3). The evidence from both Boomplaas and Bonawe indicates a dry mid-Holocene followed by a moister period. The close correlation of trends through this time period from a set of sites in the summer rainfall area and Boomplaas Cave, situated in the climatically transitional zone of the southern Cape, suggests that the changes registered in the southern Cape during the Holocene may prove to be largely attributable to changes in the summer rainfall regime.

The main conclusions reached by palynological study have already been mentioned. One interesting point

emerges from the correlation of the evidence from the Boomplaas and Norga sites. According to the Norga record, the most adverse conditions experienced in the southern Cape during the last ca 4000 years were experienced during a short 700 year period from 2500-1800 B.P. The 1950 B.P. date from the BLD occupation unit in the Boomplaas sequence falls in this time period. According to the Norga record, other evidence referred to in Chapter 2, and the Bonawe study referred to above (Fig.1.3), the period for 2 to 3000 years prior to 2500 B.P. can be considered the Holocene climatic optimum in the southern Cape, yet within this period it appears that there was little or no occupation of Boomplaas Cave. This evidence is not strong, but any suggestion that climatic factors may determine whether a cave will be occupied or not has such serious implications for the interpretation of all aspects of the archaeological record that it requires consideration.

The preceding three chapters are all concerned with ways in which charcoal can be used to reconstruct a history of vegetation and climate. Chapter 6 focuses on the way in which human behaviour is involved in creating the charcoal assemblages found in archaeological contexts and, conversely, on how to obtain evidence from charcoal assemblages concerning the patterns of human selection and use of firewood involved in their formation. Minimum Piece Diameter Analysis (MPDA) uses estimates of the diameters of branches from which pieces of charcoal were derived as its data and analyses the

distribution pattern of branch diameter sizes in an assemblage. The fossil material to which the analysis was applied was the same set of assemblages from Boomplaas Cave that were studied using MTRA and EDXA-type analyses. Evidence was produced that indicates that firewood procurement was a relatively distinctive and patterned economic activity at only one period in the past 60 000 years, between 14 and 12 000 B.P.. During this time people chose to use long burning fires and to select and transport specific types of firewood to the cave. As already mentioned, this period is also distinguished by a cool and wet, mesic climate.

The results achieved by this thesis can be summarised as follows. The palynological study has produced a vegetation and climatic history for the late Holocene time period for the area of the southern Cape coastal plain which includes the area occupied by Knysna forest (afromontane) vegetation. Two new forms of charcoal analysis, one entirely computer based, have been developed. The set of applied charcoal analyses have provided a relatively reliable and detailed climatic history for the interior of the southern Cape for the last ca 60 000 years. The fact that the evidence for palaeoclimates of the last 12 000 years derived from analysis of charcoal assemblages from the Boomplaas sequence correlates so well with similar evidence from the northeastern Cape both instils confidence in the

methods employed and suggests that the climatic history recorded in the southern Cape may be extrapolable to other areas of southern Africa. However, until climatologists can provide models which suggest how inferences based on biological evidence concerning aspects of climate in region A can predict aspects of climate in regions B, C, and D, there will be little reliable base on which to correlate observations made in different climatic regions.

#### REFERENCES

- DEACON, H.J., A. SCHOLTZ & D.L. DAITZ 1983. Fossil charcoals as a source of palaeoecological information in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis:174-182. SANSPR 75, Pretoria.
- TUSENIUS, M. 1986. Charcoal analytical studies in the north-eastern Cape. Unpublished M.A. thesis, Department of Archaeology, University of Stellenbosch.



C H A P T E R   T W O

PALYNOLOGICAL ANALYSIS OF THE NORGA PEAT, GEORGE  
DISTRICT, SOUTHERN CAPE

I N D E X

ABSTRACT

INTRODUCTION

PREVIOUS RESEARCH BEARING ON THE HISTORY OF THE KNYSNA  
FORESTS

LOCATION AND DESCRIPTION OF THE SITE

DATING

THE POLLEN DIAGRAMS

RESULTS

FACTOR ANALYSIS

DISCUSSION

Estimating the scale of vegetation and  
climatic change

The "pristine" (pre-agricultural) vegetation  
of the coastal forelands

Correlations with other evidence

REFERENCES

ABSTRACT

The Knysna forests grow on a short and narrow strip  
of coastal forelands in the southern Cape, a region which  
receives rain throughout the year, but with equinoxial

precipitation maxima. At present the climate and vegetation types in this region appear to be particularly delicately balanced. Afromontane forest is the most mesic vegetation type present in the region and is palynologically highly visible. Documentation of changes in its distribution in the past is therefore possible and would provide a record of climatic change.

Two pollen profiles from a peat deposit in the George area, southern Cape have been analysed. Three radiocarbon determinations provide dating control and the base of the sequence is estimated to be about 4000 years old. Problems of gauging the scale of vegetation and climatic changes reflected in the pollen diagrams were encountered, but the following conclusions were reached. From 4000 to 2600 B.P. conditions were generally 'optimal' within the time range concerned and conducive to the spread of forest vegetation. Drier and perhaps colder conditions were experienced between 2600 and ca. 1400 B.P. and a marked contraction in the distribution of forest occurred. Conditions then became more mesic and perhaps warmer and the present climatic norm was established. The correlations between the changes in climate inferred from this study and evidence relating to palaeoclimates of the late Holocene from other studies in the region and further afield are discussed.

## INTRODUCTION

The afro-montane forests (White 1978) of the Knysna region of southern Africa grow on a coastal plain, which varies between 8 and 48 km in width, and on the seaward slopes of the Outeniqua and Langkloof mountains (Fig.2.1). The distribution of forests to the east and west of their core area in the George and Knysna divisions, and towards the interior, is limited by sharp climatic gradients towards karroid aridity (Fig.2.1).

The Knysna forests require a comparatively uniformly distributed annual rainfall regime with a minimum of at least 45-50 mm of rain in any month and an annual figure in excess of 800 mm (Martin 1968). The region experiences an all season to bimodal rainfall regime, a high incidence of cloud, frequent light rain and changeable weather (Tyson 1971). The dominant climatic control is the passage of cold fronts which sweep the southern coast of the subcontinent. Rainfall occurs in association with these frontal weather disturbances. However, due to the nature of the topography, the distribution of rainfall over even short distances can be quite erratic. The mountains close to the coast prevent the inland penetration of shallower weather systems and frequently produce highly localised orographic mist and rain (Tyson 1971).

Because of these fluctuations in the orographic

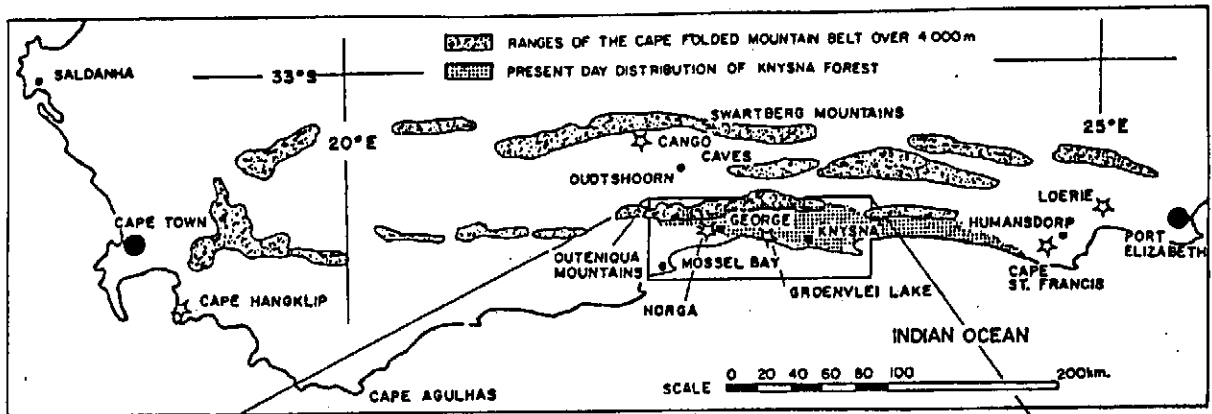


Fig.2.1a Location map for sites in the southern and southwestern Cape

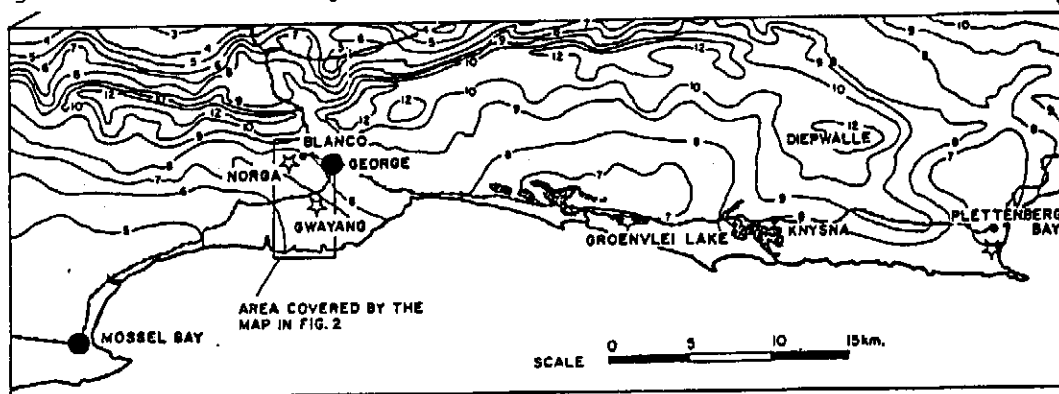


Fig.2.1b Isohyets of mean annual precipitation (mm X 100) for the Mossel Bay-Kynsna region (after Van Daalen 1980)

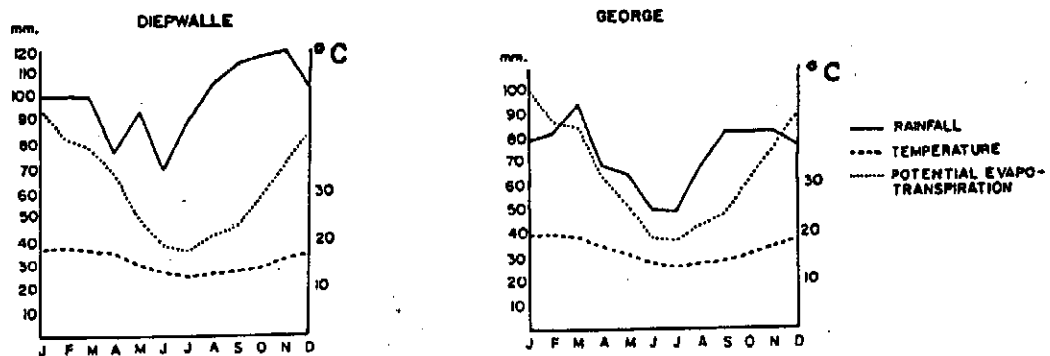


Fig.2.1c Climate diagrams with Thornthwaite's potential evapotranspiration index superimposed onto them (after Van Daalen 1980)

component of precipitation, the variable width and elevation of the coastal plain and the variety of substrates present in the region, a mosaic of vegetation types occurs (Von Breitenbach 1974).

The Knysna Forests are the southern African remnants of the ancient coniferous forests of Gondwanaland (Levyns 1964). Their history, both of the distant and more recent past, has always been a topic of interest to botanists. The aim of this study was to document the recent history of this vegetation and of climate in the region. To this end, the palynological analysis of a peat deposit in the upper Norga River valley was undertaken and has produced a ca 4000 year record.

#### PREVIOUS RESEARCH ON THE HISTORY OF THE FORESTS

Phillips (1931) described the distribution of occurrences of charcoal horizons in the uppermost layers of soil beneath both stands of forest and fynbos vegetation. On the basis of the presence or absence of fossil charcoal of forest species he concluded that the forests had been more widespread in the past and had covered some of the area which was later occupied by fynbos vegetation. In other areas, notably the upper mountain slopes and summits, part of the foothills and lateritic portions of the coastal plain, fynbos appeared to be the climax vegetation. Phillips (1931) stated a belief that in the not so distant past the long stretch of coastal plain between

the present Knysna forest area and the southwestern Cape was covered, with but minor interruptions, by a belt of forest. This idea was popularised in Acocks's (1953) *Veld Types of South Africa*. In this publication Acocks produced a map of what he thought the distribution of vegetation types would have been ca 1400 A.D., and indicated a continuous belt of forest and scrub forest blanketing the coastal plain between Knysna and Cape Town. This reconstruction was based partly on his own observations of the disjunct distribution of relict patches of vegetation, but his interpretations rested on the assumption that these distributions were all the result of recent human disturbance of the environment.

It was also Phillips's belief (Phillips 1931:234) that the forests and scrub forests were well adapted to the present climatic regime and would, if protected from exploitation, recolonise much of the coastal plains of the southern and southwestern Cape now occupied by fynbos and renosterveld vegetation. This view is contradicted by Van Daalen (1980), who concludes his study of the ecological relationships of forest and fynbos vegetation with the following remark: "These forests must be considered a relict of a much wetter climatic period. They managed to survive on the protected southern side of the Outeniqua Mountains where the evenly spread orographic mist and rain is higher than in the surrounding country. On the whole the present climate seems to be in favour of fynbos."

The most important reason cited by Van Daalen (1980) to explain why forest cannot at present colonise areas of fynbos vegetation adjacent to it, is that, "...the macroclimate is too dry for forests especially in that water deficiencies occur during the summer months" (Fig.2.1). He suggests that "A rainfall pattern peaking in summer might be more advantageous than the evenly spread one of the southern Cape, where much of the effect of the summer rainfall is eliminated by relatively high temperatures."

Van Daalen notes that the minimum annual rainfall figures for other forested areas of the southern hemisphere are comparable to the maximum annual figure of 1200 mm for the Knysna forest area recorded at Diepwalle forest station. The point is illustrated in Fig.2.1b. The steep moisture gradients which occur over the southern Cape coastal forelands suggests the tenuous nature of the occupation of portions of the area by mesic vegetation. The isohyets of annual precipitation are particularly close west and north of the town of George. The 800 mm isohyet, often quoted as the minimum required by the Knysna forests, lies close to the location of the peat analysed in this study. The two climate diagrams using Thornthwaite's potential evapotranspiration index (Fig.2.1c) indicate that while at present the George area experiences a moisture deficit during summer, a moisture surplus is always available at Diepwalle, in the heart of

the forests. These climatic data tend to support Van Daalen's estimation of the relictual status of the forests rather than Phillips's more optimistic view.

The work of Phillips and Van Daalen was based on the analysis of the present day distribution of vegetation types. The first work dealing with fossil evidence for the recent history of the forests was that of Martin (1959, 1960, 1968). He studied the ecology, geomorphology and diatom and pollen stratigraphy of Groenvlei Lake, one of a series of interdune lakes in the Wilderness embayment 20 km east of the Norga Peat (Fig.2.1). The palynological analysis of a 6,5 m core from the fen on the eastern margins of the lake revealed four vegetation/climatic phases during the last ca 8000 yrs. (Martin 1968). At some time before 7000 B.P. the distribution of forest was much restricted and a dry steppe-like heath was present in the area. An amelioration of climate occurred ca 7000 B.P. After this event the record is ambiguous and there is evidence for a marine transgression and mobilisation of coastal dunes. At about 2000 B.P. a marked increase in the representation of forest taxa occurred, indicating a shift towards more mesic climates. A period of deterioration of climate and/or the effects of European forest clearance were detected near the top of the sequence. One reason for locating the present study in the Wilderness/George area was so that it could serve as a test of the evidence

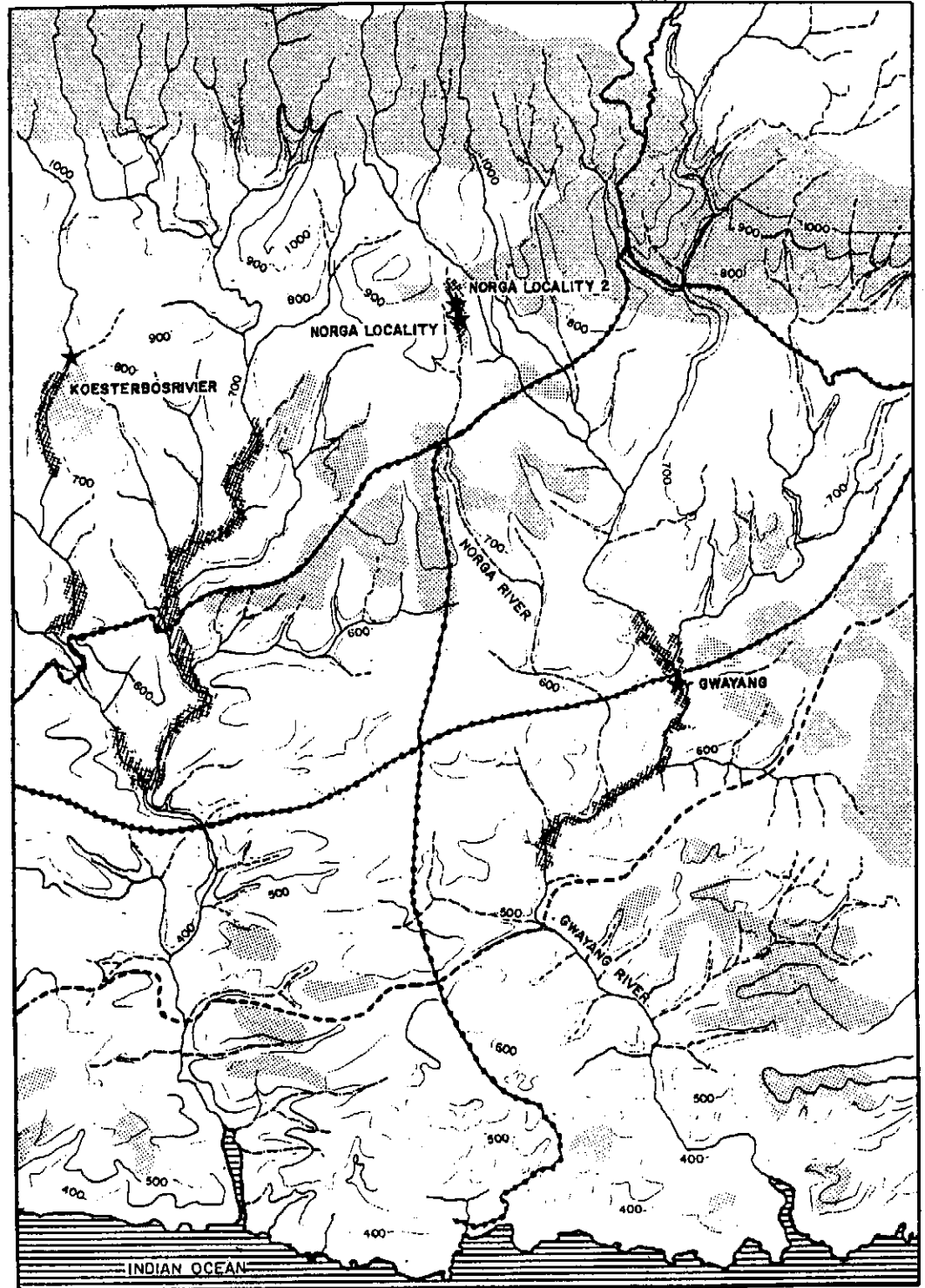



from Groenvlei. The correlations between the evidence from Martin's work and that produced in this study are discussed in the final section of this chapter.

#### LOCATION AND DESCRIPTION OF THE SITES

The town of George is situated on the southern Cape coastal platform, a marine planed surface, probably of early Tertiary age. This surface lies at an altitude 180-240 m above sea level (Tyson 1971). Close to the coast in the George area major streams have been incised into this platform and a deeply dissected landscape results. The headward incision of the larger streams terminate rapidly in nickpoints, upstream of which shallow incision and a gentle undulating landscape predominate. In this latter landscape peat deposits are found in several of the shallow valleys (Fig.2.2).

The Norga Peat (33.57 S; 22.23 E) is found about 2 km west of the hamlet of Blanco in the George area (Fig.2.1). It has been formed by a build up in organic matter in the bed of the shallow valley associated with the Norga River, a tributary of the Gwayang. The Norga does not rise in the mountains and the peat deposit occurs only about 600 m from the head of the stream which is on a low ridge to the north (Fig.2.2). At present, ploughed lands and pastures surround the peat on all sides and it is covered by infestations of black wattle (Acacia mearnsii) and bracken (Pteridium). It has also



Scale  4 km





-  Marshland
-  Soils able to support forest vegetation (after Engelbrecht 1969)
-  Main roads
-  Railway line

Fig.2.2 Topography and soil types in the vicinity of the Norga Peat sites

recently been commercially exploited as a high quality potting peat.

Fig.2.2 indicates the extent of peat deposits in the area and, more important for the interpretation of the palynological evidence, the distribution of soils which are unlikely to have supported forest in the recent past. These are shallow duplex soils with a clay horizon close to the surface (J.N.N. Lambrechts pers. comm.).

The stratigraphy of the two columns analysed and a section and schematic perspective on the Norga peat is provided in Fig.2.3. The Norga locality 2 site is situated 177 m upstream from locality 1 in the same body of peat and is 2.5 m higher than the latter site. It is also closer to the top end as well as to the margins of the peat. The layer of alluvial sediments and loam shown underlying the main peat accumulation in Fig.2.3 is composed of loam on the flanks and alluvial sediments, silts, fine sands and clays towards the centre of the valley. The yellow clay at the base of the recorded sequence is considered to be residual, weathered granite bedrock.

The commercial exploitation of the peat has resulted in large scale surficial excavation of the main peat layer above 1,2 to 1,5 m below surface between localities 1 and 2 and this has obviously disturbed the natural stream regime. When stream flow is present, water emerges at the upper end of the excavated area close to

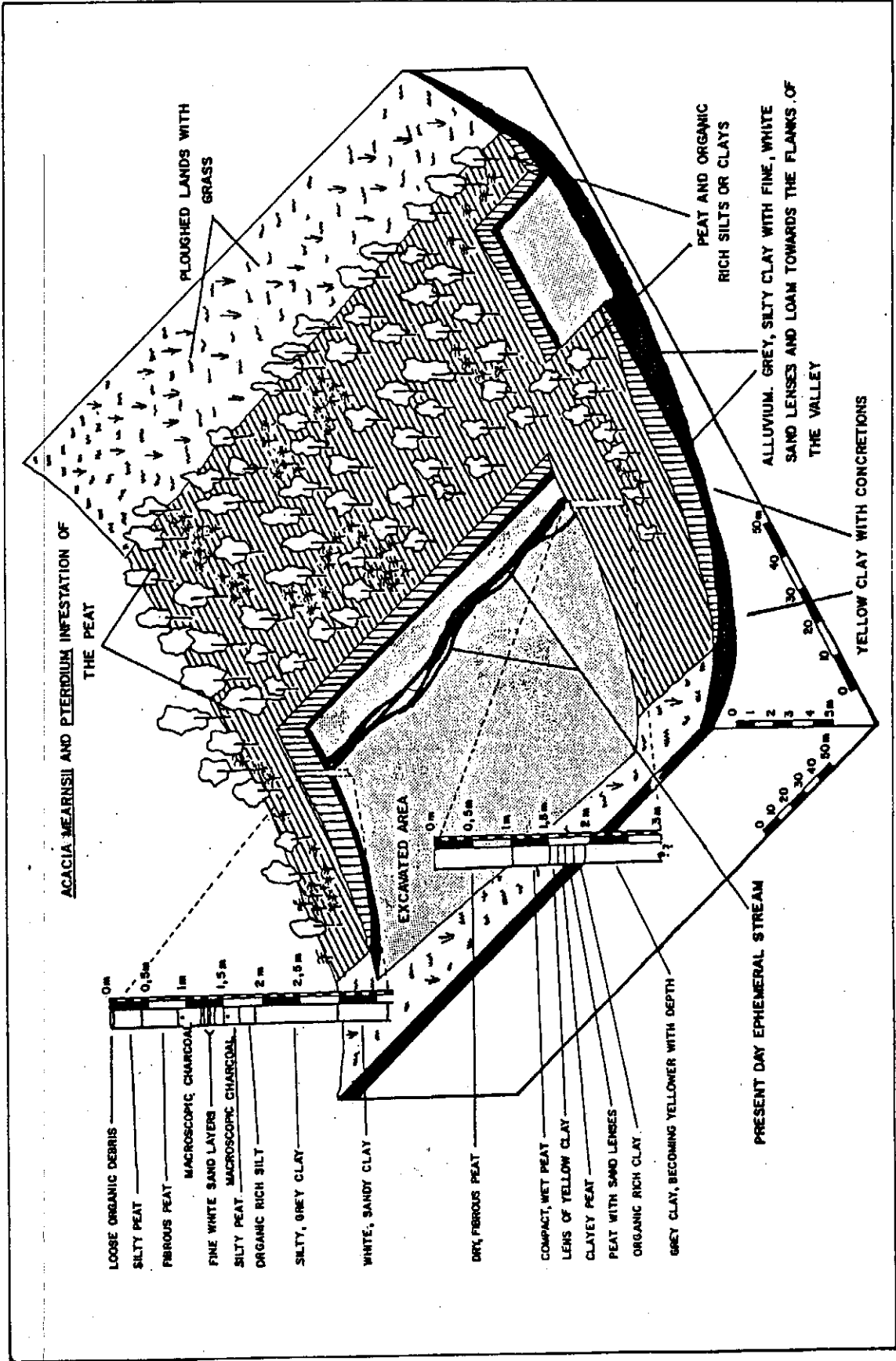


Fig.2.3 Perspective and section of the Norga Peat

locality 2, flows over the exposed surface and re-enters the unexcavated peat close to locality 1 (Fig.2.3). During coring near this locality it was observed that large cracks and cavities exist within the peat body. This has probably been caused by the drying out of the peat, but it is also possible that the more channeled flow itself has been responsible for internal excavation of the peat. Some disturbance or truncation of the record at locality 1 is therefore possible.

A marked change in sedimentology occurs in the Norga locality 1 sequence between 0,9 and 1,1 m (Fig.2.4D). Above this level less than 20% by weight inorganic material is present. Lower down the deposit consists of silts, fine sands and clays.

#### MATERIALS AND METHODS

Samples for palynological analysis were taken in the field either directly from a cleaned face (locality 1; upper section at locality 2) or from a Hiller augur (below 2 m at locality 2). The samples were dried and cleaned in the laboratory.

The following method was used to obtain the measures of pollen concentration (Colinvaux 1978) for the locality 1 sequence. Accurately weighed (dry weight) 5 g samples were submitted to a carefully controlled, standardised pollen concentration and recovery process, which included sieving, KOH, acetolysis, HF and heavy liquid flotation processes. Inorganic material recovered after sieving

and the heavy mineral separation process was washed, dried and weighed. The weight of this fraction/5 g is expressed in section D of Fig.2.4 as the "inorganic: organic" ratio. (Note that no measurement was obtained for the clay fraction eliminated in washing and in the HF acid process and the ratio is therefore to some degree inaccurate, the weight of the inorganic fraction being lower than it should be. With higher clay contents this inaccuracy would become more significant.)

After the acetolysis process the pollen preparation was suspended in a 1:1 glycerol and deionised water solution to make up 5 ml. This suspension was thoroughly agitated and 0.01 ml aliquots were then withdrawn using an automatic microlitre pipette. The total pollen content of the aliquot, or several aliquots, was then counted and, because of the quantitative control through all the stages of processing, the results could be expressed in terms of the occurrence of pollen per gram of sediment. The size of the counts ranged from 467 to more than 2000.

In the case of the locality 2 sequence, the aim of the procedure was to achieve statistically reliable measures of relative abundance and the full procedure described above (used to obtain measures of pollen concentration) was not used. Samples were submitted to standard palynological processing for recent peat deposits, the preparations were suspended in a glycerol and water solution and a minimum of 500 grains were counted for each sample.

Two types of basic data are therefore available. Firstly, the palynological record at each locality is portrayed in terms of changes in the relative abundance of 23 selected taxa (Figs 2.4A,B,C and 2.5). A simple form of diagram has been used to portray change in the local wet site environment and change in the non-local or regional environment. The first sections of Figs 2.4 and 2.5 record the relative abundance per sampled horizon of pollen of taxa which are judged to have occurred in the local environment, while the second sections record the relative abundance of the remaining taxa. These latter are referred to as the regional taxa. The usefulness of this division is that it enables different pollen sums to be used in the calculation of the percentage values in each section. Change in the regional environment can thus be portrayed on a smaller scale and without being swamped by the effects of changes in representation of pollen of taxa growing in the local environment. The 95% confidence intervals were calculated according to the formula devised by Mosimann (1965).

Secondly, the sequence at locality 1 (Fig.2.4E, F & G) was also analysed in terms of pollen counts per gram of sediment, a measure of pollen concentration (Colinvaux 1978). The manner of portrayal of these measures in Fig.2.4 requires explanation. The hatched areas of Fig.2.4, sections E, F and G, represent the counts/g sediment adjusted by a factor calculated per sampled horizon to account for the much higher inorganic:organic

A. The percentage total local component ( *Cyperaceae*, *Myriophyllum/Lauremburgia*, *Cliffortia*, *Pteridophyta* ) of the pollen sum and the 95% confidence intervals

B. The percentage individual local components of the pollen sum and the 95% confidence intervals

C. The percentage of individual regional components of, the pollen sum - the total local component and the 95% confidence intervals

D. The inorganic versus organic fraction of sediment per gram ( dry weight )

E, F and G. Individual components per gram of sediment. In E, F and G the hatched section of the diagrams represents the observed values adjusted by a factor to account for fluctuations in the organic:inorganic ratio between levels ( See text for fuller explanation )

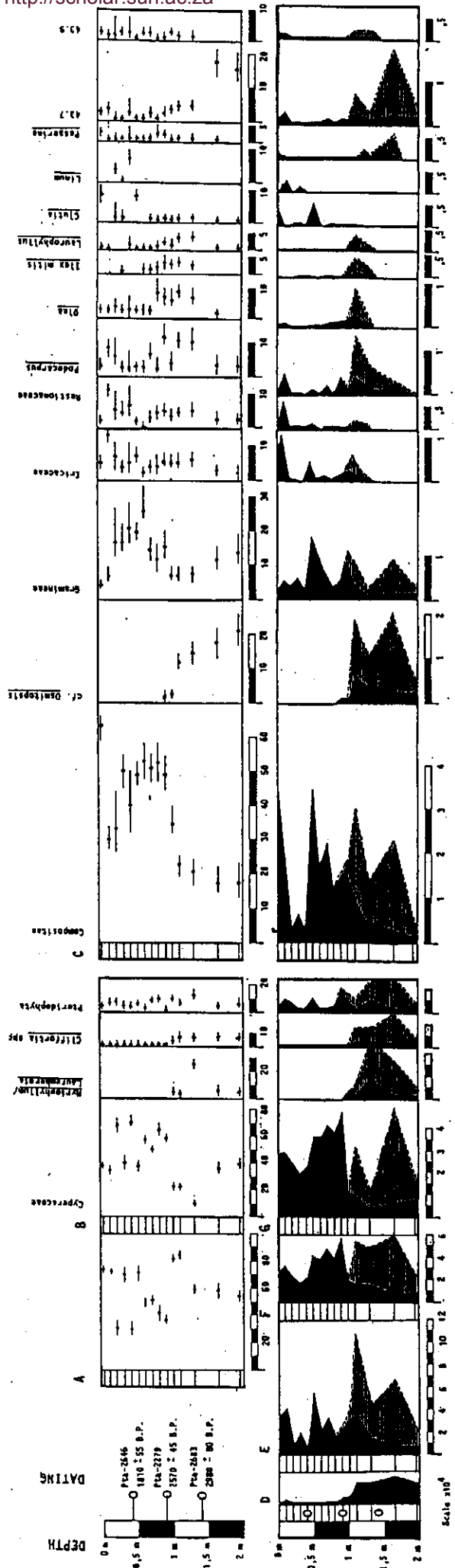


Fig.2.4 Pollen diagram. Norga Peat, locality 1



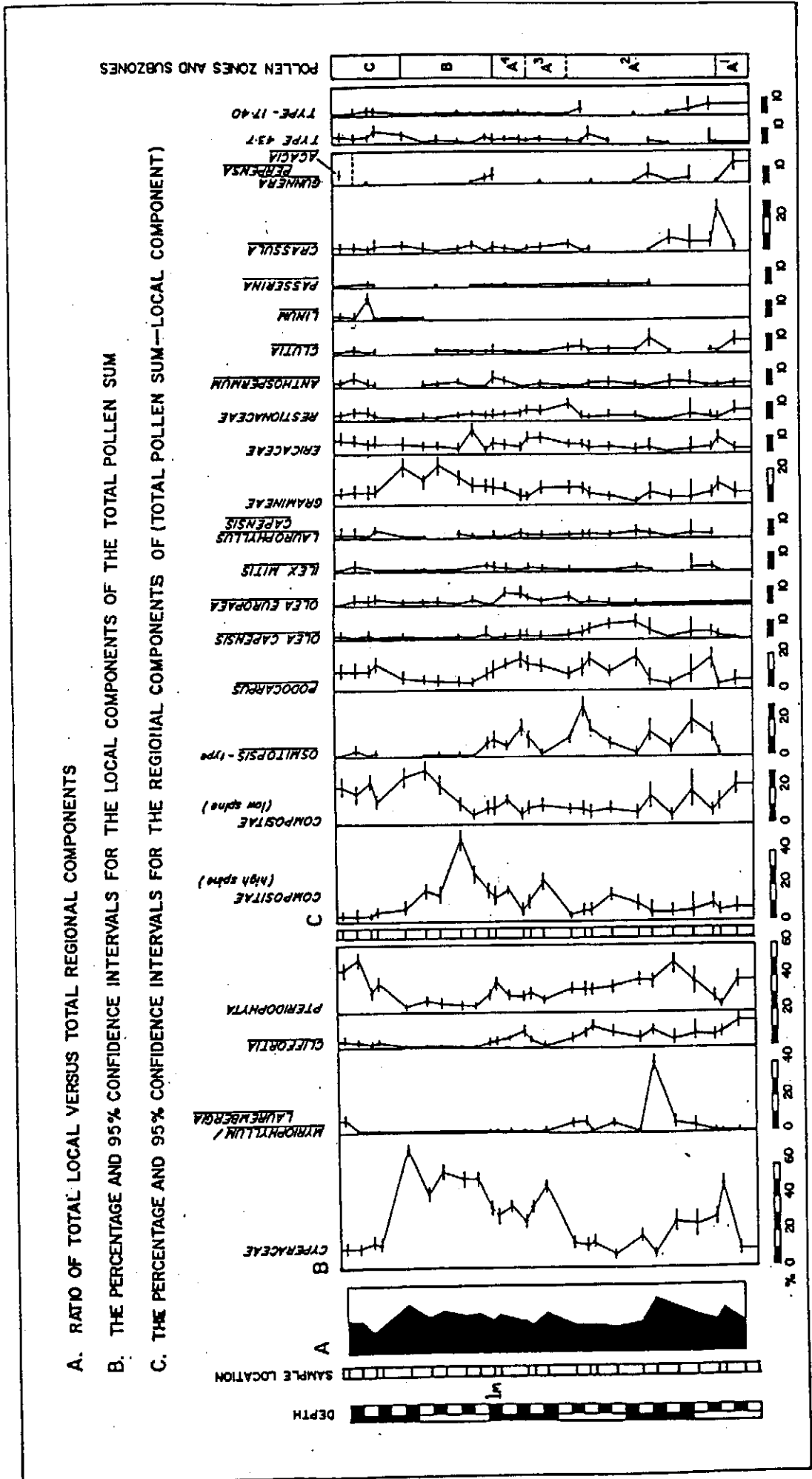


Fig.2.5 Pollen diagram. Norga Peat, locality 2

ratio (Fig.2.4D) encountered at 0,9 m and below relative to the values above 0,9 m. The factor was calculated by dividing the weight of the inorganic fraction (Y) measured at each level below 0,8 m, by the average weight of the inorganic fraction encountered above 0,8 m (X), i.e. the adjusted values = counts/g sediment multiplied by Y/X. This procedure results in the sequence of counts/g sediment graphed by the hatching in Fig.2.4E, F and G being effectively related to a roughly constant weight of organic material, i.e. counts/g organic material. In contrast, the non-hatched areas portray counts/g sediment. Given the large changes in sedimentation rates experienced in this environment, it is suggested that the former measure (counts/g organic material) may be more useful than the latter (counts/g sediment).

The ecological significance of the taxa represented in the pollen diagram are recorded in Table 2.1. As is usual in this type of palynology, it was possible to identify some forms only to family or genus level. Uncertainty exists about the identification of four taxa which show strong patterning in the diagrams and in this respect the following points should be noted.

The pollen of the closely related genera Myriophyllum and Laurembergia (Haloragidaceae) are not easily distinguishable, but their habitat requirements differ widely. Myriophyllum is a rooted, partly submerged aquatic requiring perennial, relatively still

Table 2.1 The ecological significance of taxa recorded in the Norga pollen diagrams

Pollen taxa of the Norga and Gwyang pollen diagrams and their ecological significance. (information obtained from Muir 1929, Phillips 1931, Martin and Noel 1960, Martin 1968, von Breitenbach 1974, Boucher 1978, Scott 1978)		
Diagrammed taxa	Content	Ecological significance
Cyperaceae	Many genera	Especially important in marshy places forming swards, predominant in the later stages of evolution of the hydrosere, most important locally produced element.
<u>Myriophyllum</u>	<u>M. spicatum</u>	Submerged aquatic.
<u>Laurembergia</u>	<u>L. repens</u>	Stream banks and marshy areas.
<u>Cliffortia</u>	Many species	Small to medium shrubs, dry and wet heath forest margins and glades especially common on stream banks and in wet heath.
Pteridophyta		Found in various environments. Common on wet sites, in marshes and on forest margins. Common in post devastation weed flora.
Compositae	Many genera	As a whole more common in dry heath and subkarroid heath margins.
<u>Osmitopsis</u> -type	<u>Osmitopsis</u> (+other genera?)	Common on 'seepage' peats together with <u>Erica</u> spp.
Gramineae	Many genera	Ubiquitous.
Ericaceae (tetrads)	<u>Erica</u> spp.	Numerous spp. abundant in heath and often in wet places.
<u>Podocarpus</u>	<u>P. latifolius</u> , <u>P. falcatus</u>	Major dry and wet forest trees, also in scrub along stream-banks.
<u>Olea capensis</u>	<u>Olea capensis</u>	Major forest species.
<u>Olea europaea</u>	<u>Olea europaea</u>	Small tree or shrub. Mainly in dry scrub.
<u>Ilex mitis</u>	<u>Ilex mitis</u>	Medium to large tree, moist forest and stream banks.
<u>Laurophyllus</u>	<u>Laurophyllus capensis</u>	Shrub or shrubby tree. Frequent in wet scrub and on the margins of wet mountain scrub forest and on flat waterlogged areas.
<u>Clusia</u>	<u>Clusia</u> spp.	Shrubs and small trees present in a variety of habitats. Common on forest margins, growing in the shade together with bracken ( <u>Pteridium aquilinum</u> ). Also in post devastation weed flora.
<u>Linum</u>	<u>Linum</u> spp.	
<u>Passerina</u>	<u>Passerina</u> spp.	Dry ericoid heath, fringes of scrub and forest margins.
<u>Crassula</u>	cf. <u>C. inanis</u> , <u>C. natans</u> and others	Aquatics and in wet places. Other species in the genus are found in wide range of habitats.
<u>Gunnera</u>	<u>G. perpensa</u>	Streams and marshy places.
<u>Anthospermum</u>	<u>Anthospermum</u> spp.	Small shrubs, common in heath.
<u>Pinus</u>	<u>Pinus</u> spp.	
<u>Acacia</u>	<u>Acacia mearnsii</u>	
<u>Eucalyptus</u>	<u>Eucalyptus</u> sp.	

water, while Laurembergia is found on the banks of streams and in marshy areas.

The Compositae (Asteraceae) are a large and ecologically diverse group and its members produce a number of distinctive pollen types. Most of the palynomorphs referred to this group were of a similar, high-spined morphology. Only odd specimens of other types such as Artemisia, Tarhonanthus, Lactuca or Elytropappus/Stoebe, to which more precise ecological significance could be attached, were encountered. However, the pollen of Osmitopsis, a genus of the Compositae whose members are usually associated with wetlands, is distinctive and was counted separately. Changes in the relative abundance of this type contribute a significant pattern to the pollen diagrams.

The sudden prominence of the Crassula-type towards the bottom of the Norga 1 and 2 sequences made a definition of its ecological significance important. Crassula (Crassulaceae) is a very large genus and its species are difficult to distinguish on pollen morphological grounds. Although the genus is mainly represented in relatively arid vegetation, species are found in a wide range of habitats. A thorough palynological survey of the genus was not attempted, but in terms of the species occurring at present in the region, the pollen of C. inanis and C. natans, both aquatics or semi-aquatics common in the Knysna region, are indistinguishable from the forms observed in this study.

In the pollen diagram from the Norga locality 1 site the Olea type potentially contains pollen of the species O. capensis macrocarpa, O. capensis capensis and O. europaea subsp. africana (Oleaceae). O. capensis and O. europaea have, however, different ecological significance. Although problematic, in the analysis of the Norga locality 2 sequence a distinction was made between the two Olea species on the basis of the greater size of the lumina and muri of the reticulum in Olea europaea subsp. africana (Fig.2.5).

#### DATING

Three radiocarbon dates for the Norga locality 1 sequence were obtained by Dr J C Vogel, Natural Isotopes Division, CSIR, Pretoria. These were:

1810 + 55 B.P. (Pta-2146) for a sample at 0,45 m below surface;

2570 + 45 B.P. (Pa-2279) at 0,9 m;

and 2980 + 80 B.P. (Pta-2683) at 1,4 m

Assuming constant rates of accumulation between dated horizons, it appears that sedimentation rates have decreased through time: the top 0,45 m of deposit has accumulated at 24,9 mm/yr; from 0,45 m to 0,9 m at 57,8 mm/yr and from 0,9 m to 1,4 m at 128,2 mm/yr. Applying the last figure to the 1,6 m depth of sediments below 1,4 m at locality 2 suggests that the base of this deposit might be about 4000 yrs. old.

## FACTOR AND SUMMARY STATISTIC ANALYSIS

A factor analysis was performed on the single data set composed of the relative abundances for the 23 most common taxa recorded in the sequences from both the localities. Due to the possible influence of disturbances relating to recent agricultural practices, the samples from the upper 0,4 m of both sequences were excluded from this analysis. In a three factor solution, the principal component factor 1 (F1) accounted for 52,9% of variance and F2 for 27,1%. Table 2.2 lists the factor scores for each taxon on these two factors.

"Factor analysis aims to explain observed relations among numerous variables in terms of simpler relations" (Cattell 1965). In the case of the relative abundance data produced in this study, where variability is determined by multiple factors, factor analysis may help to distinguish underlying forcing factors. In more or less direct ways, these are likely to be climatic factors. An examination of the factor loadings for the taxa on a certain factor may indicate whether a climatic variable is being registered by that factor and suggest its identity.

Podocarpus, a clear indicator of forest (Table 2.1), has a high positive score on F1 (Table 2.2). The undifferentiated Olea taxon may be taken by association to represent Olea capensis, another prominent forest species. Cliffortia has a high positive score on this factor and, as noted by Martin (1968:128), there is a correlation of Cliffortia with forest. Species of

Table 2.2 Scores for factors 1 and 2 of a factor analysis (data from localities 1 and 2)

Factor scores for individual taxa on factors 1 and 2 of a 3 factor solution. The scores are arranged from high to low on each factor

	Factor 1		Factor 2				
.77086	<u>Podocarpus</u>	.26292	<u>Clusia</u>	.55203	Ole	.13346	Cyp
.76490	<u>Cliffortia</u>	.22841	<u>Gunnera</u>	.51532	Pas	.11814	Lin
.74850	<u>Laurophyllus</u>	.10851	<u>Crassula</u>	.47348	Com	-.05130	T43-7
-.73094	<u>Olea</u>	.10305	Type 43-7	.44767	Lau	-.07766	Ant
.62496	<u>Osmitopsis</u>	.08002	<u>Anthospermum</u>	.42404	Eri	-.13260	Clt
.55678	<u>Pteridophyta</u>	.06352	<u>Ericaceae</u>	.37789	Ilx	-.21673	Ptr
.51547	Type 17-40	.03939	cf. Liliaceae	.30805	Pod	-.32414	Osm
.44771	<u>Ilex</u>	-.19203	<u>Linum</u>	.26532	Grn	-.34513	Li1
.40002	<u>Restionaceae</u>	-.50479	<u>Compositae</u>	.26406	T17-40	-.35945	Gun
.27518	<u>Myriophyllum/Laurembergia</u>	-.59987	<u>Gramineae</u>	.22685	Res	-.36238	Myr/
.26409	<u>Passerina</u>	-.84408	<u>Cyperaceae</u>			-.49146	Clf
						-.55912	Cra

Cliffortia are common in glades and on forest margins, but are also frequent on streambanks and in wet fynbos. Laurophyllus, loading positively on F1, is frequent in wet scrub and on flat waterlogged areas, Osmitopsis is common in "seepage" fynbos and Peridophyta are common on forest margins and in wet fynbos, but may also be represented in swamp vegetation.

Cyperaceae, Gramineae and Compositae are grouped on the other extreme of high negative scores on factor F1. Phillips' (1931:107-112) description of the ecology of the Knysna forest area indicates that numerous species of the Cyperaceae are common in the stages of development of the hydrosere, but that they are especially dominant in the later stages where perennial abundance of water is not typical. Although in the George-Knysna region most Cyperaceae are associated with wet habitats, there are exceptions to this rule, e.g. Tetraria and Ficinia. Grasses are common in fynbos and allied shrubland (Cowling 1983a, b) and also in karroid vegetation (Acocks 1979) and were certainly much more so prior to the intensive European exploitation of the last few centuries (Acocks 1979; Cowling 1983a). Compositae are as a whole more prominent in dry heath and karroid or subkarroid (arid) vegetation (Martin 1968).

Elements with the high negative loadings on F2 include Cliffortia and Gunnera, common in wet fynbos and on streambanks while Myriophyllum and Crassula



inanis/natans are common in the zone of semi-aquatics. On the other extreme of this factor Olea, Passerina and Compositae have high positive scores. Compositae are common in subkarroid vegetation (Martin 1968), species of Passerina are common in the medial stages of seres leading to scrub vegetation and Olea europaea subsp. africana is a prominent element of scrub vegetation. The suggestion that the Olea component with a high positive score on F2 can be identified with Olea europaea subsp. africana rather than Olea capensis is supported by the pollen analysis of the locality 2 site (Fig.2.5) where a distinction was made between O. capensis and O. europaea pollen.

In order to observe fluctuations through time in the strengths of factors 1 and 2, a summary statistic was calculated for each factor for each level. This statistic was calculated by multiplying factor scores for each taxon by its relative abundance (expressed as percentages of the total pollen sum) per level and then summing the products. In this way a single value reflecting the strength of the factor for each level is obtained. These values were calculated for factors 1 (F1) and 2 (F2) for each sequence and have been plotted in Fig.2.6 as SSF1 and SSF2 respectively. This procedure was suggested by J.F. Thackeray (pers. comm.) and the summary statistic concerned corresponds to one of the "composite statistics" described by Nie et al. (1975).

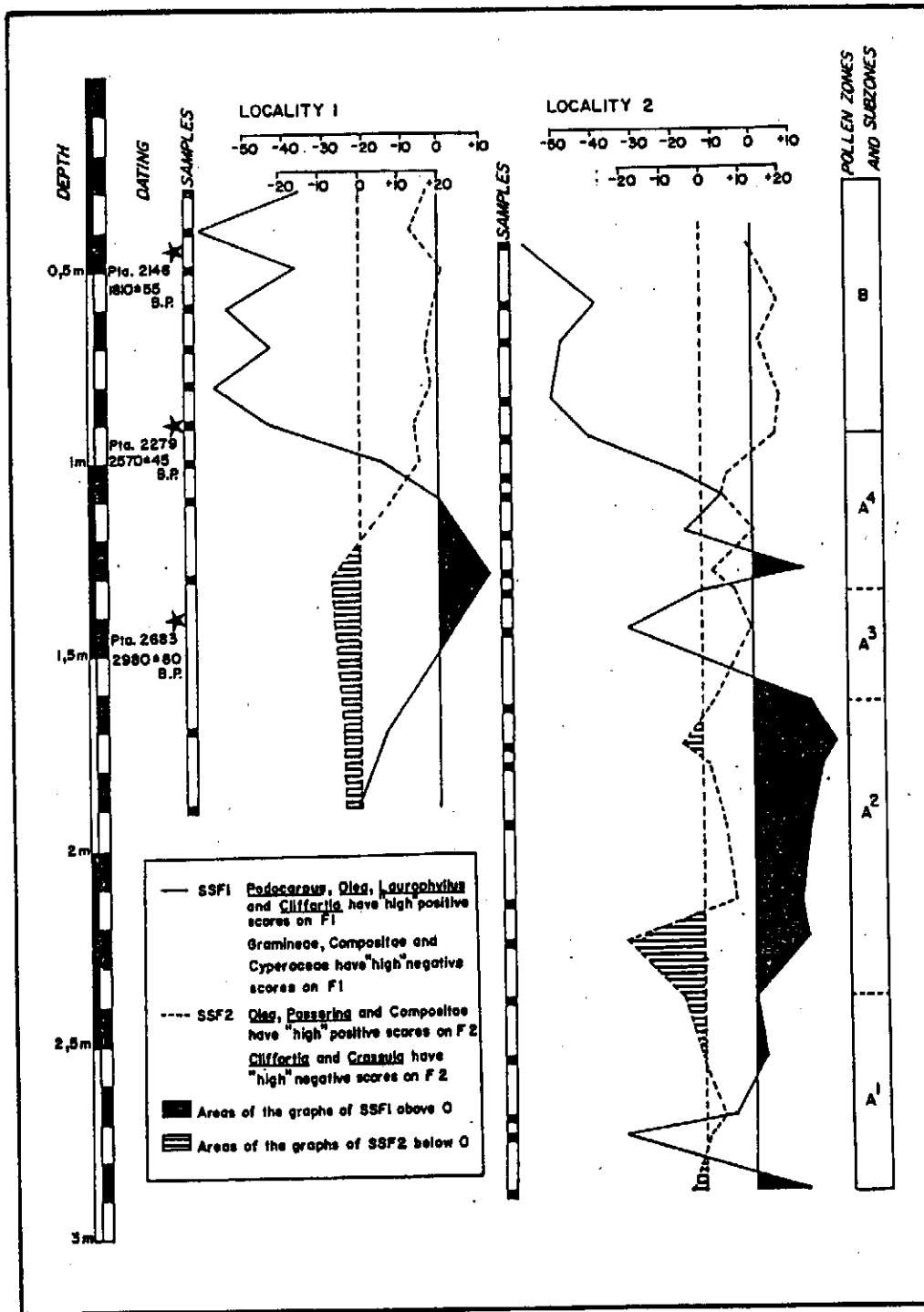


Fig.2.6 Values of a summary statistic for factors 1 (SSF1) and 2 (SSF2) for the Norga locality 1 and 2 sequences

On the basis of the observations on the habitat requirements and loadings of taxa on factors 1 and 2 it can be suggested that high values of SSF1 record relatively mesic periods during which forest and wetland vegetation was favoured. SSF2, on the other hand, can be positively correlated with scrub or subkarroid vegetation and negatively correlated with aquatic conditions in the local environment. It seems therefore that both SSF1 and SSF2 register a mesic/xeric gradient. In the latter case, however, high positive rather than negative values indicate the more xeric conditions. In terms of our present understanding of the habitat requirements of specific taxa and of the formation of the type of deposit concerned, it is not possible to attach more precise significance to the groupings of taxa in F1 and F2.

The graphs of SSF1 and SSF2 may be used to help correlate the two sequences. A comparison of the two graphs indicates that marked changes in vegetation occur at the same depth below surface in both sequences and that change in the regional environment occurs concurrently with change in the local environment. This evidence is discussed in the following two sections.

A second factor and summary statistic analysis (Fig.2.7, SSF1) was done using the data from the locality 2 sequence alone. The method employed was the same as that described above for the first analysis. Note that the four counts from the top 45 cm of the locality 2 sequence, which were excluded from the first factor

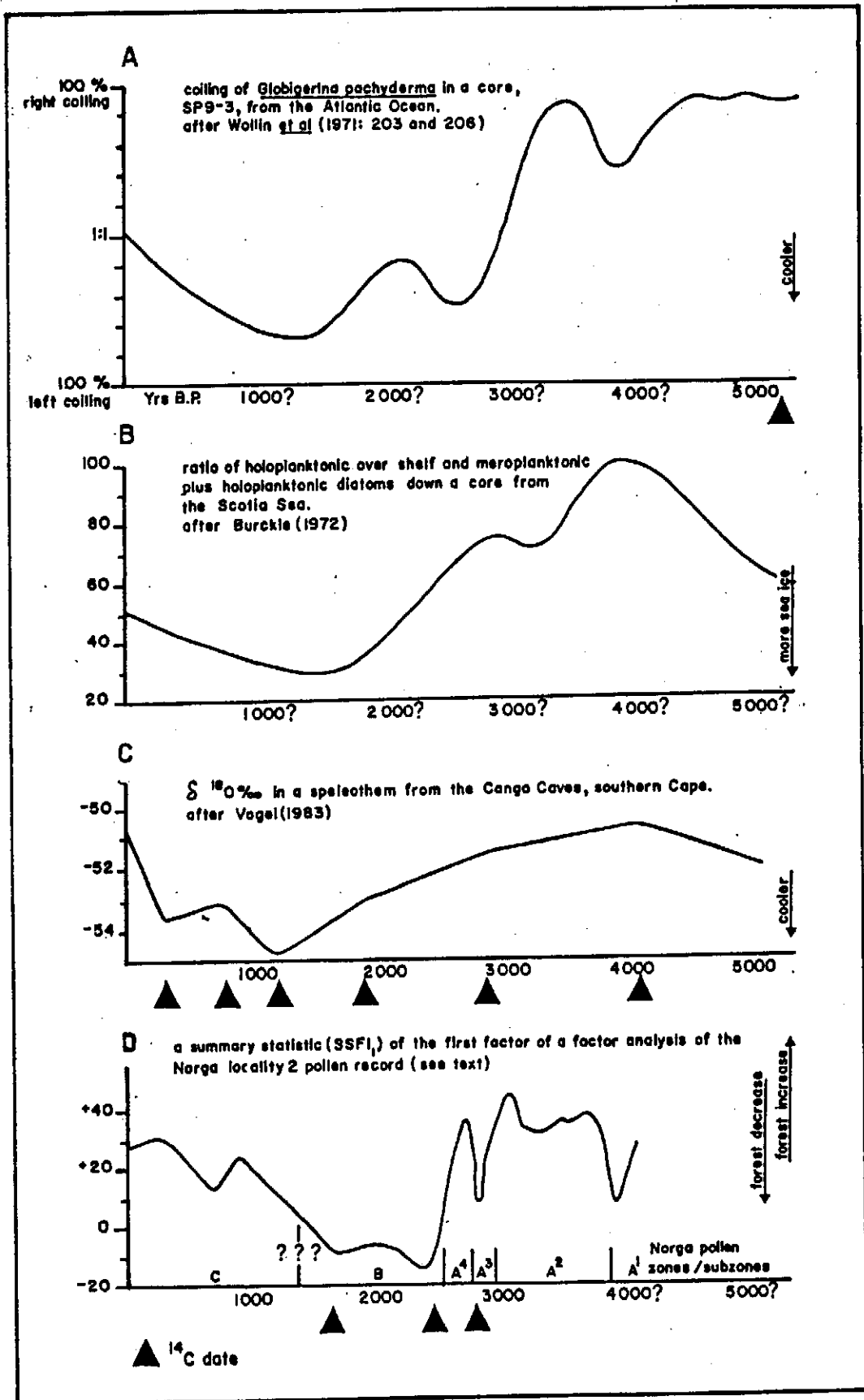


Fig.2.7 Correlating temperature curves for the late Holocene with the values for SSF1

analysis, are included in this analysis and add an important pattern to the record. The factors produced in the second factor analysis differed only slightly from those produced in the first and the SSF1 (locality 2) graph, Fig.2.7D, shows the same basic pattern as SSF1 (locality 2) in Fig.2.6. In both cases taxa such as Podocarpus, Olea capensis, Laurophyllus and Osmitopsis had high positive scores on Factor 1, while Gramineae, Compositae and Cyperaceae had high negative scores. High values for SSF1 (Fig.2.7D) can therefore be taken to indicate relatively mesic conditions.

#### RESULTS : ZONATION OF THE POLLEN DIAGRAMS AND THEIR INTERPRETATION

Before discussing the evidence which is recorded in the sequences from both localities, the patterns not recorded in both sequences should be noted. In some cases marked change in, or specific levels of representation of a certain element in the sequence from one locality are not reflected in the sequence from the second locality. An example is provided by a comparison of the values for Pteridophyta down the two sequences (Figs 2.4 & 2.5). Not only are the values for this group consistently higher at locality 2, but the marked increase in relative abundance recorded in the top four counts at locality 2 does not occur at locality 1. Similarly, the abrupt increase in representation of

Myriophyllum/Laurembergia recorded at locality 1 at 1,3 - 1,4 m is not recorded at locality 2. These inconsistencies occur mainly in the representation of taxa which might grow in the local environment and it is therefore parsimonious to regard them as a function of: i. processes determining the growth and microtopography of such a peat deposit; ii. the complex zonation of vegetation in and on the margins of a wet site and, iii. the location of the two sites relative to the shifting boundaries of local vegetation types. Unfortunately, little is known about the precise habitat requirements of the local semi-aquatic plants, so that fluctuations in their relative abundance cannot be interpreted. Also there are no studies available dealing with the processes which determine the growth of the type of peat deposit in question.

Despite these differences, visual examination of the pollen diagrams from the two Norga localities allows three pollen zones to be discerned, zones A-C (Fig.2.4 and Fig.2.5), representing two phases of increased representation of forest taxa (zones A and C) and one of low representation of forest taxa (Zone B). Zone A can be further subdivided. In the following section the evidence is described and discussed.

ZONE A (Figs 4 & 5) 2,9 m - 1,05 m at locality 2; 1,9 m - 1 m at locality 1; estimated age of zone A, 4000 - 2600 B.P. (estimation based on extrapolation from the dated

locality 1 sequence).

This zone is marked by generally high values of Podocarpus, Olea, the Osmitopsis-type, Cliffortia and Pteridophyta. Odd high counts of Myriophyllum/Laurembergia occur at 1,3-1,4 m at locality 1 and 2,25 m at locality 2. Values of Cyperaceae, Compositae and Gramineae are low compared to their representation in zone B.

The high clay content of the sample from 1,3 m in the locality 1 sequence and the sharp increase in the representation of Myriophyllum/Laurembergia at this point points to the existence of a particular habitat and a quiet sedimentary environment. It is suggested that the Myriophyllum/Laurembergia morphological type contains in this case the pollen of Myriophyllum, a rooted submerged aquatic which requires a perennial, relatively still water body. The same suggestion applies to the sudden increase in values for this type at 2,25 m in the locality 2 sequence.

Within this zone two subzones, A1 (2,9-2,4 m at locality 2) and A3 (1,65-1,45 m at locality 2) can be recognised, and are characterised by generally low counts Podocarpus, Olea, Cliffortia (at 1,45 m), Pteridophyta and the Osmitopsis-type and high counts of taxa such as Cyperaceae and Compositae. Subzone A2 includes the majority of zone A. It is present at locality 2 from 2,4 m to 1,7 m. Olea capensis is well represented in this subzone, but subsequently declines. A4 is a shorter

subzone and is present from 1,35-1 m at locality 2. The Olea peak in this latter subzone consists of Olea europaea rather than Olea capensis pollen. Due to the possible problem of disturbance of the lower part of the sequence at locality 1 and the failure to recover pollens at 1,5 and 1,6 m, it is uncertain with which of the two subzones, A2 or A4 (defined for locality 2), the counts at 1,7 and 1,9 m in the locality 1 sequence correlate. The counts at these levels are characterised by low values for Podocarpus, Olea, Cliffortia, Ilex mitis and Laurophyllus, relatively high values for Cyperaceae and high values for the Osmitopsis-type and Crassula.

There is little basis on which to evaluate the scale of the changes observed within Zone A, but they are of a lower order than the changes marking the boundary between zones A and B. Subzones A1 and A3 may indicate periods of some degree of deterioration of the environment with lower representation of forest taxa and changes in the vegetation zonation in the local wet site. Alternatively, the changes may be explained merely by some episodic or perhaps cyclical process of change in the stream flow regime, sedimentation and microgeography of the site. Although such changes were indeed occurring, as is demonstrated by the abrupt peaks in subzones A2 and A4 in the values of Myriophyllum/Laurembergia, this latter explanation is regarded as the less plausible one. The Norga River does not rise in the Outeniqua Mountains, where kloof forests and forested lower slopes could be



expected to deposit pollen onto the surface of a stream, but, as already noted, has its source on a low ridge only about 600 m north of the peat deposit (Fig.2.2). The proximity of the peat to the head of the stream reduces the possibility that differential contribution of water transported pollen to the depositional site could be a factor in explaining changes in the relative abundance of forest and streambank taxa.

A third possible explanation for the changes in zone A is that they relate to successional factors and/or disturbances of vegetation caused by events such as fire. Abundant macroscopic pieces of charcoal were observed in a sample from 1,55 m in the Norga locality 2 sequence, i.e. within subzone A3 and the relevance of this observation is discussed in the final section of this paper.

The general interpretation of zone A, particularly subzone A2 is that it represents a time of expansion of forest relative to zone B and a wet local environment. Within the bed of the shallow valley, periodic alterations in the positioning of a meandering stream and in the location of barriers of lush plant growth led sometimes to the creation of perennial pools of standing water. This is unlike the present state of peats in the area where Cyperaceae vegetation is dominant and is adapted to seasonal drought.

ZONE B (Figs 4 & 5), 0,95 m-0,45 m at locality 2; 0,9 m-0,3 m at locality 1; estimated age of Zone B, 2600-1400 B.P.

This is a very clearly defined zone in the sequences from each locality. The precise location of its lower boundary may lie between 1 m and 0,7 m at locality 1. The lower boundary is defined at 0,9 m since both SSF1 and SSF2 values in Fig.2.6 indicate that at this level a change from the values typical of subzones A2 and A4 has occurred and a plateau for values of these two summary statistics for the period 0,9-0,3 m achieved.

The relative abundance of taxa such as Podocarpus, Olea, Cliffortia, Pteridophyta and the Osmitopsis-type are low, while the relative abundances of Cyperaceae, Gramineae and Compositae are high. Myriophyllum/Laurembergia and the Osmitopsis-type are virtually absent in this zone. The values for Ilex mitis and Laurophyllus are relatively low compared to their representation in the underlying Subzone A4. These data indicate a deterioration in the environment. It seems that an expansion in the range of sub-karroid vegetation and a retraction of forest vegetation occurred.

The significance of the sequence of change in species representation documented in the Compositae group, with longer spined form(s) increasing earlier in time and then decreasing as lower spined form(s), and Gramineae increase, cannot be further elucidated with the present quality of identification.

ZONE C (Figs 4 & 5), 0,25 m-surface at locality 2; 0,2 m-surface at locality 1; estimated age of Zone C, 1 400 B.P.-Present.

In the local environment the representation of Cyperaceae declines sharply while Cliffortia and Pteridophyta increase at locality 2 and Myriophyllum/Laurembergia and the Osmitopsis-type are again present. In the regional environment Gramineae and Compositae values decrease, while the relative abundance of Podocarpus and, at locality 2, Olea europaea, Ilex mitis and Laurophyllus increases.

The odd examples of Acacia pollen in the top counts at both localities probably represent Acacia mearnsii, an exotic species introduced into the area in the mid-19th century (Phillips 1931) and at present the dominant vegetation on the Norga Peat and many other peats in the area. The occurrence of these pollens marks the period of European occupancy of the area and the associated disturbance of the environment probably explains the anomalous values of Compositae, Restionaceae and Podocarpus registered at locality 1 in the topmost count.

The interpretation of this zone is that conditions again became conducive to an expansion of forest vegetation. Locally, a high water table caused a decline in the dominance of cyperaceous vegetation. A tongue of forest possibly extended close to locality 2. The last expansion of forest recorded at the Norga localities appears to have begun between 1400 and 1000 B.P.

The initiation of the late phase of forest expansion in the Groenvlei record is dated at 1900 B.P.

## DISCUSSION

### ESTIMATING THE SCALE OF CHANGES

The data presented above indicate the direction of change in the environment better than they indicate the scale of change. The following discussion provides some perspectives on the possible scale of the vegetation and climatic changes recorded in the pollen diagrams.

To begin with, the distribution of soils (Fig.2.2) which would not have had the potential to support forest vegetation in the recent past even under optimal climatic conditions should be noted. Since the development of an extensive and unbroken area of forest on the coastal platform west of George could never have occurred in the recent past, even optimal conditions for the spread of forest vegetation would not have resulted in pollen spectra comparable to that found beneath pure stands of forest vegetation, i.e. relatively low percentage representation of pollen of forest taxa could be recording the optimal distribution of forest in the area.

The available modern spectra from the Knysna area suggest that despite the fact that Podocarpus produces abundant well dispersed pollen, the relative abundance of this pollen type, as for other forest taxa, declines sharply away from the forest margin. The suggestion is therefore that the upper (18-20%) and lower (5-7%) values

recorded for Podocarpus at Norga record very different distributions of the trees in the region. At the higher values (subzones A2 and A4) the whole band of suitable soils to the north and east of the Norga site may have been forested. This would have brought a tongue of forest close to the present site of the Norga peat. This suggestion is supported by the high representation of pollen of Olea capensis, another component of forest vegetation in these zones.

If values of 10% and below are taken to indicate that no Podocarpus trees were present in the immediate environment, this could mean that only kloof forest was present west of George during Norga Zone B times. Given the present day marginal status of the forest patches west of George and the steep rainfall gradient in the area, it is thought that only a modest decrease in effective precipitation (especially in summer) relative to the present would be required to restrict forest taxa to the relatively mesic kloofs.

It was suggested in the previous section that the occurrence of pollen taken to be that of Myriophyllum in subzones A2 and A4 of the Norga sequence indicated the presence of perennial pools of water in the local environment. During this century Myriophyllum has not been recorded in the George division (Fourcade 1941), but has been recorded in the Wilderness (Jacot Guillarmod 1982) and Knysna (Phillips 1931) areas. This suggests that an annual precipitation of at least 1000-1200 mm

is required to maintain its habitat. Because of the short length of the Norga stream above the peat and because the Norga does not rise in the mountains whose south slopes receive higher and more regular doses of orographic rain, it is suggested that an annual rainfall of at least 1000 mm, equably distributed and with sufficient rain in summer, would be necessary to maintain the required habitat at the Norga site. This implies an increase in annual precipitation of close to 400 mm in the George area during subzones A2 and A4. This estimate also supports the idea that forest occupied all areas of suitable soil in the region during Zone A.

The rainfall gradient west of George is at present very steep. It is not known whether, in terms of the macroclimatic controls operating in the region, it is justified to suggest that during the times of subzones A2 and A4, all isohyets in the region were increased by 3-400 mm. If justified, the implication is that, given suitable soils, considerable areas east, north and even west of Mossel Bay may have been able to support forest.

These suggestions are based on the assumption that the stream is not spring fed or in other ways controlled by ground water effects significantly out of phase with changes in the regional climate.

#### THE PRE-AGRICULTURAL, "PRISTINE" VEGETATION OF THE SOUTHERN CAPE COASTAL FORELANDS

In previous sections of this chapter it was stated that decline in forest vegetation during Norga Zone B times

was accompanied by an expansion of a sub-karroid vegetation type with prominent graminoid and compositoid components. On the grounds of recent accounts of the phytogeography and vegetation history of the region (Boucher & Moll 1980; Cowling 1983a,b), it appears likely that communities of what has been termed the Cape transitional shrublands (sensu Cowling 1983a) would have occurred on the granite derived soils west of George.

The ground layers of these shrublands are dominated by grasses and the vegetation requires 300-600 mm annual rainfall. Cowling (1983a,b) and Hendey (1983) review the literature which strongly suggests that prior to overgrazing by domestic livestock and increase in fire frequency following European colonisation, most of the areas in the southern and southeastern Cape now covered by transitional shrublands were grassland. In the southeastern Cape at least, these grasslands consisted of a dense growth of Themeda triandra (Cowling 1983a,c). Only recently have these grasslands come to be dominated by "weedy" composites such as members of the genera Elytropappus, Metalasia, Relhania and Euryops.

The low relative abundance of pollen of Elytropappus rhinocerotis (renosterbos) and the prominence of Gramineae in all the Norga fossil pollen spectra lends support to the contention that in relatively moist regions, Cape transitional shrublands are marginal to grassland and that the present prominence of renosterveld on the coastal forelands is a recent phenomenon which can

be related to over exploitation of the veld. The virtual absence of Elytropappus pollen throughout the Norga sequence contrasts with extremely high representation in pollen spectra from modern day renosterveld (pers.obs.) and from fossil spectra of ca 20 000 B.P. from the Congo Valley (Deacon et al 1983). The latter observation, however, indicates that the dominance of Elytropappus in an area cannot in all cases be attributed to disturbance by man.

On two points, suggestions from the present study about the history of vegetation in the region contradict ideas developed in analysis of the botanical present. Cowling (1983a), amongst others, has suggested that forest has securely held its present range of distribution during the Holocene. This study has shown that the present distribution of vegetation types in the George area reflects a delicate balance of vegetation and climate with a short, 1500 year, time depth. Cowling (1983a) also assumed "that the overall floristic structure of the major plant assemblages (of the southern Cape) and the ecological factors determining their distribution have not differed drastically in the last glacial to Holocene sequence". The evidence for a recent and perhaps quite substantial climatic 'perturbation' as well as evidence for major changes in climate during the last 14 000 years (Chapter 5) casts doubt on this assumption.

It should be noted that Acock's (1953) map purporting to represent the distribution of southern African



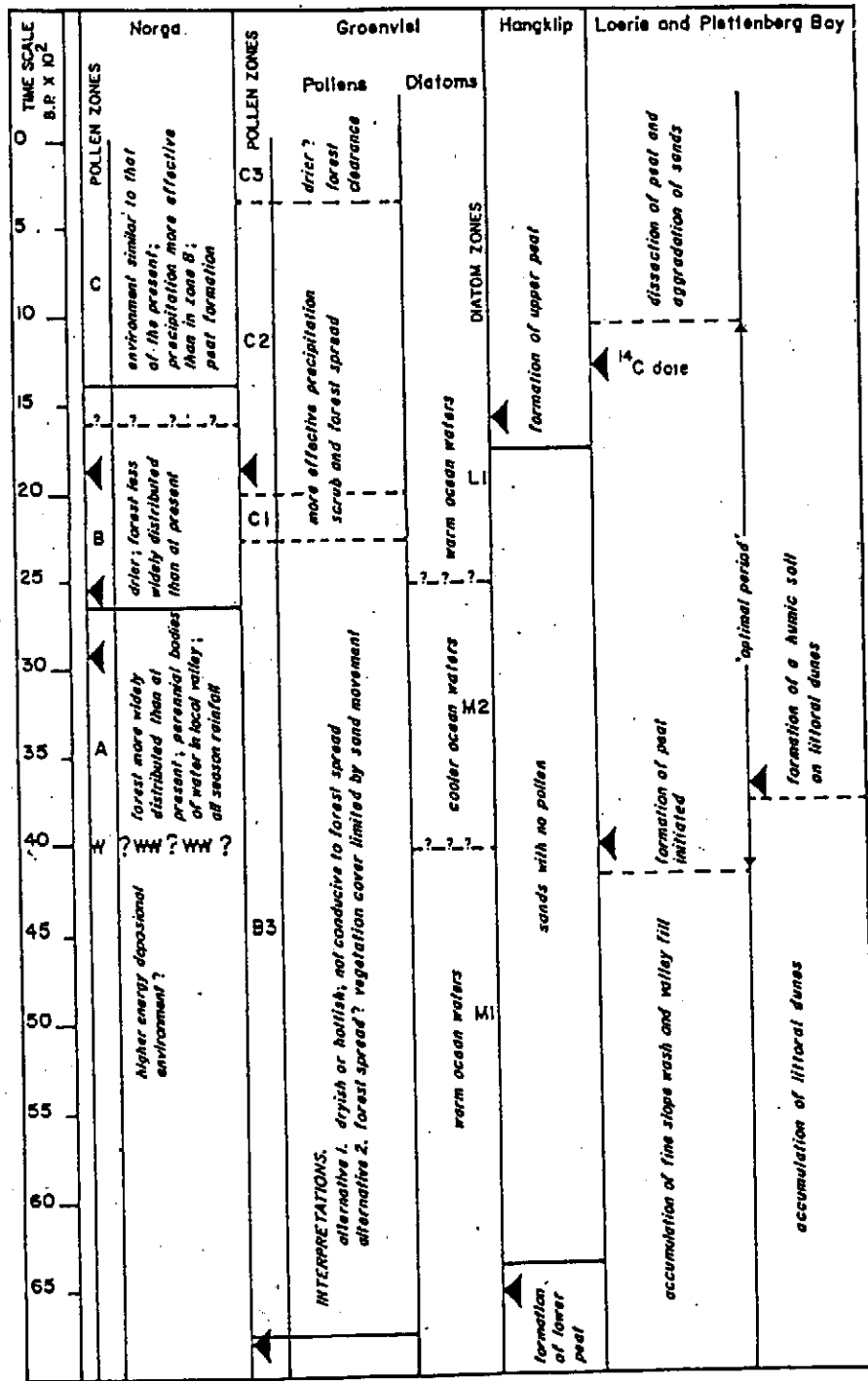
vegetation types ca 1400 A.D. stands corrected. The evidence presented in this study suggests that only before 2600 B.P. could afro-montane forest and scrub have been much more widespread than it is today. The retreat of forest since that time, leaving outliers of forest and bush/scrub in protected landscape situations, cannot all be telescoped into the last few hundred years and attributed to the impact of European colonisation.

#### CORRELATIONS WITH OTHER EVIDENCE

In this section the correlations which exist between the Norga record and the records obtained from the palynological analysis of the Groenvlei Lake sediments (Martin 1968), the Hangklip Peat (Schalke 1973) and the sedimentological evidence presented by Butzer and Helgren (1972) in their outlining of the geomorphic evolution of the southern Cape Coast are discussed (see Fig. 2.1 for location of the sites). The evidence from Norga and other relevant studies are summarised in Table 2.3.

Evidence for a late mesic period is found in the Norga (Zone C), Groenvlei and possibly Hangklip sequences and the dating of the inception of this period at Norga and Hangklip agrees closely. The apparently slightly earlier date for the beginning of this period at Groenvlei (around 1900 versus 1400 B.P. at Norga) could be explained away by a variety of factors including the different ecological settings of the sites and the fact that the relevant date from the Groenvlei sequence does

Table 2.3 Correlation of palaeoenvironmental information from sites in the southern and southwestern Cape



not come from the core which was analysed palynologically.

It is possible that the disturbance of a local geomorphic equilibrium in the Loerie Peat environment (Butzer & Helgren 1972:164-165), post-dating 1330 B.P. and marked by dissection of the peat and aggradation of coarse sands, might relate to the same change in climate. Palynological analysis of this peat might suggest how the disturbance of local equilibrium in this locality after 1330 B.P. related to changes in the regional environment and climate.

Although the late mesic period (Zone C at Norga) is recorded at Groenvlei and possibly at Hangklip (by peat formation in a dune environment), the preceding periods documented by Norga pollen zones B (relatively less mesic) and A ('optimal' for the sampled time range) are not recorded at the two coastal sites.

The obvious explanation for why the changes in climate recorded at Norga between 4000 and 2000 B.P. are not recorded at these sites is that the movement of dunes in the local environment of these sites masked changes in their regional environments. At Hangklip, 1,5 m of deposit between a lower peat with an upper date of 6520 B.P. and an upper peat with a date close to its base of 1580 B.P. (Schalke 1973: Appendix 6) consists of sands with no pollen content, while at Groenvlei, a similar depth of deposit consists of silty to sandy greenish, black mud with marine diatoms and foraminifera. This

unit, corresponding to pollen Subzone B3 at Norga, is bracketed by a lower peat and an organic rich gyttja layer with dates comparable to those from Hangklip (6870 B.P. and 1905 B.P. respectively). Martin (1959, 1968) reports sedimentological and geomorphological evidence suggesting that movement of dune sands occurred between 7000 and 2000 B.P. in the vicinity of Groenvlei Lake. The probable reason for the movement of dune sands, at least in the latter half of this period, is that the sea level was retreating from its mid-Holocene high (Mabbut 1954; Martin 1959; Butzer & Helgren 1972), leaving enlarged areas of mobile dunes in its wake.

The Loerie Peat started to form at about 4000 B.P. Butzer & Helgren (1972:165) note that at around the same time littoral dunes near Plettenberg Bay were stabilised by the development of a humic soil. Also, it is estimated that at about 4000 B.P. organic rich clays, silts and fine sands began to accumulate at the Norga site. The possible synchronicity of change in sedimentology at these three sites may indicate a change in macroclimate experienced over the region, with the post transition climate creating conditions conducive to the deposition of fine sediments and the growth of aquatic and semi-aquatic vegetation in stream beds and the development of humic soils on coastal dunes. It is suggested that these conditions are indicative of a mild climate characterised by a reliable all season rainfall regime and a moisture surplus throughout the year.

However, the synchronicity of the bottom date for the Loerie Peat and the estimated age of the base of the Norga deposit may be fortuitous and bottom dates on the Norga and other peats in the southern and eastern Cape are required to confirm this pattern.

needs confirmation  
→ WW

If the 4000 B.P. dates mark a period during which a certain climatic plateau was attained ( Butzer & Helgren (1972) refer to the period 4200-1000 B.P. as the 'optimal' period of the Holocene dynamic equilibrium ), the question is begged as to the nature of the preceding climatic regime. There is little data that relates to this period. Sands or residual clays are found beneath the organic rich clays in the Norga deposit. According to Butzer and Helgren (1972) the pre 4000 B.P. period is marked by the accumulation of littoral dunes in the Plettenberg Bay area and of fine slope wash and valley fill at the locality of the Loerie Peat. (The evidence from the Bonawe site, northeastern Cape (Tusenius 1986), which indicates a mesic period around 4000 B.P. preceded and followed by less mesic conditions was mentioned in Chapter 1.)

←

More discussion is required concerning the correlation of evidence from Martin's studies on Groenvlei and evidence from the present study. The evidence produced in this study suggests that Zone B3 in the Groenvlei sequence (7000-2000 B.P.) must contain two or three distinct phases of climate. However, Zone B3 (Martin 1968:141) is undifferentiated. Because of the potential effect of the mobilisation of large areas of

Can B3 be divided into two or three phases with WW

dunes on the vegetation in the vicinity of Groenvlei, Martin proposed alternative interpretations for the pollen record for this period. The first alternative was that conditions were hot and dry and not conducive to forest spread, while the second was that conditions were indeed encouraging of forest spread, but that locally, vegetation cover was limited by the movement of sand. Given the Norga evidence, the latter interpretation is more likely to be the correct one for the majority of Groenvlei Zone B3 times.

The diatom analysis of a core through the Groenvlei Lake sediments (Martin 1959) produced evidence more informative than the pollen analysis in this time range. Groenvlei pollen Zone B3, ca 6870-2000 B.P., includes the diatom stages M1, M2 and L1. During the lowest stage, M1 (5,2-4,4 m below the lake bottom), a marine stage, the diatom assemblage is composed of littoral, warm temperate or tropical forms, while in stage M2 (4,4-3,9 m below the lake bottom) the assemblage is composed of temperate forms with a wide temperature tolerance and cool temperate forms. Marine diatoms are present but rare during lagoon stage L (3,9-3,4 m below the lake bottom), and the forms are once again those common in M1, i.e. warm temperate and tropical forms.

Martin regarded it as unlikely that these changes in the marine diatom flora could be attributed to a local ecological effect and concluded that the changes in the

marine diatom flora suggested a decrease in mean temperature of the Agulhas current during stage M2. Such changes would probably have had some effect on the climate of the coastal region, but no changes are recorded in the palynological record through the relevant time range.

It is also useful to compare the inferred climatic phases experienced during the late Holocene in the southern Cape with putative temperature curves for this period. Three such curves are presented in Fig.2.7.

The most geographically relevant curve is that obtained from oxygen isotope and radiocarbon analysis of speleothem material from the Cango Caves (Vogel 1983). These caves are situated inland of and within 50 km of the Norga site (Fig.2.1). The curve published in Wollin et al (1971) is based on foraminiferal analysis and the curve published by Burckle (1972) is based on the diatom analysis of a core from the Scotia Sea in the South Atlantic Ocean, southeast of the Falkland Islands. This latter curve portrays a measure of the amount of sea ice present in the area through time.

The significance of the three curves is that they show a cooling event in the late Holocene after a mid-Holocene hypsithermal. This cooling event is often insecurely dated, but its inception is usually between 4000 and 3000 B.P. According to the Cango and Scotia Sea curves, lowest temperatures were recorded after 2000 B.P and were followed by an increase in temperature during the last 1500 years.

Given a degree of correlation between the graph of SSF1 and the various temperature' curves in Fig.2.7, it is an obvious suggestion that Norga pollen Zone B, which records a decline in forest in the area, occurs during a cool post hypsithermal period. Norga pollen zones A and C, during which forest advances are recorded, may apparently largely be correlated with warmer temperatures. This suggests that Norga pollen Zone B records a period of forest retreat, reduced precipitation and a cooler or even cold climate. This combination of features is unexpected. Taking the marginal viability of afro-montane forest over some of its present range of distribution into account, a more predictable scenario would be that within the 'norm' of late Holocene climates, an increase in temperature would adversely affect the forests.

Palynological evidence relevant to the late Holocene from the interior of southern Africa suggests that a slightly cooler climate prevailed over the Transvaal between about 4000 and 2000 B.P. and that since 2000 B.P. the climate has become progressively drier and warmer (Scott 1982).

The factor of seasonality of rainfall could also be implicated in the decline of forest recorded in Norga Zone B and the low oxygen isotope 18 content of the Congo Cave speleothem at this time (Fig.2.7) may be reflecting a change in seasonality of rainfall (HJ Deacon pers. comm.). As Van Daalen (1980) has noted, the distribution of forest is closely correlated with the amount of summer rainfall.



The evidence for more sea ice in the Scotia Sea may be significant for a reason other than its general reflection of colder conditions in the southern hemisphere. The area of cyclogenesis related to the disturbances in the circumpolar westerlies which regularly affect the climate of the subcontinent lie far to the southwest of the Cape (Taljaard 1967) and include the area of the Scotia Sea. Marked change in the extent and amount of sea ice in the Scotia Sea, an area where at present a particularly complex set of factors govern the location of ocean zones (Deacon 1982), could have powerful effects on the climate of southern Africa.

Before concluding this discussion, it is worth noting that climatic change involves features other than precipitation and temperature. A feature of great importance, both in its effects on vegetation and in its significance as an indicator of intensity of the general atmospheric circulation, is that of wind strength (Newell et al 1982). Recent studies by Sarnthein (1978) and Sarnthein & Koopman (1980) have suggested that in west Africa and the Sahara during the mid-Holocene hypsithermal, atmospheric circulation was slack, dune fields were not active and precipitation was relatively high. In a subsequent period atmospheric circulation was much more intense and Sarnthein (1978) goes so far as to suggest that conditions in the last 4000 yrs in west Africa have approached those which pertained during the glacial maximum in this area.

This statement is important for the present discussion because it questions the assumption that climatic changes within the Holocene are necessarily of a much lower order than changes between a Holocene 'norm' and the late Pleistocene. Evidence from the southern Cape (Vogel 1983) indicates a decline in temperatures after 4000 B.P. with minimum values approaching those of ca 20 000 B.P., while the amount of sea ice present at 1500 B.P. in the Scotia Sea apparently also rivalled that of the last glacial maximum (Burckle 1972).

A change in the intensity of the atmospheric circulation system could affect climate in the southern Cape considerably. Any northward extension of a winter rainfall climatic regime would have a great influence on a narrow transitional climatic zone like that of the southern Cape.

An increase in the intensity of atmospheric circulation could also reflect in some increase in wind strengths and duration. Story (1952:121-135) has discussed the set of factors which control the distribution of forest in the Keiskammahoek District of the eastern Cape. He emphasised that, given adequate moisture, the crucial factor determining the distribution of forest vegetation in this region is that of cold winter winds. These winds cause physiological drought and, according to the topography, as areas of landscape are exposed to or protected from them, so forest is excluded or able to grow. It is possible that an increase in the occurrence of cold winter

winds could have caused the decline in forest recorded during Norga pollen Zone B, ca 2600-1400 B.P.

## REFERENCES

- ACOCKS, J.P.H. 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, Pretoria
- ACOCKS, J.P.H. 1979. The flora that matched the fauna. Bothalia 12:673-709.
- BOUCHER, C. 1978. Cape Hangklip area 11. The vegetation. Bothalia 12:455-497.
- BOUCHER, C. & MOLL, E.J. 1980. South African mediterranean shrublands. IN F. di Castri, D.W. Goodall & R.L. Specht (eds ) Mediterranean-type shrublands:233-248 Elsevier, Amsterdam.
- BURCKLE, L.H. 1972. Diatom evidence bearing on the Holocene in the South Atlantic. Quaternary Research 2:323-326.
- BUTZER, K.W. & HELGREN, D.M. 1972. Late Cenozoic evolution of the Cape Coast between Knysna and Cape St. Francis, South Africa. Quaternary Research 2:143-169.
- CATTELL, R. B. 1965. Factor analysis: an introduction to essentials. I. The purpose and underlying models. Biometrics 21:190-214.
- COLINVAUX, P. 1978. On the use of the word "absolute" in pollen statistics. Quaternary Research 9:132-133.
- COWLING, R.M. 1983a. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome.

- COWLING, R.M. 1983b. The occurrence of C3 and C4 grass in the southeastern Cape, South Africa. Oecologia 58:121-127.
- COWLING, R.M. 1983c. Phytogeography and vegetation history in the southeastern Cape, South Africa. Journal of Biogeography.
- DEACON, G.E.R. 1982. Physical and biological zonation in the Southern Ocean. Deep Sea Research 29(A):1-15.
- DEACON, H.J. DEACON, J., SCHOLTZ, A., THACKERAY, J.F. & BRINK, J.S. 1983. Correlation of the palaeoenvironmental data from the late Pleistocene and Holocene deposits at Boomplaas Cave, southern Cape. IN: J.C. Vogel (ed) Late Cainozoic palaeoclimates of the southern hemisphere:339-351. Balkema, Rotterdam.
- ENGELBRECHT, C.J. 1969. Die gronde in die omgewing van George. Unpublished M.Sc. University of Stellenbosch.
- FOURCADE, H.G. 1941. Check-list of the flowering plants of the divisions of George, Knysna, Humansdorp and Uniondale. Memoirs of the Botanical Survey of South Africa 20. Government Printer, Pretoria.
- JACOT GUILLARMOD, A. 1982. Checklist of the aquatic and floodplain vegetation of the Wilderness Lakes, southern Cape. Bontebok 2:41-51.
- HENDEY, Q.B. 1983. Palaeontology and palaeoecology of the fynbos region: an introduction. IN: H.J. Deacon, Q.B. Hendey & J.N.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis:87-99. SANSPR 75, Pretoria.

- LEVYNS, M.R. 1964. Migrations and origins of the Cape Flora. Transactions of the Royal Society of South Africa 37:85-107.
- MABBUT, J.A. 1954. Cape Hangklip, a study in coastal geomorphology. Transactions of the Royal Society of South Africa 34(1):17-24.
- MARTIN, A.R.H. 1959. The stratigraphy and history of Groenvlei, a South African coastal fen. Australian Journal of Botany 7:142-167.
- MARTIN, A.R.H. 1960. The ecology of Groenvlei, a South African fen. Journal of Ecology 48:55-71, 307-329.
- MARTIN, A.R.H. 1968. Pollen analysis of Groenvlei Lake sediments, Knysna (South Africa). Review of Palaeobotany and Palynology 7:107-144.
- MARTIN, A.R.H., NOEL, A.R.A. & HILL, D.B. 1960. The flora of Albany and Bathurst. Rhodes University, Grahamstown.
- MERCER, J.H. 1978. Glacial development and temperature trends in the Antarctic and South America. IN: E.M. van Zinderen Bakker (ed.) Antarctic glacial history and world palaeoenvironments:73-94. A.A. Balkema, Rotterdam.
- MOSIMANN, J.E. 1965. Statistical methods for the pollen analyst. Multinomial and negative multinomial techniques. IN: Handbook of palaeontological techniques (eds) Kummel, B.G. and Raup, D.M.:636-673. Freeman, San Francisco.

- District, Cape Province. Memoirs of the Botanical Survey of South Africa 13. Government Printer, Pretoria.
- NEWELL, R.E., SELKIRK, R., EBISUZAKI, W. 1982. The southern oscillation: sea surface temperature and wind relationships in a 100-year data set. Journal of Climatology 2:357-373.
- NIE, H.H., HULL, C.M., JENKINS, J.G., STEINBRENNER, K. & BENT, D.M. 1975. Statistical package for the social sciences. 2nd Ed. McGraw-Hill, New York.
- PHILLIPS, J.F.V. 1931. Forest succession and ecology in the Knysna Region. Memoirs of the Botanical Survey of South Africa 14. Government Printer, Pretoria.
- SARNTHEIN, M. 1978. Sand deserts during glacial maximum and climatic minimum. Nature 272:43-46.
- SARNTHEIN, M. & KOOPMAN, B. 1980. The Quaternary deep sea record of northwest African dust supply and wind circulation. Palaeoecology of Africa 12:239-253.
- SCHALKE, H.J.W.G. 1973. The Upper Quaternary of the Cape Flats Area (Cape Province, South Africa). Scripta Geologica 15:1-57.
- SCOTT, L. 1978. Late Quaternary pollen analytical studies in the Transvaal (South Africa). Unpublished Ph.D. University of the Orange Free State.
- SCOTT, L. 1982. A late Quaternary pollen record from the Transvaal bushveld, South Africa. Quaternary Research 17:339-370.
- STORY, R. 1952. A botanical survey of the Keiskammahoeck District. Memoirs of the Botanical Survey of South Africa 27. Government Printer, Pretoria.

- TALBOT, M.R. & DELIBRIAS, G. 1980. A new Late Pleistocene-Holocene lake level curve for Lake Bosumtwi, Ghana. Earth and Planetary Sciences Letters 47:336-344.
- TALBOT, M.R. 1982. Holocene changes in tropical wind intensity and rainfall: evidence from southeast Ghana. Quaternary Research 16:201-220.
- TALJAARD, J.J. 1967. Development, distribution and movement of cyclones and anticyclones in the southern hemisphere during the IGY. Journal of Applied Meteorology 6:973-987.
- TUSENIUS, M. 1986. Charcoal analytical studies in the north-eastern Cape. Unpublished M.A. thesis, Department of Archaeology, University of Stellenbosch.
- TYSON, P.D. (ed.) 1971. Outeniqualand: The George-Knysna area. The South African Landscape 2. South African Geographical Society, Johannesburg.
- VAN DAALEN, J.C. 1980. The colonisation of fynbos and disturbed sites by indigenous forest communities in the southern Cape. Unpublished M.Sc. thesis, University of Cape Town.
- VOGEL, J.C. 1983. Isotopic evidence for the past climate and vegetation of southern Africa. Bothalia 14:391-394.
- VON BREITENBACH, F. 1974. Southern Cape forests and trees. Government Printer, Pretoria.
- WHITE, F. 1978. The afro-montane region. IN: M.J.A. Werger (ed.) Biogeography and ecology of southern Africa:463-513. W. Junk, The Hague.

WOLLIN, G., ERICSON, D.B. & EWING, M. 1971. Late pleistocene climates recorded in Atlantic and Pacific deep-sea cores. IN K. Turekian (ed.) Late Cenozoic Glacial Ages: 199-214. Yale University Press, New Haven.



C H A P T E R   T H R E E

ANALYSIS OF THE RELATIVE ABUNDANCE OF IDENTIFIED WOOD  
MORPHOLOGICAL TYPES PRESERVED AS CHARCOAL ASSEMBLAGES  
FROM BOOMPLAAS CAVE, CANGO VALLEY, SOUTHERN CAPE

I N D E X

ABSTRACT  
INTRODUCTION  
THE SITE  
MATERIALS AND METHODS  
DESCRIPTION OF MORPHOLOGICAL TYPES  
RESULTS AND INTERPRETATION  
CONCLUSIONS  
REFERENCES

ABSTRACT

This chapter reports the results obtained through the analysis of nine stratigraphically and temporally discrete charcoal assemblages from the sediments of Boomplaas Cave, Cango Valley, southern Cape in terms of the relative abundance per assemblage of a range of wood morphological types.

Before 32 000 B.P., the olive tree (Olea europaea subsp. africana) occurred in the valley. Between 32 000 and 17 000 B.P. the olive was absent from the valley and woody vegetation consisted mostly of a range of karroid asteraceous genera such as Euryops, Relhania, Stoebe and

Elytropappus. It is inferred that the climate was dry and cold. This interval includes the period coeval with the Last Glacial Maximum (LGM). Between 17 and 14 000 B.P. a sharp amelioration of climates occurred and the olive and other woody genera such as Rhus, Maytenus, Euclea and Tarchonanthus reappear in the record. A dominance of Acacia karroo is recorded in the late Holocene.

## INTRODUCTION

The history of this research project partly determines the construction of this chapter. Prior to the development of both the MPDA (Ch.6) and EDXA (Ch.4 & 5) forms of analysis, the charcoal assemblage from Boomplaas Cave had been processed for the purpose of Morphological Type Relative Abundance Analysis (MTRAA) and the results reported in a preliminary paper (Deacon et al 1983). For this reason, despite the fact that some substantial changes have been made in how the data are presented and interpreted, the present reporting and discussion of the study is relatively brief.

## THE SITE

Boomplaas Cave is situated in the intermontane Cango Valley, southern Cape. The setting of the site and the archaeological analysis of its sediments are described in H.J. Deacon (1979), J.C.G. Deacon (1982) and Deacon et al (1983). The cave is situated on the southeast facing slope of a low limestone hill, Drupkelderkop (33.22 S, 22.11 E), within the Cango Valley and about 60 m above the floor of the valley of the perennial Grobbelaars River.

The north and south slopes of the hill, the floodplain, the river margins and marshy areas on the floodplain, sheltered gullies and areas below cliff faces provide a diversity of habitats within the environs of the cave. The cave sediments are well stratified and occupation units are often clearly separated by sterile units (Fig.3.1). A series of 22 radiocarbon dates provides reliable chronological control within the last ca 40 000 yrs. Apart from the lithic analysis (Deacon JCG 1982), the sediments have been analysed by Webley (1979), the macrofauna by Klein (1983) and the microfauna by Avery (1982). A vegetation survey of the area recorded 70 woody species in the valley (Moffett & Deacon 1977) and samples of these woods formed the basic reference collection for this study.

#### MATERIALS AND METHOD

Charcoal was routinely recovered during excavation, either directly from exposed floors or by water flotation from excavated sediments (Deacon HJ 1979). The latter method was used only in the upper levels where charcoal was abundant. Charcoal assemblages were provenanced per excavated square or per hearth feature and dried and bagged in the field.

Subsamples for charcoal analysis were taken using two different sampling methods. In the upper levels (CL-BLD), where relatively large areas were excavated and charcoal was abundant (Fig.3.1), the total assemblage from an occupation unit was sampled by randomly selecting

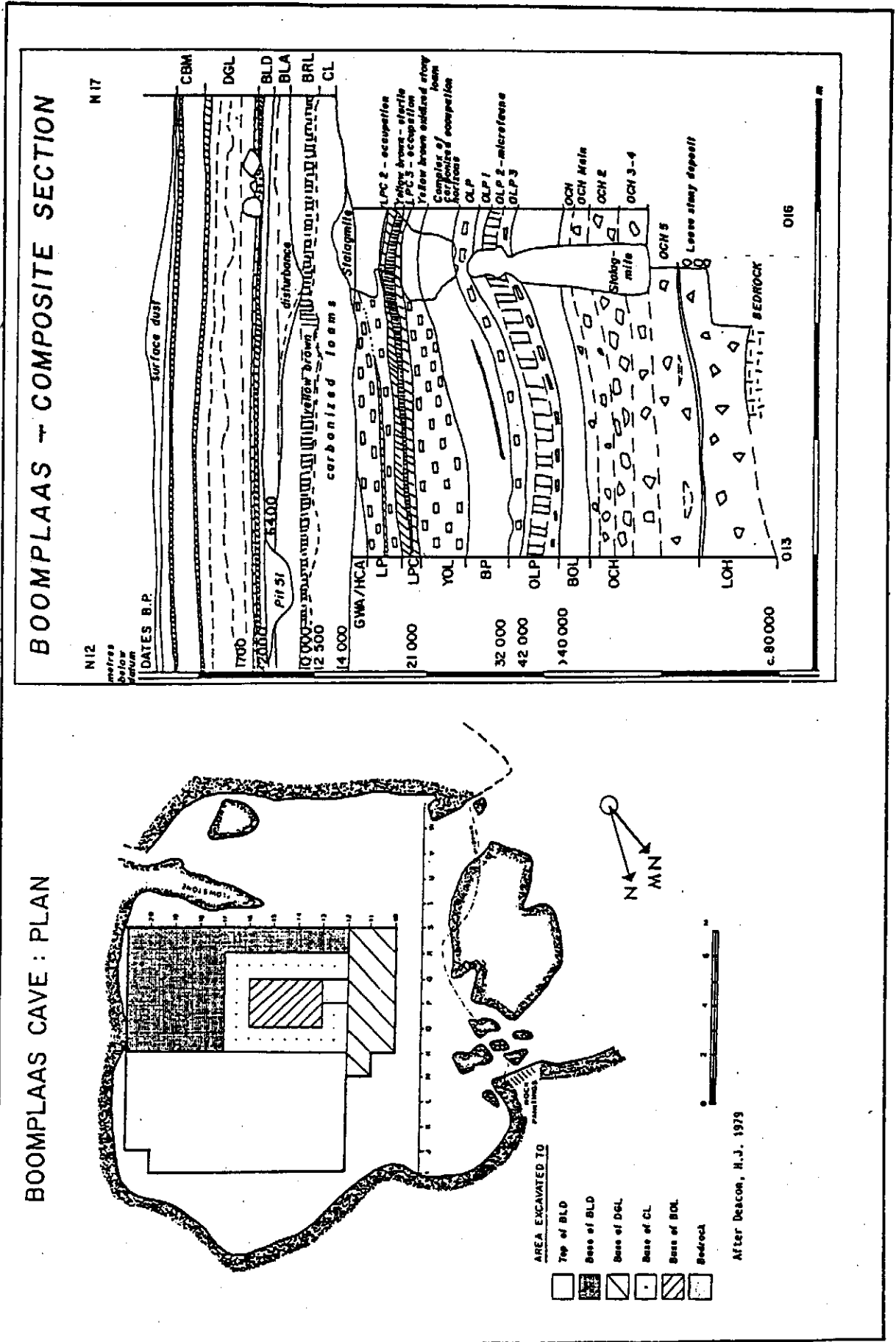


Fig.3.1 Plan and section of Boomplaas Cave (after Deacon HJ 1979)

two pieces of charcoal per hearth feature or square (Deacon HJ 1979; Deacon et al 1983). In the levels below CL, ten or more pieces were randomly selected from the pre-selected set of adequately preserved pieces per hearth or square. In some cases all available pieces from a hearth feature were analysed.

Transverse sections alone were mostly used. This was done in order to limit the bias towards the selection of larger pieces of charcoal. This bias would arise if two or more sections had to be obtained from one piece of charcoal and would make the measures of relative abundance on which comparing the assemblages was based less reliable. A second reason for using only transverse sections was that an initial phase of the project had been aimed at simply distinguishing between Acacia karroo and all other types of wood. This species is presently the most common woody plant in the vicinity of the cave and its wood is easily distinguished in transverse section from the wood of other species occurring in the valley.

Charcoal pieces were identified as belonging to a certain morphological type by comparing SEM images of the fossil material with those in a reference collection which consisted of the 70 woody species occurring in the valley (Moffett & Deacon 1977) plus a range of karroid woody taxa. The addition of the latter was necessary since, in the assemblages below CL, morphological types not encountered in the upper assemblages were dominant

and initial research showed that these types represented karroid woody taxa. In these lower levels (GWA-BOL) wood was identified both on the light microscope and from SEM photomicrographs and both transverse and tangential sections were used where possible.

Identification of any one piece of charcoal was rendered uncertain because of the limitations imposed by the state of alteration and preservation of charcoal, the availability of only single photomicrographs per section per piece, the normal factors of wood variability and the trends across phylogenetic lines towards modal xeromorphic wood anatomy. Even with modern material the taxonomic level at which identifications can be made without a sample of adequate size and exhaustive research varies. For these reasons it was decided firstly to identify pieces as belonging to morphological types, with these types in turn being identified with a taxon or set of taxa as appropriate. A total of 30 morphological types (MT 1-30) were used to sort the assemblages. The availability of both transverse and tangential sections for the assemblages below CL sometimes enabled specific identifications to be made and this, where relevant, is mentioned in the text. To limit the subjective factor, the final sorting of the 1039 pieces analysed in this study was carried out by two researchers, A. Scholtz and M. Tusenius.

In the following section the 20 most commonly occurring morphological types are described and illustrated. The relative abundances of each morphological type per

level are provided in Fig.3.2. The numbering of the morphological types was determined by the order in which they appear in this figure. This system helps to organise the evidence into an informative pattern. The types which are most abundant in the topmost assemblage (BLD) appear first in the diagram (MT 1-6), followed by the types most abundant in BLA (MT 7-9) and so on down the sequence.

A diversity index, the Shannon-Weiner diversity index (Shimwell 1971), was calculated for each assemblage and the values are provided in Fig.3.2. High values indicate assemblages composed of numerous species represented at intermediate relative abundances, while low values indicate assemblages composed of few species represented at high or low relative abundances.

#### DESCRIPTION OF THE MOST COMMON MORPHOLOGICAL TYPES (Standard magnification of all transverse sections X 60)

##### TYPE 1 Acacia karroo (Fig.3.3.1 & 3.3.2)

Large solitary vessels; occasionally smaller vessels form a cluster around a larger vessel; vessels with simple perforation plates; axial parenchyma strongly vascentric, aliform to confluent; relatively thick walled fibres in tangential bands; multiseriate rays. Fig.3.3.1 is of a branch sized piece, while Fig.3.3.2 is of a piece of twig sized diameter.

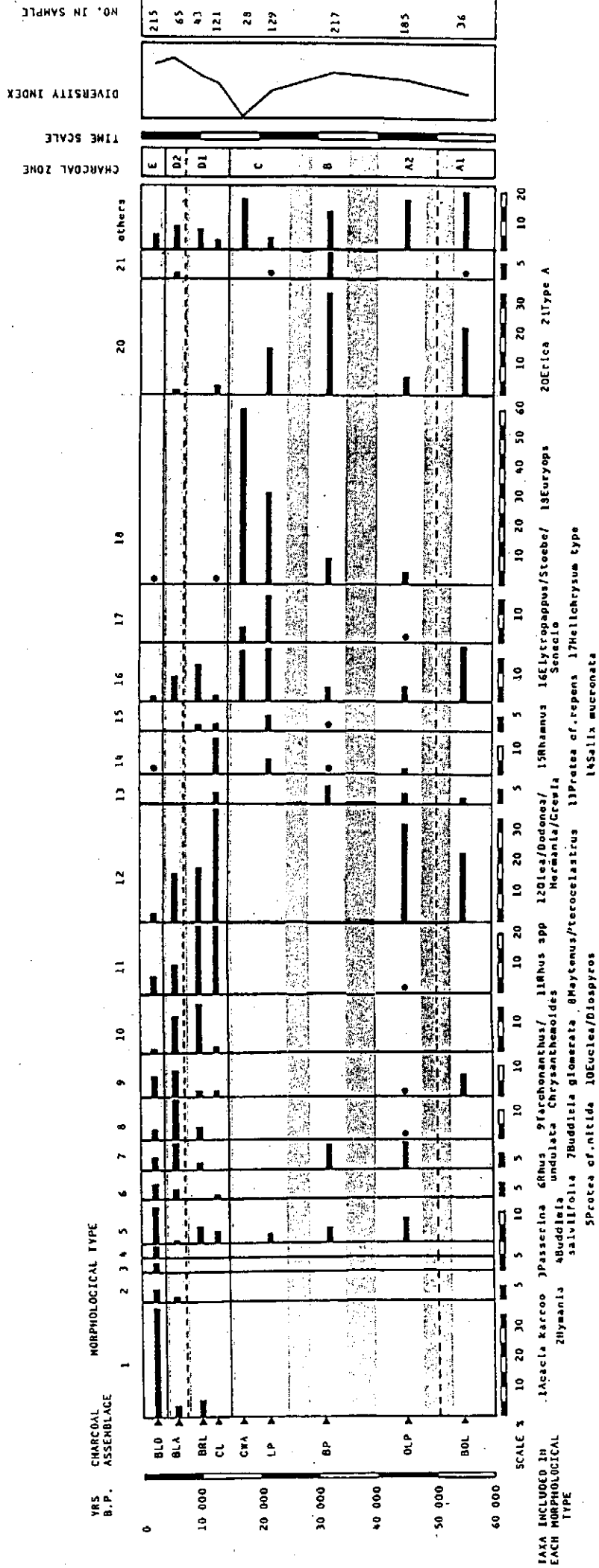


Fig. 3.2 The relative abundances of morphological types in nine assemblages from Boomplaas Cave



TYPE 2 Nymania capensis (Fig.3.3.3)

Medium sized to small vessels arranged in radial and oblique multiples, mostly more than four cells long, producing a sinuous radial pattern ; short, tangential vessel arrangements also occur; uniseriate rays.

TYPE 3 Passerina (Fig.3.3.4)

Sinuuous, oblique, radial and tangential arrangement of vessels and vessel clusters; sparse, confluent paratracheal and sometimes terminal parenchyma; relative to type 2, much more prominent 'background' fibre tissue consisting of small, uniformly sized fibre cells; uniseriate rays, often difficult to observe in transverse section.

TYPE 4 Buddleia salviifolia (Fig.3.3.5)

Vessels medium-sized, in radial multiples up to seven cells long, but also solitary; scanty parenchyma; rays 1-3 cells wide; relatively thick walled fibres in late wood and relatively more axial parenchyma in early wood.

TYPE 5 Protea nitida (Fig.3.3.6 & 3.3.7)

Large solitary vessels with no tangential arrangement; large multiseriate rays interspersed with the odd uni-seriate ray.

TYPE 6 Rhus cf. undulata (Fig.3.3.8)

Vessels smaller than type 11 (Rhus spp.); distinct

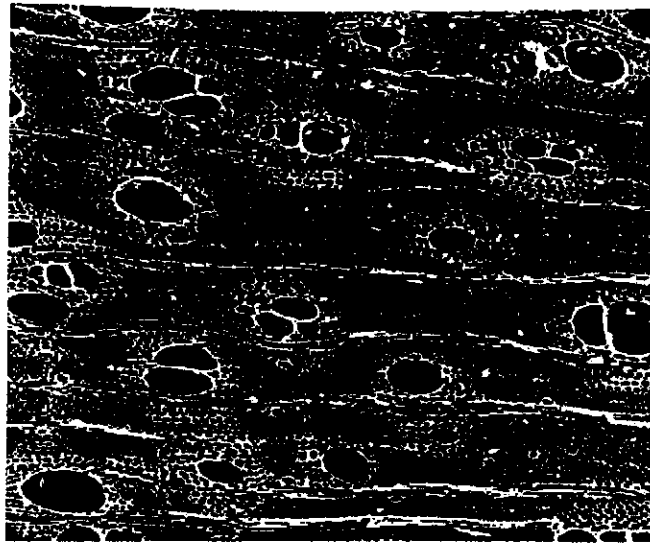


Fig.3.3.1 MTL Acacia karroo (mature wood)



Fig.3.3.2 MTL Acacia karroo (twig-sized branch)

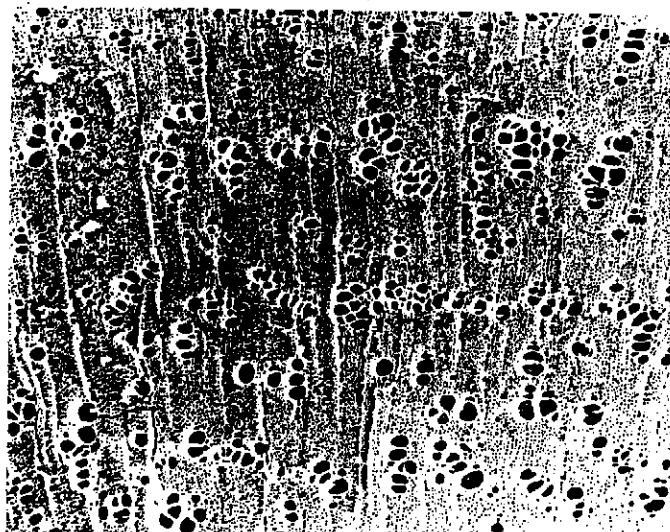


Fig.3.3.3 MT2 Nymanina capensis

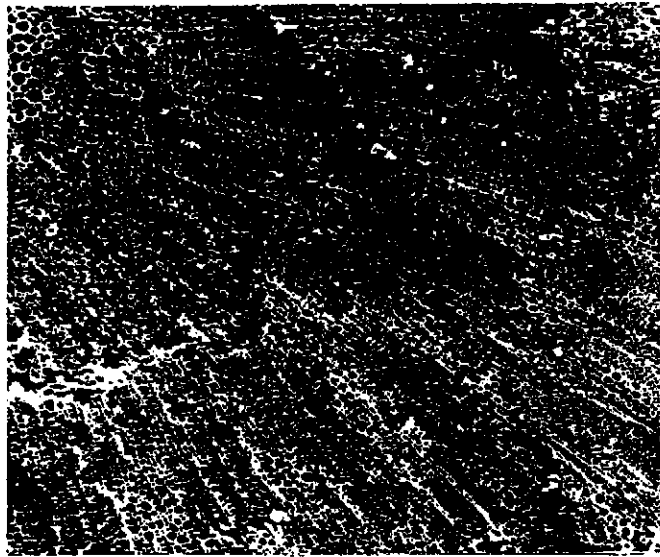


Fig.3.3.4 MT3 Passerina

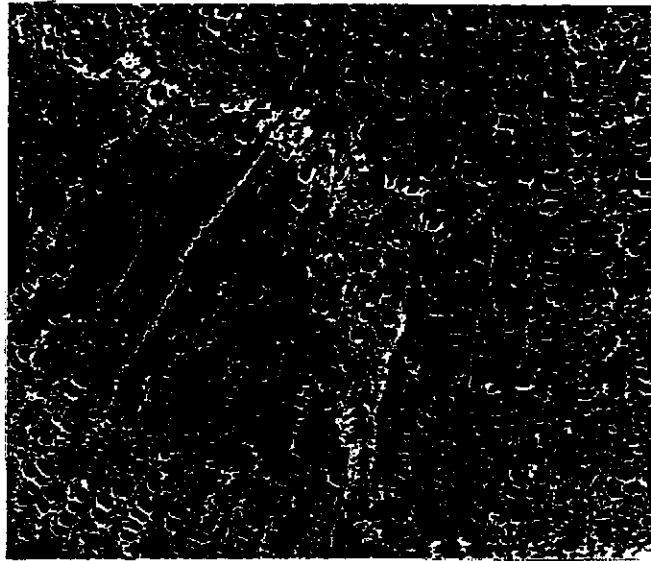


Fig.3.3.5 MT4 Buddleia salviifolia

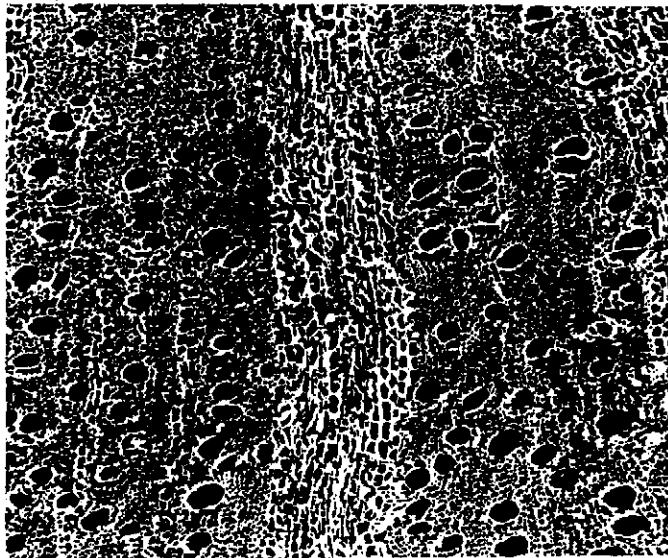


Fig.3.3.6 MT5 Protea nitida (mature wood)

radial arrangement of solitary vessels and short radial multiples; axial parenchyma, scanty paratracheal; rays uni-seriate; semi-ring porous.

TYPE 7 Buddleia glomerata (Fig.3.3.9)

Numerous small solitary vessels, sometimes in short tangential multiples; areas of crowded, relatively large vessels or uniseriate vessel strings; vessels also in tangential arrangement; growth rings prominent; rays uniseriate and biseriate with relatively large isodiametric cells.

TYPE 8 Maytenus/Pterocelastrus (Fig.3.3.10)

Medium to small-sized solitary vessels; axial parenchyma apotracheal, tangentially banded and four cells or more wide; rays uniseriate with isodiametric cells prominent in transverse section.

TYPE 9 Tarchonanthus/Brachylaena/Chrysanthemoides  
(Fig.3.3.11)

This group is as a whole characterised by an open reticulate structure formed by uniformly medium-sized vessels arranged in radial multiples and uniseriate lines of square ray cells; some tangential arrangement of vessels and apotracheal axial parenchyma; scanty, diffuse para-tracheal parenchyma.

TYPE 10 Euclea/Diospyros (Fig.3.3.12)

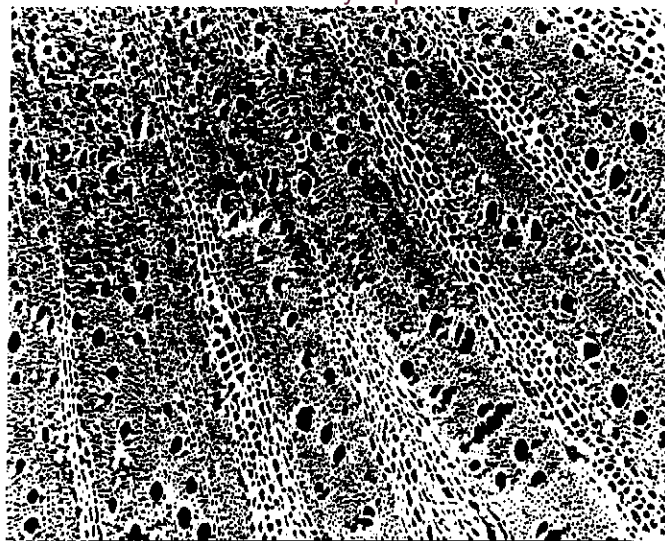


Fig.3.3.7 MT5 Protea nitida (twig-sized branch)

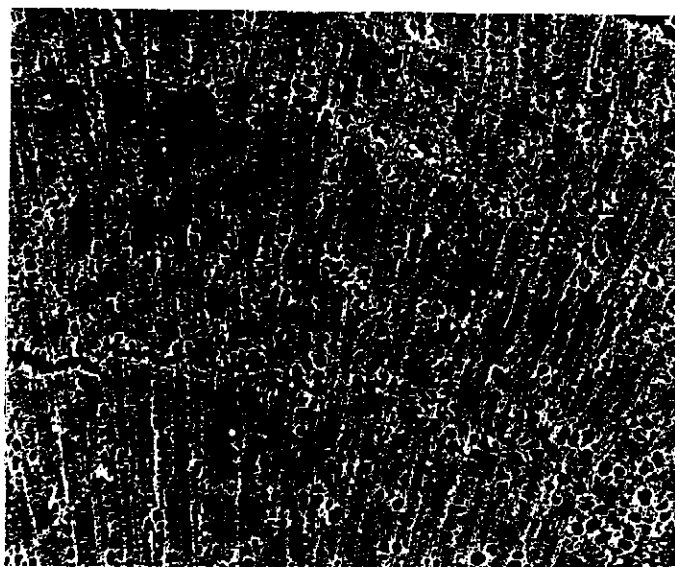


Fig.3.3.8 MT6 Rhus cf. undulata

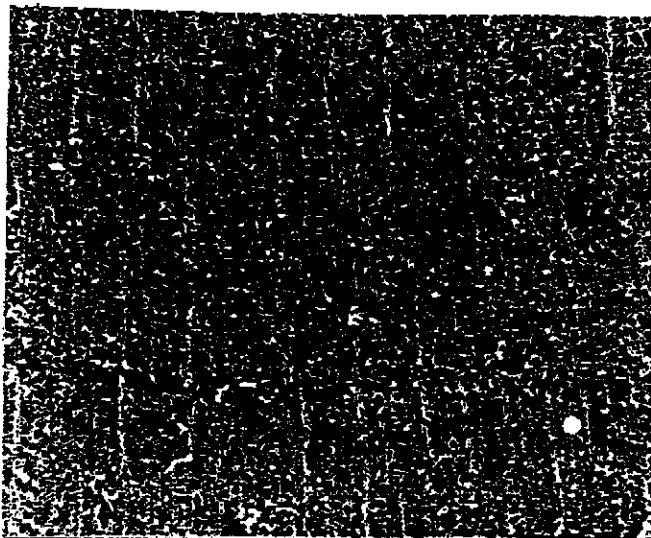


Fig.3.3.9 MT7 Buddleia glomerata

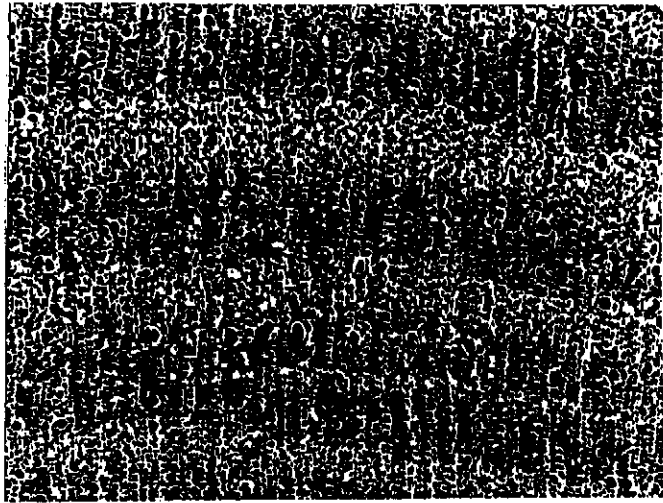


Fig.3.3.10 MT8 Maytenus/Pterocelastrus

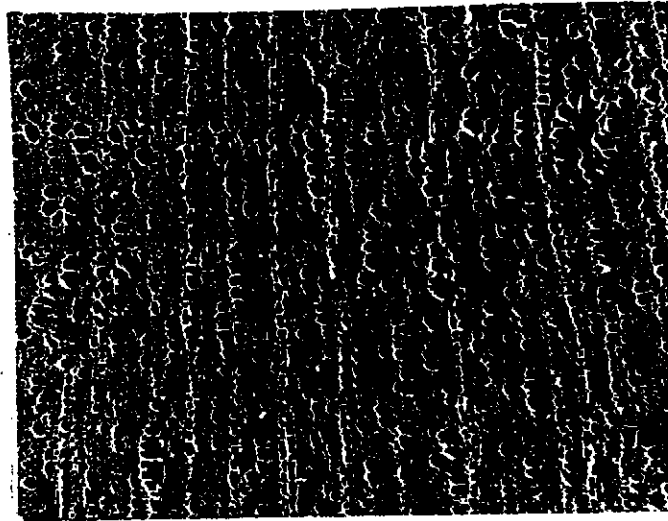


Fig.3.3.11 MT9 Tarchonanthus/Brachylaena

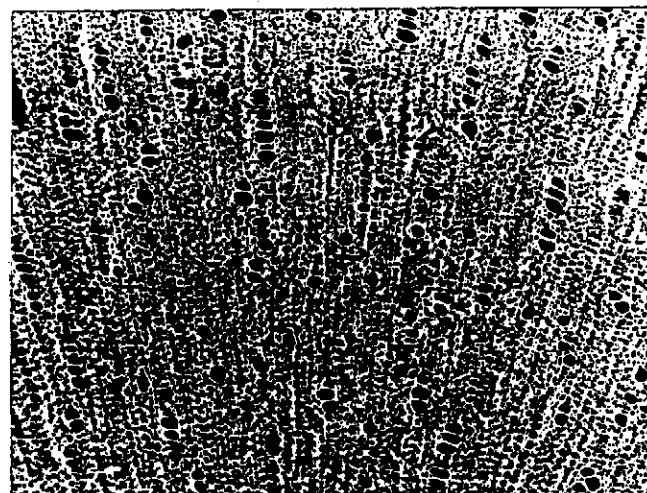


Fig.3.3.12 MT10 Euclea/Diospyros

The most prominent feature of this type is the fine reticulate structure caused by the diffuse, mainly apotracheal distribution of numerous thin walled axial parenchyma cells and radial vessel multiples against a background formed by a dense matrix of tiny fibre cells; vessels medium sized; parenchyma sometimes in small aggregates.

TYPE 11 Rhus spp. (Fig.3.3.13 & 3.3.14)

Medium to large, mostly solitary vessels; also occasional short radial multiples; uniseriate rays indistinct in transverse section; long vessel elements; resin canals almost always visible in tangential section; variation in size of fibre cells causes tangential structures (sub-growth rings).

TYPE 12 Olea/Dodonea/Grewia/Hermania (Fig.3.3.15 & 3.3.16)

It is difficult to separate these four taxa, especially the first two, on transverse section alone. Where tangential sections were available (levels OLP and BOL) Olea was positively identified.

Medium sized vessels, mostly solitary with some radial doubles and triples. In Olea the rays are usually distinct in transverse section and single radial vessel lines alternate with single rays; rays are less distinct and may be farther apart in Dodonea so that more than one radial vessel line appears between rays; in Olea, ray parenchyma consistently more prominent in both transverse

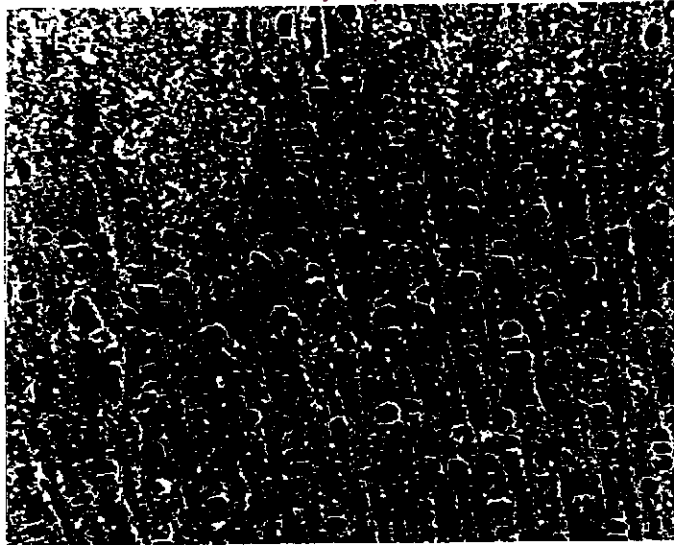


Fig.3.3.13 MT11 Rhus spp.

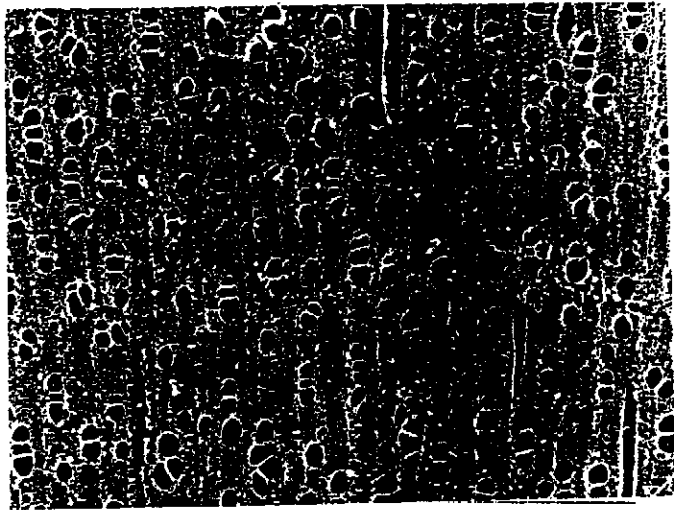


Fig.3.3.14 MT11 Rhus spp.

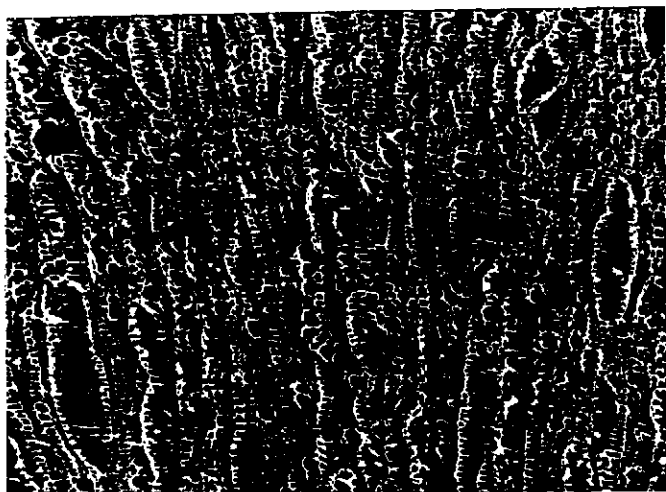


Fig.3.3.15 MT12 Olea/Dodonea



and tangential sections; radial structures caused by alternating bands of thick walled fibres and thin walled ray parenchyma are prominent in Olea, comparatively, the xylem structure of Dodonea is more uniform in the tangential direction; rays are homogeneous in Dodonea, and of the heterogeneous, types II and III in Olea; upright ray end cells (uniseriate) are most prominent in Olea with markedly smaller procumbent cells forming biseriate sections, while in Dodonea rays may be more than biseriate; Grewia and Hermania are not as robust woods (see figures for density in Kromhout 1975) with generally more axial parenchyma and tangential aggregates present.

TYPE 13 Protea/Leucadendron (Fig.3.3.17 & 3.3.18)

Medium to large sized vessels with tangential arrangement of growth rings always apparent; ring, or, semi-ring porous; broad, multiseriate rays; thin walled fibres.

TYPE 14 Salix mucronata (Fig.3.3.19 & 3.3.20)

Abundant medium to large very uniformly sized vessels, solitary, or in short radial multiples; uniseriate rays with elongated procumbent cells.

TYPE 15 Rhamnus (Fig.3.3.21)

Oblique, radial arrangement of vessels and short radial multiples form a dendritic pattern; biseriate

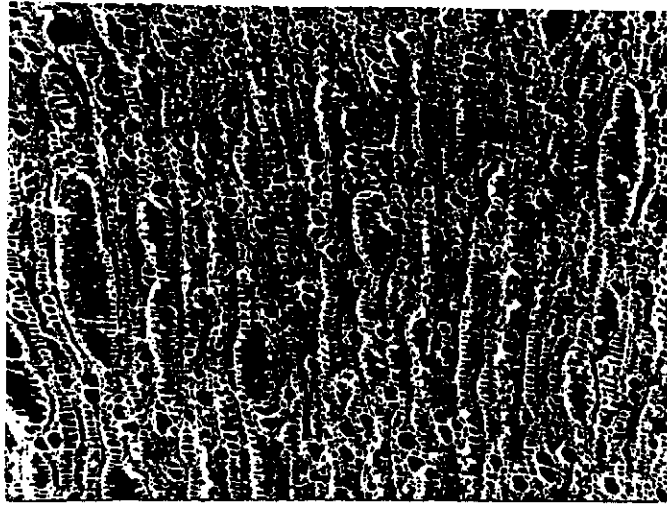


Fig.3.3.16 MT12 Olea/Dodonea

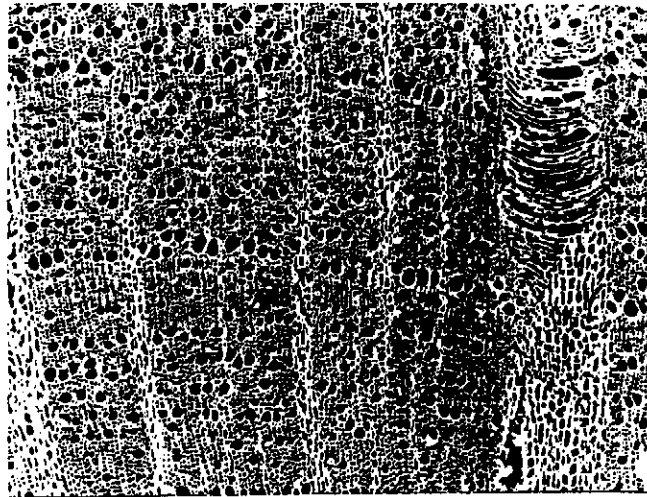


Fig.3.3.17 MT13 Protea/Leucadendron



Fig.3.3.18 MT13 Protea/Leucadendron

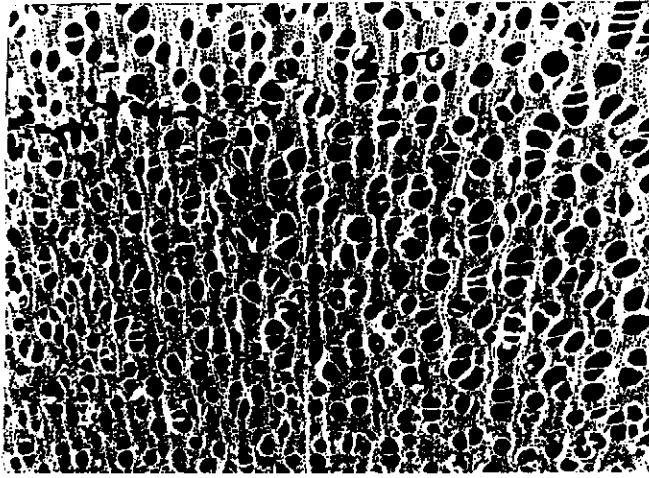


Fig.3.3.19 MT14 Salix

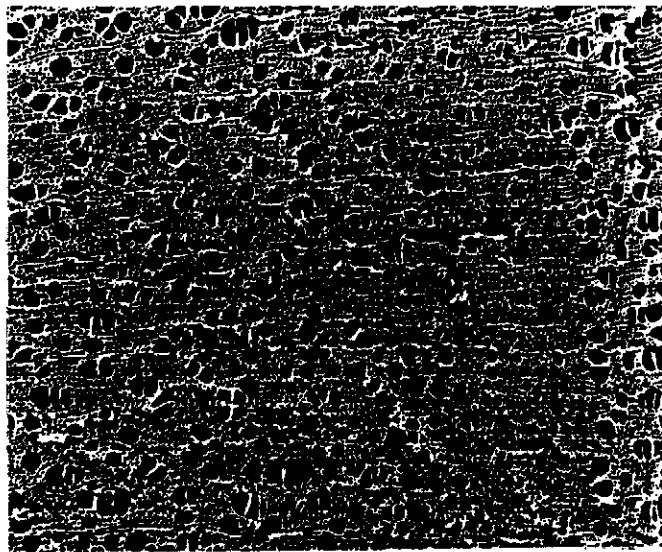


Fig.3.3.20 MT14 Salix

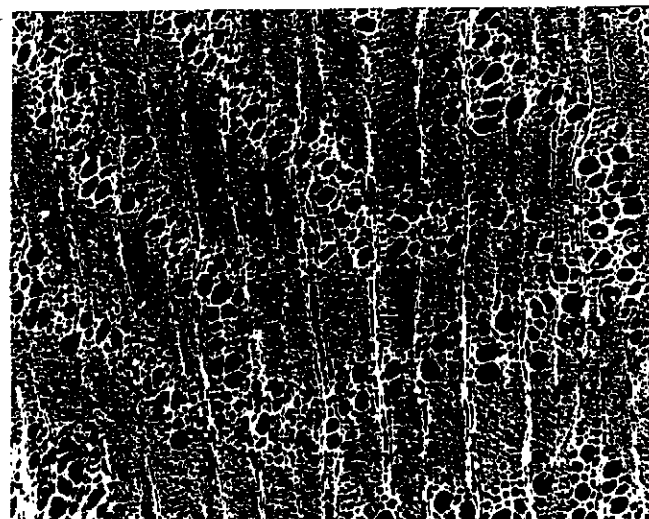


Fig.3.3.21 MT15 Rhamnus

paratracheal parenchyma emphasises this pattern.

TYPE 16 Elytropappus/Stoebe/Senecio/Metalasia

a. Elytropappus/Stoebe (Fig.3.3.22)

Wavy and dendritic tangential arrangement of abundant small tracheary elements interspersed with bands of thick walled fibres; rays absent; occasional single, extremely broad, multiseriate to chaotic rays occur.

b. Senecio/Metalasia (Fig.3.3.23)

Distinct vessel clusters relatively more common than in the Elytropappus type, often with larger central vessels; wavy tangential arrangement of vessels less prominent; uni- and biseriate rays more common and regularly spaced.

TYPE 17 Helichrysum (Fig.3.3.24)

Medium to small solitary vessels with classic growth ring structure often prominent; broad, multiseriate rays; diffuse scanty parenchyma.

TYPE 18 Euryops (Fig.3.3.25 & 3.3.26)

Small solitary vessels or in short tangential multiples; diffuse and marked tangential arrangement of vessels; in subtype 1 tending towards a classical growth ring structure; in subtype 2, an often very regular tangential arrangement of vessels with "peaks" of larger vessels; rays are multiseriate, the norm being 4-5 cells, and in tangential section are not lenticular, but long and parallel sided to continuous, with separate rays

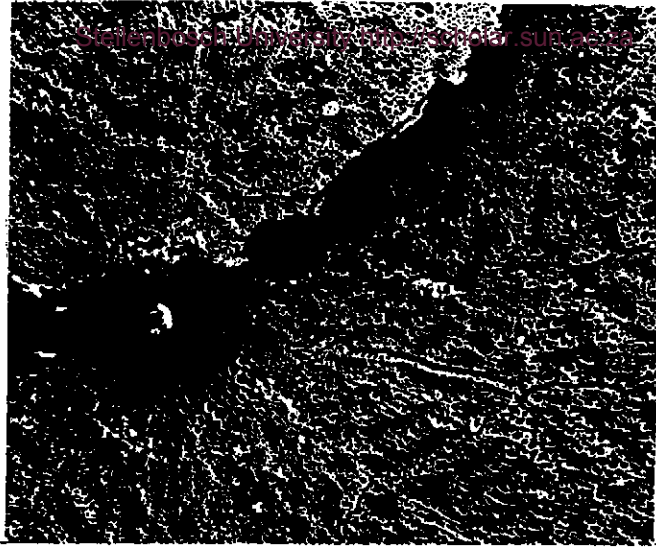


Fig.3.3.22 MT16 Elytropappus/Stoebe

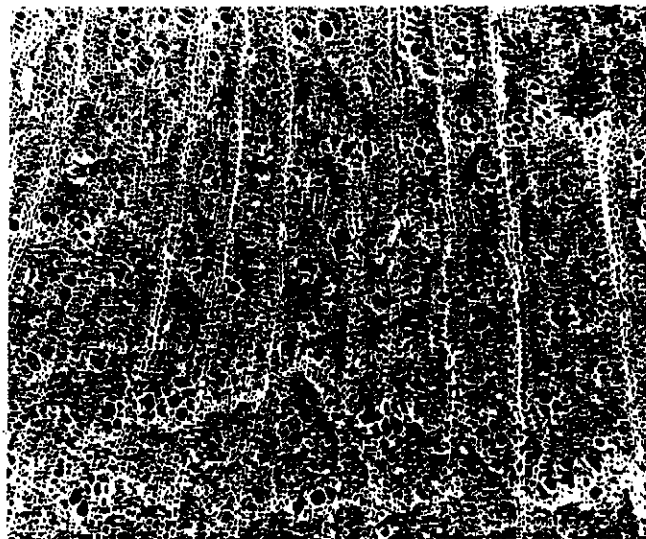


Fig.3.3.23 Senecio/Metalasia

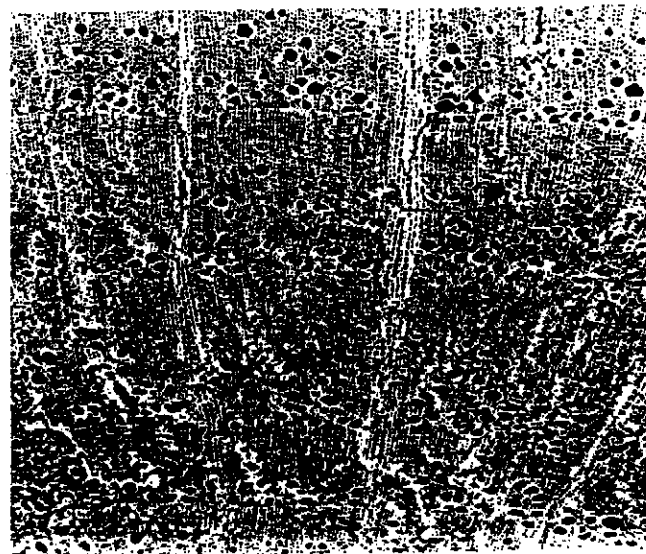


Fig.3.3.24 MT17 Helichrysum

marked only by fibre "crossovers"; scanty apotracheal parenchyma.

TYPE 20 cf. Erica (Fig.3.3.27).

Characterised by large, uniformly sized, solitary vessels, uniform sized thin walled fibres and multi-seriate (4-5 cells wide) rays with elongated procumbent ray parenchyma cells.

### RESULTS AND INTERPRETATION

Table 3.2 summarises the inferences based on the analysis of other categories of archaeological material from the Boomplaas sediments for palaeo-vegetation and climates. The discussion below follows the definition of charcoal zones in Fig.3.2.

ZONE A: ASSEMBLAGES BOL and OLP ca 60 000-35 000 B.P.

The zone is characterised by high values of MT 12 (Olea/Dodonea), MT 16 (Elytropappus-type) and MT 20 (cf. Erica). This combination is unique. Crucial to interpreting this evidence is an understanding of the ecological significance of Olea. Note that in assemblages BOL and OLP tangential and transverse sections were available and the identification of Olea europaea subsp. africana is positive. Boucher (pers.comm.) reports that the present day distribution of this very widespread and plastic species may be more limited by a temperature rather than a rainfall factor. The occurrence of high percentages of Olea in zone A suggests a similarity with

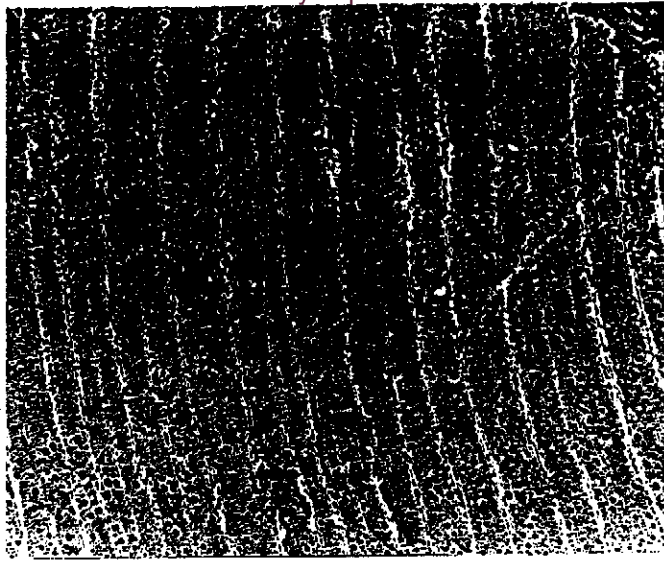


Fig.3.3.25 MT18 Euryops, type 1

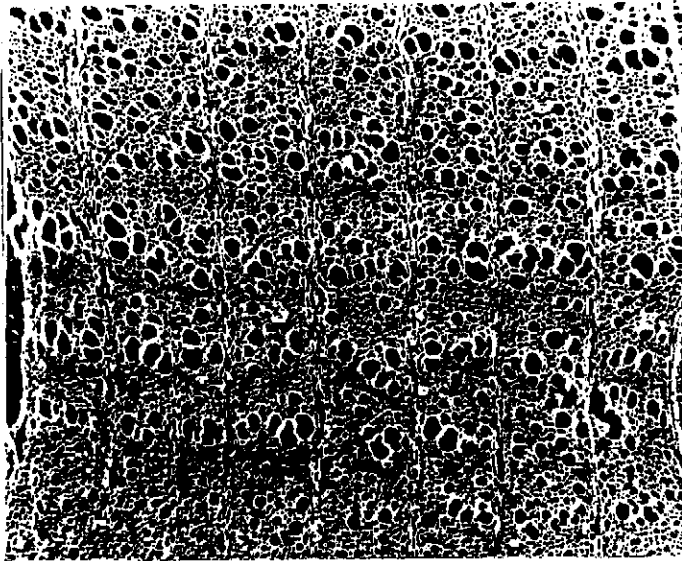


Fig.3.3.26 MT18 Euryops, type 2

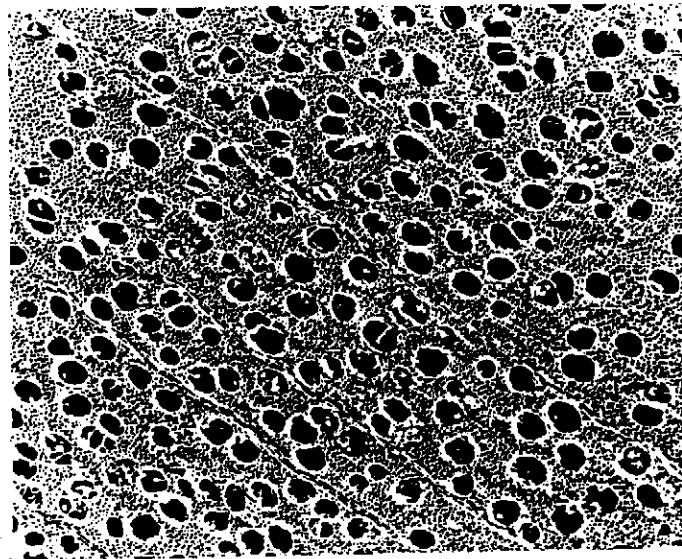


Fig.3.3.27 MT20 Erica

Table 3.1 Summary of palaeoclimatic inferences drawn from other lines of evidence (\*after Deacon et al 1984, \*\*after Avery 1982, \*\*\*after Klein 1983)

ASSEMBLAGE AND DATING	ARCHAEOLOGICAL EVIDENCE*	MICROFAUNA**	MACROFAUNA***
BLD 2000 B.P.	impersistent low density scatters of artefacts, faunal remains and plant debris; storage pits; cave occupied for short periods or days		dominant browsing fauna indicates dense vegetation
BLA 6000 B.P.	a series of elongated, charcoal filled features occurred in this level and may be related to smoking of meat	similar conditions to the present, shrubland or bush dominant; extensive, dense riverine vegetation with trees; climate more xeric around 9000 B.P.	
BRL 10 000 B.P.	the evidence suggests a series of short term occupations		mixed browsing and grazing fauna
CL 13 000 B.P.	'processor economy'; a thick occupation deposit without discontinuities and a high density of faunal remains and artefacts suggests long term occupation	dense vegetation extends onto the hillsides at the expense of grassland; semi arid shrub restricted to hillsides, some increase in temperature relative to LP	grazing fauna (equids, a celaphines) dominant indicating grassland
LP 22 000 B.P.	a well developed occupation complex indicates that during LPC the cave was used relatively infrequently	severe climate, cold and dry with at least very cold winters; grass on the hillsides and grassland and semi-arid shrub on the valley floor; dense riverine vegetation reduced to a minimum	
BP 32 000 B.P.	'processor economy'; well developed occupation complex; environment more productive than during OLP or BOL times		stronger representation of alcelaphines
OLP ca. 45 000 B.P.	low site usage and low productivity of the environment; 'traveller economy'	moderate climate; grass and semi-arid shrubland on the hillsides; an extension of dense vegetation on the valley floor	mainly a browsing fauna
BOL ca. 55 000 B.P.	ditto	open vegetation, cold climate; semi-arid shrubland on valley floor; grass on hillsides	mainly a browsing fauna



the climate of the end Pleistocene and early Holocene, zone D (CL-BRL). However, in this latter zone a variety of other tree and shrub taxa are also represented, e.g. Acacia, Rhus, Euclea.

What specific climatic conditions caused the harsher climate of Zone A relative to Zone D cannot be specified, but it is likely that both precipitation and temperature factors were involved. Zone A covers a long period of time during which numerous climatic oscillations or changes of longer duration may have occurred. The small size of the BOL sample and the apparent low order of change do not allow significance to be attached to the differences between OLP and BOL. The evidence from the microfauna indicates a cold climate and semi-arid shrubland on the valley floor (Table 3.2).

ZONE B: ASSEMBLAGE BP ca 33 000-26 000 B.P.

This zone is distinguished from zone A by the absence of MT 12 (Olea/Dodonea) and the dominance of MT 20 (cf. Erica). As suggested in the preceding discussion, low temperatures may limit the distribution of Olea. The low relative abundance of shrubby Compositae (MT 16, 17, 18) separates this zone from the subsequent Zone C.

Due to uncertainty about the specific identification of MT 20 the interpretation of the palaeoclimatic significance of the zone is problematic. If indeed an erica-

ceous taxon is represented by MT 20 and was a large component of vegetation on the south slope of Drupkelderkop, this could perhaps be taken to indicate alpine conditions. If, on the other hand, the ericaceous taxa/taxon were growing close to the river, or on marshland in the valley (the habitat of the widespread Erica caffra for example), the high relative abundance of MT 20 would suggest that little woody vegetation was present on the hillside in the vicinity of the cave. This would imply that the hillsides were dominated by grassland or other herbaceous vegetation. An ecoclimatic factor which can help to enforce grassland is low temperatures. Both the above scenarios suggest cold conditions. No tree taxa, apart from the ubiquitous Protea nitida, are recorded in the B.P. assemblage.

ZONE C: ASSEMBLAGES LP/LPC and GWA ca 26-16 000 B.P.

The interpretation of the MTRAA evidence for these zones is less problematic. The LP/LPC and GWA assemblages are dominated by a range of shrubby, karroid or subkarroid asteraceous taxa, Elytropappus, Stoebe, Helichrysum, Euryops (MT 16, 17, 18) etc. The Shannon-Weiner index of diversity is low, and no tree taxa are recorded. Cold, but especially dry conditions are clearly indicated. The extreme dominance of MT 18 in GWA is probably caused by the low sample size and the fact that only one hearth could be sampled.

ZONE D: ASSEMBLAGES CL, BRL and BLA ca 14-3000 B.P.

This zone is characterised by the reappearance and consistently high representation of wood of tree taxa (MT 10, 11, 12, 14). Three subzones may be distinguished. D1 (assemblage CL) is characterised by the first reappearance of tree taxa (MT 11 and 12). The shrubby Asteraceae (MT 16, 17, 18), ubiquitous elsewhere in the sequence, are all but absent in this assemblage. Salix mucronata (MT 14) reaches its highest relative abundance in the subzone.

It is inferred that a dramatic change in climate occurred within the 3000 year period, 17-14 000 B.P. This change was in the direction of more mesic conditions. Wood of shrubby Asteraceae is a preferred fuel with the cortex of many taxa rich in resin (Van der Watt pers. comm.) and therefore their low representation in CL may be taken to reflect their rarity in the local vegetation. This feature could be caused either by extreme cold, perhaps associated with high wind speeds, or by a high incidence of fire. Both these conditions would relate to the occurrence of grassland on the exposed hill slopes.

The high relative abundance of Salix could indicate that the river channel lay closer to the northern flanks of the valley; that flood debris provided a regular supply of dry wood; or, as suggested by the last argument, that woody vegetation was rare on the hillside and fire-

wood had to be collected from the river margins and floodplains.

The changes between subzones D1 (CL) and D2 (BRL) are of a low order. MT 1 (Acacia karroo), MT 7 (Buddleia glomerata) and MT 8 (Maytenus/Pterocelastrus) make their first appearance in this subzone, but at low percentages. Their habitat requirements suggest warmer conditions in D2 relative to D1. The relative abundance of Salix declines, the river margin was perhaps no longer a focus for firewood gathering, and MT 16 (Elytropappus-type) once again forms a major component. This evidence suggests a denser woody vegetation and a greater diversity of species, but especially more woody vegetation on the hillside in the vicinity of the cave. Relative to the climatic conditions inferred for D1, the climate of D2 may be less harsh, but what the level of precipitation of CL relative to BRL was, is unclear. The high relative abundance of MT 14 may indicate flooding or extension of a riverine habitat, but may also indicate higher annual precipitation during CL times (subzone D1).

The differences between subzones D2 and D3 are also of a low order and their ecological significance is obscure. Three groups of taxa with thicket associations, Tarchonanthus (MT 6), Euclea/Diospyros (MT 7) and Maytenus/Pterocelastrus (MT 8) reach their maximum relative abundances in this zone and the diversity index is at a maximum. It may be inferred that a thickening up of woody vegetation occurred. This might relate to warm and wet conditions, but all the taxa concerned tolerate a dry

season.

ZONE E: ASSEMBLAGE BLD ca 3000-PRESENT

This zone is characterised by an overwhelming dominance of Acacia karroo (MT 1) and maximum values for Passerina (MT 3), Buddleia salviifolia (MT 4), Rhus cf. undulata (MT 6) and Nymania (MT 7). Together these suggest warm and relatively dry conditions.

DISCUSSION

The inferences made above are informal and relatively obvious constructs placed on the evidence. They require little further discussion. However, in a more rigorous sense, interpreting the relative abundance of types of wood occurring in charcoal assemblages involves consideration of a range of factors and discussion of these is required. For present purposes, issues such as choice of sampling strategy, which are involved in establishing a reliable measure of relative abundance for an assemblage, are ignored (they are discussed in Deacon H.J. 1979 and Tusenius 1986).

In reconstructing a vegetation and a climatic history from MTRA-type data, two sorts of assumptions have to be made. Firstly, that people (the agent of deposition) will to an extent sample woody vegetation randomly. This assumption can be broken down into two

different assumptions; 1) that people collect the range of wood that is available (only) according to the principle of least effort (Tusenius 1986) and 2) that firewood will always be collected in the same manner, i.e. that environmental, social or cultural factors do not play a significant role in determining how charcoal is procured. Secondly, that the site of deposition, in this case a cave, will receive uniform input through time from the agent of deposition, i.e. that social, cultural or environmental factors will not differentially affect the use of a cave through time.

The set of factors involved in the first assumption are discussed in Chapter 6. The relative abundance of woody taxa represented in a charcoal assemblage cannot be taken to reflect the composition of a vegetation. This is so both because the natural supply of dry wood does not faithfully record the composition of live woody vegetation and because various factors affect how people procure and use firewood. The factors involved in determining a natural spectrum of dry wood include, inter alia, differences in tree and shrub shooting strategies and the effects of age of vegetation, drought and fire on the supply of dead wood. The factors affecting human exploitation of the firewood resource include the relative quality of different woods, the size spectra of dead branches, the intensity of exploitation of the natural supply and the various domestic uses of fire.

The first assumption can therefore not be made. It is possible both that considerable environmental change might take place without this being reflected in collections of firewood and that changes in exploitation patterns could alone produce changes in the composition of collections of firewood. In a general sense however, MTRA-type evidence reflects what woody material was available at a certain time and gross environmental change should be reflected in changes in the composition of the charcoal assemblages recovered from fossil hearths.

In the context of attempting to reconstruct a vegetation or climatic history for a region the second assumption, viz. that the site of deposition receives a uniform input from the agent of deposition through time, is more crucial. Once again cultural/social and environmental factors need consideration. In terms of the present study it is known that at one stage Boomplaas Cave functioned as a stock post (CBM), at another time as a storage pit facility (BLD) and in BRL as a focus for meat drying processing (Deacon H.J.1979; Deacon et al 1983; Deacon et al 1984). It is not known whether these different functions imply importantly different firewood procurement patterns.

In terms of environmental factors, the possibility arises that a climate-related factor might affect the occupation or use of a cave. Ethnographic evidence on the hunter-gatherer life-style (Lee 1979; Silberbauer

1981) as well as other life-styles (Ashton 1952; Best 1979; Jelenic & Van Vegten 1981; Archer in prep.) record that indigenous people will seek shelter from inclement weather by using topographic features, vegetation, natural or man made shelters. There is some evidence from the archaeological record that Boomplaas Cave may have been used consistently only during periods of harsh climates. EDXA analysis (Fig.5.3) provides relative measures of precipitation and temperature for periods of human occupation of the cave, whereas the microfaunal evidence provides a more continuous recorded. Summary statistics based on factor analysis of the microfaunal evidence (Thackeray in Deacon et al 1984) indicate both periods of relatively xeric and relatively mesic climates during the time span of member BP, while the charcoal evidence suggests occupation only during a period of harsh climates. Similarly, a correlation of the evidence from the Boomplaas and Norga sites suggests that in the late Holocene Boomplaas Cave may only have been occupied during a short period of relatively adverse climates.

The evidence is not strong. Stratigraphic and contextual problems have not been thoroughly considered, but any suggestion that climatic factors may determine whether a cave will be occupied or is of particular importance to the range of studies aimed at reconstructing the climatic history of a region from analysis of material transported to the cave by humans.



It may be that the archaeological record contained in cave sediments is biased in favour of certain weather conditions.

Changes in climate could influence human occupation of a particular site indirectly through affecting the accessibility of a site. For instance, dense shrub vegetation on hillslopes rather than more open grassy vegetation will hinder access to a cave. There are so few studies on contemporary habitation of caves (see Solecki 1979), especially in the southern African context, that it is at present impossible to evaluate the importance of factors such as these.

For the same reason it is not possible to evaluate the relevance of the following point to the understanding of cave occupation. Some ethnographic evidence suggests that caves might be used only infrequently. Archer (in prep.) reports that accumulations of plant food debris and old bedding material quickly attract an array of stinging insects. Even in open site situations people take care to avoid this by regular sweeping of areas close to their homes. It is likely that this factor would operate more effectively in the moister confines and half light of a cave and for this reason it can be suggested that, all other things being equal, camping in caves may have been avoided.

Finally, interpreting MTRAA-type evidence is based upon extrapolating from knowledge of the present day

ecoclimatic ranges of plant taxa. Apart from problems with achieving specific identifications and the fact that the woody taxa recorded in charcoal assemblages are often plastic, generalist species, current knowledge about which precise ecoclimatic variables control the distribution of plant species is poor. A better knowledge about the correlations between the distribution of plant taxa and ecoclimatic variables will allow more confident interpretation of evidence about the composition of past woody vegetation.

In the Boomplaas sequence gross changes in the percentage representation of species occur, notably between assemblages CL and GWA, assemblages BP and OLP and assemblages BLA and BLD. These changes must reflect changes in climate and are readily interpretable. Because of the factors mentioned above the interpretation of lower order changes is problematic. Until more is known from ethnoarchaeological studies about the relationship between the composition of firewood collections and of woody vegetation, only relatively obvious inferences about past woody vegetation and climates will be justified on the basis of MTRA-type alone. However, MTRA-type analysis remains the basic form of charcoal analysis in that the ability to make good use of other forms of analysis rely on some previous identification of material. MTRA-type analysis should therefore be evaluated as one component of charcoal analysis, the other

components being xylem analysis (Chapters 4 & 5) and analysis of the size class distribution of the diameters of the branches from which pieces of charcoal were derived (Chapter 6).

#### REFERENCES

- ARCHER, F. in prep. An ethnographic study of the edible plants of Namaqualand.
- ASHTON, H. 1952. The Basotho. Oxford University Press. Oxford.
- AVERY, D.M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum 85:183-374.
- BEST, M. 1979. The scarcity of domestic energy: a study in 3 villages. SALDRU working paper no.27, University of Cape Town.
- DEACON, H.J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10:241-257.
- DEACON, H.J., A. SCHOLTZ & D.L. DAITZ 1983. Fossil charcoals as a source of palaeoecological information in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis: 174-182, SANSPR 75, Pretoria
- DEACON, H.J. DEACON, J., SCHOLTZ, A., THACKERAY, J.F. & BRINK, J.S. 1984. Correlation of the palaeoenvironmental data from the late Pleistocene and Holocene deposits at

- Boomplaas Cave, southern Cape. IN: J.C. Vogel (ed) Late Cainozoic Palaeoclimates of the southern hemisphere:339-351. Balkema, Rotterdam.
- DEACON, J.C.G. 1982. The Later Stone Age in the southern Cape, South Africa. Ph.D thesis, University of Cape Town.
- JELENIC, N.E. & VAN VEGTEN, J.A. 1981. A pain in the neck: The firewood situation in south-western Kgatleng, Botswana. NIR research note 5, University of Gaborone, Gaborone.
- KLEIN, R.G. 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis:116-138. SANSPR 75 Pretoria.
- KROMHOUT, C.P. 1975. 'n Sleutel vir die mikroskopiese uitkenning van die vernaamste inheemse houtsoorte van Suid-Afrika. Departement van Bosbou Bulletin 50:1-140.
- LEE, R.B. 1979. The !Kung San. Cambridge University Press, Cambridge.
- MOFFETT, R.O. & DEACON, H.J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Cango Valley. South African Archaeological Bulletin 32:127-145.
- SILBERBAUER, G.B. 1981. Hunter and habitat in the central Kalahari Desert. Cambridge University Press, Cambridge.
- SHIMWELL, D.W. 1971. The description and classification of vegetation. Sidgewick and Jackson, London.

SOLECKI, R.S. 1979. Contemporary Kurdish winter-time inhabitants of Shanidar cave, Iraq. World Archaeology 10:318-330.

TUSENIUS, M. 1986. Charcoal analytical studies in the north-eastern Cape. Unpublished M.A. thesis, Department of Archaeology, University of Stellenbosch.

WEBLEY, L. 1979. A sedimentological analysis of the Boomplaas Cave sequence. Unpublished Hons. project, Department of Archaeology, University of Stellenbosch.

C H A P T E R F O U R

ECOLOGICALLY DIAGNOSTIC XYLEM ANALYSIS: THEORY AND  
METHODOLOGY

I N D E X

ABSTRACT

INTRODUCTION

INTEGRATED AND COMPARATIVE PLANT ECOPHYSIOLOGICAL/  
ANATOMICAL STUDIES

BASIC PROBLEMS AND GENERAL CONSIDERATIONS

METHODOLOGY

    General description

    Direct measurements

    Calculated variables

    Indices

    BASIC Program EDXA2

THE DIAGNOSTIC VALUE OF VARIABLES

EDXA AND TAXONOMIC/ECOLOGICAL WOOD ANATOMY

EDXA AND EXPERIMENTAL BOTANY

EDXA AND DENDROCLIMATOLOGY: CONTRASTING TWO APPROACHES TO  
THE DIAGNOSIS OF PAST CLIMATES FROM WOOD ANATOMY

CONCLUSIONS

REFERENCES

ABSTRACT

This chapter describes the basic methodology of a

computer based approach to quantitative and comparative wood anatomical studies. The methods of obtaining measurements from an image of the transverse section of a piece of wood, including a point counting method for counting the areas of the various tissues found in xylem and the measurement of radial and tangential diameters of vessels, are described. These measurements are input into a computer and program EDXA2 then calculates, outputs and manipulates a range of wood anatomical variables and indices. The formulae used in the program are described and the significance of the variables and indices is discussed. Attention is focussed on the use of the variable of relative conductivity (RELV) in measuring the ability of xylem tissue to transport water, on various ways to analyse the size distribution of elements of the tracheary system and on the potential value of indices in correlating wood anatomical and ecoclimatic variables.

The EDXA-type approach is compared to the traditional approaches of ecological wood anatomy and, as a method to reconstruct past climates from the analysis of wood anatomy, to the approach of dendroclimatology. Since EDXA is based on the analysis of variables more basic than tree-ring widths and on qualitative changes in wood anatomy rather than on changes in the quantity of wood produced per time unit, it is argued that the the EDXA approach will produce more reliable data than dendroclimatology in the analysis of the wood of temperate and subtropical hardwoods.

## INTRODUCTION

This chapter describes the methodology of a computer based approach to quantitative and comparative wood anatomical studies. The approach contributes towards the study of the relationships between plant anatomy, physiology and ecology and, since it developed out of a consideration of how the anatomy of fossil wood might be used to infer past climates, has been termed Ecologically Diagnostic Xylem Analysis (EDXA). EDXA is not designed to describe the anatomy of a particular piece of wood in any comprehensive sense, but rather to measure a wide range of the functionally significant wood anatomical variables which are observable in transverse section.

In the first section of the chapter the need for comparative and integrated research into plant ecophysiology/anatomy is emphasised. In the next section, three problems encountered in research in ecological wood anatomy, namely that of the generally low level of comparability of descriptive wood anatomical data, that of the integrity or indivisibility of xylem tissue, and that of the variability of wood anatomy are discussed in order to introduce EDXA as an approach aimed at resolving these problems. Subsequently, the methods used in EDXA are described under the headings:- (a) general considerations, (b) variables directly measured, (c) calculated variables, (d) indices and, (e) software. The section on methods is concluded by a discussion illustrating the diagnostic value of selected variables.



The last three sections of this chapter review the relationship of EDXA to traditional taxonomic/ecological wood anatomy, experimental plant physiology and dendroclimatology. Since, as already stated, the EDXA approach developed out of a consideration of how the anatomy of fossil wood might be used to infer past climates, the relationship between dendroclimatology and EDXA is discussed in some detail.

#### THE NEED FOR INTEGRATED AND COMPARATIVE PLANT ECOPHYSIOLOGICAL/ANATOMICAL STUDIES

During the latter part of the last and the early years of this century, the studies of comparative plant physiology and ecological anatomy were active and promising fields of research (Baas 1982). However, the study of these fields did not develop in as integrated a fashion as was anticipated. A contributory factor was the work of Maximov (1929, 1931)(Mooney 1974:115). He demonstrated that desert plants can transpire freely and thereby invalidated what had become an implicit law of ecophysiology, namely, that the anatomy of xerophytes was designed to prevent loss of water. It was probably not merely in invalidating a single correlation between anatomical, physiological and ecological variables (APE variables), even if this correlation had been almost symbolically clear, that Maximov's results threatened a program of research. The wider implication of his results was that, since there was no simple relationship

between plant anatomy and physiology, research in the sciences of comparative plant physiology and ecological anatomy should be decoupled. It was clear that a general understanding of the relations between plant anatomy, physiology and ecology would rest on a more complex synthesis of knowledge than had been previously anticipated.

Yet, Maximov (1931) concluded one of his papers by stating that his data did not entirely contradict the idea that the anatomy (particularly of the leaves) of xerophytes is designed to reduce water loss. By making distinctions between cuticular and stomatal transpiration and transpiration in turgid versus wilting states, these ideas were qualified and a sounder relationship between anatomy and physiology established.

Maximov had been most concerned that plant physiology be given its rightful place, ("..... anatomical investigations should always be followed by physiological experiments in order to show the real correlation between structure and function" (Maximov 1931: 274)). He was less insistent on the related, but different point, that plant form and function should always be studied as part of a single, integrated system. His work was concerned with the external morphology of plants and the measurement of physiological parameters such as transpiration. Even today, this type of data is often not placed in perspective in terms of a more holistic and comparative understanding of the adaptive mechanisms of xeromorphism.

The following example illustrates the point. It is well known that vessel diameter decreases whilst vessel frequency increases with increasing drought (Carlquist 1966, 1977a, Baas 1982). Carlquist (1975) has proposed that this pattern is explained by the ability of narrower vessels to resist greater negative pressures (suction) and by the value of vessel 'redundancy' in enabling tracheary systems to survive a high incidence of vessel disabling, air embolism events. In other words Carlquist suggests that the typical xeromorphic wood anatomy is functionally related to the most adverse conditions the plants must endure. While the xylem of desert plants may fulfil the functions ascribed to it by Carlquist, in the light of Maximov's findings (confirmed by Cunningham & Strain 1969 and Mooney et al 1968), it would be important to understand the role xylem anatomy plays in enabling xerophytes to transpire so freely in the turgid state. Does the xerophyte not make use of its ability to achieve /resist greater negative pressures under conditions of both water surplus and deficit ?

A study by Rundel & Stecker (1977) suggests that narrower conducting elements are, in some ways, more efficient than larger elements under conditions of relative water stress; it is also suggestive that leaf specific conductivity (LSC) is often higher in xerophytes than mesophytes (Zimmerman 1983).

A second obvious example relevant to the lack of understanding of the adaptive mechanisms of xerophytism concerns the relationship between xylem anatomy, high negative pressures and depth of root penetration (Kozlowski 1972:241).

The lack of integration of studies of comparative plant physiology and anatomy has meant that the potential significance of wood anatomy in explaining ecophysiological problems is often overlooked. The following example is illustrative. Australian acacias are aggressive plant invaders in the winter rainfall fynbos biome area of the Cape and for this reason their ecology has been the subject of intensive research (Macdonald & Jarman 1984). The wood anatomy of Acacia cyclops is characterised by the large vessels typical of the genus, with vasicentric parenchyma and unusually thick vessel walls (pers. obs.). This combination of features results in a system optimal for transporting large volumes of water under high negative pressures and it is likely that this feature alone gives these plants a competitive advantage in low lying areas with deep, free draining, sandy soils. In these areas Acacia cyclops can indeed competitively exclude indigenous vegetation, apparently by lowering the water table (Boucher pers. comm.).

A number of themes central to this paper have been raised in the above paragraphs. The plant functions as a unit and its physiology and anatomy, including that of its tracheary system, should be studied accordingly. Yet the first study dealing in detail with the interrelation-

ships between wood and leaf anatomy and plant habit was only recently published (Rury & Dickison 1984). The relationships between APE variables as they occur in nature reveal forceful and prevailing correlations between these variables. The current state of knowledge in regard to quantifying relationships between APE variables, separating the components of phylogenetic and ecological variability (see Novruzova 1968; Akachuku & Burley 1979) and modelling the root, xylem and leaf system, is poor. Nevertheless, many correlations between APE variables are reported in the literature, there are anatomical features to which positive (if sometimes provisional) ecological meaning can be attached and there are hypothetical physiological 'rules' concerning adaptive character syndromes which can help to focus further research.

#### BASIC PROBLEMS AND GENERAL CONSIDERATIONS

The three most basic problems encountered in research in ecological wood anatomy, are that of the low level of comparability of descriptive wood anatomical data, that of the integrity or indivisibility of xylem tissue, and that of its variability. These are discussed in order to introduce the EDXA approach at resolving them.

The first problem concerns the issue of comparability of data, i.e. of basic methodology. Researchers need to measure the same range of variables and measure them in a similar (described) manner in order that their results be comparable (Rendle & Clark 1934). In EDXA the

methods used to obtain measurements are described and the use of the computer helps to standardise the measurement and calculation of variables.

Both conceptually and practically, the fact that in their integration in the xylem the various tissues incorporated affect one another hinders progress in the field of ecological wood anatomy. One anatomical feature may fulfil various functions, different functions at different times or be influenced by more than one ecoclimatic variable. Change in one anatomical variable may also have a significant influence on other anatomical variables. For one thing, the cross sectional area available for the disposition of the various component types of xylem tissue is limited and, despite the exploratory work of Carlquist (1975), no working model of the dynamics of this basic aspect of the system has been developed. In practice however, researchers are often forced to use arguments about the functional balance achieved by combinations of wood anatomical features in coping with the contradictory demands for mechanical strength and optimum sap flow, e.g. Rundel & Stecker (1977) and Carlquist (1978).

The integrity of the tissue and the lack of a mechanical model with which to interpret the functions of the various xylem strategies makes it difficult to relate basic wood anatomical variables to single ecological variables. A particularly important case involves the effects of high negative pressures on xylem anatomy.

Both low soil water potential and low temperatures cause high negative pressures in the tracheary system and result in the development of wood with numerous small vessels and a high density (Carlquist 1975; Baas 1982).

Excluding experimental work where certain variables can be controlled, there are three ways to attempt to distinguish the effects of specific wood anatomical/ecoclimatic relationships on xylem anatomy. One is to measure as full a set of functional wood anatomical variables as possible. From the ecological perspective, it is important that not only mean values, or other summary statistics, but also the more sensitive distribution of dimensions within a tissue be analysed. Only appropriate methods can achieve this latter goal. The second, but related approach, involves using a range of basic wood anatomical variables to construct indices or correction factors of various kinds. These may allow stronger or as yet unsuspected relationships between wood anatomy and ecoclimatic variables to be discovered. This approach demands a practical facility which allows for ease of exploratory data analysis, i.e. a computer based approach. The third approach revolves around the mathematical/mechanical modelling of the system. Such an approach would, at various stages, make use of the data produced by the first two approaches.

The variability of wood causes problems for all wood anatomical studies and this variability is known to be caused by a several factors (Rendle & Clark 1934;

Barefoot & Hankins 1982). In terms of research design for specific goals, the problem of variability reduces to a problem of choice of sampling strategy. However, some of the decisions about sampling strategy have to be made at an early stage of research, in fact at the level of basic data gathering methods, and there are contradictory demands to be met. In ecological wood anatomy tensions arise in the appropriation of time between the necessity to accumulate a large body of data in order to register certain patterns, the measurement of a large range of variables and the demand for statistical reliability.

Three principles are used here to resolve these tensions. Firstly, the use of the computer enables values for a wide range of variables to be obtained in a comparatively short time and the researcher consequently need not preselect which variables to measure. Secondly, small areas of xylem tissue, usually between 1,2-4,5 mm<sup>2</sup>, are analysed, but the set of measurements for one area is attained relatively quickly and therefore more individual areas can be processed. Thirdly, the EDXA2 program options include the production of basic statistics for a data set. Other statistical tests could be included as desired.

In a discussion of the issues involved in obtaining reliable measurements for taxonomic purposes, Rendle & Clark (1934) state that, "A few measurements on many samples are preferable to many measurements on a few



samples." Apart from being incorporated in the basic methodology of the approach, this latter principle is central to the EDXA-based approach to reconstructing components of past climates (see Chapter 5).

## METHODOLOGY

### GENERAL DESCRIPTION

The aim of this study was to produce an efficient, computer based method to quantify relationships both between and within the types of tissue of which the xylem is composed. The approach involves the analysis of transverse sections alone and is flexible in that, within limits, any magnification, any size of area and any amount of actual measures, may be used. Photomicrographic prints or direct microscope images, fresh wood thin sections or SEM prints can be analysed and the results are calculated by the computer and expressed in standard units such as  $\mu\text{m}$ ,  $\text{mm}^2$ , %, or other ratios. The system is also flexible in that several variables which are not calculated and saved in the standard program (in order to save storage space and because their relevance is questionable), but have been used by other researchers, e.g. mean diameter of the larger vessels (Ingle & Dadswell 1953), means for radial or tangential vessel diameter (Dodd 1984), or mean fibre wall width/fibre cell diameter (Barajas-Morales 1985) can be requested. The data produced are automatically filed and are easily

accessible for further statistical analysis. The aim of the system is to :-

(1) measure the areal relationships of three components of xylem tissue, namely, the tracheary system, the mechanical support system and the ray system and

(2) measure and record the distribution of dimensions of the individual elements (vessels) of the tracheary system.

(3) facilitate exploratory data analysis, e.g. by automatically calculating a range of indices or applying certain correction factors specified by the user at the start of a work session.

At present 30 variables and indices are employed in these tasks. In addition a new descriptive device, the distribution of relative conductivity (RELV) per vessel diameter size class, is produced by program EDXA2 and describes the distribution of functional dimensions of the tracheary system. It is an important device, since those variations in tissue whose analysis requires measurements of both individual cell dimensions and their distribution, rather than just their dimensions, appear to be more affected by ecoclimatic factors than those variations which can be described by a single summary statistic (Rendle & Clark 1934:33).

For comparison with a stereological method in some ways similar to that described here, a method designed to analyse the transverse section of wood in order to represent, in three dimensions, components of its structure, see Steele et al (1976).

The variables and indices at present produced by program EDXA2 are listed in Table 4.1. In Table 4.2, four examples of complete sets of inputs prompted by program EDXA2 are provided. The areas of xylem analysed together with the resultant EDXA variables are illustrated in Fig.4.1. The description provided below of the methods used to measure and calculate these EDXA variables follows the order and numbering system of Table 4.1.

#### DIRECT MEASUREMENTS (Table 4.1, nos 1-9)

##### 1. Total vessel area (TVESA)

This variable is measured by means of a point count. The general features of point count methodology are well described in a number of publications (see Clark 1983). The method involves laying a grid of points over an area in which two or more components (phases) are represented and counting the intersection of a particular phase with the points in order to measure the proportion of the total area occupied by that phase. If the total number of points in the grid is 100 and the number of points intersected by a particular phase is 23, then .23 (23%) of the area is occupied by that phase. If the area counted was actually 2 mm<sup>2</sup>, then the area occupied by the measured phase would be .46 mm<sup>2</sup>.

Clark (1983) discusses the statistical reliability of the method and the criteria to be used to determine an adequate density of points for a given problem area/phase

Table 4.1 Variables produced by program EDXA2

EDXA VARIABLES				
Description	Computer acronym	Methodology/formula		
<b>A. VARIABLES DIRECTLY MEASURED</b>				
1. Total vessel area per mm <sup>2</sup>	TVESA	the sum of point counts in up to 3 vessel diameter size classes. (TVESA <sub>C</sub> (larger) + TVESA <sub>C</sub> (medium) + ...)	RELY	12. Relative conductivity  the sum divided by 2 * 10 <sup>6</sup> of the mean radius <sup>4</sup> for each vessel measured multiplied by the corresponding NVESty. NVESty is divided by the no. of vessels actually measured in that size class (see table 2) to obtain NVESty for that size class.
2. Ray area per mm <sup>2</sup>	RAYA	point count	RFIB1	RFIB * FIBA
3. Parenchyma area per mm <sup>2</sup>	PARA	point count	FWA1	FMA * FIBA
4. Total area of fibre tissue per mm <sup>2</sup>	FTBA	1 - (TVESA + RAYA + PARA*) * expressed as fractions	FLA1	FLA * FIBA
5. Fibre wall area per mm <sup>2</sup> of fibre tissue	FMA	point count: light dot method	MFWT	$\frac{\text{mean fibre cell area} * \pi}{\pi}$ * mean fibre lumen area = area of analysed fibre tissue / MFIB ** mean fibre lumen area = area of analysed fibre tissue * FLA / MFIB
6. Fibre lumen area per mm <sup>2</sup> of fibre tissue	FLA	additive inverse of FMA expressed as a fraction	MTANG	1/TANG
7. Number of fibres per mm <sup>2</sup> of fibre tissue	MFIB	direct count	DIENS1	1/FLA
8. Number of tangential structures per radial mm.	TANG	direct count	DENSE2	1/FLA1
9. Number of rays per tangential mm.	RAYNO	direct count	DENS3	1/(TVESA + RAYA + PARA + FLA1)
10. Vessel diameters i) Mean vessel diameter ii) Maximum vessel diameter iii) Vessel diameter size range	MWESD MAX RANG	tangential and radial diameters are directly measured in up to 3 vessel size classes. Using NVES, MWESD is calculated (see discussion)	VULR MES01 MES02 MES03 D1V	MWESD/NVES (defined by Carlquist 1976) RELY * VULR RELY/NVES RELY/TVESA RANG * MAX/MEAN
<b>B. VARIABLES CALCULATED</b>				
11. Number of vessels per mm <sup>2</sup>	NVES	NVES is the sum of the no. of vessels per mm <sup>2</sup> for each of up to 3 vessel size classes (NVES (large) etc.) The NVESty are calculated by dividing each TVESA <sub>C</sub> by its corresponding mean vessel area.	STR AXRAD1 RAY1 AXRAD2 RAY2	MFIB1 * MFVT * NVES TVESA/RAYA RAYA * RAYNO TVESA/RAY1

Table 4.2 List of computer prompts and examples of inputs

<u>EXAMPLES OF INPUTS</u>				
COMPUTER PROMPT	piece no.	piece no.	piece no.	piece no.
	35	701	455	523
	assemblage	assemblage	assemblage	assemblage
	BLD	BLD	BLD	LP
Piece number ?	35	701	455	523
Morphological type ?	1	24	14	18
Assemblage ?	BLD	BLD	LP	LP
Photograph orientation ?	2	2	3	2
Magnification ?	75	75	150	75
Shrinkage factor ? (Y/N)	1	1	1	1
Piece radius (in cm) ?	237	128	95	144
Point count total ?	360	180	180	165
Point count (large vessels) ?	43	17	28	-
Point count (medium vessels) ?	-	10,5	39	19
Point count (small vessels) ?	11	-	8,5	-
Point count (ray tissue) ?	48,5	36	11,5	33
-----				
<b>VESSEL DIAMETERS</b>				
Large vessels (in mm)	9,5x9,2	7,4x7,4	7,8x8,6	-
	8,5x8,1	6,8x6,8	10x6,6	-
	9x8,4	6,8x5,9	6,9x6,4	-
	9,1x7,2	4,9x6,6	7,6x5,5	-
	7,6x5,1	5x5,5	6,2x6,2	-
	8,6x5,2	5,2x5,2	7x5,2	-
	7,3x5	4,4x4,7	6,3x6,9	-
	6,9x6,5	5,1x4,9	6,9x5,4	-
-----				
Medium vessels (in mm)	-	4x2,7	6x4	2x1,5
	-	2,7x3	5,6x4,4	1,6x1,3
	-	4,2x3,4	4,4x5,5	1,1x1,1
	-	4,1x3	3,9x3,5	0,6x0,6
	-	3,2x3,9	4x5,4	0,9x0,9
	-	2x3,9	4,3x5	0,8x0,8
	-	3,6x2,7	3,8x3,7	0,5x0,5
				1x1,2
-----				
small vessels (in mm)	5,6x3,1	-	-	-
	4,5x2,6	-	-	-
	6,3x4,7	-	4,2x3	-
	3,4x3,8	-	3,9x2,8	-
	5,5x2,7	-	3,7x3	-
	3x3,6	-	3,2x3,3	-
	3,7x3,3	-	4x2,9	-
-----				
No. of tangential structures?	0	0	1	4
No. of rays?	13	6	16	19
Mean ray width (in mm) ?	6	7,85	1,4	3
Mean ray seriate?	10	2,5	1	4
-----				
Fibre tissue (Y/N) ?	1	1	1	1
Magnification ?	75	75	150	75
Shrinkage factor ?	1	1	1	1
Dimensions of image ? (L x b; in mm)	15x15	15x15	15x15	15x15
Point count total ?	100	100	100	100
Point count lumen ?	25	40	29	21
No. of fibre cells?	304	75	152	480

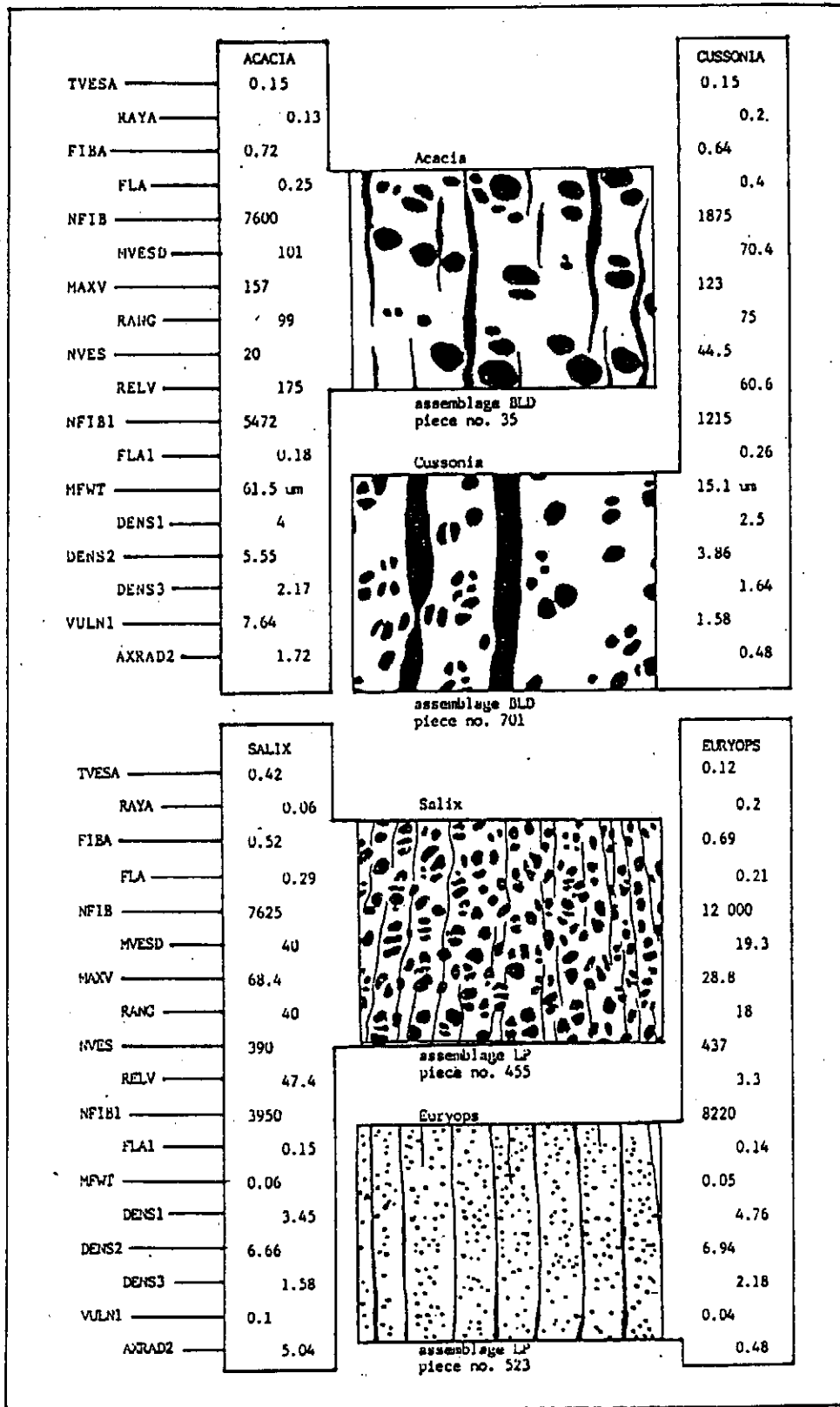


Fig.4.1 EDXA analysis of four areas of xylem tissue

relationship. Program EDXA requires input of the total number of points counted and the number of point intersects with the specific phase area being measured (see Table 4.2). The values reported in Fig.4.1 were obtained using a plastic sheet marked with a 7 x 7 mm grid of points (360 in all) overlain on standard 120 x 150 mm SEM photomicrograph prints.

Although preferable statistically, a random point count (Ladel 1959; Clark 1982) considerably increases the difficulty and time taken to complete a count (since there is no regular pattern for the eye to scan) and was therefore not used. Rather, in order to reduce the negative effect of degrees of conjunction occurring between regularities in the xylem tissue and the point counting grid, the grid was orientated so that one axis of the grid's rectangular pattern lies at 15-25° to the visible radii in the wood (if, as is usual, tangential and radial arrangements are most prominent).

Vessel area is counted in up to three vessel diameter size classes, large, medium and small. This is a heuristic and flexible device employed in order to increase the accuracy of the calculations of numbers of vessels per mm<sup>2</sup> as well as the resultant vessel diameter size distributions. These classes are intuitively and relatively defined for each area analysed, i.e. if the observer can easily distinguish three size classes, then the appropriate option in program EDXA2 is chosen and the vessels are counted accordingly. However, if a smaller

vessel size range is present then the vessels would be point counted in only one or two size classes. Whether one, two, or three size classes are to be counted they should be counted on one unbroken sequence of transects, i.e. following the rows of the grid, covering the area to be analysed. Ray area (RAYA) and parenchyma area (PARA), the latter not always applicable, should also be counted on the same sequence of transects.

In the analysis of fossil charcoal assemblages, areas of xylem tissue are sometimes badly preserved, obscured or deformed by bursts. These areas are simply pointcounted and the score subtracted from the number of points in the grid to give a new divisor for the calculation of TVESA, RAYA, etc.

#### 2. Ray area per mm<sup>2</sup> (RAYA)

This variable is measured by the point count method as described above.

#### 3. Parenchyma area per mm<sup>2</sup> (PARA)

This variable is measured by the point count method, but is only measured in the way already described in cases where obvious and relatively extensive areas of parenchymous tissue are present, i.e. extensive areas of vasicentric banded, confluent or boundary parenchyma. Scanty, diffuse parenchyma is ignored in this count, but its incidence is measured in the point count of fibre tissue described below.

#### 4. Total area of fibre tissue per mm<sup>2</sup> (FIBA)

This is an approximate measure defined as the additive inverse of (TVESA+RAYA+PARA), these three



variables being expressed as fractions.

5. Number of fibre cells per mm<sup>2</sup> of fibre tissue (NFIB),

6. Fibre wall area per mm<sup>2</sup> of fibre tissue (FWA) and

7. Fibre lumen area per mm<sup>2</sup> of fibre tissue (FLA)

These three variables are measured in a single procedure. The method described is an adaptation of that of Ladel (1959) and is quick and efficient.

A high contrast, high magnification slide is taken of a selected area which consists, as far as possible exclusively, of fibre tissue. The negative (or positive) is then projected onto a screen so that approximately 100 fibre cells are contained in a 200 x 200 mm square. Standard magnifications and enlargements should be used throughout.

A thin card of opaque material with 100 randomly arranged 0,5 mm holes drilled into it and held by a suitable stand and clamp is then inserted into the beam about 200 mm before the screen. With due consideration for counting fractions of cells, the number of cells appearing on the card is then counted. Since the magnification, area of card and number of fibre cells is known the number of fibres per mm<sup>2</sup> of fibre tissue (NFIB) can be calculated.

The number of light dots in the dark rectangle cast by the card on the screen is then counted. If a negative is being projected, a fibre lumen area intersecting a hole in the screen will produce a bright dot of light while a fibre wall area will not; in this way counting

light dots on the screen achieves a point count of the fibre lumen area. The fibre lumen area (FLA) is expressed as a fraction or percentage of the unit area, while FWA is the additive inverse of FLA.

If xylem tissue characterised by scanty, diffuse parenchyma is to be analysed, a different procedure is followed. Instead of only the fibre cells being counted, the image is point counted to record the relative proportions of fibre and parenchyma tissue. Accounting for this difference, program EDXA2 then calculates the same set of variables as before. For the purposes of measuring the fibre lumen:wall ratio, the presence of the parenchyma cells is ignored, i.e. in effect a cell lumen:wall ratio for the selected area is measured.

#### 8. Average width of tangential structures (TANG)

Knowing the magnification of the image, the average width of the tangential structures can be simply calculated from the count of the number of tangential structures observed over a standard radial transect.

If areas of xylem large enough to display regularly four or five tangential structures are being analysed, their widths can be measured in the sequence in which they occur and a measure of mean sensitivity (Fritts 1976) obtained.

#### 9. Number of rays per tangential mm (RAYNO)

RAYNO is measured similarly to TANG. Given a standard methodology with SEM prints of regular dimensions being analysed, program EDXA2 requires only an input indicating the orientation of the photograph, i.e.

indicating whether radii are parallel to the longer or shorter axis of the rectangle of the photograph or diagonal to these axes, and an input of the number of rays counted in a tangential transect in order to calculate RAYNO.

CALCULATED VARIABLES (Table 4.1, numbers 11-19)

10. Measurements of vessel diameters:

- i. mean vessel diameter (MVESD);
- ii. maximum vessel diameter (MAXV);
- iii. vessel diameter size range (RANG) and;

11. number of vessels per mm<sup>2</sup> (NVES)

These four variables are measured and calculated in a single procedure. As described in the point count method used to measure TVESA, vessel diameters are measured in up to three intuitively and relatively defined size classes. These measurements are correlated with the point count measurements of TVESA so that the same size range of vessels which have their diameters measured in the large vessel size class, have their combined area measured in the corresponding point count. If the boundaries between size classes are easily intuited, no aid is required to achieve concurrence. In more problematic cases, plastic sheet overlays on which vessels of a size class whose boundaries are uncertain can be temporarily marked, can be used. Alternatively, the point count transects can be interrupted in order to measure the diameter of vessels. Depending on the

distribution of vessel dimensions, some overlapping of size classes must occur but this will not affect the accuracy of the method. Acquaintance with the method quickly produces a standard technique.

Because accurate measures both of vessel diameters and areas are required to calculate the important variables RELV and NVES, EDXA requires the measurement of both radial and tangential vessel diameters. This is in contrast to much common practice in wood anatomical studies. As many vessels as are necessary can be measured per size class. The vessels to be measured are randomly chosen with the proviso that due to the significance of larger vessels for calculating relative conductivity (RELV), the largest vessels must be relatively well sampled. Therefore for each area of xylem tissue analysed, the large vessel size class should be defined as a relatively small class.

Program EDXA2 uses the formula for an ellipse to calculate the area and average diameter for each vessel measured. The maximum (MAXV) and minimum (MINV) vessel diameters for each area of xylem tissue are recorded and the vessel diameter size range (RANG) calculated.

To calculate the mean vessel diameter (MVESD), not only the vessel diameter size range, but also the distribution of vessel diameter size classes is required. The mean vessel area per vessel diameter size class is calculated by first dividing the sum of the areas of the set

of vessels measured in that class by the number of vessels measured. This value is then divided into the total vessel area for that size class (known from the point counts) to obtain the number of vessels for that size class per  $\text{mm}^2$  (NVESc). The total number of vessels per  $\text{mm}^2$  for the analysed area is the sum of NVESc (large vessels) + NVESc (medium) + NVESc (small). Desch (1932) used a method involving similar principles to calculate total vessel area and was satisfied of its reliability compared to that of other methods he had tested.

NVESc (the no. of vessels per a specific vessel diameter size class) is divided by the number of vessels actually measured in that class to obtain NVESv, the no. of vessels per  $\text{mm}^2$  for each size class of vessel for which a measurement was obtained. Note that each vessel diameter measured in a size class is, in this procedure, assigned the same NVESv. For this reason the selection of vessels to be measured within a size class should reflect the vessel diameter size class distribution within that class.

In the final stage of this procedure, MVESD is calculated by first summing the products of each average vessel diameter (calculated using the formula for an ellipse) multiplied by their respective NVESvs and then dividing the total by the total NVES.

#### 12. Relative conductivity per $\text{mm}^2$ (RELV)

This variable is calculated by summing the products of each vessel mean radius measured per unit area raised

to the power four, and multiplied by its associated NVESv. Vessels are not ideal capillaries, often being less than 50% efficient (Zimmerman 1983), so the answer is divided by two. As suggested by Van den Oever et al (1981:20), the answer is further divided by 10 to create a useful scale of values.

Note that because of the power of the  $r^4$  relationship and its sensitivity to small increases in diameter, using  $MVESD \times NVES$  to calculate RELV could give a widely incorrect result. It is unclear whether this latter formula was used by Van den Oever et al (1981). As far as is known, this latter work is as yet the only applied study which tries to use an estimate of relative conductivity to analyse wood anatomical and ecoclimatic covariability.

### 13. Number of fibres per $\text{mm}^2$ of xylem tissue (NFIB1)

This variable is calculated by multiplying NFIB by the fibre tissue area (FIBA). FIBA is calculated by the formula  $(1 - (TVESA + RAYA + PARA))$ , the three latter variables being expressed as fractions. In other words, FIBA is taken as the additive inverse of the total area occupied by the other xylem tissue.

The calculation of the remaining variables (14-19) employ measures already defined and these calculations are adequately described in Table 4.1.

### INDICES (Table 4.1, numbers 20-28)

The calculation of the indices is described in Table 4.1. The rationale for their construction and use is discussed in Chapter 5. The VULN1 index was defined and

has often been used by Carlquist (1977b and elsewhere)

#### PROGRAM EDXA2

The program was originally written in Microsoft BASIC on an Olivetti M10 notebook computer. To increase the speed of operation, it has now been rewritten in Turbo-Pascal. With slight modifications it will run on any IBM compatible machine. It requires at least 10K of memory and a disk copy will be available shortly.

As has already been stated, the program requires input of certain basic parameters, such as whether a shrinkage factor should be applied (fresh wood versus charcoaled wood), magnification and the dimensions of the analysed image before input of the values for the set of direct measurements described above. The EDXA variables are then calculated. For an illustration of this cycle see Table 4.2 and Fig.4.1.

Program EDXA2 stores the inputs as entered in data file INPUTS, the EDXA variables in data file "ASSEMBLAGE NAME" and vessel diameter distribution data (each mean vessel diameter together with its corresponding RELV and NVESv values) in data file VESDIS. The data are stored in easily accessible form and are available for further manipulation. After a set of data has been entered, program EDXA2 will calculate maximum, mean and minimum values as well as the standard deviation and coefficient of variation for each variable for a selected morphological type in an assemblage, or for a whole assemblage.

Subprogram VESDIS2 uses data file VESDIS to produce vessel diameter distribution data as well as to calculate the distribution of relative conductivity (RELV) per vessel diameter size class (see Fig.4.2 for an example of the latter type of graph, the RELV:vess graph).

The indices listed in Table 4.1 are regarded as hypotheses to be tested, initially, by whether the patterns they produce can be interpreted. Indices that prove uninformative can be replaced by others.

Although work remains to be done on defining the statistical parameters of the basic data capturing system, it is not anticipated that it will require amending. Hopefully, other researchers will critically experiment with the system so that standardisation can be rapidly achieved. The field of study will benefit by this process and a large body of comparable data could subsequently be rapidly accumulated.

#### THE DIAGNOSTIC VALUE OF THE VARIABLES : TWO ILLUSTRATIONS

Reported correlations between basic wood anatomical and ecoclimatic variables are listed in Table 4.3.

Several of the indices, variables and graphs used in this study have, however, not been used before and two of them are discussed in this section.

Perhaps the most diagnostically important wood anatomical variable is that of relative conductivity (RELV). A description of the full rheological formula



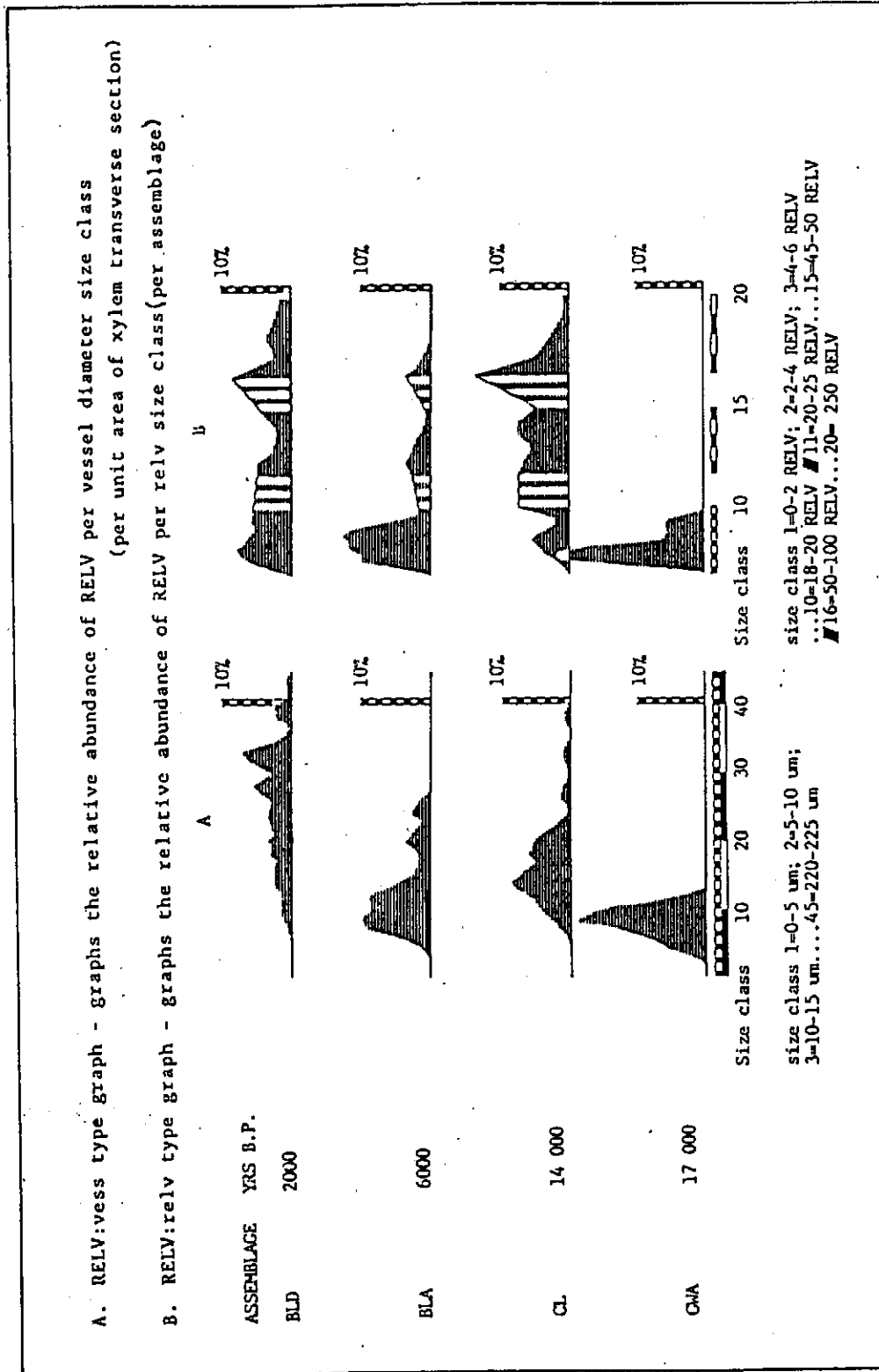


Fig.4.2 Examples of RELV: vess and RELV: relv type graphs (examples from the analysis of Boomplaas Cave)

Table 4.3 Reported correlations between wood anatomy and climate

## VESSELS

1. Correlations of an increase in vessel diameter with:
    - a. decreasing altitude- Baas (1973) Ilex; Styer & Stern (1979) Deutzia; Versteegh (1978) Indonesia  
decreasing latitude- Baas (1983) review; Van der Graaf & Baas (1974); Van den Oever et al (1981) Symplocos; Dickison & Phend (1985) Styracaceae; Forsaith (1920) alpine.
    - c. increasing rainfall- Carlquist (1966) Asteraceae; Baas (1983) review; Dickison & Phend (1985) Styracaceae; Baas et al (1984) dwarf trees; Van Vliet (1979) Combrataceae
    - d. trees versus shrubs- Carlquist (1966) Asteraceae; Forsaith (1920) alpine
  2. Correlations of increase in no. of vessels per mm<sup>2</sup> with:
    - a. increasing altitude- Carlquist (1966) Asteraceae; Novruzova (1968) USSR
    - b. increasing cold- Carlquist (1982a) Illicium; Baas (1983) review
    - c. increasing latitude- Carlquist (1966) Asteraceae; Baas (1976) review; Van den Oever et al (1981) Symplocos; Dickison & Phend (1985) Styracaceae
    - d. increasing variability of precipitation- Carlquist (1982a) Illicium
  3. correlations of increasing incidence of two vessel size classes with:
    - a. increasing variability of precipitation- Baas et al (1983) Israel
  4. Correlation of thicker vessel walls with:
    - a. low rainfall- Baas (1982) review
    - b. low latitude- Dickison & Phend (1985) Styracaceae
  5. Correlations of increase in vessel element length with:
    - a. decreasing latitude- Van der Graaf & Baas (1974) review;
- 
- Van den Oever et al (1981) Symplocos; Dickison & Phend (1985) Styracaceae
  - b. decreasing altitude- Carlquist (1966) Asteraceae; Baas (1973) Ilex
  - c. trees versus shrubs- Carlquist (1966) Asteraceae; Baas (1982) review; Michener (1981) Keckiella
  - d. independent or constant- Baas (1976) review
  - e. increased precipitation- Carlquist (1966) Asteraceae; Baas (1982) review; Dickison & Phend (1985) Styracaceae; Novruzova (1968) USSR; Styer & Stern (1979) Deutzia; Dickison et al (1978) Hibbertia; Akachuku & Burley (1979) Gmelina; De Buhr (1977) Sarracenaceae; Carlquist (1977b) Onagraceae
- 
6. Correlations of increasing total vessel area with:
    - a. reduced precipitation- Den Oeter & Van Veenendal (1976) Ivory Coast
    - b. constant- Akachuku & Burley (1979) Gmelina
  7. Correlations of increasing incidence of vessel clusters with:
    - a. reduced precipitation- Carlquist (1966) Asteraceae; Baas (1982) review
    - b. low latitude- Carlquist (1966) Asteraceae
  8. Correlations of increased incidence of helical thickenings with:
    - a. reduced precipitation- Carlquist (1966) Asteraceae
    - b. high latitude- Carlquist (1966) Asteraceae; Van den Oever et al (1981) Symplocos
    - c. high altitude- Baas (1973) Ilex
    - d. shrubs versus trees- Vander Graaf & Baas (1974) review

Table 4.3 continued-

RAYS	
9. Correlations of an increase in ray tissue with:	
a. decreasing latitude- Van der Graaf & Baas (1974) review; Robertse et al (1980) <u>Acacia</u>	b. increasing var ability of precipitation- Dickison et al (1978) <u>Hibbertia</u> .
b. increasing latitude- Carlquist (1966) <u>Asteraceae</u>	c. constant <u>Parameswaran &amp; Conrad (1982) Balanites aegyptica</u>
c. decreasing altitude- Forsaith (1920) alpine	d. increasing precipitation- Fritts (1976) softwoods
d. decreasing precipitation- Den Oeter & Van Veenendal (1976) Ivory Coast	
e. constant- Akachuku & Burley (1979) <u>Gmelina</u>	
FIBRES	
10. Correlation of increase in fibre lumen area with:	
a. decreasing latitude- Van der Graaf & Baas (1974) review; Van den Oeter et al (1981) <u>Symplocos</u>	AXIAL PARENCHYMA
11. Correlation of an increase in fibre length with:	
a. decreasing latitude- Van der Graaf & Baas (1974) review; Van den Oeter et al (1981) <u>Symplocos</u> ; Dickison & Phend (1985) <u>Styracaceae</u>	a. Correlations of an increase in axial parenchyma with:
b. decreasing altitude- Carlquist (1966) <u>Asteraceae</u> ; Baas (1973) <u>Ilex</u> .	a. increased predipitation- Dickison et al (1978) <u>Hibbertia</u>
c. trees versus shrubs- Carlquist (1966) <u>Asteraceae</u> ; Baas (1982) review; Michener (1981) <u>Keckiaella</u>	b. constant- Den Oeter & Van Veenendal (1976) Ivory Coast
d. constant- Baas (1976) review	
e. increased precipitation- Baas (1976) review; Carlquist (1966) <u>Asteraceae</u> .	INDICES
f. increased growth rates- Baas et al (1984) dwarf trees	15. Correlations of an increase in the indices of 'vulnerability' and 'mesomorphy' with:
GROWTH RINGS	
12. Correlations of increasing growth ring width with:	a. increasing precipitation? Carlquist (1982a) <u>Illicium</u>
a. tropical versus temperate areas- Dickison & Phend (1985) <u>Styracaceae</u> :	Carlquist (1981) <u>Chloanthaceae</u> ; Carlquist (1977) <u>Onagraceae</u> ;
	Carlquist (1978) <u>Bruniaceae</u> ; Carlquist (1977c) <u>Pentaceae</u> ;
	Carlquist (1977a) <u>Australia</u> ; Michener (1981) <u>Keckiaella</u> ;
	Creber & Chaloner (1984) review.
	b. constant- Robbette et al (1980) <u>Acacia</u>
	c. contradictory- Van Vliet (1979) <u>Combrataceae</u> .

which describes laminar flow in capillaries and on which the calculation of RELV is based, is given in Zimmerman (1983). RELV, as used here, must not be confused with the measure of relative conductivity defined by Heine (1971). This latter variable represents an attempt to quantify the factors, such as pitting and degree of vessel overlap, other than vessel diameter, which affect sap flow in the tracheary system.

Zimmerman (1983:149) has emphasized the importance of the measure of relative conductivity, "... if we want to compare conductivities of different woods we should not compare their respective transverse-sectional vessel area, vessel density or any such measure. We must compare the sum of the fourth powers of their inside vessel diameters." This  $r^4$  relationship means that a slight increase in vessel diameter results in a considerable increase in ability to transport sap.

To illustrate the power of the relationship Zimmerman (1983:14) notes that vessels of relative diameters 1, 2 and 4 will have relative surface areas of 1, 4 and 16, but relative conductivities of 1, 16 and 256 respectively. The percentage of the total volume of sap transported, which will be transported by each of the three vessels, is 0.4, 5.9 and 93.7.

The sum of the relative conductivity of each vessel in a  $\text{mm}^2$ , or RELV, is the best comparative measure of the ability of an area of xylem tissue to transport sap and, as such, it is the best indicator of the adaptation of the plant to a specific supply of water.

RELV is important for another reason too. As opposed to measures of vessel diameter, RELV can be considered to measure the dimensions of the tracheary system in units of equivalent functional value to the plant. This allows a detailed analysis of the distribution of these dimensions (see Fig.4.2). The potential of the graphs representing these distributions to describe the functional characteristics of the tracheary system has yet to be explored.

Lastly, it is clear from studying the examples given in Table 4.2 and Fig.4.1, that relative conductivity per  $\text{mm}^2$  (RELV) is a very different variable to either total vessel area per  $\text{mm}^2$  (TVESA) or mean vessel diameter (MVESD). The variable may therefore prove to be of use in helping to penetrate the integrity of xylem tissue and distinguish the influence of specific ecological variables on its formation. For example, if RELV is most sensitive to conditions requiring optimal volume of sap transport, TVESA and MVESD are probably more sensitive to the influence of temperature as well as to the distribution of moisture availability through the year.

In terms of xylem anatomy, RELV is most sensitive to changes in vessel diameter even amongst a small percentage of the larger vessels in a population, TVESA is most sensitive to changes in vessel density and MVESD reflects the size of a large proportion of vessels. The distribution of RELV per vessel diameter size class, the so-called RELV:vess distribution, provides a description of the

xylem which is also sensitive to the seasonal distribution of water availability and to changes in temperature.

Analysis of wood preserved as charcoal from archaeological contexts (Chapter 5) has suggested that under colder conditions, an increase in precipitation will cause some increase in vessel diameter, but a proportionately larger increase in vessel density, i.e. in TVESA, while, if precipitation increases under warmer conditions, the diameter of larger vessels, i.e. RELV, increases most markedly. Note that for this reason alone those hardwoods which have the ability to vary their vessel diameters (RELV) will be favoured under warm and wet conditions, while the softwoods (and slower growing hardwoods whose ability to increase their vessel diameter is limited) will react more favourably to cold and wet conditions.

Such patterns can be revealed by comparing the values of RELV, TVESA and MVESD, but also by analysis of the distribution of RELV. Fig.4.2 portrays the distribution of RELV recorded for selected charcoal assemblages from Boomplaas Cave (see Chapter 5). The data from occupation unit CL, during which time the climate is inferred to have been cool and wet, indicate that the mean and modal values of RELV rise while the modal vessel diameter class for the distribution of RELV remains relatively low, i.e. individual vessels remain small, but

more are present per  $\text{mm}^2$ . In contrast, the graphs for assemblage BLD, during which time the climate is inferred to have been warm and wet, shows a relatively high modal vessel diameter size class.

The second variable to be discussed in this section is the index of AXRAD2 (TVESA/(RAYA X RAYNO)). It was selected for discussion not because of its proven value as an ecoclimatic indicator, but because, in contrast to most other variables, it would appear to provide evidence directly concerning the growth habit of a plant. In terms of field data not much is known about the functional significance of variability of ray tissue. Forsaith (1920) reported reduction in ray parenchyma tissue with increasing cold and Den Oeter & Van Veenendal (1976) report an increase in the area of ray and vessel tissue within the same species in savanna versus tropical forest environments. Bannan (1954) notes that for the stem wood of Thuja occidentalis, the fastest growing trees have the largest rays and greatest mean ray height.

A recent study by Lynham (1985) involved using xylem analysis to compare the anatomy of two populations of the same species of Passerina, one from a relatively mesic habitat and the other from a more xeric site. On the latter site the Passerinas grew as tall, lanky, but still relatively thick stemmed, tree-shrubs, while on the former, the plants grew as low shrubs in a stunted vegetation. AXRAD2 values were much higher in the low shrubs. This suggests that in some species the amount of ray tissue is correlated with the degree of radial growth

and/or with the overall rate of growth. A reduction in the AXRAD1 and AXRAD2 indices might therefore signal a relatively low rate of secondary, or radial growth (these indices are very high in vines and riverine species).

#### EDXA AND TAXONOMIC/ECOLOGICAL WOOD ANATOMY

This section comprises a critical review of current approaches in the field and a discussion of the potential contribution of an EDXA-type approach to ecological wood anatomy. The discussion is organised as follows. The most glaring inadequacies of the contemporary study of ecological wood anatomy relate to the fact that methodology appropriate for the field has not been developed. The reasons for and effects of this failure are discussed first. Other issues are discussed around the headings: correlations of wood anatomy with habit, growth rate, phylogeny and climate; phylogenetic versus genotypic variability; species, genus and florule levels of analysis; the use of indices; and lastly, criticism of assumptions that the relationships of wood anatomy and climate are predictable enough for components of climate to be diagnosable from the analysis of wood anatomy.

#### APPROPRIATE METHODOLOGY

Why has the development and standardisation of a methodology appropriate for the study of ecological wood anatomy not occurred? One reason is that ecological



wood anatomy has never been sufficiently detached from its mother discipline, wood taxonomy. The three branches of the study of wood anatomy, ecological, taxonomic and evolutionary have not been distinguished clearly enough and therefore descriptions of wood anatomy gathered for taxonomic purposes have been uncritically accepted as adequate for the study of the relationship between wood anatomy and climate. "In the onset of this paper, it should be stressed that the search for adaptive and functional correlations in wood anatomy is complementary to the purely phylogenetic and systematic approach" Baas (1976:159). Wood anatomical variability is caused by the interaction of several different components of variability (e.g. genetic, hormonal, ecological, within-tree), and inadequate theory and methodology will not allow progress in trying to define the variability attributable to only one component.

Before elaborating on the effects of this failure, its origins in the history and practise of wood anatomical studies in general should be noted. The success of Bailey & Tupper (1918) and Bailey (1944, 1954) in establishing the so-called Baileyan trends of xylem evolution, as well the propagation of Bailey's approach through his training of students has had a strong influence on the development of the field of ecological wood anatomy. This approach was, however, essentially taxonomic in nature. Much work in ecological wood anatomy is

still cast in the form of providing the functional, ecological basis to explain the Baileyan trends (Carlquist 1975; Baas 1982). This is, up to a point, a viable aim, but has encouraged anatomists to be satisfied with demonstrating that correlations between wood anatomical and ecoclimatic variables do exist, rather than with quantifying and exploring them further. The result is, on the one hand, a plethora of studies which repeat the observation of certain relationships, and on the other, a list of exceptions to the rule. What has been lacking is the progress associated with problem orientated research.

Practical considerations have probably also helped to retard the development of appropriate methodology. Measuring wood anatomical variables is a laborious activity and together with the fact that most wood anatomists are occupied mainly with taxonomic work, this encourages the use of taxonomically orientated descriptions of xylem in related studies, including ecological wood anatomy. In addition, a wealth of such descriptions is already available for analysis and reasons of comparability of data therefore encourage continued use of the traditional type of descriptions.

The effects of this failure on individual studies are apparent in the methods chosen to measure wood anatomical variables and in the units chosen for analysis (many of the points made in the section on methods are again at issue).

The present situation is that, apart from the two basic variables of mean vessel diameter and number of vessels per  $\text{mm}^2$ , researchers measure an unstandardised and variable set of features. This set will often contain qualitative features whose functional significance is unknown or low, while contrariwise, some of the most functionally significant variables (e.g. RELV or NFIB1) may not be measured. From a taxonomic point of view, Rendle & Clark (1934) and Wheeler & Pearson (1985) have emphasised how important it is that standardisation occurs and that researchers describe how their measurements are obtained. If anything, the objective problems faced by ecological wood anatomists are larger than those faced by taxonomists.

The units of analysis, ecoclimatic, anatomical and floristic, used by ecological wood anatomists reflect the failure to develop appropriate methods. The selection of anatomical variables has already been discussed. Latitude (which can be obtained from any map) is often used in correlating ecoclimatic and wood anatomical variables, e.g. Baas (1973), Van der Graaf & Baas (1974). Considering the eight ecoclimatic variables which have been shown most powerfully to determine the life forms of plants (Box 1979, see also Table 4.4), it is clear that several of them may change over a latitudinal gradient and to different degrees, while others need not change at all. The correlation of wood anatomical variables with this ecoclimatic variable therefore produces ambiguous

Table 4.4 Ecoclimatic variables which determine plant life forms

List of 8 ecoclimatic variables which express the most important aspects of annual precipitation, temperature and evaporation regimes as they affect plant energy and water budgets (after Box 1981)

ECOCLIMATIC VARIABLE	SIGNIFICANCE
1. Mean temperature of the warmest month (TMAX)	the minimum value for TMAX represents the minimum temperature required for growth; a measure of solar energy; the maximum value for TMAX estimates the point at which some form of metabolic collapse may occur and the point at which respiration begins to out weigh production.
2. Mean temperature of the coldest month (TMIN)	lower values specify minimum temperatures which can be tolerated; the upper limit indicates temperatures required to induce dormancy or vernalisation; separates evergreen and summergreen plants.
3. Annual range of monthly mean temperatures (DTY)	separates only slightly seasonal tropical plants from seasonal extra-tropical types.
4. Average annual precipitation (PRCP)	relates to potential evapotranspiration and measures total amount of water available for storage in the soil and use by vegetation.
5. Annual moisture index (MI)	annual precipitation divided by the Thornthwaite estimate of annual potential evapotranspiration; this index expresses the relationship between potential water loss and total water available (PRCP), i.e. the general wetness or dryness of a climate; this is the most important variable for predicting the dominant plant structural types.
6. Highest average monthly precipitation (PMAX)	the lower limit for PMAX represents the minimum amount of water needed to sustain growth; the upper limit for PMAX indicates the point at which true xerophytes will be disadvantaged.
7. Lowest average monthly precipitation (PMIN)	the lower limit of PMIN indicates the greatest degree of drought which can be tolerated; the upper limit represents the degree of drought required to induce dormancy or other life cycle functions; separates evergreen from summergreen vegetation.
8. Average precipitation of the warmest month (PNTMAX)	expresses the degree of summer drought; separates mediterranean from summergreen forms.

results. While Baas and his co-workers tend to use broad ecoclimatic variables such as latitude or altitude, Carlquist, who focuses more on describing the wood anatomy of selected families or genera, uses anecdotal descriptions of specific plant habitats to record correlations between wood anatomy and ecology. Both of these levels of description are difficult to translate into the type of ecoclimatic variables used by Box (1979). Again, the lack of standardisation contributes to the low level of comparability of data. Despite the obvious deleterious effects (see DeBuhr 1977:166-167), researchers have not made demands for standardisation.

In respect of the floristic units used for analysis, appropriate units must be chosen for specific research goals. This issue is discussed below in more detail. For the purposes of this discussion it is sufficient to note that the lack of definition of research goals has resulted in the genus and family becoming the preferred units of analysis. For obvious reasons these are not the best units to use when investigating the relationships between wood anatomy and ecology.

#### CORRELATIONS OF WOOD ANATOMY WITH HABIT, GROWTH RATE, PHYLOGENY AND CLIMATE

Table 4.3 summarises most of the reported correlations between wood anatomical and ecoclimatic variables. Carlquist (1966) has noted that "The most useful features (of wood anatomy) taxonomically, are ones which

relate to habit... Systematists seem often to over-estimate the taxonomic value of wood anatomy... Woods of Compositae are indistinguishable from woods of other specialised families which may not be at all closely related". That convergent evolution and fundamental eco-climatic forcing causes xeromorphs to have xylem structures tightly constrained around certain norms, and that a trend exists across the ecological gradient of increased incidence of these characteristics, is well accepted (Carlquist 1975; Baas 1982) (The reverse trend, i.e. towards mesomorphy, does not apparently produce such uniform results; the phylogeny of tropical trees is usually clearly displayed in their wood anatomy). According to Carlquist therefore, convergent evolution sets limits to the value of the qualitative descriptions of wood anatomy used for taxonomic purposes. More particularly, it sets limits to the identification of fossil wood (Barefoot & Hankins 1982).

Also according to Carlquist (1966), variability of precipitation is most comprehensive in its effects on xylem morphology and all wood anatomical features are affected by increasing growth form xeromorphy. With increasing dryness, width of vessels and fusiform initial length decreases and the number of vessels per  $\text{mm}^2$  increases (Table 4.3). The same author introduced the idea that xylem might exhibit "modal" conditions within various growth forms (Carlquist 1966). On a very general

level for instance, trees tend to show 'mesomorphic' and shrubs, 'xeromorphic' features. However, little progress has since been made in the definition of modal xylem states, but the concept remains an important one.

Although growth form is not a fully independent selective force, the correlations between habit and wood anatomy in certain families, e.g. Cactaceae, may override correlations such as those between anatomy and climate (Gibson 1973). In their study of the wood anatomy of dwarf trees, Baas et al (1984) have gone even further in suggesting that wood anatomical variables may be correlated with ecological variables, not via phylogeny or growth form, but via the effect of differential growth rates. As suggested in the discussion of the AXRAD2 index, this is an insight that can potentially be exploited within an EDXA-type approach.

Special mention should be made here of the work by Creber (1977) and Creber & Chaloner (1984). These authors have made a detailed review of the influence of environmental factors on the wood anatomy of living and fossil trees and have shown that a study of the anatomy of assemblages of fossil wood can produce good evidence about past environments. They have applied their method to the analysis of fossil woods dating as far back as the Upper Devonian. However, their approach is not quantitative in the sense of the approach described here and their analysis of fossil woods is mainly based on the

recognition of types of tree-ring formation. Mention should also be made of the work of Niklas (1985). In a paper entitled 'the evolution of tracheid diameter in early vascular plants and its implications on the hydraulic conductance of the primary xylem strand', he makes use of several of the suggested functional relationships of elements of the morphology of tracheary systems to interpret the major changes in tracheid morphology recorded for tracheophyte fossils during the Silurian and Devonian.

Recent work by Rury & Dickison (1984) has demonstrated the existence of environmentally related "adaptive character syndromes", or multiple correlations between plant stature and qualitative and quantitative features of both wood and leaf anatomy in the genera Hibbertia and Erythroxyllum. They suggest that components such as the xylem, the leaves and plant habit should be viewed as facets of the plant hydrovascular system, or continuum, which have evolved as structural/functional units. Although their study confirms that "foliar buffering" of xylem, i.e. the retention of mesomorphic wood structure in xeric habitats, can occur and that the foliage constitutes the most significant interface between the plant and the environment, their study strongly confirms the general rule that "adaptive character syndromes" relate to environment.



#### PHYLOGENETIC VERSUS GENOTYPIC VARIABILITY

The problems of distinguishing phylogenetic and ecological components of variability does not arise in all applications of EDXA. Genotypes, growth forms and xylem modes tend to segregate along ecological gradients. Within the genotype itself, sufficient wood anatomical variation may or does occur to make it useful to analyse.

A schematic illustration of the relationship between change in the mean vessel diameter of a species across an ecoclimatic gradient is provided in Fig.4.3. Within the assemblage based form of EDXA analysis of the relationship between wood anatomical and ecoclimatic variables, it is those relationships which override phylogenetic related variability which are studied, i.e., it is immaterial whether the environment selects a certain wood morphology by selecting a taxon whose morphology is relatively rigidly genetically predetermined, or by influencing the growth of a more plastic species. What is important are the trends towards modal states and the correlations with values for variables whose ecological significance at those levels is already known.

#### SPECIES AND FLORULE LEVELS OF ANALYSIS

Appropriate floristic units must be chosen for analysis in terms of divergent research goals. As discussed above, research may be focused on the relationships between ecoclimatic and wood anatomical variables which override phylogeny, or those which occur

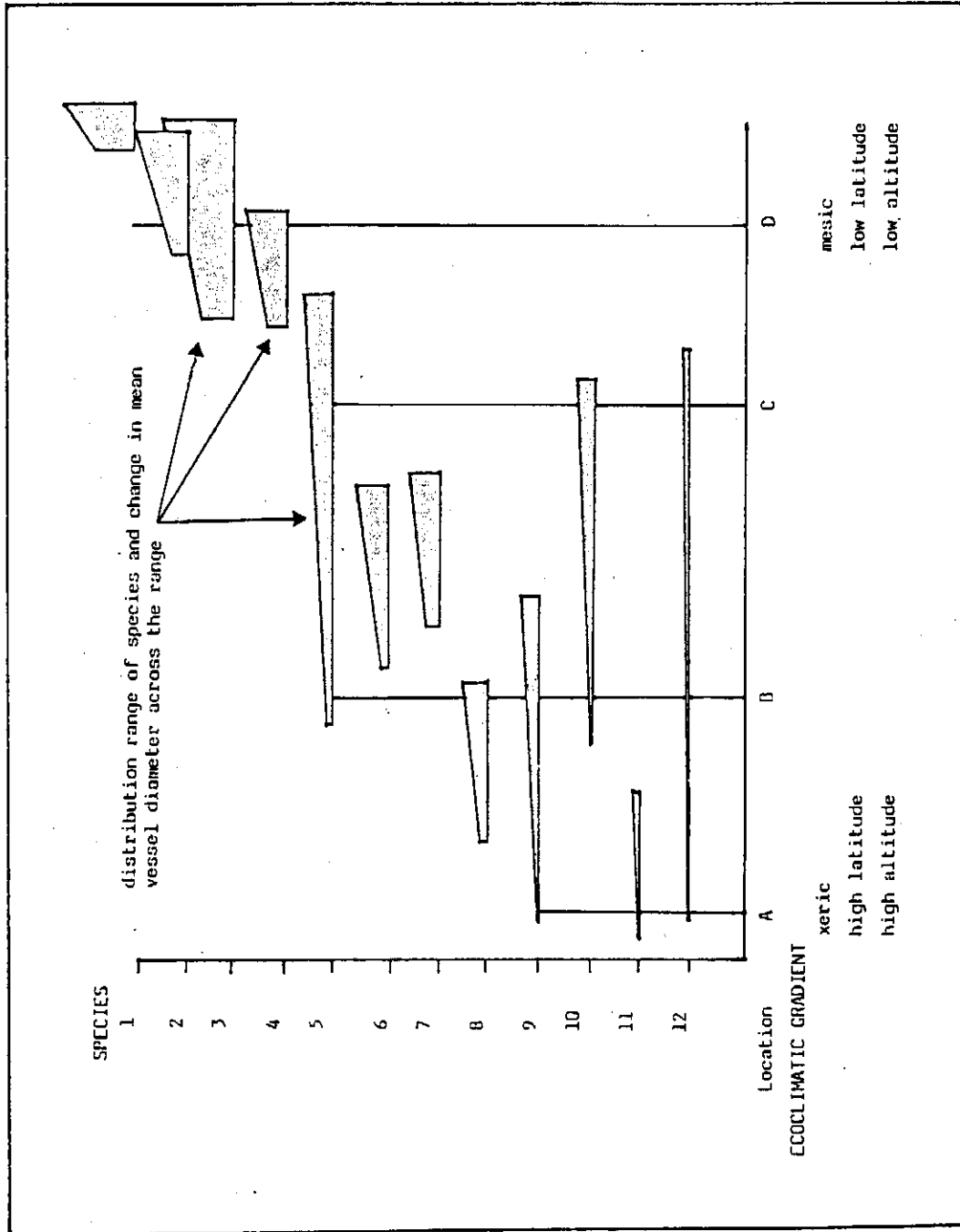


Fig.4.3 Schematic illustration of how mean vessel diameter relates to provenance on an ecoclimatic gradient

within a phyla/genotype. In the first case the appropriate unit for analysis is the florule, while in the second, the most useful unit to use is that of the species. Yet these are arguably the units which are least analysed by ecological wood anatomists, most studies focusing on the distribution of wood anatomical and ecoclimatic variables within families or genera, e.g. Carlquist (1966, 1977b,c, 1980b), Baas (1973). This again reflects the taxonomic bias characteristic of the field of ecological wood anatomy. Units of analysis such as the genus or family are usually unsatisfactory from the wood ecological point of view since the historical or evolutionary component incorporated in the unit cannot be adequately accounted for.

Although numerous papers have dealt with variability in the anatomy of commercially important plantation species from the point of view of the mechanical properties of the wood, there is as yet no study from the purely wood ecological/anatomical point of view on change in the anatomy of a single species along an ecological gradient.

The floristic approach was pioneered by Webber (1936) and was used by Carlquist (1977a) to analyse five wood florules along an ecoclimatic gradient in southwestern Australia. The rationale for the approach was stated thus, "If wood characteristics of particular florules tend to conform to particular plans and to dif-

fer modally from those of other florules ... we have a tool for... developing criteria for (defining) xylem adaptation to varying ecological regimes" (Carlquist 1977a:888). In this study, Carlquist showed that the means for the indices of 'vulnerability' and 'mesomorphy' for the florules correlated with the respective rainfall figures.

The EDXA approach applied to wood anatomy preserved in fossil charcoal assemblages (Chapter 5) is based on a similar principle as the floristic approach. The latter forms part of a general attempt to understand the relationship between physiological ecology and wood anatomy, while EDXA makes use of that understanding to diagnose the existence of certain climatic conditions from an analysis of xylem morphology.

Some of the principles employed to determine aspects of a past climate from the mean values for wood anatomical variables are illustrated in Fig.4.3. This figure portrays schematically the distributions of a range of taxa, each possessing a certain vessel size range, along an ecoclimatic gradient and shows how a measure of the mean vessel diameter at locations A, B, C and D could be used to diagnose those locations on the gradient.

## INDICES

The usefulness of the indices of vulnerability and mesomorphy as ecological indicators seems well established and they have been employed by several researchers

apart from Carlquist, e.g. DeBuhr (1977), Michener (1981), Robbertse et al (1980) and Creber & Chaloner (1984). However, Carlquist has not gone on to develop other ecologically significant indices. Perhaps this is explained by the initial criticism, well founded or not, of the Dutch school of wood anatomy (Van Vliet 1979; Van den Oever 1981) against his exploratory approach. It may also be a result of the constraints of his own basic wood anatomical descriptions. These include only measures of three variables, mean vessel diameter, mean vessel element length and number of vessels per  $\text{mm}^2$ , which can be used to construct ecologically diagnostic indices. A number of indices which have ecological significance have been proposed in this paper. These include indices using the variable of relative conductivity (RELV), total vessel area (TVESA)/ray area (RAYA), mean fibre wall thickness (MFWT)/mean fibre diameter and various indices reflecting density.

#### CRITICISM OF TWO ASSUMPTIONS BASIC TO ECOLOGICAL WOOD ANATOMY

Baas (1976:159,175) has attempted to use the idea that within the plant kingdom there has been much scope for 'free form making' (Van Steenis 1981) to explain the lack of consummate patterning, i.e. the existence of exceptions to the rule, in the relationship between xylem morphology and ecology. In his own words, "The absence of indications of any effects of selection in these cases

(the cases of exceptions) reveals the true nature of xylem evolution as a random process leading to wood anatomical diversity which is not necessarily advantageous or disadvantageous for efficient water transport or for mechanical requirements." Apart from the perverse logic involved in using acknowledged exceptions to a general pattern as evidence for a theory which cannot explain the patterns themselves, Baas's statement is based on a questionable claim, viz. that the quality of his evidence is such that he can state with certainty that no detectable functional relationship exists between a certain wood anatomical feature and ecological variables. As already noted, the use of crude ecological categories alone produces ambiguities. A remark of Zimmerman's (1983:1) is also pertinent, "The concept of evolutionary adaptation, i.e. the concept that everything about a plant has a specific purpose, can be misleading in those cases where a feature serves more than one purpose, but where the investigator is preoccupied with a single one."

There is a second line of criticism which is potentially more damaging to the project of ecological wood anatomy. "Variation of anatomical characteristics from roots to twigs in an individual tree make it extremely dangerous to set up correlations of certain xylem features (such as vessel diameter) with habitat and draw conclusions about functional adaptations when one has only a random sample of wood from each species. Wood

ging process". Zimmerman's warning assumes that comparisons are to be made between wood drawn from a variety of locations on a tree. However, wood samples drawn from similar locations, for example, branches of similar age and diameter, may be compared, while it is well known that within-tree variability is higher in deciduous trees than in evergreen trees or in shrubs (Farmer Bretland 1919).

To conclude, the main point made in this section is that standardisation of methods designed to measure wood anatomical variables appropriate for studying the relationships with ecoclimatic variables is necessary for progress in the field of ecological wood anatomy.

#### EDXA AND EXPERIMENTAL BOTANY

"...the sort of work I do (a synthesis between anatomy, systematics and ecology, based upon field work) will soon be overtaken by a new synthesis between anatomy and physiology" (Carlquist 1982c)

Experimental work produces more precise knowledge about basic matters than does field work. There is a wealth of information in the literature on experimental botany/plant physiology of relevance to ecological wood anatomy. However, little of this detail has been synthesised into a form which makes it available for applied wood taxonomic/ecological studies.

In this respect the work of Zimmerman (1982, 1983) is valuable. He defined some of the basic physiological and mechanical parameters which govern the movement of

ging process". Zimmerman's warning assumes that comparisons are to be made between wood drawn from a variety of locations on a tree. However, wood samples drawn from similar locations, for example, branches of similar age and diameter, may be compared, while it is well known that within-tree variability is higher in deciduous trees than in evergreen trees or in shrubs (Farmer Bretland 1919).

To conclude, the main point made in this section is that standardisation of methods designed to measure wood anatomical variables appropriate for studying the relationships with ecoclimatic variables is necessary for progress in the field of ecological wood anatomy.

#### EDXA AND EXPERIMENTAL BOTANY

"...the sort of work I do (a synthesis between anatomy, systematics and ecology, based upon field work) will soon be overtaken by a new synthesis between anatomy and physiology" (Carlquist 1982c)

Experimental work produces more precise knowledge about basic matters than does field work. There is a wealth of information in the literature on experimental botany/plant physiology of relevance to ecological wood anatomy. However, little of this detail has been synthesised into a form which makes it available for applied wood taxonomic/ecological studies.

In this respect the work of Zimmerman (1982, 1983) is valuable. He defined some of the basic physiological and mechanical parameters which govern the movement of



between and within cells enable a plant to resist both frost injury and desiccation. In an analysis of the wood anatomy of dwarf trees Baas et al (1984) suggest that the features commonly associated with resistance to cold and drought may be caused by slow growth rates alone. Rudman (1970) suggests that for physiological reasons growth at lower temperatures is associated with an earlier onset of lignification and a higher lignin content. Slow growth rates therefore result in early lignification of cell walls, a concomitant lack of expansion of the cell and high wood density. It can be inferred that the smaller size of cells and relatively heavily lignified walls lend rigidity to the xylem tissue and cause internal resistance to water flow. This would help to enable dry habitat plants to minimise their transpiration when suffering a water deficit.

Another example concerns fibre tissue. At present it is not known whether lignified tissue fulfils any function other than that of mechanical support. If fibre tissue fulfilled another function, for example, insulation, which related more directly to some ecoclimatic variable, then measures of fibre tissue variables such as wall thickness or cell abundance could be used in addition to measures of the tracheary system to infer aspects of past climates. Ecological wood anatomists may speculate about these factors, but they all require investigation by experimental botany.

between and within cells enable a plant to resist both frost injury and desiccation. In an analysis of the wood anatomy of dwarf trees Baas et al (1984) suggest that the features commonly associated with resistance to cold and drought may be caused by slow growth rates alone. Rudman (1970) suggests that for physiological reasons growth at lower temperatures is associated with an earlier onset of lignification and a higher lignin content. Slow growth rates therefore result in early lignification of cell walls, a concomitant lack of expansion of the cell and high wood density. It can be inferred that the smaller size of cells and relatively heavily lignified walls lend rigidity to the xylem tissue and cause internal resistance to water flow. This would help to enable dry habitat plants to minimise their transpiration when suffering a water deficit.

Another example concerns fibre tissue. At present it is not known whether lignified tissue fulfils any function other than that of mechanical support. If fibre tissue fulfilled another function, for example, insulation, which related more directly to some ecoclimatic variable, then measures of fibre tissue variables such as wall thickness or cell abundance could be used in addition to measures of the tracheary system to infer aspects of past climates. Ecological wood anatomists may speculate about these factors, but they all require investigation by experimental botany.

for xylem based on engineering principles. The largely mechanical nature of the functioning of the xylem, and particularly of the tracheary system, makes the anatomy of the tissue particularly amenable to modelling. An example of the usefulness of developing mathematical models for biological systems which involve both anatomical and physiological components is provided by Parkhurst & Louck's (1983) work on predicting optimal leaf size and shape in a given environment. Because of the precision of the science, work within experimental botany should define the functional significance of the range of wood anatomical variables.

#### EDXA AND DENDROCLIMATOLOGY: CONTRASTING TWO APPROACHES TO THE DIAGNOSIS OF PAST CLIMATES FROM WOOD ANATOMY

Since the EDXA approach developed out of a consideration of how the anatomy of fossil wood might be used to infer past climates, and since dendroclimatology is a successful approach to the same problem, the similarities and contrasts between the two are discussed in detail.

The science of dendrochronology/climatology is based on measurements of growth ring widths. The method is based exclusively on these measures; even an understanding of the qualitative differences in growth ring types (see Carlquist 1980a) is ignored. Tree-ring sequences are correlated with historical climatic records and individual tree sequences are correlated between

trees and across regions. Aspects of the knowledge produced by the background and methodological studies of dendroclimatology are clearly important to ecological wood anatomy. The tree-ring is, however, not a basic wood anatomical variable, in the sense that a change in its dimensions can be caused by change in a number of more basic variables, e.g. no. of vessels per  $\text{mm}^2$ , mean diameter of vessel or fibre cells, and the limitations of dendroclimatology are linked to this fact.

Dendroclimatology is in effect based upon measurements of the quantity of xylem tissue produced per unit of time. For this reason the approach works best with species which alter the rate of their production of wood in reaction to changing conditions for growth, rather than altering the quality of their wood. Dendroclimatology is therefore suited to the analysis of some of the morphologically (and physiologically) relatively simple softwoods. In contrast, EDXA is designed to measure change in the quality of wood of hardwoods. Dendroclimatology is limited in two other ways not entailed in EDXA. Firstly, every correlation between a tree-ring and a climatic record and every calibration of a synthetic tree-ring curve is unique (and to some extent impenetrable, see Pittock 1982). If a different species is studied, or the same species from a different location, an entirely new analysis, correlation and calibration has to be done. Progress in the field there-

fore occurs in the development of improved statistical procedures with which to correlate tree-ring and climatic records (sometimes also the use of better climatic records leads to improved results! see Pittock 1982:37) and in improved techniques of correlating individual studies in a region, rather than in the development of knowledge about how wood anatomical variables relate to ecoclimatic variables.

Secondly, dendroclimatology is limited in its extension back into time. To achieve correlations with climatic variables, a dendrochronology must first be established. The correlations will only be reliable if all environmental conditions to be diagnosed in the past also occurred within the time range of the relevant historical record (Pittock 1982:32).

In contrast, the EDXA-type approach to reconstructing past climates is not linked to a time sequence and the correlations used to infer past climates are those observed in the present between ecoclimatic and basic wood anatomical variables. Since these relationships can be studied using material from a wide geographical area, a much wider range of past climatic changes can be diagnosed than is possible in dendroclimatology.

The great advantage of dendroclimatology is that it provides a year on year reconstruction of past climates. In contrast, in most applications of the EDXA-type approach, the level of temporal resolution will be determined by the actual archaeological provenancing of

charcoal assemblages and the accuracy of radiocarbon determinations. In practice, temporal resolution of less than 100 years is unlikely to be achieved.

Two recent advances in dendroclimatological method have highlighted the advantages of using basic wood anatomical variables. The traditional tree-ring analysis is not very successful when applied to the study of temperate hardwoods (LaMarche 1982:4). Schweingruber et al (1978) report that analysis with X-ray densitometry produces four significant variables other than total growth ring width, namely, early wood width, latewood width, and maximum and minimum wood densities. When these variables are then analysed, improved correlations between climatic and tree-ring records are achieved. This is so essentially because these variables are more basic than is total growth ring width.

The work of Eckstein & Frisse (1979), also on temperate hardwoods, has demonstrated that better correlations with ecoclimatic variables can be achieved when using measures of mean vessel diameter within growth rings than when using measures of growth ring width. Due to its time-consuming nature (Eckstein pers. comm.), this work has been discontinued, but it is possible that with the use of EDXA-type methodology, perhaps in conjunction with an image analyser, this line of research could be continued.

These two developments suggest that an interdisciplinary approach involving dendroclimatology and eco-

logical wood anatomy may be possible. Within the field of ecological wood anatomy, EDXA is concerned with those wood anatomical variables whose spatial proportions can be measured in transverse section, and its interests are thus especially close to those of dendroclimatology.

The following example illustrates the contribution that insights gained from ecological wood anatomy can make to dendroclimatology. The problem concerned was encountered in extending the application of dendroclimatology to temperate hardwoods. Jones et al (1984) report the results achieved using ring widths of oaks to reconstruct river flow in southern Britain. They note that the reconstructions are more reliable for low flow events. It seems likely that the lack of success in accurately diagnosing periods of highest rainfall relate to limitations of dendroclimatological method rather than insensitivity of the trees. Measures of tree-ring width are linear measures, but, as already discussed, flow in capillaries is proportional to the fourth power of the conduit radius. The effects of this relationship are magnified as the diameter of the conduit increases, so that linear measures of the tracheary system become progressively less reflective of the actual capabilities of the system and of high moisture availability in the environment. As discussed in this chapter, only measures of individual vessel diameters allow calculation of relative conductivity (RELV), the variable based on the  $r^4$  relationship.

Finally, two recently developed branches of dendroclimatology should be mentioned. Both employ the analysis of anatomical features other than the growth ring which are visible in the transverse section and therefore aspects of both approaches have potential use in a xylem analytical approach. Hill (1982) reports that the analysis of the spacing of parenchyma bands and of vessel density can produce evidence about past climates. Work done by Yanonsky (1984) is dependant on the location of trees in a flood plain environment. He has demonstrated that analysis of changes in the distribution and dimensions of the fibre tissue in the wood of ash trees can produce a record of river flooding.

Since dendroclimatology is based upon analysis of a single composite variable, tree-ring width, it is possible that further limitations will be revealed in attempts to apply the method to the wood of temperate hardwoods. Dendroclimatologists are beginning to pay more attention to xylem analysis and clearly, the comparative analysis of radial transects of wood by the dendroclimatological and xylem analytical methods will benefit both approaches.

#### REFERENCES

- AKACHUKU, A.E. & J. BURLEY 1979. Variation of wood anatomy of Gmelina arborea Roxb. in Nigerian plants. International Association of Wood Anatomists Bulletin 4:94-99.



- BAAS, P. 1973. The wood anatomical range in Ilex (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21:193-258.
- BAAS, P. 1976. Some functional and adaptive aspects of vessel member morphology. IN: P. Baas, A.J. Boulton & D.M. Catling (eds) Wood structure in biological and technical research. Leiden Botanical Series 3:157-181, Leiden University Press, The Hague.
- BAAS, P. 1982. Systematic, phylogenetic, and ecological wood anatomy - history and perspectives. IN: P. Baas (ed.) New Perspectives in Wood Anatomy. Nijhoff/Junk, The Hague.
- BAAS, P., E. WERKER & A. FAHN 1983. Some ecological trends in vessel characters. International Association of Wood Anatomists Bulletin (n.s.) 4(2-3):141-1.
- BAAS, P., CHENGLER, L., XINYING, Z., KEMING, C. & YUEFEN, D. 1984. Some effects of dwarf growth on wood structure. International Association of Wood Anatomists Bulletin (n.s.) 5:45-63.
- BAILEY, I.W. 1944. The development of vessels in angiosperms and its significance in morphological research. American Journal of Botany 31:421-429.
- BAILEY, I.W. 1954. Contributions to plant anatomy. Chronica Botanica Company, Waltham, Massachusetts.
- BAILEY, I.W. & TUPPER, W.W. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proceedings of the American Academy for Arts and Sciences 54:149-204.

- BAILEY, I.W. & FAULL, A.F. 1934. The cambium and its derivative tissues. IX. Structural variability in the redwood, Sequoia sempervirens, and its significance in the identification of fossil woods. Journal of the Arnold Arboretum 15:233-253.
- BAILEY, I.W. & HOWARD, R.A. 1941. The comparative morphology of the Icacinaceae II. Vessels. Journal of the Arnold Arboretum 22:174-187.
- BANNAN, M.W. 1954. Ring width, tracheid size and ray volume in stem wood of Thuja occidentalis L. Canadian Journal of Botany 32:466-479.
- BARAJAS-MORALES, J. 1985. Wood structural differences between trees of two tropical forests in Mexico. International Association of Wood Anatomists Bulletin (n.s.) 6:355-364.
- BAREFOOT, A.C. & HANKINS, F.W. 1982. Identification of Modern and Tertiary Woods. Clarendon Press, Oxford.
- BOX, E. 1979. Macroclimate and plant forms: An introduction to predictive modelling in phytogeography. W. Junk, The Hague.
- CARLQUIST, S. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. ALISO 6:25-44.
- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley.
- CARLQUIST, S. 1977a. Ecological factors in wood evolution: a floristic approach. American Journal of Botany 64:887-896.

- CARLQUIST, S. 1977b. Wood anatomy of Onagraceae: Additional species and concepts. Annals of the Missouri Botanical Gardens 64:627-637.
- CARLQUIST, S. 1977c. Wood anatomy of Penaeceae (Myrtales): comparative, phylogenetic, and ecological implications. Botanical Journal of the Linnean Society 75:211-227.
- CARLQUIST, S. 1977d. Wood anatomy of Tremandraceae: phylogenetic and ecological implications. American Journal of Botany 64:704-713.
- CARLQUIST, S. 1978. Wood anatomy of Bruniaceae: correlations with ecology, phylogeny, and organography. ALISO 9:323-364.
- CARLQUIST, S. 1980a. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. ALISO 9:499-553.
- CARLQUIST, S. 1980b. Wood anatomy of the Vochysiaceae. International Association of Wood Anatomists Bulletin (n.s.) 1(4):172-179.
- CARLQUIST, S. 1981. Wood anatomy of Chloanthaceae (Dicrastylidaceae). ALISO 10:19-34.
- CARLQUIST, S. 1982a. Wood anatomy of Illicium (Illiciaceae): phylogenetic, ecological, and functional interpretations. American Journal of Botany 69:1587-1598.
- CARLQUIST, S. 1982b. Wood anatomy of Daphniphyllaceae: ecological and phylogenetic considerations, review of pittosporalean families. Brittonia 34:252-266.
- CARLQUIST, S. 1982c. Review of New Perspectives in Wood

- Anatomy, P. Baas (ed). International Association of Wood Anatomists Bulletin (n.s.) 3:216-218.
- CLEMENS, J. & JONES P.G. 1978. Modification of drought resistance by water stress conditioning in Acacia and Eucalyptus. Journal of Experimental Botany 29(111):895-904.
- CLARK, R.L. 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. Pollen et Spores 24(3-4):523-530.
- CREBER, G.T. 1977. Tree rings: a natural data-storage system. Biological Review 52:349-383.
- CREBER, G.T. & CHALONER, W.G. 1984. Influence of environmental factors on the wood structure of living and fossil trees. The Botanical Review 50(4):357-448.
- CUNNINGHAM, G. & B. STRAIN 1969. Ecological significance of seasonal leaf variability in a desert shrub. Ecology 50:400-408.
- DEBUHR, L.E. 1977. Wood anatomy of the Sarraceniaceae; ecological and evolutionary implications. Plant Systematics and Evolution 128:159-169.
- DEN OUTER, R.W. & VAN VEENENDAAL, W.L.H. 1976. Variation in wood anatomy of species with a distribution covering both rain forests and savanna areas of the Ivory Coast, West-Africa. Leiden Botanical Series 3:182-195, Leiden University Press, The Hague.
- DESCH, H.E. 1932. Anatomical variation in the wood of some dicotyledonous trees. New Phytologist 31:73-117.

- DICKISON, W.C. 1979. A note on the wood anatomy of Dillenia (Dilleniaceae) International Association of Wood Anatomists Bulletin 79(2-3):57-78.
- DICKISON, W.C., RURY, P.M. & STEBBINS, G.L. 1978. Xylem anatomy of Hibbertia (Dilleniaceae) in relation to ecology and evolution. Journal of the Arnold Arboretum 59:32-49.
- DICKISON, W.C. & PHEND, K.D. 1985. Wood anatomy of the Styracaceae: evolutionary and ecological considerations. International Association of Wood Anatomists Bulletin (n.s) 6:3-22.
- DODDS, R.S. 1984. Radial and tangential diameter variation of wood cells within trees of Acer pseudoplatanus. International Association of Wood Anatomists (n.s) 5:253-257.
- ECKSTEIN, D. & FRISSE, E. 1979. Environmental influences on the vessel size of beech and oak. International Association of Wood Anatomists Bulletin (n.s) 1:36.
- FARMER BRETLAND, J. 1919. On the quantitative differences in the water conductivity of the wood in trees & shrubs. Part 1, The evergreens; Part 2, The deciduous plants. Royal Society Proceedings. Series B 90:218-250.
- FORSAITH, C.C. 1920. Anatomical reduction in some Alpine plants. Ecology 1:124-135.
- FRITTS, H.C. 1976. Tree rings and climate. London: Academic Press.
- GIBSON, A.C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). Biotropica 5:29-65.

- GIRAUD, B. 1980. Correlation between wood anatomical characters in Entandrophragma utile (Meliaceae). International Association of Wood Anatomists Bulletin (n.s.) :73-75.
- HABERLAND, G. 1928. Physiological plant anatomy. MacMillan, London.
- HEINE, R.W. 1971. Hydraulic conductivity in trees. Journal of Experimental Botany 22:503-511.
- HILL, J.F. 1982. Spacing of parenchyma bands in wood of Carya glabra (Mill.) Sweet, pignut hickory, as an indicator of growth rate and climatic factors. American Journal of Botany 69(4):529-537.
- IAWA Committee. 1981. Standard list of characters suitable for computerised hardwood identification. International Association of Wood Anatomists Bulletin (n.s.) 2:99-110.
- INGLE, H.D. & H.E. DADSWELL 1953. Anatomy of timbers of the South-West Pacific area. III. Myrtaceae. Australian Journal of Botany 1:353-401.
- JONES, P.D., BRIFFA K.R. & PILCHER J.R. 1984. Riverflow reconstruction from tree rings in southern Britain. Journal of Climatology 4:461-472.
- KACPERSKA-PALACZ, A. & S.E. EGIERSDORFF 1972. Effects of cold hardening and CCC treatment on hydration and frost and desiccation hardness of plant tissue. Botanical Gazette 133:355-360.
- KOZLOWSKI, T.T. 1972. Physiology of water stress. III: Wildland shrubs-their biology and utilisation.

Proceedings of an international symposium, Utah State University, July 1971 :229-244. USDA Forest Service General Technical Report.

LADEL, J.L. 1959. A method of measuring the amount and distribution of cell wall material in transverse microscope sections of wood. Journal of the Institute of Wood Science 3:43-46.

LAMARCHE, V.C. Jr. 1982. \_\_\_\_ IN: M.K. Hughes, P.M. Kelly, J.R. Pilcher & V.C. LaMarche Jr. (eds) Climate from tree rings. Cambridge University Press, Cambridge.

LARSON, P.R. 1964. Some indirect effects of environment on wood formation. IN: M.H. Zimmermann (ed.) The formation of wood in forest trees :345-365. Academic Press, New York.

LEGGE, N.J. & D.J. CONNOR 1985. Hydraulic characteristics of mountain ash (Eucalyptus regnans F. Muell.) derived from in situ measurements of stem water potential. Australian Journal of Plant Physiology 12:77-88.

LEVITT, J. 1956. The hardiness of plants. Academic Press, New York.

LYNHAM, T. 1985. Third year project in ecophysiology. Department of Botany, University of Cape Town

MACDONALD, I.A.W. & M.L. JARMAN 1984. Invasive alien organisms in the Terrestrial Ecosystems of the Fynbos Biome, South Africa. SANSPR 85, Pretoria.

MAXIMOV, N.A. 1929. The plant in relation to water. George Allen and Unwin, London.

- MAXIMOV, N.A. 1931. The physiological significance of the xeromorphic structure of plants. The Journal of Ecology 19:273-283 .
- MICHENER, D.C. 1981. Wood & Leaf anatomy of Keckiella (Scrophulariaceae): ecological considerations. ALISO 10:39-57.
- MILBURN, J.A. 1979. Water flow in plants. Longmans, London.
- MOONEY, H.A. 1974. Plant form in relation to environment. IN: B.R. Strain & W.D. Billings (eds) Vegetation and environment. Junk, The Hague.
- MOONEY, H.A. & KUMMEROW, J. 1971. The comparative water economy of representative evergreen sclerophyllous and drought deciduous shrubs of Chile. Botanical Gazette 132:245-252.
- NIKLAS, K.J. 1985 The evolution of tracheid diameter in early vascular plants and its implications on the hydraulic conductance of the primary xylem strand. Evolution 39:1110-1122 .
- NOVRUZOVA, Z.A. 1968. The water-conducting system of trees and shrubs in relation to ecology. Izd. AN Azerb. SSR, Baku, 230 pp.
- OETER, R.W. den & VAN VEENENDAAL W.L.H. 1976. Variation in wood anatomy of species with a distribution covering both rain forest and savanna areas of the Ivory Coast, West Africa. IN: P. Baas, A.J. Boulton & D.M. Catling (eds) Wood structure in biological and technical research. Leiden Botanical Series 3:132-195. Leiden



University Press, The Hague.

ORSHAN, G. 1972. Morphological and physiological plasticity in relation to drought. IN: Wildland shrubs-their biology and utilisation. Proceedings of an international symposium, Utah State University, July 1971. USDA Forest Service General Technical Report :245-254

PARAMESWARAN, N. & CONRAD, H. 1982. Wood and bark anatomy of Balanites aegyptiaca in relation to ecology and taxonomy. International Association of Wood Anatomists Bulletin ( n.s.) 3(2):75-8.

PARKHURST, D.F. & LOUCKS, O.L. 1983. Optimal leaf size in relation to environment. Journal of Ecology 60:505-537.

PITTOCK, A.B. 1982. \_\_\_\_ IN: M.K. Hughes, P.M. Kelly, J.R. Pilcher & V.C. laMarche Jr. (eds) Climate from tree rings. Cambridge University Press, Cambridge.

QUIRK, J.T. 1975. Dot-grid intergrating eye piece. Two easy techniques for estimating cell wall areas. Wood Science 8:88-91.

RENDLE, B.J. & CLARKE, S.H. 1934. The diagnostic value of measurements in wood anatomy. Tropical Woods 40:27-37.

RENDLE, B.J. & CLARKE, S.H. 1938. The problem of variation in the structure of wood. Tropical Woods 38:1-8.

ROBBERTSE, P.J., VENTER, G. & JANSE VAN RENSBERG, H. 1980. The wood anatomy of the South African Acacias. International Association of Wood Anatomists Bulletin (n.s.) 1:93-103.

- RUDMAN, P. 1970. The influence of genotype and environment on wood properties of juvenile Eucalyptus camaldulensis Dehn. Silvae Genetica 19(2-3):49-54.
- RUNDEL, P.W. & STECKER, R.E. 1977. Morphological adaptations of tracheid structure to water stress gradients in the crown of Sequoiadendron giganteum. Oecologia 27:135-139.
- RURY, P.M. & DICKISON, W.C. 1984. Structural correlations among wood, leaves and plant habit. IN: R.A. White & W.C. Dickison (eds) Contemporary problems in plant anatomy :495-540. Academic Press, Orlando, Florida.
- SCHWEINGRUBER, F.J., FRITTS, H.C., BRANKER, O.U., DREW, L.G. & SCHAR, E. 1978. The x-ray technique as applied to dendroclimatology. Tree-Ring Bulletin 38:61-91.
- SHIELDS, L.M. 1950. Leaf xeromorphy as related to physiological and structural influences. The Botanical Review 16:399-447.
- STEELE, J.H., IFJU, G & JOHNSON, J.A. 1976. Application of stereological techniques to the quantitative characterisation of wood microstructure. Journal of Stereology 3:245-256.
- STYER, C.H. & STERN, W.L. 1979. Comparative anatomy and systematics of woody Saxifragaceae Deutzia. Botanical Journal of the Linnean Society 79:291-319.
- VAN DEN OEVER, L., BAAS, P. & ZANDEE, M. 1981. Comparative wood anatomy of Symplocos and latitude and altitude of provenance. International Association of Wood Anatomists Bulletin (n.s.) 2:3-24.

- VAN DER GRAAFF, N.A. & BAAS, P. 1974. Wood anatomical variation in relation to latitude and altitude. Blumea 22:101-121.
- VAN STEENIS, C.G.G.J. 1981. Rheophytes of the world. An account of flood-resistant flowering plants and ferns and the theory of autonomous evolution. Sijthoff & Noordhoff, Alphen a/d Rijn.
- VAN VLIET, G.J.C.M. 1979. Wood anatomy of the Combretaceae. Blumea 25:141-223.
- VERSTEEGH, C. 1968. An anatomical study of some woody plants of the mountain flora in the tropics (Indonesia). Acta Botanica Neerlandica 17:151-159.
- WALSH, M.A. 1975. Xylem anatomy of Hibiscus (Malvaceae) in relation to habit. Botanical Gazette 13:56-71.
- WEBBER, I.E. 1936. The woods of sclerophyllous and desert shrubs and desert plants of California. American Journal of Botany 23:181-188.
- WHEELER, E.A. & R.G. PEARSON 1985. A critical review of the IAWA standard list of characters formatted for the IDENT programs. International Association of Wood Anatomists Bulletin (n.s.) 6:151-160.
- WHITEHEAD, F.H. 1957. Wind as a factor in plant growth. IN: J.P. Hudson (ed.) Control of the environment :59-70. Butterworth, London.
- YANONSKY, T.M. 1984. Documentation of high summer flows on the Potomac River from the wood anatomy of ash trees. Water Resources Bulletin 20:241-250.

ZINNERMAN, M.H. 1982. Functional xylem anatomy of angiosperm trees. IN: P. Baas (ed.) New Perspectives in Wood Anatomy. Nijhoff/Junk, The Hague.

ZINNERMAN, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

C H A P T E R 5

APPLICATION OF THE EDXA-APPROACH IN ANALYSIS OF CHARCOAL  
ASSEMBLAGES FROM BOOMPLAAS CAVE

I N D E X

ABSTRACT

INTRODUCTION

MATERIAL AND METHODS

RESULTS AND INTERPRETATION

CONCLUSIONS

REFERENCES

ABSTRACT

The methodology of an approach to xylem analysis described in Chapter 4 is applied in the analysis of charcoal assemblages from Boomplaas Cave, Cango Valley, southern Cape. Assemblages from nine cave members, from member BLD (ca 2500 B.P.) to member BOL (ca 60 000 B.P.) are analysed in this way. The data produced are examined in three ways; firstly, as the mean values for a selected set of EDXA variables for the whole assemblage; secondly, as the mean values for a selected set of EDXA variables for individual morphological types per assemblage and; thirdly, as a detailed analysis per assemblage of the

distribution of dimensions in the tracheary system of a constructed "typical" or average area of xylem tissue for that assemblage.

The inferences that can be placed on the evidence from these three ways of looking at the data are compared and in almost all cases harmonise. The results can be summarised as follows.

From ca 60 000 to 17 000 B.P. a harsh climate, cold and dry prevailed. A major change toward more mesic conditions occurred between 17 and 14 00 B.P. The climate then became optimum, mesic and equable, during the end Pleistocene Zone E, ca 14-12 000 B.P. Subsequently, warmer temperatures were experienced. Within the scale of Holocene climates, xeric conditions were experienced during the mid-Holocene, 7-5000 B.P.. There is evidence for summer rainfall during the late Holocene.

#### INTRODUCTION

The methodology of an approach to xylem analysis termed Ecologically Diagnostic Xylem Analysis, or EDXA, was described in Chapter 4. This chapter reports the results of a first trial application of the method to the study of fossil charcoal assemblages. Assemblages analysed were those from nine occupation units from Boomplaas Cave, Cango Valley, southern Cape.

The setting of the site and the archaeological analysis of its sediments are described in Deacon HJ (1979), Deacon JCG (1982) and Deacon

et al (1983). The cave is situated on the southeast facing slope of a low limestone hill, Drupkelderkop (33° 22'S, 22° 11'E), within the Cango Valley and about 60 m above the floor of the valley of the perennial Grobbelaars River. The cave sediments are well stratified and occupation units are often clearly separated by sterile units (Fig.3.1). A series of 22 radiocarbon dates provides reliable chronological control within the last ca 40 000 yrs. Apart from the lithic analysis (Deacon J 1982), the sediments have been analysed by Webley (1979), the macrofauna, by Klein (1983) and the microfauna by Avery (1982).

EDXA is a computer based system designed to measure a range of functional wood anatomical variables visible in the transverse section. The rationale for its use in the analysis of the anatomy of fossil wood is that modern day comparative studies have shown that predictable relationships exist between wood anatomical and eco-climatic variables (Carlquist 1977). Most of the analysis reported in this paper is based on the mean values for various variables which measure the functional attributes of the tracheary system. At present the xylem analytical approach can be used as a relative method to diagnose components of past climates from the analysis of wood anatomy.

#### MATERIALS AND METHODS

The basic sampling and processing of material from

Boomplaas Cave has been described in Chapter 3 in the context of the MTRA-type analysis. It must be emphasised again that the sampling, processing and photography was designed for the purposes of the latter approach. The EDXA approach was developed only later in the research program.

A set of 670 photomicrographs of transverse sections with total magnification of either 75X or 150X was submitted to Minimum Piece Diameter Analysis (MPD analysis) and the results are reported in Chapter 6. Branch diameter size estimates for each of these pieces were obtained and the branch diameter size class distribution data are summarised in Fig.5.1. Since a relationship exists between branch diameter and wood anatomy, these MPD measures are integral to the EDXA approach.

The subsequent sampling for EDXA was as follows; Only photomicrographs of relatively well preserved areas of xylem tissue were considered and within each morphological type (MT 1-30), the five (if possible) pieces with the largest estimated branch diameters (more accurately, the MPD values indicate distance from the pith) were selected for each assemblage.

It was decided to analyse the pieces originating from the largest size of branches for two reasons. Firstly, the anatomy of mature wood is a more reliable reflection of the adaptation of the structure than immature wood. Secondly, any other selection criterium, for example selecting pieces of a standard diameter,



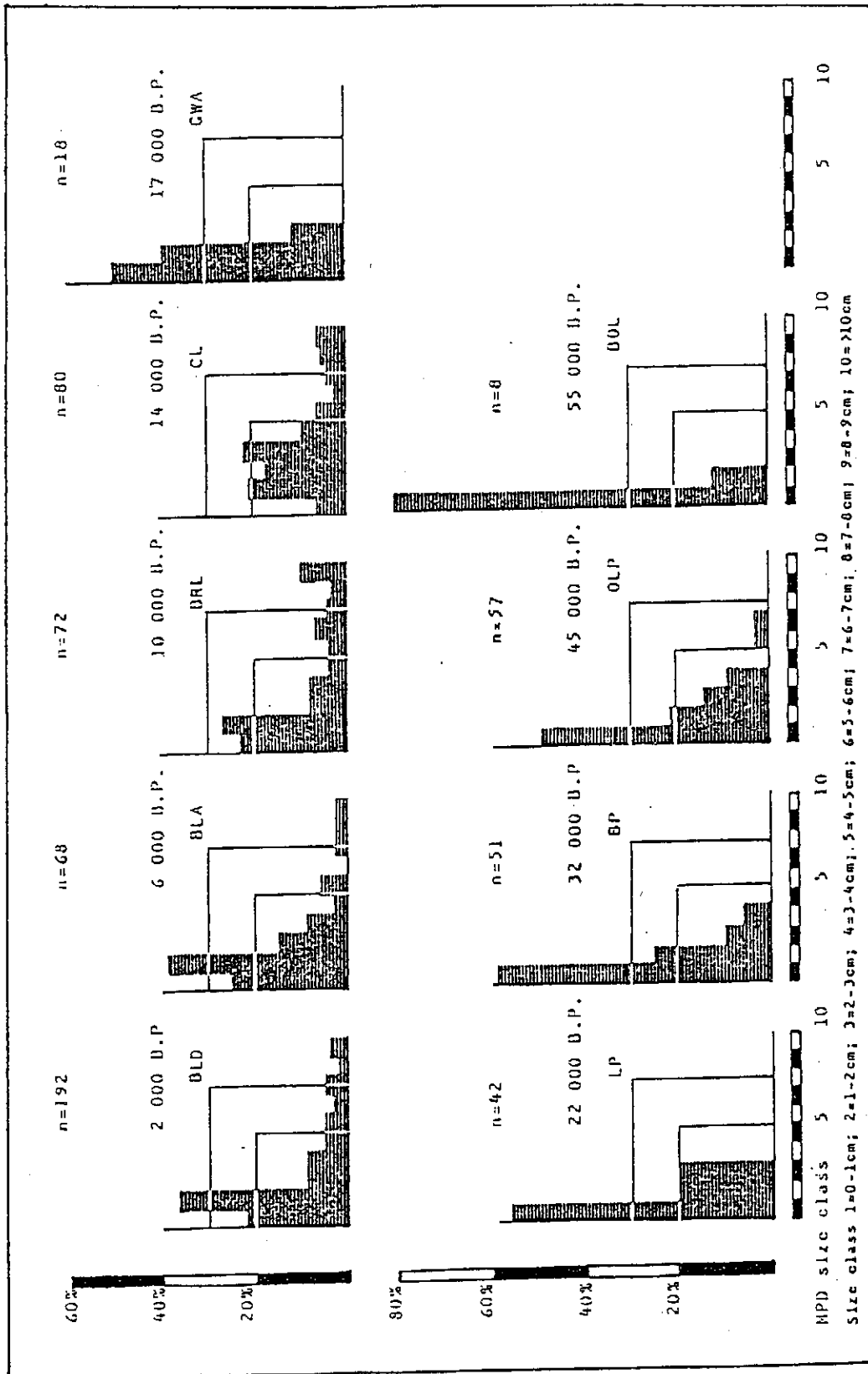


Fig.5.1 Minimum piece diameter (MPD) size class distribution for assemblages from Boomplaas Cave (graphed by assemblage)

would have introduced an artificial bias into the samples.

Of course, due to the large differences in mean MPD values, some bias already exists in the assemblages, and this factor must be evaluated. To the extent that these differences reflect differences in the natural spectra of dry wood, they reflect the carrying capacity of the environment, and should not adversely affect the comparability of EDXA values. In other words, mature wood from different environments is being compared. To the extent that differences in mean MPD values reflect human selection (see Chapter 6), the diagnostic value of the EDXA variables is reduced. In this trial application the full set of EDXA variables described in Chapter 4 were not used; due to the poor state of understanding of the relationship between the mechanical support tissue (fibres), the other subsystems of the xylem and ecological variables, this subsystem was not analysed.

To illustrate the method of the EDXA system in practice, Table 5.1 provides a list of program EDXA2 prompts and examples of actual inputs. Fig.5.2 illustrates the transverse sectional areas of xylem tissue analysed in the examples together with the resultant values for selected EDXA variables.

The analysis proceeded on two levels; analysis by assemblage (Figs 5.3-5.5) and analysis by morphological type (Figs 5.6-5.10). Mean values and means of means are used in these analyses in order to exclude the components

Table 5.1 List of computer prompts and examples of inputs

EXAMPLES OF INPUTS				
COMPUTER PROMPT	piece no.	piece no.	piece no.	piece no.
	35	701	455	523
	assemblage	assemblage	assemblage	assemblage
	BLD	BLD	BLD	LP
Piece number ?	35	701	455	523
Morphological type ?	1	24	14	18
Assemblage ?	BLD	BLD	LP	LP
Photograph orientation ?	2	2	3	2
Magnification ?	75	75	150	75
Shrinkage factor ? (Y/N)	1	1	1	1
Piece radius (in cm) ?	237	128	95	144
Point count total ?	360	180	180	165
Point count (large vessels) ?	43	17	28	-
Point count (medium vessels) ?	-	10,5	39	19
Point count (small vessels) ?	11	-	8,5	-
Point count (ray tissue) ?	48,5	36	11,5	33
-----				
VESSEL DIAMETERS				
Large vessels (in mm)	9,5x9,2 8,5x8,1 9x8,4 9,1x7,2 7,6x5,1 8,6x5,2 7,3x5 6,9x5,5	7,4x7,4 6,8x6,8 6,8x5,9 4,9x6,6 5x5,5 5,2x5,2 4,4x4,7 5,1x4,9	7,8x8,6 10x6,6 6,9x6,4 7,6x5,5 6,2x6,2 7x5,2 6,3x6,9 6,9x5,4	- - - - - - - -
Medium vessels (in mm)	- - - - - - -	4x2,7 2,7x3 4,2x3,4 4,1x3 3,2x3,9 2x3,9 3,6x2,7	6x4 5,6x4,4 4,4x5,5 3,9x3,5 4x5,4 4,3x5 3,8x3,7	2x1,5 1,6x1,3 1,1x1,1 0,5x0,6 0,9x0,9 0,8x0,8 0,5x0,5 1x1,2
small vessels (in mm)	5,6x3,1 4,5x2,6 6,3x4,7 3,4x3,8 5,5x2,7 3x3,6 3,7x3,3	- - - - - - -	4,2x3 3,9x2,8 3,7x3 3,2x3,3 4x2,9	- - - - - -
No. of tangential structures?	0	0	1	4
No. of rays?	13	6	15	19
Mean ray width (in mm) ?	6	7,85	1,4	3
Mean ray seriate?	10	2,5	1	4
-----				
Fibre tissue (Y/N) ?	1	1	1	1
Magnification ?	75	75	150	75
Shrinkage factor ?	1	1	1	1
Dimensions of image ? (L x b; in mm)	15x15	15x15	15x15	15x15
Point count total ?	100	100	100	100
Point count lumen ?	25	40	29	21
No. of fibre cells?	304	75	152	480

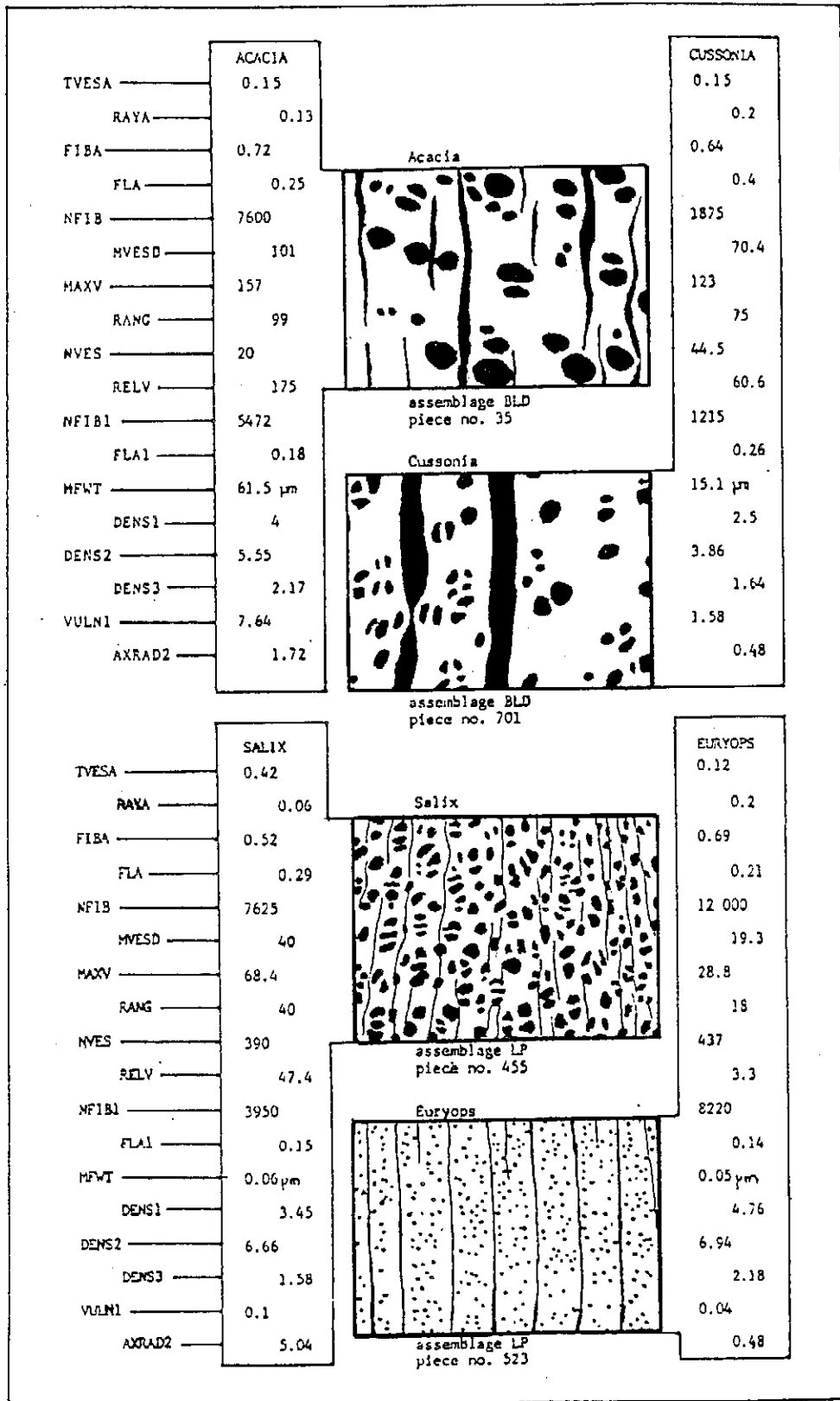


Fig.5.2 EDXA analysis of four areas of xylem tissue

of variability attributable to factors other than climatic (see discussion in Chapter 4). In the analysis by assemblage, the possible effects of the factor of human selectivity on the EDXA variables are reduced by calculating the mean values for each assemblage the basis of each morphological type being counted as one. These values are therefore only affected by human selection as far as selection of particular types and branch size diameters is concerned. The analysis by morphological type was done for those types which were adequately represented in more than one assemblage. The two levels of analysis provide complementary evidence, with the analysis by morphological type to some extent avoiding the component of variability related to phylogeny and divergent xylem strategies, while the analysis by assemblage is valuable because it is based on mean values for relatively large samples.

RELV distribution data are graphed in Figs 5.4 to 5.10. These graphs serve as descriptive tools for analysis of the distribution of dimensions in the tracheary system. Although the two types of graph both make use of the RELV variable, it is important to note that they are quite different sorts of graphs and provide different information (for a full discussion of RELV see Chapter 4. RELV is the sum of the relative conductivity of all the vessels per square  $\text{mm}^2$  of xylem tissue. The RELV of an individual vessel is proportional to the fourth power of the internal radius of that vessel). In

the first type of graph (RELV:vess, Fig.5.4A and 5.5A & B), the distribution of RELV in an assemblage is plotted by its total percentage representation per vessel diameter size class (Figs 5.4A and 5.5A & B). Size class increments of 0,005 mm or 0,002 mm are used and the vessel size range is from 0,005-0,250 mm. In the second type of graph (RELV:relv), the RELV values for all the pieces in an assemblage are size classed and their relative abundances per size class are graphed (Figs 5.4B and 5.5C). Since a very left skewed range of RELV values is typical, three different scales are required to portray the full range of values on the latter graph. Simply put, the RELV:vess type graph indicates the distribution and preferred size of vessels, while the RELV:relv type graph indicates the distribution and preferred range of RELV values.

The RELV:vess distribution data, the most sensitive descriptive analysis of the tracheary system used in this study, was calculated in two ways. Firstly, as already stated, with each type counting equally (each type=1) and, secondly, using the associated relative abundance factors for each type (Fig.5.5A & B respectively). A comparison of the results indicates that the EDXA analysis by assemblage is little affected by changes in the proportion of constituent types. To some degree this evidence supports the contention that relationships exist between wood anatomy and ecology which override phylogeny.

Throughout this chapter values for EDXA variables

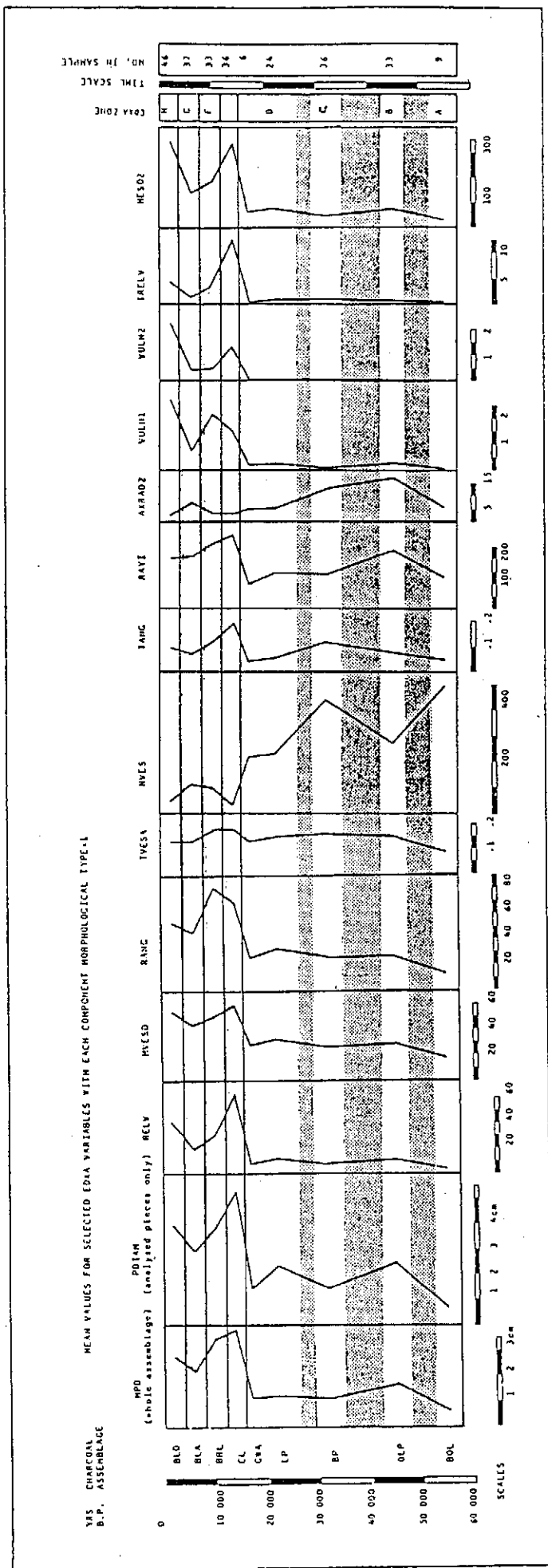


Fig.5.3 EDXA analysis by assemblage : mean values for a selected set of variables for nine assemblages from Boomplaas Cave dating within the last ca 60 000 years

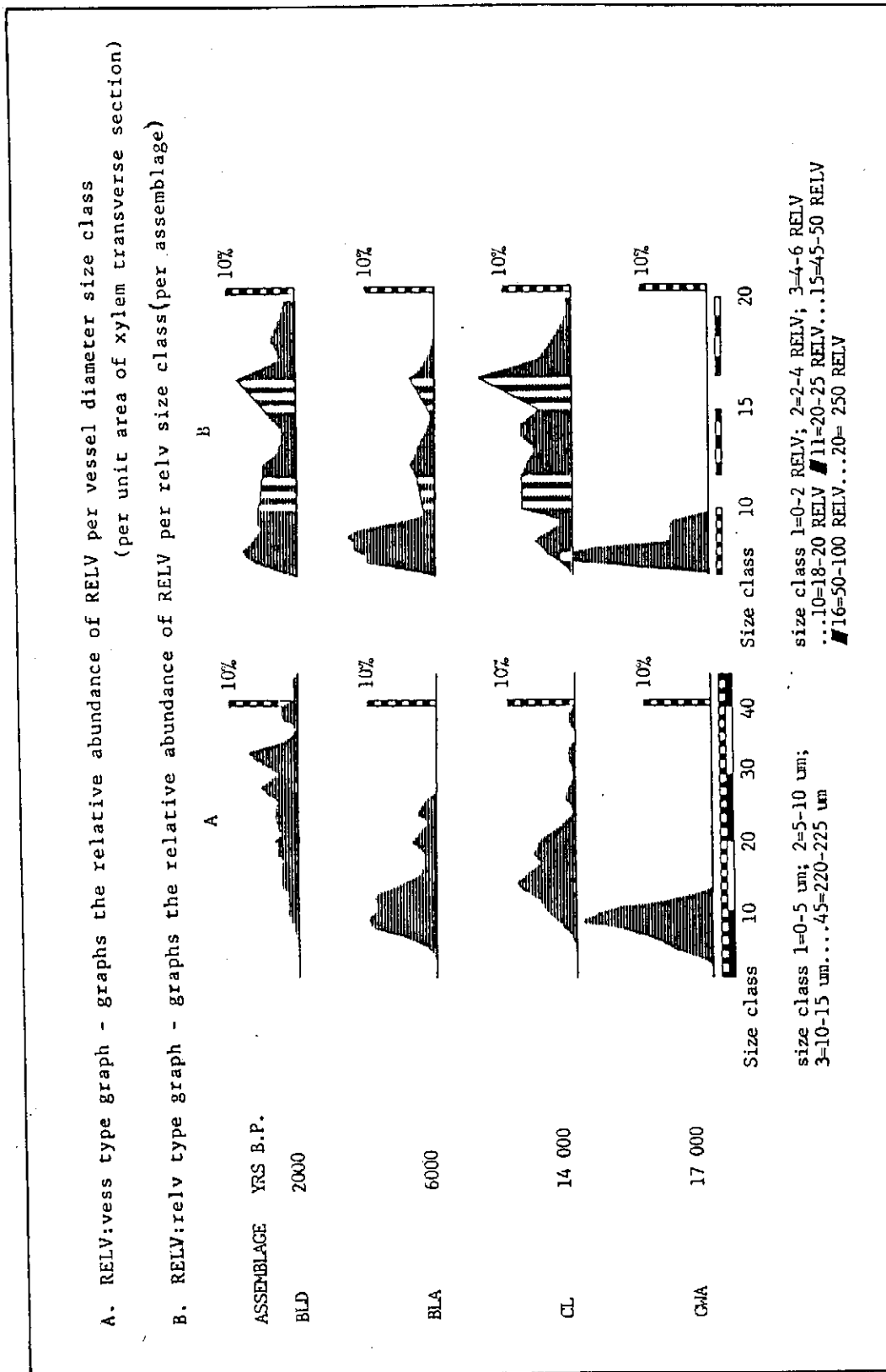


Fig.5.4 Examples of RELV:vess and RELV:relv type graphs (examples from the analysis of Boomplaas Cave)



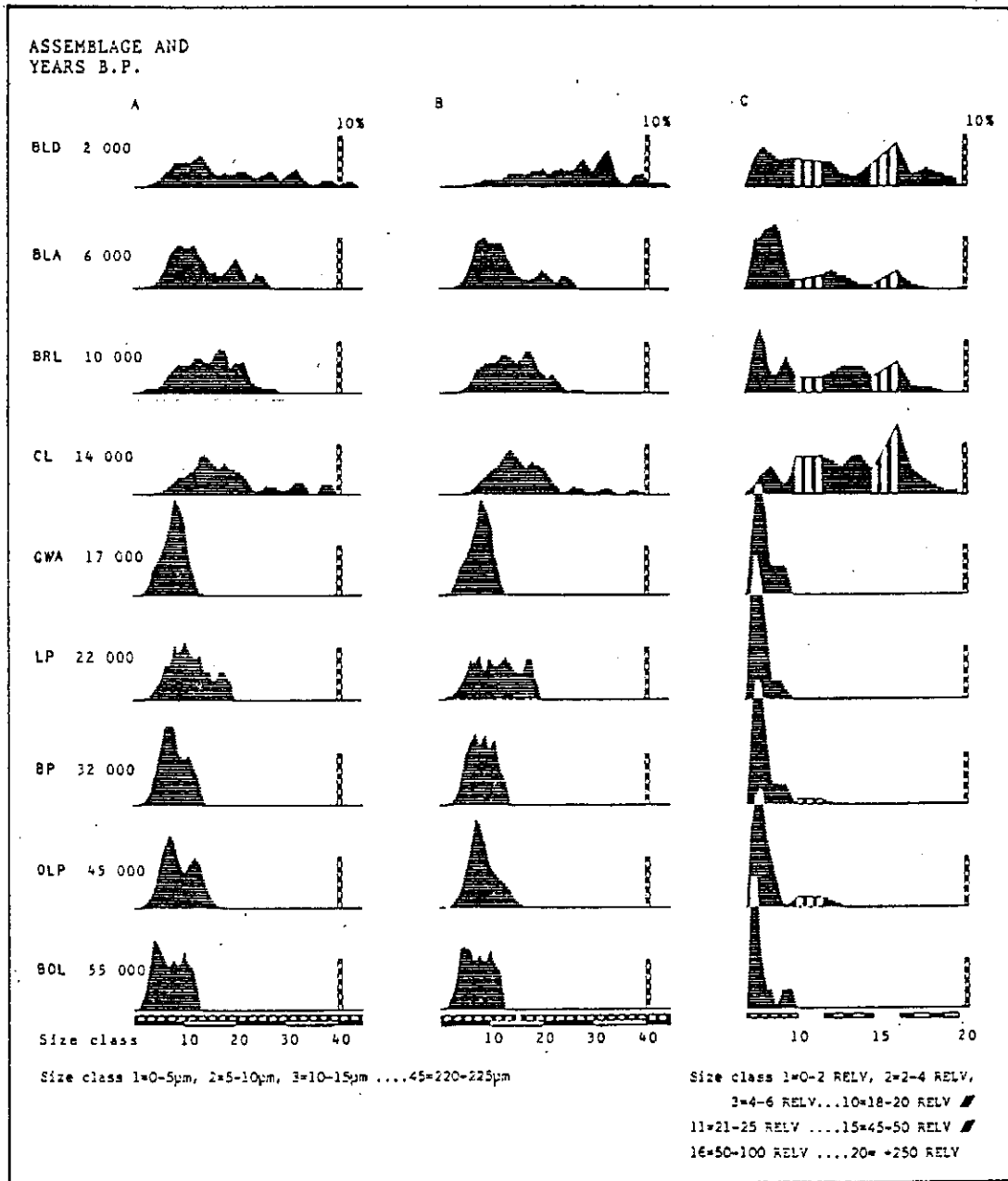


Fig.5.5 RELV:vess and RELV:relv type graphs for assemblages from Boomplaas Cave

5.5 A RELV:vess (distribution of total RELV per vessel diameter size class) with each morphological type = 1

5.5 B RELV:vess graph with the contribution of each morphological type multiplied by its relative abundance per assemblage

5.5 C RELV:relv type graph for each morphological type = 1

are treated as relative values. In other words, change is interpreted. This approach will not always be necessary. The limitation is at present imposed by the fact that little work has been done on recent woody florules from southern Africa in order to specify relationships between wood anatomical and ecoclimatic variables. When such background work is available, values for EDXA variables, both on the assemblage level and for specific taxa, will become interpretable as absolute values.

Table 5.2 lists the wood anatomical (EDXA) variables used in this study and their suggested ecoclimatic significance. Given the present state of ignorance concerning the correlation between climate and wood anatomy for woody florules from southern Africa, it is not known how reliable these relationships are in the local context. In this study however, being the first trial application of the approach, the suggested relationships have been freely used in interpreting (in a relative sense) the changes in the value of variables recorded in the sequence. As stated, studies on present day woody florules will demonstrate the strength and precise value of the relationships. At this stage of research some measure of reliability is lent by the fact that in most cases all lines of evidence produced by the analysis suggest similar palaeoclimatic inferences.

## RESULTS AND INTERPRETATION

The results are discussed by EDXA period as indicated in Fig.5.3. For each period the evidence is

Table 5.2 List of wood anatomical variables and their suggested significance

<p>The definition and suggested ecoclimatic significance of selected EDXA variables (see Chapter 4 for a description of methodology)</p>	<p>growth increments or the frequency of the intervention of factors limiting to growth. Low values indicate xeric conditions</p>
<p>MF0 The mean minimum piece diameter reflects the size of branches in a total assemblage and as such, the structure of vegetation. Larger values indicate the presence of trees</p>	<p>RAYA High values for the mean ray area are predicted to relate to high growth rates and tall vegetation</p>
<p>FD/AM The mean piece diameter of the pieces chosen for analysis alone</p>	<p>RAYI (RAYA <math>\times</math> the no. of rays per tangential mm)</p>
<p>RELV The mean relative conductivity is at present the best comparative measure of the capability of the tracheary system to transport sap. To the extent that this ability correlates with the availability of water, it is, in terms of wood anatomy, the best proxy measure of precipitation</p>	<p>AXRAD2 (TVESA/RAYI) This ratio measures the relative investment of energy in the axial versus radial system. High values may indicate stunted and spindly vegetation.</p>
<p>MAXV Mean maximum vessel size is also a measure of the capabilities of the tracheary system, but, more specifically, high values indicate high temperatures (high sun) during the growing season</p>	<p>VULNI (MVESD/NVES) Increased values for this ratio have been demonstrated by Carlquist (1977a,b) to indicate increasing vulnerability to drought (or cold).</p>
<p>MVESD The average mean vessel diameter is an important variable descriptive of the tracheary system since it allows the separation of two basic types of xylem variability, namely those based on altering MVESD and those based on altering NVES</p>	<p>VULN2 (RELV/NVES) This ratio is similar to VULNI, but, since RELV is a less composite measure than MVESD, may be a more reliable measure.</p>
<p>RANG A high value for the mean size range of vessels indicates either a warm, mesic climate with one dry season, or a cool, wet climate. Low values indicate cold and/or dry conditions</p>	<p>TRELV (TANG*RELV) This index combines a measure of the quality of the tracheary system with a rough estimate of the associated quantity produced per unit of time. (If TANG were measured as width of growth rings sensu stricto this would be a more reliable measure.)</p>
<p>TVESA Only climatic changes of some magnitude, or marked changes of habit affect the mean total vessel area per mm. Higher values indicate mesic conditions and high growth rates</p>	<p>MESQ2 (RELV/TVESA) This index provides another measure of the capabilities of the tracheary system.</p>
<p>NVES High values for the mean number of vessels per mm indicates adaptation to drought or low temperatures</p>	<p>RELV:ves (RELV distribution/vessel diameter size class) This type of distribution data provides a quantitative description of the distribution of functional dimensions in the tracheary system. This is more sensitive than summary statistics such as RELV or MVESD in registering and defining change in a system</p>
<p>TANG The mean width of tangential structures measures the size of radial</p>	<p>RELV:relv (RELV distribution per RELV size classes) This data describes the range and distribution of xylem strategies tolerated in a certain environment. Together with the RELV:ves distribution, RELV:relv provides an ecoclimatically sensitive description of the general capabilities of the tracheary systems selected by an environment.</p>

discussed as follows; firstly, in terms of the mean values for selected EDXA variables per assemblage (Fig.5.3); secondly, in terms of the evidence per morphological type per assemblage (Fig.5.6-5.10); and thirdly, in terms of the two types of RELV distribution data, RELV:vess and RELV:relv, per assemblage (Fig.5.5). The last paragraph in the discussion of each EDXA zone notes the correlations between palaeoclimatic inferences drawn from the EDXA data with those drawn from other lines of evidence. This latter evidence is summarised in Table 5.4.

EDXA ZONE A: ca 65 000-55 000 B.P. ASSEMBLAGE BOL (BOL, BOL.ys, BOL.bo(n=9)).

Mean values for selected EDXA variables (Fig.5.3)

The sample is small and comes from only one hearth feature and MPD and PDIAM have minimum values. All other variables except NVES also have minimum values. The characteristic wood anatomy for this zone shows numerous small vessels (NVES, MVESD), no large vessels (MAXV), a low size range of vessels (RANG), low total vessel area (TVESA), closely spaced tangential structures (TANG) and numerous rays per tangential mm (inferred from RAYI). This set of features suggests that the harshest climates of the last ca 60 000 years were experienced during Zone A.

However, the small size of the sample, the age of the material and the minimum MPD value suggest that these

Table 5.3 Correlating the palaeoclimatic inferences based on MTRA and EDXA-type analyses for the Boomplaas sequences

ASSEMBLAGE AND DATING	MTRAA: PERIOD AND EVIDENCE	EDXA: PERIOD AND EVIDENCE
BLD 2000 B.P.	E: dominance of <i>A.karoo</i> , <i>Nymania</i> and <i>Rhus cf. undulata</i> suggests warm and relatively dry conditions.	H: mesic, warm and wet with summer rainfall, low resistance to drought but some stress relative to E.
BLA 6000 B.P.	D3: high diversity index; thicket taxa indicate a hot, relatively dry climate; dense shrubby vegetation.	G: shrubs rather than trees; xeric conditions; episodic rainfall and low annual precipitation; spindly growth form and high resistance to drought.
BRL 10 000 B.P.	D2: slightly warmer than D1 with shrubs on the hillsides; precipitation similar or slightly lower than D1.	F: less mesic than E; climate less equable especially in summer; more seasonal climate with increased incidence of drought and/or frost.
CL 12- 14 000 B.P.	D1: dominance of <i>Olea/Dodonea</i> and <i>Rhus</i> spp. high representation of <i>Salix</i> and virtual absence of <i>Compositae</i> indicate trees on floodplain or in riverine or sheltered habitats and few shrubs on the hillsides.	E: trees well represented; climate very equable and mesic; high precipitation, tall, fast growing vegetation and large growth increments.
GWA 17 000 B.P. LP/LPC 22 000 B.P.	C: assemblages dominated by shrubby, karroid or subkarroid composite taxa; low diversity, cold and especially dry conditions.	D: episodic summer rainfall warmer temperatures and more moisture than in C during the growing season; extremely low rainfall in GWA; harsh climate and woody vegetation consisting exclusively of shrubs.
B.P. 32 000 B.P.	B: <i>Olea/Dodonea</i> absent, and <i>cf. Erica</i> dominant; cold, perhaps Alpine conditions and little woody vegetation.	C: cold and also dry conditions; winter rainfall only; small, spindly shrubs.
OLP ca.45 000 B.P.	A: <i>Olea/Dodonea</i> , <i>Elytropappus</i> -type and <i>cf. Erica</i> dominant; climate less harsh than in Periods B and C, but not as mesic as during the end Pleistocene and Holocene	B: higher precipitation than in A; some indications that this period is considerably more mesic than other periods in the late Pleistocene; slow growth rates and spindly vegetation; precipitation perhaps similar to period G.
BOL ca.55 000 B.P.	A: see above	A: very harsh climate; cold and dry but not as cold as in Periods C and D; slow growth rate for <i>Olea</i> .

results should be treated with caution. The small size of branches could reflect the carrying capacity of the environment, or be partly an artefact of human selection. Since wood of a twig-sized branch from a plant can often be more dense than the wood of a larger branch, wood of twig-sized material might be preferentially preserved through time. On the other hand, other lines of evidence (see Table 5.4) support the suggestion of a harsh climate during this time period.

#### Analysis by morphological type

##### i. MT 12 (Olea/Dodonea) Fig.5.6

The mean values for all EDXA variables confirm the analysis by assemblage. The wood structure probably reflects a slow growth rate and early onset of lignification. The RELV:vess distribution data indicates a harsh climate.

#### RELV distribution by assemblage (Fig.5.5)

The RELV:vess distribution confirms the small size class and size range of vessels in Zone A. The RELV:relv distribution indicates a uniformly low capacity to transport sap.

#### Correlations with other lines of evidence (Table 5.4)

Low site usage may indicate a poorly productive environment. The microfaunal evidence suggests open vegetation, semi-arid shrubland on the valley floor, grass on the hillsides and a cold climate. This evidence complements the evidence from xylem analysis

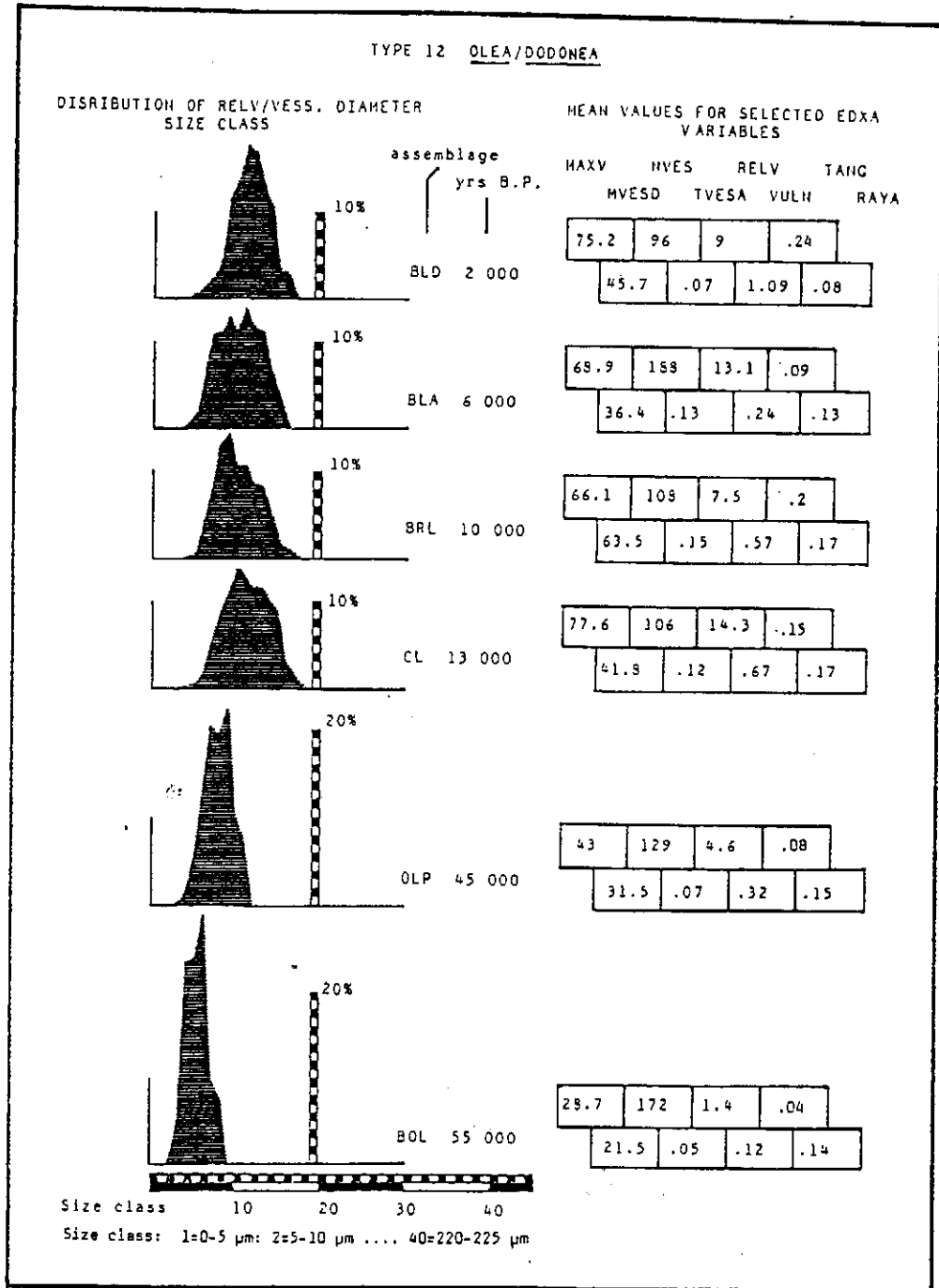


Fig.5.6 EDXA: values for selected variables, MT12

EDXA ZONE B: ca 55 000-40 000 B.P. ASSEMBLAGE OLP OLP,  
OLP1, OLP2, OLP3, OLP.b(n=33)

Mean values for selected EDXA variables by assemblage  
(Fig.5.3).

A much larger assemblage could be analysed and PDIAM is double its value in the previous zone. RELV, NVESD, RANG, TVESA, TANG, VULN1 and MES02 all increase slightly, indicating increased precipitation, while NVES declines sharply, perhaps indicating, in addition, less cold stress. High values for RAYI and AXRAD2 distinguish this zone. This may reflect low growth rates and little secondary thickening. It is suggestive that these features are not recorded for Zone A, for which a harsher climate is indicated.

Analysis by morphological type

i. MT 7 (Buddleia glomerata) Fig.5.7.

The wood structure of this taxon is remarkably stable and the vessel size range is always small. The smaller scale (vessel diameter size class increment) has therefore been used in the RELV:vess graph for this type. The RELV:vess distribution data indicate most mesic conditions in Zone B relative to other periods for which there are samples for this morphological type. The RELV value is also highest in this Zone, the TANG value indicates a comparatively equable climate, but the NVES value associates this Zone with Zones G and F. In the case of Zone B the relatively low NVES and VULN scores probably



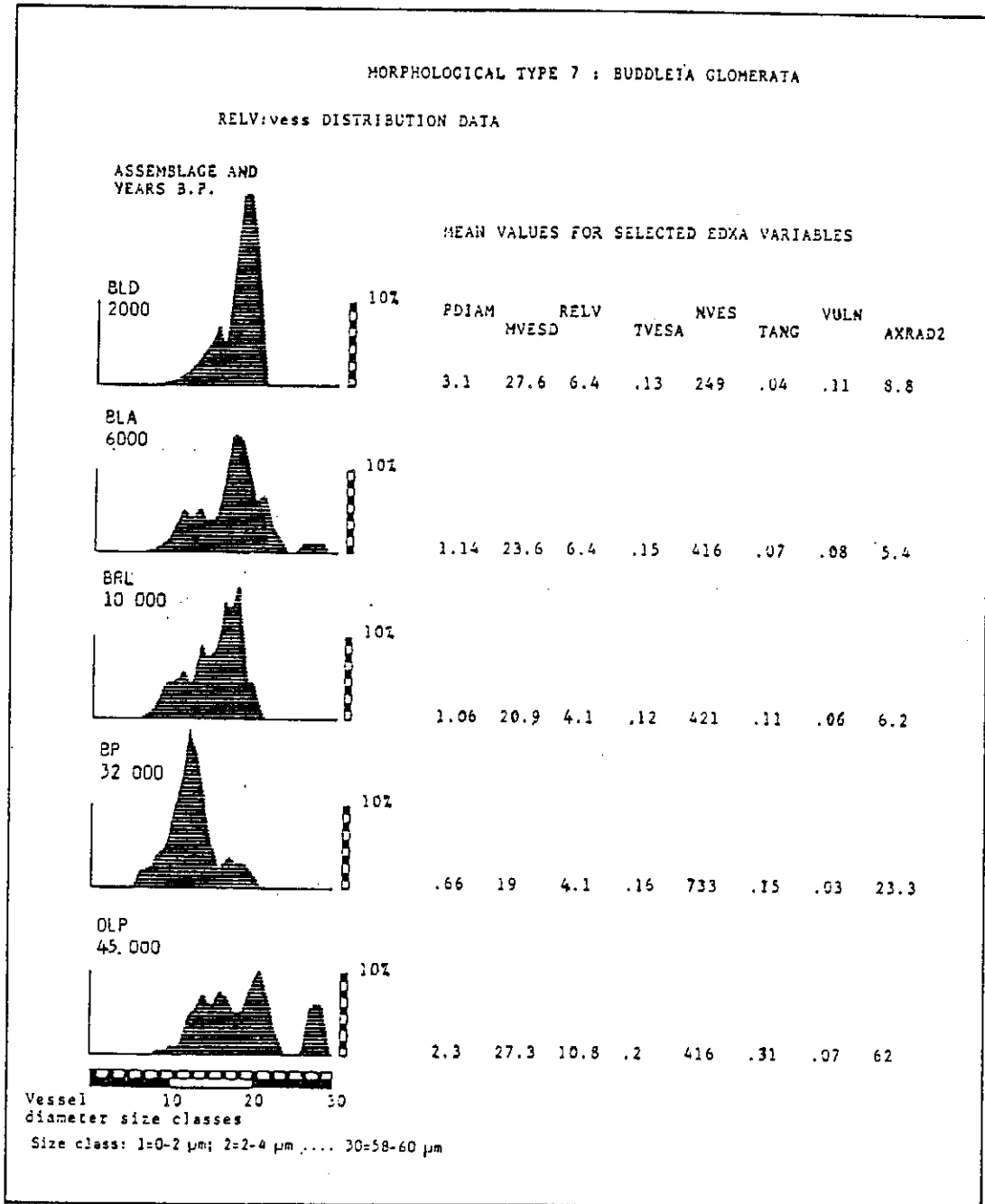


Fig.5.7 EDXA: selected variables, MT7

indicate adaptation to cold. The high AXRAD2 value suggests a thin, spindly growth form.

ii. MT 12 (Olea/Dodonea) Fig.5.6

This is the only type recorded in abundance in both the end Pleistocene to Holocene (CL-BLD) and late Pleistocene (BOL-OLP) time periods. MAXV, MVESD, RELV and TANG are higher in Zone B than Zone A, but are still lower than in Zones E to H (CL-BLD). The average wood anatomy of MT 12 in Zone B most closely approaches that of Zone G (BLA), but from the RELV:vess distribution data it can be seen that a wider size range of vessels is present in Zone G and that RELV is concentrated in smaller vessel size classes in Zone B. This suggests that, although wetter than Zone A, the climate in Zone B is still relatively cold and/or drv.

iii. MT 20 (cf. Erica) Fig.5.9

All data indicate a similarity between the wood of this type in Zones B and C in contrast to the Zones D and E. In the former Zones, relatively cold and/or dry conditions are indicated.

RELV distribution by assemblage (Fig.5.3)

The distribution is similar to that of Zone A, although some pieces with a slightly higher total RELV value (Fig.5.5C) are recorded.

Correlations with other lines of evidence (Table 5.4)

The microfauna indicate a moderate climate with grass and semi-arid shrubland on the hillslopes and denser vegetation on the valley floor. The macrofauna indicates

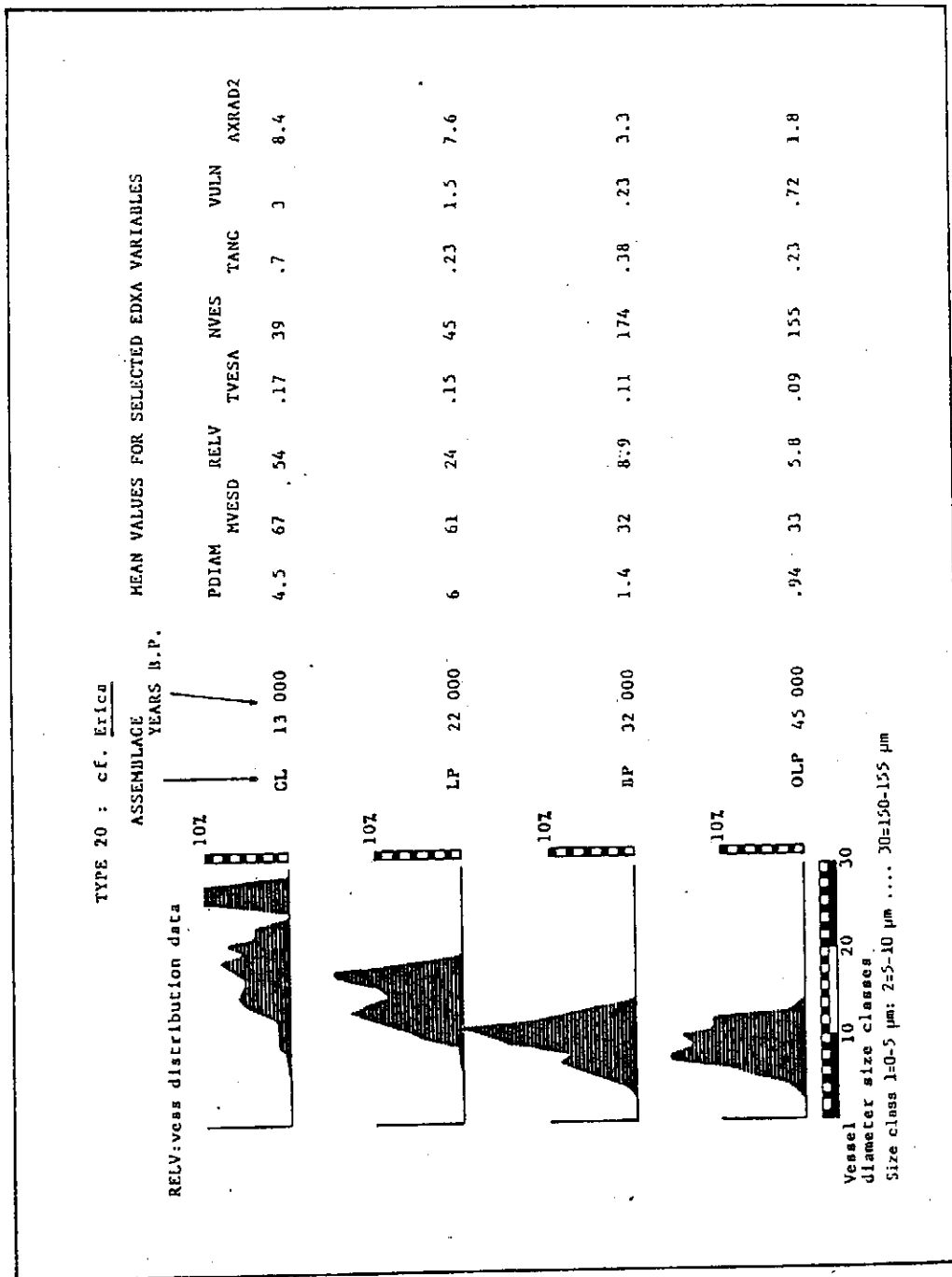


Fig.5.8 EDXA: selected variables, MT20

a browsing fauna. The microfaunal evidence corresponds well with the evidence gained from xylem analysis.

EDXA ZONE C: ca 33 000-26 000 B.P. ASSEMBLAGE BP (BPH, BPK, BPR (n=36)

Mean values for selected EDXA variables by assemblage  
(Fig.5.3)

Compared to the other late Pleistocene periods, Zone C is distinguished by a high value for NVES and TANG. The former suggests cold conditions and the latter, either the rare occurrence of conditions limiting to growth or a non-erratic climate. This may indicate winter rainfall. The values for other variables in Zone C are slightly lower than elsewhere in the late Pleistocene, except for Zone A. The set of features for Zone C suggests that annual precipitation was similar to that of Zones A and D and slightly lower than during Zone B, but that this precipitation may have been received only during winter. The low MPD value indicates a vegetation composed exclusively of (probably small) shrubs with thin branches.

Analysis by morphological type

i. MT 7 (Buddleia glomerata)

As already indicated the wood morphology of this species is relatively stable, but the RELV:vess graphs show a distribution concentrated in the small vessel size classes. All other data (NVES, RELV, MVESD, RANG, VULN)

also indicate adaptation to high drought or cold stress, particularly the latter, during Zone C.

ii. MT 20 (cf. Erica)

As already noted, the data indicate that a very similar wood morphology occurs during Zones B and C.

RELV distribution by assemblage (Fig.5.5)

The RELV:vess graph is very clear in distinguishing the OLP (Zone B) and BP (Zone C) samples from the LP (Zone D) and CL (Zone E) samples. The distributions of BOL, OLP and BP are constrained to smaller vessel size classes, indicating cold and/or dry conditions.

Correlations with other lines of evidence (Table 5.4)

The microfaunal evidence suggests rapidly changing climatic conditions during the BP time period. High percentages of Otomys saundersae in BP3 and BP4 indicate cold conditions, while Myosorex varius is well represented in BP1, indicating moister conditions and dense vegetation. Alcelaphines dominate the macrofaunal assemblage. The faunal evidence does not contradict the EDXA evidence.

EDXA ZONE D: ca 26-16 000 B.P. ASSEMBLAGES LP/LPC (LP, LPC.1, LPC.2, LPC.B (n=24) AND GWA (n=6)

Mean values for selected EDXA variables by assemblage (Fig.5.3)

Low TANG values especially for GWA indicate an erratic supply of water and may indicate episodic summer rainfall. NVES values are lower than in the other late

Pleistocene time periods and this may be interpreted to mean either generally warmer temperatures or warmer temperatures when water is available for growth, i.e. rain in the warm season. The capabilities of the tracheary system to transport sap remain low (RELV, MUESD, RANG) and it is inferred that precipitation is low.

#### Analysis by morphological type

##### i. MT 20 (cf. Erica) Fig.5.9

The RELV:vess distribution graphs suggest either increased precipitation or rain during the high sun season for Zone D versus Zone C. The more mesomorphic structure of the wood of this type for Zone E versus Zone D is evident.

#### RELV distribution by assemblage (Fig.5.5)

The RELV:vess distribution shows that vessels of a relatively large size are better represented in LP/LPC than GWA. This suggests that the climate was somewhat milder during the former period. Total RELV values are low indicating a harsh cold and/or dry climate.

#### Correlations with other lines of evidence (Table 5.4)

An array of evidence confirms the harsh nature of the climate during this time period. Palynological analysis records low diversity and a dominance of one or two species of Compositae (Scholtz in Deacon et al 1983). A large grazing fauna is recorded and the microfauna indicates a severe climate, very cold winters and a reduction in riverine vegetation. The microfaunal evidence indicates that grassy vegetation occurred on the

hillslopes and the high representation of Mvosorex varius in LPC.2b indicates moist conditions. The indications from EDXA are also that more precipitation was received during LPC times relative to GWA times, at least during the warm season.

EDXA ZONE E: ASSEMBLAGE CL (n=36)

Mean values for selected variables by assemblage

(Fig.5.3)

The values for all variables except AXRAD2 change dramatically between Zones D and E. MPD and PDIAM rise from 10,5 mm to 40 mm and this indicates a change from woody vegetation consisting exclusively of small shrubs to a vegetation in which trees are well represented.

The ability of the tracheary system to manage high rates of flow under low negative pressure is best developed in this period (RELV, TRELV, MVESD and TVESA) and NVES is at a minimum. The former evidence indicates high precipitation and the latter, a low level of drought or cold stress. One may tentatively suggest that the higher values for TVESA during Zones E and F, and the pattern of this graph for the whole sequence, indicate that some higher "adaptive plateau" has been achieved. Apart from Carlquist (1966), who discusses the possibility that "modal states" for the xylem may exist, no studies can be quoted to support the claim for the existence of "adaptive plateau" of the tracheary system. TANG is high, indicating an equable, mesic climate. The low

AXRAD2 value suggests a tall, relatively fast growing vegetation. The reasons why maximum values for RANG and VULN1 are not recorded in CL are discussed in the context of the evidence for the following zone (BRL).

Analysis by morphological type

i. MT 11 (Rhus spp.) Fig.5.10

All variables indicate that the wood of this morphological type is most adapted to mesic conditions during Zone E. The high TANG values indicate large growth increments and little incidence of growth limiting conditions. VULN1 is high indicating that the wood is ill-adapted to withstand drought. The RELV distribution data shows a normal-type distribution with consistent representation in relatively large size classes of vessels.

ii. MT 12 (Olea/Dodonea) Fig.5.6

RELV and MAXV values are highest in Zone E compared to all other periods and the high values for RAYA for Zones E and F suggest the increased degree of secondary thickening that might accompany relatively tall tree growth.

iii. MT 20 (cf. Erica) Fig.5.9

The RELV:vess distribution data clearly show the mesic nature of the wood from CL.

RELV distribution by assemblage (Fig.5.3)

The RELV distribution data adds considerable detail to the reconstruction of the climate associated with Zone E. The change between Zones D and E is striking. Firstly, considering Fig.5.3C, it is clear that Zone E



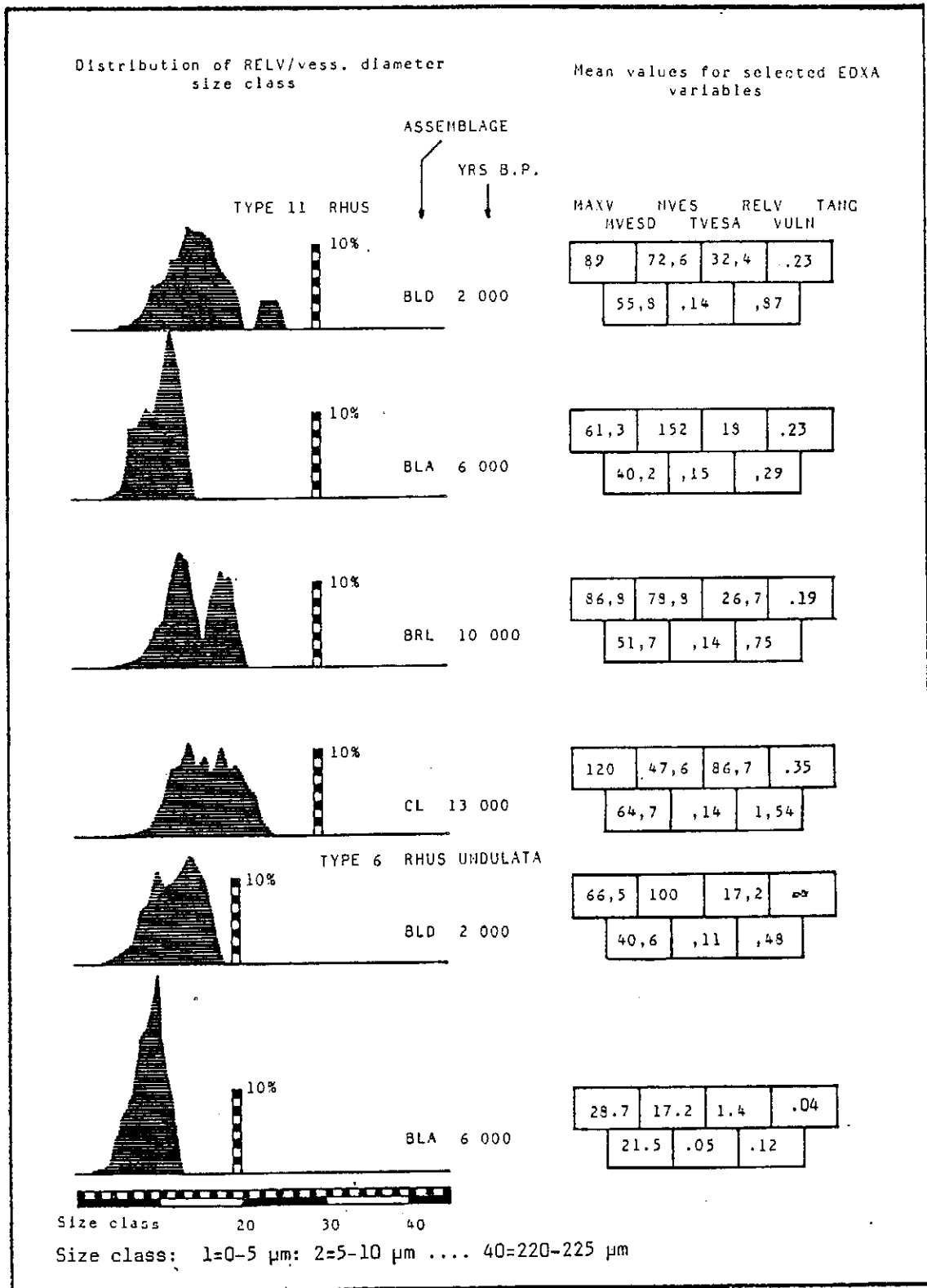


Fig.5.9 EDXA: selected variables, MT11 and MT6

(CL) is best represented in the medium to large RELV classes. Secondly, considering Fig.5.3A & B, it is clear that medium/small sized vessels, rather than relatively large vessels (as is the case in BLD) contribute most towards the total RELV values. One can deduce that the xylem strategy favoured by the climate of Zone E entailed few large or small vessels, but numerous medium sized vessels per mm<sup>2</sup>. A cool, mesic, equable climate is indicated.

Especially for evergreen species, large vessels may be taken to indicate sufficient water for growth during a high sun growing period. Although some large vessels do occur in CL, large vessels are more characteristic of the late Holocene (BLD. Fig.5.5A & B).

#### Correlations with other lines of evidence (Table 5.4)

CL is a thick occupation unit without discontinuities. A high density of artefacts and faunal remains suggests long term occupation and a particularly productive environment. The dominance of a large grazing fauna indicates grassland and the microfaunal evidence indicates dense vegetation on the hill slopes and some increase in temperature relative to LP times.

#### EDXA ZONE F: ASSEMBLAGE BRL (n=39)

#### Mean values for selected EDXA variables (Fig.5.3)

Values for MPD, PDIAM, RELV, MVESD and TANG decrease from their maxima in Zone E and this indicates a climate

in some way less mesic. The relatively sharp decline in TANG indicates a less equable climate, perhaps especially in summer. The higher RANG value indicates that more areas of xylem tissue than was the case in Zone E contain small vessels and this must reflect an increased incidence of drought or frost, more likely the former (denser vegetation can also lead to narrower tangential formations (Phipps 1982)). This is also reflected in an increase in NVES. It is unclear why the VULN1 index should be higher in BRL than in CL, but the VULN2 index may be more reliable.

#### Analysis by morphological type

##### i. MT 11 (Rhus spp.) Fig.5.10

All mean EDXA values for this type confirm the trend apparent on assemblage basis. The increased proportion of smaller vessels and the marked bimodality of the patterns of RELV distribution may indicate a less mesic and more seasonal climate.

##### ii. MT 1 (Acacia karroo) Fig.5.11

The PDIAM values are so different for the three assemblages in which *A. karroo* occurs, that comparisons may be misleading. The high MPD values during the late Holocene Zone H (BLD) probably indicate proximity of the trees (see Chapter 3). All the indications are that the climate during Zone F was more mesic than during the subsequent Zone G, but less mesic than during Zone H.

##### iii. MT 10 (Euclea/Diospyros) Fig.5.12

Once again there is an unfortunately large

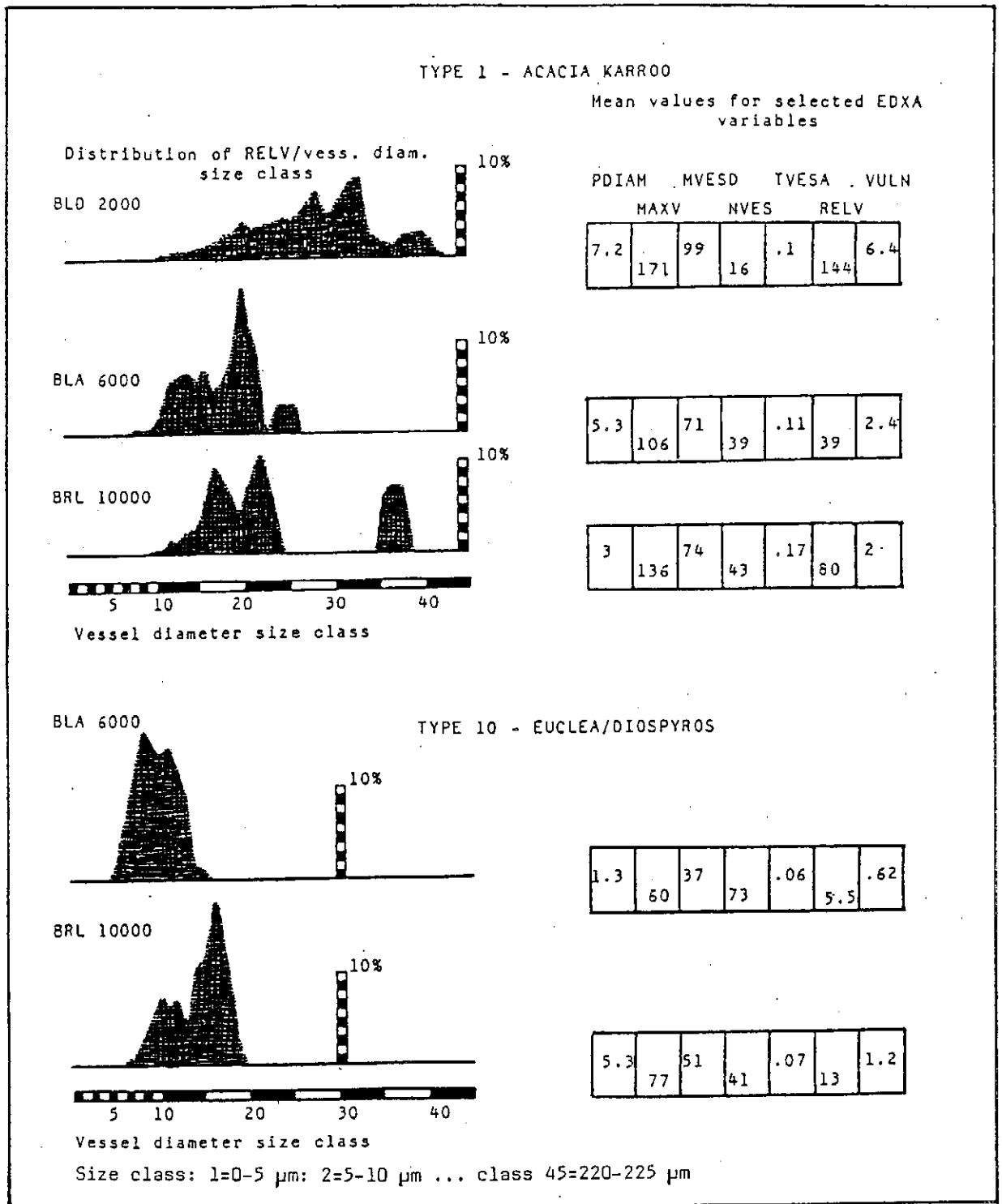


Fig.5.10 EDXA: selected variables, MT1 and MT10

discrepancy between the PDIAM values. All variables indicate that the wood in BRL is considerably more mesomorphic than in BLA.

v. MT 7 (Buddleia glomerata) Fig.5.7

The morphology of this species is remarkably uniform and it is assumed that this indicates a specific and unusually integrated xylem, leaf and root strategy.

vi. MT 12 (Olea/Dodonea) Fig.5.6

The EDXA variables for this type for Zones E-H provide evidence, which, at first glance, might be taken to contradict the evidence from the assemblage-type analysis. Complicating factors may be the small size of the sample in the BLD assemblage and the possibility that more than one taxon is represented in the morphological type, but a third and more important factor is involved.

Attempts to find correlations between wood anatomical and ecoclimatic variables are often predicated on a single classic pattern which is that with increasing drought or cold MVES increases, MVESD decreases and fibres become more numerous etc. An inverse relationship between MVESD and MVES is commonly reported. However, this pattern is only typical of wood whose xylem strategy is focused around changing MVESD. A suggestion made here is that slower growing plants may instead focus on changing MVES. Due to some developmental factor (perhaps related to early onset of lignification and the production of radial bands of extremely lignified fibres) Olea varies MVES more than MVESD. This causes confusing

results, since, if NVES increases in response to drought stress, RELV will be affected and will also increase, suggesting an increase in precipitation.

Nevertheless, the evidence for MT 12 substantially confirms the trends established in the analysis by assemblage. Despite the higher MVESD values in Zone F, the class of larger vessels cause the RELV value for MT 12 in Zone E (CL) to be high. The RELV:vess distribution data record the shift towards smaller vessels in Zone F versus Zone E.

#### RELV distribution by assemblage (Fig.5.5)

In terms of the RELV:relv distribution data, Zone F has much lower representation than Zone E (CL) in the middle to large size classes, while Zone G (BLA) has the most noticeably consistent representation in the small RELV size class. The shift to smaller vessels in Zone G versus Zones F or H is also clear in the RELV:vess graphs. The main difference between Zones E and F is that the latter lacks the larger vessel component and this may indicate less rain in summer during Zone F (BRL).

Together these data indicate that the wood of Zone F is less mesomorphic than that of Zone E, but more mesomorphic than that of Zone G.

#### Correlations with other lines of evidence (Table 5.4)

The archaeological evidence suggests a short term occupation and evidence for a mixed grazing and browsing fauna, in contrast to the pure grazing fauna recorded in

CL. This may indicate denser and more extensive shrubland during the BRL time. This evidence does not contradict the xylem analytical evidence.

#### EDXA ZONE G: ASSEMBLAGE BLA (n=32)

##### Mean values for selected EDXA variables by assemblage

MPD is low suggesting a paucity of trees and the capabilities of the tracheary system (RELV, MVESD, RANG, TRELV) to transport sap at high rates is low. TANG is low, indicating small growth increments and a rise in the AXRAD2 ratio may indicate stunted, spindly growth form. A high value for NVES and a low value for VULN1 and VULN2 indicate resistance to drought and cold. The mean values for the selected EDXA variables all indicate that, during the Holocene, the most xeric conditions were experienced during this time period.

##### Analysis by morphological type

###### i. MT 1 (Acacia karroo) Fig.5.10

All the data indicate clearly that the climate during Zone H was more mesic than during Zone G.

###### ii. MT 6 (Rhus undulata) Fig.5.9

All data indicate that conditions during Zone G were more xeric than during the subsequent Zone H.

###### iii. MT 7 (Buddleia glomerata) Fig.5.7

No significant change is recorded between Zones F, G and H.

###### iv. MT 10 (Euclea/Diospyros) Fig.5.10

The RELV:vess distribution graph and all EDXA

variables indicate more xeric conditions during Zone G relative to the preceding Zone F.

v. MT 11 (Rhus spp.) Fig.5.10

All data confirm the relatively xeromorphic nature of wood in Zone G (BLA).

vi. MT 12 (Olea/Dodonea) Fig.5.6

See discussion for Zone F. The very high NVES value is significant and indicates adaptation to drought and/or cold. The low TANG value indicates small growth increments.

RELV distribution by assemblage (Fig.5.5)

All the data confirm the xeromorphic nature of the wood of this zone.

Correlations with other lines of evidence (Table 5.4)

The inference based on the microfaunal evidence that the climate during this period was mild, is strongly at variance with the evidence gained from xylem analysis.

EDXA ZONE H: ASSEMBLAGE BLD (n=36)

Mean values for EDXA variables by assemblage (Fig.5.3)

The contrasts with Zone G (BLA) have already been mentioned. The high values for VULN1 and VULN2 indicate that the characteristic wood of this zone is not drought or cold resistant. Given the indications for higher precipitation (RELV, TRELV) in the end Pleistocene Zone E, this latter evidence may indicate both adequate water and relatively warm temperatures in Zone H. The low TANG value probably records oscillations in growing conditions



caused by episodic summer rainfall rather than small annual growth increments.

Analysis by morphological type

i. MT1 (Acacia karroo) Fig.5.10

The wood of this species is most mesomorphic in BLD. The greater investment in large vessels suggests sufficient water during a high sun growing period. As already discussed, the high MPD value indicates the proximity of relatively large trees.

ii. MT 6 (Rhus cf. undulata) Fig.5.9

The general nature of the comparison between BLD and BLA is confirmed. As with Olea, Rhus cf. undulata seems variable as regards NVES and relatively inflexible as regards MVESD.

iii. MT 11 (Rhus spp.) Fig.5.9

The wood of Zone H (BLD) is most similar to the wood of Zone F (BRL) with Zone E (CL) considerably more mesomorphic.

iv. MT 12 (Olea/Dodonea) Fig.5.6

As discussed, Olea may produce apparently contradictory evidence in terms of the classic pattern. An enormous increase in NVES in BLA boosts the RELV values for this assemblage higher than that for BLD. The MVESD values indicate that these numerous vessels are mainly small vessels. TUESA is markedly lower in Zone H (BLD), again an unusual feature, and the high VULM1 value indicates vulnerability to drought and/or cold stress. These data apparently contradict the other evidence for this zone.

### RELV distribution by assemblage (Fig.5.5)

The change caused by applying relative abundance factors before calculating the RELV:vess data is most apparent for Zone H (compare Fig.5.3A & B). This reflects the high relative abundance of Acacia karroo. However, even without applying the relative abundance factors, the pattern of a larger investment in big vessels in Zone H compared to any other period is clear. This probably indicates sufficient moisture for growth during the high sun period. The better representation of small vessels and of low RELV values in the RELV:relv distribution data for BLD versus CL indicates some drought stress in the former time period. This could partly have been caused by higher temperatures adversely affecting the P:E ratio and by less efficient precipitation.

### Correlations with other lines of evidence (Table 5.4)

There is little clear evidence from the analysis of the other categories of material as to whether the climate of this period is distinctive relative to other periods in the Holocene. The dramatic increase in the representation of Acacia karroo recorded by charcoal analysis is not easily interpretable in terms of palaeoclimate, since it is not known what specific climatic variable most controls its distribution. Xylem analysis suggests that an increase in the incidence of summer rainfall may have caused the increase in its representation in the late Holocene.

## CONCLUSIONS

In this section the EDXA data is reviewed briefly before comparing the approaches and the evidence produced by the two forms of analysis employed in this study. The three forms of EDXA have mostly produced corroborating evidence (Table 5.3). This may be summarised by zone as follows:-

i. A very harsh climate (cold and dry) was experienced during Zone A, ca 65-55 000 B.P.

ii. The evidence for Zone B (OLP), ca 55-40 000 B.P., is more ambiguous. Analysis by assemblage indicates a climate not as harsh as during Zone A. On both analysis by assemblage and by morphological type, the AXRAD2 ratio indicates a particularly spindly growth habit. This may be caused by a combination of eco-climatic factors, but variables other than precipitation or temperature, for example high wind speeds, may also be involved. Modern day comparative studies would probably resolve the problem. In addition, the evidence for MT7 and MT16 indicate that the climate during Zone B was more mesic than at any other stage during the late Pleistocene.

iii. All variables and analyses indicate cold conditions during Zone C, ca 40-26 000 B.P., with signs that winter rainfall was perhaps characteristic.

iv. The climate during Zone D, ca 26-18 000 B.P., was dry and cold.

v. A major change in climate towards more mesic conditions occurred between 17 and 14 000 B.P. The

Table 5.4 Summary of palaeoclimatic inferences drawn from other lines of evidence (\*after Deacon et al 1984, \*\*after Avery 1982, \*\*\*after Klein 1983)

ASSEMBLAGE AND DATING	ARCHAEOLOGICAL EVIDENCE*	MICROFAUNA**	MACROFAUNA***
BLD 2000 B.P.	impersistent low density scatters of artefacts, faunal remains and plant debris; storage pits; cave occupied for short periods or days		dominant browsing fauna indicates dense vegetation
BLA 6000 B.P.	a series of elongated, charcoal filled features occurred in this level and may be related to smoking of meat	similar conditions to the present, shrubland or bush dominant; extensive, dense riverine vegetation with trees; climate more xeric around 9000 B.P.	
BRL 10 000 B.P.	the evidence suggests a series of short term occupations		mixed browsing and grazing fauna
CL 13 000 B.P.	'processor economy'; a thick occupation deposit without discontinuities and a high density of faunal remains and artefacts suggests long term occupation	dense vegetation extends onto the hillsides at the expense of grassland; semi arid shrub restricted to hillsides, some increase in temperature relative to LP	grazing fauna (equids, alcelaphines) dominant indicating grassland
LP 22 000 B.P.	a well developed occupation complex indicates that during LPC the cave was used relatively infrequently	severe climate, cold and dry with at least very cold winters; grass on the hillsides and grassland and semi-arid shrub on the valley floor; dense riverine vegetation reduced to a minimum	stronger representation of alcelaphines
BP 32 000 B.P.	'processor economy'; well developed occupation complex; environment more productive than during DLP or BOL times		mainly a browsing fauna
OLP ca. 45 000 B.P.	low site usage and low productivity of the environment; 'traveller economy'	moderate climate; grass and semi-arid shrubland on the hillsides; an extension of dense vegetation on the valley floor	
BOL ca. 55 000 B.P.	ditto	open vegetation, cold climate; semi-arid shrubland on valley floor; grass on hillsides	mainly a browsing fauna

climate then become optimum, mesic and equable, during the end Pleistocene Zone E. Some rain at least was received during summer, drought was seldom experienced and temperatures were low during this time.

vi. The climate during Zone F, ca 12-8000 B.P., was slightly less mesic with some summer drought stress indicated. Relative to Zone E, warmer temperatures prevailed.

vii. Within the scale of Holocene climates, extremely xeric conditions were experienced during Zone G, ca 7-5000 B.P.. There are marked signs of drought stress in the wood anatomy. It is likely that summers were long, dry and hot and the typical growth form became more spindly.

viii. Finally, all the indications are that the climate during Zone H, 3000 B.P.-present, was warm and mesic with sufficient moisture to promote a warm season growing cycle and cause a low incidence of drought relative to Zones F and G. Increased temperatures however contributed towards a higher water stress than experienced in the cool and mesic Zone E.

These inferences are summarised in Table 5.3 where they are contrasted with the evidence produced by the Morphological Type Relative Abundance Analysis (MTRAA, Chapter 3). Examination of this table reveals that the evidence from the two forms of analysis is largely complementary. This allows a comparatively confident and detailed reconstruction of past climates. Resolving of

the few occasions where the evidence may not harmonise must await further development in both fields of research.

The most significant trends revealed by xylem analysis of wood from nine charcoal assemblages from Boomplaas Cave are summarised in Fig.5.11 in terms of the mean values per assemblage for the variables RELV and VULN. The late Pleistocene assemblages cluster together in an area of the graph which, accepting the suggested significance of the two variables, indicates low precipitation and adaptation to cold and/or drought. The values for CL indicate high precipitation and adaptation to cold temperature. Precipitation is less in BRL, but there are indications for higher temperatures. Within the Holocene, precipitation is lowest and resistance to drought highest during the mid-Holocene BLA. Precipitation is relatively high in the late Holocene BLD and little cold or drought stress is indicated.

Fig.5.12 shows the distribution of values for the variables RELV and MESO for each piece of morphological type 12 (Olea/Dodonea) analysed in the sequence. The clustering of values for pieces from from the same assemblages is marked and constitutes strong evidence both for the power of the xylem analytical approach and the correctness of the palaeoclimatic inferences based on the EDXA data. The same trends per time period as were indicated by the forms of analysis reported above are once again evident.

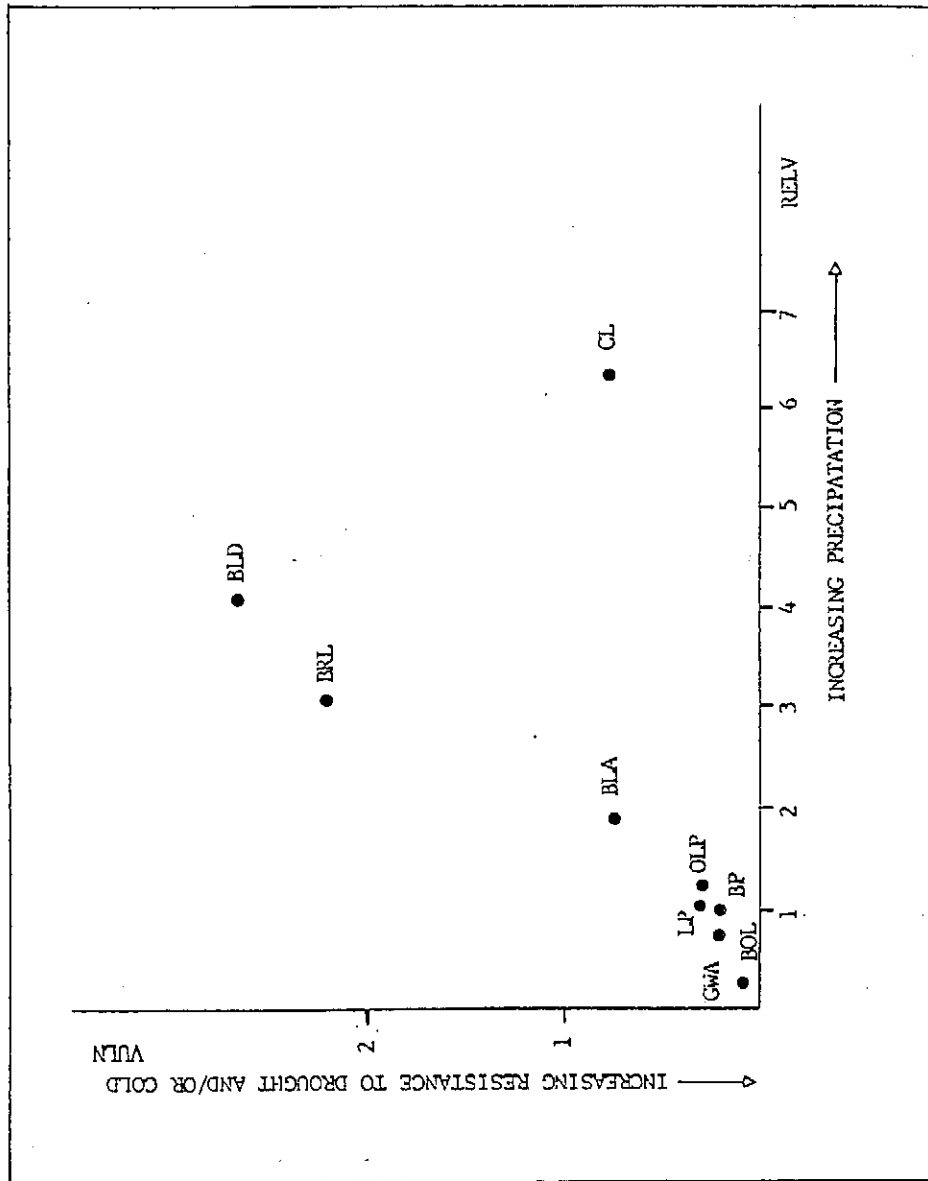


Fig.5.11 Summarising the results of the EDXA analysis of assemblages from Boomplaas Cave in terms of the mean values per assemblage for the variables RELV and VULN

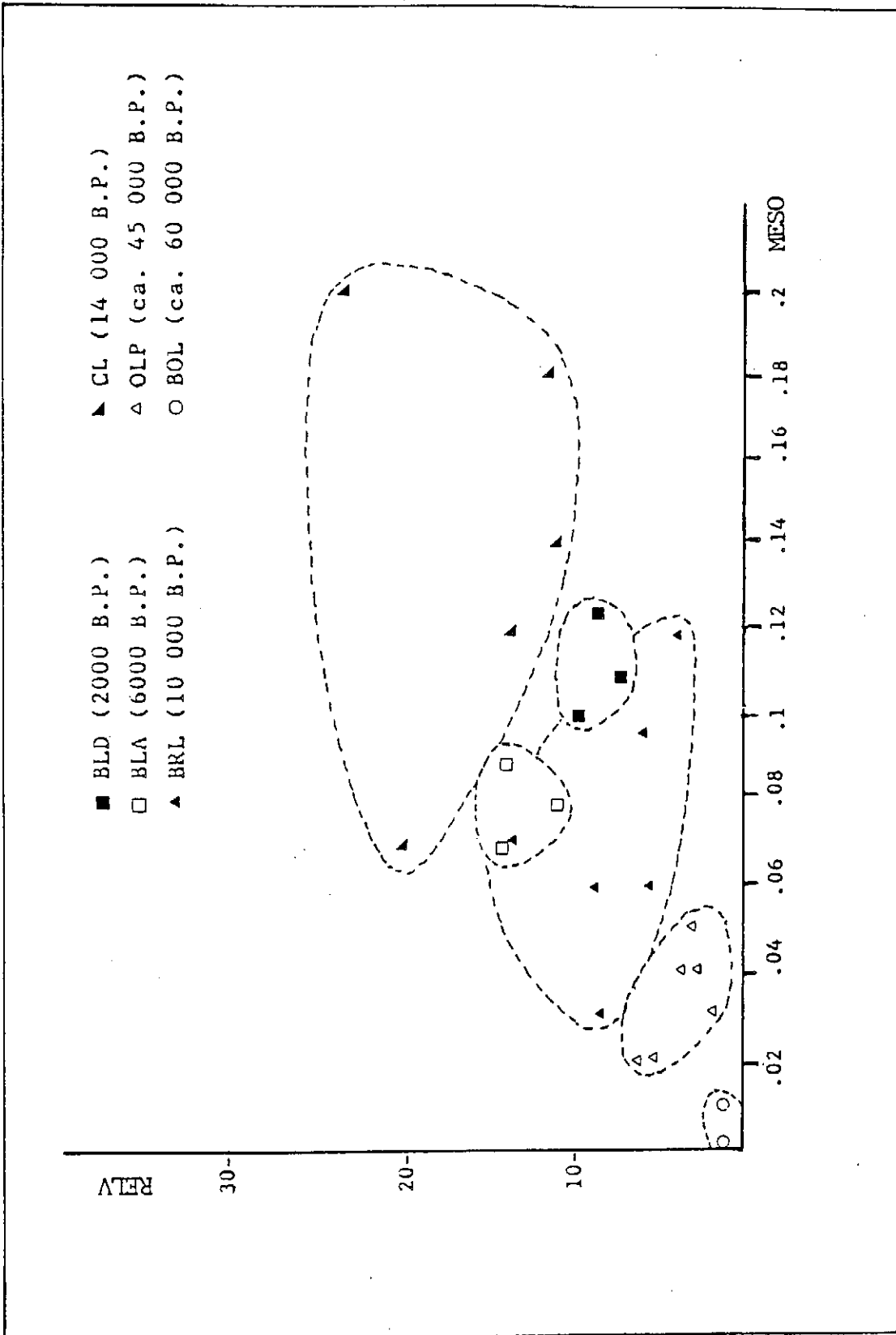


Fig.5.12 The distribution of the values for the variables RELV and MESO for each piece of Mf12 (Olea/Dodonea) analysed in the assemblages from Boomplaas Cave



To conclude this chapter, the two forms of analysis, MTRA and xylem analysis are briefly compared.

MTRA identifications lay the basis for the analysis-by-morphological-type form of xylem analysis. The value of this latter form of analysis has been amply demonstrated in this study. MTRAA produces descriptive type evidence on which inferences about past climates can be based. The quality of the inferences based on MTRA evidence is dependant on the quality of identifications and of knowledge about the ecoclimatic significance of identified taxa. Given peculiar sets of evidence (cf. assemblage CL) such inferences can sometimes produce tantalizingly clear pictures of a past climate and vegetation, but these reconstructions rely on interpretations of evidence, not direct, measureable correlations. MTRA is strongly affected by patterns of human selection of firewood, about which, at present, little is known. In contrast, xylem analysis is relatively unaffected by the factor of human selectivity, but may be affected by differential preservation of denser wood through time.

MTRA produces measures of relative abundance, while xylem analysis provides values for a wide range of independant and semi-independent, wood anatomical variables. These values can be interpreted in a relative way, but, as the system expands in application and the relationship between the wood anatomy of modern day florules and taxa and climate is studied, they will become

progressively more interpretable in absolute terms. It is probable that, in time, xylem analysis of the wood anatomy of selected taxa will provide the most precise palaeoclimatic information obtainable from the range of biological material commonly recovered from archaeological sites.

Evidence produced in this study suggests that xylem analysis may be successfully applied to a randomly selected sample of unidentified wood and can therefore be practised by a non-specialist in wood identification. In contrast, MTRA requires a specialist wood anatomist.

#### REFERENCES

- AVERY, D.M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum 85(2):183-374.
- CARLQUIST, S. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. ALISO 6:25-44.
- CARLQUIST, S. 1977. Ecological factors in wood evolution: a floristic approach. American Journal of Botany 64:887-896.
- DEACON, H.J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10:241-257.
- DEACON, H.J., A. SCHOLTZ & D.L. DAITZ 1983. Fossil charcoals as a source of palaeoecological information in the

- fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.N.N. Lambrechts (eds) Fynbos palaeoecology: a preliminary synthesis:174-182. SANSPR 75, Pretoria.
- DEACON, H.J. DEACON, J., SCHOLTZ, A., THACKERAY, J.F. & BRINK, J.S. 1984. Correlation of the palaeoenvironmental data from the late Pleistocene and Holocene deposits at Boomplaas Cave, southern Cape. IN: J.C. Vogel (ed) Late Cainozoic Palaeoclimates of the southern hemisphere :339-351. Balkema, Rotterdam.
- DEACON, J.C.G. 1982. The Later Stone Age in the southern Cape, South Africa. Ph.D thesis, University of Cape Town.
- KLEIN, R.G. 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: a preliminary synthesis:116-138. SANSPR 75 Pretoria.
- PHIPPS, R.L. 1982. Comments on interpretation of climatic information from tree rings, eastern North America. Tree-Ring Bulletin 42:11-22.
- TUSENIUS, M. 1986. Charcoal analytical studies in the north-eastern Cape. Unpublished M.A. thesis, Department of Archaeology, University of Stellenbosch.
- WEBLEY, L. 1979. A sedimentological analysis of the Boomplaas Cave sequence. Unpublished Hons. project, Department of Archaeology, University of Stellenbosch.

C H A P T E R   S I X

MINIMUM PIECE DIAMETER ANALYSIS (MPDA) AND THE  
TAPHONOMY OF CHARCOAL ASSEMBLAGES

I N D E X

ABSTRACT

INTRODUCTION

THE TAPHONOMY OF CHARCOAL ASSEMBLAGES

THE NATURAL SPECTRUM OF DRY WOOD

HUMAN SELECTION AND USE OF FIREWOOD

    Quality of wood

    Transportation and the shape and size of branches

    Patterns of firewood exploitation

    The domestic use of firewood

METHODS

PREDICTING MPD DISTRIBUTIONS

INTERPRETING MPD DATA

APPLICATION

    The site

    Materials and methods

    Results

    Discussion

CONCLUSIONS

## ABSTRACT

This chapter is concerned with understanding how human behaviour contributes towards creating the type of charcoal assemblages found in archaeological context and, conversely, with how to obtain evidence from such assemblages about patterns of human behaviour. A review is presented of the factors which can influence the composition of the natural supply of dry wood and the range of environmental, practical and cultural factors which co-determine human procurement and use of firewood. An approach designed to produce data from the analysis of fossil charcoal assemblages which will allow the recognition of certain patterns of selection and preparation of firewood and the use of certain types of fires is then described. This approach is based on estimates of the diameters of the branches from which identified pieces of charcoal were derived and the subsequent analysis is of the distribution of branch diameter sizes for an assemblage and for identified species per assemblage. This form of analysis has been termed Minimum Piece Diameter Analysis (MPDA).

The analysis is applied in the study of nine charcoal assemblages from Boomplaas Cave. At least two different types of dry branch supply, two different types of fire and three different types of procurement strategy were recognised. The proximity of certain trees to the cave site at various periods and the distance of other types could also be discerned and these findings constitute proof of the value of the method.

## INTRODUCTION

Charcoal assemblages are commonly recovered from archaeological sites and are, to a considerable degree, a product of past human activity. It is peculiar that in a field characterised by a concern with extracting all possible evidence about past human behaviour from scraps of material remains, the potential for studying these assemblages has remained almost unexplored. The study reported here is an investigation of this potential. It is exploratory in nature and should be seen as an attempt to develop a new form of archaeological analysis.

Specifically, this chapter is concerned with understanding how human behaviour contributes towards creating the type of charcoal assemblages found in archaeological contexts and, conversely, with how to obtain evidence from such assemblages about patterns of human behaviour. The approach which has been developed is based on estimates of the diameters of the branches from which identified pieces of charcoal were derived. The subsequent analysis is of the distribution of branch diameter sizes for an assemblage and for identified species per assemblage. This form of analysis has been termed Minimum Piece Diameter Analysis (MPDA). Considering the problems of interpreting branch diameter size distributions, the approach is concerned with understanding those processes of production, selection, transportation and preservation which operate in transforming the living

woody plant tissue in a vegetation into the charcoal assemblages found in archaeological contexts. Thus MPDA may be regarded as the study of charcoal taphonomy.

In outlining this new field of study, not only an analysis of fossil material, but a range of studies, from ethnographic studies related to firewood, to studies of the natural spectra of dry wood in various vegetation types, were involved. Only the analysis of fossil material could be dealt with at any length in this thesis. Information concerning the other fields had to be culled from the literature and, as could be expected, not much of the desired type of information has yet been recorded. Apart from describing the methods of obtaining the basic data from the fossil material, a primary aim of this chapter was therefore to discuss the range and type of information which would be required to base the interpretation of fossil evidence. Since the second half of the chapter is concerned with an applied study, it was also necessary to note substantive information concerning patterns of indigenous use of firewood.

In the analysis of the fossil assemblages, three different patterns of branch diameter size distributions could be recognised and at present this constitutes the most positive evidence that the approach has merit.

The remainder of the introduction discusses an early attempt (Salisbury & Jane 1940) to reconstruct some aspects of past human use of firewood and exploitation of an environment through the analysis of charcoal assem-

blages. The subsequent section discusses the factors which affect the spectrum of dry wood in a vegetation type and the environmental, practical and cultural factors which influence human selection and use of firewood. The techniques involved in obtaining estimates of branch size diameters from pieces of charcoal and the geometry of the production of pieces of charcoal from a charred piece of wood are then discussed. In the last section the results of applying Minimum Piece Diameter Analysis (MPDA) in the study of nine charcoal assemblages from Boomplaas Cave are reported, the types of problems encountered discussed, and the approach evaluated in terms of prospects for future research.

As already noted, the analysis of the charcoaled remains of firewood has seldom been used to reconstruct aspects of human behaviour involved in the gathering of firewood and its use. The exception is the work of Salisbury & Jane (1940). They examined large charcoal assemblages from Maiden Castle, Dorset, England. The pieces of wood preserved as charcoal were identified and deductions about past climates were made on the basis of analysis of the growth ring structure preserved in isolated pieces of wood. Because of the unusual fact that the assemblages consisted exclusively of the remains of wood of twig-sized diameter, the size of the branches used as fuel was clear merely from macroscopic observation.

Assuming that only branches of a reasonable diameter



will be transported for use as firewood, the researchers interpreted the fossil evidence to mean that all firewood had been gathered in the immediate vicinity of the camp site. They could therefore suggest that the species identified and the growth habit indicated by the uniformly small diameters of the branches would have occurred on the local chalk down itself.

Salisbury & Jane (1940:311) also assumed that little or no human selectivity had been involved in determining the composition of the assemblages they were studying. They therefore simply took the composition of the charcoal assemblages to reflect the actual composition of the source woody vegetation. As argued in this chapter, despite being a common assumption, it is one to be treated with caution.

Godwin & Tansley (1941) were critical of some of the conclusions reached by Salisbury & Jane (1940). They argued that people living on a possibly treeless down would have been obliged to gather their firewood, even if of small diameter, from the closest source. They did not state why prehistoric peoples may have chosen to stay far from such a basic resource, but to explain away the lack of larger pieces of wood, suggested that branches could have been introduced butt first into the fires, leaving only their extremities, charred twigs, as remains.

This was a pioneering study and, in an almost casual fashion, the authors, Salisbury & Jane (1940), and their critics Godwin & Tansley (1941), suggest that a range of

information about past societies, information not available then or now to archaeologists through any other form of analysis, was potentially obtainable through analysis of charcoal assemblages. The types of arguments employed by these authors are discussed below in the context of general principles of use in interpreting MPDA-type data. The possibilities suggested by the Maiden Castle study, particularly as regards producing information about human behaviour, were never developed and the analysis of charcoal assemblages has yet to become a standard form of archaeological analysis.

#### THE TAPHONOMY OF CHARCOAL ASSEMBLAGES

##### THE NATURAL SPECTRUM OF DRY WOOD

Apart from contexts of serious over exploitation of the resource, it can probably safely be assumed that wood to be used as fuel is collected as dry wood. Best (1979) notes that in areas of the Transkei tribal laws protect trees from being cut. Sheddick (1954) and Ashton (1956) mention that the natural trees and forests of Lesotho are traditionally protected and deadwood is only collected at certain times of the year. On the other hand, brushwood (mostly Asteraceae) which is the most important source of firewood, is not protected. In Zululand, green woody material may not be cut for firewood either (Best 1979: 12). Interestingly, Jelenic & Van Veeten (1981) record that Bakgatla women will not collect deadwood lying on the ground, but prefer to tear dead branches off trees.

Archer (in prep.) reports that deadwood lying on the ground is tested for decay before being collected. Stone Age hunter-gatherer peoples may have lacked the technology or motivation to cut down trees, although today the G/wi and !Kung Bushmen will use metal tools to fell trees in order to provide wood for woodworking (Lee 1979; Silberbauer 1981).

The composition of a collection of firewood will therefore in the first instance bear a relationship to the composition of the supply of dry wood. There is abundant evidence that because of factors such as different shooting strategies, the different ages of plants in a vegetation, different ages at which species begin to produce dead wood and differences in structure of vegetation, the composition of the supply of dry wood can differ considerably from the composition of the living vegetation.

The rate at which plants or florules of the same age produce dry wood (usually measured as the ratio between functional and non-functional components) can vary significantly depending on species, age and climate. For instance, under relatively mesic conditions an Acacia karroo will grow rapidly and produce much dry wood, while under the same ecological regime an Olea europaea subsp. africana might produce hardly any dead wood, forming instead a dense, multistemmed shrub. However, under more xeric conditions the particular shooting strategy of the Acacia can be inhibited and the plants will then produce

similar amounts of dry wood (pers. obs.). This factor could clearly have important implications for the interpretation of changes in charcoal assemblage composition.

There are other ways in which dry wood is produced in the natural environment; namely through disease, unusual drought or cold and fire.

Extremes of drought can kill all woody vegetation. Plants will employ various dieback strategies in reaction to lesser degrees of stress (Rutherford pers. comm.). To the extent that a fire in vegetation might produce a different supply of dry branch size classes to that produced by the living vegetation (by analogy with faunal analysis, a catastrophic versus an attritional age mortality profile!) the occurrence of markedly different fire regimes might be reflected in the charcoal assemblages from fossil hearths.

As noted by Axelrod (1984), amongst others, the incidence of fire in grassland can be such that, despite a favourable climate, woody vegetation is unable to survive except in locally protected sites. Many studies of the modern day distribution of forest, scrub-forest and grassland have concluded that it is an artificially high incidence of fire which maintains areas of grassland within ecozones suitable for the growth of woody vegetation (see Van Daalen 1980). In general an increase in the incidence of fire in a region in which grassland occurs can be expected to result in less abundance and a more patchy distribution of woody vegetation. The com-

position of woody vegetation will also be altered by changes in fire frequency.

#### HUMAN SELECTION AND USE OF FIREWOOD

Not much ethnographic work is available which deals with indigenous human selection and use of firewood. Lately however, researchers in the field of alternative energy resources have become aware of the crisis in firewood supply in many areas of southern Africa (more often than not in areas where resettlement has occurred). In the context of work related to alleviating the current crisis several recent publications refer to topics such as firewood preferences, calorific value of local woods, transport problems, selection of tree species for planting in woodlots etc. (Gwaitta-Magumba 1983; Gandar 1983a, b, c, Liengme 1983; Kgathi 1984; Cunningham 1984; Eberhard 1986; Eberhard & Poynton in press). These studies often refer to observations made about people in disturbed social and environmental settings and the results might therefore not be extrapolable to other contexts.

All indigenous peoples use considerable amounts of firewood (Ashton 1956; Best 1979; Jelenic & Van Vegten 1981; Silberbauer 1981) but the effort required to procure the firewood differs according to the environment and the pressures on the resource. The importance of firewood for sedentary populations is well known (Ashton 1956; Best 1979; Jelenic & Van Vegten 1981; Eberhard 1986; Archer in prep.) and its importance in a hunter-

gatherer context can be gauged by the fact that the proximity of a supply of firewood is important in deciding the location of the G/wi Bushman campsite (Silberbauer 1981:222).

In the arid Richtersveld certain substrates do not support woody vegetation and the local pastoralists travel long distances to secure a supply. On the other hand, in a woodland environment like that inhabited by the !Kung bushmen, where dry wood is plentiful and well distributed, firewood gathering seems to be such a casual activity that it was apparently judged not worth describing as part of the material base of society (Lee 1979).

The degree of effort required to procure firewood determines to what extent the activity is developed as a distinct economic activity. It is the signs of this formalization, or adherence to a pattern of behaviour, which are of importance to the approach described here. These signs consist of patterns in the taxonomic and branch diameter size composition of charcoal assemblages. The primary aim of this study was to develop a method to recognise these signs.

There will obviously be considerable differences in the patterns of firewood exploitation in nomadic versus sedentary contexts. Therefore only the more general factors which might influence human selection of firewood are discussed below. The discussions are organised under the following headings: quality of wood; the shape and size of branches; the domestic use of fuel; and social and economic factors.

### Quality of wood

In a paper reporting the results of measuring the calorific value of 108 South African grown fuelwood species Eberhard & Povnton (in press) state that the calorific value of all woods varies within narrow limits and that, allowing for differences of site and age, the variation within a single species is as significant as that between different species. The data presented by Bialy (1982) show clearly that while the calorific value of types of wood by dry weight is more or less a constant, the inclusion of even small amounts of resin considerably increases this value. In terms of the use of energy it is therefore more economic to select wood which contains resin. However, a further advantage is involved; wood containing resin will, even if wet, ignite more easily and be more inclined to burn than other wood. Consequently, it is particularly preferred during wet weather (Archer in prep.).

In the context of the applied section of the present study, wood of the taxa Acacia and Rhus and the family Asteraceae are known to contain large amounts of resin. The resin of Acacia karroo is concentrated in large quantities close to the cambium, whereas in Rhus, the resin is also contained in canals within the xylem and in the heartwood. Wood of the former ignites easily and burns powerfully while wood of the latter burns well, but can produce the potentially unpleasant effects of crackling and explosive burning.

The data presented by Bialy (1982) also indicate that, by volume, wood with the highest specific gravity has highest calorific value. Best (1979) and Eberhard & Povnton (in press) mention calorific values of between 19 and 25 MJ/kg for local hardwoods. In the case of softwoods the slowest growing wood is usually the most dense, while with hardwoods the pattern is not so clear. This factor could prove to be significant, especially where questions of plant succession are involved (cf. Salisbury & Jane 1940:311): Denser wood does not only release more calories per volume when burnt but, since it forms better coals, will release this energy at a slower, steadier and often more useful rate. Eberhard & Povnton (in press) suggest that properties such as "combustibility", which relate to density, may be better measures of fuelwood quality than calorific value.

Archer (in prep.) records the range of domestic uses of firewood for which coals are not required, but in general, good coal producing wood is sought after. This is especially so where long burning, winter fires are concerned.

#### Transportation and the shape and size of branches

Godwin & Tansley (1941) suggested that the necessity to transport firewood is not always a product of over exploitation of the resource. Transport distance is a function of the relative locations of the camping site and available fuel supplies. Since certain substrates may not support woody vegetation, but be rich in other



resources, the situation could arise where a particular occupation site becomes to an extent fixed and the location of the firewood alone then determines the transport distance.

It would seem unlikely that within hunter-gatherer economies the situation would often have arisen in which firewood was so exploited that for this reason alone transport of firewood to a camping site would have become necessary. However, in the applied section of the present study, data from one occupation unit does suggest transport of firewood.

Where transport is a factor, the shape (i.e. essentially whether long straight branches are produced), regularity and size of material are important firewood selection criteria. The ideal of long straight branches allows large bundles of firewood to be packaged and balanced on the head (see the paper by Jelenic & Van Vegten 1981 entitled "A pain in the neck ...") and in more extreme cases even longer and heavier branches may be used to help lever heavy bundles onto the head and thus avoid the strain of crouching or bending (Best 1979:23). This technique can considerably increase the weight of a package of wood which one person can bear " ... it seems that the weight of a bundle of wood depends on the shape and size of the individual pieces of wood" (Best 1979: 22).

There are no doubt a number of other simple methods of improving the economics of cartage of firewood. In

Namaqualand at present wood is strapped to the back (Archer in prep.). However, it is likely to be a common feature that straight branches with slighter wood extremities which can be easily broken off by heating will be selected if wood is to be packaged.

It can be predicted that where there is a size range of regular straight branches available, it will not only be the size (diameter) of branches, but also the differential abundance of sizes which will constitute a selection criteria. People will prefer to collect a standard size of wood and this, within bounds, will be that size which is most abundant in a particular area. This prediction may only hold for vegetation types where large branch diameters are rare. Best (1979:23) notes that where people are exploiting forest vegetation, very large single pieces of wood may be collected. The !Kung, living in a rich woodland environment, likewise use logs for long burning fires (Yellen 1976:68, Fig.2.3).

On the other hand L.Botha (pers.comm.) reports that amongst the Xhosa, regular and medium sized branches are preferred above large pieces of wood since the former allow more control over the intensity of the fire. This also suggests that evidence for the use of regular and medium sized, straight branches cannot always be interpreted as evidence for the transport of firewood.

#### Patterns of firewood exploitation

No data exists on this subject, but the logic involved is simple. The application of a certain firewood

procurement strategy to a given supply of dry wood will, through time, alter the type and size distribution of that supply of wood. Conversely, a certain supply of dry wood obviously constrains firewood procurement strategy. Three variables are therefore involved, an original supply of dry wood, a firewood procurement strategy and the duration of application of the strategy. The following simple example is quoted in order to suggest the potential importance of the interaction of these factors.

Let us suppose a supply of dry wood characterised by a large size range of branches, but with an abundance of branches of medium size and a casual exploitation strategy (whatever dry wood is close to the site is collected for firewood). Exploitation alone could, either progressively through time or in demanding collecting episodes, result in the scant supply of larger dry branches becoming exhausted and branches of medium diameter being most commonly collected. On the other hand, a lower intensity of firewood exploitation could result in dry larger branches close to a site (a rare natural occurrence) always being available. If larger dry branches were preferentially selected in casual firewood gathering they would thus make up a greater proportion of the final firewood supply.

The domestic use of fuel: social and economic factors

There are many different domestic uses for fuel. It is likely that the range of types of fires and their use relate to a limited set of functional variables which determine the qualities of the small open fire. What qualities can be required of firewood is largely determined by what firewood is actually available.

Much of the domestic use of firewood relates to cooking. Cooking fires may differ as to whether coals, flames, ashes, hot rock surfaces or smoke is required. Fires can be of long or short duration and be cool or intense. A fire made for lighting purposes requires a light, volatile wood, while the qualities that make a wood good for ash production ("ashlom", literally ash flower) as required for certain purposes by people in Namaqualand are only possessed by select species (Archer in prep.). Most ethnographic studies suggest that indigenous peoples have an intimate knowledge about the firewood qualities of woods and that the selection of firewood is quite precise (Ashton 1956; Best 1979; Jelenic & Van Vegten 1981; Archer in prep.). The latter two works note that people will choose to walk considerable distances to obtain the wood of preferred species rather than to collect inferior wood.

Eberhard & Poynton (in press) state, "Rural households generally possess a very detailed local knowledge of the natural flora and have different vernacular

names for the most subtly different tree species". Eberhard (1986) mentions the reasons why the wood of certain species is not used for firewood. These range from functional reasons such as unpleasant smell, to beliefs that the burning of particular woods will result in cows producing only bull calves. Gandar (1983a) notes that in Kwazulu the wood of species of Euclea, a common and high quality fuelwood, is avoided because of the belief that its burning will cause strife in the family.

From the archaeological point of view, a potentially informative pattern concerns seasonal differences in the use of firewood. This pattern is both widespread and would appear to be easily recognisable in charcoal assemblages. In all three villages (concerned with three different tribes and situated in different ecological settings) studied by Best (1979), marked changes were recorded in the summer, winter and autumn patterns of firewood procurement and use. A common fact was that in winter hearth fires are kept burning day and night. Yellen (1976:65) also notes that during winter the !Kung will keep fires burning throughout the night and most of the day. The winter campsites are also larger and care is taken to remove the large amounts of ash which result. At present, the pattern amongst the semi-sedentary pastoralists in Namaqualand is to use large branches and keep fires smouldering through the night during winter and to make smaller, single episode fires in summer. The tendency is also that smaller, strong burning fires are made under windy conditions (Archer in prep.).

There is evidence that under colder and wetter conditions people would tend to use the available natural refuges (Silberbauer 1981). This behaviour might emphasise the patterns mentioned above since the extended use of a refuge, such as a cave, would entail greater transport of firewood. It can be predicted that under such conditions people will maintain relatively large stockpiles of fuel collected during relatively infrequent but efficient collecting episodes.

Conceptions about firewood, firewood procurement and the use of fires, also play a role in maintaining a pattern of behaviour. Indigenous, "technical" terms reveal established conceptions. In Namaqualand at present two modes of firewood collection are clearly distinguished. Firewood collection proper, termed "houtmaak" (to make wood) and more casual gathering, termed "sa-y". Correspondingly, firewood is known as "dorrogod" (dry stuff) and kindling as "krummels" (crumbs). A feature of firewood gathering proper is the definite preparation of wood for packaging and transport. The extremities of large, dry branches are beaten on the ground to strip sticks and twigs prior to packaging and transport. A similar process of preparation is reported by Jelenic & Van Vegten (1981) and the distinction between casual firewood collection and firewood collection proper is apparently widespread (Ashton 1956; Best 1979; Van Vegten 1981).

It is also important that the available ethnographic evidence suggests that casual firewood collection usually occurs close to camp and/or while performing another task and that smaller packages and generally smaller size classes of wood (mainly for kindling purposes) are concerned. This pattern can be used to help reconstruct the palaeovegetation mosaic in the environs of a site and the pattern of human exploitation of that mosaic.

#### METHODS

An estimate of the original diameter of the branch from which a piece of charcoal was derived can be obtained by extension and measurement of the radii observed in the transverse section of that piece of charcoal. If SEM photomicrographs are available this can be done using only two 3 m measuring tapes marked in cm (alternatively, a sector of a circle with 3 m radius and with selected radial and tangential markings may be inscribed on a transparent plastic sheet and used as described below).

The end of the tapes at 0 cm are anchored together loosely enough to allow movement around the axis of the anchor. With the tapes held taut to imitate radii and ensure straight lines, the SEM photomicrograph is aligned so that the visible rays coincide with the radii defined by the movable arms of the tapes. The length of the radius, (X), is measured by reading off the value at the intersection of the tape with the outer margin of the

illustrated area of xylem tissue. The estimated 'real diameter', (D), of the branch from which the piece of charcoal was derived is then calculated by the formula,  $D=2.X.S/MAGN$ , where S = a shrinkage factor of 25% and MAGN = magnification factor. Only total magnifications of 75 X or 150 X were used in this study.

This description outlines the basic method of obtaining measurements. The following preparatory technique improves the accuracy of the method and should be regarded as integral to it. Before aligning the photograph as indicated above, the intersections of three or more radii with the margins of the photograph should be marked. This is done most precisely by laying a ruler along the selected radii. This procedure eliminates much subjectivity, especially as the radius increases and adjacent radii tend progressively to appear parallel. It also indicates immediately whether a 'deformed' radial structure has been encountered. A variation of this technique is to draw three radii on a transparent overlay and take the MPD measures from this overlay.

The radial structure in xylem is indicated mainly by the ray system, but also by radially arranged vessels and other tracheary elements and similarly arranged fiber cells and axial parenchyma. The arc defined by a tangential structure as well as the radius to the tangent can also help to define a radial structure. Apart from badly preserved charcoal or pieces with large or numerous radial bursts, the most common problems encountered are



with pieces evidencing a twisting of a 'branch' around its axis or where the wood is knotted.

The method for obtaining measures of MPD is based on two assumptions, viz., that the transverse section of branches (the concept is used inclusively) is more or less round and/or that rays usually lie on radii and that no strong or systematic bias exists across the diameter of a charcoaled stump as to the production of different sized pieces of charcoal. From the point of view of interpretation of MPDA data, aspects of these two assumptions clearly require investigation.

Wood shrinks when charcoaled and this has been accounted for in the formula given above by a shrinkage factor of 25%. While earlier authors (Cousins 1975; Schweingruber 1978) quoted reasonably similar figures for the radial and tangential shrinkage of wood when charcoaled (20-30% for the transverse plane depending on the type of wood and variables of the charcoaling process), more recent work (Eberhard & Poynton in press) records shrinkage factors by volume ranging from 7 to 30%. Until more is known about the relationship between wood quality, temperature of the charcoaling process and shrinkage to allow the shrinkage factor to be predicted from wood anatomy, a standard shrinkage factor will have to be used in MPDA. All researchers agree that areal relationships such as that between various tissues and the ratio between cell diameter and cell wall thickness remain very similar through the charcoaling process.

(McGinnes et al 1971; Cousins 1975, Zicherman & Williamson 1981).

The adjective 'minimum' is used to qualify the piece diameter measurements since estimation of the diameter of the mother branch through extension of the radii observed in an isolated area of xylem tissue can only indicate that the branch was at least that diameter. It cannot indicate how much bigger the branch could have been. There are however four other reasons why the adjective is appropriate :-

- a. the preservation of woody tissue external to the cambium is probably selected against
- b. wood shrinks when charcoaled and, as described above, a relatively conservative shrinkage factor is applied in this study
- c. in the present application of the general method the areas of xylem tissue selected for SEM photography were selected in order to include the best preserved area of xylem tissue rather than the area furthest from the pith and
- d. the method of notching charcoal to induce a break in the required plane (see Tusenius 1986) reduces the outer margins of the transverse sectional area of xylem tissue potentially available for observation. The influence of some of these four factors can be limited in future research.

## INTERPRETING MPDA DATA

The interpretation of MPDA data yields four main categories of information. Firstly, a distinction can be made between wood of kindling size and that of firewood proper (kindling, or brushwood, is defined as the firewood used to start a fire and is distinguished from tinder, which is the very fine material, dry grass or paper, used initially to sustain the flame). This distinction may provide information useful for reconstructing the woody vegetation mosaic in a site catchment area, in particular for suggesting what woody plants occurred close to a specific site, and human exploitation of that area.

Secondly, the distinction between firewood and kindling allows a kindling:firewood ratio to be determined. This statistic provides information about an important variable, namely the duration of burn of a single fire.

If, all other things being equal;

- i. the amount of kindling required to start a fire can be taken to be relatively constant;
- ii. the longer a fire burns the less remains of the initial fuel supply survive (the longer a fire burns the more the charcoal recovered from the cold fire reflects the subsequent additions of fuel rather than the initial supply) and;
- iii. no wood of kindling size is added to a fire subsequent to the phase of ignition,

then changes in the kindling:firewood ratio should reflect changes in the size of fires and their duration of burn, i.e. the ratio distinguishes short, single episode small fires on the one hand from the larger, multipurpose fires which are often kept smouldering for days, on the other.

Other factors may of course affect the kindling:firewood ratio. Wood of kindling size can be used as firewood proper. There is little ethnographic evidence describing situations where a size range of branches is available and yet people choose to use wood of kindling size as firewood proper. Archer (in prep.) records that larger and heavier pieces of wood tend to be used for cooking, while brushwood is used for heating and light and to welcome people to a fireside chat and Jelenic & Van Vegten (1981) note a similar pattern. Wood of kindling size burns quickly and feeding a fire for any length of time with wood of this size would be uneconomical.

Markedly patterned and differing ways of introducing wood into fires (for which there is at present little ethnographic evidence) and factors related to the frequency of rekindling, ventilation characteristics and how economically wood is being used might also affect the kindling:firewood ratio. However, the most basic variable measured by the ratio is probably the duration of burn.

Thirdly, MPDA can produce indications about possible differential degrees of transport of firewood; about whether firewood was collected on an ad hoc and casual basis in the immediate vicinity of a proposed fire, or whether firewood procurement and use was a more distinctive economic activity and about whether the wood of a specific taxon was valued as firewood and if it grew close to the camping site. Transport is only involved when firewood gathering is a distinct economic activity and ethnographic studies indicate that transport of firewood is preceded by selection, preparation and packaging of material (Jelenic & Van Vegten 1981; Archer in prep.). The signs of this selection and preparation of material may be preserved in the remains of hearths and via MPD analysis these signs may be recognised.

Lastly, MPDA produces gross information about the habit of woody vegetation. Analysis of the maximum MPD measures recorded, the mean MPD values and the pattern of the MPD size class distribution graphs for various taxa can distinguish whether the source of fuel was scrub vegetation, shrubs or trees. In the case of trees, MPDA can distinguish whether the trees grew close to the camping site or not. MPDA may also record changes in the growth habit of plastic species and as well as suggest the duration or intensity of application of a firewood gathering strategy.

In conclusion, humans do not necessarily sample either woody vegetation or the available size range of

wood randomly. This filter of human selection naturally limits the confidence with which the composition of past woody vegetation can be reconstructed. The MPDA approach is designed to determine something about the filter (the set of factors influencing human selection of firewood) and the natural spectrum of woody vegetation filtered by it and does this by analysis of the filtrate, so to speak. Therefore, alternative hypotheses will exist to explain a certain pattern, one placing emphasis on the component of human behaviour, the other emphasising the determining influence of a naturally occurring spectrum of dry wood. To choose between these will often require recourse to other types of information, i.e. information from other relevant palaeo-environmental or archaeological analyses.

#### PREDICTING MPD DISTRIBUTIONS

In order to interpret MPD spectra of fossil assemblages, it is necessary to determine some of the typical patterns of MPD spectra. These can be derived theoretically or through experimentation.

The theoretical reconstruction of size class distribution can be calculated by using the assumptions basic to MPDA, i.e., that the transverse section of wood is round and that regularly shaped and sized pieces of charcoal are produced across the diameter of a piece of wood. A further assumption is that only a narrow zone of char-

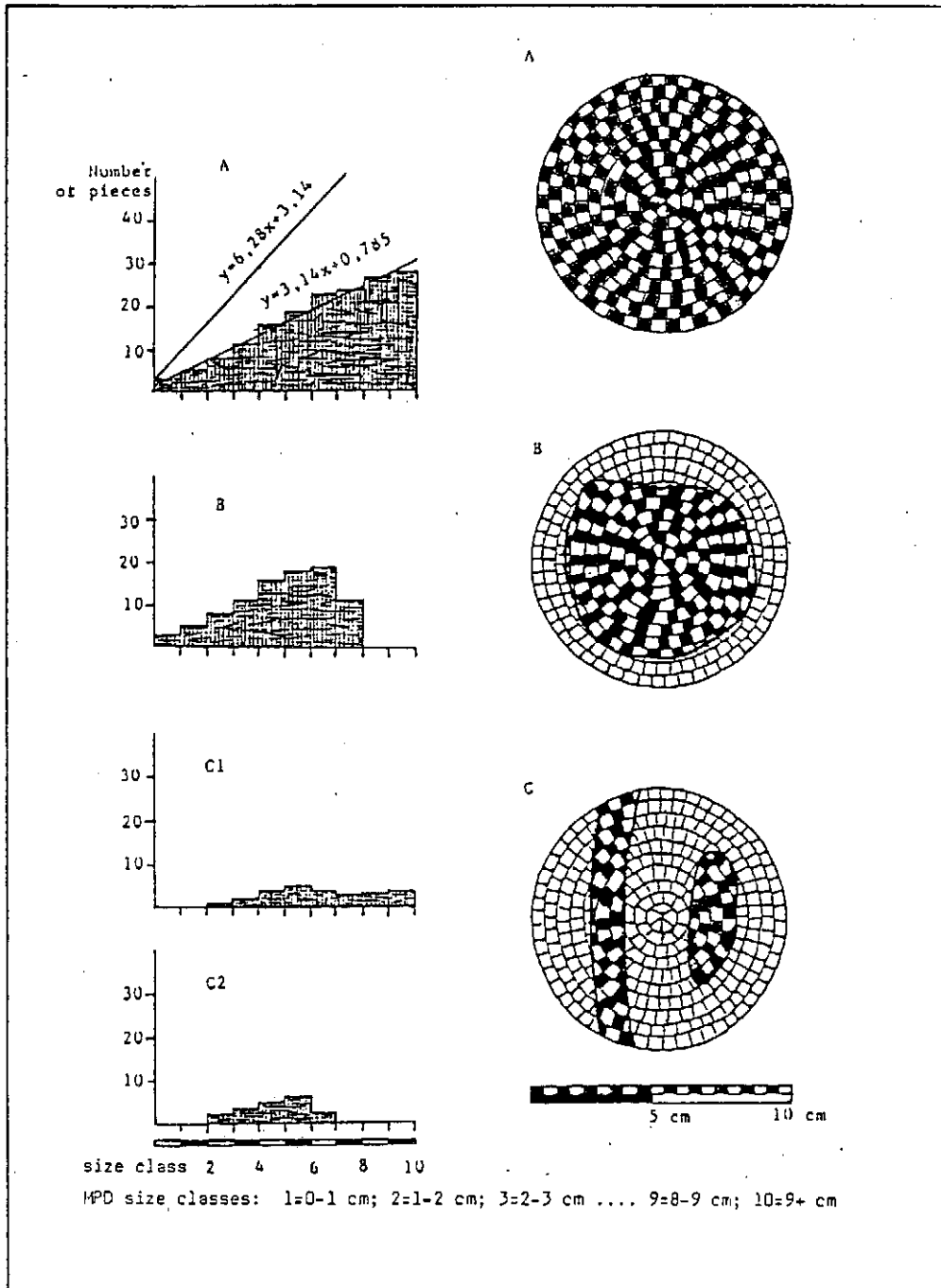


Fig.6.1 Predicted charcoal production and MPD distribution for three burning patterns

coaled wood sandwiched between the zone of ashed and scorched or unburnt wood will produce charcoal, except in circumstances where the supply of oxygen is limited. In Fig.6.1 the MPD distributions which should result when a single piece of wood is charcoaled are predicted for contrasting burning patterns; namely, one in which wood is burnt from the end (probably the most common mode of burning) and representative samples of charcoal are recovered for the full diameter of the wood (Fig.6.1A), one in which wood is also burnt laterally and some portion of the circumference is lost (Fig.6.1B) and, lastly, one where a branch is only burnt laterally (Fig.6.1C).

From these simple contrasting situations a number of patterns emerge which are of immediate relevance to the interpretation of the fossil data. For the first case, that in which branches are burnt from the end, the predicted distribution approximates a straight line whose gradient is given by the formula  $\pi \cdot (r+C) - \pi \cdot r$  (where C is the average radial extent of the pieces of charcoal produced by the charcoaling and subsequent processes) and whose maximum X value is the greatest value for r (see Fig.6.1A). In the second case, where a branch is also burnt laterally, the resultant size class distribution tends towards a normal type skewed to the left or right according to the exact transverse sectional profile of the remaining cone of charcoal. Note that the slope of the graph defined by the formula is a constant for the



first two cases and that in the second case merely the right gradient and location of the peak Y value (% representation per size class) changes. This peak obviously occurs on the X-axis at the largest value for r at which the circumference is complete. Thirdly, if wood is burnt mainly laterally, charcoal will be produced in a tangential or subtangential zone and a variety of MPD distribution patterns could result.

The two lines and associated formulae in Fig.6.1B indicate the slopes of the graphs which would result from two different charcoal mean piece size (to be precise, mean length in a radial direction) values. The steeper slope would result from pieces with an average radial length of 10 mm, while the shallower slope would be produced if pieces of an average radial length of 5 mm were produced by a charred stump.

It is obvious from these data that burning branches of large diameter can only under unusual circumstances (lateral burning leaving charcoal close to the pith) produce a maximum Y score in a low size class. Such a peak would regularly only be produced by the introduction of large amounts of kindling sized wood. Note that where wood of various diameters is fed into a fire, the contribution of the various diameter sizes to the total assemblage composition is more likely to be proportional to the relative numbers of individual pieces of wood of different diameters rather than to their volumes. In the simplest case where branches are burnt from the terminal

end, each branch in a fire will produce charcoal in only the one, narrow transverse zone.

In order to test these predictions and to demonstrate experimentally the viability of the MPD approach, small fire charcoal production experiments could be performed. Three such experiments were in fact performed. The results were satisfactory at a crude level and are portrayed in Fig.6.2, but experiments controlling more variables and replicating different types of fires are required to demonstrate relationships between firewood supplies, types of fires and the data recoverable by MPDA-type analysis from charcoal assemblages.

## THE APPLICATION OF MINIMUM PIECE DIAMETER ANALYSIS (MPDA) TO CHARCOAL ASSEMBLAGES FROM BOOMPLAAS CAVE

### INTRODUCTION

Boomplaas Cave is situated in the intermontane Cango Valley, southern Cape. The setting of the site and the archaeological analysis of the sequence are described in H.J. Deacon (1979), J.C.G. Deacon (1982) and Deacon et al (1983). Apart from the lithic analysis, the cave sediments have been analysed by Webley (1979), the macrofaunal record by Klein (1983) and the microfauna by Avery (1982). The cave is situated on the southeast facing slope of a low limestone hill, Drupkelderkop (33°22'S, 22°11'E), within the Cango Valley and about 60m above the floor of the valley of the perennial

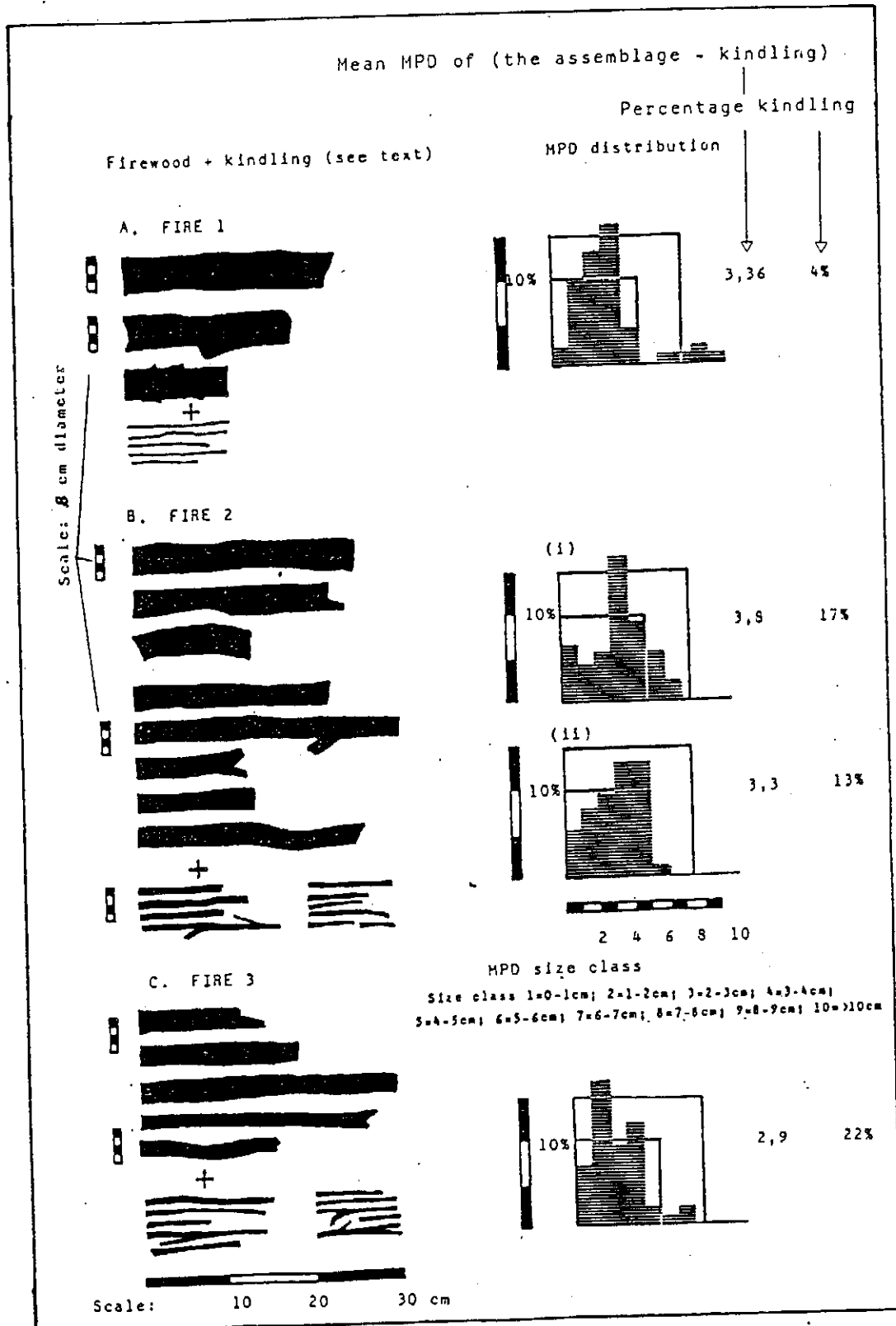


Fig.6.2 Results of three small fire, charcoal production experiments  
 Firewood supplies, MPD size class distributions, mean MPD values and Kindling: non-kindling ratios

Grobbelaars River. The river margins, marshy areas on the floodplain, sheltered gullies, exposed hillslopes and areas below cliff faces provide a diversity of habitats within the environs of the cave. A plan and section of the cave excavations are shown in Fig.6.3. In a baseline study for the palaeobotanical analysis of material from the cave sediments, the vegetation in the vicinity of the cave was described by Moffett & Deacon (1977).

#### MATERIALS AND METHODS

The analysis (MPDA) of charcoal assemblages from Boomplaas Cave was based on measurements of 580 individual pieces. These pieces had been selected and photographed under the SEM with the aim of analysing the relative abundance of wood types (Chapter 3) and prior to the development of the MPDA approach. The sampling and the techniques used to prepare the pieces for SEM microphotography were therefore not ideal for the purposes of MPDA. The sample sizes are detailed in Fig.6.6 and the techniques used in the original preparation and photography of the sections are described in Tusenius (1986).

The sampling strategy was not consistent through the sequence. Down to layer CL, where a relatively large area was still excavated (see Fig.6.3), numerous hearth features and excavation squares could be sampled. This was done by randomly selecting two pieces of charcoal per hearth feature or excavation square from the separately

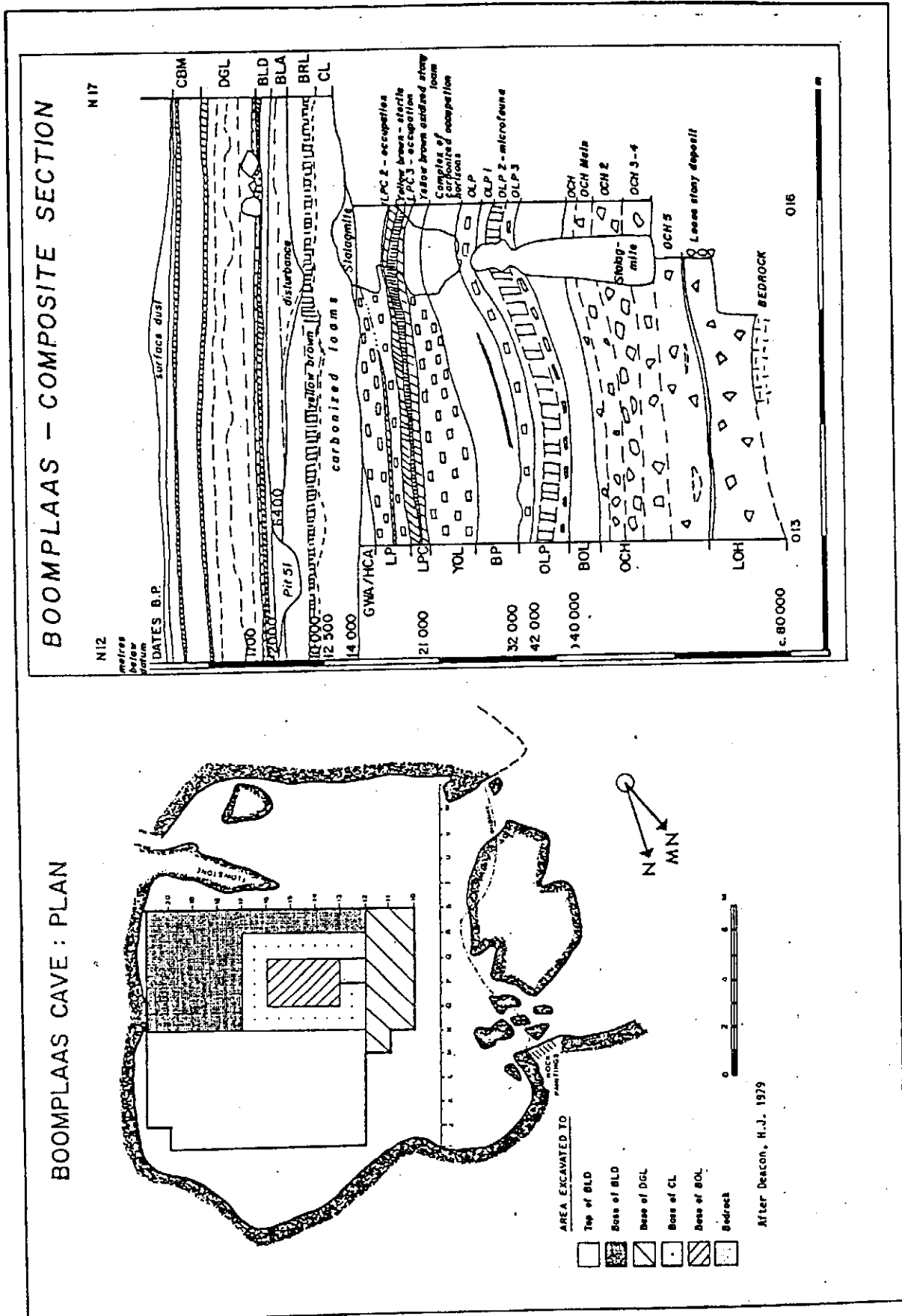


Fig.6.3 Plan and section of Boomplaas Cave (after Deacon 1979)

bagged and curated samples. Below level CL charcoal was not so abundant and here between 10 and 20 pieces were photographed per hearth feature or square. The standard total magnifications employed were either 75 X or 150 X and the assemblages came from the nine most prominent occupation units in the cave predating 2000 B.P. (Fig. 6.3).

## RESULTS

The MPD size class distributions for the total assemblages are presented in Figs 6.4 and 6.5, both percentage based diagrams. The diagrams portray the same data but highlight different patterns. Fig. 6.4 presents the data per MPD size class per assemblage, making it easy to compare changes in specific diameter size classes. Fig. 6.5 presents the data for all size classes for an individual assemblage in a single bar diagram. This allows the typical pattern for each assemblage to be readily discerned. Note that the sample sizes are sometimes low (Fig. 6.5). The Chi-square table (Table 6.1) provides a measure of the degrees of confidence with which the distribution patterns from successive layers can be regarded as distinctive.

Fig. 6.6 presents the data on mean MPD values and the ratio of kindling:firewood for each assemblage. For ease of reference these data are again presented in two forms (Figs 6.6A,B). The MPD size class distribution data for a few selected morphological types per assemblage are

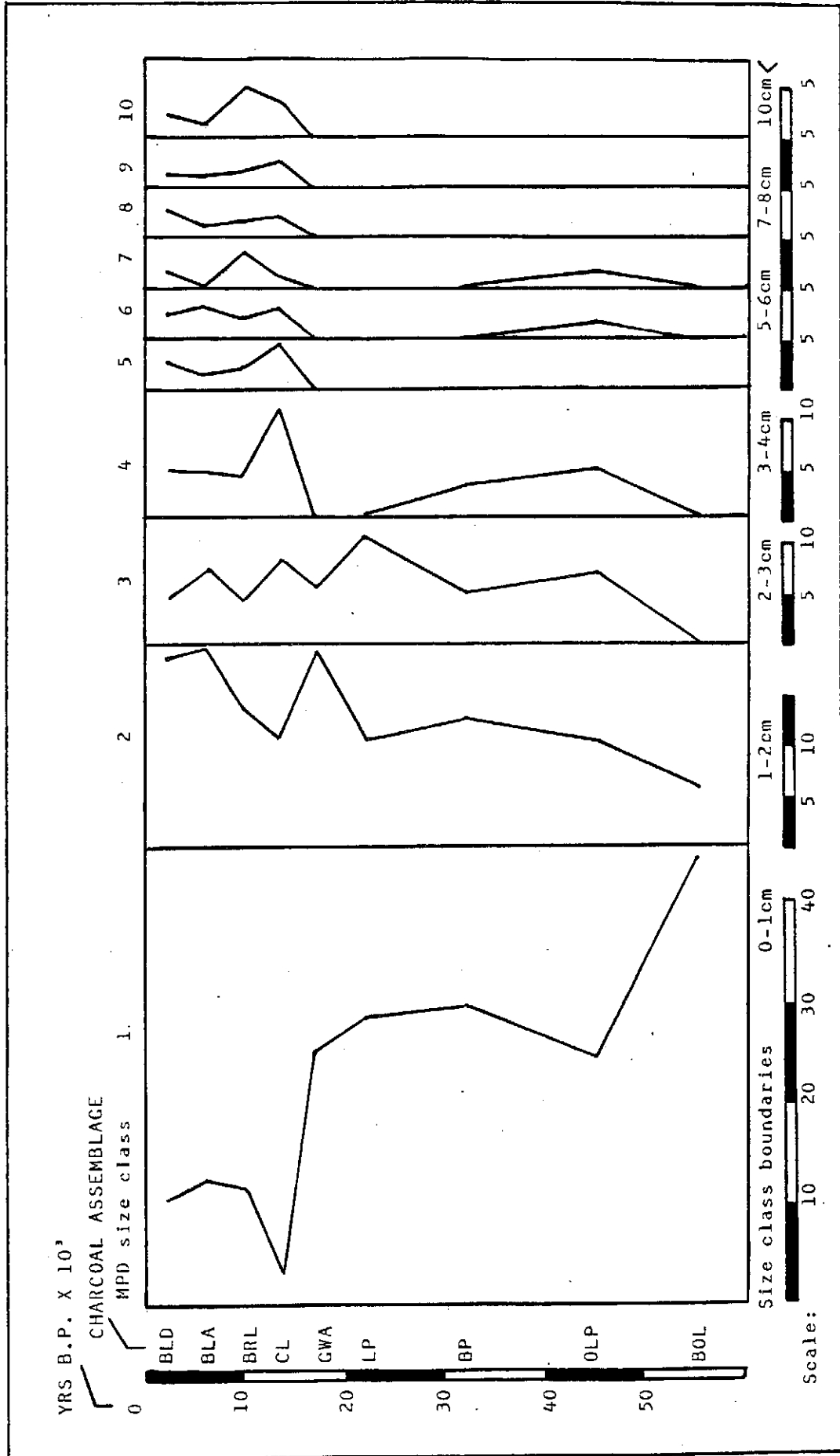


Fig.6.4 MPD (estimated branch minimum diameter) size class distributions for assemblages from Boomplaas Cave (by size class)

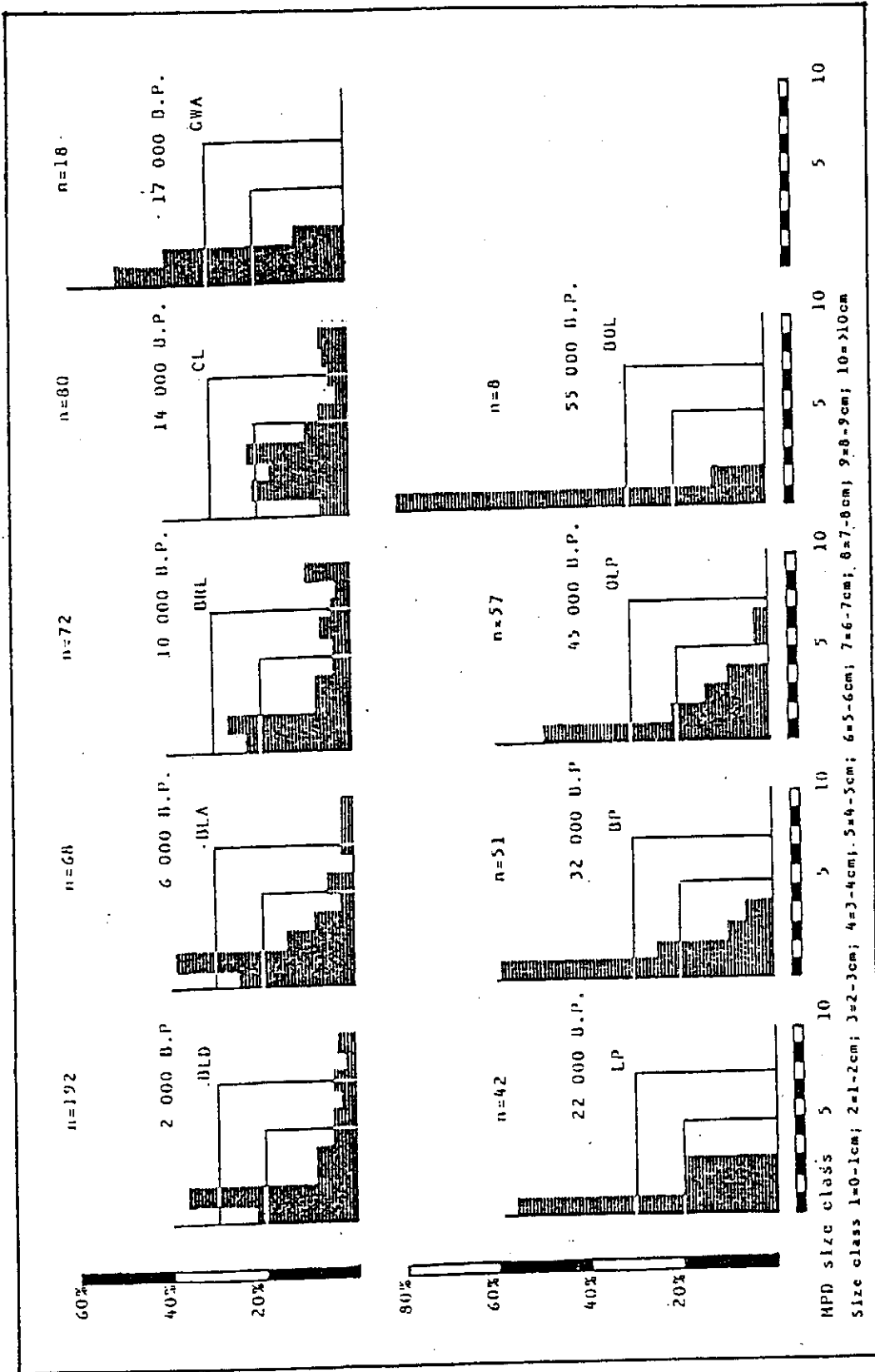


Fig.6.5 MPD size class distribution for assemblages from Boomplaas Cave (by assemblage)



Table 6.1 Chi-square values for the top four assemblages from Boomplaas Cave  
(calculated using Yates' correction for continuity)

	BLD	BLA	BRL	CL
BLD	-	7.38	8.8	30.8
BLA	7.38	-	11.4	18.5
BRL	8.79	11.4	-	13.5
CL	30.8	18.5	13.5	-

Upper percentage points for the chi-square distribution with nine degrees of freedom

0.500	0.250	0.100	0.050	0.025	0.010	0.005	0.001
8.34	11.38	14.68	16.91	19.02	21.66	23.58	27.87

presented in Fig.6.7, starting with an example from assemblage BP at the top left and proceeding down the page and from left to right to the most recent assemblage, BLD, at the bottom right.

Fig.6.7 presents examples of the MPD distribution patterns for individual morphological types per assemblage. Sample sizes are in many cases too small to be statistically reliable, but the grossly different patterns recorded for individual types within the same assemblage and for the same type between assemblages adds a valuable dimension of evidence to this exploratory analysis.

The discussion of the MPD size class distribution is based mainly on examination of Fig.6.5. Comparing the Holocene (BLD, BLA and BRL) and end Pleistocene (CL) assemblages first, the similarity of the two late Holocene assemblages (BLD, BLA) is obvious, while the BRL pattern, despite being clearly more similar to that of the members above it, tends to be intermediate between those of BLA and CL. The BLD and BLA patterns are characterised by a high relative abundance of wood in size classes 1 and 2 (diameters less than 2 cm) and low but steady representation in the larger size classes, including class 10 (diameters of 10 cm and more). The CL pattern is unique in its very high values for class 4 (see also Fig.6.4). Both CL and BRL are well represented in size classes 7 and above.

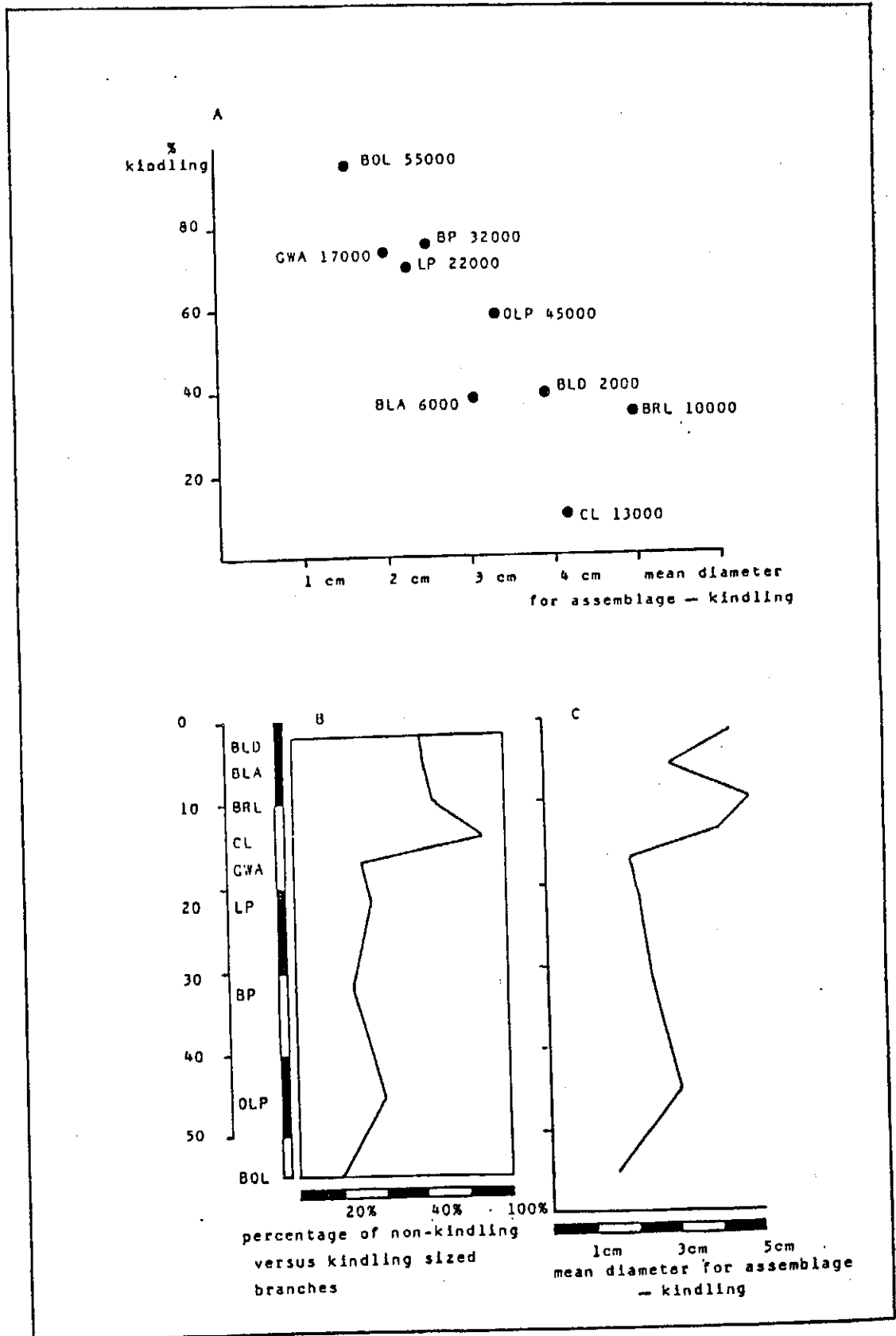


Fig.6.6  
 A. Mean minimum piece diameter (MPD) values for each assemblage graphed against the associated kindling:non-kindling ratio  
 B. Kindling versus non-kindling ratio  
 C. Mean MPD values (for the assemblage minus pieces of kindling size)

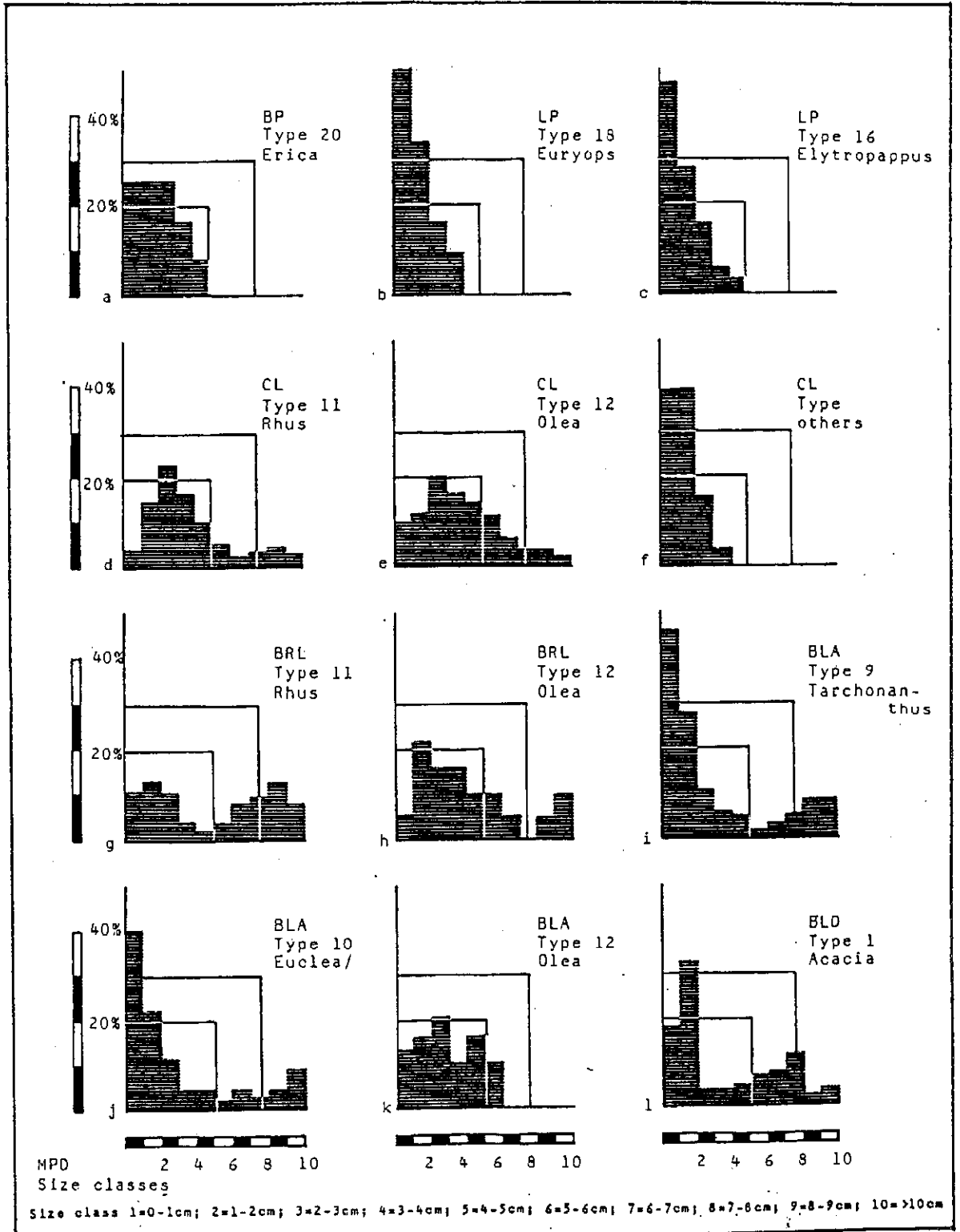


Fig.6.7 Examples of minimum piece diameter (MPD) size class distributions for individual morphological types (per assemblage)

The late Pleistocene assemblages (GWA, LP, BP, OLP and BOL ) indicate a scrub habit for woody vegetation and thus harsh climates. All the assemblages below CL have their mode in class 1 and their next most common values in class 2. Apart from OLP, none have MPD scores above 4 cm. The BOL assemblage only has wood less than 2 cm in diameter, GWA and LP, wood of less than 3 cm and BP wood less than 4 cm. Some wood of diameter 6-8 cm is recorded in the OLP population.

Fig.6.6A and C graph the mean MPD values for the nine assemblages. Apart from OLP, the values for the late Pleistocene assemblages are uniformly low ( 2.5 cm). Apart from BLA the values for the end Pleistocene and Holocene assemblages are uniformly high ( 4 cm). Fig. 6.6A and B graph the ratio of kindling to non-kindling diameters for the nine assemblages and a clear pattern emerges. Values for the three Holocene assemblages are similar, the end Pleistocene CL assemblage has very little wood of kindling size and the late Pleistocene assemblages are largely composed of wood of kindling size.

Several features revealed by the the MPD size class distribution data for selected morphological types per assemblage (Fig.6.7) should be noted. The pattern presented by the MPD size class distributions for LP and the other late Pleistocene assemblages (Fig.6.5) are repeated in the distributions for individual types (Fig.6.7b,c). In contrast, a diversity of patterns for individual types

occur in the end Pleistocene and Holocene assemblages (e.g. Fig.6.7 d,e,f or i,j,k). Looking at the pattern within the CL assemblage (Fig.6.7 d,e,f), the Olea and Rhus types are represented mainly by wood 2-3 cm in diameter or larger, while the other types occurring in the assemblage are mostly represented by wood of kindling size. This pattern suggests that selection and transport of branches of Olea and Rhus was occurring.

Fig.6.7g,e (Rhus type) and e,h,k (Olea type) provide comparisons of the patterns for a single type between levels. The patterns for the Rhus type for assemblage CL and BRL are markedly different. In CL the type is mainly represented by branches in the 2-5 cm diameter size class and little wood of kindling size is found. In BRL more fine wood occurs, less wood in the 2-5 cm size range and more wood of large diameter.

Finally, the pattern presented by the Acacia type in BLD (Fig.6.7i) is unusual with high representation in the 0-2 cm diameter size class and progressive increase in abundance of wood from the 3-4 cm to the 7-8 cm size class. The latter pattern is that predicted on theoretical grounds to correspond to a supply of firewood consisting of branches 7-8 cm in diameter.

## DISCUSSION

Table 6.2 summarises the most important aspects of the archaeological record for the nine occupation units, BLD through BOL. For present purposes particularly

Table 6.2 Summary of palaeoclimatic inferences drawn from other lines of evidence (\*after Deacon et al 1984, \*\*after Avery 1982, \*\*\*after Klein 1983)

ASSEMBLAGE AND DATING	ARCHAEOLOGICAL EVIDENCE*	MICROFAUNA**	MACROFAUNA***
BLD 2000 B.P.	impersistent low density scatters of artefacts, faunal remains and plant debris; storage pits; cave occupied for short periods or days		dominant browsing fauna indicates dense vegetation
BLA 6000 B.P.	a series of elongated, charcoal filled features occurred in this level and may be related to smoking of meat	similar conditions to the present, shrubland or bush dominant; extensive, dense riverine vegetation with trees; climate more xeric around 9000 B.P.	
BRL 10 000 B.P.	the evidence suggests a series of short term occupations		mixed browsing and grazing fauna
CL 13 000 B.P.	'processor economy'; a thick occupation deposit without discontinuities and a high density of faunal remains and artefacts suggests long term occupation	dense vegetation extends onto the hillsides at the expense of grassland; semi arid shrub restricted to hillsides, some increase in temperature relative to LP	grazing fauna (equids, alcelaphines) dominant indicating grassland
LP 22 000 B.P.	a well developed occupation complex indicates that during LPC the cave was used relatively infrequently	severe climate, cold and dry with at least very cold winters; grass on the hillsides and grassland and semi-arid shrub on the valley floor; dense riverine vegetation reduced to a minimum	
BP 32 000 B.P.	'processor economy'; well developed occupation complex; environment more productive than during OLP or BOL times		stronger representation of alcelaphines
OLP ca. 45 000 B.P.	low site usage and low productivity of the environment; 'traveller economy'	moderate climate; grass and semi-arid shrubland on the hillsides; an extension of dense vegetation on the valley floor	mainly a browsing fauna
BOL ca. 55 000 B.P.	ditto	open vegetation, cold climate; semi-arid shrubland on valley floor; grass on hillsides	mainly a browsing fauna

relevant are the recording of elongated hearth features, containing large volumes of charcoal in member BLA and the indications of differential occupation intensity in the various members. In Fig.6.8 the relative abundances of the charcoal morphological types identified in the assemblages are plotted through time. A large change over of types occurs through the ca. 60 000 year time span represented by the nine assemblages and this factor affects the nature and quality of the inferences about human behavior which can be placed on the MPDA data. In particular a dramatic change of vegetation and climate occurred between 14 000 and 17 000 years ago (Chapter 4 and Fig.6.8). Identification of the charcoal morphological types with woody plant taxa indicates that, contrary to the post 14 000 B.P. time period when trees are recorded, during the 30 000 years prior to 14 000 B.P. only smallish shrubs and bushes grew in the valley. This change in vegetation reflects strongly in the distribution of MPD values.

The evidence from the late Pleistocene assemblages suggests that short, single purpose fires were the norm during this time period. Only fine wood is represented in these assemblages; fine wood burns quickly and a fire of any duration being fed with wood of this size would be uneconomical. The incidence of a few larger branches in OLP probably registers a change in vegetation rather than a change in behaviour.

The large environmental change which occurred



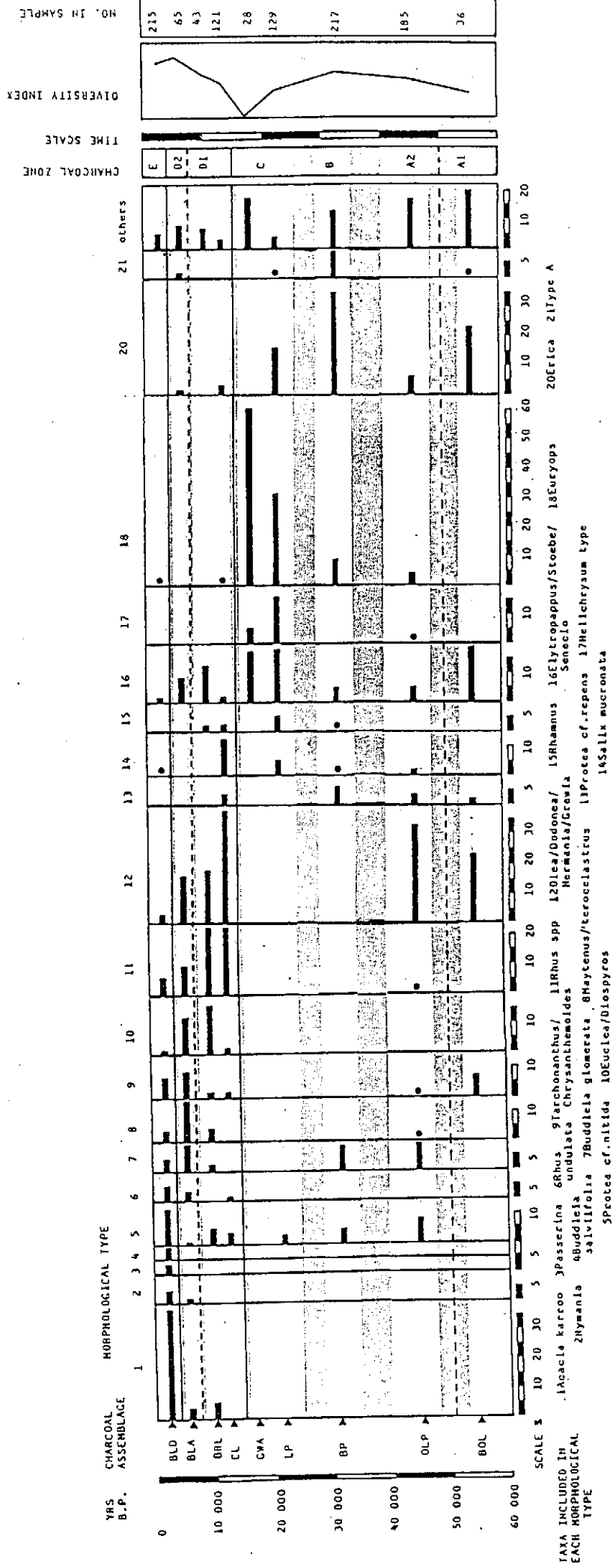


Fig.6.8 The relative abundances of morphological types in nine assemblages from Boomplaas Cave

between 14 and 12 000 years ago renders the changes in MPD distribution recorded over this boundary difficult to interpret in terms of human behaviour. However, a similar set of woody taxa was present in the valley during the Holocene and end Pleistocene (Fig.6.8) and it is therefore less hazardous to interpret changes in various MPD statistics during this time period in terms of changes in human behaviour.

The MPD data from the CL occupation unit provides the clearest evidence for a distinctive pattern of human exploitation of firewood. Firstly, CL has a much lower kindling:firewood ratio than any other level (note that the kindling wood diameter size class boundary was taken as 1,3 cm and not as 1 cm). Secondly, this pattern is further defined by the patterns for individual morphological types in CL (Fig.6.7, d-f). The two most prominent types in this assemblage, morphological types 11 (Olea) and 12 (Rhus) contain almost no wood of kindling size. Yet other types that contribute towards the total pattern for this assemblage are represented largely by wood of small diameter (Fig.6.7f). This evidence indicates that only wood of medium to large diameter of types 11 and 12 was being selected, wood falling in the 3-6 cm diameter size range being preferred.

In terms of ethnographic analogy, this is the pattern predicted when wood is systematically transported from some distance to a site, this preference being based

on the relative abundance and regularity in size and shape of branches of this diameter as well as the quality of the wood.

The overall low kindling:firewood ratio for CL suggests that long burning fires fed by wood of medium to large diameter were common during this period. The only alternative explanation is that during CL times wood of kindling size was dear, i.e. kindling was (also) having to be transported to the cave, and that it was therefore being used sparingly. This hypothesis suggests environmental conditions which could cause the local absence of scrub. The unusual feature of a virtual absence of the drier Compositae types from CL (Fig.6.8, types 16,17 and 18) suggests the same (Chapter 4). The only set of conditions which can cause the absence of woody vegetation from open slopes in a well watered area are those such as cold winds (Story 1952) or fire (Axelrod 1984) which favour and/or are maintained by grassland. Other lines of archaeological evidence (see Table 6.2) also indicate the existence of grassland during CL times.

However, evidence for the absence of woody vegetation from an area when other ecoclimatic factors are favourable for its occurrence is evidence that a relatively pure grassland existed, rather than just associations in which grass was well represented.

Comparing the HPDA data from BRL to that of CL, wood of larger diameters is relatively better represented in

BRL (but the BRL sample is small and the chi-square test shows no significant difference between the CL and BRL assemblages at the 5% level). The kindling:firewood ratio for this assemblage is, however, close to the mean for the other Holocene assemblages. The likely inference is that, in contrast to CL, during BRL times single episode fires were employed.

The fact that larger pieces may be better represented in BRL than in CL suggests that trees may have been relatively closer to the cave, or more common during BRL times. An alternative explanation is that the rare natural occurrences of dry larger branches close to the cave, a lower intensity of firewood exploitation and preferential selection of larger dry branches may have caused the BRL pattern. Conversely, a more intense or continuous exploitation of the resource during the CL occupation may have exhausted the limited supply of larger dry branches (+ 10 cm in diameter). Charcoal assemblages formed subsequently within the same occupation would thus be under represented in this size class.

The fact that the kindling:firewood ratios for BLD, BLA and BRL are so similar, while their mean MPD values differ considerably, suggests that the former statistic has some validity and reflects a pattern of use of firewood. The differences in mean MPD values recorded in the Holocene probably mainly reflect changes in the resource itself, i.e. changes in the habit and structure of woody

vegetation. The low mean MPD values for assemblage BLA for example may reflect the sampling of a drier, stunted, more spindly vegetation. The taxa prominent in BLA are thicket indicators (Euclea/Diospyros, Mavtenus/Pterocelastrus and Tarchonanthus).

On the other hand, as was argued in the case of CL, the low mean MPD value for BLA might be a product of intensive exploitation of the supply of firewood. Branches of relatively small diameter can be the most common size class in a natural size spectrum. This could, either progressively through time or because of particularly demanding collecting episodes, result in branches of relatively small diameter being most commonly collected.

The MPD size class distribution for individual types for BLD is informative. The pattern for Type 1 (Acacia karroo) from this assemblage (Fig 6.71) strongly suggests that the source was trees rather than shrubs and that these were close by. A large percentage of kindling sized wood and wood under 2 cm in diameter is present and this indicates a lack of transport. The uniform slope of the graph above size class 2 suggests that, apart from branches in the first 2 size classes, pieces of wood between 6-7 cm in diameter and branches > 10 cm in diameter were being collected and this evidence also suggests proximity of the trees.

It is known from the modern day botanical survey of the valley (Hoffett & Deacon 1977) that a grove of Acacia karroo occurs on the slope below and close to the cave.

## CONCLUSIONS

MPD analysis clearly registers the dramatic change in environment which occurs between CL and GWA and which has been recorded by all the other forms of analysis which use biological remains as proxy evidence for past climates (Avery 1982; Klein 1983). The analysis was able to distinguish three clearly different MPD size class distribution patterns for assemblages and this constitutes the most positive proof of the value of the approach. The fact that MPDA could produce evidence that a unique pattern of behaviour related to firewood gathering and use (and perhaps to other aspects of society too) existed during CL times demonstrates the potential of the method. EDXA and other analyses suggest that the environment was very productive at this time and that occupation of the cave was intense. The diagnosis of the proximity of a grove of Acacia karroo in the late Holocene (BLD) also constitutes proof of the potential of the method.

The approach is still in a developmental stage in terms of knowledge about human behaviour related to firewood procurement and use. Much scope exists for ethnographic work in this direction. In terms of analysis of fossil material, it is clear that larger samples should be studied in order to make more of the changes recorded statistically reliable. Also, if the type of deposit and excavation techniques allow it, assemblages should be analysed by hearth feature rather than occupation unit. Apart from problems with

excavation techniques not designed to recover charcoal, the main problems in achieving these aims are technical, i.e. how to process large samples. The methods of taking measurements described in this chapter are simple and the procedure could be made faster by computer processing of data, especially if the basic data capturing were done directly on a digitising tablet linked to the computer.

#### REFERENCES

- ARCHER, F. in prep. An ethnographic study of the edible plants of Namaqualand.
- ASHTON, H. 1956. The Basotho. Oxford University Press, Oxford.
- AVERY, D.M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum 85:183-374.
- AXELROD, D.A. 1984. The evolution of the grasslands of the American Mid-West. Botanical Review 51:163-202.
- BARTHOLIN, T.H. 1979. Environment and dating - Wood anatomy applied to a Neolithic settlement. International Association of Wood Anatomists Bulletin 10: 49
- BEST, M. 1979. The scarcity of domestic energy: a study in 3 villages. SALDRU working paper 27, University of Cape Town, Cape Town.
- BIALY, J.R. 1982. Energy flows in subsistence agriculture. A study of a dry zone village in Sri Lanka. Ph.D. thesis, University of Edinburgh.

- COUSINS, W.J. 1975. Optical microscopy of charcoal. Journal of Microscopy 105:15-18.
- CUNNINGHAM, T.T. 1984. The resource value of indigenous vegetation to rural people in an area of low agricultural potential. Unpublished Ph.D thesis, University of Cape Town.
- DEACON, H.J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10:241-257.
- DEACON, H.J., A. SCHOLTZ & D.L. DAITZ 1983. Fossil charcoals as a source of palaeoecological information in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis:174-182. SANSPR 75, Pretoria.
- DEACON, H.J. DEACON, J., SCHOLTZ, A., THACKERAY, J.F. & BRINK, J.S. 1984. Correlation of the palaeoenvironmental data from the late Pleistocene and Holocene deposits at Boomplaas Cave, southern Cape. IN: J.C. Vogel (ed.) Late Cainozoic Palaeoclimates of the southern hemisphere:339-359. Balkema, Rotterdam.
- DEACON, J.C.G. 1982. The Later Stone Age in the southern Cape, South Africa. Ph.D thesis, University of Cape Town.
- EBERHARD, A.A. 1986. Energy consumption patterns in undeveloped areas in South Africa. Unpublished report. Energy Research Institute, University of Cape Town.
- EBERHARD, A.A. & POYNTON, R.J. in press. Fuelwood calorific values and preferences as criteria for the



- choice of tree species for planting in southern Africa. Proceedings of the conference for alternative energy resources, Energy Research Institute, University of Cape Town. ( August 1986 )
- GANDAR, M.V. 1983a. The utilisation of trees and the impact on the environment: A study in Mahlabatini District, Kwazulu. Institute of Natural Resources, University of Natal, Pietermaritzburg.
- GANDAR, M.V. 1983b. Wood as a source of fuel in South Africa. Monograph 4, Institute of Natural Resources, University of Natal, Pietermaritzburg.
- GANDAR, M.V. 1984. The poor man's energy crisis: domestic energy in Kwazulu. Carnegie Conference paper 156, SALDRU, University of Cape Town.
- GODWIN, H. & TAMSLEY, A.G. 1941. Prehistoric charcoals as evidence of former vegetation, soil and climate. Journal of Ecology 29:117-126.
- GWAITTA-MAGUMBA, D.A. 1983. Woodfuel and other energy resources in Swaziland , SADDC Woodfuel Seminar, Luanda, Angola (October 1983).
- JELENIC, N.E. & VAN VEGTEN, J.A. 1981. A pain in the neck: The firewood situation in south-western Kgatleng, Botswana. NIR research note 5, University of Botswana, Gaborone.
- KGATHI, D.L. 1984. Aspects of firewood trade between rural Kweneng and urban Gaborone: a socio-economic perspective. Working paper 46, NIR, University of Botswana, Gaborone.

- KLEIN, R.G. 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos region. IN: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (eds) Fynbos palaeoecology: A preliminary synthesis:116-138. SANSPR 75 Pretoria.
- LEE, R.B. 1979. The !Kung San. Cambridge University Press, Cambridge.
- LIENGME, C.A. 1983. A study of wood use for fuel and building in an area of Gazankulu. Bothalia 14:245-257.
- MCGINNES, E.A., KANDEEL, S.A. & SZOPA, P.S. 1971. Some structural changes observed in the transformation of wood into charcoal. Wood and Fibre 3:77-83.
- MOFFETT, R.O. & DEACON, H.J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Congo Valley. South African Archaeological Bulletin 32:127-145.
- SALISBURY, E.J. & JANE, F.W. 1940. Charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times. Journal of Ecology 28:310-325.
- SCHWEINGRUBER, F.H. 1978. Microscopic wood anatomy: structural variability of stems and twigs in recent and subfossil woods from Central Europe. Swiss Federal Institute of Forestry Research, Birmensdorff.
- SHEDDICK, V.G.J. 1954. The Southern Sotho. International African Institute, London.
- SILBERBAUER, G.B. 1981. Hunter and habitat in the central Kalahari Desert. Cambridge University Press, Cambridge.

- STORY, R. 1952. A botanical survey of the Keiskammahoek District. Nemoirs of the Botanical Survey of South Africa 27. Government Printer, Pretoria.
- TUSENIUS, M. 1986. Charcoal analytical studies in the north-eastern Cape. Unpublished M.A. thesis, Department of Archaeology, University of Stellenbosch.
- VAN DAALEN, J.C. 1980. The colonisation of fynbos and disturbed sites by indigenous forest communities in the southern Cape. Unpublished M.Sc. thesis, University of Cape Town.
- WEBLEY, L. 1979. A sedimentological analysis of the Boomplaas Cave sequence. Unpublished Hons. project, Department of Archaeology, University of Stellenbosch.
- YELLEN, J.E. 1976. Settlement patterns of the !Kung. IN: R.B. Lee & I. DeVore (eds) Kalahari Hunter-Gatherers:47-72 Harvard University Press. Cambridge, Massachusetts.
- ZICHERMAN, J.B. & WILLIAMSON, R.B. 1981. Microstructure of wood char. Wood Science and Technology 15:237-249.