THE UNIVERSITY OF HULL

LATE QUATERNARY MONTANE VEGETATION DYNAMICS IN BWINDI-IMPENETRABLE FOREST, CENTRAL AFRICA

being a Thesis submitted for the Degree of

Doctor of Philosophy

in the University of Hull

by

Robert Marchant BSc (Hons.)

November 1997

To Caroline, Laura and Myooba

Contents

Page number

PART 1: BACKGROUND TO THE THESIS AND STUDY AREA

Chapter 1

Research context

Chapter 2

The central African environment

Chapter 3

The present-day environment of the Rukiga highlands and the Mubwindi Swamp catchment

PART 2: METHODS AND RESULTS

Chapter 4

Collection and radiocarbon dating of sediments

Chapter 5

Analysis of sediments from Mubwindi Swamp

Chapter 6

Modern vegetation surveys, palynology and the pollen-vegetation relationship

Chapter 7

Fossil pollen analysis of the Mubwindi Swamp sediments: methodology, zonation and relationship to sedimentary analysis

Chapter 8

Interpretation of the pollen and spores retained within the Mubwindi Swamp sediments

PART 3

DISCUSSIONS AND CONCLUSIONS FROM THE THESIS

Chapter 9

A discussion of Late Quaternary sedimentary and vegetation dynamics within the Rukiga highlands

Chapter 10

Conclusions from the thesis and future research possibilities

10.1 Introduction

List of Figures

List of Tables

Following
page number

List of Plates

Acknowledgements

The work presented in this thesis was financed by the University of Hull, the Natural Environment Research Council, the British Institute in East Africa and the Bill Bishop Memorial Fund. Logistical support in Uganda was provided by the Institute of Tropical Forest Conservation (ITFC). This funding and support is sincerely acknowledged.

I am indebted to my supervisor, Dr. David Taylor for advice and encouragement throughout the period of research. More than a source of help, David has been a valued friend. In addition I would like to thank Dr. Alan Hamilton, from whom David has learnt the craft of African palaeoecology, and whos energies are still enthusing.

The help from staff at various institutions was also very much appreciated. Here in the University of Hull, thanks are due to Dr. Steve Ellis, Dr Jack Hardisty and Dr. David Watts for valuable discussions and friendship; to Keith Scurr for drafting some of the figures; and to John Garner who scanned and printed the plates. Furthermore, I am indebted to Makerere University, Kampala, for the use of coring equipment and to the Government of Uganda for research permission.

I am indebted to the help I received during fieldwork in Uganda, particularly from Jonathan Baranga, the Director of the ITFC who made much of the work possible. Special thanks must go to Myooba Godfrey who worked as field assistant during the majority of the time at Mubwindi Swamp; his knowledge of the Bwindi-Impenetrable Forest and appreciation of the environment was inspirational.

Finally, I would like to thank Caroline, and latterly Laura for providing support throughout the thesis.

Abstract

Mubwindi Swamp in the Rukiga Highlands of south west Uganda is today surrounded by dense stands of moist lower montane forest. A survey of the present-day vegetation combined with an investigation of the surface pollen spectra indicate pollen accumulating on the swamp surface mainly result from taxa within the catchment. This survey also highlights that a combination of climatci, edaphic, demographic and human factors control the present-day composition and distribution of montane forest.

Mubwindi Swamp comprises deep accumulations of peat-rich deposits. Pollen data from three cores of sediment provide a partial record of montane vegetation history since at least 43,000 yr B.P. This record is broken by at leat two, and possibly three, sedimentary hiati. Twelve radiocarbon ages, charcoal data from two cores using combination of three methods, and investigations into particle size characteristics place this record of montane vegetation dynamics within a wider palaeoenvironmental debate concerning Pleistocene climates, forest refugia, and human induced impacts on montane forests. Pollen deposited before and soon after the last glacial maximum represents a vegetation composition very different to that of the modern vegetation within the Mubwindi Swamp catchment. Specifically there were increased amounts of *Artemisia*, Ericaceae, *Faurea* and *Stoebe*. However, some elements found within the modern vegetation persisted during these periods, these include *Ilex*, *Olea*, *Podocarpus* and *Zanthoxylum*. These taxa may have persisted possibly because of favourable topography or soils.

The uppermost 5 m of deposits in core MB6 from the site are dated to the last 2100 years, and thus provide an opportunity, so far unique for Uganda, and much of central Africa, to record variations in the composition of montane vegetation during the late Holocene. Results of analyses of pollen indicate that lower montane forest has been present in the catchment for Mubwindi Swamp throughout the last 2100 years, despite extensive clearance in other parts of the region over the same period. A transition to a more open - and possibly drier - form of forest is apparent from around 680 yr B.P. This montane forest composition is thought to stem from a recent period of climatic change to less

humid conditions. This change is followed by an increased occurrence of pollen from plants presently associated with areas of degraded forest from around 200 yr B.P. and a decrease in pollen from important sources of timber. Some recovery of timber trees is apparent from around 50 yr B.P.

Changes in forest composition around 200 years ago could be interpreted as representing slightly increased humidity. However, in view of the nature of these changes, a low level of human impact was probably the most important causal factor. The gazetting of Bwindi-Impenetrable Forest as a Forest Reserve in the early 1930s may have facilitated a recovery of timber trees during the present century.

PART 1: BACKGROUND TO THE THESIS AND STUDY AREA

CHAPTER 1

Research context

1.1 Introduction

Within the current chapter the aims of the thesis, and the structure that the thesis takes is presented. Theoretical principles inherent in palaeoenvironmental research will be discussed and the approach adopted for the thesis outlined.

1.2 Aims of the thesis

The primary aim of this thesis is to provide a palaeoecological record for the Mubwindi Swamp catchment. First, it is necessary to describe the present-day composition and distribution of vegetation within the Mubwindi Swamp catchment (2100m). This catchment is located within Bwindi-Impenetrable Forest National Park, Rukiga highlands, south-west Uganda. Using this information, how representative pollen spectra accumulating within surface sediments are of the surrounding vegetation will be determined. Pollen retained within accumulated sediments at Mubwindi Swamp, combined with sedimentology will be investigated to provide a palaeoecological record during the Late Quaternary period from a catchment that presently supports montane forest.

As palaeoecological research is not new to the Rukiga highlands (Hamilton, 1982; Hamilton *et al*, 1986; Morrison, 1961; 1968; Morrison and Hamilton, 1974; Taylor, 1990; 1992; 1993; 1996), a second aim is to incorporate the new data from Mubwindi Swamp within existing data to develop a regional model for changes in the composition and distribution of montane vegetation. Which of the various potential forcing mechanisms (exogenic: climate, anthropogenic; and endogenic: successional) responsible for montane vegetation dynamics within the Rukiga highlands is suggested during the Late Quaternary.

Bwindi-Impenetrable Forest is the only significant area of lower moist montane rain forest remaining in the Rukiga highlands. It has major international, national and local importance; Bwindi-Impenetrable Forest is a locus of high biodiversity and natural resources, and performs an important role in catchment protection. Thus, a third aim of this thesis is to place the current debates over managing, monitoring and utilising this forest in a longer, and more biologically meaningful time perspective than is currently available.

1.3 Research philosophy

Reconstruction of vegetation composition and distribution usually has two foci; the past and the future. This temporal focus appears to be something of a short-coming, as environmental reconstruction is based on the assumption of uniformitarianism, or 'the present is the key to the past'. This assumption must be treated with caution. Present-day environmental controls are unique to the present. This uniqueness means that a thorough understanding of present-day environmental controls (be they climatic, anthropogenic or ecological) on the resultant vegetation, and how a record of these factors is commuted to a sedimentary record is essential for the reconstruction of past environments, and production of future scenarios. For example, presently in central Africa humans do, and it seems likely will continue to, impart the dominant control on vegetation composition and distribution. The present-day controls are protective legislation, high population densities resulting in environmental pressure and loss of biodiversity. Seemingly, these will be more important in the future. However, these were almost non-existent, or certainly much reduced, in the non-too-distant past. Therefore, forcing mechanisms on montane vegetation composition and distribution have moved from environmental controls towards the anthropogenic arena. Here, economical, political and social agendas 'battle it out' to determine the composition and distribution of montane vegetation.

Under reduced human influence a range of other factors were responsible for the composition and distribution of montane vegetation. Climate has been the main determinant, manifesting itself as fluctuations in temperature and/or precipitation. These changes would lead to a change in humidity, and in diurnal and seasonal patterns of atmospheric moisture transfers. Importantly, the influence imparted on the local climatic regime, and therefore the vegetation by factors such as topography, edaphic conditions and the position and type of water course, would be in a state of flux as the ambient climate changes.

Therefore, in the application of an uniformitarian approach, the present should not be seen as the definitive key to the past. Present-day environmental controls on vegetation composition and distribution should not be blindly applied to past vegetation composition and distribution, but should be applied with caution. Initially, there should be an inherent requirement in any palaeoenvironmental study to understand fully the environmental controls operating at present, before launching through the process of 'time-travel'. For this study, the reconstruction of past vegetation composition and distribution will be viewed as the key to the present-day situation. Reconstructions that follow will not merely focus on the present-day controls, but will be based on the preceding and proceeding vegetation associations. Hence, as well as the present being the key to the past, the past is viewed as the key to the present.

1.4 Thesis organisation

The following text of this thesis is arranged into three sections: background to the thesis and study area; methods and results; and discussion and conclusions. The first section contains three chapters, including the current. The second chapter details the environmental setting of central Africa, and places the current research in context of the available evidence for regional environmental change and archaeological history, while exposing some of the deficiencies in this evidence. The third chapter outlines the environment of the Rukiga highlands in terms of the geology, topography, drainage, climate, soil, flora and fauna, and management of Bwindi-Impenetrable Forest. The chapter then details the present-day environment of Mubwindi Swamp.

The method and results section is arranged into five chapters that describe: collection and dating of sediment cores; surveys of present-day vegetation and modern pollen rain; core-based sedimentary and fossil pollen data from Mubwindi

Swamp; and identification of stratigraphic zones derived from the pollen and sedimentary data.

The third section comprises two chapters. In chapter nine, evidence described in section two is used to reconstruct the sediment and vegetation history within the Mubwindi Swamp catchment, then the Rukiga highlands. Chapter ten summarises the conclusions from the thesis, and outlines suggestions for the future of palaeoenvironmental research in the region.

CHAPTER 2

The central African environment

2.1 Introduction

Central Africa extends in an arc from northern Malawi to north-east Zaire (Figure 2.1). Regional boundaries are arbitrary, resulting from political division rather than geographical or ethnographic characteristics. For the purposes of this thesis the region includes the boundaries of Rwanda, Burundi, eastern Zaire and western Uganda. Initially, the present-day environment will be detailed for central Africa. This will then focus on past evidence for change in the composition and distribution of montane vegetation. This evidence has been derived from micro-fossil, geomorphology and archaeological sources.

2.2 Geology, topography and drainage

Since the Precambrian, Africa has been little affected by the major global orogonies. This stability has resulted in a gentle topography for much of the African continent. However, central Africa has undergone tectonic dislocation, beginning in the Mesozoic (Summerfield, 1996). This was most active since mid-Tertiary times, particularly around 22, 6 and 2.5 million years ago (Grove, 1986). This tectonic activity resulted in the formation of the Western Rift Valley, with uplift ranging from 700 m to over 4000 m (Hamilton, 1982). The Virunga volcanoes in eastern Zaire, northern Rwanda and western Uganda originated during the Quaternary period. In contrast to this volcanic activity, the Ruwenzori mountains are formed by a block of up-thrust Precambrian crystalline rock (Livingstone, 1967). This tectonic activity has produced the high Plateau that characterises much of central Africa (Figure 2.1). Most of the uplift was completed before the Quaternary glaciations (Rosquist, 1990). Each tectonic phase was associated with erosion of the uplifted geology and subsequent deposition, resulting in a topographically complex landscape along the Western Rift Valley.

One of the characteristic features of central Africa is the numerous deep lakes. Towards the south of the region, Lake Tanganyika dominates, with a chain of

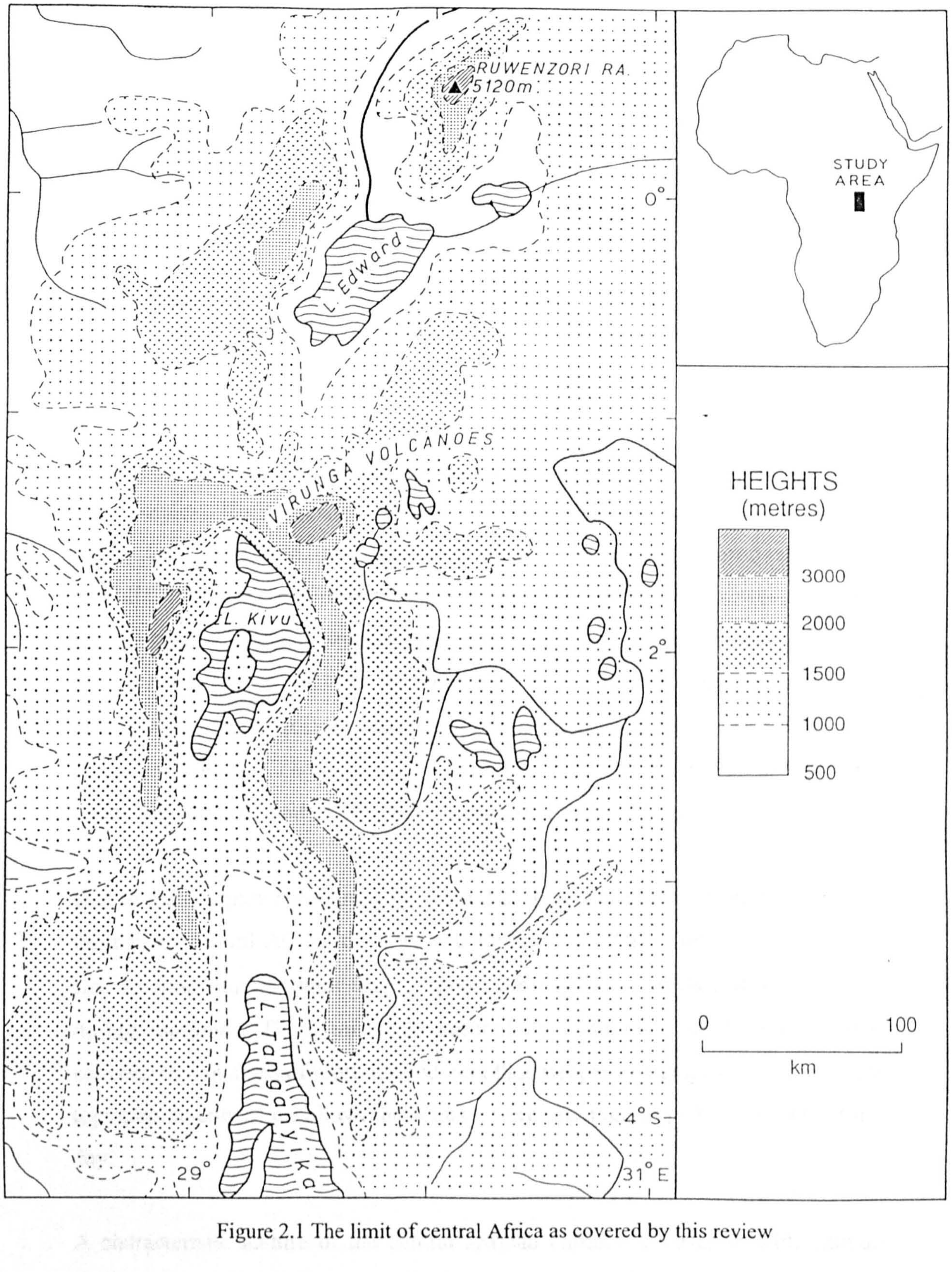


Figure 2.1 The limit of central Africa as covered by this review

lakes (Albert, Edward, George and Kivu) along the arc of the rift valley (Figure 2.1). The rifting process has had considerable affect on central African watersheds (Walling, 1996). There has been a reversal of previously west-flowing rivers, and the creation of Lake Victoria. The Virunga Volcano chain marks the hydrological divide between the headwaters of the Congo and Nile river systems.

2.3 Climate

Central Africa lies between the axes of the sub-tropical high pressure cells (Kenworthy, 1966). Large migrations of these cells manifest themselves as a reversal of winds, resulting from differential heating, and an excursion of the Inter-Tropical Convergence Zone (ITCZ). The present-day climate of central Africa is tropical, and thus almost entirely dominated by monsoonal systems (Goudie, 1996). A complicating factor is a zone of convergence between westerly and the south-easterly air streams, which normally lies over the eastern part of the Congo Basin (Maley, 1995a). Accompanied by a belt of rainfall (Baker, 1958), this frontal zone frequently moves over western central Africa, bringing moist climatic conditions. The influence of these can be felt as orographic precipitation on the highlands of central Africa (Livingstone, 1967).

Due to the complex topography (Section 2.2) there are marked climatic variations throughout central Africa. Cool air accumulates in valleys during the night; this can become saturated with water vapour, forming heavy mists that are common during mornings. These mists are particularly common after the rains, being concentrated in areas of more incised, and thus steeper topography. In areas where topographic conditions allow, these mists were observed to persist throughout the day.

A characteristic feature of the central African climate is variation with altitude (Davies *et al*, 1977). The climate in areas over 3800 m is characterised by severe diurnal temperature changes, intense nightly frosts and strong daytime radiation (Hedberg, 1951). Down to about 2600 m, the climate is strongly influenced by diurnal temperature changes; mid-day temperatures vary from 6 °C to 10 ^{0}C, and night temperatures are often much lower with frequent frosts (Hedberg, 1951).

Within this altitudinal range the ground can be locally saturated (Hedberg, 1951), due to a combination of mists, rainfall, low levels of evapo-transpiration and seepage from snow-melt above. Between approximately 2800 and 2000 m the climate is characterised by strong diurnal fluctuations in temperature (5 °C to 30 °C), and consequently evapo-transpiration. Orographic precipitation is common in incised, steep sided valleys and depressions. Land from approximately 2150 to 1000 m is characterised by diurnal temperature ranges of 10 °C to 30 °C.

Climatic variations with altitude are complex, resulting from various factors superimposed on the general climatic regime for a given latitude. This factor-complex can be summarised as an adiabatic lapse rate. Although lapse rates have often been 'determined' from altitudinal changes in temperature, results vary considerably. One standard that is constant is the dry adiabatic lapse rate; this can be defined as the cooling of an absolute dry parcel of air as it passes to higher altitudes (Barry and Chorley, 1990). The laws of thermodynamics fix this rate of cooling at - 9.8 °C 1000 m^{-1}. However, cooling air invariably produces condensation, and the liberalisation of latent heat, which reduces the rate of temperature decrease (Barry and Chorley, 1990). A crucial, and often overlooked aspect of the saturated adiabatic lapse rate is that the rate of temperature decrease varies considerably with ambient temperature. At high temperatures, the rate can be as low as - 4 °C 1000 m^{-1}, and increases with decreasing ambient temperature; to approaching - 9 °C 1000 m^{-1} at - 40 °C (Barry and Chorley, 1990).

Thus, the actual adiabatic lapse rate, or environmental lapse rate, varies according to levels of ambient moisture and temperature. The environmental lapse rate for east and central Africa is - 6.5 °C 1000 m^{-1} (Kenworthy, 1966). This was computed from a wide range of climatic and altitudinal data, principally from Kenya. However, this rate is likely to vary according to aspect, topography, and to have been different under past climatic regimes. Thus, caution is prudent when applying lapse rates to points in the past, or indeed different areas from where the rate was computed from.

2.4i Present-day composition and distribution of montane vegetation

Common to all montane areas are rapidly changing climatic conditions as one passes up an altitudinal gradient (Section 2.3), thus the resultant vegetation changes rapidly with altitude. Before highlighting the composition of specific vegetation assemblages, it should be emphasised that the altitudinal divisions are flexible and change over space and time.

Central African montane vegetation belongs to three phytochoria (White, 1983); these are the Afroalpine, Afromontane and Guineo-Congolian. These phytochoria are regional divisions of vegetation, based upon floristic composition and distribution. There is a noticeable altitudinal overlap between the different phytochoria and significant within phytochoria differences; this has led to the grouping together of some phytochoria, and sub-divisions of others. Therefore, an altitudinal approach (Figure 2.2) to describing vegetation composition is more suitable to this thesis. Hedberg (1951) classified vegetation into a series of belts (regionally recognisable vegetation associations), and zones (locally based altitudinal bands). Within the Afroalpine and Afromontane phytochorias of White (1983), Hedberg (1951) recognised three belts. In ascending order these are: the Montane Forest Belt, the Ericaceous Belt, and the Afroalpine Belt.

Montane forest (3300 to 1700 m) contains broad-leaved, hardwood trees, and less frequently conifers (Hamilton, 1982). Several different zones are recognised within this broad classification by different authors (Chapman and White, 1970; Eggeling and Dale, 1951; Hedberg, 1951; Langdale-Brown *et al*, 1964; Lind and Morrison, 1974; Livingstone; 1967; White, 1983). Unfortunately, the published accounts have used different terminology for similar zones, and have delimited different 'transitional altitudes' between the zones. Indeed, Boughey (1955b) identified a total of thirty-nine different synonyms for montane forest. This has led to confusion, and possible mis-interpretation, of data on vegetation distribution. Therefore, with standardisation in mind, I shall use the classification proposed by Hamilton (1982) and used by Taylor (1990, 1992). According to this scheme montane forest is divided into lower and upper altitudinal zones, the adjectives moist and dry being used where appropriate.

At lower altitudes the forest has structural and floristic similarities to lowland forest, although being more species rich than the dry lower montane forest (Chapman and White, 1970). The vegetation is now dominated by *Celtis* spp., *Juniperus procera* and *Olea capensis* ssp. *hochstetterii.*

Frequently occurring species of moist lower montane forests on the lower slopes of valleys include *Entandrophragma excelsum*, *Neoboutonia macrocalyx*, *Parinari excelsa* and *Syzygium cordatum*. On land at mid-altitudes *Cassipourea ruwensorensis*, *Chrysophyllum albidum*, *Drypetes albidi*, *Ilex mitis*, *Strombosia scheffleri* and *Zanthoxylum* spp. are present. At higher altitudes, or within edaphically drier areas, taxa such as *Faurea saligna*, *Hagenia abyssinica*, *Nuxia congesta*, *Olea capensis* ssp. and *Podocarpus milanjianus* are common. Some taxa found in dry-land situations at high altitudes are present at wetland locations at lower altitudes. For example, *Podocarpus milanjianus*, a taxon normally associated with a dry upper montane habit is present on the north-west side of Lake Victoria at 1200 m (Lind and Morrison, 1974). Species of *Ilex*, *Rapanea* and Ericaceae all exhibit a similar distribution trend (Hamilton, 1982).

Within the Rukiga highlands, Bamboo (*Synarundinaria* spp.) dominated forest is restricted to the south-eastern parts of Bwindi-Impenetrable Forest (Cahusac, 1958), and Euchoya Forest (Hamilton, 1969). In the context of central Africa, and possibly further afield, bamboo is thought to represent a successional stage within montane forest, rather than a distinct vegetation type. This is supported by the presence within bamboo of taxa normally associated with regenerating lower montane forest (Section 2.4iii).

The upper altitudinal limit of the upper montane forest varies from place to place, and reaches up to 4000 m along stream courses on Mount Kenya (Coe, 1967). The arboreal flora of the upper montane forest zone appears to vary little from locality to locality, possibly because of a more uniform climate at higher altitudes (Hamilton, 1974). *Rapanea rhododendroides* and *Hagenia abyssinica* are usually prominent members of the vegetation, *Stoebe kilimandsharica* and *Artemisia afra* can also be present (Hamilton, 1969). *Anthospermum*, *Cliffortia*, Ericaceae,

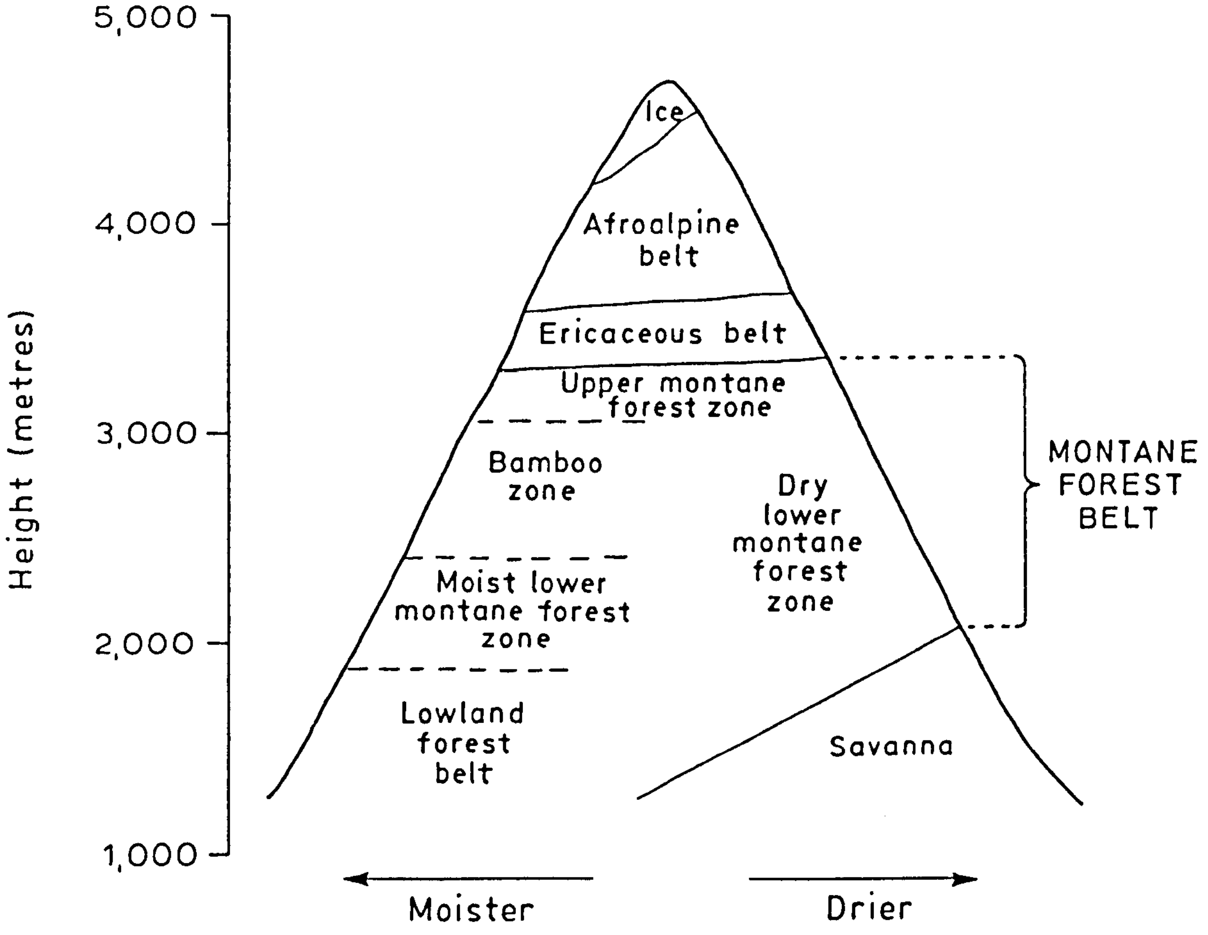


Figure 2.2 Altitudinal distribution of vegetation types (after Hedberg, 1951)

Myrica, *Olea* and *Podocarpus* can also be important elements of the vegetation (Hamilton, 1969). Notwithstanding the general similarity of upper montane forest composition, the upper altitudinal limits occur at higher altitudes in drier places (Bouxin, 1976). This may be related to the mean maximum temperature of such sites being higher comparable to wetter sites. Similarly, many taxa descend to lower than expected altitudes in areas that are climatically moister or are situated in edaphically moist river valleys.

In the lower parts of the Ericaceous Belt (3300 to 2700m) montane forest taxa can be present experiencing nightly conditions of frost, over-heating and physiological drought. More regular rainfall, or occult precipitation, can encourage tree growth at higher altitudes, as can be seen in topographically protected, humid valley slopes (Coetzee, 1967; Coe, 1967). These locally moist conditions cause higher temperatures (Section 2.3). Therefore, the floristic composition of the lower part of the belt is very sensitive to the local climatic regime.

Ericaceous Belt (4000 to 2700 m) vegetation is characterised by a microphyllous, thorny habit, other xeromorphic features are common. Three main communities (zones) are recognised from this vegetation belt (Snowden, 1953). Sub-Alpine arboresent Ericaceous and *Senecio* forest is dominated by *Agauria salicifolia*, *Artemisia afra*, *Cliffortia nitidula*, *Erica arborea*, *E. ruwenzoriensis*, *Hypericum* spp., *Philippia johnstonii*, *P. keniensis* and *Stoebe kilimandscharica*. Sub-Alpine ericaceous and mixed bush communities are dominated by species of *Alchemilla* and *Helichrysum*. Thirdly, Sub-Alpine herb-rich grassland communities are dominated by members of the Gramineae. There is relatively close floristic similarity between the composition of Ericaceous Belt vegetation on different mountains of east and central Africa; the following genera being common; *Alchemilla*, *Artemisia*, *Cliffortia*, *Deschampsia*, *Helichrysum*, *Hypericum*, *Philippia* and *Stoebe* (Hedberg, 1951).

Although poor in species diversity, the Afro-Alpine flora (> 3800 m) is sufficiently distinct from the surrounding lower floras to warrant its own class (Hedberg, 1963). No less than 80% of the taxa are endemic to the high mountains of east and central Africa, indicating that as a vegetation type it has long been isolated from other African mountains and more temperate areas (Hedberg, 1961). *Alchemilla* spp., *Helichrysum* scrub and *Scenico* spp. are the dominant taxa in this zone (Hedberg, 1951; Hamilton, 1972), other genera present include *Carduus*, *Festuca* and *Lobelia*. As one moves into the lower altitudes, Afro-Alpine vegetation intergrades with microphyllous thicket (Hedberg, 1961). Within this *Philippia* and more rarely *Erica* dominate. These can form dense forest or open scrub depending on local edaphic and climatic factors (Harmsen *et al*, 1991).

2.4ii Swamp vegetation

A wide range of swamp vegetation occurs within the highland environments of central Africa. These are concentrated within poorly drained valleys, around lake margins and within topographic depressions. Tussock forming species of the sedge *Carex*, principally *C. ruwenzoriensis* but more locally *C. monostachya*, dominate at high altitude (Hamilton and Taylor, 1986). *Pycreus nigricans*, another tussock-forming sedge, replaces *Carex* at lower altitudes (Morrison, 1968). A wide range of other grasses and sedges grow on swamps in central Africa; the large tussock-forming grass *Pennisetum mildbraedii* can be abundant. Species of *Cyperus*, particularly *C. denudatus* and *C. latifolius* can dominate swamp vegetation at mid-altitudes. Whereas, *C. papyrus* will dominate the vegetation at lower altitudes (Morrison, 1968). *Myrica* swamp forest, dominated by *Myrica kandtiana* and *M. salicifolia* is widely distributed in wet places of central Africa (Lind and Morrison, 1974), as is *Syzygium* swamp forest, dominated by *Syzygium guineense* and the probably conspecific *S. staudtii*. Taxa characteristic of moist lower montane forest can be found within this vegetation association. *Sphagnum* spp. are recorded as a minor element of *Carex*, *Erica* and *Pycreus* dominated swamps. Occasionally, *Sphagnum* spp. can dominate, such as at Butungo Swamp in the Rukiga highlands (Morrison and Hamilton, 1974), here it forms *Sphagnum* 'lawn'.

2.4iii The intergrade between vegetation associations

The nature and number of vegetation belts, and the factors governing their altitudinal limits are different in different upland areas (Figure 2.3), being

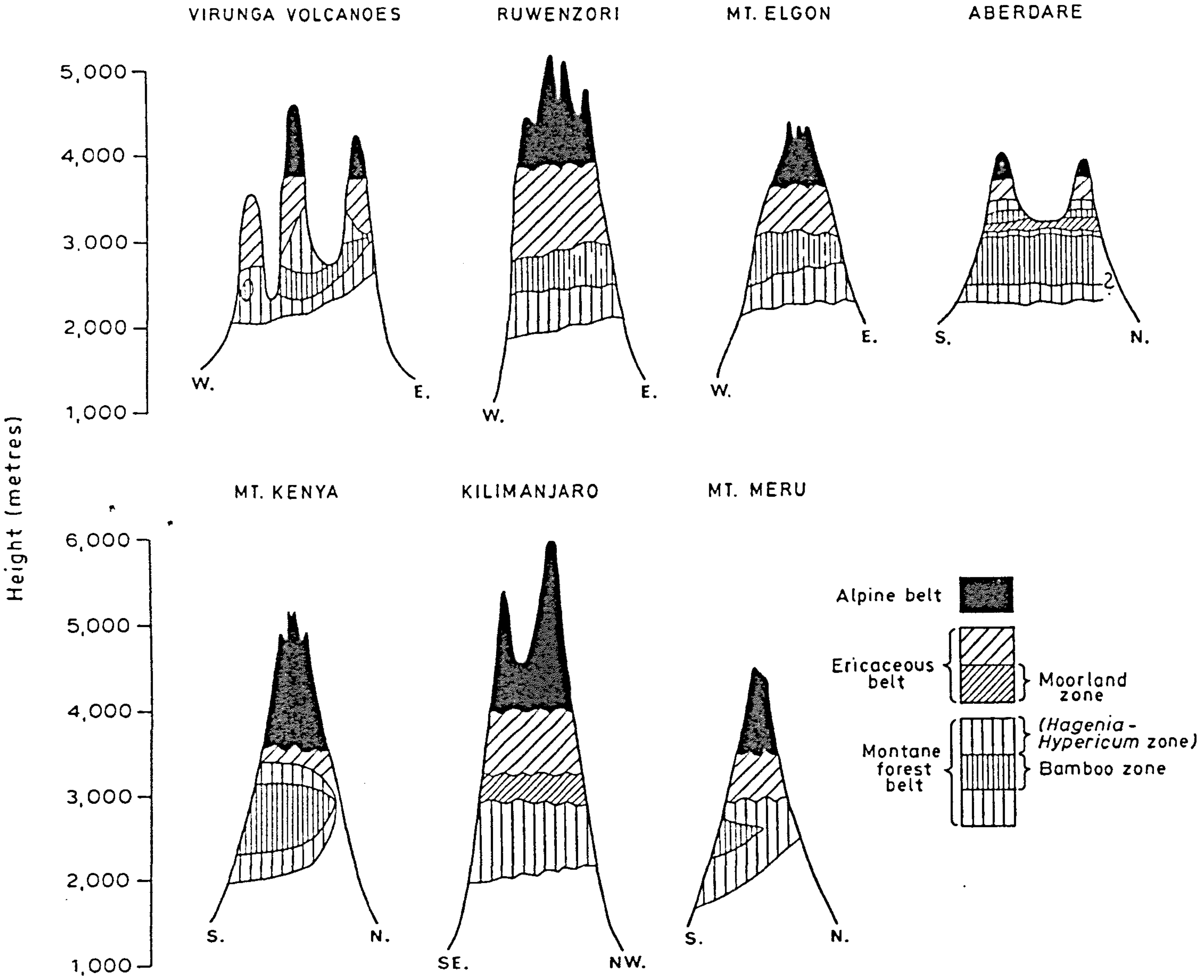


Figure 2.3 Altitudinal distribution of vegetation types on different highland locations in east and central Africa

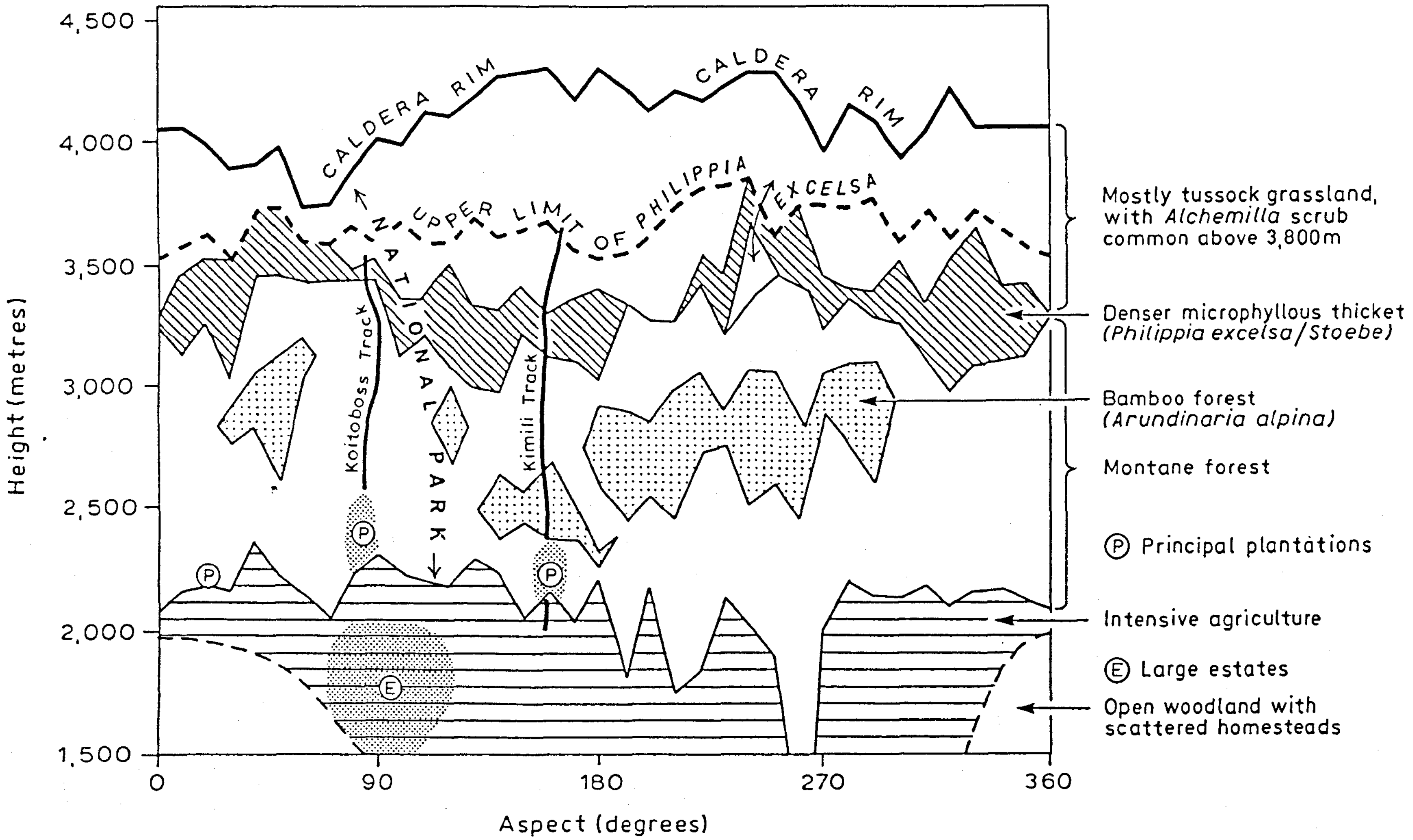


Figure 2.4 Altitudinal distribution of vegetation types on Mount Elgon (after Hamilton and Perrot 1982)

dependent on the latitude and the relative influence of continental or oceanic climatic conditions. Super-imposed on these controls vegetation composition and distribution expresses local micro-climatic, edaphic and topographic influences as demonstrated by work carried out on Mount Elgon (Figure 2.4).

Lebrun (1935), investigating forests in Congo, noticed a transitional zone between lowland and montane forest; these vegetation types were separated by a relatively thin altitudinal range within which the vegetation composition changed rapidly. These altitudes between different vegetation types were termed 'critical altitudes'. Between lowland and montane forest this critical altitude varied from 1100 m to 1750 m (Lebrun, 1935). Hedberg (1951) and Boughey (1955a), also identified thin altitudinal divides between different vegetation types to produced the widely used, but over-simplified model of vegetation zonation on a mountain in tropical Africa (Figure 2.2). However, Hamilton (1975b), investigating vegetation composition within Ugandan forests was unable to delimit critical altitudes for species type, although some physiological characteristics were found to change dramatically over relatively narrow altitudes, thus casting doubt on this simple model. Similarly, Hall (1973) records a lack of distinct vegetation zones on Mount Cameroon. Indeed, there is wide altitudinal variation in the distribution of various vegetation belts on mountains in east and central Africa (Figure 2.3). Some of the variation can be attributed to the Massenerburg affect (Grubb, 1971); the amount by which the given massif can modify its climate. On the smaller scale, the influence that local topographic and edaphic conditions impart on the vegetation can be important. This was very apparent from a study (Hamilton and Perrot, 1981) of the distribution of vegetation on Mount Elgon (Figure 2.4). This clearly showed there was wide-scale variation in the altitudinal distribution of vegetation belts, this variation can be attributed to local climatic and human-induced influences.

2.4iv The influence of human activity on vegetation composition and distribution

The preceding description is based on the species distribution when climate is the determining factor. With the long-term record of human inhabitation in central

Africa (Section 2.8), there has been extensive clearance of upland vegetation throughout central Africa. Indeed, very little montane forest presently exists between the altitudes of 1500 and 2500 m, because these are the altitudes most favoured by farmers (Taylor, 1996). Montane vegetation is now largely restricted to protected areas such as Bwindi-Impenetrable Forest and the Virunga Volcanoes National Park. Eastern Zaire also contains large tracts of 'unprotected' montane forest. However, a rapidly growing population (Kingdon, 1990), and mass population migration resulting from political instability threatens many of these remaining montane forest habitats.

Relatively small patches of montane forest do exist outside protected areas but these are becoming increasingly influenced by human populations such as Rugege Forest in Rwanda (Bouxin, 1976; 1977). Thus, much of the remaining montane vegetation has been modified to varying degrees by the presence of human populations. The resultant vegetation often has components indicative of disturbance, such as ruderal species of *Chenopodium*, *Dodonaea*, *Plantago*, *Rumex* and *Vernonia*. Tree genera also indicative of disturbance can be locally common; such as species of *Alchornea*, *Croton*, *Dombeya*, *Erythrina*, *Hagenia*, *Harungana*, *Macaranga* and *Polyscias*. However, care must be taken when translating the presence of these taxa to a particular type of disturbance as they all occur naturally within montane vegetation, albeit at relatively low values. For example, *Hagenia abyssinica*, being widely distributed in the upper montane forest zone is restricted to forest edges and derived woodland at low altitudes. Furthermore, it should be noted that human disturbance can result in changes in vegetation similar to those which are induced by a drier climate, or a shift to lower altitudes (Hamilton, 1982).

2.5 Present composition and distribution of montane vegetation, the relationship to the past: Refugia hypothesis

There have been many theories to account for the high diversity of tropical forests. A particularly popular one in recent years has been the refugia theory; this suggests during past cool and arid climatic conditions montane communities were constrained in discrete refuges (Flenley, 1993). These were reunited by climatic ameriolation. Lönnberg (1929) was the first to suggest an oscillating distribution of montane forest in response to an oscillating climate. Botanists such as Aubréville (1949), zoologists such as Booth (1958), Colyn *et al* (1991), Diamond and Hamilton (1980), Jones (1987), Kingdon (1990) Moreau (1966) and palaeoecologists such as Hamilton (1982), Livingstone (1982) and Maley (1987; 1989; 1991; 1995a; 1995b) have added support to the concept that tropical forests may have been restricted to refugia at points in the past.

Since the first location maps of possible refugia were published by Aubréville (1962) there has been a two pronged thrust to the research regarding forest refugia. Firstly, to locate more precisely the possible refugia, and secondly, to study speciation associated with geographical isolation (Goldberg, 1985). Central to the question of where forest refugia may have been located is the question of what was the reason for their persistence. The locations of montane forest refugia have yet to be established although these are thought to be associated with the Western Rift Valley and the eastern Zaire Basin (Figure 2.5). Taylor (1993) suggests the nearest late glacial refuge for moist montane forest was about 100 to 150 km westward, on the Hombwe mountains. Here levels of precipitation are higher than in south-west Uganda, and are believed to have been so during the Late Pleistocene period (Hamilton and Taylor, 1991). Others suggest that forest remnants persisted in isolated pockets where local environmental conditions acted as a buffer against a cool, dry climate (Butynski, 1984). This formulates the so-called mini-refugia hypothesis and accounts for the discrete forest blocks along the Western Rift, indicated in Figure 2.5 (Maley, 1995b). Following a study of Begoniaceae distribution in tropical Africa, Sosef (1994) provided additional support for the presence of mini-refugia. It is suggested in view of the generally arid nature of the last glacial period (Section 2.6), the majority of the area presently able to support montane forest supported savannah, intermixed with forest patches. Where the forest patches (mini-refugia) existed these would act as 'stepping stones' for the migration of flora and fauna following climatic amelioration.

As yet there is no way of dating when forest were last restricted to refugia. This could be much improved by pollen analysis (Maley, 1995b). Similarly, there has

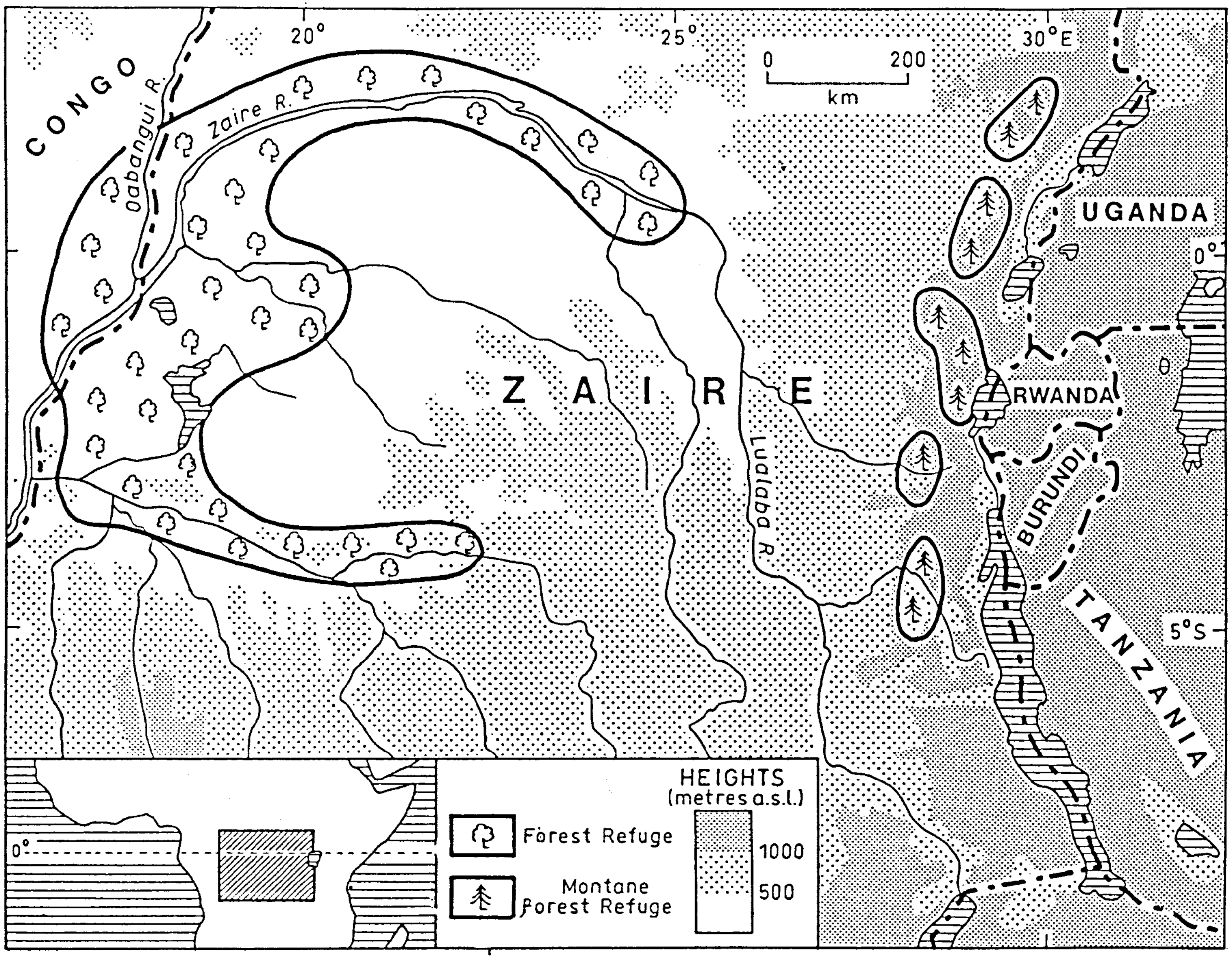


Figure 2.5 Location of montane and lowland forest refugia in tropical Africa during the last glacial period (After Maley, 1995b)

been no documenting of the composition of the proposed refugia, a facet not attempted in the seemingly blind search for the location, assuming that the theory is correct. The delimiting of composition, distribution and timing of floristic change within forest refugia would provide information why the specific locality was able to sustain montane vegetation during a cooler, drier past climate. Hence, these areas would be able to indicate whether the local conditions could impart vegetation stability for future predicted climatic changes.

2.6 Sedimentary evidence for changes in montane vegetation composition and distribution

Since its beginnings (Hedberg, 1954; Morrison, 1961; van Zindderen-Bakker, 1962; Coetzee, 1964; Flenley, 1979), palaeoenvironmental research in equatorial Africa has focused on environmental records retained within swamp and lake sediments. Environments surrounding the sites have been reconstructed using micro-sedimentology, charcoal analysis and examination of macrofossils and microfossils incorporated within these sediments. Changes in the composition and distribution of montane vegetation inferred from pollen analysis have been well documented in reviews for east Africa (Coetzee, 1967; Hamilton, 1982; Jolly *et al*, in press; Street-Perrot and Perrot, 1988) and for central and southern Africa (van Zindderen Bakker and Coetzee, 1988). Although selected late glacial and Holocene data are discussed in Jolly *et al* (in press), a full review of the extensive data specifically from central Africa has yet to be undertaken.

2.6i Sediment accumulation within swamps

Swamp based pollen based records within central Africa are available from a wide altitudinal spread (1360 to 2340 m), from different types of swamp, with a range of basin topographies. Combined, these provide one of, if not the most intensively studied area in the tropics. This Section will focus on the sedimentary and pollen data from swamps in central Africa. The locations of swamps with sediment and pollen records covered by this review are shown in Figure 2.6, with a description of their stratigraphies in Figure 2.7. Prior to discussing the palaeoenvironmental records retained within the swamps a description of the sites is essential.

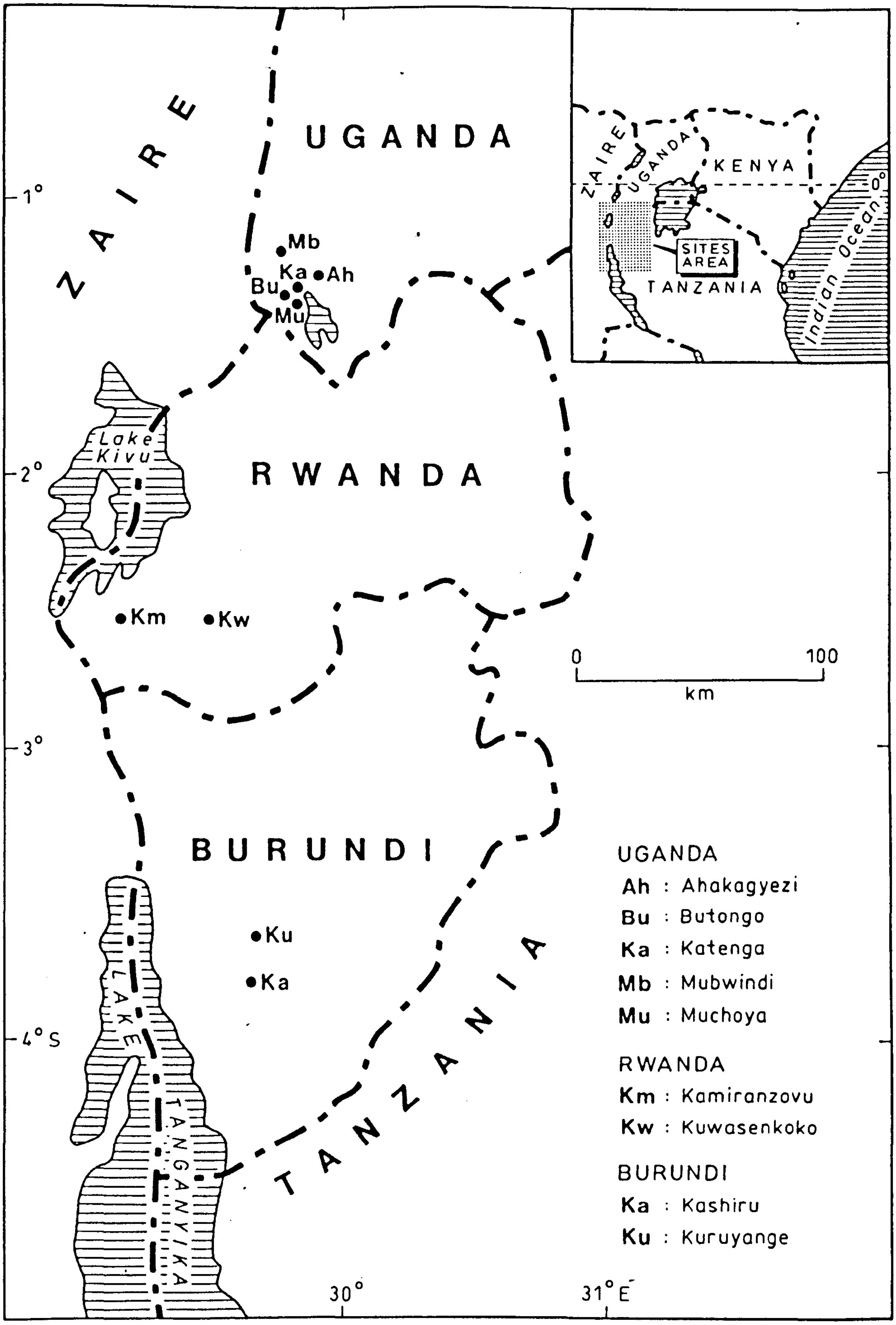


Figure. 2.6 Location of swamps in central Africa with pollen records

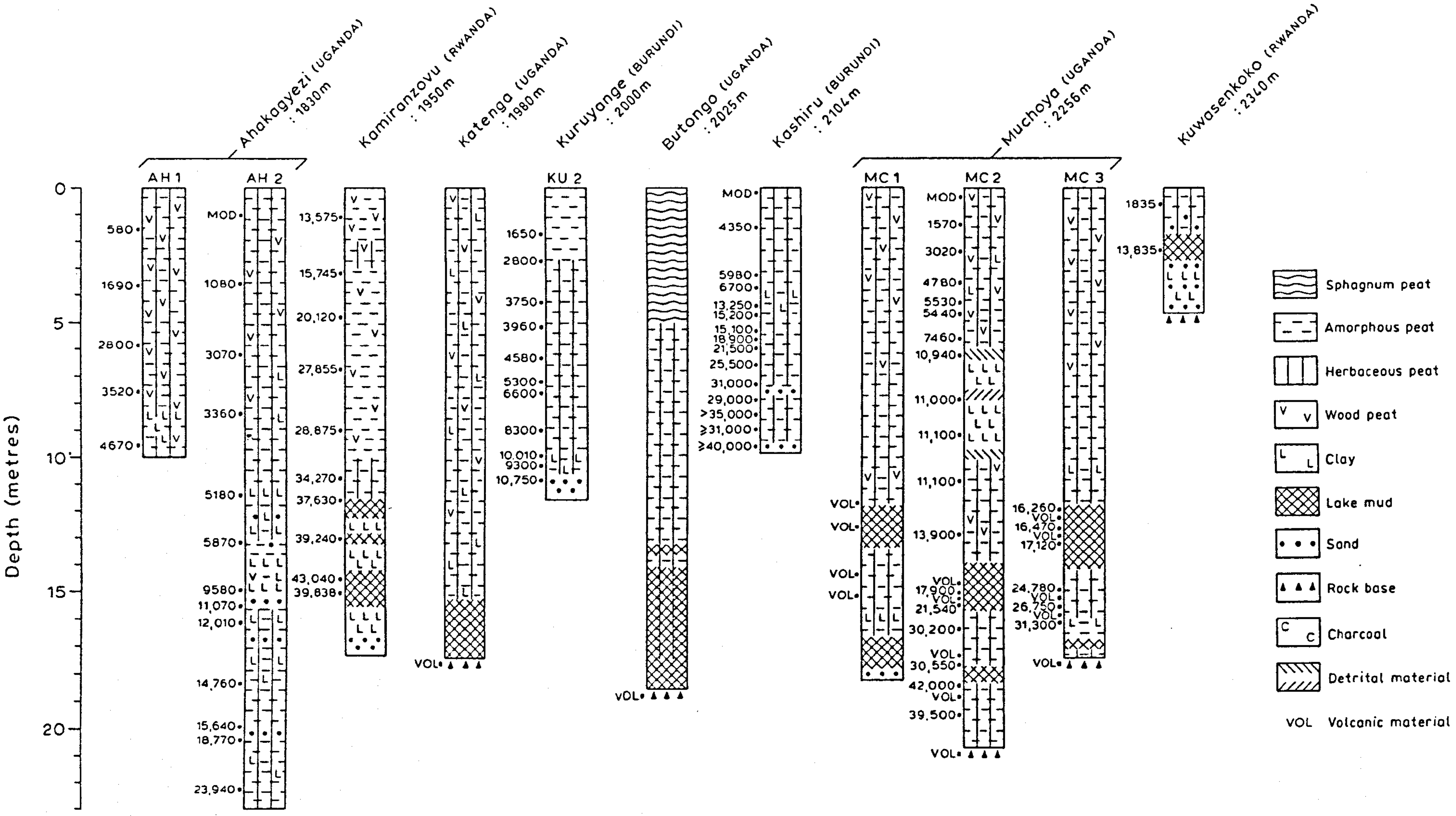


Figure 2.7 Sediment stratigraphies from swamps in central Africa

2.6 ii Description of swamps with palaeoecological records

Prior to discussing the palaeoecological records retained within swamp sediments, it is imperative to first described the swamp's location in terms of altitude, drainage, topography and present-day vegetation. These descriptions will be confined to those catchments within the altitudes covered by the montane forest vegetation zone (Section 2.4).

Ahakagyezi Swamp (1860 m OD, 1° 05' S, 29° 54' E) covers an area of approximately 1.5 km^2, it forms part of a much larger swamp occupying a series of bifurcating basins centred upon the Ishasha - Kiruruma valley. Drainage from the Ishasha - Kiruruma valley is bi-directional (the valley has been upwarped). The precise timing of this dislocation is unknown as the cores extracted from Ahakagyezi Swamp did not reach the basal sediments. The swamp's catchment, at about 8 km^2, is described by ridges that rise to a maximum elevation of 2487 m (Taylor, 1990; 1993). Much of the swamp surface today supports agriculture as do the surrounding hill-sides. However, parts of the swamp still support *Syzygium*-dominated swamp forest. A belt of wetter conditions forms a marginal zone around the swamp in which *Cyperus papyrus* and *Typha* spp. dominate (Taylor, 1993). Two cores (AH1 and AH2) have been extracted from Ahakagyezi Swamp using a Russian (D-Section) corer; the stratigraphies are portrayed in Figure 2.7. Radiocarbon control indicates a sedimentary record just in excess of 24,000 years old.

Kamiranzovu Swamp (1950 m OD, 2° 40' S, 29° 05' E) is described by Hamilton (1982) as 'one of the largest peat bodes in Africa' and has a surface area of c. 13 km^2. The swamp is situated within a flat-bottomed valley within Rugege Forest, which is one of the two significant areas of moist montane forest remaining in Rwanda today. Bouxin (1976, 1977) made a detailed survey of the forest and found floristic variation to be strongly influence by moisture availability. The 1775 cm long core of sediment was collected using a combination of Russian and Hiller corers. 10 radiocarbon dates are available. These range from > 43,040 yr B. P. to 13,575 +/- 130 yr B. P. Thus the sediments from this presently-forested catchment lack any sediments from the Holocene period. The reason for the cessation of peat accumulation is unclear although Hamilton (1982) indicates a single climatic event was responsible.

Katenga Swamp (1980 m OD, 1° 05' S, 29° 47' E) measures about 0.75 km by 0.75 km at its maximum dimensions. At the time of coring (1974) vegetation on the swamp surface was dominated by a tall growth of *Typha* spp. along with *Alchemilla* spp. (Morrison and Hamilton, 1974). Today the swamp surface has been drained and cultivated. The single sediment core (Figure 2.7) was extracted from the middle of the swamp basin using a Hiller corer (Morrison and Hamilton, 1974). The sedimentary record is not radiocarbon dated.

Kuruyange Swamp (2000 m OD, 3° 35' S, 29° 41' E) is situated in eastern Burundi. The valley swamp is located 20 km to the south-east of Kashiru Swamp and 50 km east of Lake Tanganyika. The adjacent hillsides are mainly covered by fieldcrops. Kuruyange Swamp is fed by rainfall and river water which then joins the general drain into Lake Victoria and the Nile system. Part of the swamp has been drained and converted to agricultural land. Two cores of sediment were collected from Kuruyange Swamp using a Russian corer, these are described in Jolly and Bonnefille (1982) and Jolly *et al* (1994). 10 radiocarbon dates were obtained for one of the cores. This indicates a virtually continuous record for the last 11,600 years (Jolly *et al*, in press), although pollen from the period 1000 to 500 yr B.P. were not collected.

Butongo Swamp (2025 m OD, 1° 05' S, 29° 38' E) is located within a steep-sided valley, at its closest point being 1.8 km west of Muchoya Swamp. The formation of this mire is thought to stem from blocking of the valley by lava (Morrison and Hamilton, 1974). The swamp is only 1 km long with an average width of 200 m. The vegetation consists of an even and luxuriant carpet of *Sphagnum* spp. with occasional specimens of *Cyperus papayrus* and *C. latifolius*, particularly around the swamp margins (Morrison and Hamilton, 1974). A 18.4 m sediment core (Figure 2.7) was extracted with a Hiller corer from near the lava dam, although the uppermost 5.5 m were not sampled as the sediment was too un-consolidated (Morrison and Hamilton, 1974). The sedimentary record is not radiocarbon dated.

Rusaka Swamp (2070 m OD, 3° 34' S, 29° 37' E) is a small swamp with a catchment area of about 1 km^2. It is situated within the Burundi highlands, 9 km east of Kashiru Swamp. The adjacent hillsides are mainly covered by fieldcrops. Rusaka Swamp is fed by rainfall and springs, part of the swamp has been drained and converted to agricultural land. Core Ru-3 was taken with a Russian corer to a depth of 1090 cm. 31 samples were processed for radiocarbon dating; 18 by AMS. These dates indicate a sedimentary record in excess of 35,000 years although the record before 12,260 +/- 210 is characterised by a number of sedimentary hiati, or sediment contamination (Bonnefille *et al*, 1995).

Kashiru Swamp (2104 m OD, 3° 34' S, 29° 33' E) is located on the south-eastern slope of the Burundi highlands. The swamp is occupied by a *Xyris - Sphagnum* association with *Cyperus denudatus* also common. The adjacent hillsides are covered by fieldcrops. Recently, parts of Kashiru Swamp have been drained and converted to agricultural land. A 10 metre core was abstracted with a Russian corer. A total of 15 radiocarbon dates have been obtained that indicate the sedimentary record dates from at least 40,000 yr B.P.

Muchoya Swamp (2260 m OD, 1° 05' S, 29° 45 E) is 600 m across at its widest point with a total catchment area of 30 km^2. The swamp is enclosed by hilly ridges, the highest point being 2554 m (Morrison, 1968). Muchoya Swamp is set within Euchoya Forest (Section 3.5), with land immediately next to the swamp having been cleared for agriculture (Morrison and Hamilton, 1974). Vegetation on a frequently burnt part of the swamp is dominated by the tussock forming sedge; *Pycreus nigricans*. The northern-most part of the swamp, where the incidence of fire is thought to be less frequent, supports *Erica kingaensis* ssp. *rugegensis*, *Lobelia mildbraedii* and *Myrica kandtiana* (Taylor, 1990; 1992). A total of nine cores have been collected from Muchoya Swamp (Morrison, 1968; Morrison and Hamilton, 1974; Taylor, 1990; 1992), using a combination of Hiller and Russian corers, for the most compacted sediments a screw auger was used. Records are presented from the longest three of these cores (MC1, MC2 and MC4) on Figure 2.7. Radiocarbon dating of these sediments indicate a date for the basal sediments in excess of 40,000 years old (Taylor, 1990).

Kuwasenkoko Swamp (2340 m) is situated in Rugege forest. The small (250 by 75 m) valley swamp is surrounded by a fairly extensive area of tussock grassland. It is suggested this has originated, at least in part, as a consequence of forest clearance, followed by repeated burning (Hamilton, 1982). Kuwasenkoko Swamp is covered by large tussocks of *Pycerus nigricans*. Three cores were abstracted from Kuwasenkoko Swamp with a combination of Hiller and Russian corers. Two radiocarbon dates are available for the 350 cm core. These indicate a record dating back to 13,835 +/- 120.

2.6i.ii Palaeoecological reconstruction from swamp sediments

The period before 32,000 yr B.P. is represented by the records from Kamiranzovu Swamp (Hamilton, 1982), Kashiru (Bonnefille, 1987; Bonnefille, 1993; Bonnefille and Riolett, 1988; Bonnefille *et al*, 1990; Bonnefille *et al*, 1992) and Muchoya (Taylor, 1990) swamps.

The fossil pollen record from Muchoya Swamp (Taylor, 1990) indicates that before approximately 40,000 yr B.P. *Cyathea* spp. dominated the vegetation within the catchment with taxa from high montane and moist lower montane forest at low levels. From about 40,000 yr B.P. there was a change in the forest composition, becoming of a higher altitude type, represented by pollen from high montane forest and ericaceous belt vegetation. Between 43,000 and 32,000 yr B.P. montane vegetation in south-west Uganda was of a slightly higher altitudinal nature than those further south (Kashiru and Kamiranzovu swamps), more so than can be attributed to the small differences in altitude between the two swamps.

This period from 32,000 to 21,000 yr B.P. is represented by sediments from Ahakagyezi (Taylor, 1990), Kamiranzovu, Kashiru, Muchoya and Rusaka (Bonnefille, *et al* 1995) swamps. Fossil pollen from Muchoya Swamp highlights the dominance of high montane forest within the catchment. The pollen flora at Kashiru Swamp is quite different being dominated by members of Gramineae, with Ericaceae sub-dominant. Pollen from other montane forest taxa are present, albeit only at very low levels. These suggest the presence of an ericaceous grassland flora within the catchment. This is also supported by the low levels of $\delta^{13}C$ recorded from cellulose, charcoal and total organic matter (Aucour *et al*, 1993). Pollen from the Kamiranzovu Swamp sediments suggests a higher altitudinal vegetation type than that recorded at other sites in central Africa during this period. Pollen from Rusaka Swamp indicates the vegetation was dominated by Gramineae, with a small amount of arboreal pollen. At Ahakagyezi Swamp high montane forest was present within the catchment towards the end of this period. Combined, these data indicate that slightly different types of vegetation were growing within the swamp catchments; ericaceous grasslands and high montane forest were more prevalent in southern central Africa while high montane forest became more dominant towards the north of central Africa during this period. This gradient of a lower altitudinal vegetation type towards the north of the region is the reverse of that highlighted previously.

The period from 21,000 to 14,000 yr B.P. is represented by all but one of the sedimentary records so far discussed, and that from Kuwasenkoko (Hamilton, 1982). Possibly the undated records from Katenga and Butongo swamps (Morrison and Hamilton, 1974; Hamilton, 1982) may extend into this time period. Rusaka Swamp is thought to have a sedimentary hiatus between 21,000 and 12,000 yr B.P.

From 21,000 yr B.P. high montane forest and ericaceous belt vegetation was present within all the swamp catchments. Pollen retained within the basal sediments from Butongo and Katenga swamps indicate that high montane forest was present within their catchments. This suggests these records stem from the end of this time period. An interesting feature from all the sedimentary records that cover this period, is the occurrence of pollen (albeit sometimes at very low levels) from montane forest taxa. This suggests four possible situations: 1. montane forest taxa were either present near to, but not within the swamp catchments so far studied, 2. montane forest taxa were present at relatively low densities within all the swamp catchments, 3. montane forest taxa were present in discrete core areas that have yet to be delimited, or 4. pollen was transported long distances into sedimentary basins from montane forest at lower altitudes.

This period from 14,000 to 10000 yr B.P. is recorded by all the swamps so far described apart from the record from Kamiranzovu Swamp. Rusaka Swamp accumulated sediment from about 12,000 yr B.P., following the break in sedimentation.

Hagenia dominates the pollen spectra at Ahakagyezi, Butongo, Katenga and Muchoya swamps. Combined, these indicate a specific type of high montane forest was present throughout the Rukiga highlands. Pollen derived from a range of montane forest taxa, other than *Hagenia*, was more prevalent at the lower altitude sites, and towards the top of this period. There was a rise in montane forest pollen recorded at Kashiru Swamp after 13,000 yr B.P. The presence of a hiatus, or a very low sedimentation rate, makes interpretation of this period from the Kashiru sequence very difficult.

A re-interpretation of the radiocarbon data places this rise in montane forest pollen approximately 1000 years before the 12,000 yr B.P. suggested by Taylor (1990). It should be emphasised the transition from ericaceous belt mixed with high montane forest vegetation to a high montane forest composition is transitional rather than instantaneous. Thus, the spread of lower altitudinal forest types is some 1500 to 2000 years earlier in south-west Uganda than that recorded in Burundi. Within the Rukiga highlands the precursor of montane forest may be *Hagenia* dominated forest, rather than a steady increase in mixed montane forest taxa. These between-site differences could result from spatially transgressive regional climatic change diachronic north to south, or result from local climatic change in south-west Uganda.

The period from 10000 to 4000 yr B.P. is represented by all the swamps so far highlighted and Ndurumu Swamp from Burundi (Jolly and Bonnefille, 1992) and Kuruyange Swamp (Jolly *et al*, 1991). Apart from at Rusaka Swamp, the dominant sedimentary signal is one of continuing hiati throughout this period. Indeed, hiati recorded at Kamiranzovu and Kuwasenkoko swamps cover the whole of this period, in the case of Kashiru and Muchoya swamps the hiati extend well into the Holocene. When sedimentation was resumed around 7500 yr B.P. at Muchoya Swamp the pollen sum is dominated by moist montane forest taxa.

There are similar pollen spectra at Ahakagyezi, Katenga and Butongo swamps, although at Ahakagyezi Swamp this change is recorded earlier at around 9000 yr B.P. These data indicate the presence of moist lower montane forest throughout central Africa during this period. Moist lower montane forest reached its maximum extent in the period covered by this review; being present at a range of different altitudes throughout central Africa. The Montane vegetation in the southern part of central Africa was of a slightly higher altitudinal nature than that towards the north.

This period from 4000 years to present is represented by sediments from all the sites in central Africa. It is quite clear from the pollen records the Late Holocene period experienced marked change in the composition and distribution of montane vegetation. The first major change is a transition to a dryer type of montane forest from about 3500 yr B.P. This change is more prevalent in the Rukiga highlands than elsewhere. Specifically, there was a transition to a drier type of forest dominated by *Podocarpus* spp. At Kashiru Swamp and latterly Ndurumu Swamp the change is recorded as a steady decline in moist montane forest taxa, rather than the '*Podocarpus* rise' recorded further north. All the records from central Africa indicate the presence of more open forest, possibly originating from human-induced forest disturbance during the past few thousand years. This is recorded as a gradual transition at Kashiru Swamp, unlike within the Rukiga highlands sites, where distinct phases of vegetation change are recorded. These changes centred at 2200 yr B.P. and 800 yr B.P. are thought to be related to technological innovation among the developing agricultural communities (Taylor and Marchant, 1996). These late Holocene, human-induced changes in the composition and distribution of montane vegetation have obscured the influence of any sub-Milankovitch climatic induced changes.

2.6 ii Sediment accumulations within lakes

The lakes associated with the Western Rift Valley of central Africa (Section 2.2) are thought to contain sediments that span the whole Quaternary period (Hamilton, 1982). There has been a focus of research to obtain palaeoenvironmental information from the sediments dating to the Late Quaternary. Sediments dating from 29,500 to 25,350 yr B.P. at Lake Mobutu Sese Seko (619 m) contain pollen derived from forest, presently at higher altitudes than the lake (Sowunmi, 1991). A recorded overflow of the lake between 28,000 and 25,000 yr B.P. is thought to indicate a high lake level and hence moist and/or cool climate. Pollen from Zambezian woodland, indicative of drier conditions also dominated the sediments from Lake Tanganyika between 35,000 and 15,000 yr B.P. (Vincens, 1993). From 25,000 yr B.P. Williamson *et al* (1991) record a complex sediment history: a sedimentary hiatus lasted until 21,500 yr B.P. Initiation of sedimentation is thought to possibly result from a local humid phase, prior to full glacial conditions (Williamson *et al*, 1991).

Pollen retained in the sediments of Lakes Mobutu Sese Seko, Kivu and Tanganyika indicate that from about 21,000 yr B.P. there was a spread of vegetation from higher altitudes than previously present (Harvey, 1976). At Lake Mobutu Sese Seko the surrounding catchment carried open grassland with isolated forest patches (Ssemmanda and Vincens, 1993), this relatively dry vegetation type corresponds to a lake level approximately 100 m lower relative to present-day levels. Similarly, at Lake Kivu there was a low stand of between 90 m and 300 m lower than present-day levels recorded for the period before 13,400 yr B.P. (Vincens, 1993). This fall was also recorded for Lake Tanganyika (- 250 m to - 400 m) between 16,000 and 9900 yr B.P. (Haberyan and Hecky, 1987; Gasse *et al*, 1989). Further to the south, Lake Malawi water levels were - 125 m relative to present-day levels at approximately 10,700 yr B.P. (Finney and Johnson, 1991).

There is not such a consensus of the information regarding the transition to post late glacial conditions. At Lake Mobutu Sese Seko pollen from lower altitudinal vegetation is recorded from 14,700 yr B.P., increasing in abundance until 12,500 yr B.P. (Ssemmanda and Vincens, 1993). The lake level did not show a recorded rise until about 9000 yr B.P. (Ssemmanda and Vincens, 1993). At Lake Kivu, water levels rose at about 12,500 yr B.P., a transitory low stand being recorded from 11,000 to 10000 yr B.P. before the lake overflowed into Lake Tanganyika at 9500 yr B.P. (Hamilton, 1982). However, the timing of overflow was latterly estimated to be between 6800 and 6700 (Vincens, 1993). According to Williamson *et al* (1991) a rise in water level of Lake Tanganyika is dated to 13,000 yr B.P. These differences are thought to result from different responses of lake basins following a period of rapid environmental change.

During the early to mid Holocene there was an expansion of vegetation from previously low altitudes within the lake catchments. Around the shores of Lake Mobutu Sese Seko there was an expansion of semi-deciduous forest (Ssemmanda and Vincens, 1993). Similarly, around Lake Tanganyika Guinean Forest components colonised the catchment (Vincens, 1993). The sediments from Lake Tanganyika record an increase in sedimentation from 8000 to 5000 yr B.P. The lake was most stable around 5200 yr B.P. when there was no mixing or lake-overturn (Haberyan and Hecky, 1987).

Around 4000 yr B.P., temporally corresponding to the *Podocarpus* rise detected within the Rukiga highlands, there was a notable change in the lacustrine sediment records. At Lake Mobutu Sese Seko from about 5000 yr B.P. there was an increase in the pollen from semi-deciduous forest, particularly in *Celtis* spp., and establishment of swamp forest around the lake; dominated by *Phoenix reclinata* and *Anthocliesta* spp. (Ssemmanda and Vincens, 1993). The outflow from Lake Kivu to Lake Tanganyika was interrupted from about 3500 yr B.P., this altered the salt balance in Lake Tanganyika and changing the resultant diatom flora (Haberyan and Hecky, 1987). Similarly, the Lake Tanganyika outflow was closed from about 4000 yr B.P. with lake levels lowered by about 75 m. At Lake Kivu from about 3000 yr B.P. there is a reduction in forest and expansion of the savannah without any indication of human agency (Ssemmanda and Vincens, 1993). Lake Tanganyika sediments record a deterioration of the arboreal cover and extension of grasses after 2600 yr B.P.; thought to indicate a transition to modern climatic conditions rather than human impact on the local vegetation (Vincens, 1993).

The reconstructions from swamp and lake sediments indicate very significant changes during the late Holocene. Initially these were linked to human impact (Hamilton *et al*, 1986), but subsequently are thought to result from regional climatic change. However, the latter changes in forest composition from 2200 yr B.P. are still thought to relate to human-induced forest clearance. Due to the lack of spatially related archaeological data (Section 2.8), and lack of palaeoenvironmental data from sites that have not been heavily influence by human activity, the possibility of other forcing mechanisms for these late Holocene changes in the vegetation cannot be fully discounted. The present study will contribute significantly to this on-going debate as it will provide evidence from a site that appears not to have been heavily degraded by human activity.

2.7 Geomorphic evidence for change in montane vegetation composition and distribution

It is difficult to extract a precise palaeoenvironmental signal from geomorphic evidence. Specifically, geomorphic processes operate at the landscape surface, and hence the most obvious signal is that of the present-day process, often this will obscure past evidence for environmental change.

2.7i Glacial evidence

Evidence from montane glaciation has been successfully used to reconstruct environmental change in tropical Africa. Specifically in central Africa, the first extensive discussion of the glaciers on the Ruwenzori were carried out by Nilsson (1931; 1940) and de Hienzelin (1952), these proposed a spatial correlation and chronology of glacial events. A relative chronology was not produced until Osmaston (1989) had mapped the moraines and correlated these to the more extensively documented studies in East Africa (Rosquist, 1990). There were three main Late Pleistocene glaciations on the Ruwenzori; the first two were estimated to have occurred before 100,000 yr B.P. (Livingstone, 1980) whereas the latter one took place before 14,700 yr B.P. (Osmaston, 1989) when the glaciers started to retreat. The timing of this retreat, ties in with the expansion of lower altitudinal vegetation following late glacial climates.

A succession of small moraines has fuelled the debate as to the extent of neoglacial advances, Taylor (1996) suggests one group represent a re-advance about 2000 yr B.P., although Osmaston (1989) suggests these are associated with the previous glacial period. Above 4000 m fresh, sharp crested moraines, thought to be a few hundred years old, are possibly representative of the Little Ice Age (de Hastenrath, 1984b). Considering lichenometry, soil development and growth of *Scenicio friesiorum* a date of between 100 and 700 yr B.P. has been suggested for these moraines (de Heinzelin, 1952). Since the turn of the century the glaciers on the Ruwenzori have retreated rapidly (Rosqvist, 1990). Further south, the only land high enough to support glaciers are Muhabura and Karisimbia volcanoes of the Virungas; however, both these only exhibit the influence of periglacial activity. Even during the last glacial period of the Ruwenzori they did not support small cirque glaciers (Mahaney, 1990). These late Holocene changes in the glacial evidence indicates that there has been significant climatic changes. As suggested previously, the potential impact of these sub-Milankovitch climatic changes on montane forest composition and distribution have been obscured by human induced forest clearance.

2.7ii Pedological evidence

There is very little published pedological evidence for environmental change in central Africa. On the Virunga Volcanoes dating of buried palaeosols (Mahaney, 1990) on the saddle between Visoke (3711 m) and Karisimbi (4507 m) shows the most intense period of weathering to have taken place between 35,000 and 25,000 yr B.P. Further up the same sequence, glacially crushed quartz grains are present. These are thought to date from 18,000 yr B.P. and to have originated from the Ruwenzori Mountains (Mahaney, 1990); being transported by aeolian processes. It is suggested that the palaeowind system associated with the last glacial period was intensified as a result of an increased north-south temperature gradient and more open vegetation cover (Mahaney, 1990). Records of pedogenesis dating from 18,000 yr B.P. on an exposed long Section in a study from eastern Zaire (Kivu province), suggested by numerous authors as a Pleistocene core area for montane forest (Maley and Elenga, 1993; Sosef, 1994; Maley, 1995), indicate that the soil forming process has not been constant. There were periods of increased hill-wash recorded at 18,000 and 2000 yr B.P. and change in pedogenesis (Runge and Runge, 1996). In what way human activity may have influenced these changes cannot be stated as the site presently supports dense rainforest vegetation.

2.8 Archaeological and historic evidence for human impact on montane vegetation composition and distribution

Central Africa contains archaeological evidence indicative of long-term human inhabitation. However, the distribution of past populations can only be reconstructed according to the spread of archaeological remains (Mitchell, 1988), which are relatively scarce within central Africa. Thus, the following review will encompass material from outside the central African region. The changes that have taken place within central Africa will be dealt with in three major development stages; hunter-gatherer populations, with stone technology, agricultural communities without iron; and ultimately those practising agriculture with iron technology. As with the data from sedimentary sequences (Section 2.6), these temporal divisions should be viewed as fluid, the reality being a transgressive development from nomadic, hunter-gatherer populations to a food producing society that is settled and socially structured.

2.8i Hunter gathers

Tool-using hominids are thought to have been present in east and central Africa since the end of the Pliocene (Wayland, 1924), with *Homo sapiens sapiens* present since 75,000 yr B.P. (Hamilton, 1982). Indeed, some of the earliest fossilised human remains have come from the Kenyan Plateau (Phillipson, 1988). The succession of post-Acheulian stone industries in central Africa is similar to, and lasts as long as that revealed by the more intensive research to the south (Phillipson, 1988). This suggests the established archaeology for this region can be applied to central African; indeed Uganda has been proposed as a possible centre for the diffusion of these early Pebble Cultures, recognised elsewhere in Africa (van Riet-Lowe, 1952).

In some parts of central Africa, bladelet production can be traced back to 50,000 yr B.P., a similar age to that derived from some palaeoenvironmental studies (Section 2.6). For example, the Matupi Caves of eastern Zaire have revealed a quartz based industry dated to approximately 40,000 yr B.P. (van Norton, 1977). Similarly, finds from Kandalo (Rwanda) are dated to about 35,000 yr B.P. (Lugan *et al*, 1979), also some skeletal parts of a pygmy individual associated with broken crystal micro-lithes were dug out of pisolithic red earths at Bugungu (Wayland, 1921), on the northern shores of Lake Victoria. Specifically in south-west Uganda, Cunningham (1992) estimates human occupation of the area by the BaTwa pygmies dates to between 32,000 and 40,000 yr B.P. A similar age of occupation has been suggested for the Mbuti pygmies of the Ituri Forest in Zaire (Turnbill 1961; 1965; 1966).

The existence of a 'Neolithic period' in east Africa was recognised as early as the 1930's (Leakey, 1931). Neolithic implements have been documented for east and central Africa from 18,000 yr B.P., although it was only around 12,000 yr B.P. (Phillipson, 1988) that they became widespread. Analysis of bone at several sites indicates a change in hunting practice around this time, with the emphasis on smaller, less gregarious prey (Phillipson, 1977). Indeed, Phillipson (1988) has argued the adaptation of backed micro-lithic technology was linked to the development of new hunting techniques, permitting the exploitation of forested environments. Alternatively, it has been suggested that the development of microlithic technology could have occurred as a response to increased population density with greater subsistence requirements (Bower, 1988; Bower and Lubell, 1988). Communities would have been centred on areas that could support quasi-stable settlements, such as the fishing communities that developed near water courses. One such settlement at Ishango, on the western shores of Lake Mobutu Sese Seko has been identified as a specialised harpoon fishing settlement, dated to between 11000 and 6000 yr B.P. (Phillipson, 1986).

For the Rakai District of Uganda it has been suggested that Neolithic communities settled on ridge top locations (MacLean, 1996), the higher ground possibly being the focus of early settlement as this was easier to work, offered some natural protection, and was relatively free from disease. Although soil in these upland locations was very thin and relatively unproductive the possibility of early agriculture cannot be excluded. Indeed, further west in the Central Africa Republic, polished stone axes and megaliths associated with food producers date to between 2700 and 3500 yr B.P. (de Maret, 1985). The longevity of food production is highlighted to the north of the central African region; carbonised seeds have been found that date to approximately 8000 yr B.P. (Wendorf *et al*, 1992). Around the south, east and western shores of Lake Victoria, Kansyore pottery associated with the Neolithic has been dated to about 3000 yr B.P. Although there is no evidence to suggest its makers had any degree of iron technology, this pottery type is likely to be associated with early pastoralism and/or agricultural technology (Robertshaw, 1991). This further suggests the presence of a more semi-settled society within central Africa at this time. Due to very low population densities during these periods impact on the extant vegetation is thought to have been localised and relatively negligible (Phillipson, 1988).

2.8ii Pastoral Neolithic

The 'Pastoral Neolithic' (PN) is a regional development stage between the Later Stone Age and the Pastoral Iron Age (Bower and Lubell, 1988). There is an argument for earlier pastoral development; perhaps in excess of 7000 yr B.P. (Bower and Nelson, 1978). Due to the few sites this period is difficult to document with any precision. The transformation to a pastoral lifestyle is thought to be associated with the arrival of people from elsewhere, rather than independent domestication (Schroenbrun, 1993). It is likely this arrival is part of a general southward movement of pastoralists across Africa after 4500 yr B.P. Overwhelming evidence indicates pastoralism had begun in the Lake Turkana basin of northern Kenya by 4500 yr B.P., although it was not until about 3000 yr B.P. (Ambrose, 1982) that the pastoralists moved south. These ideas are further supported by rock art around Lake Victoria (Chaplin, 1974), indicative of a society without iron technology but practising pastoralism.

The PN contains well defined developmental stages. This allows the transition to a food producing society to be reconstructed. Starting in northern Africa (Ethiopia and Sudan) at about 4500 yr B.P. the PN spreads southward in a complex 'bow wave' form (Bower and Lubell, 1988). The rate and direction of this spread are partly determined by mid to Late Holocene shrinkage of the Rift Valley lakes (Butzer *et al*, 1972; Richardson and Richardson, 1972), this exposed large areas of previously inundated grazing land. It is suggested there was a major rise in livestock levels about 3000 yr B.P. (Bower, 1988; Schoenburn, 1993), probably as a result of a transition to a more intensive and established pastoral system. The areal extent of the PN is unknown; linguistic work by Schoenburn (1993) suggests the presence of southern Cushitic cattle-herders in Rwanda and northern Tanzania from about 3000 yr B.P. Dated remains of goat and sheep teeth in Rwanda suggest mixed pastoralism had become established between 2500 and 2000 yr B.P. (van Norton, 1979). Thus by about 2500 yr B.P. pastoralists were widely spread throughout central Africa.

As with the hunter-gather populations, due to low population densities, impact on vegetation composition and distribution would have been localised and relatively negligible at the start of the period. As populations became increasingly settled, and the number of people seeking a agricultural base grew, impact on vegetation would have been increasing noticeable.

2.8iii Iron Age and the spread of agriculture

There is a consensus that Iron Age technology reached Zaire, Rwanda, Burundi, south-west Tanzania and southern Uganda between 2500 and 2000 yr B.P., (Phillipson, 1988). Due to the complexity of the artefacts, Meroe has been presented as a possible place of origin for the spread of iron technology through Sub-Saharan Africa (van Norton, 1979). Indeed it is known that there was well-developed iron working at Matara, in Ethiopia by 2500 yr B.P. (Anfray, 1967) and Meroe by 2600 yr B.P. (Shinnie, 1967). Meroe was developing rapidly as a major centre of iron working with a trade hinterland developing (Shinnie, 1967; Haaland and Shinnie, 1985), reaching its height between about 2300 and 2000 yr B.P.

(Oliver and Fage, 1984). Furthermore, large slag heaps have been found between Lakes Edward and George. Many are perforated and were possibly used as filters for the abstraction of the final raw iron (Heinzelinsee, 1959). Combined, these finds suggest that Western Lake Victoria populations had developed a sophisticated iron smelting technology from 2500 to 2000 yr B.P. However, charcoal associated with pottery of an Early Iron Age type in Burundi radiocarbon date to 3500 yr B.P. (de Maret, 1985). Similarly, at Gasiza in Rwanda, charcoal from a slag furnace has been dated to 2700 yr B.P. (de Maret, 1985). Although these Early Iron Age dates are still the exception to the norm, it is possible there was an Early Iron Age cluster in central Africa, independent to that in the north.

If we reject independent invention of iron smelting in central Africa, due to the extant archaeological and linguistic evidence for the spread of iron technology, we are left with the most likely carrier to be Bantu-speaking people from the north-west. Today, linguists are virtually unanimous in the belief that the ancestral Bantu language originated close to the north-western border of the present Bantu speaking area, in what is now Cameroon and Nigeria (Hiernaux, 1968, Vansina, 1984). However, there is not unanimous agreement on the date of initiation for Bantu migration; these vary between 5000 yr B.P. (Oslisly, 1994) to the more accepted 3000 yr B.P. (Vansina, 1984). It is difficult to suggest what initiated the population movement from the Bantu homeland, increased population growth was probably one of the causal factors (Phillipson, 1988). Whatever the direction of this migration, passage was rapid, the Bantu probably followed river courses within the intervening forest, these not being so dense during this period (Schroenburn, 1992; Schwartz, 1992).

For archaeological reconstruction, pottery styles are often used to recreate the migrations of different cultural groups, particularly as there is a well-documented temporal succession of pottery styles. Changes in pottery styles (particularly non-functional changes) are likely to indicate a population change (Soper, 1971a). The widespread Dimple Wares, found throughout east and central Africa, unlike the previous Kansyore Ware, do have an affinity with iron technology (Phillipson, 1986). In Rwanda and Burundi, Dimple Ware has been found at twenty sites, seven of which are associated with slag heaps dated to approximately 1700 yr B.P.

(Sutton, 1971). Iron Age sites with Dimple based pottery *in situ* have also been described from Lolui and Ssese islands, where they have been dated to 1600 yr B.P. (Soper, 1971b). The areas settled by people responsible for this pottery complex experienced rapid cultural change around 1000 yr B.P. (Phillipson, 1988). This can be temporally correlated with the introduction of cattle on a large scale and the concentrated grazing of inter-lacustrine grasslands, these cattle are thought to have arrived with the Chwezi, from the north-east (Chaplin, 1974). This 'population influx' was relatively transitory, disappearing and leaving an advanced pastoral legacy (Chaplin, 1974; Lanning, 1970; Sutton, 1993). The extent, and legacy of this culture is highlighted in Mubende District where there is a great line of earthworks dated to between 650 and 500 yr B.P. (Robertshaw 1996).

The cultural assimilation of iron technology and agricultural practice should be viewed as more than just a simple development stage; there were important socio-economic connections between the iron smelters/smiths and the levers of political power (Schroenburn, 1993). Specifically, in the Rukiga highlands, iron working was a jealously guarded secret, only being carried out by given clans: the Basingola from Bwindi, and the Barunga and Baheesi from Bukova, near Lake Bunyonyi (Turyahikayo-Rugyem, 1942). Although there were plenty of iron ore deposits, and forests for charcoal production, the smelting industry was maintained by these clans. Prominent iron workings are to found at Kayonza (Baitwabobo, 1972a) and at Nyabwinhenye in Bufumbia and Muko in Rubanda county (Turyahikayo-Rugyem, 1942). Trade hinterlands are thought to cover Zaire, Rwanda and western Tanzania (Kamuhangire, 1975) with iron goods being traded over a large area using existing salt routes (Turyahikayo-Rugyem, 1942).

Population influx and expansion of iron and agricultural technology led to a widespread, agricultural and pastoral community throughout Kigezi (Rwandusya, 1972). Population movements into the Rukiga highlands increased; by 150 yr B.P. the BaKiga were making large movements into Kigezi driven by attacks from the BaTwa in the south-west and the BaTutsi in the south (Kagambirwe, 1972). Indeed, the resulting high population of the Rukiga highlands today has been attributed to tribal wars in Rwanda and internal religious rising (Kagambirwe, 1972). The BaTwa, BaTutsi and Bakiga lived together, albeit in precariously harmony, being hunters, pastoralists and agriculturists respectively (Turyanhikayo-Rugyem 1942; Baitwabobo, 1972b). However this 'social harmony' was under continual pressure from the surrounding environment, a rinderpest epidemic swept the area in the 1880's, a widespread famine also occurred in 1897 (Turyanhikayo-Rugyem, 1942). These events within the backdrop of BaTwa raids, particularly under the leader Basebya who was killed in 1913 (bringing much rejoicing to the surrounding BaKiga), brought a chaotic situation to the southern parts of Kigezi by the end of the 19th century (Turyahikayo-Rugyem, 1942). A series of bitter wars with the BaTwa, quelled by the British administration in 1912, caused indelible bitterness and animosity between certain clans.

Sporadic famines in Rwanda, such as the one from 1927 to 1928, caused massive population influxes into Kigezi. A severe drought in 1943, coupled with continued population movements from Rwanda made it clear, due to lack of land and continued soil deterioration, that the area could not continue to support the dense populations. There was no foreseeable decline in the resident population; there was improved health care, mitigation of famine, reduced internal warfare and a stabilisation of law and order (Purseglove, 1950). A solution to the problem was to resettle some of the population to land above Lake Edward. However, the native council was in favour of de-reservation of Chelima and Mafuga forests, stating that their fore-fathers had lived in these areas and they should be allowed to move back (Turyanhikayo-Rugyem, 1942). It is possible these areas may have been deserted during warfare between the BaKiga and BaTwa. Even with active population management, today central Africa supports a densely settled agriculturally based population that in places reaches population densities up to 500 km^{-2} (Section 3.6).

Unlike previous periods, the development and growth of settled, agricultural populations has substantially modified the vegetation over large tracts of central Africa. In many areas this has led to complete deforestation and transition to permanent agriculture. In other areas the composition of the remaining montane forest has been significant modified by human activity (Section 2.4iv).

CHAPTER 3

The present-day environment of the Rukiga highlands and the Mubwindi Swamp catchment

3.1 Introduction

Within this chapter the present-day environment of the Rukiga highlands will be described. Many of the physical aspects are applicable throughout the Rukiga highlands, smaller-scale variations are emphasised when pertinent. As work presented in part two of this thesis is derived from the Mubwindi Swamp catchment, within Bwindi-Impenetrable Forest, this Chapter will focus on this forest. Specifically, the fauna and flora of Bwindi-Impenetrable Forest will be described. How Bwindi-Impenetrable Forest has been managed by the various organisations (past and present), and how this management has affected the surrounding populations will be discussed. The present-day environmental setting of Mubwindi Swamp will be described.

3.2 Geology, Topography and Drainage

The Rukiga highlands (Plate 3.1) are situated in south-west Kigezi, south-west Uganda. This area is associated with up-warping and faulting during the formation of the Western Rift Valley (Section 2.2). The area is underlain by rocks of the Karagwe-Ankolean System, comprising of phyllites and shales, with some quartz, quartzites and granite outcrops (Coombe and Simmons, 1933). Occasionally, the parent rock is mineralised with metals such as copper, gold, microlite, tantalite, tin and wolfram resulting. Three large volcanoes, Mgahinga (3475 m), Muhavura (4128 m) and Sabino (3654 m) dominate the Rwanda / Uganda border. Numerous small volcanic ash cones and lava flows are concentrated within the southern part of the Rukiga highlands, these being part of the larger Virunga Volcano field (Section 2.2).

The area covered around the southern part of Bwindi-Impenetrable Forest is more rugged and dissected than other areas of the Rukiga highlands (Figure 3.1), presumably as the area has been subjected to more recent or vigorous uplift than

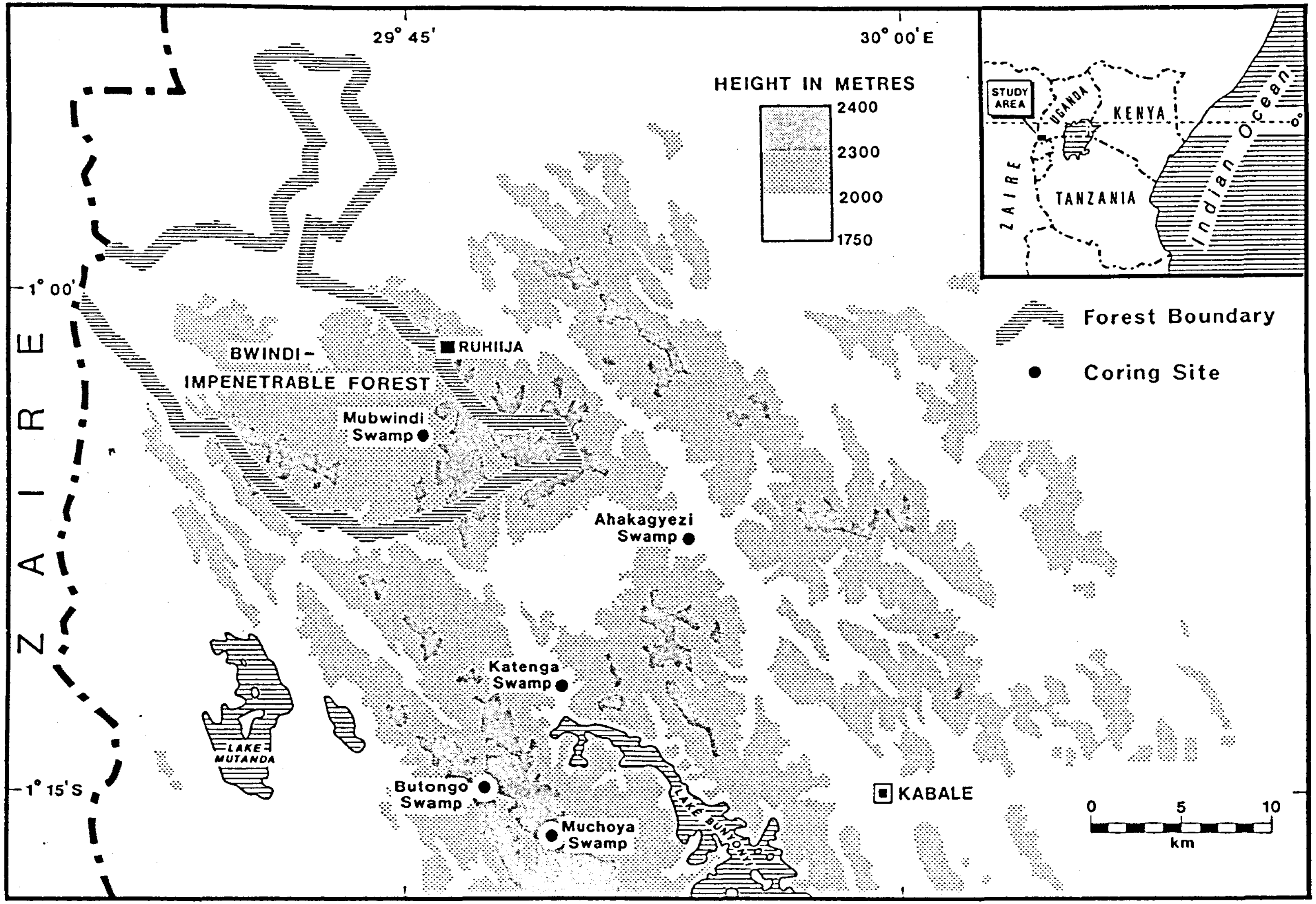


Figure 3.1 Location map of the Rukiga highlands, south-west Uganda

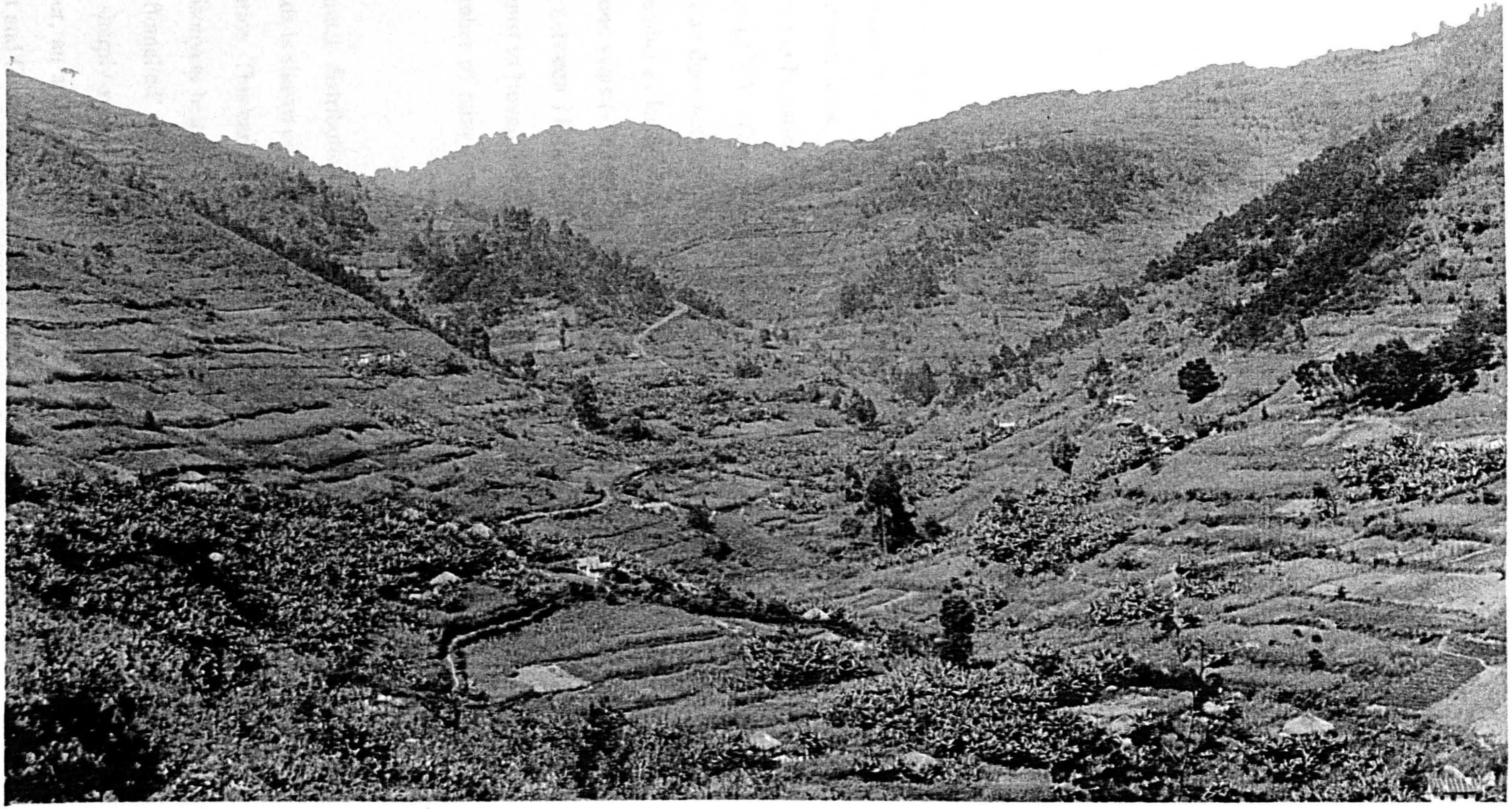


Plate 3.1. Typical view of the Rukiga highlands

other areas (Hamilton, 1969). The topography is extremely rugged comprising narrow, very steep-sided valleys that have a north-west to south-east to north-north-west to south-south-east trending, although there are exceptions to this. These valleys are bound by emergent hill crests lying between altitudes of 1190 m in the north and 2607 m in the south.

Bwindi-Impenetrable Forest is a vital catchment area and contains the sources of several perennial rivers that are important to the populated agricultural areas. About four-fifths of the total drainage is to lake Edward. The remainder is into lakes Mutanda and Bunyonyi (Deny, 1972).

3.3 Climate

The climatic regime is typical of central Africa (Section 2.3). Using existing data from Kabale town and applying climatological considerations, particularly the environmental lapse rate (Section 2.3), the mean annual temperature at Ruhiija (2300 m) can be estimated at 13 ^{0}C, with a mean daily maximum of 20 ^{0}C and a minimum of 7 ^{0}C. The coolest period is June to July, however the mean monthly temperature does not vary by more than 4 ^{0}C through the year. The driest months are December to January (sometimes extending to February) and June to July. The twenty-one years (1963 to 1983) mean annual rainfall at Ruhiija is 1440 mm yr $^{-1}$ ranging between 1130 to 2390 mm yr $^{-1}$. The wettest months are March to April and August to November, these correspond to the passage of the equatorial trough. The number of rainy days per year varies between 122 and 177 with a mean of 148.

The annual distribution of the present-day rainfall (cm yr^{-1}) for the Rukiga highlands is shown on Figure 3.2. This highlights the considerable variation in the distribution. This can be related to the regional topography with the concentration of the isohyets being related to the passage of the rain-bearing weather systems being ‘funnelled’ into the area presently covered by Bwindi-Impenetrable Forest by the sharply rising high ground of the Virunga Volcanoes to the south-west. However, an additional explanation for the rainfall distribution has come from Leggart and Osmaston (1961); this suggests that Bwindi-Impenetrable Forest may

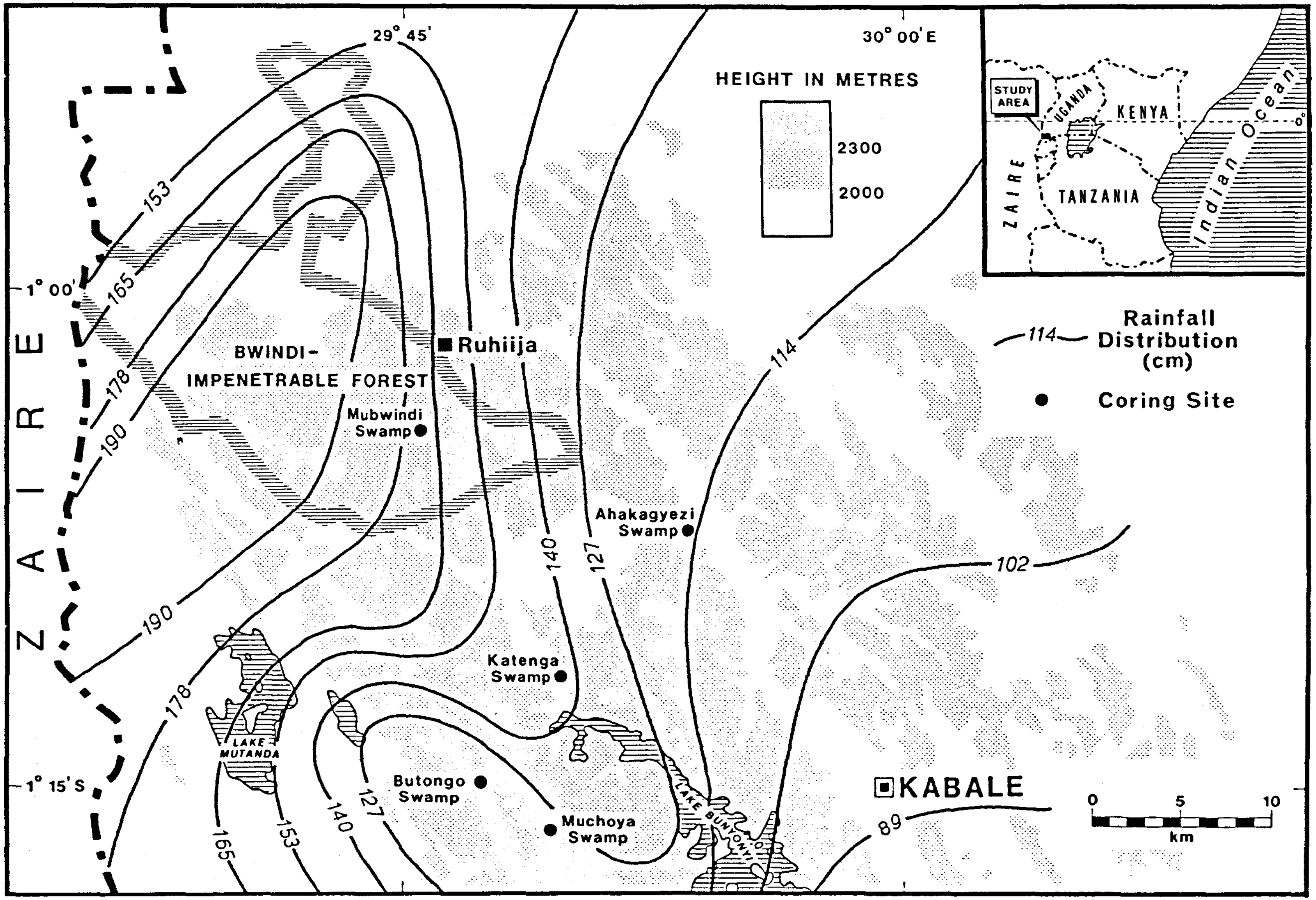


Figure 3.2 Rainfall distribution in the Rukiga highlands

affect the regional climate, especially by influencing the number of rainy days and the amount of rain that falls. Although not dismissed outright, I suggest the influence of Bwindi-Impenetrable Forest as a modifier of climate will be felt mainly on a local, rather than regional scale.

3.4 Soils

The soils of the Rukiga highlands are derived primarily from Precambrian phyllite of the Karagwe-Ankolean system (Coombe and Simmons, 1933). The Atlas of Uganda (1967) classifies the soils as being of two major types; 'non-differentiated humic ferralitic soils of high altitudes' and 'non-differentiated ferralitic soils with dark horizons'. Harrop (1960) recognised two soil series for Bwindi-Impenetrable Forest; the 'Mafuga Series' covering the upland sites, and the 'Ntendule Series'. The soils of Bwindi-Impenetrable Forest have poor structure, moderate to high acidity, and are very deficient in bases, thus rendering them low in productivity (Baker, 1958). The soils become very loose and friable as they dry, and they are highly susceptible to erosion, especially once the forest vegetation has been removed and cultivation is undertaken. Elsewhere in the Rukiga highlands the soils are tropical red earths (Kabale Catena), overlain with a spongy humus. Clays occur under a layer of peat in the swampy valley bottoms (Leggart and Osmaston, 1961). Within these swamps debris mixed with alluvium from the surrounding slopes produces a peaty clay soil (Kagambirwe, 1972).

3.5 The flora and fauna of the Rukiga highlands

As discussed in Chapter 2 the composition and distribution of the central African flora has changed significantly over the late Quaternary period. These changes have ultimately determined the composition and distribution of flora and fauna in the Rukiga highlands today.

3.5i Flora of the Rukiga highlands

Present-day vegetation in the Rukiga highlands is largely the product of intense human activity (Section 2.8). However, three major forested areas remain. The most important of the three forest blocks is Bwindi-Impenetrable Forest, which represents the largest fragment of what is believed to be the dominant vegetation type for much of the area in the absence of intense human activity (Hamilton, 1969; 1974). As such Bwindi-Impenetrable Forest has been described in part, or in full by Burtt (1934), Cahusac (1958), Hamilton (1969; 1974), Lind and Morrison (1974), Morrison (1968), Snowden (1933; 1953) and Watt (1956). Although these descriptions have been driven by different agenda, all have fallen into the idea that the forest is 'natural' and has undergone very little, if any, anthropogenic disturbance. However, Howard (1991) suggests that 90% of Bwindi-Impenetrable Forest has undergone intensive, selective forest clearance, (Section 3.7). Consequently, only the most isolated areas resemble primary montane forest. The flora of Bwindi-Impenetrable Forest has been described by different authorities as 'moist montane', 'tropical lower montane evergreen', 'medium altitude moist evergreen', 'undifferentiated moist montane', '*Parinari* and *Pygeum* moist montane' and 'mixed forest with *Chrysophyllum*'. Absence of agreement on which vegetation category the forest belongs to within the literature is a clear indication of the vegetation complexity, being greatly affected by altitude, topography and soil depth. Within the scheme outlined in Section 2.4 Bwindi-Impenetrable Forest comprises dry lower montane forest, moist lower montane forest and upper montane forest components.

Bwindi-Impenetrable Forest can be divided into northern and southern sectors by climatic, floristic and topographic differences (Butynski, 1984). The northern sector is characterised by lower elevation, lower rainfall, a relatively subdued topography and taxa associated with the lower altitudinal limits of dry lower montane forest; species such as *Celtis* spp., *Newtonia buchananii*, *Strombosia scheffleri*, and *Symphonia globulifera* are common (Kakuru, 1993). A herbaceous layer is particularly well developed under open forest (Plate 3.2). In swampy areas dense stands of *Syzygium guineense* occur. Vegetation on the swamp surfaces is dominated by *Alchemilla loberia*, *Cyperus* spp., *Miscanthus* spp. and *Myrica kandtiana* communities.

By comparison, the southern sector is altitudinally higher, wetter and has a much more rugged topography. The southern sector includes a number of deeply incised,

Plate 3.2 Herbaceous understory in the southern sector of Bwindi-Impenetrable *Forest*

poorly drained valleys, one of which contains Mubwindi Swamp (Plate 3.3). Within the southern sector species composition varies with altitude (Hamilton, 1969). *Neoboutonia macrocalyx* and *Syzygium cordatum* are common on the lower slopes of valleys. On land at mid-altitude *Chrysophyllum albidum* and *C. gorungosanum* are abundant in association with *Cassipourea ruwensorensis, Drypetes albidi* and *Strombosia scheffleri.* At higher altitudes, taxa such as *Faurea saligna, Hagenia abyssinica,* and *Nuxia congesta* become common. *Olea capensis, Podocarpus milanjianus,* previously common on ridge and hill top locations (Hamilton, 1969), have now largely been removed by pit-sawyers (Howard, 1991). *Synarundinaria alpina* occurs in two small patches, mainly in the south-east of the southern sector; the total area covered is extremely small (about 2%). Fire induced, and possibly maintained, sub-climax woodlands are characterised by *Agauria* spp., *Dodonaea viscosa* and *Panicum* spp. These are common towards settlements adjoining Bwindi-Impenetrable Forest.

The other remaining forested areas in the Rukiga highlands (Mafuga and Euchoya Forest) are of a secondary nature (Taylor, 1990). Mafuga Forest is only about sixty years old. This age is particularly useful because of the light it throws on forest regeneration (Hamilton, 1969). The most common trees are *Agauria salicifolia, Hagenia abyssinica, Macaranga kilimandscharica, Maesa lanceolata, Psychotria megistosticta* and *Nuxia floribunda.* Small tree seedlings of species recorded in the more remote parts of Bwindi-Impenetrable Forest are also found at Mafuga Forest, these include *Chrysophyllum albidum, Cassipourea ruwenzorensis, Entandrophragma excelsum, Fagaropsis angolensis, Newtonia buchananii, Strombosia sheffleri, Symphonia globulifera* and *Zanthoxylum gilleti* (Hamilton, 1969). Euchoya Forest is dominated by *Synarundinaria alpina,* this is patchy in structure with broad-leaved forest taxa present in the gullies. The most common species are *Macaranga kilimandscharica* and *Neoboutonia macrocalyx,* both are well-known colonising tree species (Hamilton, 1974). Other species presents include *Bersama abyssinica, Maesa lanceolata, Nuxia* spp. and *Polyscias fulva* (Hamilton, 1969; Morrison, 1968).

Agricultural land covers the majority of the Rukiga highlands. The main agricultural crops of the region are bananas, beans, Irish and sweet potatoes,

Plate 3.3 Southern view of Mubwindi Swamp

millet, plantain, sorghum and wheat. Hill-slope terracing is the most common form of land management, this allows for agricultural production on the steep slopes and is most suited to the subsistence requirements of the large number of small-holdings. More recently, many of the swamps have been drained as population density increase.

3.5ii Fauna of the Rukiga highlands

Bwindi-Impenetrable Forest has great faunal diversity. It is a particularly important locality for many species that are endemic to the highlands of the Western Rift. The forest has at least 336 species of birds, 19 (53%) of the region's endemic species (Butynski, 1986). There are no less than twelve threatened, or near-threatened species; the mountain gorilla (*Gorilla gorilla beringei*), chimpanzee *(Pan troglodytes*), l'hoest's monkey (*Cercopithecus l'hoesti*), elephant (*Loxodonta africana*), dwarf honey guide (*Indicator pumilio*), African green broadbill *(Pseudocalyptomena graueri*), Kivu ground thrash (*Tardus tanganjicae*), Grauer's swamp wabler (*Bradypterus graueri*), Chapin's flycatcher (*Muscicapa lendu*), Shelley's crimson wing (*Cryptospiza shelleyi*), African giant swallowtail butterfly (*Papilio antimachus*) and cream-banded swallowtail (*Papilio leucotaenia*) (Butynski, 1984). The most conspicuous mammals in Bwindi-Impenetrable Forest are the primates; the forest contains ten species (58% of Uganda's total) of primates and, is the only forest with both mountain gorilla and chimpanzee. Gorillas are a highly endangered species, there are only around 280 individuals remaining in the forest (nearly 40% of the world's total). Censuses for the rest of the large mammals are yet to be undertaken.

3.6 Population distribution and land-use within the Rukiga highlands

Populations within the Rukiga highlands can be divided into two main categories; those who have been resident for a considerable time, and those that have migrated into the area following agricultural revolution and population migration (Section 2.8).

3.6i Indigenous populations

The indigenous inhabitants of Bwindi-Impenetrable Forest were the BaTwa pygmies. Bwindi-Impenetrable Forest, once under National Park control became 'out of bounds' for human inhabitation. Most of the BaTwa now work for farmers close to the forest edge, a few act as guides and trackers. The BaTwa are numerically few, their influence and numbers have been swamped by the expansion of their neighbours. These are politically organised and demand land for settlement. One of the prominent BaTwa often laments that they were once mortal enemies of the pioneering agriculturists, keeping all strangers out of the forest (Kingdon, 1990).

3.6ii Migrant populations

The majority of the people living within the Rukiga highlands are migrants (Section 2.8). According to the 1991 national census the total population in the districts surrounding Bwindi-Impenetrable Forest was nearly 1,000,000 people. Annual mean growth rate since the previous census (1981) was 2.7%, which is 0.2% above the national Figure. Population density averaged over 230 persons km^{-2}. This is about three times the national average. As happened for many centuries, this population meets its life needs almost entirely from subsistence farming. Nearly all the land outside Bwindi-Impenetrable Forest has been cleared and is intensively cultivated (Plate 3.1). In the face of continuing population growth and declining soil fertility land shortages are, and will continue to be, a serious problem.

3.7 Past human activities within Bwindi-Impenetrable Forest

Before demarcation, land currently within the boundaries of Bwindi-Impenetrable Forest was used for materials that could not be obtained from the homesteads. These activities have been focused on three major types of resource; mineral, timber, and subsistence requirements.

3.7i Mineral activities within Bwindi-Impenetrable Forest

Mining of gold has been carried out both within, and outside Bwindi-Impenetrable Forest for a considerable time. It was a significant source of local income until 1991, when the activity was proscribed by the National Park legislation. Two wolfram mines, one at Ruhiija and the other at Kakangaga, were operational during the 1930s, these have closed since the late 1970s when political instability caused the foreign owners to return to Kenya.

Smelting of hematite is carried out only very locally, if at all. Scrap metal is re-worked into tools and hardware. Because of the presence of iron-ore containing rocks, blacksmiths are found in villages bordering the southern part of Bwindi-Impenetrable Forest. Due to competition from industrially produced goods, the technology and the traditional knowledge this activity represents are disappearing,. Subsequently, the number of operational blacksmiths has declined (White, 1969). Only two to four blacksmiths work in each parish today, while in some parishes they are completely absent (Rob Wild pers. comm.). Most blacksmiths have one set of bellows, usually made from the wood of *Polyscias fulva*. This species is favoured for its softness, allowing to be hollowed-out to form the drums and pipes of the bellows. These last between 20 and 30 years (Rob Wild pers. comm.). Although *Polyscias fulva* occurs at low densities within Bwindi-Impenetrable Forest, the longevity of bellows is thought to exceed replacement time of the parent tree. Both exotic and indigenous woods are used for charcoal production, with black wattle being most favoured. This is unchanged since the late 1960s, when White (1969) recorded that nearly all the blacksmiths produce their charcoal from locally grown black wattle. Favoured indigenous species for charcoal production are *Aguaria salicifolia* and *Syzygium* spp. (White, 1969).

3.7ii Timber activities within Bwindi-Impenetrable Forest

Timber abstraction through pit-sawing has been a major impact on the resultant flora of Bwindi-Impenetrable Forest (Howard, 1991). As well as removal of specific trees there is considerable damage to the surrounding vegetation. Saplings and poles cut for the construction of the pit-sawing trestles and shelters are rarely re-used. In some cases only a small portion of the felled tree is converted to timber. Thus, pit-sawing can be a very wasteful form of timber abstraction.

Official records for timber abstraction date from the 1940s, although casual extraction is thought to predate this. In 1947 pit-sawing into large planks for subsequent re-sawing on small saw-benches was officially recommended by the Forest Department as the best approach to abstract timber. In 1948, the forest was inventoried at a 3% sampling intensity with a view of giving a timber concession to meet anticipated timber demand in the area. It was estimated that there was about 20 m^3 ha^{-1} of wood from the then saleable species namely *Chrysophyllum* spp., *Entandrophragma excelsum*, *Ficalhoa laurifolia*, *Maesopsis eminii*, *Newtonia buchananii*, *Podocarpus* spp., *Symphonia globulifera* and *Zanthoxylum* spp. The affect of the increased demand for timber was soon noticed as a decrease in the standing stock. Indeed, by 1954 no licences were issued for *Podocarpus* spp., except for windthrows and trees with a minimum diameter at breast height (dbh) of 2.3 m. By 1957, pit-sawing had become such a popular occupation that it was decided to restrict it to 100 licences, and to confine these within a distance of about 6 km from access roads. By 1961, only 85 licensed pit-sawyers were operating in the forest. Table 3.1 shows the 'total' outputs for the years 1940-61.

The Forest Department's proposed working plan for the 1961 to 1971 period states; 'Natural irregular forest was to be converted to the uniform shelterwood system with the aim of establishing a normal forest with a cropping rotation of 100 years. The harvesting of the main crop was to be controlled in a manner that was always to give priority to protect the haunts of the mountain gorilla. This was to be achieved through a range of management practices; harvesting was to be arranged in three felling series, two nature reserves were established, all dead and dying trees were to be felled for timber by pit-sawyers throughout the forest, except in nature reserves, and 'quota species' were determined. For each felling series, the aggregate annual allowable cut (AAC) was to be limited to 2832 m^3 for each quota species. In each of the felling series, harvesting was to be limited to one compartment at a time. In the event of the AAC not being achieved during the year the balance was to be carried forward to the next year. The number of species in the quota list was to be balanced with volume in such a way that if other species

Table 3.1 Timber Output From the IFCR (BIFNP): 1940-61.

(Source: Forest Department Records)

Year	Volume cut (m^3)
1940	421
1941-1944	1584
1945	432
1946	619
1947	700
1948	1044
1949	1110
1950	1188
1951	1260
1952	1332
1953	1438
1954	1519
1955	1728
1956	2157
1957	2559
1958	2717
1959 (6 months)	896
1959/60	1459
1960/61	760

became acceptable on the market, the AAC would correspondingly be increased. Similarly, if species were removed from the list, the AAC would be reduced. Felling was to be controlled by the Forest Department office in Kabale through a licensing system. Issue of licences was to be stopped when the AAC was reached.

The subsequent years were characterised by breakdown of civic order and a severe inability of government to finance its activities. Consequently, the official records from 1971 to 1984 (Table 3.2) are in sharp contrast to eye-witness and informed estimates of the total sawn timber removed. Towards the end of 1984, the Forest Department resumed its control mechanisms; the number of pit-sawing licences were reduced by almost 50%. When the forest became a National Park, pit-sawing was banned throughout Bwindi-Impenetrable Forest. Now it is only an occasional illegal activity (Rob Wild pers. comm.).

The end-point of this timber extraction has meant that Bwindi-Impenetrable Forest has been heavily pit-sawn. Indeed, only 10% of the Bwindi-Impenetrable Forest remains free from exploitation by pit-sawyers, 61% has been heavily exploited and 29% has been 'creamed' of its best timber trees (Howard, 1991).

3.7iii Subsistence activities within Bwindi-Impenetrable Forest

There have been, and continue to be a number of subsistence requirements on Bwindi-Impenetrable Forest from the surrounding populations. Bwindi-Impenetrable Forest has been used extensively as a supply of meat. Hunting of wild animals in the forest predates gazetted protection of the area, the African buffalo (*Syncerus caffer*) and the leopard (*Panthera pardus*) have been poached into local extinction. The threat from poaching on existing animals is reportedly being brought under firm control (Rob Wild pers. comm.).

Basketry produces a range of vessels for harvesting, drying, winnowing, grinding and storing agricultural produce. Plant materials used, range from fast growing wetland species such as *Cyperus papyrus* to scarce, slow growing climbers such as *Loesneriella apocynoides*. *Synarundinaria alpina* and *Smilax kraussiana* are also used.

Table3.2 Licensed Pitsawyers in Bwindi Forest in 1971-84

(Source: Forest Department Records)

Year	no. of pitsawyers	Revenue (USH)	Round vol.(m^3)
1972	30		54
1973			486
1974			710
1975			
1976			181
1977		20530	798
1978		35573	2346
1979	54	81300	2412
1980		88174	1180
1981	73	66751	906
1982		354849	1015
1983	73	191993	1152
1984	42	527310	

Bee-keeping is a popular and widespread activity. The majority of beekeepers have hives inside Bwindi-Impenetrable Forest; hives can be hidden away from the general public and are less susceptible to theft or spells placed by jealous people directed at anyone with many high yielding hives (Rob Wild, pers. comm.). Areas with high densities of flowering trees, such as *Faurea saligna*, *Nuxia congesta* and shrubs like *Brilliantasia* spp. are well known to bee-keepers; hills near these areas are favoured for placing hives. Bee keepers also know which areas have plants with toxic pollen, producing diarrhoea-causing honey.

Fire is a threat to bee-keeping. It would appear that beekeepers (although often the cause of fire) are genuinely prepared to prevent runaway fires. Large trees are felled for hive construction, *Faurea saligna* being the preferred species; *Alangium chinense*, *Albizia gummifera* and *Polyscias fulva* are also used but to a lesser extent. Although no data are available on growth rates of *F. saligna*, it is likely that tree growth exceeds the rate of hive deterioration (Rob Wild, pers. comm.).

Most people have to travel long distances to clinics in Kabale, Kisoro, Kisiizi and Kambuga. Thus, there is considerable reliance on herbal remedies for many ailments. Commercial trade in herbal medicine is not well developed and the impact of medicinal plant harvesting is low, even for popular remedies, such as provided by *Rytigynia kigeziensis* for the treatment of worms.

Bean-stakes are essential for climbing bean production, cutting of bean-stakes is an important seasonal agricultural activity during May and June. With densities reaching 50,000 bean-stakes ha^{-1}, and only lasting for 2 to 3 seasons (Rob Wild, pers. comm.), huge quantities of bean-stakes are needed every year. The under-storey tree *Alchornea hirtella* is one of the most favoured sources of bean-stakes. Coppicing readily and occurring in high density patches. Other species used include *Acacia mearnsii*, *Acanthus arboreus*, *Eucalyptus* spp. and *Sapium ellipticum* (Rob Wild pers. comm.).

Communities have depended on the use of building poles for construction of homesteads. Selection of poles for this purpose is based on a need for straight, durable trees. Favoured forest species are *Drypetes gerrardii*, *D. ugandensis*, *Harungana madagascariensis*, *Tabernaemontana* spp. *Cyathea maniana* is used for durable support poles and roofing. *Synarundinaria alpina* is favoured for cross pieces. Harvesting of these from Bwindi-Impenetrable Forest would be labour intensive due to the comparatively low density of suitable poles ha^{-1} (Cunningham, 1992) and is thought to have negligible impact on the vegetation apart from *Synarundinaria alpina* which occurs within relatively small areas at high densities.

As elsewhere in rural areas of central Africa, the major source of household energy for cooking and heating for the communities around Bwindi-Impenetrable Forest is fuelwood. Wood is also used for distilling waragi, baking bricks and clay pots. Although the highest consumption of wood in the area is for fuelwood use (approximately 140,000 m^3 yr^{-1}), a recent survey showed that most of this originates from cultivated trees and only a small proportion (7.5%) originates from non-cultivated sources (Rob Wild pers. comm.).

3.8 Past and present management of Bwindi-Impenetrable Forest

Bwindi-Impenetrable Forest was originally gazetted as undemarcated forests in 1932, then known as Kasatora Crown Forest (181 km^2) and Kayonza Crown Forest (26 km^2). In 1942 the Kasatora Crown Forest and Kayonza Crown Forest were combined with additional forest to establish the Impenetrable Crown Forest Reserve(324 km^2). In 1948 this was redesignated as the Impenetrable Central Forest Reserve (ICFR), and reduced in size to 298 km^2. Demarcation of the boundaries of the forest (where they did not follow natural features) was carried out between 1939 and 1947, with exotic tree species (*Cupressus* spp.) as boundary markers. Further, but smaller excisions were made in 1958 to shorten the boundaries and make them easier to maintain and patrol.

In 1961 the forest was gazetted as an Animal Sanctuary, with boundaries as those of the ICFR. Two local forest reserves, namely Bikingi and Ishaya bordered the ICFR and were incorporated in 1968 after the republican constitution of 1967. After 1968, the word Bwindi was added at the beginning of the title, being the local name for 'place of darkness'. Until 1991, the forest was administered from both the Rukungiri and Kabale district Forest Department offices, and small field stations at Ruhiija and Rushaga. A WWF-USAID supported research project based at Ruhiija also provided additional infrastructure, logistical management and an administrative backstop. The Forest Department played the leading role in the management and administration of the forest until designation as a National Park in late 1991, with its administrative headquarters at Buhoma. Considerable confusion has been caused by the fact that Bwindi-Impenetrable Forest (and various portions of it) has been referred to by different names. This forest has been called the 'Kayonza' (Kingdon, 1971; Pitman, 1937), 'Impenetrable-Kayonza' (Hamilton, 1974, 1975b, 1976), 'Impenetrable' (Leggart and Osmaston, 1961), 'Bwindi-Kayonza' (Hamilton, 1981; Kingdon, 1987), and 'Bwindi' (Harcourt, 1981).

National Park designation in 1991 was shrouded in intra-governmental wrangling, politicking and bickering, donor pressure and hence controversy. The idea of creating a National Park in this area was first suggested by Ugandan National Parks (UNP) in 1971, but the idea was never pursued any further (Rob Wild, pers. comm.). UNP revived the suggestion in 1983, reasoning that the Forest Department was no longer capable of protecting these vital and environmentally fragile ecosystems. Also, gorillas could be a major tourist attraction, hence an important source of foreign income. A series of intra-government consultations ensued in the subsequent few years, culminating in a common position that Bwindi-Impenetrable Forest, was to remain a forest reserve, the Forest Department was regaining its capability for affective management. In 1989, UNP requested cabinet to endorse designation of Mugahinga, Bwindi-Impenetrable and Mount Ruwenzori forest reserves as National Parks. Cabinet gave the approval, and during August 1991 UNP announced through the British Broadcasting Corporation that the three areas 'are now national parks'.

Bwindi-Impenetrable Forest is now managed according to the National Parks Act of 1952 and the management plan for the period 1993 to 1997. The overriding goal for this plan is 'maintain and enhance the biological diversity and the ecological and physical processes of the forest, while allowing sustainable utilisation of the forest's resources'. The principle *modus operandi* is the four zones into which the forest and environs have been sub-divided. The high protection zone includes all rare habitats, all national and regional endemic species and the largest area of water catchment. Multiple use zones are located within 2 km from the forest edge and must have resources that local people need; the resource must be identified, quantified and classified, alternative sources should not be available outside Bwindi-Impenetrable Forest. The tourism zone should be well protected and in such a state that low-impact tourism can take place without disturbing biodiversity and ecological processes, and will enhance conservation. The sustainable development zone includes all parishes bordering the park. Depending on the needs of the people, services may go beyond one parish limit, but in any case not beyond two. In this zone, members of the local community must have food security, adequate education, health-care, communication services, energy and other natural resources.

3.9 Mubwindi Swamp topography, drainage and vegetation

Mubwindi Swamp (Plate 3.4) is situated in the south-east of Bwindi-Impenetrable Forest at an altitude of 2100 m. The hills surrounding Mubwindi Swamp rise to over 2500 m although 2350 m is more common. Mubwindi Swamp is constrained within four valleys (Figure 3.3) these all support vegetation (Plate 3.5) characteristic of the southern sector (Section 3.5). Four streams feed the swamp; the Kanyambogo, Kiruhura, Nyakigali and Kajembejyembe, all flowing north to south along the geological strike. In the northern parts of Mubwindi Swamp the gentle gradient almost brings the flowing water to a standstill during the dry seasons. Mubwindi Swamp is periodically flooded by a dramatic increase in the hydrological budget during the monsoonal seasons. There is a confluence of the rivers at the southern end of the swamp, where the resultant single river is of considerable size (Plate 3.6). Where the rivers join there is a drop in the swamp surface of approximately 1.5 m this appears to result from headward fluvial erosion. The single river meanders through the accumulated sediments (Plate 3.7), often against an incut wall of incised organic sediment. The river flows through a small lake-like depression in the southern part of Mubwindi Swamp this may become periodically wet during the height of the monsoon. The river then flows

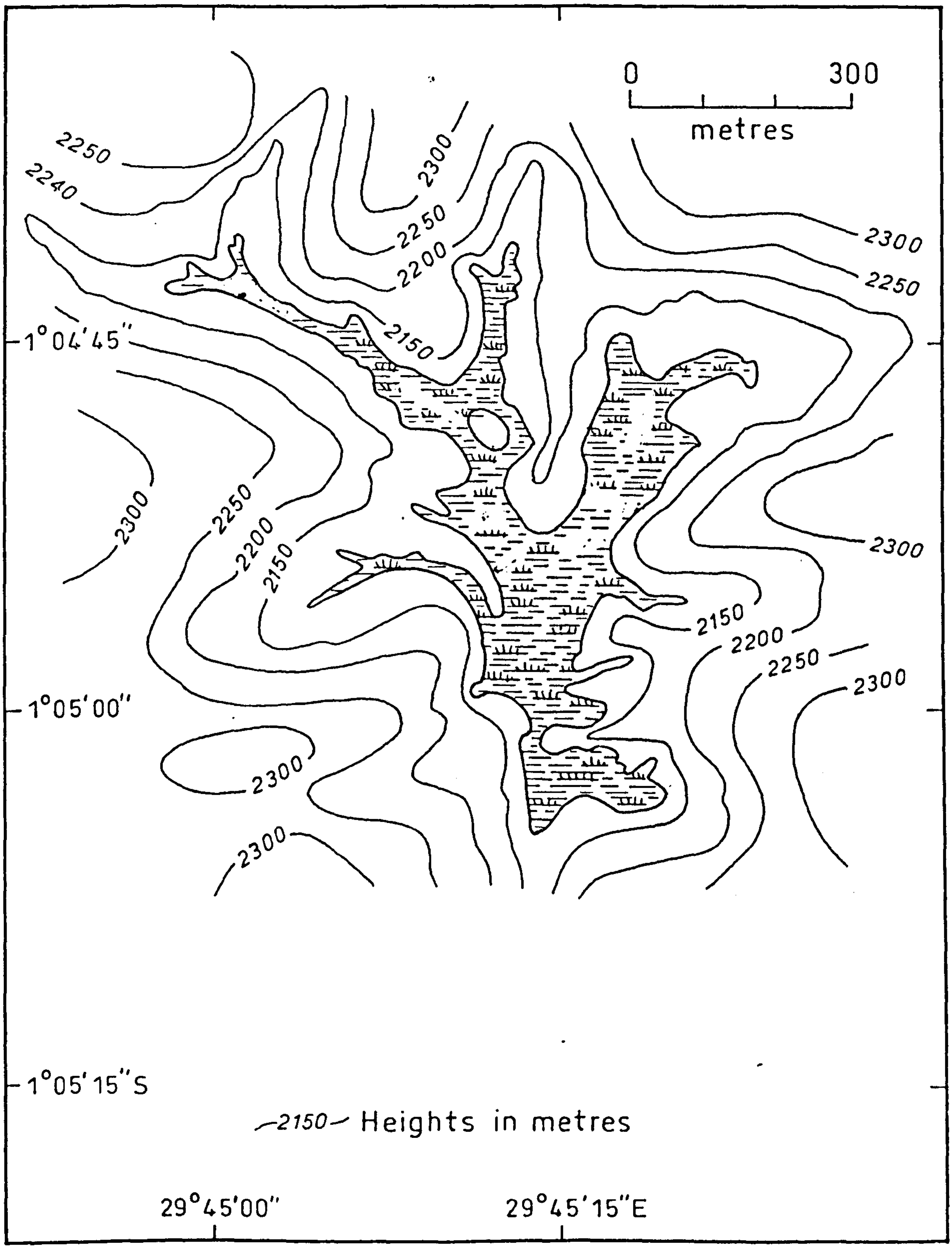


Figure 3.3 Mubwindi Swamp topography and location

Plate 3.4 Mubwindi Swamp.

Plate 3.5 Setting up base camp.

Plate 3.6 The resultant river after the confluence in the southern part of Mubwindi Swamp

Plate 3.7 Meandering river in the southern sector of Mubwindi Swamp

out of the basin to the west of a massive tongue of unconsolidated, slumped material and joins the general drain into Lake Mutanda.

The surface vegetation of Mubwindi Swamp was mapped by Katende (1984). The surface vegetation of Mubwindi Swamp varies considerably from fringing swamp forest dominated by *Usnea*-clad trees (Plate 3.3) such as *Myrica kandtiana*, *Syzygium cordatum*, and the swamp grass *Miscanthus violaceus*. Away from marginal areas the vegetation is dominated by *Cyperus denudatus* in the wettest areas and *C. latifolius* in the dryer areas. Other common components of the vegetation at Mubwindi Swamp are *Alchemilla* spp. and several species of ferns including *Blechnum* spp. Occasional tree heathers and patches of Elephant grass, (Plate 3.8) are also found. A broken, fringing band of *Alchornea hirtella* is found on the dry land immediately next to the swamp.

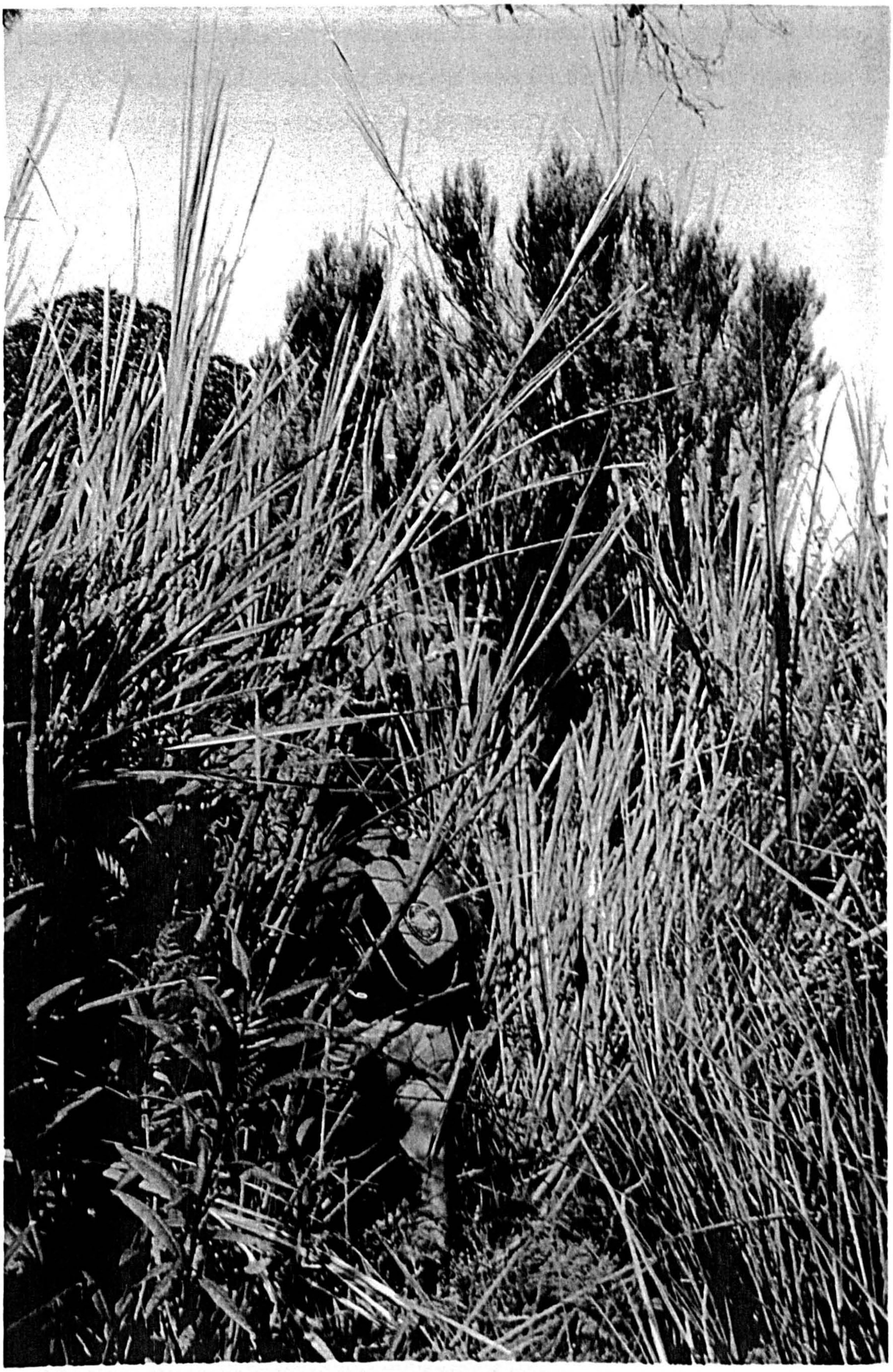


Plate 3.8 A patch of Elephant grass and *Erica arborea*.

PART 2 METHODS AND RESULTS

This section of the thesis describes field and laboratory methods used to acquire data on aspects of Mubwindi Swamp and its catchment. Results yielded by these methods are described. These will form the basis for the discussion of vegetation dynamics and environmental change in part three.

CHAPTER 4

Collection and radiocarbon dating of sediments

4.1 Introduction

The current chapter details the extraction of sediment cores from Mubwindi Swamp. These will form the basis for a reconstruction of the vegetation and sedimentary environment within the Mubwindi Swamp basin. The radiocarbon chronology is described for two of the cores (MB3 and MB6). From this chronology, age-depth curves are constructed. In addition, the environmental significance of $\delta\ ^{13}C$ values assigned to the radiocarbon dates from core MB6 is also investigated.

4.2i Abstraction, logging and collection of sub samples from the sediment cores

A total of twenty-three cores of sediment were collected along five transects (Figure 4.1) from Mubwindi Swamp in three separate visits. Mubwindi Swamp occupies a Y-shaped, bifurcating valley. During 1990, three exploratory cores (MB3, MB4, MB5) were collected from the central part of the widest arm of Mubwindi Swamp by David Taylor, using a Hiller, and Russian (D-Section) samplers. During 1992, a further eleven cores were collected by Mike Atkinson. These included five more cores along transect 1 (Figure 4.1). Additional cores were collected along a transect on the north-western arm (transect 2), and a transect just south of where the valley bifurcates.

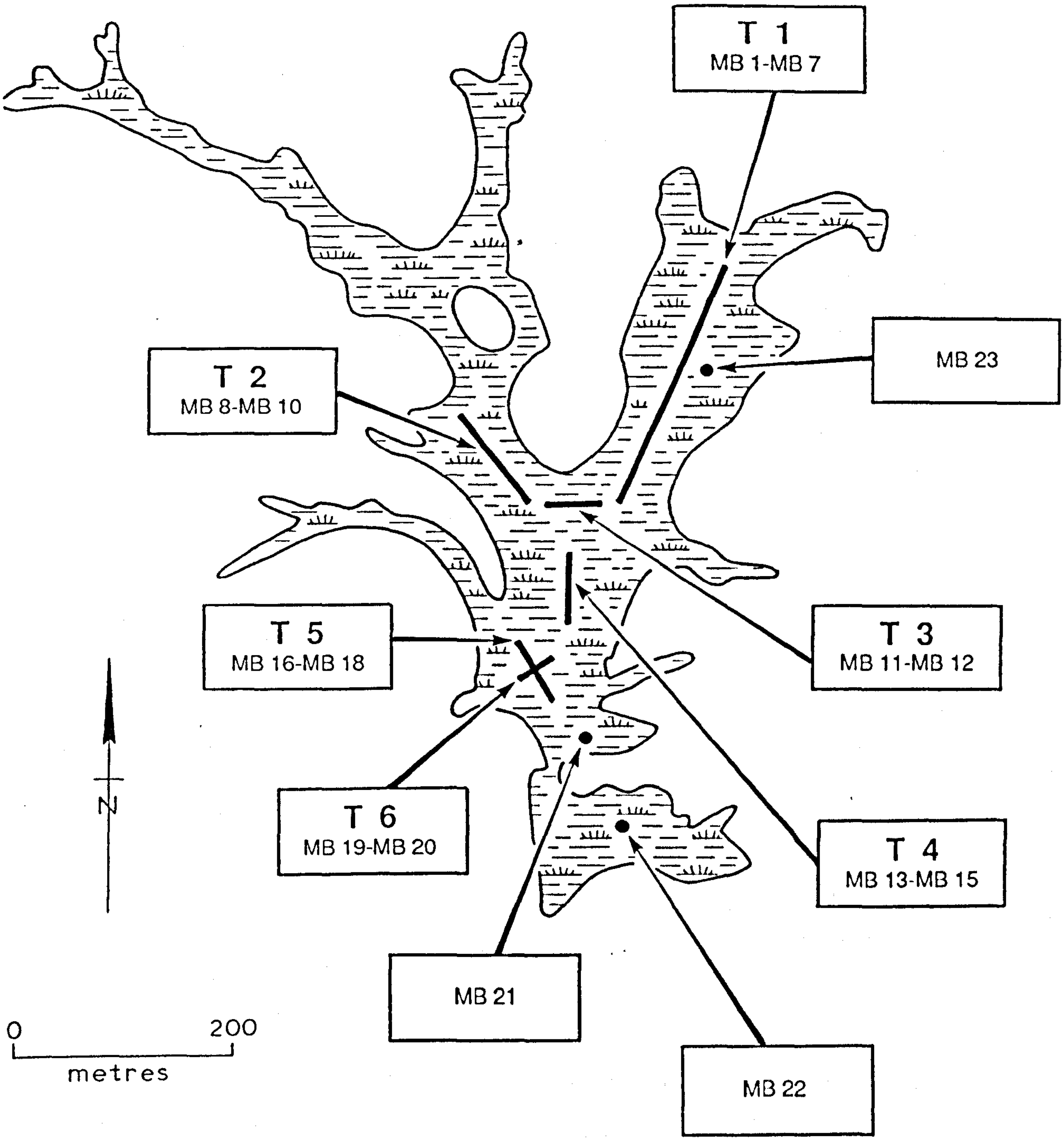


Figure 4.1 Location of sediment cores on the Mubwindi Swamp surface

Transects 1 to 3 are located in the northern most part of Mubwindi Swamp. In order to provide a more complete stratigraphic record, cores of sediment were collected along three transects (T4 to T6) from the southern part of Mubwindi Swamp, during 1994. Transect 4 was located in the central part of the swamp, and comprised three cores (MB13 to MB15). Transect 5 comprised three cores (MB16 to MB18), and ran longitudinally along a main river channel (Section 3.9). Two additional cores (MB19 and MB20) were collected either side of the core situated in the lowest part of this transect, forming transect 6. These cores were placed specifically with a view to try and determine the extent and influence of any transverse migration of the main river channel. Cores MB21 and MB22 were taken from the southern-most end of Mubwindi Swamp. During 1994 an additional core, core MB23 was collected from the northern part of the swamp, adjacent to transect 1.

All sediment cores were extracted in 50 cm sections and sub-sampled in the field (Plate 4.1), with the outer-most layer of sediment removed before sub-sampling in order to minimise contamination. Sediments were described on site using the Tröels-Smith (1955) method. Presentation of sediment stratigraphies in Figure 4.2 is based on the simplification of Tröels-Smith's (1955) system as suggested by Aaby (1979). Figure 4.2 shows the location of these cores, and their stratigraphies within the Mubwindi Swamp catchment.

Cores MB3, MB4, MB6, MB7 and MB10 were sub-sampled for subsequent laboratory analysis, as these cores accounted for the range of variation in sediment type logged on site. During field work in 1991 and 1992, sub-samples of between 3 and 8 cms were collected. As a rule, larger samples were collected from the more inorganic sediments to allow for the possibility of low amounts of pollen present, or, in the case of the samples collected for radiocarbon analysis, low amounts of carbon present. These large samples were deemed unnecessary following pollen analysis carried on sub-samples from cores MB3 and MB6.

During 1994, core MB23 was sub-sampled at 1 cm slices every 5 cm throughout its length (Plate 4.2). Where there were obvious changes in sedimentation, the sampling interval was reduced to samples taken every other centimetre. This high

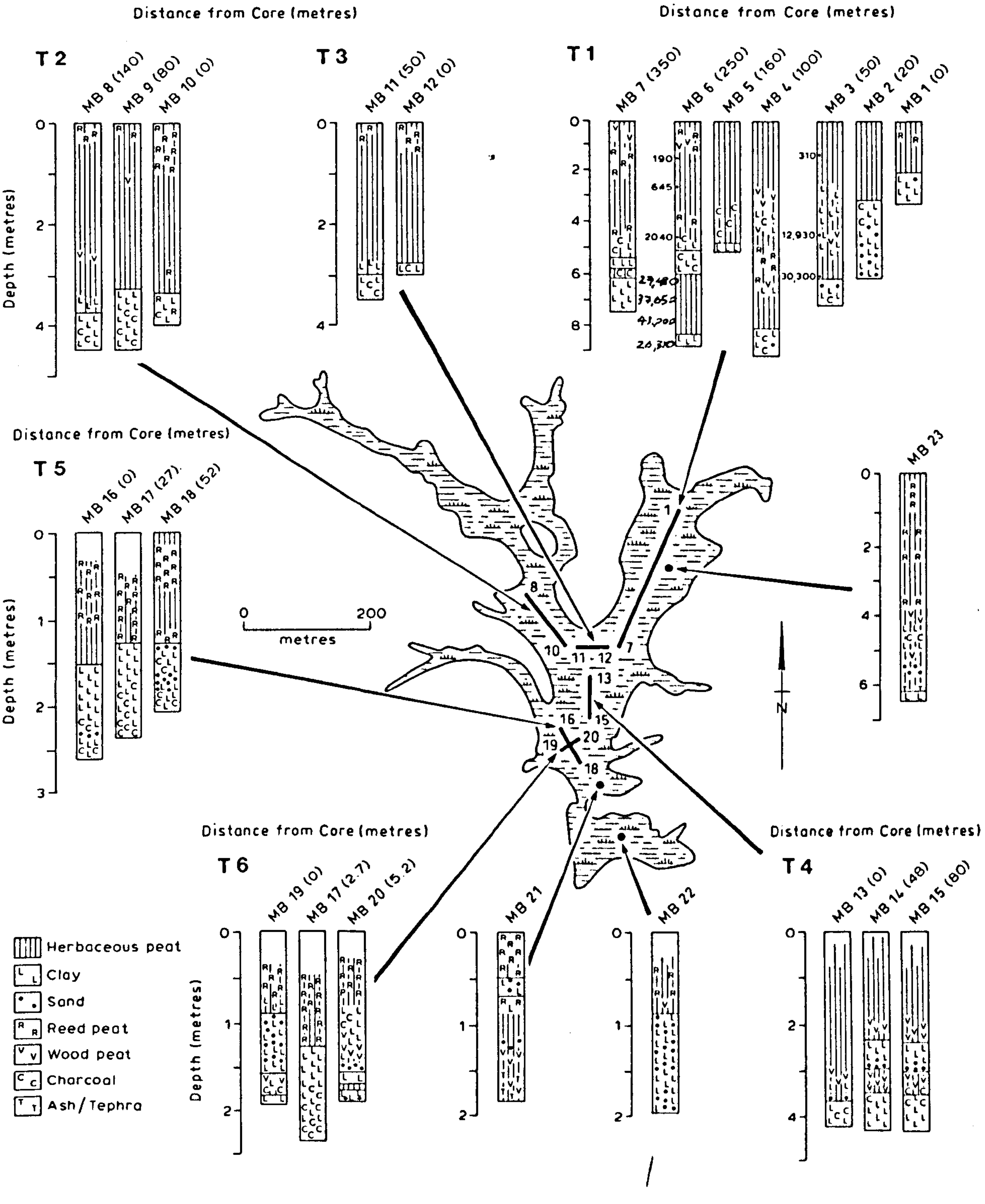
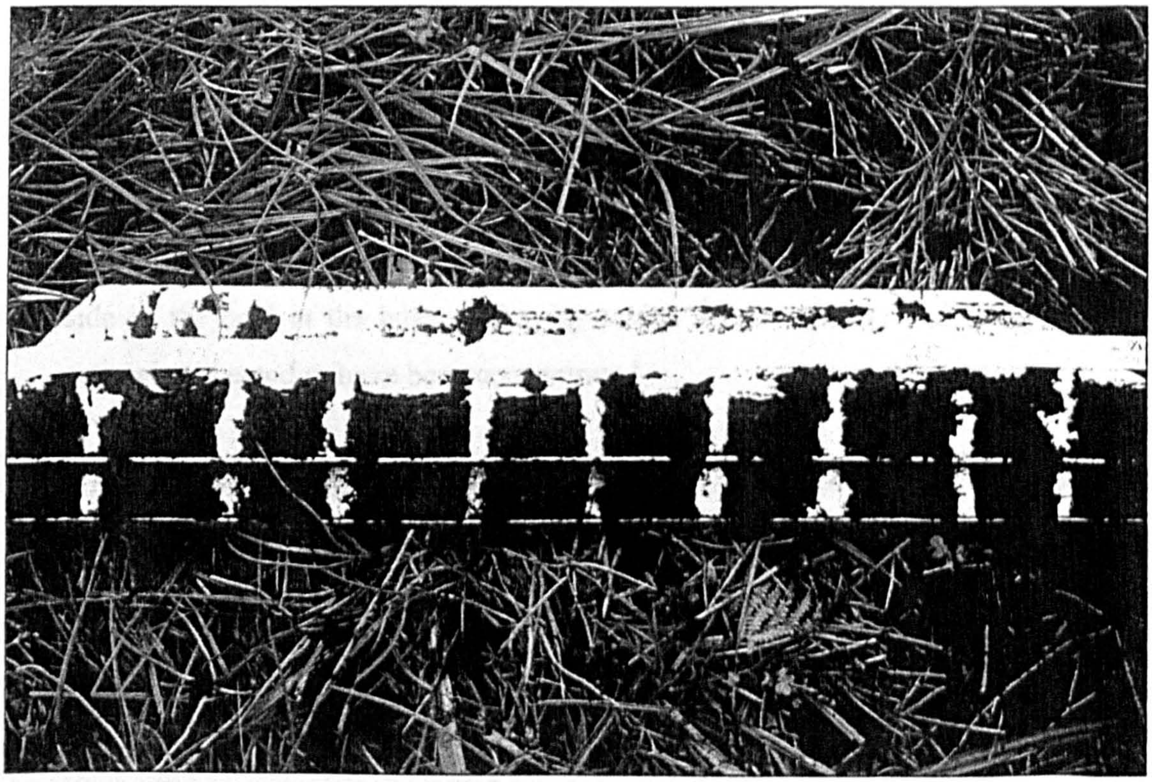


Figure 4.2 Sediment stratigraphy of Mubwindi Swamp

Plate 4.1. Coring at Mubwindi Swamp.

Plate 4.2 Samples taken at 5cm. intervals.



resolution resulted in very small samples being taken. The small size allowed for pollen analysis but did not allow for other analysis of the sediments. All sediment samples for laboratory analysis were collected in a standard manner to reduce the likelihood of differential contamination. The inner-most sediments were collected with a clean spatula and transferred to a bag pre-labelled with sample depth and core number. The sample was then double bagged. Samples for radiocarbon analysis were triple bagged. Samples were freighted back to the University of Hull where they were stored in a cold room at 4 °C.

4.2ii Sediment stratigraphy of Mubwindi Swamp

The stratigraphy from the twenty-three cores is presented in Figure 4.2. The longest cores of sediment (up to 9 m) were taken from the north-eastern arm, along transect 1. The cores from the southern and western parts of Mubwindi Swamp are much shorter than those from the north-east arm. There is a notable decrease in the length of sediment cores, to approximately 2 m south of transect 4. The differences in core length through Mubwindi Swamp are thought to result from a combination of several factors: increased time that sediments have accumulated over, the rate of sediment accumulation, decreased influence of fluvial activity, and the ability of the coring equipment to penetrate relatively solid basal clay sediments. The short, southern sequences are sedimentologically very complex being composed of charcoal, clay, gravel, peat and sand. This stratigraphy is most complex along transects 5 and 6, close to the location of a main river channel. Here the sediments consist of a complicated depositional sequence with bands of sand deposits; these are most apparent in the cores either side of the core at the base of the depression (Core MB 17) where any fluvial action is expected to have been concentrated.

For ease of description, the sediments from Mubwindi Swamp have been divided into four main stratigraphic zones, labelled A to D. Although there are only four major changes in sediment composition identified throughout the Mubwindi Swamp catchment, there is significant within-zone variation. This variation will be highlighted within the text.

A characteristic feature of all the extracted cores, apart from core MB21, was a basal clay horizon, stratigraphic zone A. In the shorter cores, i.e. those from the south and west, the basal clay is thought to be contemporaneous with the mid-core clay deposit (stratigraphic zone C) present in the longer cores. In those cores with two clay-rich horizons the basal deposit forms stratigraphic zones A. Stratigraphic zone A was only recorded in the longest cores from the eastern part of the swamp, along transects 1 and 4. This basal clay varied considerably in length, attaining its greatest length (1.2 m) in core MB7. As the bedrock was not reached on any of the cores, the different lengths of stratigraphic zone A are likely to result from differential penetration by the coring equipment. Stratigraphic zone A also varied in composition. In some of the cores (MB3, MB4, MB13, MB14 and MB15) charcoal was recorded on-site. In other cores (MB3 and MB4), sand particles were recorded on-site.

Overlying the basal clay along transect 1 and 4 is a horizon of herbaceous peat; this forms stratigraphic zone B. A characteristic feature of this zone is that it attains different lengths in different cores - attaining its greatest length in core MB6. Stratigraphic zone B is composed of herbaceous peat along transect 1. Along transect 4 the herbaceous peat is mixed with wood peat. Within stratigraphic zone B two of the cores (MB21 and MB23) record the presence of volcanic material. Unfortunately, the extractions in 1991 and 1992 did not highlight the presence of volcanic material. The use of these volcanic sediments as a stratigraphic, or indeed, a chronological marker, was not possible. The isolated record of volcanic material further indicates the highly variable sedimentary environment at Mubwindi Swamp. The different lengths of stratigraphic zone B indicate the possible presence of an erosional hiatus. The shorter the depth of stratigraphic zone B, the greater the impact of erosion on the sediments. If this relationship holds true there was a relatively longer break at the location of core MB3 in comparison to core MB6.

A feature of the Mubwindi Swamp sediments in the north and east of the basin, particularly in the area along transect 1, is the presence of a second clay rich horizon; this forms stratigraphic zone C. In many of the short cores (i.e. those not from transect 1 and 4) stratigraphic zone C forms the base of the sedimentary record. The rationale for this is that the cores that contain only a single clay-rich horizon, particularly those from the southern part of the swamp, are relatively short. Furthermore the single clay band is at a similar stratigraphic depth to the mid-core clay deposits in the longer sediment cores. The composition of stratigraphic zone C is mainly clay which often contained relatively large amounts of charcoal fragments. In cores MB2, MB20 and MB22 this stratigraphic zone also contains sand. The inclusion of sand in this stratigraphic zone possibly suggest the presence of migrating rivers of some considerable force were responsible for these deposits.

In some of the cores (MB6, MB7, MB14 and MB15) containing a second clay rich horizon, the upper and lower sediment boundaries are very sharp. In others (MB3, MB4, MB13 and MB23) the boundaries are much more gradual. It is possible that sediment hiati are represented by sharp boundaries between clay-rich and organic-rich horizons. Differences in the nature of the boundaries between stratigraphic zones may indicate that sedimentation on the swamp responds differently to changes in the hydrological budget depending on the location of the core on the swamp surface. Cores from the central part of the swamp are generally less responsive than those from a more marginal position.

All the cores contain an uppermost band of herbaceous peat; this forms stratigraphic zone D. Stratigraphic zone D varies both in length and composition throughout Mubwindi Swamp. The maximum depth (495 cm) of stratigraphic zone D is recorded in core MB6. Other cores record a depth of between 450 and 90 cm. In all the cores in the northern part of Mubwindi Swamp, stratigraphic zone D is greater than 200 cm in depth.

The composition of this upper herbaceous peat horizon shows a noticeable variation; it comprises reed peat, wood peat and clay-rich sediments. Reed peat is increasingly common towards the top of the sediment cores, particularly in the southern part of the swamp. This compositional change may result from a recent change in sedimentary conditions, such as a change in the hydrological budget. Alternatively, the reed peat may result from recent sediment deposition, and subsequent low levels of humification.

The cores along transect 1 (Figure 4.2) have the longest, and hence potentially the most complete environmental records, containing all four stratigraphic zones. Subsequent analysis has been concentrated on two of the cores (MB3 and MB6), with supplementary microfossil analysis from core MB23. Due to the core containing the longest stratigraphic zone D, and hence potentially the most complete recent palaeoenvironmental record, the main focus of subsequent analysis is on core MB6.

4.3i Radiocarbon dating: providing a chronology

A chronology for cores MB3 and MB6 is provided by radiocarbon dating. The standard gas counting technique as described in Bradley (1985) was used for some samples (Table 4.1). For small samples, or those with low carbon content, the atomic mass spectroscopy (AMS) technique was used. As this is the first site within the Rukiga highlands to have sediments dated by the AMS technique, a brief introduction to the technique is warranted.

Since the inception of the AMS technique, a range of applications throughout environmental and physical sciences has emerged, the most commonly used being the dating of materials that contain radiocarbon. The first count of radiocarbon using AMS in 1977 (Bennett *et al*, 1977) heralded a revolution in the field of carbon dating. The AMS technique counts atoms of radiocarbon rather than the emitted radiation. For every atom of radiocarbon that decays there are between 10^9 and 10^{12} more radiocarbon atoms remaining in the sample, and therefore a much larger data base is available if the raw sample is examined rather than the tiny part that undergoes Beta transformation during the counting period. The advantages of AMS over the standard gas counting technique are the smaller sample sizes required, the shorter measuring times and greater precision afforded (Grove, 1992). Greater accuracy is also possible: assuming the samples are contaminant free after sampling, the potential for contamination during processing is negligible, as no extraneous carbon needs to be introduced (Beukens, 1992).

4.3ii Sample preparation and treatment

For both the gas counting and AMS dating methods, initial sample preparation involved triple wrapping the sediment samples in silver foil, oven drying and weighing the sediment sample prior to dispatch. Samples were dated at two counting facilities in America; the first was a commercial radiocarbon laboratory - Beta-Analytic, (laboratory notation Beta-). Secondly, the NERC appointed radiocarbon facility was used at Arizona (initial sample preparation being carried out at Kilbride, laboratory notation AA-).

For dating by gas counting, the sample was pre-treated by picking out any rootlets. The raw sample was digested in 2M HCl at 80 ^{0}C for 24 hours to eliminate any carbonates, repeatedly rinsed to neutrality, filtered and dried to a constant weight. Conventional radiometric dating uses the benzene method: samples are converted to benzene, these are then oxidised to CO_2, within a closed system and β-particle emissions determined from aliquots of the resultant radiocarbon CO_2. A date is produced as variations in output voltage are proportional to the rate of β-particle emission, therefore radiocarbon content of the sample.

For the AMS method, the count of radiocarbon atoms present in the samples was achieved using particle accelerators as very sensitive mass spectrometers (Lowe and Walker, 1991). After pre-treatment, the sample is converted to CO_2, and reduced to graphite. The ratio of ^{14}C - ^{13}C in the graphite is measured by small differences in mass between the radiocarbon ^{14}C and ^{13}C components of the sample measured in the accelerator. These differences are used to calculate a radiocarbon age.

4.4i Results and construction of age-depth curves for cores MB3 and MB6

Results from the radiocarbon analysis (Table 4.1) are expressed as yr B.P. (years before AD 1950) using the conventional half life of 5730 +/- 40 years. Results are described for each core with the tabulated results presented as age-depth curves (Figures 4.3 and 4.4). Further refinement of age-depth curves, using evidence from subsequent analytical techniques, is discussed in part 3.

Table 4.1 Radiocarbon results for core MB6 and MB3

(Lab codes with a * are AMS dates)

Lab. Code	Sample depth (cm)	Date (years BP)	δ 13C (%)
AA-12396*	163-167	190 +/- 55	-27.1
AA-12397*	273-277	645 +/- 55	-27.8
AA-12398*	473-477	2110 +/- 55	-26.8
AA-13909*	473-477	1970 +/- 55	-27.2
AA-17153	590-595	27,480 +/-300	-26
Beta-82554	628-635	37,650 +/- 850	-27
AA-17154	683-690	33,150 +/- 620	-21.8
Beta-82553	748-755	>43,000	-25.9
AA-17155	886-894	26,310+/- 340	-27.9

Lab. Code	Sample depth (cm)	Date (years BP)
Beta-61809	170-177	310 +/- 100
Beta-60065	430-443	12,930 +/- 100
Beta-60066	580-588	30,030 +/- 1250

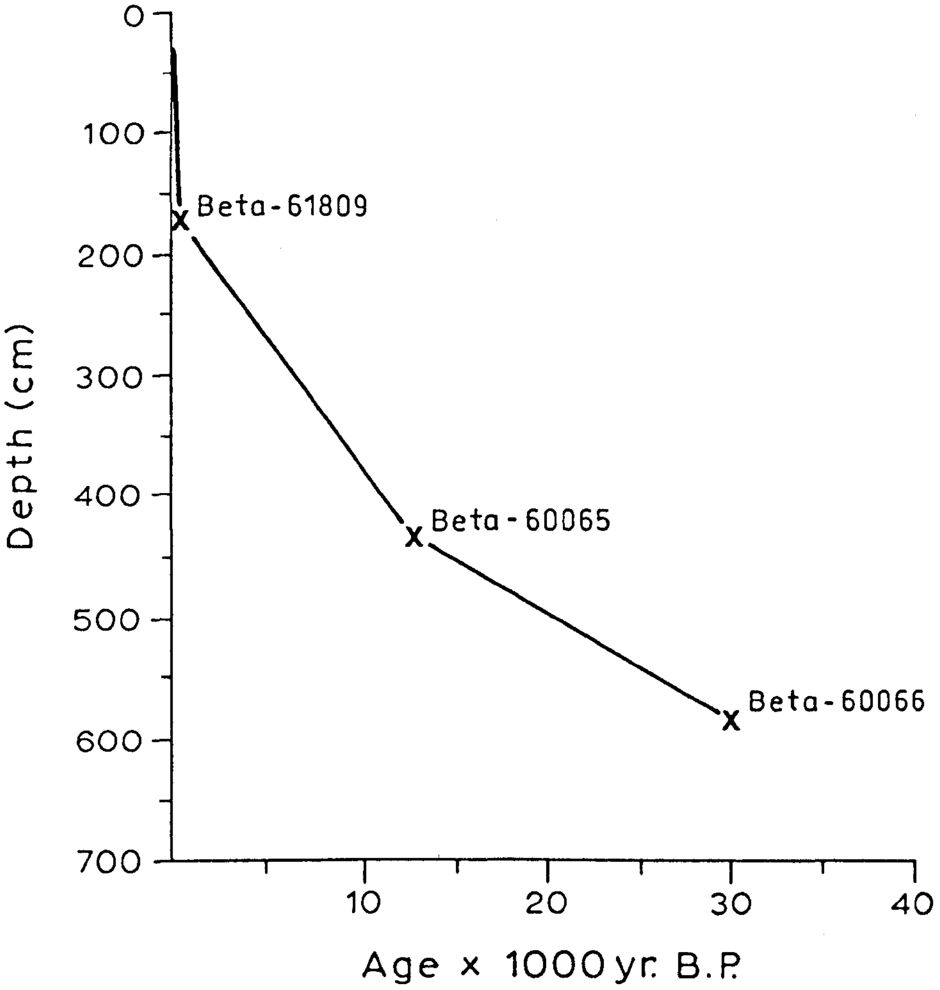


Figure 4.3 Core MB3 age-depth curve

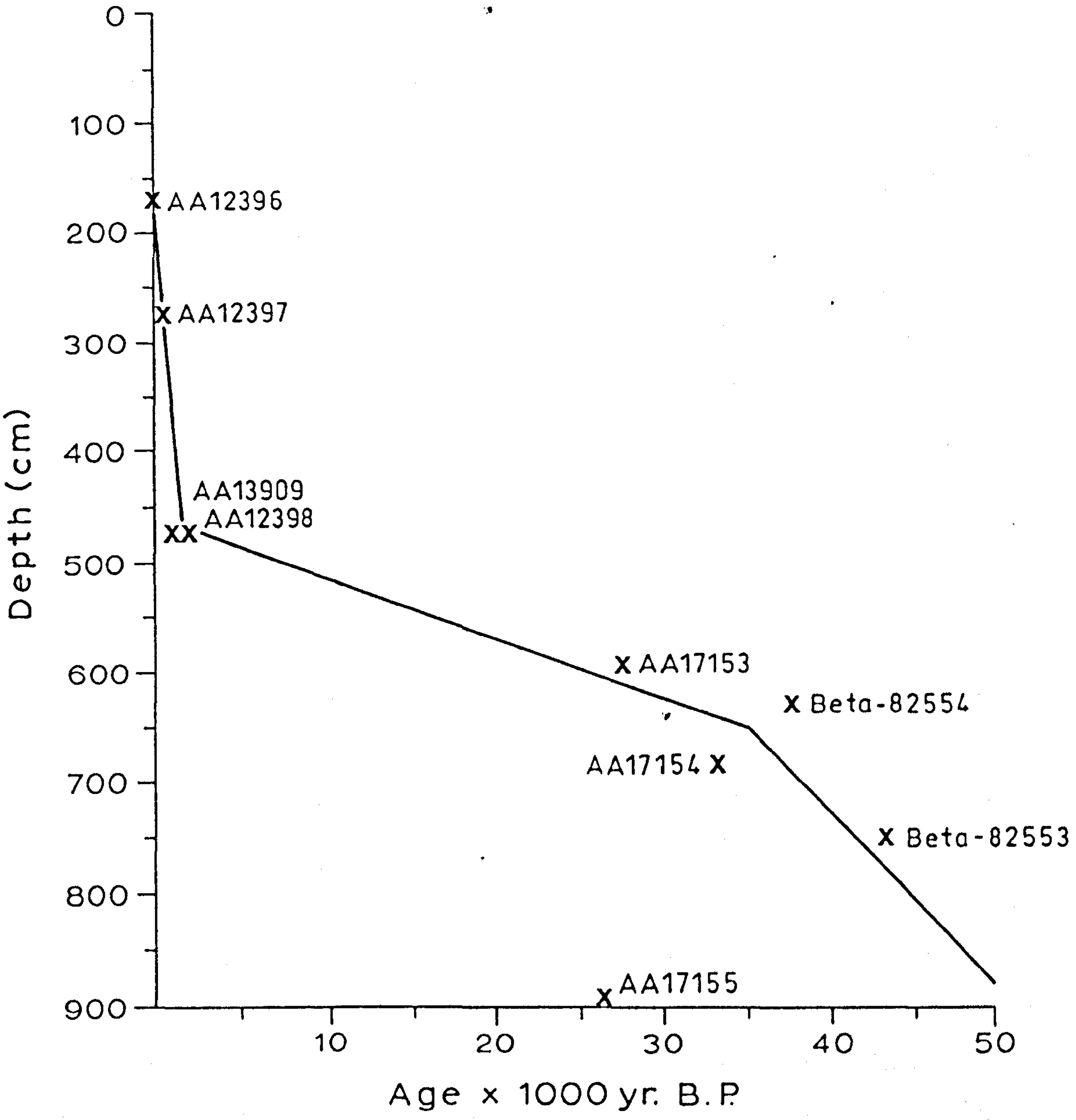


Figure 4.4 Core MB6 age-depth curve

4.4ii Core MB3

Figure 4.3 represents an age-depth curve for core MB3. The radiocarbon dates of 30,030 +/- 1250 yr B.P. for 580 to 588 cm (Beta-60066) and 12,930 +/- 100 yr B.P. (Beta-60065) for 430 to 433 cm indicate the presence of Mubwindi Swamp sediments deposited during the last ice age. Due to the large temporal gap of 17,000 radiocarbon years between these bottom two dates (within only 140 cm of sediment) the presence of at least one hiatus in sedimentation is likely. A second unconformity appears to be represented by the age-depth anomaly between the two dates of 12,930 +/- 100 yr B.P. (Beta-60065) for 430 to 433 cm and the date of 310 +/- 100 yr B.P. for 170 to 177 cm (Beta-61809). The uppermost date of 310 +/- 100 yr B.P. for 170 to 177 cm (Beta-61809) suggests a very high rate of sedimentation during the late Holocene, or some contamination by younger material.

4.4iii Core MB6

Figure 4.4 represents the age-depth curve for MB6, based upon the five standard and four AMS radiocarbon dates. The oldest date obtained (> 43,000 yr B.P., Beta-82553) for 748 to 755 cm indicates that basal sediments in core MB6 may extend back in excess of 50,000 years. However, the basal date of 26,310 +/- 340 yr B.P. for 886 to 894 cm (AA-17155) does not support this. Due to the 'younger than expected' age of the basal date, it is suggested the basal date has been influenced by contamination, either in the initial sample collection or subsequent analysis. This line of reasoning suggests some form of contamination could be applied to the other radiocarbon dates. However, given the outlying position of date AA-17155 from the age-depth curve (Figure 4.4), this contamination is thought to be most pronounced in date AA-17155. Furthermore, on the basis of the tightly grouped nature about the age-depth curve of the three radiocarbon dates of 33,150 +/- 620 yr B.P., 37,650 +/- 850 yr B.P. and 27,480 +/- 200 yr B.P., for 683 to 690, 628 to 635 and 590 to 595 cm respectively, it is suggested the dating of sediments in this part of the core is generally reliable and that the date of >

43,000 yr B.P. (Beta-82553) for 748 to 755 cm is likely to be more accurate than the date of 26,310 +/- 340 yr B.P. for 886 to 894 cm (AA-17155).

The repeat dating counts for 473 to 477 cm were due to a check run by the dating facility, as the results from the first count were considerably 'younger than expected'. The dates of 2110 +/- 55 yr B.P. and 1970 +/- 55 yr B.P. for 473 to 477 cm (AA-12398 and AA-13909 respectively) indicate the presence of at least one sedimentary hiatus between 590 and 477 cm, or during the late last glacial to the late Holocene period, as suggested for core MB3. The fact that similar age-depth anomalies are found in core MB3 and MB6 is perhaps sound evidence that these anomalies represent sedimentary hiati, rather than contamination of radiocarbon-dated samples. According to the four radiocarbon dates available for the uppermost five m of sediment in MB6, sediments have accumulated rapidly during the late Holocene. By applying a linear relationship between each of the samples four different gradients of sediment accumulation rate are recorded for this part of the core. However, sediment accumulation rate is likely to be influenced by the degree of sediment compression. Thus, the sedimentation rate is more likely to be a gradual curvilinear change rather than four individual, linear changes. Figure 4.5 highlights the age-depth curve for core MB6 from 495 cm to 23 cm. The high regression coefficient (R^2 0.99) indicates a very close fit of the best-fit line to the dated samples.

4.5 The significance of $\delta\ ^{13}C$ in radiocarbon samples

Levels of $\delta\ ^{13}C$ are routinely calculated during radiocarbon dating to correct for possible isotopic fractionation. Expression of $\delta\ ^{13}C$ represents the ratio of ^{13}C to ^{12}C, which in air is normally -6.3 ‰ (Colinvaux, 1989). During photosynthesis plants discriminate against the heavier carbon isotopes, ^{14}C and ^{13}C, which are thus found at lower levels in plants than in the ambient atmosphere (Smith and Epstein, 1971). Measurements of $\delta\ ^{13}C$ for different plant taxa show that those plants that initially fix CO_2 into carbon-4 compounds (C-4 types) have $\delta^{13}C$ ratings from -10 to -19 ‰, whilst the more common plants, assimilating 3-carbon compounds (C-3 types) have $\delta\ ^{13}C$ values less than -21 ‰ (Wang *et al*, 1993). Different photosynthetic pathways (C-3 or C-4) tend to be used at different

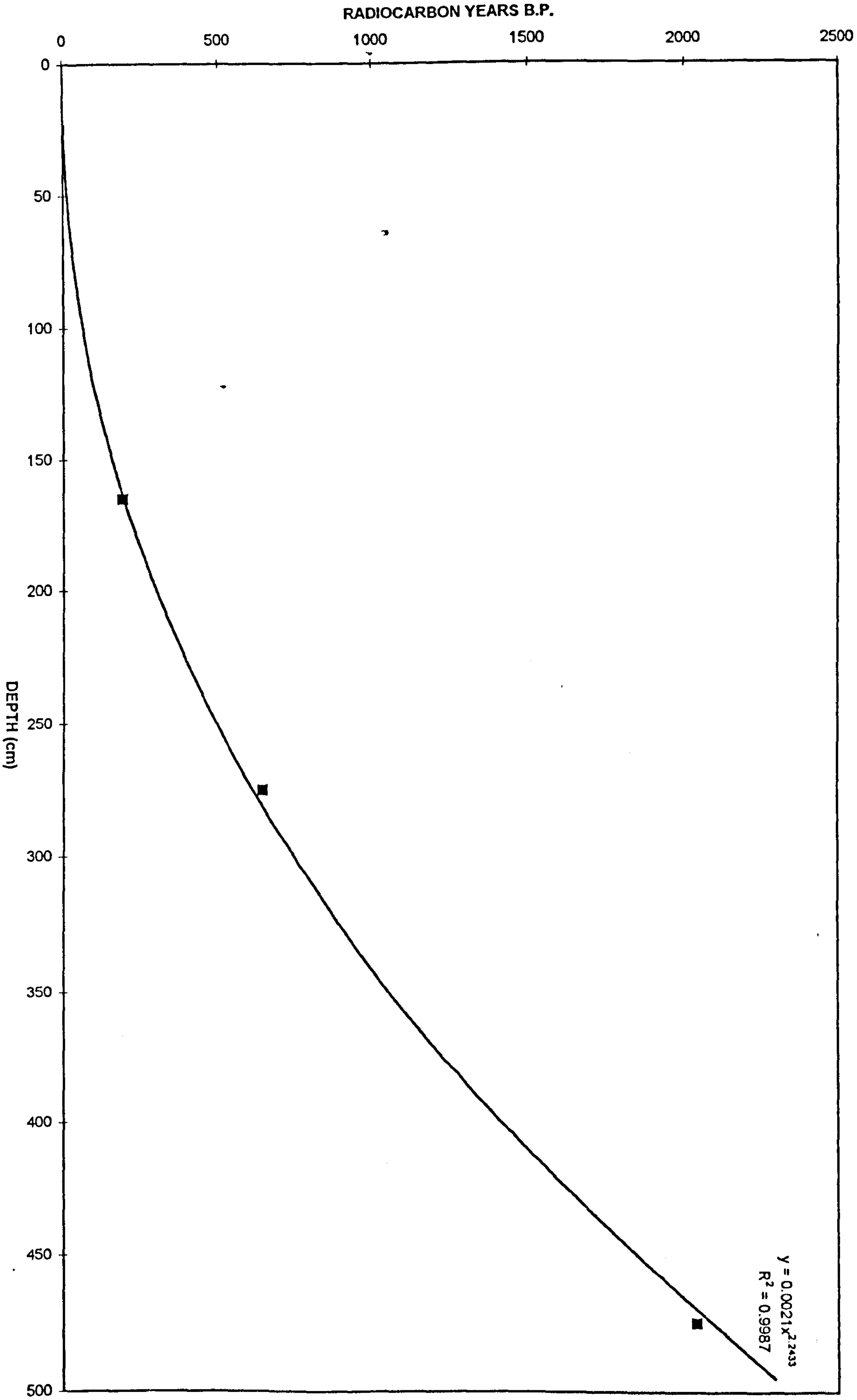


Figure 4.5 Core MB6 age-depth curve for the late Holocene

temperatures, and at different levels of atmospheric CO_2. The C-4 pathway predominates in hot, dry places, or in areas of low CO_2 concentration, whereas the C-3 pathway dominates in environments with opposite temperature, moisture and CO_2 regimes (Colinvaux, 1989). Livingstone and Clayton (1980) showed that for grasses, the relative importance of C-3 or C-4 taxa in the local vegetation depends on altitude and temperature. $\delta\ ^{13}C$ values for preserved plant material thus, potentially, can provide additional palaeoenvironmental information. As a benchmark, $\delta\ ^{13}C$ values less than - 21 ‰ are deemed consistent with a predominantly C-3 carbon source (Aucour *et al*, 1994).

However the relationship between $\delta\ ^{13}C$ values and photosynthetic pathway (and hence environmental conditions) is not simple. Many aquatic taxa, such as algae and submerged higher plants, in which assimilated carbon is often in the form of bicarbonate, yield $\delta\ ^{13}C$ values (Aucour *et al*, 1994) similar to those of C-4 plants. Indeed, $\delta\ ^{13}C$ values published by Smith and Epstein (1971) indicate that algae possess $\delta\ ^{13}C$ values that range between -12 to -23‰. whilst some aquatic monocotyledons, including members of the Potamogetonaceae, have values between -10 and -5.6 ‰. Taxa that fringe Mubwindi Swamp, such as *Syzygium cordatum* and *S. guinense*, have very low values (> -27 %) (Hillaire-Marcel *et al*, 1989).

$\delta\ ^{13}C$ values for samples from core MB6 are shown in Figure 4.6. Unfortunately, the radiocarbon dating from core MB3 was not accompanied by $\delta\ ^{13}C$ values. The consistently low $\delta\ ^{13}C$ values from core MB6 sediments indicate the radiocarbon dates are largely based on debris from swamp plants which followed a C-3-photosynthetic pathway. Indeed, the consistent and low $\delta\ ^{13}C$ values of about -27 ‰ suggests that there has been very little input into the sediment record from C-4 plant sources. There is only one major deviation from this trend, as noted by sample AA-17154. Although this is still less than the -21 ‰ $\delta\ ^{13}C$ benchmark, it highlights a change in the constituent vegetation, such as the incorporation of the remains of aquatic taxa, such as members of the Potamogetonaceae, or even C-4 plants, the most likely examples being C-4 swamp taxa, such as *Papyrus* or *Miscanthus*.

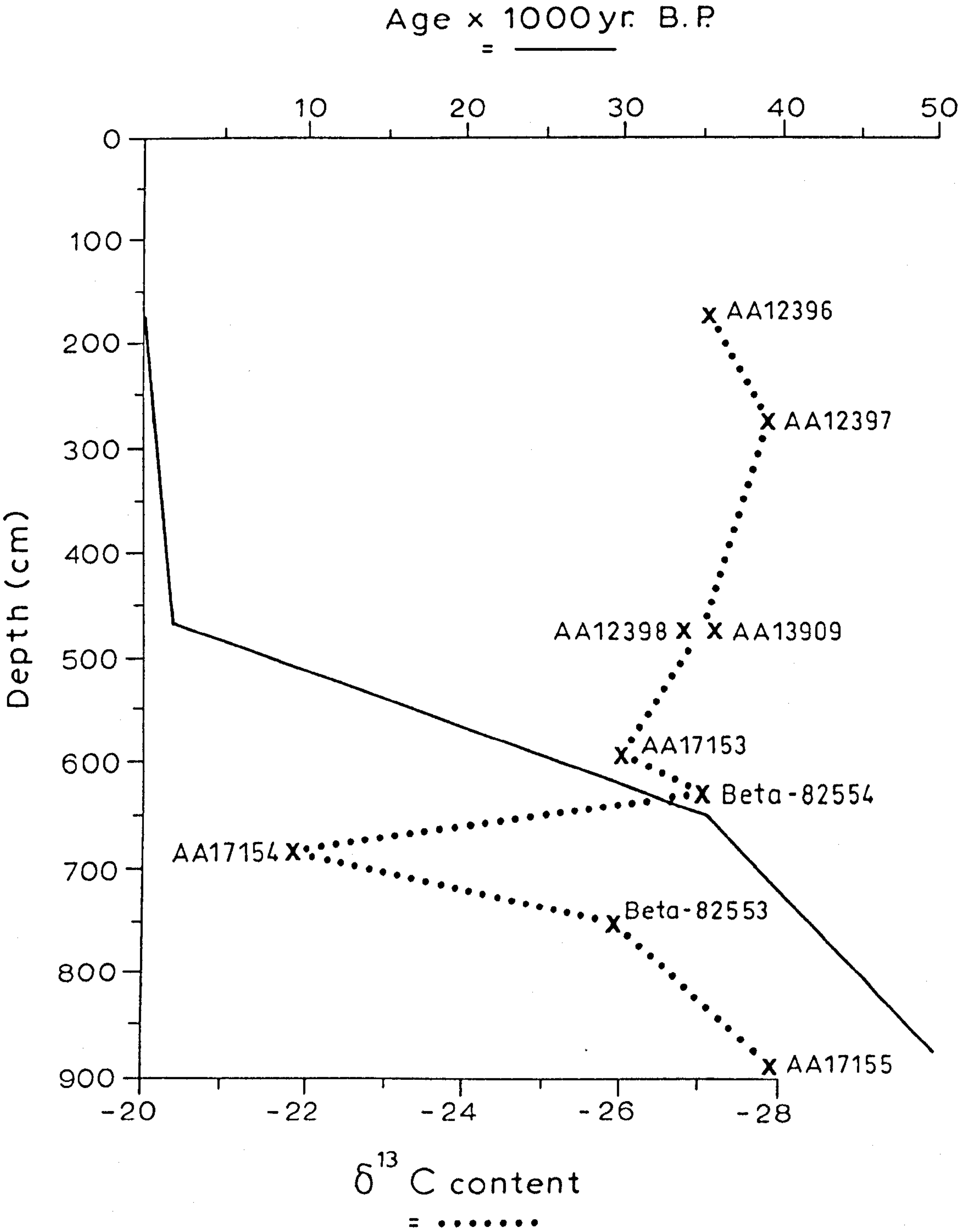


Figure 4.6 Core MB6 δ ^{13}C content with age-depth curve

4.6 Summary of the stratigraphy and radiocarbon control

The composition and age of sediments from Mubwindi Swamp indicate a highly variable sedimentary environment, with a number of sedimentary hiati possible. Four stratigraphic zones are identified within the Mubwindi Swamp sediments. The longest, and most complete sedimentary record is from the north-eastern arm of the swamp, which contains all four stratigraphic zones. The oldest radiocarbon dates indicates that organic-rich sediments began accumulating in the northern part of the Mubwindi Swamp possibly as long as 50,000 years ago. Stratigraphic zones A and B predate the last glacial maximum. Stratigraphic zone C is thought to contain sediments that date from after the last glacial maximum. This stratigraphic zone is thought to be bracketed by sedimentary hiati. Stratigraphic zone D dates to the late Holocene, more precisely approximately the past 2500 years.

Determining the presence and cause of sedimentary hiati can supply useful palaeoenvironmental information. The main causes of sedimentary hiati are either a lack of sediment accumulation, or post-depositional erosion of the sediments (David Thomas; pers. comm.). In the case of Mubwindi Swamp, possible hiati are thought to be of erosional origin, particularly as sediment erosion can be observed at present within the southern part of Mubwindi Swamp. The dating of parts of the core where hiati appear likely supports this suggestion as they occur during periods of significant climatic change. The hydrologically active nature of the present-day drainage on the swamp, and its ability to erode accumulated sediments, can be seen in the southern part of Mubwindi Swamp today, where a confluence streams forms a river of considerable discharge (Section 3.9). The influence of this river on accumulated sediments is further apparent in the stratigraphy of cores taken from this part of the swamp. These contain highly sorted sand deposits. These suggestions will be discussed in more detail in Part 3 within the context of the vegetation reconstruction within the Mubwindi Swamp catchment.

CHAPTER 5

Analysis of sediments from Mubwindi Swamp

5.1 Introduction

Within this chapter, the use of charcoal as an indicator of the history of past fires in and around Mubwindi Swamp is examined. Two methods of charcoal determination were applied to sediment samples from cores MB3 and MB6. For the uppermost sediments of core MB6 (which are also relatively well dated), a further method is applied to determine charcoal areal influx rates. Results from an investigation of particle size distribution of the inorganic fraction are also described for core MB6. Results for both cores are described in relation to loss on ignition (LOI) analysis.

5.2 Charcoal as an indicator of past environmental events

Charcoal is amorphous inorganic carbon produced by the incomplete combustion of organic material in the absence of oxygen, commonly occurs in lake and mire sediments (Taylor, 1988). Charcoal preserved within accumulated sediments can provide a record of past fire occurrence. Indeed, an understanding of burning history is important in evaluating interactions between vegetation, climate and human disturbance (Patterson III *et al*, 1987), and thus can provide a valuable insight into the causes of vegetation dynamics (Hart *et al*, 1996). High charcoal concentrations within accumulated sediments probably represent increased fire frequency, and/or magnitude during the time period represented by the sediments (Winkler, 1985). However, there are many inter-related factors that are ultimately responsible for the amount and type of charcoal present within a sedimentary record (Clark, 1988b). First, the total amount of charcoal produced by a fire will be dependent on many variables, the most important of these are the amount, type, flammability and moisture content of the material being burnt. Local meteorological conditions (especially relative humidity and wind speed), the temperature of burn and amount of O_2 available (Clark, 1983) will also be important. Also, it must be considered that not all of the charcoal will have originated from vegetation within the surrounding catchment; some could be due to post-depositional burning and diagenesis of the sediment itself (Schopf, 1975).

Similarly, the transport of charcoal from source to sink is under control of several factors. Some charcoal is carried directly from the fire as particles in smoke; these may travel vast distances (Clark, 1984). The transport of particulates produced by fires varies greatly, and is dependent on the type and amount of gases and particles produced, the intensity of the fire and the ambient meteorological conditions (Clark, 1983). However, most charcoal will remain on the ground or be attached to standing vegetation (Clark, 1988a), where it can be blown or washed away from the burned area long after the fire event. Charcoal particles may fall directly into streams or be washed in by rainfall. Once within a transporting system they can be eroded, transported and deposited in the same way as other components of the suspended sediment load. Thus, with fluvially transported charcoal particles, the final deposition point will be under the control of the terminal velocity of the transported particle, and the speed and turbulence of the transporting water (Petts and Foster, 1991).

In the case of Mubwindi Swamp, much of the deposited charcoal is likely to have originated from the burning of swamp vegetation. Patterson III, *et al* (1987) recognised that the amount of charcoal produced by localised fires, from a range of localities, can dominate the charcoal record. The importance of local fires as a source of charcoal in swamp sediments in western Uganda has been highlighted by Taylor (1990). To a degree, the origin of charcoal can be deduced from its size: according to Swain (1973), fragment size can be inversely related to the distance from source. However, Clark and Hussey (1996) suggests that the relationship is not so simple, being influenced by the mechanisms of particle transport, catchment hydrology, and the techniques applied to sediments during sample preparation. The sieving of material during preparation for pollen analysis can be particularly important in the removal of large charcoal particles.

Therefore, the amount and characteristics of charcoal deposited will depend as much on the rainfall, soil moisture conditions, stream morphology and sample preparation as on the amount of charcoal initially produced by a fire. The amount of charcoal present in sediments is thus not necessarily directly related to fire frequency, magnitude, or intensity within the catchment. Increased fire occurrence itself can result from a range of external variables, such as increased temperature, decreased precipitation, changes in seasonality, human impact or any combination of the preceding factors. This range of factors responsible for charcoal being incorporated into sediments is present throughout the sedimentary record; it is the frequency, magnitude, or intensity of the events that varies considerably.

Because of the potential problems outlined above, sedimentary charcoal data are best interpreted in conjunction with other forms of evidence of environmental history. Indeed, more information can be gleaned from the sediments if the nature of the charcoal particles, in terms of size characteristics, as well as the overall amount (estimates of area, or proportion of sample weight) is determined. Indeed, the failure to identify charcoal size distribution has been one of the drawbacks of recent trends in charcoal analysis (Patterson III *et al*, 1987; Clark and Hussey, 1996). Combined, a range of information of charcoal weight, area and size characteristics can provide evidence pertaining to the source of the charcoal and/or the mode of transport, thus being able to account for the influences of environmental change outlined above.

5.3i Investigation of charcoal content by surface area

Two methods of areal estimates are applied to the sediments from Mubwindi Swamp. The first method, a point-count estimate after Clark (1982), is quantitative; the second method, a semi-quantitative investigation, has been devised for sediments that do not meet the experimental criteria of the point-count method, specifically the ability to standardise the results against time (radiocarbon dating control).

5.3ii Point count estimate of charcoal area in core MB6

According to Clark (1982), the standard method of concentrating pollen in sediments (Faegri and Iversen, 1989) does not affect either the number, or the area of the charcoal fragments present within a sample. However, it should be emphasised that the preparation technique may alter the size characteristics of the charcoal spectra (Clark, 1984). The standard method of concentrating pollen in a sample involves sieving. Charcoal particles greater than the mesh size of the sieve used are excluded from any subsequent analysis. Also, the mounting of the pollen concentrate in different mounting media may cause differential swelling of the particles (Winkler, 1985). In support of the preparation technique, reactions involved in concentrating pollen in sediments may remove other black particles, such as iron pyrites and insect cuticles, that can be mistaken for charcoal.

One of the major problems in attempting to quantify microscopic charcoal is that of correct identification (Winkler, 1985). In samples there are often jet black, opaque, angular particles which are clearly charcoal, and there are brown, weakly structured particles that are clearly vegetal matter (Patterson III *et al*, 1987). It is the intergrade between these two groups that poses identification problems. There are many different constraints used to ensure only charcoal is counted, the main two being applied here: one, only 'jet black' angular material is counted, and two, the particle should be uniformly opaque (Waddington, 1969).

Point counting is a suitable method for determining charcoal quantity within a sediment sample, as it is easy to use, repeatable and takes a short time to achieve an accurate result of the areal density of charcoal fragments present within a sample (Clark, 1982). The point-count sampling theory is based on work by Glagoleff (1933), who demonstrated that "by applying a number of points (the increments on a graticule) to a plane surface (pollen preparation smeared on the slide), the ratio of the number of points intercepting a particular phase (charcoal fragments), within that plane surface is equal to the areal density of that phase".

The technique involved the smearing of weighed and dried sediment samples, previously prepared for pollen analysis, onto glass slides. During the preparation procedure one tablet (Batch no. 201890) containing 10,850 +/- 200 *Lycopodium* spores was added as exotic markers prior to the concentration reactions. For each sample at least 500 fields of view were counted along transects spaced 2 mm apart. Using an eye-piece graticule (grid), a note was made of the number of points falling on the charcoal fragments in each field of view. In addition, a record was made of the number of fields of view. As a means of standardising the method, only completely charcoal fragments with a long axis greater than 7.5 µm were tallied. Where the particles did not lie within the same plane as the graticule this was rotated to gain an accurate measurement. A record was kept of the number of *Lycopodium* spores, occurring within each field of view. To minimise the problems of differential swelling of charcoal particles, the time the samples were stored in silicone oil prior to counting was kept to a minimum.

By multiplying the area of charcoal on the slide by the ratio of the spores added : spores counted, it was possible to estimated the total amount of charcoal in the sample prepared. The stages in the estimation of charcoal surface area per sample, using the point-count method, are as follows:

1: Calculate the probability (P) of a random point falling on charcoal fragments:

$P = C/N$, where
C = number of points falling on charcoal
N = total number of points applied

2: Calculate the area of charcoal (A) occurring in the fields of view:

$A = P\,(N_{FW} * A_{FW})$, where
N_{FW} = number of fields of view
A_{FW} = area of field of view

3: Calculate the standard deviation (S_A) of A

$$S_A = (N_{FW}\,A_{FW}) * \sqrt{\,}\,(P\,(1 - P)\,/\,N)$$

4: Calculate the 95 % confidence limits (cl)

$$cl = (2\,(S_A))$$

5: Calculate the area of charcoal (A_C) per unit weight of sediment

$$A_C \quad = (A * M)\,/\,(M_P * W)$$

M = number of exotic grains added

Mp = number of exotic grains counted

W = dry weight of material used

6: Estimate the annual influx of charcoal

$A_I = A_C / T$

A_I = Estimated annual influx of charcoal to the sediment

T = Number of years incorporated within the sediment sample

As a result of the small sediment sample sizes there was not enough material to replicate the counts, thus stages 3 and 4 were omitted. Due to the complex age-depth relationship, as described in Chapter 4, this method can only be applied to sediments from the upper herbaceous peat horizon of core MB6. In these sediments there is sequential dating, and the unlikely presence of sedimentary hiati.

Using the curve fitted to the radiocarbon dates from the upper herbaceous peat horizon of core MB6 (Figure 4.5), the mid-depth of each sample used for charcoal analysis was used to calculate the sediment accumulation rate during the time represented by the sediment sample.

The results from the point-count method for the sediments between 473 and 23 cm in core MB6 are presented in Figure 5.1. In minerotrophic swamps, such as Mubwindi, the bulk of the inorganic fraction will be water-borne. Other types of allochthonous material will also be incorporated into the sedimentary record in this way, including charcoal. Hence, changes in sedimentary environment, such as caused by sediment focusing, channelling of water, or indeed any changes in the hydrological budget, could affect the amount of charcoal being deposited, irrespective of changes in burning regime (Taylor, 1988). Thus, expression of charcoal percentage present is likely to be influenced by fluctuating amounts of organic and inorganic matter content. As the amount of charcoal present within the sediments is likely to fluctuate with the amount of inorganic sediment, the

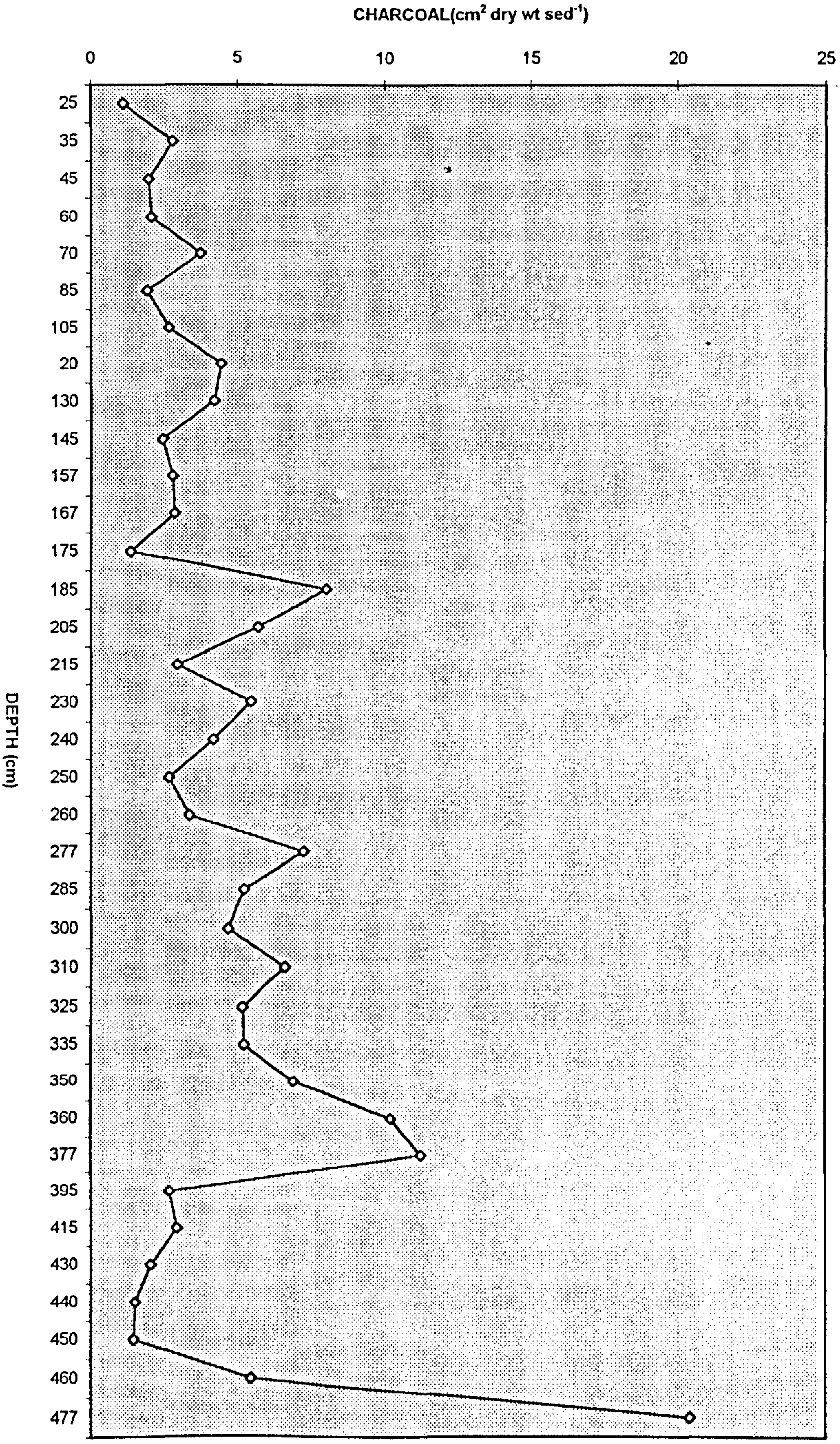


Figure 5.1 Point count results for stratigraphic zone D in core MB6

charcoal areal data was standardised against inorganic sediment content (Figure 5.2). These results were then transformed to give a measurement of the influx of charcoal per year (Figure 5.3).

5.3iii Assessment of charcoal particle-size distribution in core MB6

The point-count method of Clark (1982) can only be applied to the sediments where the sediment volume, and time-frame represented by the sediment samples can be standardised. Due to the inconsistent dating control for the Mubwindi Swamp sediments (Chapter 4), in all but the uppermost herbaceous peat horizon from core MB6 (473 to 23 cm), this method could not be applied to sediments from the remainder of core MB6, or other cores of sediment collected. However, when counting charcoal area, the importance of size class is not made specific. Although larger particles are recorded by more points within the point-count method, the differentiation between a number of small fragments and a single large fragment is not recorded. Large and small fragments are likely to have been derived from non-local and local sources respectively. Charcoal within the sediment sub-samples from cores MB3 and MB6 will be described according to the charcoal particle size distribution.

Size class distributions can be determined from the areal measurements of individual particles or, more rapidly by measuring the maximum dimension of each particle when counting charcoal particles (Clark, 1984). The majority of the size classes used for this study (5 μm to 12.5 μm, 12.5 μm to 25 μm, 25 μm to 37.5 μm, 37.5 μm to 50 μm, 50 μm to 62.5 μm, 62.5 μm to 75 μm and 75 μm to 125 μm) fit the scale on the calibrated graticule. The size limits of the lower and upper size classes were set so as the exclude very small fragments (<5 μm), and incorporate the few large particles that had passed though a 125 μm sieve, respectively. Samples were prepared in the same manner as for the point-count method. The number of charcoal particles recorded falling into the size classes outlined were recorded within at least 500 fields of view.

The results from the charcoal fragment particle size distribution from cores MB3 and MB6 are portrayed as fluctuations in charcoal particle size against sample

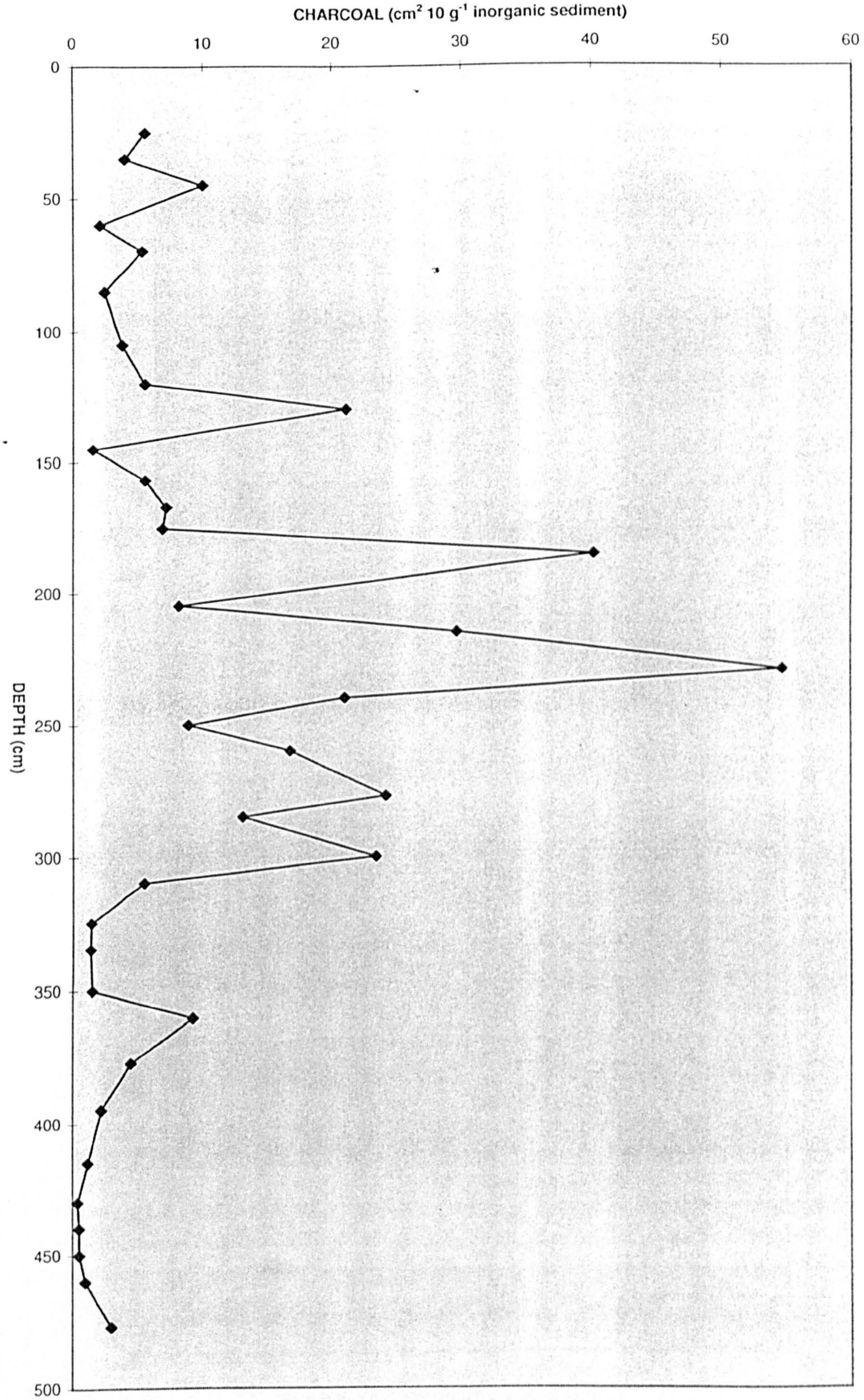


Figure 5.2 Point count results standardised against inorganic sediment for stratigraphic zone D in core MB6

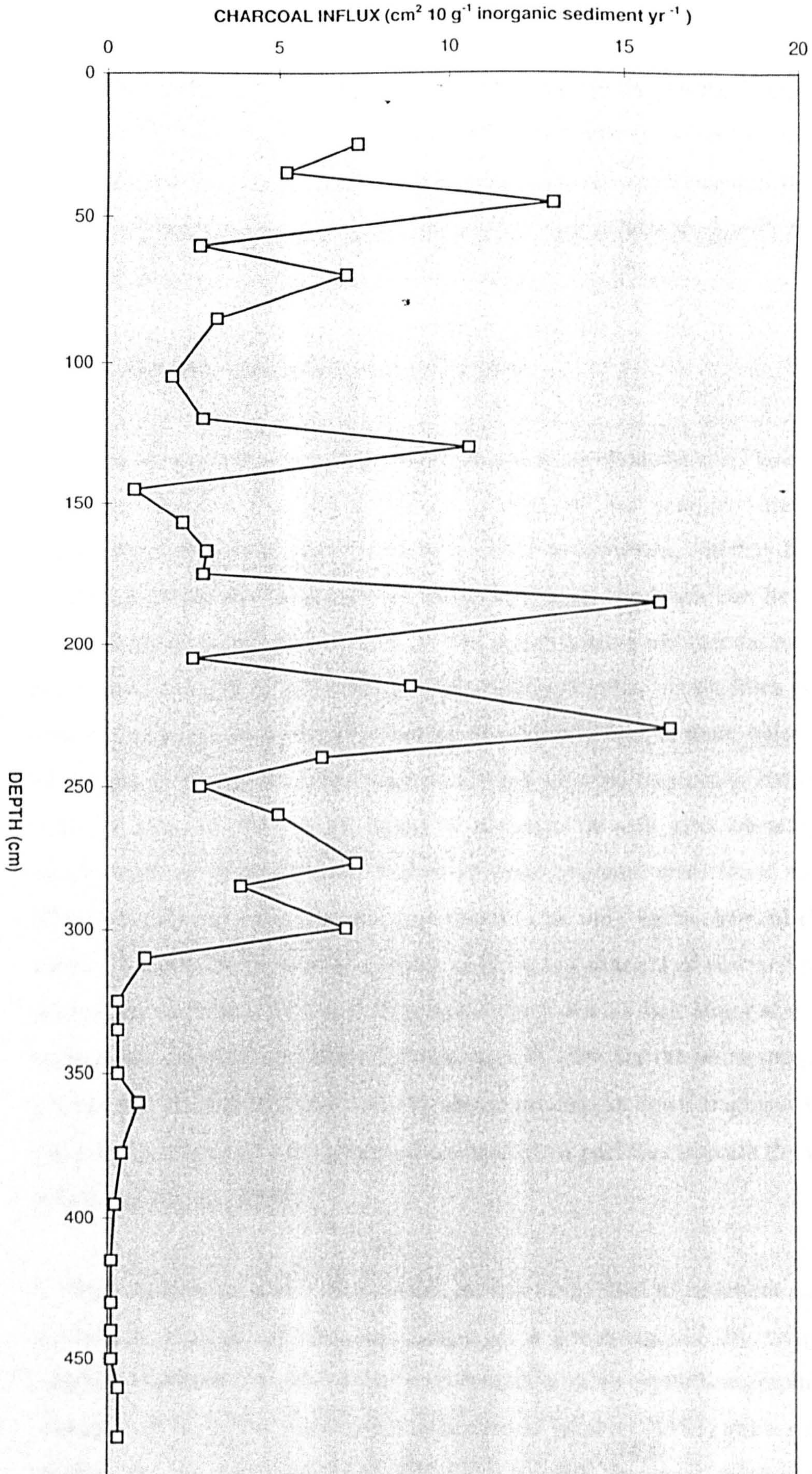


Figure 5.3 Point count influx rates for stratigraphic zone D in core MB6

depth. The scale on the X-axis is number of charcoal fragments recorded within fifty fields of view. Figure 5.4 depicts the spread of charcoal size-class distribution down-core for core MB3. Figure 5.5. shows the down-core charcoal distribution within sediments from core MB6. These results will be described and compared in Section 5.7.

5.4 Investigation of charcoal content by mass

Although the point-count method is considered to be quantitative (Clark, 1984), it does not measure the actual carbon content of the samples. Because the relationship between observed and actual carbon is unknown, and may be variable for different deposits (Patterson III *et al*, 1987), an argument can be made for determining elemental carbon directly. The quantification of charcoal by chemical assay has a number of advantages over visual estimates. Apart from being less time-consuming, measuring charcoal as elemental carbon is more objective as it avoids the problems of correct identification of charred fragments. Indeed, many types of charcoal have been found to decrease in size after burning due to development of charcoal skins. Pieces of wood charcoal were found to be only 30% charcoal, and bone charcoal was found to be only 16 % charcoal (Winkler, 1985). This potentially erroneous assay of the actual amount of charcoal present is particularly important for larger fragments, which due to their larger size are more likely to develop charcoal skins. Another area of error for the point-count method is that areal estimates of charcoal abundance assume an equal fragment thickness and may be affected by the preferred orientation of particles beneath the coverslip (Clark and Hussey, 1996)

A relatively simple, gravimetric technique can be applied to sediment samples to provide an estimate of charcoal content as a percentage of dry weight. This technique measures the amount of 'acid-insoluble micro crystalline graphite' (inert elemental carbon). The gravimetric technique of Winkler (1985) utilises the entire sample, is not influenced by different charcoal fragment thickness or by preferential orientation of the charcoal fragments under the cover-slip, or by differential swelling of the particles. However, Winkler's (1985) method does not provide additional information on the charcoal particle size or area, and thus any

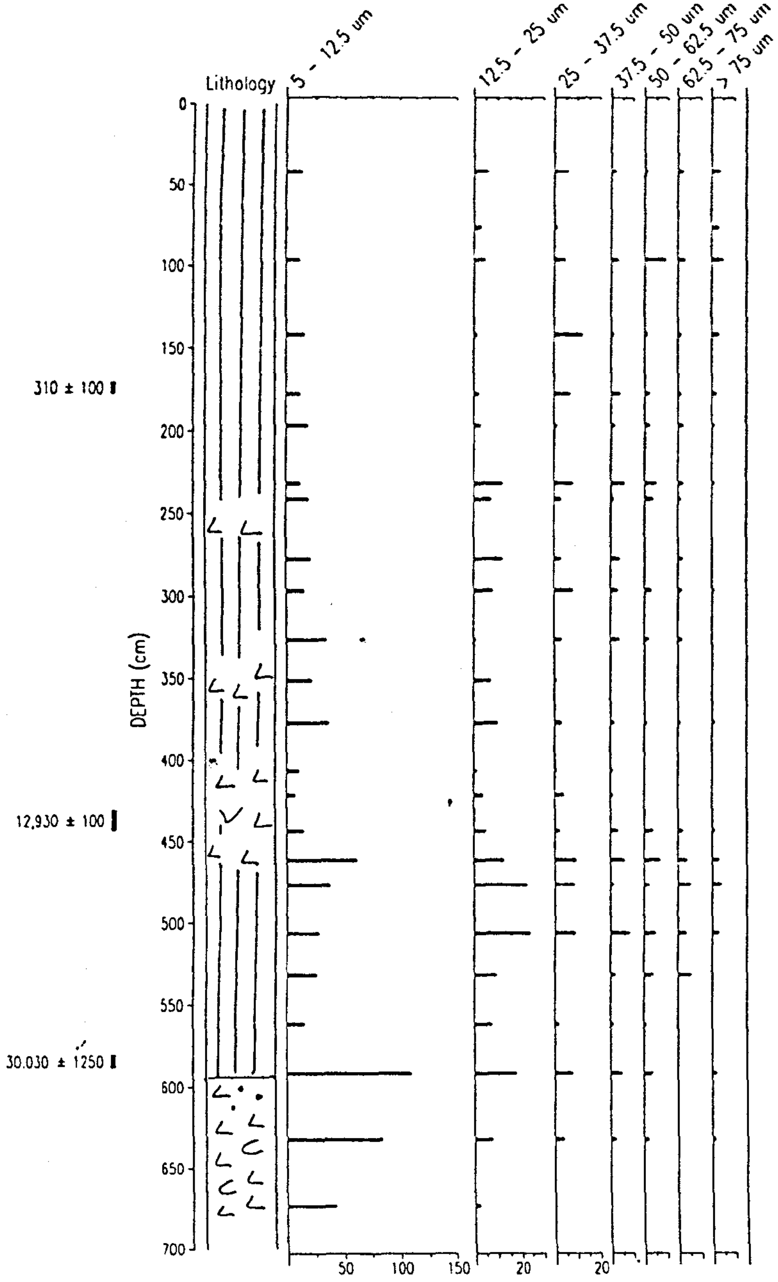


Figure 5.4 Core MB3: charcoal particle size distribution down-core

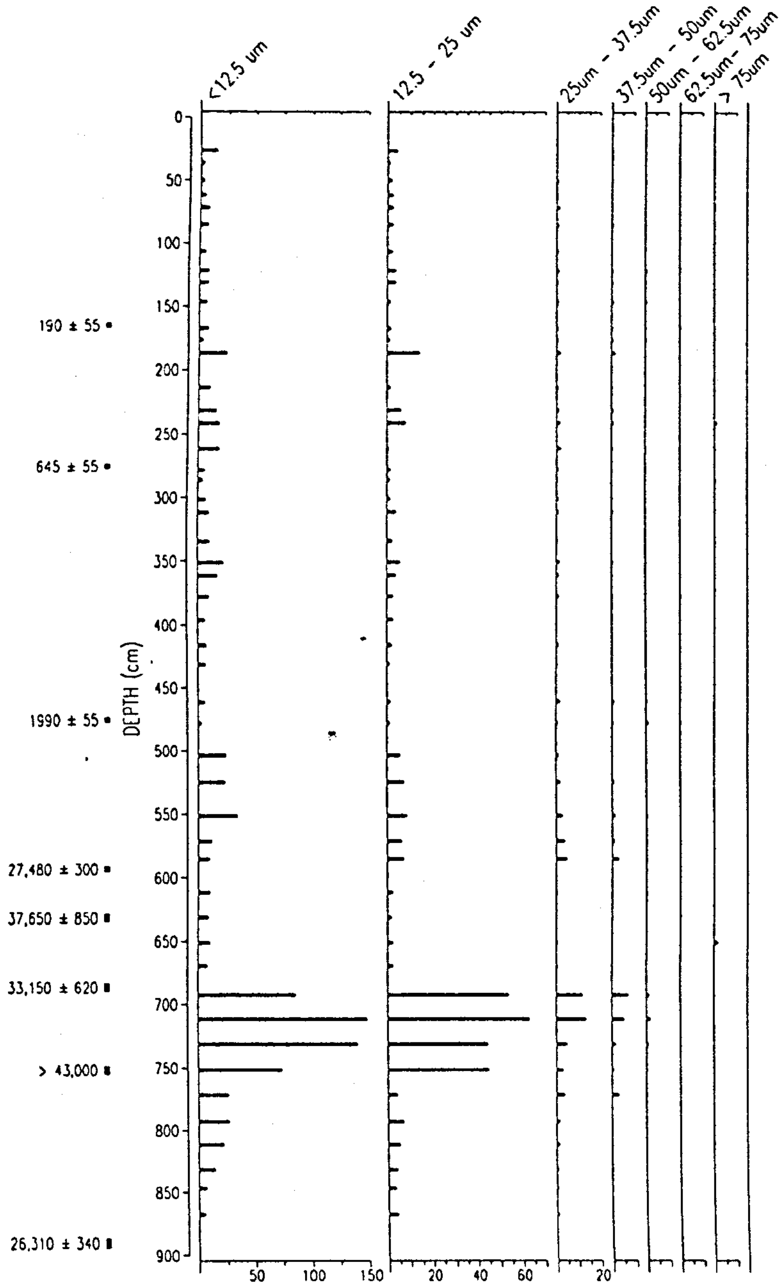


Figure 5.5 Core MB6: charcoal particle size distribution down-core

potential indication of the origin of the charcoal, both of which are likely to be of palaeoenvironmental significance.

Although there were slight modifications to reaction times the technique follows that of Winkler (1985) as outlined below. Microscopic examination at the end of the nitric acid treatment (charcoal present in the samples) and again after the ignition (charcoal not present in the samples) corroborated the expected content of the end products of each stage.

1. 1 cm^3 of wet sediment was dried at 90 ^{o}C, cooled in a desiccator and then weighed (DW).
2. 5 ml of concentrated Nitric acid was added to the samples in labelled test-tubes. This stage removed all organic material, carbonates and pyrite.
3. The samples were placed in a hot water bath for 3 hours.
4. The samples were washed with distilled water, centrifuged at 2500 rpm and the supernatant decanted. This stage was repeated until the supernatant was clear.
5. The samples were transferred to crucibles and dried over-night in an oven at 60 ^{0}C.
6. The samples were placed in a desiccator until cool and weighed (NW).
7. The samples were ignited at 480 ^{0}C for 3 hours to remove the remaining charcoal.
8. The samples were placed in a desiccator until cool and weighed (IW).

Charcoal was calculated as a percentage of the dry weight of the sample using the following equation:

$$\% \text{ charcoal} = \frac{(NW - IW) * 100}{DW}$$

Results from the analysis are portrayed as percentage of charcoal of the dry sediment weight for cores MB3 and MB6 (Figure 5.6). As with the point-count method, variations between samples in the amount of inorganic matter is likely to

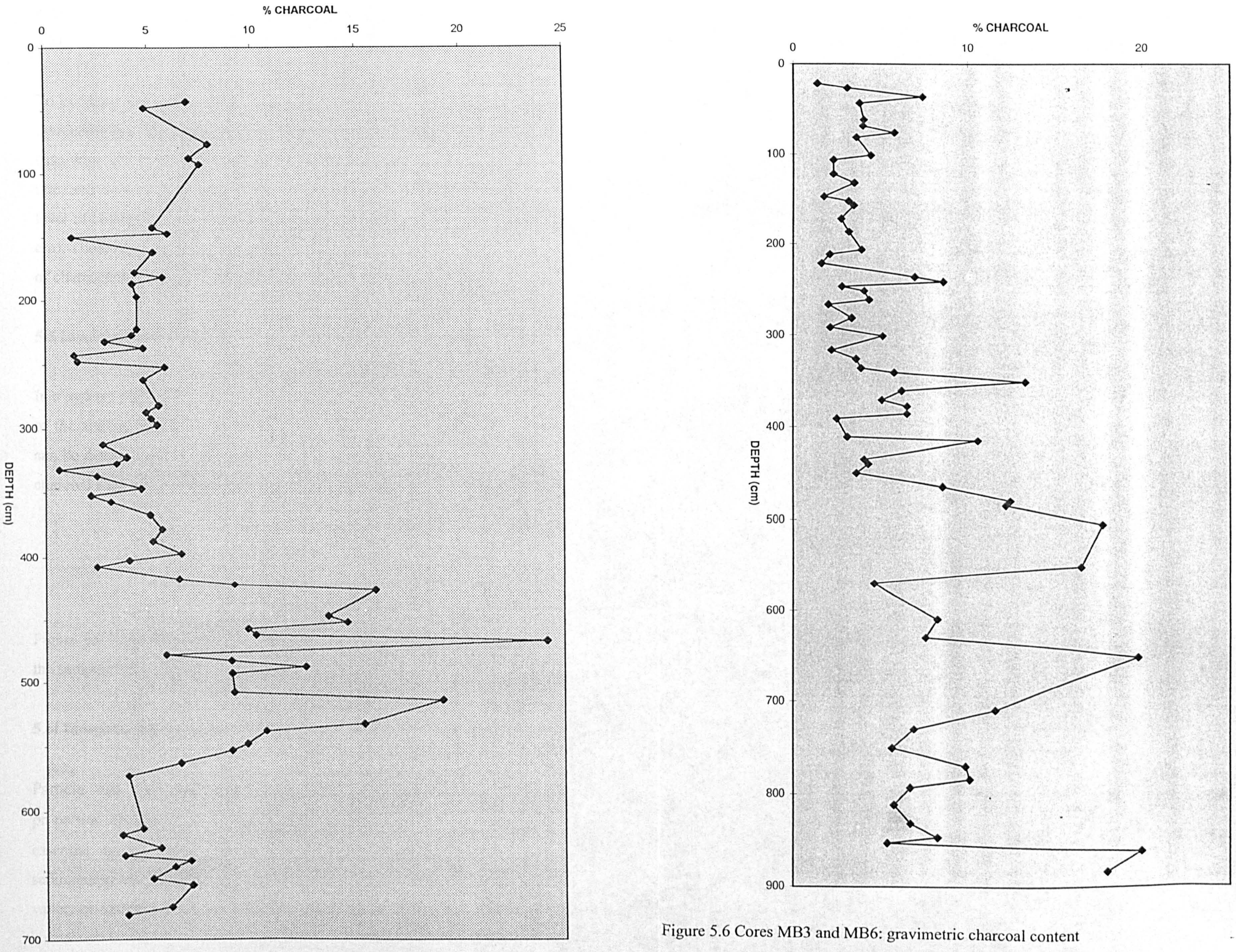


Figure 5.6 Cores MB3 and MB6: gravimetric charcoal content

influence the level of charcoal, when expressed as a percentage of dry weight. Hence, results for cores MB3 and MB6 have been standardised to account for between sample differences in the proportion of inorganic matter. These results are expressed as unit weight of charcoal unit weight of inorganic matter^{-1} (Figure 5.7).

To express the amount of charcoal present in influx terms the results have been divided by the number of years incorporated by the sediment samples. As was the case with the point-count method, this approach requires a known sedimentation rate, and hence a high degree of dating control. As described in Chapter 4, this level of control is only available for stratigraphic zone D of core MB6 (477 to 23 cm). These late Holocene sediments have the charcoal content expressed as weight of charcoal unit weight of inorganic matter^{-1} yr $^{-1}$ (Figure 5.8).

5.5 Investigation of loss on ignition

In a swamp environment the organic matter-inorganic matter ratio is an indicator of the amount of allochthonous sediment input into the swamp basin. This ratio can be determined by LOI. LOI can be computed from the Winkler technique for charcoal determination (Section 5.4) by the following equation.

$$\%\text{ organic matter} = \frac{(DW - NW) * 100}{DW}$$

Figure 5.9 illustrates variations in the ratio of inorganic and organic fractions in the samples from, respectively, cores MB3 and MB6.

5.6i Inorganic sediment particle size as an indicator of past environments

Particle size, and particle-size distribution are amongst the basic physical properties of inorganic sediments. The determination of these parameters is essential in any attempt to characterise inorganic sediments. Changes in sedimentary environment, such as caused by sediment focusing, channelling of water, or variations in the hydrological budget, could influence the amount and

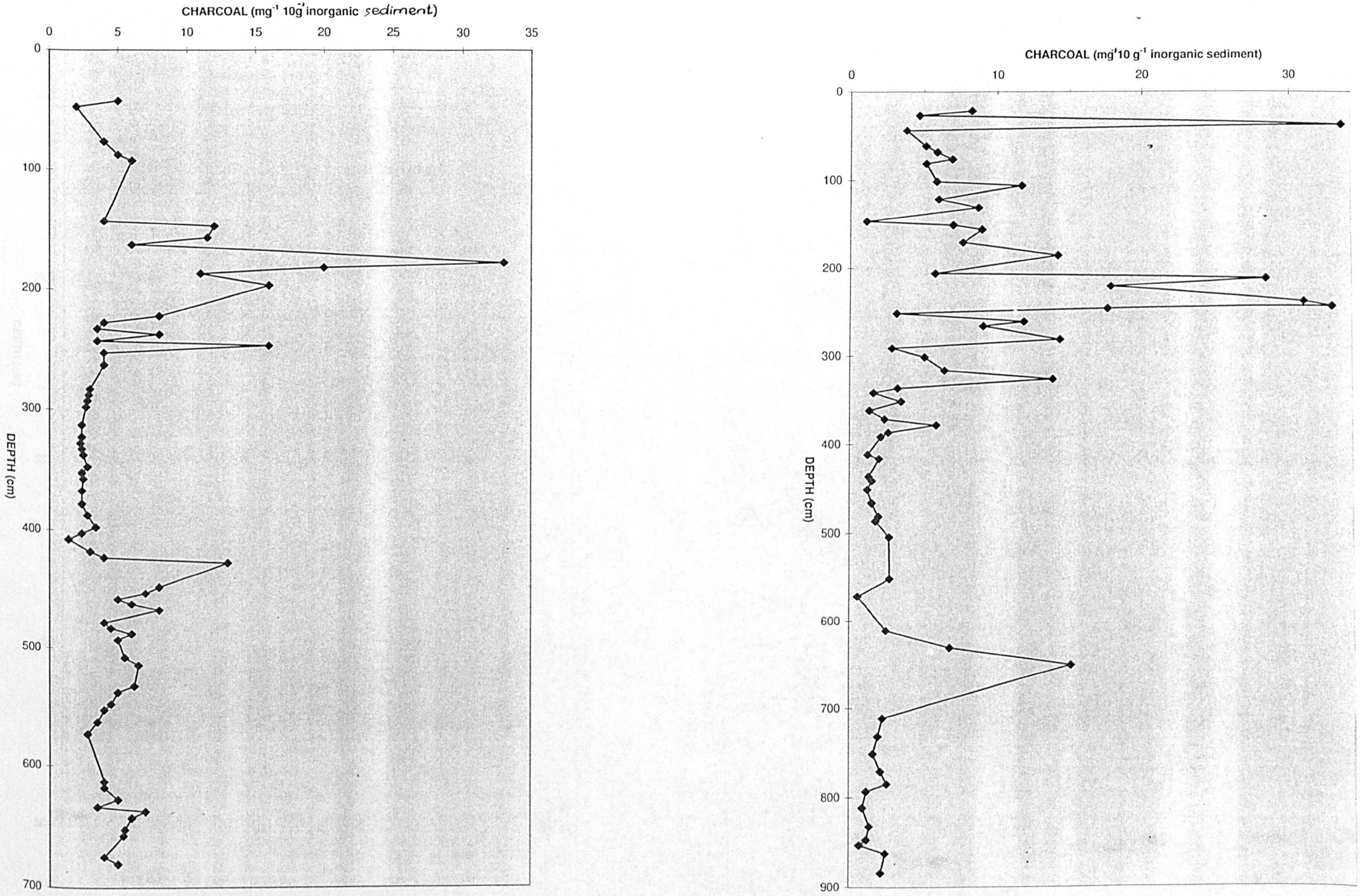


Figure 5.7 Cores MB3 and MB6: gravimetric charcoal content standardised against inorganic matter content

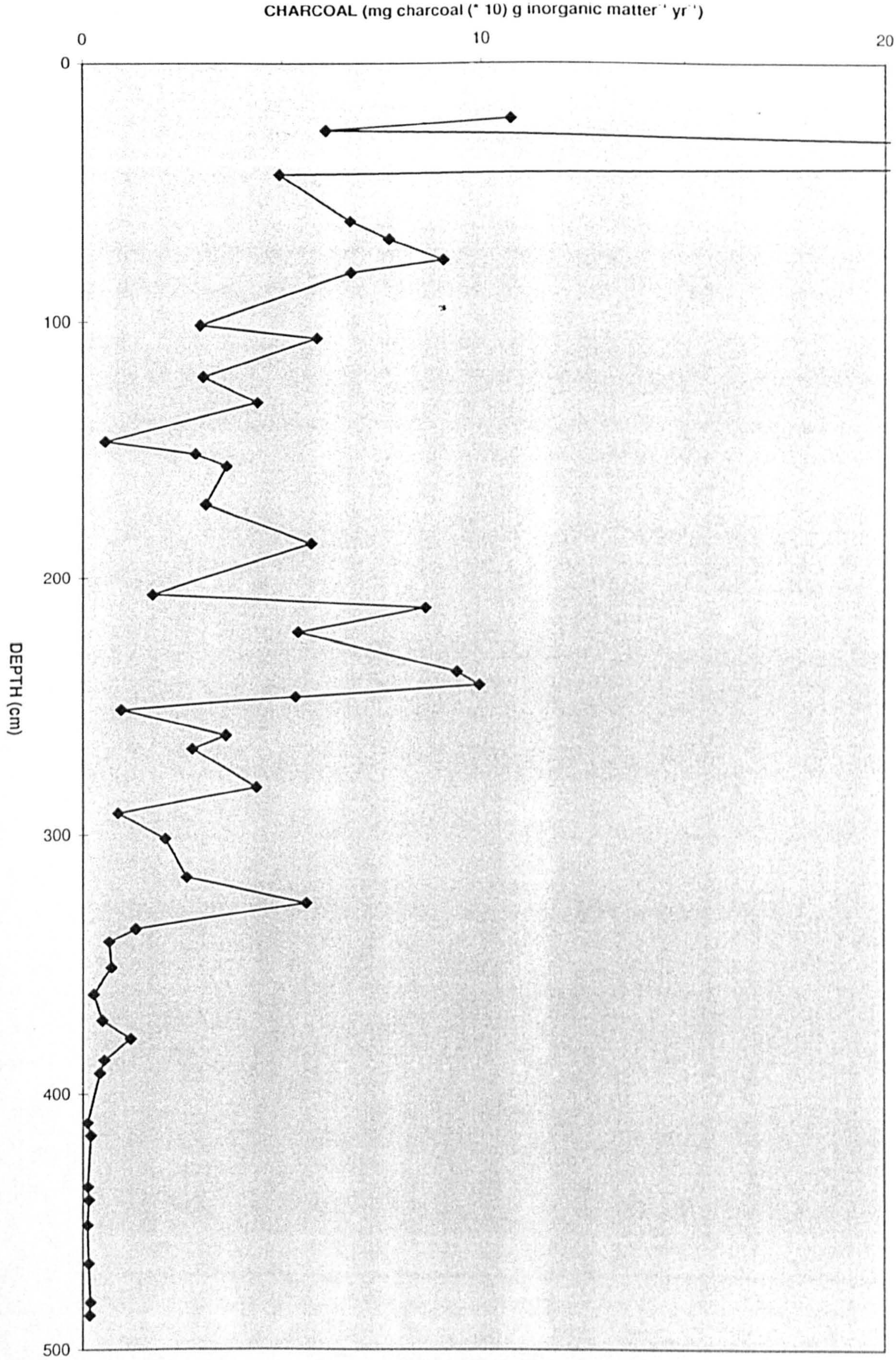
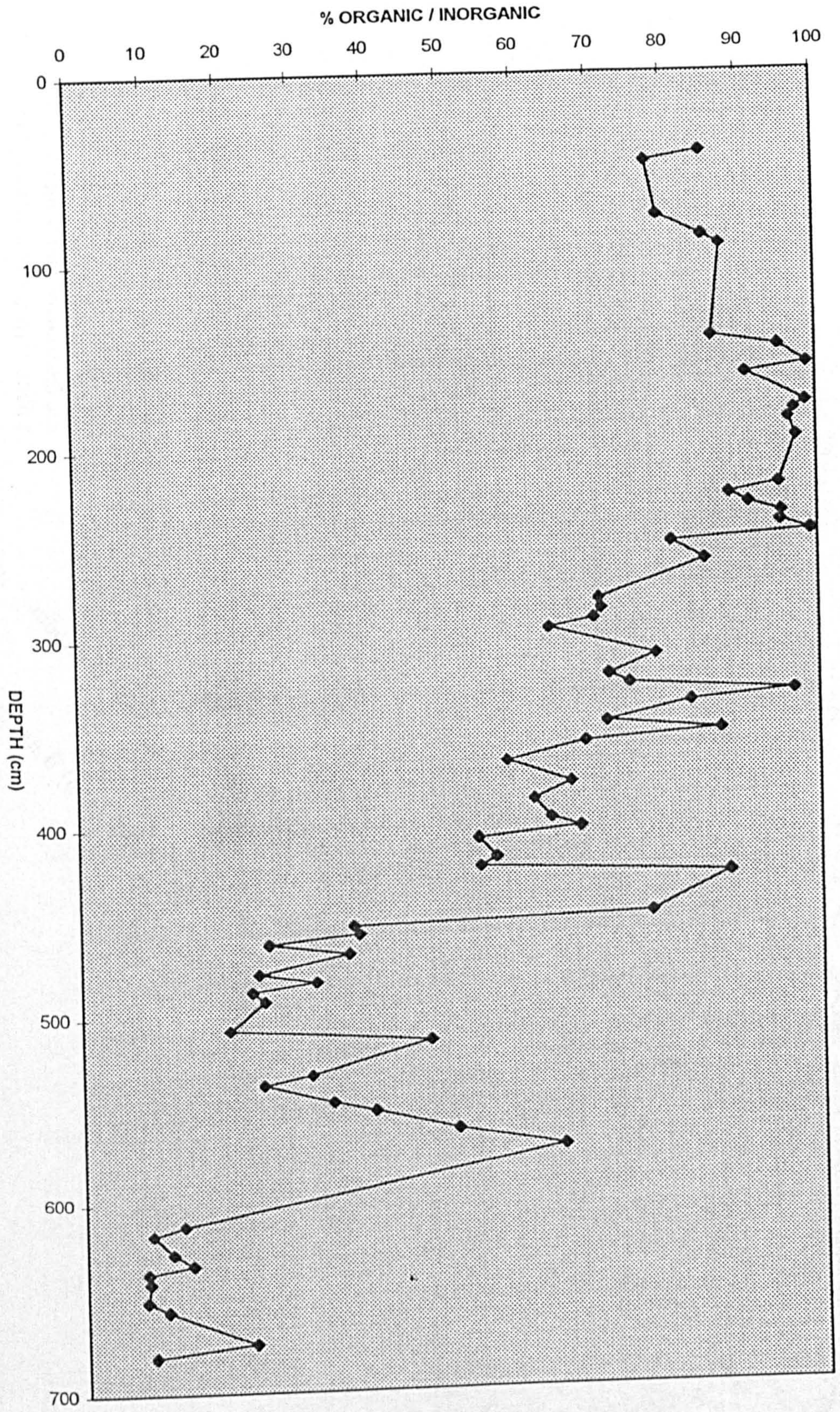


Figure 5.8 Core MB6: gravimetric charcoal content standardised against inorganic matter content and time



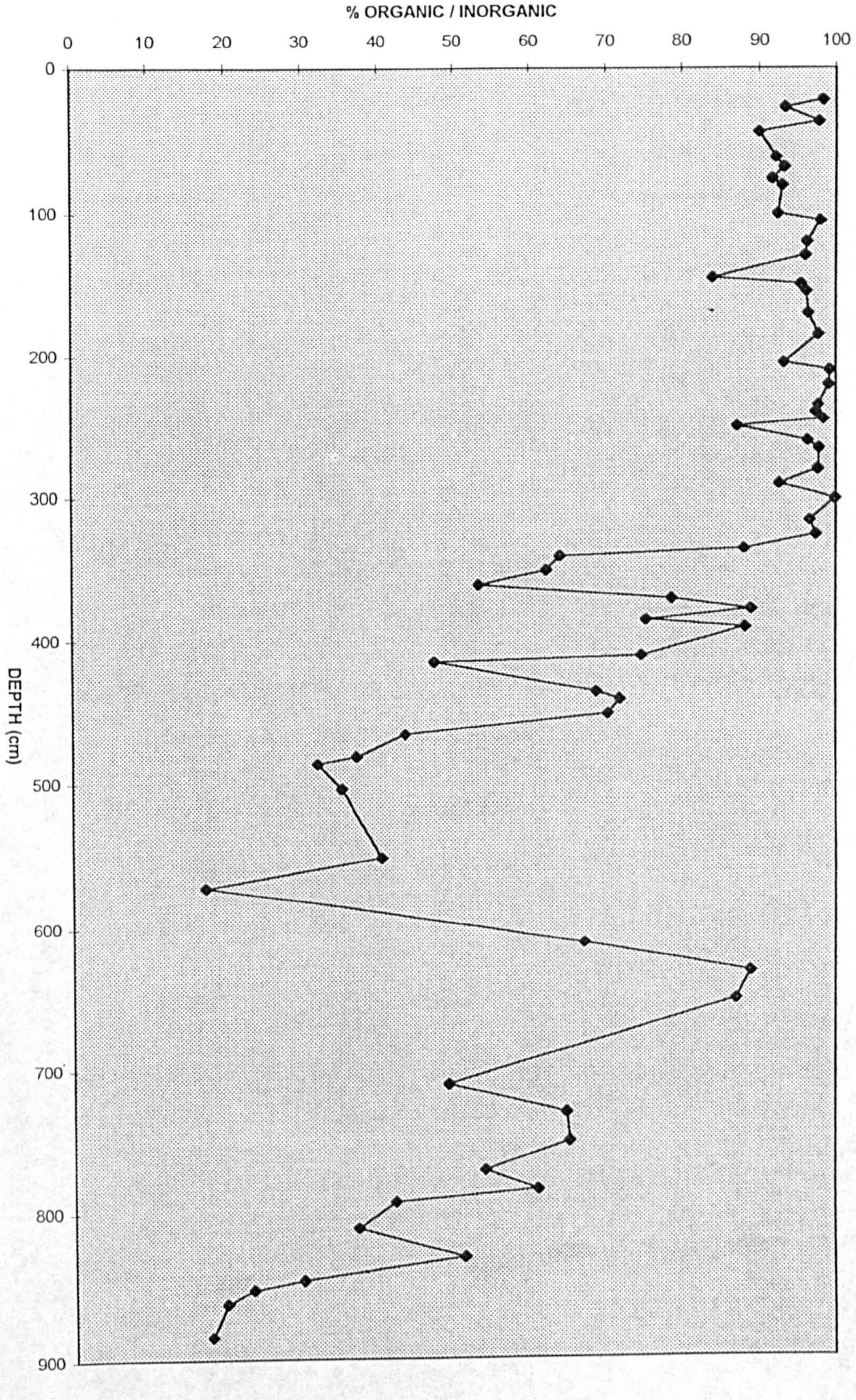
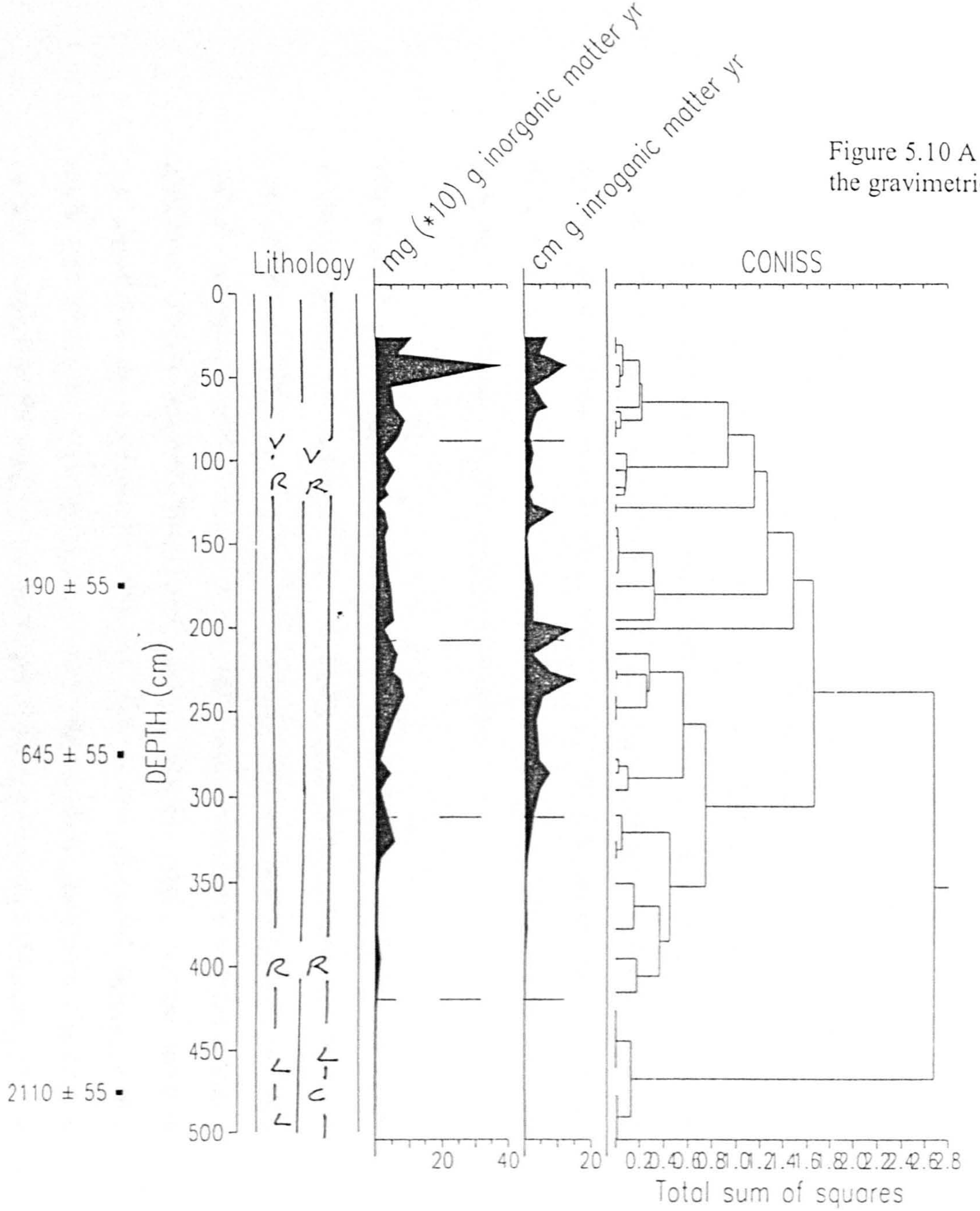


Figure 5.9 Cores MB3 and MB6: Loss on ignition

Figure 5.10 A comparison of charcoal fluctions derived from the gravimetric and point count methods



characteristics of inorganic matter deposited. Indeed, particle size distribution has been used as a sensitive palaeohydrological indicator in lake sediments, indicative of changing flow regimes to the lake body (Costa, 1978). The main assumption for the investigation of inorganic matter particle size here is that the presence of large diameter, inorganic particles in core MB6 indicates relatively high discharges in the past. Once variations in the accumulation rates have been accounted for, fluctuations in particle size spectra will provide a means of reconstructing changes in the hydrological budget of Mubwindi Swamp.

Given a range of particle sizes at source, mechanisms of erosion will be able to liberate a range of particle sizes. These will be sorted and/or reduced in size by the processes of transportion. Particles will be deposited where the competence of the transporting medium falls below a critical level. Therefore, deposited sediments have a distinctive particle size distribution imparted by the transporting regime. However, source control, and temporary stores between the primary erosion point and the final deposition point, may play an important role in determining the distribution of particle-size. Despite these limitations, it is possible to make some inferences on the nature of past environments, particularly when used in combination with other palaeoecological evidence.

The basal inorganic sediments within the Mubwindi Swamp catchment are likely to be endogenic, i.e. *in situ* soil on the valley floor before swamp development commenced. However, it is possible they were derived from exogenic sources. Indeed, inorganic material at any depth within the accumulated sediments could have been derived from aeolian, fluvial and/or lacustrine origin. Aeolian input is not thought to be significant at present due to the sheltered nature of the catchment. However, wind intensity, as with other climatic parameters, is known to have changed in the period covered by the sedimentary record (Mahaney, 1990; Mahaney *et al*, 1991)). Lacustrine deposits are not thought to be particularly important in the upper part of the Mubwindi Swamp catchment although there is evidence from the basin morphology for the seasonal presence of a small lake within the southern part of the swamp (Section 3.9). The present-day influence of fluvial activity is evident in the highly flashy nature of the rivers entering Mubwindi Swamp, which can cause flooding of the swamp surface during the monsoon season. Therefore, inorganic sediments retained within core MB6 are thought to be predominantly of fluvial origin, with the basal sediments possibly resulting from paludification of soils *in situ*.

5.6ii Measuring particle size

The size of a particle can be expressed in several ways, although there are three common expressions: linear dimensions, volume diameter and the hydraulic-equivalent diameter. Linear dimensions are determined by measuring the axes. Volume diameter is the diameter of a sphere of the same volume as the particle in question. It is approximated by the nominal diameter (De) where De = (a b c) /3 (a is a-axis length, b is b-axis length and c is c-axis length). Hydraulic-equivalent diameter is the diameter of a sphere of quartz density which has the same settling velocity in a fluid as the particle in question. It takes into account the density as well as shape of the particle. Volume diameter was used in this study as a measure of particle size because of the small particle sizes involved (0.5 - 600 µm), and hence methodological difficulties in measuring linear dimensions and hydraulic-equivalent diameters.

Due to the large range of particle sizes involved, distribution results are often displayed on a log scale, as phi units (∅). This suffers from two main drawbacks. Although the use of phi units is well known to sedimentologists, it is not widely used by workers in other disciplines (Kochel *et al*, 1982). Secondly, the use of a phi scale implies acceptance that particle size distributions are skewed and uni-modal, therefore a -log^2 transformation converts the distribution to normality. This assumption is not always the case with sediment size distribution data, where bi-modal or multi-modal distributions of particle size can be common. These complex distributions would be particularly expected from fossil sediment samples where the time-frame is incorporated into each sediment slice, and hence the range of particle sizes, is likely to vary due to different within sample flow regimes. Indeed, a single sample may contain sediment size distributions originating from a number of fluctuations in the hydrological budget. Therefore, it was decided that results should be expressed as micrometers (µm). This measurement is understood throughout a range of disciplines, and it is on a graduated, rather than a log, scale. To enable a fast, repeatable, accurate and precise measurement of the particle-size distribution, a Malvern particle sizer was used.

The Malvern particle sizer (MSX02LM) uses two forms of optical configuration to enable a wide range of particle size measurement; Conventional Fourier Optics (CFO) and Reverse Fourier Optics (RFO). In the former, light from a low powered Helium-Neon laser is used to form a monochromatic beam of light (analyser beam), typically 18 mm in diameter. Particles to be measured are introduced to the analyser beam by sample presentation units. Light scattered by the particles are incident on a receiver lens. Here a detector (a series of angular mirrors) gathers the light over a range of angles of scatter. The un-scattered light is brought to focus on the detector, before being passed through a small aperture in the detector and out of the optical system. The total laser power passing out of the system is monitored allowing the sample volume concentration to be determined. For RFO, the order of the components is altered to allow the measurement of scattering at much higher angles than is possible by the conventional method, although in principle the measurement is made in the same manner. The laser beam is expanded, as in CFO, but instead of forming a collimated analyser beam, the output beam is focused onto a point in the plane of the detector. The presentation unit is moved closer to, and further from, the detector to achieve this focus. The amount of light falling onto the detector being a product of cell to detector length and the characteristics of the particle size to be measured. It should be emphasised that results are volume based. For example, a result of 10 % of the distribution in size category < 0.5 μm means that the total volume of all particles in this size range represents 10 % of the total volume of all particles in the distribution, and not 10 % by number.

In a typical measurement run, the number of particles needed to obtain an adequate measurement would be in the region of 1000 to 10,000, depending on their size. However, this could produce under-representative sampling of the bulk material, which can be avoided by time averaged observation of scattering with the material being continuously passed through the analyser beam. By making many measurements of the detector readings (sweeps) and averaging over many such sweeps, it is possible to build up an integral light scattering characteristic based on millions of individual particles. The detector thus provides an electronic output signal proportional to the light energy measured over all the separate angles of collection. The computer software is set to collect this information, and performs time averaging by summing data from the detector over a period of time (5 seconds).

5.6iii Sample preparation for particle size analysis

For each sample depth, 2 cm^3 of sediment was placed in 30 % Hydrogen Peroxide (H_2O_2) and heated in a water bath until all the organic material was removed (as denoted by the cessation of effervescence). To prevent the flocculation of the fine sediment particles, the inorganic residue was placed in a solution of 4 % Calgon (sodium hexa-meta-phosphate). Prior to being placed in the Malvern sample presentation unit, each sample underwent ultrasonic stirring. This ensured that the measurements were an accurate measurement of particle size, and not a measurement of the degree of flocculation. Each sample was suspended in distilled water and stirred to ensure complete dispersion of the sediment in solution. The suspended sediment was drawn off from just above the bottom of the beaker using a high powered syringe, and placed in the sample presentation unit containing distilled water. While in the presentation unit, further mechanical stirring and the use of ultrasound prevented any flocculating of sediments prior to analysis. Enough of each sample was placed in the presentation unit to produce an obscuration of the analysing beam of between 10 and 30 %, an ideal obscuration being around 15 %. Measurement of the sample was set at 32 size classes between 0.5 μm and 600 μm. This size range, and the divisions within the range, were chosen as being the most appropriate to pick up the range of inorganic sediment particle sizes. This choice was validated by the subsequent results, which showed a small percentage of sediments falling within the extreme size classes.

The results of particle size distribution for each sample are presented in a Table (Table 5.1) consisting of a relative volume of material in 32 size bands. The data are described using the first four moments of the distribution; the mean, standard deviation, skewness and kurtosis. However, because many particle size

Table 5.1 Output Table from the particle size analysis with distribution statistics

MALVERN MASTERSIZER X

Version 1.2b 08 Jan 1995 13:46

MB6 783-790 :Run Number 4

MUBWINDI SWAMP.
ANALYSIS: R.A.MARCHANT.

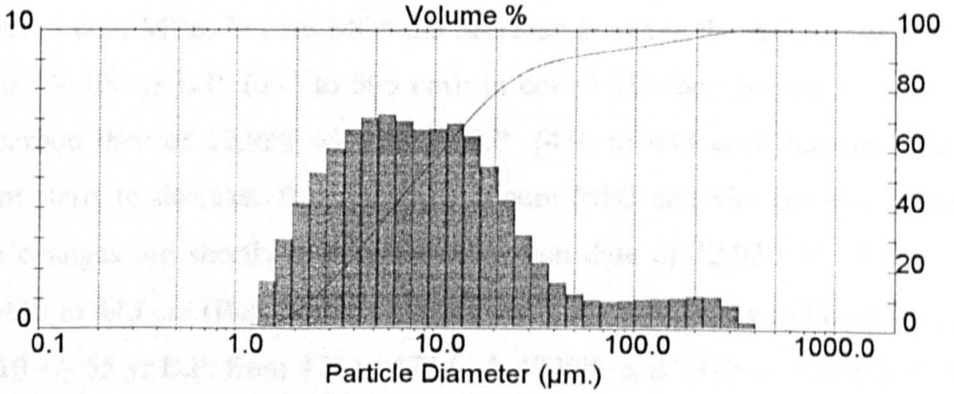
SMALL PRESENTATION UNIT.
Sample File Name: UGANDA2 , Record: 4 Source: Analysed
Measured on: 08 Jan 1995 10:26 Last saved on: 08 Jan 1995 10:26

Presentation: 2OHD
Polydisperse model Volume Result Focus = 300 mm.

Residual = 0.412 % Concentration = 0.012 % Obscuration = 14.85 %
d (0.5) = 8.39 µm d (0.1) = 2.51 µm d (0.9) = 44.61 µm
D [4, 3] = 23.78 µm Span = 5.02
Sauter Mean (D[3,2]) = 5.85 µm Mode = 5.50 µm
Specific Surface Area = 1.0258 sq. m. / gm Density = 1.00 gm. / c.c.

Size (Lo) µm	Result In %	Size (Hi) µm	Result Below %
0.50	0.12	1.32	0.12
1.32	1.55	1.60	1.68
1.60	2.92	1.95	4.59
1.95	4.12	2.38	8.71
2.38	5.14	2.90	13.85
2.90	5.97	3.53	19.82
3.53	6.61	4.30	26.43
4.30	7.02	5.24	33.45
5.24	7.12	6.39	40.57
6.39	6.90	7.78	47.46
7.78	6.62	9.48	54.08
9.48	6.65	11.55	60.74
11.55	6.82	14.08	67.55
14.08	6.38	17.15	73.93
17.15	5.35	20.90	79.28
20.90	4.21	25.46	83.50

Size (Lo) µm	Result In %	Size (Hi) µm	Result Below %
25.46	3.06	31.01	86.56
31.01	2.15	37.79	88.71
37.79	1.50	46.03	90.21
46.03	1.12	56.09	91.32
56.09	0.93	68.33	92.25
68.33	0.87	83.26	93.13
83.26	0.89	101.44	94.02
101.44	0.94	123.59	94.96
123.59	0.96	150.57	95.91
150.57	1.00	183.44	96.91
183.44	1.05	223.51	97.96
223.51	1.04	272.31	99.00
272.31	0.78	331.77	99.78
331.77	0.22	404.21	100.00
404.21	0.00	492.47	100.00
492.47	0.00	600.00	100.00



Malvern Instruments Ltd. MasterSizer X Ver. 1.2b
Malvern, U.K. Serial No. 6492 08 Jan 95 13:46

distributions do not approach log-normality, these summary statistics are of limited interpretative value. As the analysis was aimed at delimiting down-core changes in particle size, the results for each size class were combined for each sample, and expressed as variations in percentage according to depth (Figure 5.11), these will be described in Section 5.8.

5.7 Description and comparison of the results for LOI and charcoal analysis

Results will be described initially for the LOI analysis. The results from the methods for charcoal determination will be described, and intra-core correlations highlighted. Leading from these descriptions a comparison between the methods applied to determine charcoal fluctuations will be made.

5.7i LOI results

The LOI curves for both cores (Figure 5.9) show high amounts of inorganic material at between 680 and 610 cm, 530 and 430 cm for core MB3, and 884 and 850, 570 and 480 cm for core MB6. These depths correspond respectively to stratigraphic zones A and C (Chapter 4). Core MB3 has a higher amount of inorganic material than core MB6. This is thought to result from the relatively marginal position of core MB3 on the swamp surface, compared to that of core MB6.

Sharp decreases in inorganic sediment occur above 450 cm in core MB3 and at 560 cm in core MB6. In core MB6 the decrease is above the radiocarbon date of 27,480 +/- 300 yr B.P. (590 to 595 cm); in core MB3 the decrease is below the radiocarbon date of 12,930 +/- 100 yr B.P. (430 to 443 cm). Inorganic matter content starts to decrease from 420 cm in core MB3 and 480 cm in core MB6. These changes are shortly after the radiocarbon date of 12,930 +/- 100 yr B.P. from 430 to 443 cm (Beta-60066) in core MB3, and before the radiocarbon dates of 2110 +/- 55 yr B.P. from 473 to 477 (AA-12398) and 1970 +/- 55 yr B.P. from 473 to 477 cm (AA-13909). These abrupt changes in the organic - inorganic ratio may add further support to the presence of hiati in sedimentation, as suggested in Chapter 4.

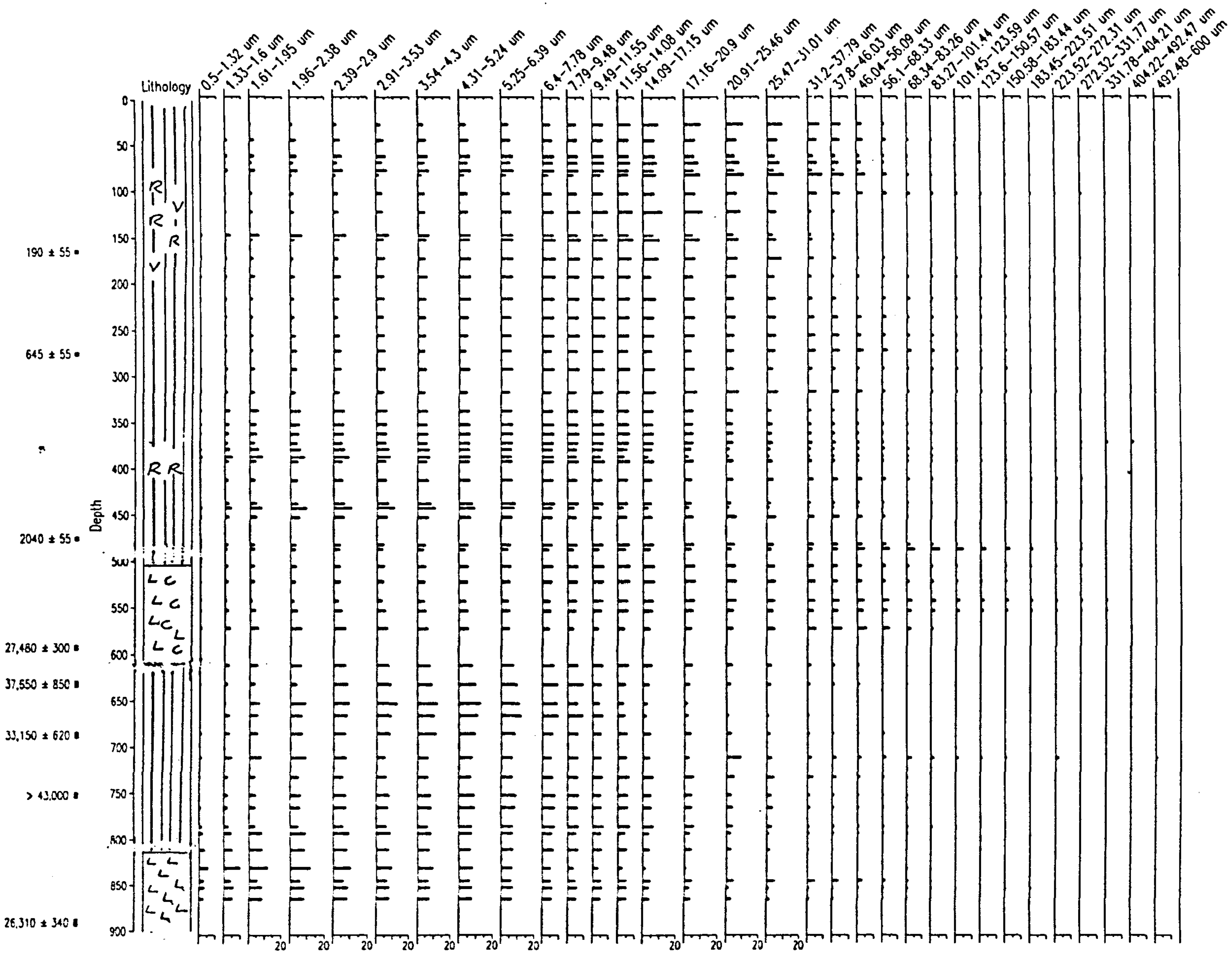


Figure 5.11 Variations in inorganic particle size down-core for core MB6

High and sustained levels of inorganic material, not recorded by the on-site stratigraphy, are recorded by the LOI analysis. These increases in inorganic matter content are recorded for horizons described in the field as herbaceous peat, particularly within stratigraphic zone D. In core MB3 there are four distinct horizons within stratigraphic zone D within which the level of inorganic matter content is relatively high, whereas in core MB6, levels of inorganic sediment fluctuate more erratically. Based on the age-depth curves (Section 4.4) the uppermost sediments of the cores (from approximately 400 cm in MB3 and from 490 cm in MB6) are thought to represent a similar time period, i.e. the Late Holocene period. The composition of the Mubwindi Swamp sediments have not been constant throughout this period; there are several peaks of inorganic material. These peaks in inorganic matter content are more sustained in core MB3, such as those centred around 400 cm and 290 cm. This may be a result of the location of core MB3, closer the swamp's margin, where it is likely to receive a higher proportion of in-washed allochthonous material. There are increases in inorganic material recorded from core MB6 at 420 and 350 cm. Although more prominent, these are less sustained than those recorded in core MB3. One peak, from 150 cm in core MB3, is sustained until all but the last sample. A similarly sustained peak is also recorded in core MB6, although not so prominently. On the basis of the radiocarbon dates date of 310 +/- 55 yr B.P. from 170 to 177 cm (Beta-61809) in core MB3 and 190 +/- 55 yr B.P. from 163 to 167 cm (AA-12396) in core MB6 it is suggested these upper peaks date from the last few hundred years.

5.7ii Charcoal point-count results

The initial results from the charcoal point-count method (Figure 5.1) for stratigraphic zone A of core MB6 highlight a decreasing amount of charcoal towards the top of the core, particularly after 180 cm. When the data are transformed to take into account the amount of inorganic matter (Figure 5.2), the area of charcoal fragments per sample is highest between 310 and 170 cm, or between approximately 800 yr B.P. and 200 yr B.P. The rise is most pronounced soon after the radiocarbon date of 645 +/- 55 yr B.P. These high levels become even more pronounced when the charcoal influx rate is calculated (Figure 5.3).

Further peaks in charcoal area are also highlighted by the influx rate data, such as that at 125 cm and a secondary sustained peak from 80 cm. These are thought to result from increased charcoal production during the past 150 years.

5.7iii Charcoal particle size results

When differentiated charcoal particle size according to size classes, the charcoal data shows one major peak for core MB6 at 710 cm (Figure 5.5). This increase in charcoal correlates to an increase in the amount of organic matter (Figure 5.9). In core MB3 (Figure 5.4) a similar rise in charcoal is present, reaching a peak at 595 cm. Within core MB6, a peak in charcoal particle size and number (although considerably smaller than the peak already described) occurs from 575 cm to 480 cm. This is associated with a peak in inorganic matter (Figure 5.9) that spans the same depths. There is an increase in charcoal content and size in core MB3 recorded between 525 and 450 cm, again associated with a peak in inorganic material. These similar signals recorded within stratigraphic zone C, in different cores, are thought to reflect a contemporaneous sedimentary environment. The uppermost 477 cm of core MB6 contains a relatively small amount of charcoal. The main point of note is a slight increase in the amount of large fragments centred about 240 cm. A similar record of small charcoal particle size is recorded in core MB3. However, in this core there is significantly more charcoal recorded, particularly larger sized fragments, than in core MB6. As with the inorganic results, this difference is thought to result from the more marginal position of core MB3. The high amount of small fragments, combined with the saw-toothed profile for this part of the core, indicate that in comparison to core MB3, the charcoal recorded within the MB6 sediments are derived from fires away from the swamp's surface.

5.7iv Gravimetric assay of charcoal results

For the description of the gravimetric results the charcoal record for core MB3 will be described and compared to the LOI curve. The same procedure will be applied to core MB6 and correlations drawn with the record from core MB3.

Core MB3 has a low consistent amount of charcoal up until about 580 cm (Figure 5.6). This corresponds to the radiocarbon date of 30,300 +/- 1250 yr B.P. from 580 to 588 cm (Beta-60066). These sediments are also characterised by high amounts of inorganic material (Figure 5.9). At 580 cm there is a rapid rise in the amount of charcoal until 520 cm, followed by a rapid decrease until 480 cm. This decrease corresponds to relatively low amounts of inorganic matter. The highest amount of charcoal is recorded between 470 and 420 cm, within stratigraphic zone C, which incorporates the radiocarbon date of 12,930 +/- 100 yr B.P. (430 to 443 cm). However, the high amounts of charcoal are not sustained, with rapid fluctuations apparent. As with the LOI curve, the charcoal curve for core MB3 fluctuates significantly in the upper Section of the core. There are four main phases of increased charcoal presence within the late Holocene sediments of core MB3, with a distinct peak above 150 cm.

The charcoal record from core MB6 (Figure 5.6), although broadly similar to that of core MB3, is more variable. Unlike core MB3, the bottom two samples from stratigraphic zone A have very high amounts of charcoal. At approximately 700 cm, within stratigraphic zone B there is a large, unsustained rise in the amount of charcoal present. This is thought to correspond stratigraphically to the rise at 570 cm in core MB3. In core MB6 this falls off dramatically at 630 cm with a relatively low amount being recorded until 560 cm. A similar fall in charcoal is recorded in core MB3 between 510 and 470 cm, where it is also associated with increased inorganic matter.

When charcoal data are standardised against the amount of inorganic matter, the results for core MB3 (Figure 5.7) highlight a significant peak in charcoal between 580 and 420 cm. This is thought to correspond stratigraphically to a peak recorded between 700 and 600 cm in core MB6. Following this peak there is a low, consistent level of charcoal until 250 cm, after which there is an abruptly fluctuating rise, which attains a peak at 170 cm (310 +/- 100 yr B.P.). A gradual decline in the amount of charcoal occurs above 170 cm.

When charcoal data are standardised against inorganic material, the record for core MB6 (Figure 5.7) highlights a significant peak at 650 cm. The other peaks associated with the inorganic matter horizons (Figure 5.6) are significantly reduced. As with core MB3 the most interesting results are within the upper band of herbaceous peat. As with the results from the point-count method, there is a very significant peak in the charcoal record from approximately 350 cm through to approximately 180 cm. As was the case from the areal method, and the results from core MB3, this overall peak is composed of widely fluctuating amounts of charcoal. Similarly to core MB3, this relatively high amount of charcoal decreases towards the top of the core. There is a single high value recorded at 30 cm. As this is not recorded within core MB3, nor in samples either side of 30 cm, the single high value is thought to reflect incorporation of a single large charcoal fragment, rather than being reflective of increased charcoal production / mobility within the Mubwindi Swamp catchment.

As with the point-count method an account was made of the time-frame incorporated by each sediment sample (Figure 5.8). This can only be applied where there is sufficient dating control. Similarly to the point-count method the increase in charcoal from approximately 800 yr B.P. to 200 yr B.P. is recorded, as is the uppermost peak in charcoal. This uppermost peak is much more pronounced than that indicated from the point-count method.

5.7v Comparison of the results for charcoal determination

When comparing the results from the three different methods of charcoal determination (point count, particle size and gravimetric) the major peaks recorded by the gravimetric technique are also recorded by the point-count and particle-size methods. This is particularly so for the large changes in charcoal content. The division of charcoal fragments into particle size classes adds information to that obtained from the quantitative estimates of charcoal area and mass. Where possible, the influence on the amount of charcoal recorded by both the inorganic matter content, and the time-frame incorporated by the sediment sample, is shown to be very important in determining the overall charcoal signal. Overall the class-size method highlighted considerably less variation in the charcoal abundance; this is thought in part due to changes in charcoal presence being diluted by the distribution between the seven class sizes.

When the results from the point count and gravimetric determination of charcoal that have been standardised against inorganic matter and time are plotted together (Figure 5.10) some notable similarities are apparent. To highlight these the data were zoned using a dissimilarity measure (Section 7.3). Both methods highlight the low amount of charcoal until approximately 1600 yr B.P. There is a slow, steady increase in the amount of charcoal, which is more marked by the gravimetric method, until approximately 900 yr B.P. Both techniques highlight a notable rise, this is thought to date from approximately 800 yr B.P. to 300 yr B.P. There is a steady amount of charcoal until approximately 50 yr B.P. when there is a significant increase in the amount of charcoal, this then tails off towards the top of the core.

5.8 Analysis and presentation of Malvern results

The stratigraphic zones of core MB6 characterised by clay bands recorded by the on-site stratigraphy (Chapter 4) have very different particle size signatures (Figure 5.11). Stratigraphic zone A is composed of relatively fine material compared to stratigraphic zone C which has a very high proportion of coarse inorganic sediments. This suggests that the two stratigraphic zones have been deposited under different sedimentary environments. Stratigraphic zone A could have resulted from paludification, or a shallow lake deposit. This latter suggestion is not supported by diatom analysis carried out on eight samples of basal clay which yielded no diatoms. Stratigraphic zone C is thought to result from an inwash of inorganic material, thus reflecting an increase in the hydrological budget of Mubwindi Swamp.

Stratigraphic zone B is characterised by the relatively small size of the inorganic sediment fraction, particularly between 700 cm and 600 cm. However, there is a transitory rise in the amount of large-sized material recorded about 710 cm. This corresponds to the period of a significant increase in the amount of charcoal (Figure 5.8). Throughout stratigraphic zone D the size of inorganic material varies considerably. At 480 cm there is a significant decrease in the inorganic sediment particle size as the total amount of inorganic matter decreases. The sediments between 480 and 350 cm are characterised by a considerable spread throughout the size range. This corresponds to a period of a relatively large amounts of inorganic matter. As the percentage of inorganic matter falls rapidly at about 340 cm so does the particle size. The sediments from 340 to 175 cm are characterised by a large amount of mid-sized material with a relatively stable particle size signature. This is at odds with the fluctuating amount of charcoal for this part of the core. Hence, it is suggested the increases in the charcoal, recorded in both cores MB3 and MB6, result from increased burning rather than a change in the mobility of charcoal that result from a change in the hydrological budget of the Mubwindi Swamp catchment. This particle size distribution changes quite dramatically at 175 cm with a very rapid decrease in sediment size to produce a very fine sediment spectra. This is thought to indicate a period of low flows within Mubwindi Swamp catchment. Conversely, the small particle sizes could represent a period of disturbance within the Mubwindi Swamp catchment and increased mobility of the fine material. There is a rapid increase in sediment size at 100 cm that corresponds to an increase in the overall amount of inorganic matter and the secondary peak in charcoal as highlighted when results are standardised against inorganic matter content. This uppermost peak in charcoal recorded within core MB6 is thought to result from increased mobility of charcoal within the Mubwindi Swamp catchment, rather than a direct increase in the amount of charcoal production. The amount of large fraction tails off towards the top of the core, indicative of increased stability within the Mubwindi Swamp catchment relative to the previous period.

CHAPTER 6

Modern vegetation surveys, palynology and the pollen-vegetation relationship

6.1 Introduction

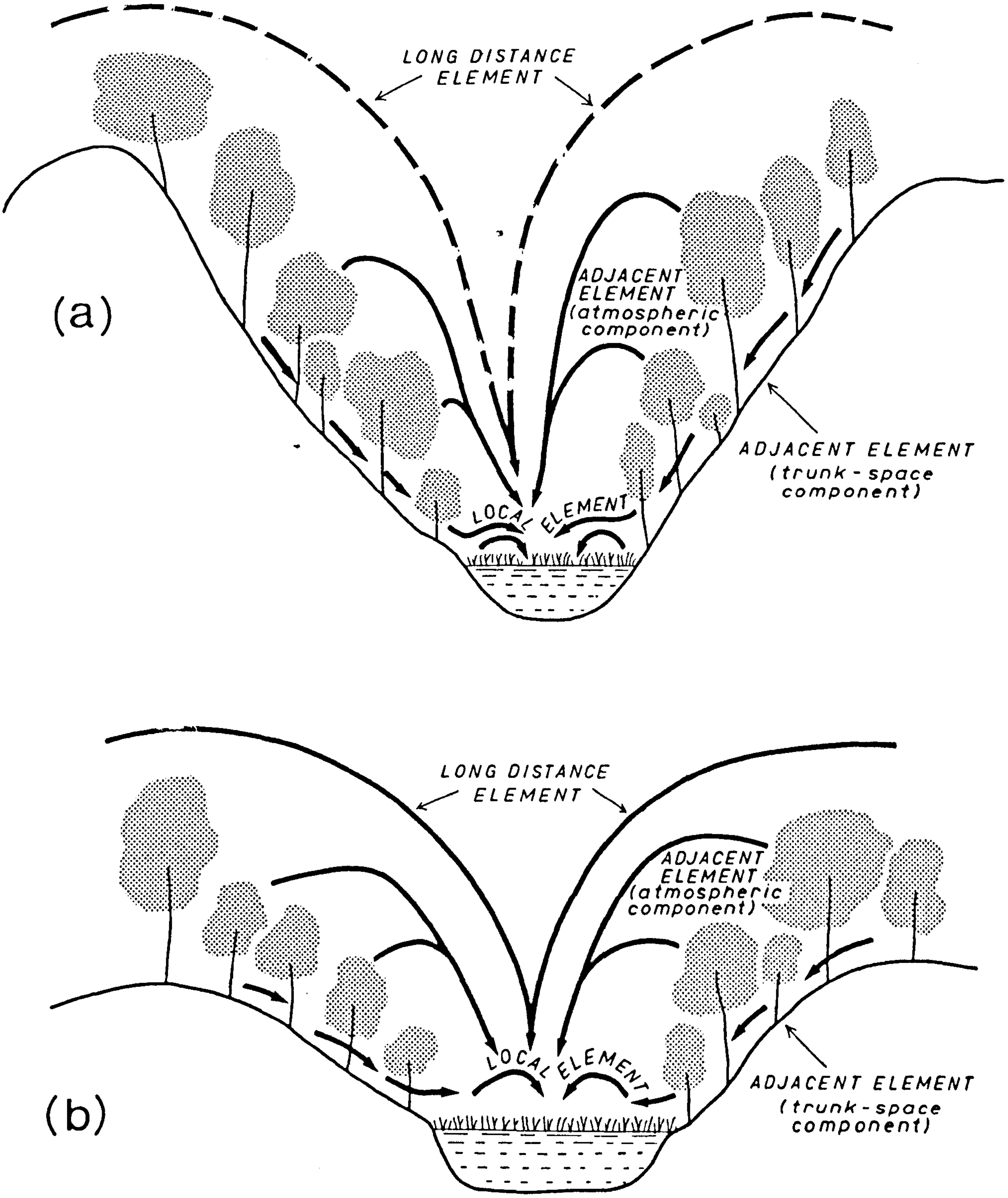
Within this Chapter the present-day composition and distribution of vegetation surrounding Mubwindi Swamp will be described. Pollen spectra from a range of locations on the surface of Mubwindi Swamp will be described. The two data sets are compared to investigate the relationship between pollen in surface samples from the swamp, and the parent taxa within the surrounding vegetation. This will provide a test of how representative pollen in the Mubwindi Swamp sediments is in recording the surrounding vegetation. The data will also provide a test of Hamilton's (1972) model of interpreting fossil pollen sequences in highland Uganda. A morphological description of the main pollen types encountered, their likely source and potential value as ecological indicators is given in Appendix 1.

6.2 Vegetation surveys and determination of pollen origin

Much of the uncertainty in the interpretation of Late Quaternary pollen assemblages can be removed by the judicious use of pollen surface samples (Wright and Wright, 1967). A quantitative relationship is assumed to exist between the number of pollen grains incorporated within sediment at a given site, and the number of individuals of the parent taxon present within the surrounding vegetation. Such a relationship is undoubtedly very complex (Flenley, 1973), being influenced by genetic, physiological, climatic and ecological factors. These factors control the pollen production of the individual plant, the abundance of the taxon within the vegetation, the structure of the community in which the taxon occurs, and the mode of pollen dispersal. Physical, chemical, and biological conditions also interact to influence the incorporation of pollen into sedimentary sequences, and determine the level of preservation. The interaction of these factors is complex, and poorly understood. No completely satisfactory model of taxon-specific pollen representation has been devised for central Africa. Quaternary palynologists have studied the final product of pollen deposition, namely modern pollen spectra preserved in the most recently accumulated surface sediments (Hamilton, 1972; Hamilton and Perrot, 1980; Meadows, 1984). These studies have used visual estimates of parent taxon density within the surrounding vegetation, to determine how representative accumulated pollen on swamp surfaces is of surrounding vegetation, rather than the quantitative survey presented here.

On a basic level, pollen input to a sedimentary basin can be classified into three pathways (Hamilton, 1982), each of which has a separate environmental significance. Firstly, pollen from local sources is indicative of aqueous and sedimentary features close to the sample site; secondly, pollen from non-local sources is indicative of the climate, land use and microclimate within the catchment; and thirdly, pollen from distant sources is indicative of a wide range of regional conditions. The division between non-local and distant sources is difficult to determine. The main determinant is that if pollen types known to be well dispersed are recorded at low levels, then it is likely these have originated from extra-catchment parent taxa. The importance that can be assigned to each pathway is dependent on the morphology of the basin, and the characteristics of the vegetation on the swamp surface, within the catchment and throughout the region.

A model of pollen transport and ultimate incorporation into the sedimentary record (Figure 6.1), highlights the influence of basin morphology on the pollen transport pathways. Within a steep-sided catchment, topographically protected from external winds (hence pollen transport), the importance of the long distance element will be reduced. Pollen originating from within-catchment vegetation is also less likely to leave the catchment due to reduced winds. Thus, it is suggested here that within a steep-sided, topographically enclosed catchment there is less likely to be a substantial contribution from the long distance element. Pollen accumulating on the swamp surface is likely to be more representative of the within-catchment vegetation than within a more open catchment. The aim of this Chapter is to determine just how reflective the pollen spectra in surface sediments is of the surrounding vegetation within the Mubwindi Swamp catchment.



THEORETICAL MODEL OF POLLEN DEPOSITION IN
TWO SEDIMENTARY BASINS IN HIGHLAND UGANDA

(a) Steeper sided slopes surrounding a restricted catchment

(b) Gentle sided slopes surrounding a more extensive catchment

Figure 6.1 The influence of different basin topographies on the components of pollen transport

6.3i Vegetation surveys: the composition and distribution of vegetation within the Mubwindi Swamp catchment

To determine the composition of vegetation within the Mubwindi Swamp catchment (Plate 6.1), and in order to quantify the relationship between this and the composition of the pollen flora within surface sediments, it was necessary to first survey the vegetation. It was decided that a belt transect survey would be the most appropriate method to use. This would identify floristic changes along altitudinal (environmental) gradients, and allow for a comparison to be made with a previous survey of the vegetation carried out in Bwindi-Impenetrable Forest (Hamilton,1969).

The sediment cores used for pollen and sediment analysis were extracted from the north-eastern arm of Mubwindi Swamp. Therefore, it was decided the surveys should be concentrated in this region. Tree species were recorded along eleven, five metre-wide, belt transects (Plate 6.2), running perpendicular from the swamp margin to the surrounding hill crests. At the start of each transect, the position was marked by a stake and a compass bearing was taken along the line the transect would follow. This was periodically checked to ensure the transect was still progressing in a straight line. At twenty metre intervals along the transects, five recordings of slope angle were taken with a compass-clinometer and averaged to give a mean slope angle.

The results from the vegetation surveys are shown on Figures 6.2 to 6.5. These Figures are drawn to scale, and each includes a location map showing the position of the transect within the catchment. Each transect records species, the position along the transect, tree height, diameter at breast height, canopy density, slope angle and the occurrence of non-arboreal ground cover. The species are represented by the codes used on the Figures are shown in Table 6.1. Where no trees were present for a distance of five metres (Plate 6.3), the nature of the ground flora was noted and placed in four main categories; *Mimulopsis* dominant (Plate 6.3); shrub and herb association; Elephant track; and *Brilliantasia* dominant.

Plate 6.1 Vegetation within the Mubwindi Swamp catchment

Plate 6.2 Transect 3 showing young *Neoboutonia*, *Prunus africana* and elephant track

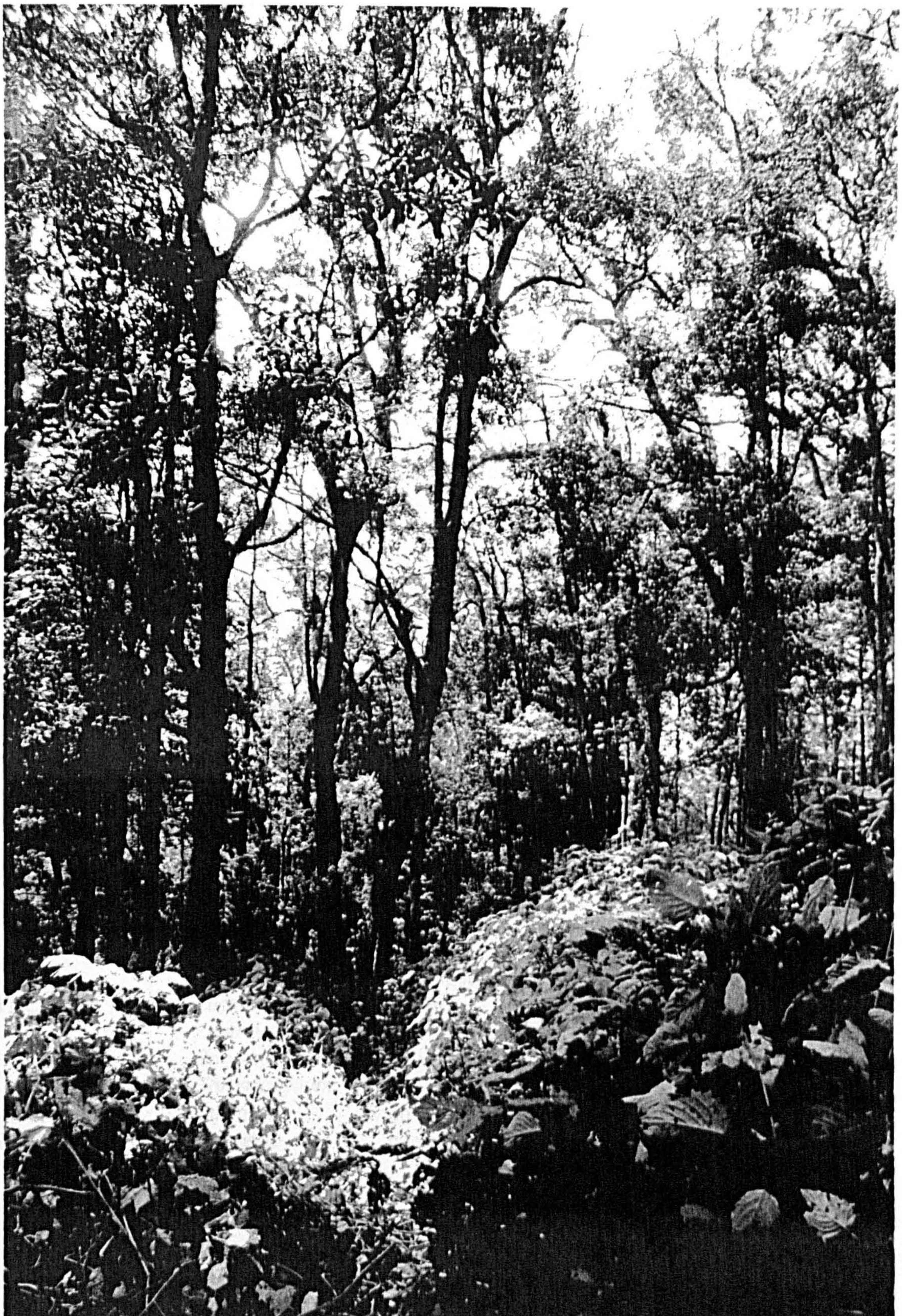


Plate 6.3 *Mimulopsis* dominated shrub complex

FAMILY	GENUS	SPECIES	CODE	AUTHORITY
APOCYNACEAE	*Tabernaemontana*	*pachysiphon*	Th	K. Schum.
AQUIFOLIACEAE	*Ilex*	*mitis*	Im	(L.) Radlk.
ARALIACEAE	*Polyscias*	*fulva*	Pf	(Hiern) Harms.
CAPPARIDACEAE	*Ritchiea*	*albersii*	Ra	Gilg.
CELASTRACEAE	*Maytenus*	*acuminata*	Ma	(L. f.) Loes.
CYATHEACEAE	*Cyathea*	*manniana*	Cm	Hook.
EUPHORBIACEAE	*Alchornea*	*hirtella*	Ah	Benth. f.
	Croton	*macrostachyus*	Cm	Hochst. Ex A. Rich.
	Croton	*megalocarpus*	Cm	Hutch.
	Drypetes	*gerrardii*	Dg	Hutch.
	Drypetes	*ugandensis*	DU	(Rendle) Hutch.
	Macaranga	*kilimandscharica*	Mk	Pax.
	Neoboutonia	*macrocalyx*	Nm	Pax
GUTTIFERAE	*Harungana*	*madagascariensis*	Hm	Poir.
	Symphonia	*globulifera*	Sg	L. f.
LAURACEAE	*Ocotea*	*kenyensis*	Ok	(Choir.) Robyns & Wilczek.
LEGUMINOSAE	*Newtonia*	*buchananii*	Nb	(Baker) Gilb. & Bout.
LOGANIACEAE	*Anthocleista*	*zambesiaca*	Az	Baker.
MELIANTHACEAE	*Bersama*	*abyssinica*	Ba	Frensen.
MONIMIACEAE	*Xymalos*	*monospora*	Xm	(Harv.) Warb.
MORACEAE	*Myrianthus*	*holstii*	Mh	Engl.
MYRSINACEAE	*Rapenea*	*rhododendroides*	Rr	(Gilg) Mez.
	Maesa	*lanceolata*	Ml	Forsk.
MYRTACEAE	*Syzygium*	*cordatum*	Sc	Hochst ex Krauss.
OLACAEAE	*Strombosia*	*schefflera*	Ss	Engl.
OLEACEAE	*Olea*	*capensis* ssp. *hochstetteri*	Ol	Baker.
	Olea	*capensis* ssp. *welwitschii*	Ow	(Knoble) Gilg. & Schellenb.
OLINIACEAE	*Olinia*	*usambarensis*	Ou	Gilg.
PITTOSPORACEAE	*Pittosporum*	*mannii*	Pm	Hook. F. 253.
PODOCARPACEAE	*Podocarpus*	*latifolius*	Pl	Rendle.
	Podocarpus	*flacatus*	Pg	Pilger.
RHIZOPHORACEAE	*Cassipourea*	*gummiflua*	Cg	Tul.
	Cassipourea	*ruwensorensis*	Cr	(Engl.) Alston.
ROSACEAE	*Prunus*	*africana*	Pa	(Hook.f.) Kalkman.
RUBIACEAE	*Aidia*	*micrantha*	Am	K. Schum.
	Galiniera	*coffeoides*	Gc	Del.
	Oxanthus	*spp.*	Os	
	Psychotria	*megistosticta*	Pm	(S. Moore.) Petit.
	Rhytigynia	*beniensis*	Rb	K. Schum.
RUTACEAE	*Teclea*	*noblis*	Tn	Del.
	Zanthoxylum	*gilleti*	Fm	de Wild.
SAPOTACEAE	*Chrysophyllum*	*albidum*	Ca	G. Don.
	Chrysophyllum	*gorungosum*	Cg	Engl.
STERCULIACEAE	*Dombeya*	*goetzenii*	Dg	K. Schum.
THYMELIACEAE	*Peddieae*	*fischeri*	Pf	Engl.

Mimulopsis dom.	51
Scrub complex	52
Brilliantasia	53
Elephant Damage	54

Table 6.1 Species list for the Mubwindi Swamp sediments

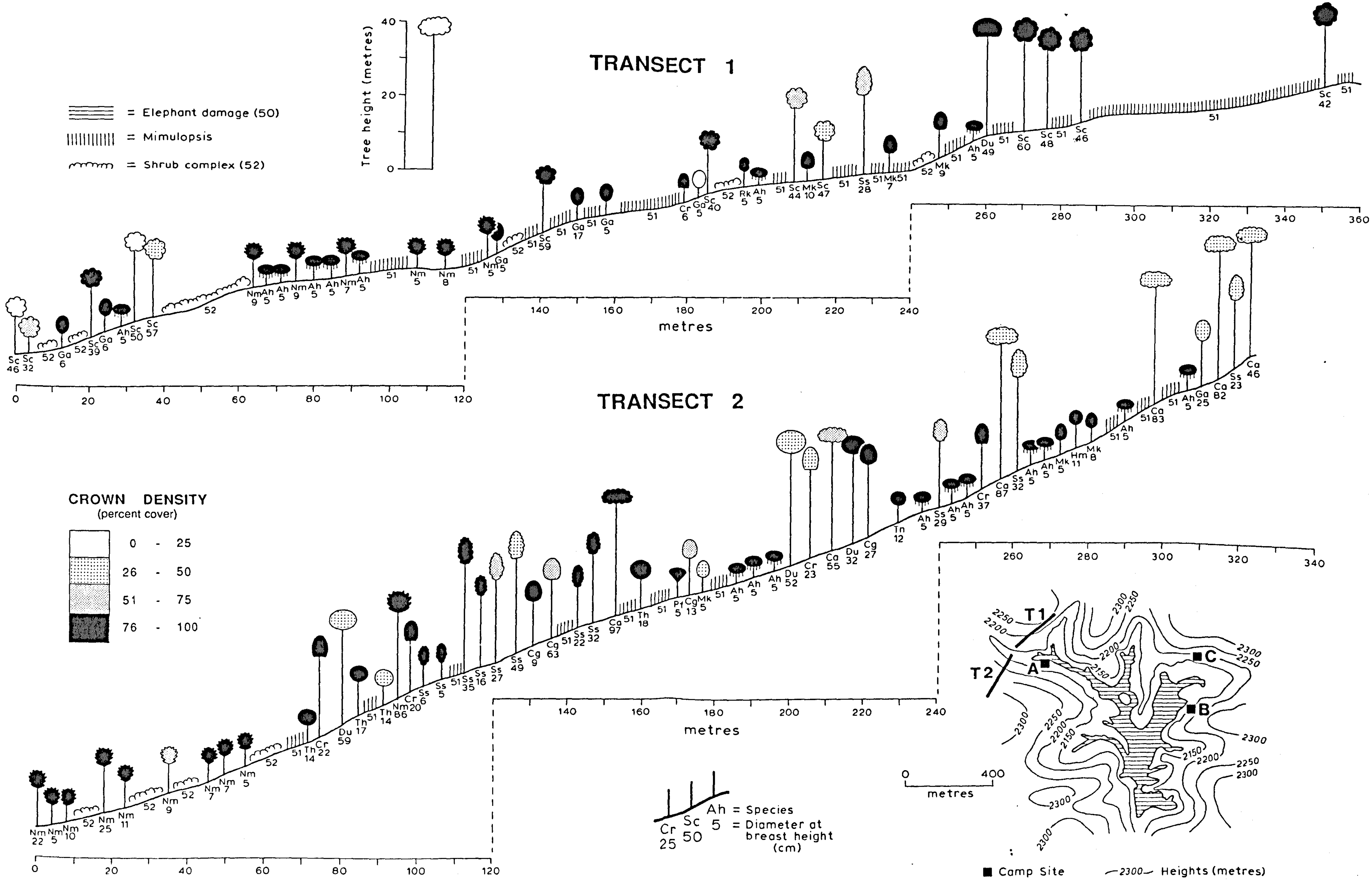


Figure 6.2 Vegetation attributes, composition and distribution along transects 1 and 2

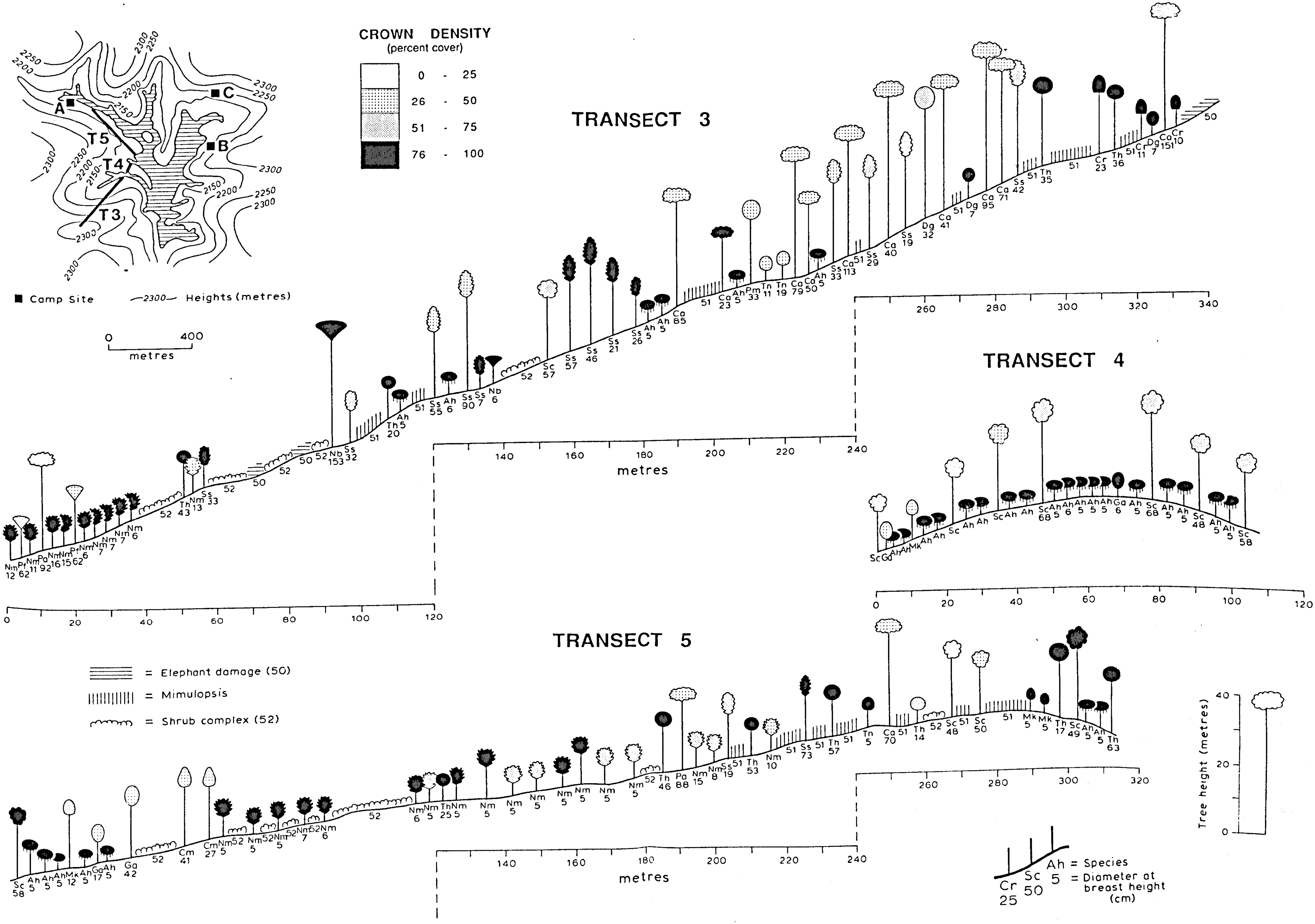


Figure 6.3 Vegetation attributes, composition and distribution along transects 3, 4 and 5

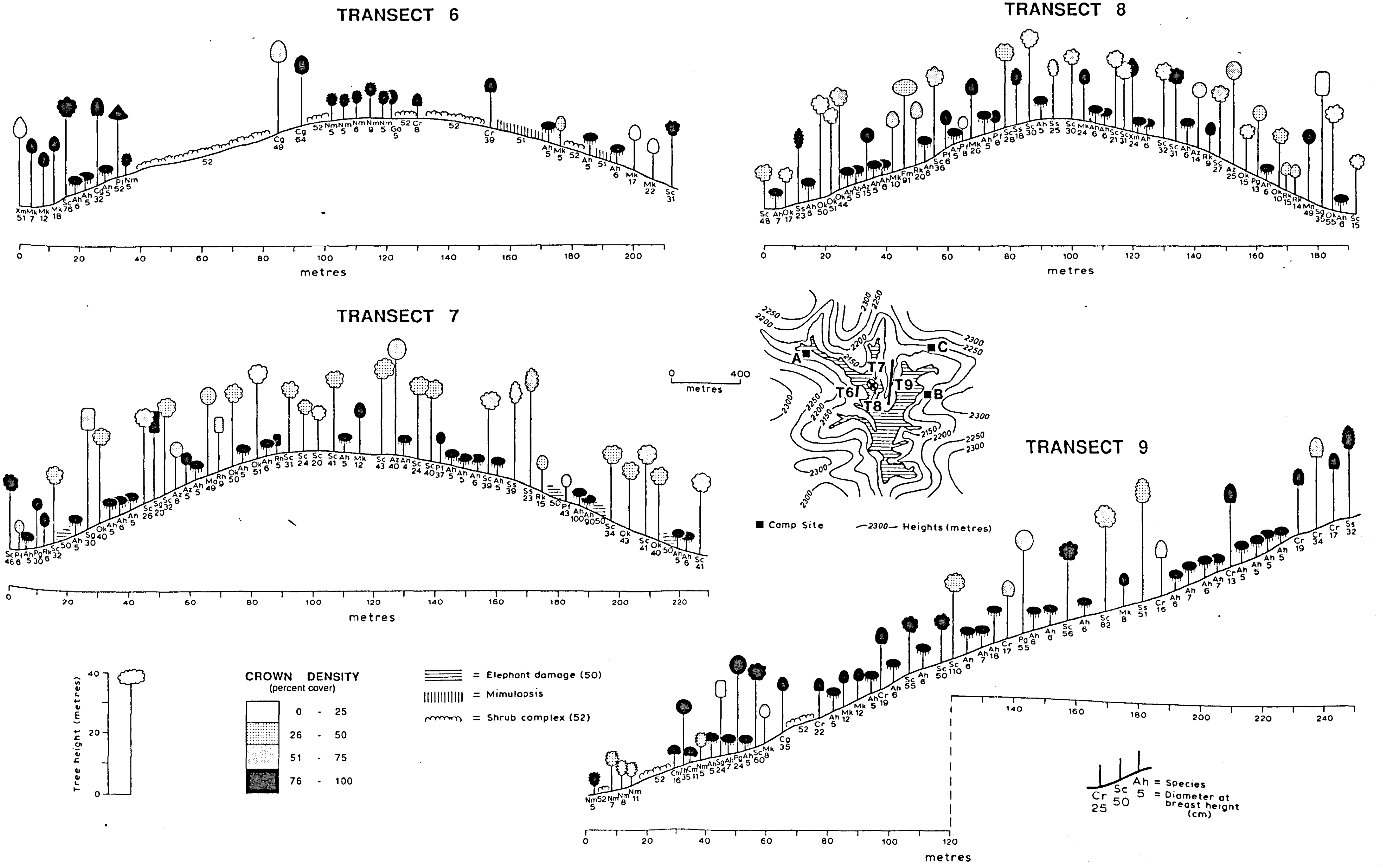


Figure 6.4 Vegetation attributes, composition and distribution along transects 6, 7, 8 and 9

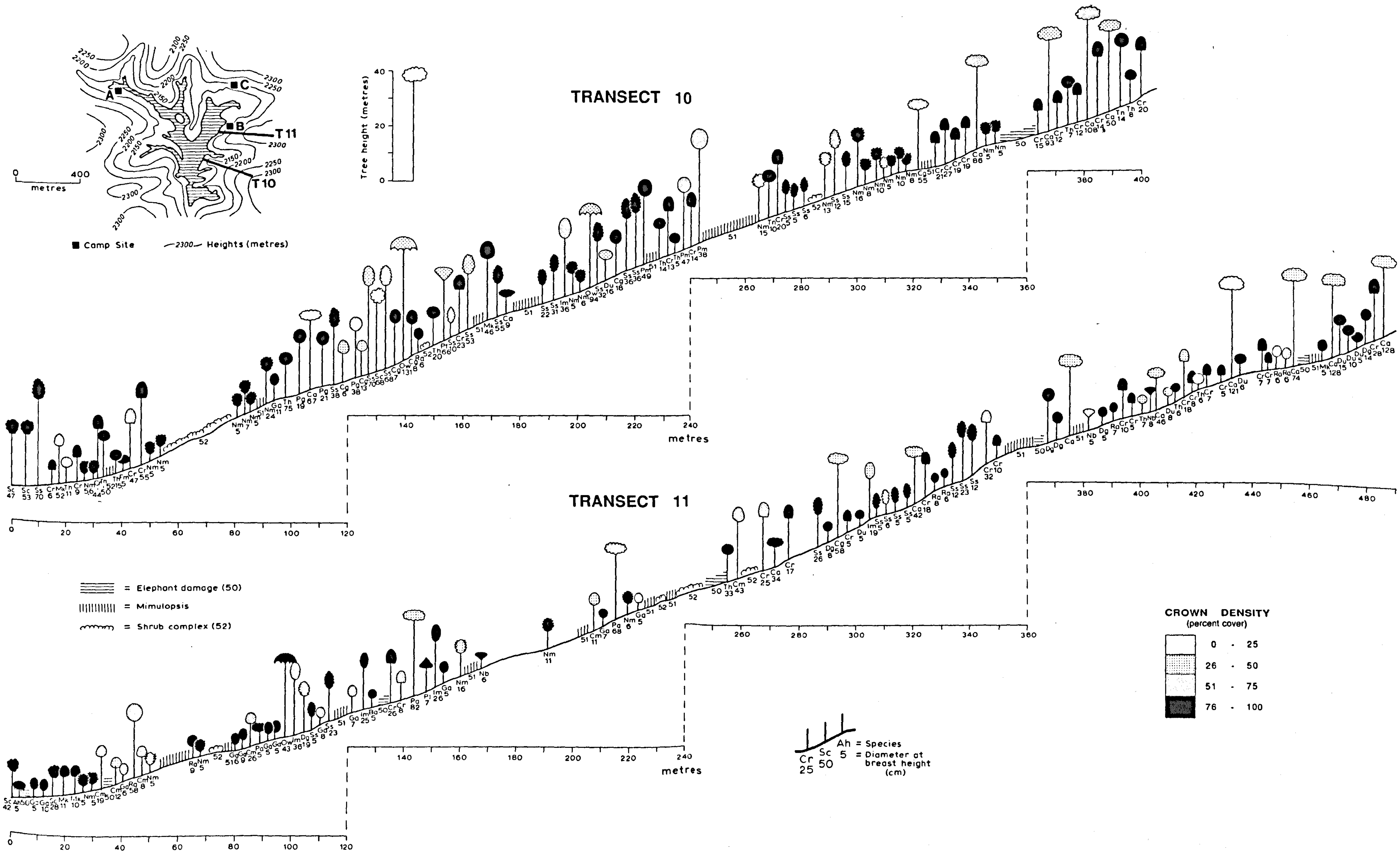


Figure 6.5 Vegetation attributes, composition and distribution along transects 10 and 11

6.3ii Results of the vegetation surveys

The results from each transect are described individually and an interpretation assigned to account for the local vegetation composition. The information from the individual transects is combined and a summary of the results presented. This will be used for a correlation with surface pollen spectra (Section 6.6).

Transect 1 (Figure 6.2) comprises a very open type of vegetation with *Mimulopsis* species dominant along the transect length. The shrub complex is also an important component of the vegetation. Trees, where present, were either *Syzygium cordatum* or young specimens of *Alchornea hirtella*, *Macaranga kilimandscharica* or *Neoboutonia macrocalyx*. Occasional specimens of *Drypetes ugandensis* and *Strombosia scheffleri* were also recorded. Throughout the transect, trees are either young specimens, or isolated from other trees. This resulted in the canopies being particularly dense. This transect is thought to be in an area recently pit-sawn. The area appears to have been almost clear-felled, as there were no large specimens present. Direct evidence to support this was found along transect 1 in the form of 'rounds' from an unidentifiable source; these are cut off and discarded prior to converting the felled tree to planks to be transported out of the forest.

Transect 2 (Figure 6.2) has a large proportion of small, young specimens of *Neoboutonia macrocalyx* in the lower part and *Alchornea hirtella* in the upper part of the transect. There is a mid-transect association of *Strombosia scheffleri* and *Tabernaemontana pachysiphon* in the lee of a large specimen of *Chrysophyllum albidum*. There are young specimens of *Harungana madagascariensis*, *Macaranga kilimandscharica* and *Polyscias fulva* present along the transect. The top part of the transect is dominated by a large *Chrysophyllum albidum* specimen. This transect is thought to be in an area recently pit sawn, albeit quite selectively, with only the more profitable species being taken out.

Transect 3 (Figure 6.3) starts with a large specimen of *Prunus africana* near the Mubwindi Swamp edge, which is surrounded by *Neoboutonia macrocalyx* and the shrub complex, interspersed with elephant tracks. A very large *Newtonia buchananii* is recorded without a surrounding under-story. There follows a

Strombosia scheffleri stand, with a young *Newtonia buchananii* present. This grades into an area dominated by *Chrysophyllum albidum* interspersed with *Cassipourea ruwensorensis*, *Drypetes ugandensis* and *Tabernaemontana pachysiphon*. The frequency of these species falls off as one gets onto the high ground, where there is increasing evidence of elephant activity. Due to the relatively large size of the trees present, and the lack of young colonising trees, it is thought the area represented by the transect has been selectively pit-sawn, approximately 20 to 40 years ago. Subsequent elephant movements and resultant damage have since been important in determining the vegetation composition and distribution along the transect.

Transect 4 (Figure 6.3) is situated on the low-lying ground close to Mubwindi Swamp. It comprises *Alchornea hirtella*, *Macaranga kilimandscharica* and *Syzygium cordatum*; *Alchornea hirtella* forming almost pure stands. It is thought his area has been very recently influenced by the activities of pit-sawing.

Transect 5 (Figure 6.3) is situated on low-lying ground although the vegetation is of a slightly more mature state than in transect 4. *Neoboutonia macrocalyx* dominates, with occasional specimens of *Croton macrostachyus* and *Macaranga kilimandscharica* present. Throughout the transect, the vegetation is quite open, being dominated by the shrub complex and latterly *Mimulopsis* species. There are occasional specimens of *Cassipourea ruwensorensis*, *Prunus africana*, *Strombosia scheffleri* and *Tabernaemontana pachysiphon* present, although these do not form forest of any discernible structure. As was the case with transect 4, it is suggested this area has recently been influenced by pit-sawing activity.

Transect 6 (Figure 6.4) intersects with transect 5. Consequently the vegetation composition and distribution is very similar, apart from the start of the transect, where *Podocarpus latifolius* and *Xymalos monospora* are found. This small stand has an under-story of *Macaranga kilimandscharica* and a ground flora of *Alchornea hirtella*. Why this enclave of vegetation remains is possibly explained by the relatively small dbh of the *Podocarpus latifolius* specimen. Presumably the *Podocarpus* would have been too small to cut during the period of pit-sawing activity. Overall, the transect is dominated by the shrub complex, interspersed with *Neoboutonia macrocalyx*. As with transect 5, the vegetation is thought to have been influenced by pit-sawing activity (Section 3.7), followed by subsequent grazing presence (supported by numerous animal tracks). This grazing is likely to have prevented colonisation by arboreal taxa.

Transect 7 and 8 will be considered together as they are both situated on a small island in Mubwindi Swamp (Figure 6.4). The composition and distribution of the vegetation is very different to what has been described so far; *Anthocleista zambesiaca*, *Ocotea kenyensis*, *Rytigynia kenyensis*, *Symphonia globulifera* and *Zanthoxylum gilleti* are present, with *Ocotea kenyensis* being common. Throughout the transects, there is a developed structure to the forest, with a canopy, sub-canopy and *Alchornea hirtella* commonly growing within the gaps. *Syzygium cordatum* is still a major component of the vegetation, although it is sub-dominant rather than dominant. Unlike the other transects the gaps are thought to originate from natural tree falls and elephant damage, rather than pit-sawing, because of the relative isolation of forest on the island. The vegetation along the two transects is thus thought to represent forest composition in the absence of past pit-sawing activity.

In the lower part of transect 9 (Figure 6.4) the vegetation is composed of *Croton macrostachyus*, *Cyathea manniana* and *Neoboutonia macrocalyx*. *Syzygium cordatum* is also present, with an under-story of *Alchornea hirtella* and *Macaranga kilimandscharica*. This association is present further up the slope than along the other transects. Further along the transect, *Cassipourea ruwensorensis* and *Strombosia scheffleri* start to dominate the vegetation, apart from a forty m long stand of *Alchornea hirtella*. The vegetation along this transect is thought to represent the influence of pit-sawing activity within the past twenty years.

Transect 10 (Figure 6.5) highlights three major points regarding the vegetation composition and distribution within the Mubwindi Swamp catchment. The vegetation at the lower part of the slope is characterised by *Cassipourea ruwensorensis*, *Neoboutonia macrocalyx*, *Syzygium cordatum*, *Tabernaemontana pachysiphon* and the shrub complex. The vegetation along this transect is thought to indicate a stage in montane forest regeneration, further supported by the young specimens of *Zanthoxylum gilleti* and the presence of the shrub complex. The Section from about 80 to 250 m is characterised by a well structured patch of forest with species not previously recorded. These include *Ilex mitis*, *Olea capensis* ssp. *welwitschii*, *Podocarpus flacatus* and *Podocarpus latifolius*. There is an under-story composed of *Cassipourea ruwensorensis*, *Strombosia scheffleri* and *Tabernaemontana pachysiphon*, together with occasional patches of *Mimulopsis*. The third feature of this transect is the transition into *Chrysophyllum*-dominated forest at the top of the slope, with a poorly developed under-story containing specimens of *Cassipourea ruwensorensis* and *Tabernaemontana pachysiphon*, which may have been effected by elephant damage. On a cautionary note, the differences in vegetation composition along transect 10 to those already described may be partly due to micro-climatic differences resulting from a change in aspect. The influence of environmental factors will be discussed in a summary of all the transect data. Vegetation along transect 10 is thought to represent either a latter stage in forest succession following pit-sawing activities, or a relatively undisturbed forest. The small dbh of the key timber species (Section 3.7) indicates the former is true.

Transect 11 (Figure 6.5) is quite different to transect 10, although it is on a similar aspect. Overall the species present are quite similar to transect 10 although the specimens are much smaller, well distributed and interspersed with large stands of *Mimulopsis* and elephant induced damage. However, one interesting similarity to transect 10 is recorded at the top of the transect, where *Chrysophyllum albidum* and *C. gorungosanum* dominate the forest, *Cassipourea ruwensorensis*, *Drypetes ugandensis* and *Tabernaemontana pachysiphon* being the principle sub-canopy forming species. The vegetation represented by transect 11 suggests the occurrence of pit-sawing activity within the past 20 to 30 years. This further supports the idea the vegetation along transect 10 represents a latter stage of forest recovery following on from pit-sawing. A possible explanation of this difference between the two transects is that transect 10 is located further away from the main path into Mubwindi Swamp, and hence it would have been logistically more difficult to abstract timber from this area.

6.3iii Summary of the vegetation surveys

The abundance of each species was calculated as a percentage value of the total number of specimens encountered within the Mubwindi Swamp catchment. This approach was used to provide a similar output to that from the surface pollen spectra (Section 6.5). The abundance of any given taxa is dependent on the abundance of all the other taxa recorded. The results are displayed as a bar chart (Figure 6.6), which includes only taxa that have an abundance of greater than 1% of the total number of taxa recorded. The results show *Neoboutonia macrocalyx* to be the dominant taxon within the Mubwindi Swamp catchment, accounting for 16 % of all specimens recorded, with *Alchornea hirtella* accounting for 14 % of all specimens recorded. The high percentage of these two taxa, both being characteristic of open forest, highlight the open nature of the montane forest, and thus the extent of past disturbance, within the catchment. *Cassipourea ruwensorensis* and *Strombosia scheffleri* are both present at densities of approximately 12 % of the total number of specimens recorded within the Mubwindi Swamp catchment. These two species were often found in close association, forming the dominant forest type with occasional species of *Drypetes* spp and *Tabernaemontana pachysiphon*. *Syzygium cordatum* is also present at approximately 12 % of the total number of specimens recorded. This species usually occupied a niche fringing Mubwindi Swamp, but did extend to higher altitudes. *Chrysophyllum albidum* was the next most common species, dominating the vegetation at the highest altitudes, often with an under-story of *Drypetes* spp. *Anthocleista zambesiaca*, *Cyathea manniana*, *Croton macrostachyus*, *Dombeya goetzenii*, *Ilex mitis*, *Macaranga kilimandscharica*, *Myrica kandtiana*, *Podocarpus* spp., *Olea* spp., *Polyscias fulva*, *Prunus africana*, *Rapanea* spp. and *Zanthoxylum gilleti* were all present at low quantities, *M. kilimandscharica* being the most common. All other species were recorded at abundances below 1 %.

6.3iv Discussion of the vegetation survey results

The combined results from the vegetation transects highlight significant differences in the present composition and distribution of the montane vegetation within the Mubwindi Swamp catchment. From the position of the transects within

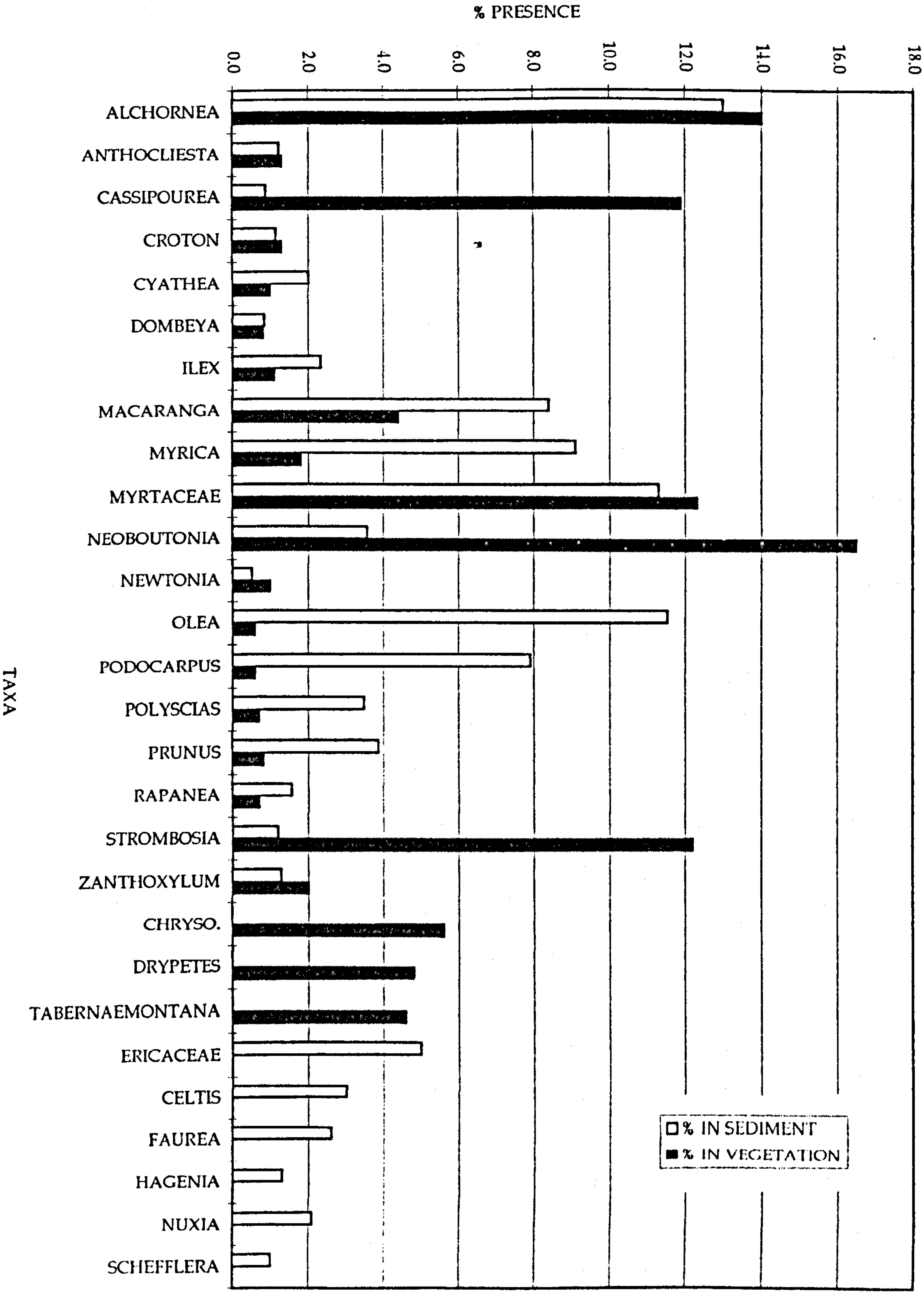


Figure 6.6 Chart showing % pollen form the surface sediments and % vegetation within the Mubwindi Swamp catchment

the catchment it is possible to infer the driving mechanism, or mechanisms, responsible for the present-day composition and distribution of vegetation.

The data indicate an important influence has been pit-sawing activity in the past (Section 3.7), and the recovery time lapsed since pit-sawyers ceased to operate in the areas covered by the transects. Indeed, the majority of the forest within the Mubwindi Swamp catchment can be described as secondary; the only site suggested not to have been influenced by pit-sawing activity is the small island, most probably because of logistical difficulties in abstracting timber across the swamp. It is suggested the vegetation recorded by transects 10 and 11 have had the longest time to recover, possibly up to 50 years in the southern-most parts of the Mubwindi Swamp catchment. The areas to the north and west of the swamp have been most recently influenced, possibly only five or ten years ago. As well as reflecting the influence of human-induced disturbance, the vegetation has been influenced by the locally catastrophic influence impact of large, forest dwelling mammals, such as elephant. One such area, along transect 11, coincided with the main migratory route from the bamboo zone to Mubwindi Swamp, the favoured habitats for elephants during the monsoonal and dry seasons respectively (Butynski, 1986). It is thought that forest gaps, and the forest shrub complex found therein, once produced by human activity, are maintained by elephants and more general mammal-induced grazing pressure.

All the differences in vegetation composition and distribution cannot be explained purely by past human activity and the activities of forest dwelling mammals. Indeed, transects 3, 10 and 11 were located on slopes of similar length, angle and altitudinal range, but of different aspect. Differences in vegetation, other than those attributed to disturbance, along the two transects are clearly visible, particularly in the lowermost parts of the profiles. For example, *Ilex mitis* and *Olea capensis* ssp. *welwitschii* are found on the colder, wetter, west-facing slopes of transects 10 and 11. The larger trees of *Newtonia buchananii* and *Prunus africana* are found on the relatively dryer, warmer, east facing slopes of transect 3. The influence of topography can also be seen in transect 9 where *Cyathea manniana* is recorded, this is possibly due to the locally cooler, wetter conditions created by the transect being on a promontory, and therefore surrounded on two sides by the swamp. This is also thought to account for the higher up-slope record of *Syzygium cordatum* along this transect. Similarly, the composition of the vegetation on the island (Transects 7 and 8), can be partly explained by being disturbance free. However, the different species recorded may result from the close proximity of Mubwindi Swamp and the influences this may have such as a wetter microclimate, wetter soils, period flooding etc.

There are some notable similarities in the data obtained during the vegetation survey. Vegetation on the highest points reached by the transects shows marked similarities: the main component is a canopy formed by *Chrysophyllum albidum*, with *Cassipourea ruwensorensis*, *Drypetes* spp. and *Strombosia scheffleri* forming a second strata. These taxa forming the second stratum on the upper hill-slopes form an association in their own right along the mid-slope areas. *Syzygium cordatum* is generally found in close proximity to Mubwindi Swamp, where it forms a fringing band, possibly aided by the locally wet edaphic and climatic conditions. This distribution of the species outlined is in agreement with catenary distribution suggested by Hamilton (1969) although without the transition into *Olea* and *Podocarpus* dominated forest on the ridge-tops.

Much of the vegetation within the Mubwindi Swamp catchment is comprised of immature trees, in particular *Neoboutonia macrocalyx* within the more open habitat and *Alchornea hirtella* within more enclosed areas. In smaller openings, *Croton macrostachyus*, *Dombeya goetzenii* and *Macaranga kilimandscharica* are also present as isolated individuals. The distribution of these specimens indicate that the colonising taxa within the surrounding vegetation have very specific roles, collectively these are able to occupy a range of specialist niches.

The composition and distribution of the vegetation within the Mubwindi Swamp catchment has been shown to be a mosaic composed of several different associations, some of these are driven by local climatic and edaphic conditions, others are a result of past human-induced disturbance. Superimposed on these are the ecological constraints of forest regeneration and niche occupation.

6.4i Surface sediment sample collection and analysis of modern pollen samples

Surface sediment samples were collected in 1994 at 15, 30 and 45 m intervals along four transects on the swamp (Figure 6.7). Two of these transects continued the line from belt transects 3 and 10. One further transect was located on each of the arms of Mubwindi Swamp. Moss polsters and *Usnea* samples were collected from trees fringing the swamp, as these were thought to be effective pollen traps. An attempt was made to collect pollen from the surface traps being placed on the Mubwindi Swamp surface after one year, although only two of these could be retrieved, and one of these was contaminated by *Ficus* pollen. This was known as *Ficus* spp. have a very specialised pollination mechanism involving close association with wasps. To increase the number of surface samples used, David Taylor collected a further twelve samples from the northern arms of Mubwindi Swamp in 1995 (Figure 6.7). Therefore, a total of twenty-four surface samples from a range of locations on Mubwindi Swamp were analysed for their pollen content.

6.4ii Preparation technique for pollen analysis

Pollen was concentrated from all surface samples using the standard preparation procedure of Faegri and Iversen (1989). Due to the fibrous nature of the surface sediment, the samples were left in KOH for up to 30 minutes to allow for easier sieving of the material. Throughout the preparation, a standard amount of sample (5 cm^3), and reagent (5 ml) were used. Reaction and centrifuge times were also kept constant.

6.4iii Pollen counting and determination of the 'optimum count'

The optimum count can be defined as the number of pollen grains required to be counted per sample, so that the pollen sum is representative of the total number of pollen grains present in the sample. An optimum count of 500 grains $sample^{-1}$ has been computed from a range of swamps in Uganda by Hamilton (1972). To verify Hamilton's (1972) estimate, ten sediment samples were counted in increments of

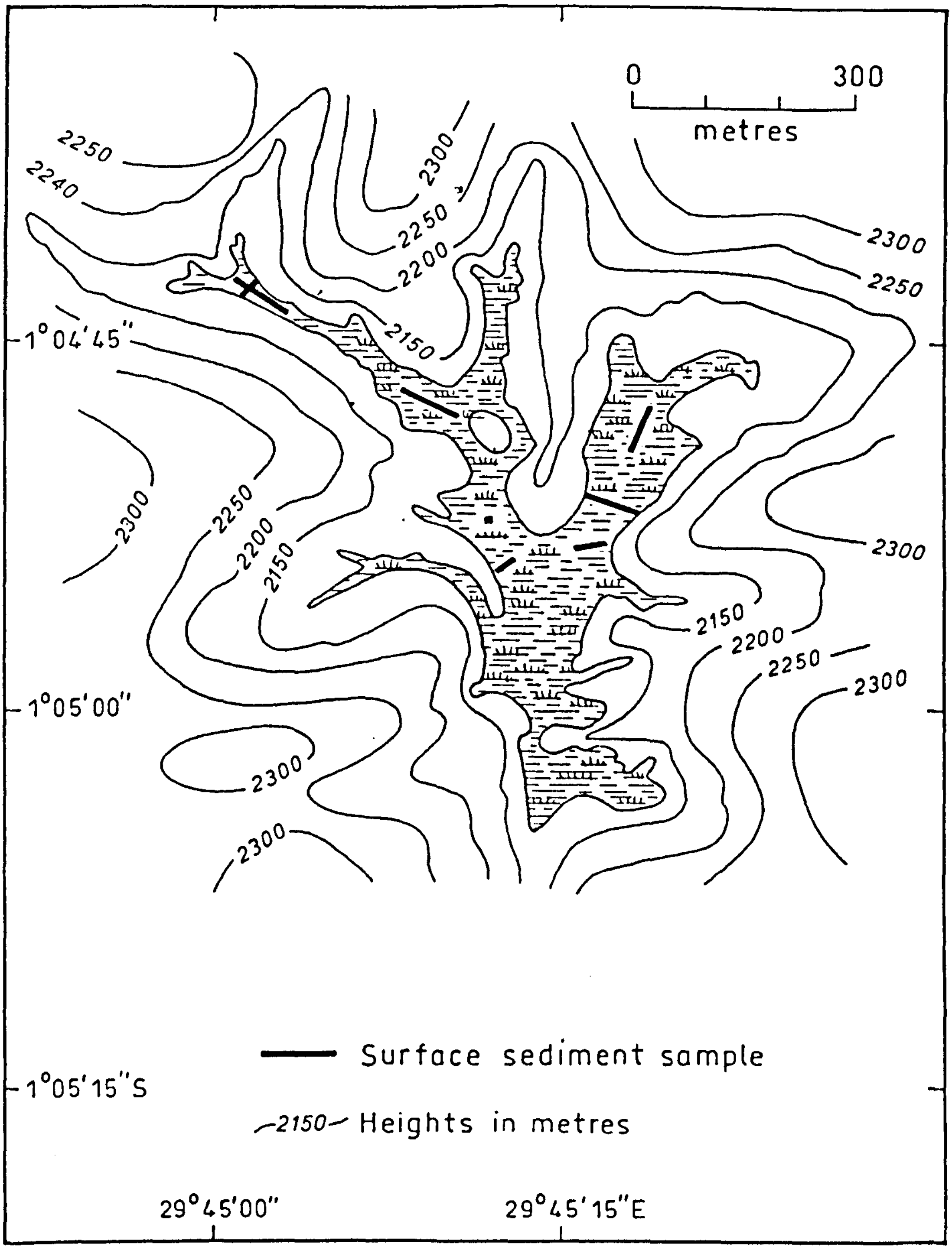


Figure 6.7 Location of surface sediment samples on Mubwindi Swamp surface

100 grains to a total of 1000 grains. At each increment a note was made of the number of taxa recorded. The results supported Hamilton's (1972) estimates; new taxa were not recorded at every increment, and commonly not at all, on reaching the fifth increment (500 grains). As a result, the optimum count was set at 500 grains for future counts. Pollen was counted along vertical transects, 2 mm apart. The area on each slide was completely covered, so as to counteract possible differential pollen migration within the slide (Brooks and Thomas, 1967).

6.5 Pollen composition within the Mubwindi Swamp surface sediments

Once the pollen content of surface samples had been determined, the non-local pollen retained within the surface sediments were separated. This sub-set comprised all pollen types likely to have originated from parent taxa growing on hillsides adjacent to the swamp. This sub-set formed the non-local pollen sum, the counts for individual taxa being converted to a percentage value. Pollen data from the twenty-four surface samples were summed, and a mean percentage value for the individual pollen types produced (i.e. a percentage for each non-local pollen type present within the surface sediment samples). These percentage data were displayed as a separate bar corresponding to the percentage value of the parent taxa within the surrounding vegetation (Figure 6.6).

Alchornea, Myrtaceae and *Olea* pollen dominate the non-local pollen, each accounting for approximately 12 % of the non-local pollen. *Macaranga*, *Myrica*, and *Podocarpus* pollen each account for about 8 % of the non-local pollen. Ericaceae, *Neoboutonia*, *Polyscias* and *Prunus* pollen all contribute approximately 4 % of the non-local pollen. There are low amounts of *Celtis*, *Faurea*, *Ilex* and *Nuxia* pollen present. Other pollen types recorded were present at levels of 2 % or lower.

6.6 The relationship between the vegetation transect and modern pollen data

So that comparisons could be drawn between the vegetation and pollen percentage data, a bar chart was produced with the percentage vegetation and pollen data forming the two series (Figure 6.6). These data were arranged into three groups:

taxa that were present within the surrounding vegetation, and in surface pollen samples; taxa that were present in the vegetation but not in the surface pollen data; and taxa that were not present in the vegetation, but were represented in surface pollen samples.

The concentration of *Alchornea*, *Anthocleista*, *Croton*, *Cyathea*, *Dombeya*, *Ilex*, Myrtaceae, *Newtonia*, *Rapanea* and *Zanthoxylum* pollen and spores within the surface sediments closely reflect the density of their parent taxa within the vegetation surrounding the swamp. For these taxa, the close relationship suggests that pollen accumulating within the swamp sediments are an accurate reflection of the parent taxa being present within the surrounding vegetation. This result is particularly interesting for *Croton* and *Dombeya*; both pollen types have very large pollen grains (Appendix 1), and have been traditionally thought of as very poorly dispersed (Hamilton, 1972; Taylor, 1991; 1993). This relationship may not hold true where the parent specimens are growing relatively close to the pollen deposition site, as is the case at Mubwindi Swamp. Furthermore, the *Croton macrostachyus* and *Dombeya goetzenii* specimens recorded from the vegetation survey are relatively large, thus providing an increased capacity for pollen dispersal.

Cassipourea ruwensorensis, *Neoboutonia macrocalyx* and *Strombosia scheffleri*, although common in the surrounding vegetation, were poorly represented by their pollen. All these taxa have been classified by Hamilton (1972) as poorly dispersed types. *Macaranga*, *Myrica*, *Olea*, *Podocarpus*, *Polyscias* and *Prunus* pollen types were present in the surface sediment samples at much higher percentages than their parent taxa were in the vegetation surrounding Mubwindi Swamp. This finding agrees with Hamilton's (1972) classification for these pollen types. Even so, particularly for *Olea*, the high amount of pollen present is quite remarkable, given the low presence of the parent taxa recorded along the vegetation transects. It is quite possible there has been additional input of some of these pollen types from extra-catchment sources. The relatively high amount of *Myrica* pollen can be explained by the localised growth of *Myrica kandtiana* on the Mubwindi Swamp surface.

Species of *Chrysophyllum*, *Drypetes*, and *Tabernaemontana* are relatively common within the surrounding vegetation, but are not recorded by their pollen in the surface sediments. This finding is very important as they were significant components within the surrounding vegetation, each species being responsible for approximately five percent of all those recorded. The total lack of pollen from these taxa indicate these species either have a specialised pollination mechanism, such as present within *Ficus*, or their pollen is not well preserved. Due to the lack of pollen commuted to the accumulating sediments these taxa are excluded from any reconstruction of past vegetation patterns from fossil pollen data. This omission, when the parent taxa are important components of the surrounding vegetation, indicates that former reconstructions of montane vegetation from palaeoecological data have only been 'partial' with some substantial omissions in the 'reconstructed vegetation'. That said, it is only possible to reconstruct the vegetation on the information (pollen) available.

Celtis, Ericaceae, *Faurea*, *Hagenia*, *Nuxia* and *Scheffleri* pollen are recorded, albeit at low percentages, in the surface sediments, but not by their parent taxa within the surrounding vegetation. Species of these genera were noted within the Mubwindi Swamp catchment (but not recorded by the vegetation transect), or were recorded at slightly higher altitudes elsewhere within Bwindi-Impenetrable Forest. Consequently these must be viewed as moderately to well dispersed pollen types, with a record of pollen within the accumulated sediment not necessarily being derived from vegetation within the Mubwindi Swamp catchment. The major difference from Hamilton's (1972) classification is that *Faurea*, which is classed as a poorly dispersed type, was recorded at relatively low levels. Thus, it is suggested that *Faurea* should be re-classified as a moderately well dispersed type, particularly for the Mubwindi Swamp catchment.

The results from the surface pollen spectra and vegetation surveys generally indicate that pollen accumulations within the sediments at Mubwindi Swamp reflect the vegetation growing within the immediate catchment. This is particularly so as the modern samples were taken from a location and environment similar to those from where the fossil sequences were collected, and therefore not subjected to the biases which may be found in studies of pollen in forest hollows (Calcote, 1995), moss polsters (Spieksma *et al*, 1994; Kershaw and Bulman, 1994; Ritchie, 1974) and pollen traps (Davis and Thompson-Webb III, 1975; Meadows, 1984; Hamilton and Perrot, 1980). This finding supports further the suggestion by Taylor (1993) that the tightly constrained catchments of the swamps within the Rukiga highlands, makes them ideal locations for palynological study. However, the specific elements of the pollen-vegetation relationship determined for Mubwindi Swamp could not be directly applied to the other swamps within the Rukiga highlands due to the range of factors determining this relationship (Section 6.1), many of which are individual to the Mubwindi Swamp catchment.

CHAPTER 7

Fossil pollen analysis of the Mubwindi Swamp sediments: methodology, zonation and the relationship to sediment analysis

7.1 Introduction

Within this Chapter, an account is given of the problems associated with palynology in tropical environments. Results derived from the numerical zonation of pollen and spore concentrations from three sediment cores (MB3, MB6 and MB23) will be presented. Using information from Chapters 4 and 5, the relationship between the stratigraphic zones, dating control, variations in charcoal and inorganic matter particle size and the zones derived from pollen analysis will be determined.

7.2 Pollen and spore analysis

Pollen and spores were concentrated from 1 cm^3 sub-samples taken from cores MB3, MB6 and MB23. The preparation procedure used (Faegri and Iverson, 1989) was the same as in the concentration of pollen and spores from surface sediment samples (Chapter 6). Samples prepared in the above fashion were smeared onto microscope slides and sealed beneath coverslips. Their pollen and spore content was determined along a series of vertical transects using * 400 and * 1000 magnifications under a Nikon Optiphot microscope. These transects started at the left edge of the slide and were spaced 2 mm apart. Each slide was counted up to the edge of the cover-slip, so as to counteract possible differential pollen migration within the slide, and the 'edge effect' (Brooks and Thomas, 1967). In accordance with the recommendations of Hamilton (1972), and the investigation undertaken in chapter 6, at least 500 pollen grains and spores were identified and counted for each sub-sample. A list of the more common pollen types identified, along with morphological descriptions, an indication of probable source and the ecological range of the parent taxa is provided in Appendix 1.

The amount of a taxon's pollen in a sample is usually expressed in pollen analytical work as either relative to that of other taxa in the sample, or as an absolute figure, independent of other types. The abundances of a given pollen taxon in cores MB3, MB6 and MB23 presented in Chapter 8 are expressed as a percentage values. Therefore, any value is relative to that of all the other taxa in the pollen sum. In common with calculations of relative frequency, percentage values invoke a mathematical problem - that of determining the pollen sum. The influence of large changes in the presence of a given pollen type, or under-representation of other pollen types, can be negated by carefully choosing the components of the pollen sum. Indeed, the pollen sum upon which the percentage calculations are based can vary according to the requirement of the analyst (Birks and Gordon, 1985). In the present work, three pollen sums were used. The first, *non-local pollen*, comprised all pollen types thought to have originated from taxa growing on the hillsides surrounding Mubwindi Swamp. The second, *local pollen and spores*, was based on all the local pollen and spore types. Due to the dominance of the parent taxa on the Mubwindi Swamp surface, Cyperaceae pollen and *Psilate* Fern spores dominated the local pollen spectra, so much so that other local pollen types were thought to be under-represented. Thus, these two palynomorphs were removed from the local pollen sum, and percentage values recalculate to form a third sum; *non-dominant local pollen and spores*. The pollen taxa used to produce each pollen sum are portrayed in Table 7.1.

Based on the assumption that vegetation occupying the hill-sides adjacent to Mubwindi Swamp is a more precise indicator of the general composition of the forest than taxa found on Mubwindi Swamp, the non-local pollen sum is the most important pollen sum for inferring changes in vegetation of the Mubwindi Swamp catchment over the cored record. Conversely, pollen produced by local vegetation is liable to considerable fluctuations in frequency over short vertical and horizontal distances in sediment (Hamilton, 1972). Therefore the zonations presented in this Chapter will focus on the non-local pollen data.

7.3 Construction and zonation of the pollen data

Percentage pollen data from the three sediment cores are portrayed using histogram diagrams. In order to facilitate description, comparison and discussion of the pollen data, each core was divided into a series of pollen zones. Pollen

NON -LOCAL POLLEN	LOCAL POLLEN	NON-DOMINANT LOCAL POLLEN
Acalypha	Alchemilla	Alchemilla
Alangium	Anthoceros	Anthoceros
Afrocrania	Balinites	Balinites
Alchornea	Callitriche	Callitriche
Anthocleista	Canthium	Canthium
Anthospermum	Carduus	Carduus
Araliaceae type	Caryophyllaceae	Caryophyllaceae
Artemisia	Clutia	Clutia
Augaria	Compositae type	Compositae
Bersama	Crassulaceae	Crassulaceae
Bidens	Cruciferae	Cruciferae
Brilliantasia	Cyperaceae	Epilobium
Buddleia	Epilobium	Eriocaulon
Cassipourea	Eriocaulon	Erythrococoa
Celestraceae	Erythrococoa	Gramineae
Celtis	Gramineae	Grammitis
Chenopodium	Grammitis	Gunnera
Chrysophyllum	Gunnera	Helichrysum
Clematis	Helichrysum	Hydrocotyle
Cliffortia	Hydrocotyle	Hypericum
Combretaceae	Hypericum	Impatiens
Commiphora	Impatiens	Labiatea
Croton	Labiatea	Laurembergia
Cussonia / Schefflera	Laurembergia	Lobelia
Dendroscencio	Lobelia	Loganiaceae
Dodonaea	Loganiaceae	Lythrum
Dombeya	Lythrum	Lycopodium
Ebernaceae	Lycopodium	Monolete Fern Spores (Polypodium)
Entandophragma	Monolete Fern Spores (Polypodium)	Monolete Fern Spores (Echinate)
Ericaceae	Monolete Fern Spores (Psilate)	Myrica
Erythrina	Monolete Fern Spores (Echinate)	Potamogeton
Fagaropsis	Myrica	Pteris
Faurea	Potamogeton	Selaginella
Fichalhoa	Pteris	Silene
Ficus	Selaginella	Sphagnum
Hagenia	Silene	Trilete spores (other)
Ilex	Sphagnum	Typha
Jasminum	Trilete spores (other)	Umbelliferae
Juniperus	Typha	Damaged
Loranthaceae	Umbelliferae	Unidentified
Macaranga	Damaged	
Maesa	Unidentified	
Maesopsis		
Maytaynus		
Meliaceae / Sapotaceae		
Mimulopsis		
Mitragyna		
Morus		
Musanga / Myrianthus		
Myrtaceae		
Neoboutonia		
Newtonia		
Nuxia		
Olea		
Olinia		
Pilea		
Plantago		
Podocarpus		
Polyscias		
Premna		
Prunus		
Psychotria		
Rapanea		
Rumex		
Stoebe		
Symphonia		
Teclea		
Thalictrum		
Trema		
Urticaceae		
Vernonia		
Zanthoxylum		

Table 7.1 Pollen types comprising the three pollen sums

zones are delimited on the criteria of their pollen and spore content, without reference to time-scale, sediment stratigraphy or inferences concerning past climate or vegetation. Therefore, pollen zones are bio-stratigraphic units (Moore *et al*, 1991), purely defined by pollen content.

All pollen diagrams produced in this thesis have been zoned numerically. Gordon and Birks (1972) state that in numerical zonation schemes, pollen produced by local sources should be removed, as these may be subject to large fluctuations. Once the percentage calculations had been completed, any taxa that did not appear at concentrations of greater than 2 % throughout the sediment cores were removed from the percentage matrix, prior to zoning and construction of the pollen diagrams. Pollen zone boundaries were identified by a clustering program within the Tilia software package. This is based on the coefficient of the squared Euclidean distance between individual values of the data matrix. Squared Euclidean distance is a measure of dissimilarity between paired objects (Birks and Gordon, 1985), i.e. the dissimilarity between two samples brought about by differences in the types and percentages of pollen taxa. The coefficient is based on the Euclidean properties of a right-angled triangle, and the square of the hypotenuse (Euclidean distance) is equal to the sum of the squares of the two opposite sides, the sum of the squares being determined by the characteristics of adjacent pollen samples.

The Euclidean coefficient is calculated by the formulae

$$Dab = \sqrt{\sum_{k=1}^{m} (Xak - Xbk)}$$

Dab = Squared Euclidean distance between sample depth a, b
m = number of samples
Xak = the abundance of the kth species in sample depth a
Xbk = the abundance of the kth species in sample depth b

The lower the value of the squared Euclidean distance between two pollen counts, the more similar their pollen composition. The lowest limit of the coefficient is 0, representing complete similarity. There is no fixed upper limit. As a result of this scale, there is likely to be a skewed distribution of the coefficients around 0. Thus, the squared Euclidean distance is likely to emphasise the effect of the more abundant taxa even more strongly, through the square power (Birks and Gordon, 1985).

Clustering of similar samples (in terms of their pollen spectra) produces a hierarchical dendrogram (Chapter 8). This allows the major pollen zones and pollen sub-zones to be identified (Figure 7.1). The zonation scheme used is a numbered sequence that increases from the bottom. Numbers attached to the pollen zone are prefixed by the core notation; for example MB3.1, MB6.1 and MB23.1. Where the pollen zone has been divided into sub-zones, as highlighted by the numerical analysis, sub-zones carry the same notation as the pollen zone but with the additional label of a lower case letter. A similarity of numbering for pollen zones from different cores denotes a similarity of the pollen flora between the different cores. This cross-core correlation was not possible for all the sub-zones; where a relationship does exist, it will be highlighted within the interpretation of the pollen data (Chapter 8). The division between the pollen zones is drawn as a long dashed line, the sub-zone division is recorded as a short dotted line.

Birks (1986), Gordon, (1982) and Birks and Gordon (1985) recommend the additional analyses should always be undertaken on any data set so as to guard against unwarranted conclusions being drawn on the basis of one particular method of analysis. As the Euclidean dissimilarity measure within Tilia was stratigraphically constrained, the effectiveness of this method was checked by a stratigraphically unconstrained technique. Similar to the construction of the pollen diagrams, the non-local pollen sum is deemed most sensitive to, and indicative of, vegetation dynamics surrounding Mubwindi Swamp. Therefore, this data sub-set was the focus of further analysis. To verify the results from the constrained zonation method, and to highlight relationships which may exist between non-contiguous samples of the non-local pollen data, a non-constrained numerical method was applied to the data. The technique applied was detrended correspondence analysis (DCA), through the use of the computer program CANOCO (ter Braak, 1988). This technique was chosen from a range of

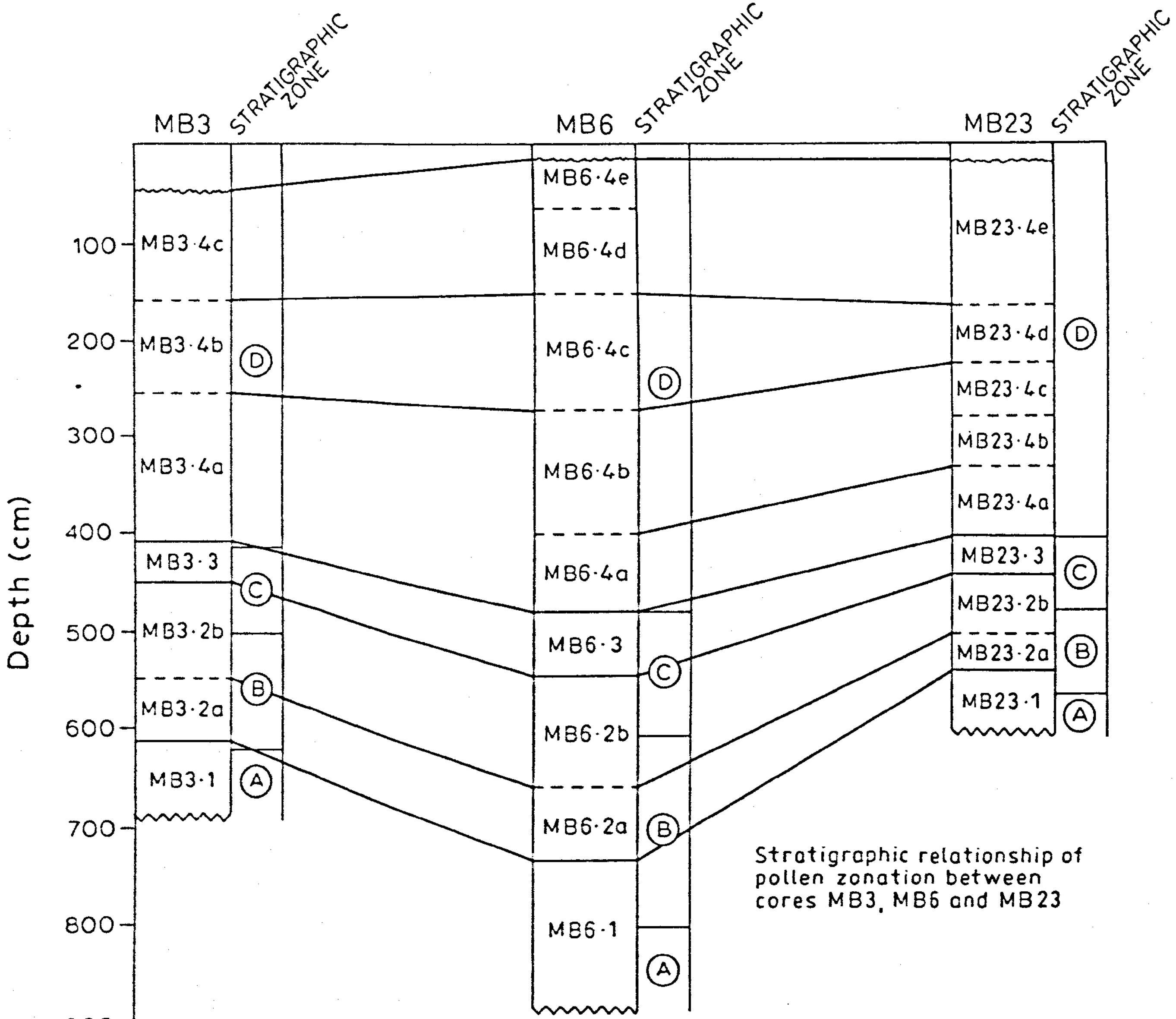


Figure 7.1 Stratigraphic relationship of pollen and stratigraphic zones in cores MB3, MB6 and MB23

ordination techniques as it mitigates some of the problems associated with earlier techniques (Hill and Gauch, 1980). A brief introduction to this method will be given, and some of the associated problems will be outlined. For a full review of the method see Birks and Gordon (1985) and Kent and Coker (1992).

DCA ordinates multivariate data sets, such as a pollen v. sample-depth matrix. In order to grasp the rational of DCA it is necessary to appreciate the faults of reciprocal averaging (RA), upon which DCA is based. DCA overcomes two of the major methodological problems associated with RA. Of these, perhaps the worst is the 'arch effect' (Gauch *et al*, 1977). The arch effect is a mathematical artefact, corresponding to no numerical structure within the data. The artefact arises because the second axis of the RA is constrained to be uncorrelated with the first axis, but is not constrained to be independent of it. For the subsequent axes of the ordination to be separately interpretable they need to be independent of previous axes, not merely constrained to be uncorrelated (Hill and Gauch, 1980). The second main fault of RA manifests itself as similar paired ecological distances from the raw data are not always apparent in the output data. Sample pairs with equivalent compositional distances within the data appear further apart in the middle of, than towards the ends of, the RA axis. Hence, there is compression of the data at either ends of the ordination axes.

The arch effect can be eliminated by ensuring that subsequent axes are independent of each other. The DCA analysis recalculates the second axis scores so as to have an average of zero. This is then repeated on an axis by axis basis up to the fourth axis. The other problem of differential compression of data is overcome by detrending the data. Detrending places data points equidistantly along each axis used for the ordination (Kent and Coker, 1992). When coming to calculate the placing of the data points in ordination space the points are expressed as a deviation from zero. Thus, the output data from the DCA analysis are scaled in units of standard deviation.

Although DCA is one of, if not the best ordination techniques available, there can still be problems if the affects of outliers are not accounted for (Kent and Coker, 1992). The only way to cope with extreme outliers is to remove them (CANOCO allows for the removal of unwanted samples). As the data were in percentage format there were no extreme outliers within the non-local pollen sum.

A problem that can never be eliminated is how to interpret the axes (van der Maarel, 1979). As a default, DCA via CANOCO uses four axes to account for the variation apparent within the data matrix. Usually, as was the case with the Mubwindi Swamp data, the first two axes explain the majority of the original variability within the data matrix, and can thus be regarded as providing a reasonably accurate summary of the information contained in a full four dimensional plot (Birks and Gordon, 1985). Everitt (1978) described a procedure which he calls the biplot; this allows for a graphical display of the relationship between individual data points. To plot the results from the DCA analysis, the DCA output files are converted to a CALIBRATE format, for use within the software CALIBRATE (Juggins and ter Braak, 1994). This package was preferred to the others available as it was the most flexible within its plotting options. As a rule, samples placed close together on the bi-plot will have a close association in the data set, and hence are likely to be associated ecologically and/or stratigraphically. Conversely, those placed far apart from each other in ordination space are likely to be quite different from each other.

7.4 Presentation and description of the results

Due to the core having the longest length of those analysed, the best dating control, and the most detailed sedimentary analysis the presentation of results will focus on data generated from core MB6. Data from cores MB3 and MB23 will be used to support the data from MB6, to clarify anomalies within the record, and allow for extrapolation and verification of the radiocarbon (Chapter 4) and sedimentary (Chapter 5) data. The pollen zones produced for each of the cores by the stratigraphically constrained analysis are portrayed in Figure 7.1. This also highlights the relationship of the stratigraphic zones presented in Chapter 4 to the pollen zones. The stratigraphic relationship between pollen zones and sub-zones is highlighted in Figure 7.1. Results from the DCA analysis of core MB6 are plotted in Figure 7.2. A high resolution DCA bi-plot of pollen zone MB6.4 is presented in Figure 7.3. Results from the DCA analysis of core MB3 are plotted in Figure 7.4.

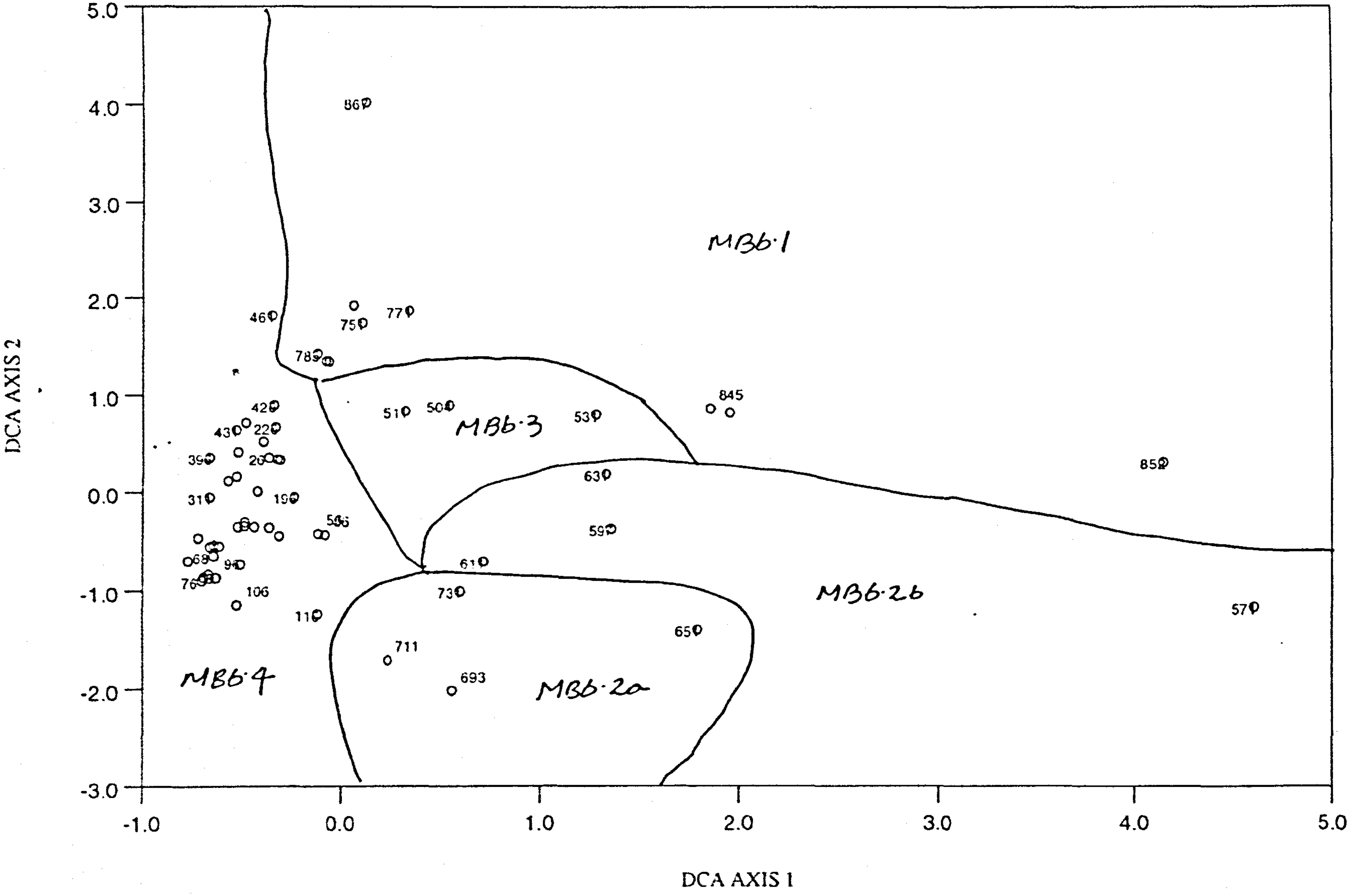


Figure 7.2 Core MB6: DCA plot highlighting sample depths for the non-local pollen sum

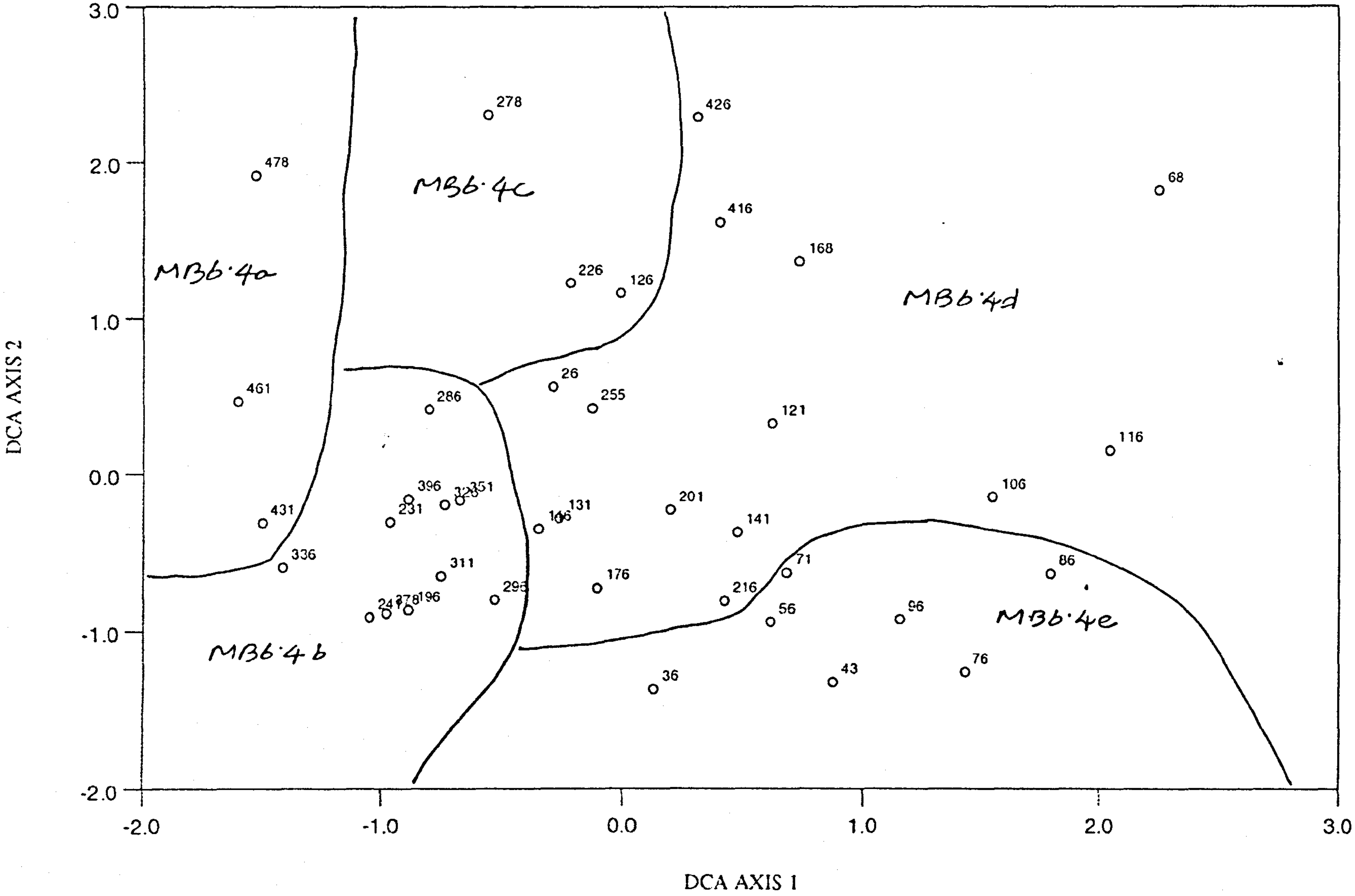


Figure 7.3 DCA plot highlighting sub groupings within pollen zone MB6 4

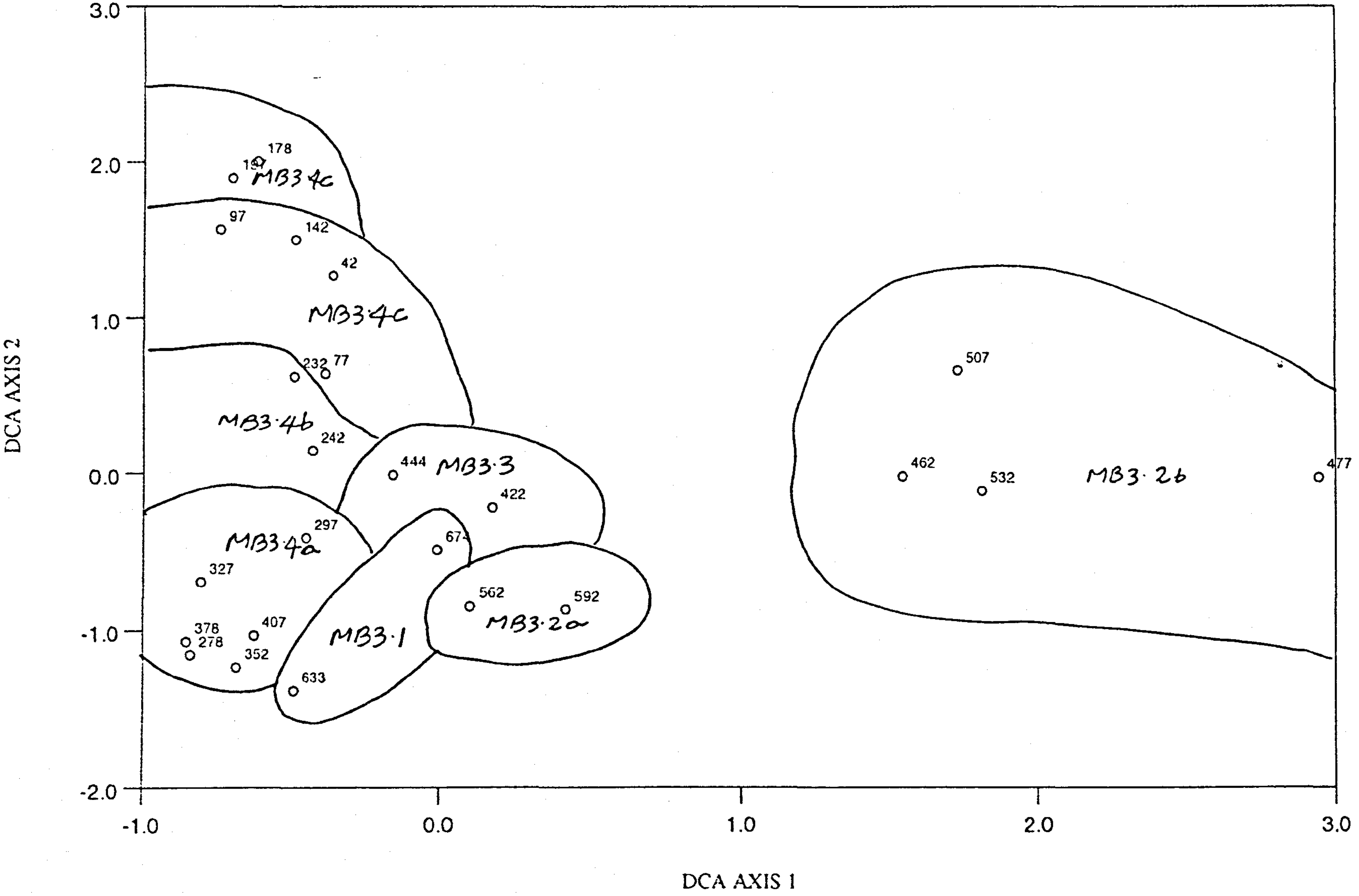


Figure 7.4 Core MB3: DCA plot highlighting sample depths for the non-local pollen sum

To identify the relationship between the positioning of the pollen zones in Figure 7.1, and the changes identified from the sedimentary analysis (Chapter 5) key results from Chapter 5 are plotted and zoned numerically. Plots of the gravimetric determination of charcoal, when standardised against inorganic matter, for cores MB3 and MB6 are presented in Figures 7.5 and 7.6 respectively. A plot of inorganic particle size changes for core MB6 is presented in Figure 7.7. So that changes in charcoal abundances within pollen zone MB6.4 could be identified, results portrayed in Figure 5.10 will be described in relation to the pollen sub-zones identified within pollen zone MB6.4.

Both the stratigraphically constrained and unconstrained numerical clustering techniques applied to core MB6 (Figures 7.1 and 7.2) have identified four major pollen zones (MB6.1 to MB6.4). Pollen zone MB6.2. is further sub-divided into two sub-zones. The DCA plot (Figure 7.3) of pollen zone MB6.4 weakly identifies a total of five clusters. These clusters within pollen zone MB6.4 are more apparent from the stratigraphically constrained analysis (Figure 7.1). It should be emphasised the clusters annotated within the DCA plots highlight some similarities between samples from different pollen zones. This facet of the results, particularly within the Holocene record, is due to a similarity of the pollen data from some non-contiguous levels. The implication of these results will be discussed for each pollen zone where appropriate within Chapter 8. Conversely, the considerable distance apart in ordination space of some of the clusters emphasises the very different characteristics of some of the pollen zones.

Stratigraphic zone A contains the base of pollen zones MB3.1, MB6.1 and MB23.1. The base of pollen zone MB6.1 is characterised by a very fine inorganic fraction (Figure 7.7). Both in cores MB3 and MB6 stratigraphic zone A is characterised by low levels of charcoal (Figures 7.5 and 7.6). As the boundary between stratigraphic zones A and B is recorded closest to the depth of the MB3.1 to MB3.2 and MB23.1 to MB23.2 pollen zone boundaries, it is suggested there may be a relatively short sedimentary hiatus at the position of the pollen zone boundaries in cores MB3 and MB23. This may also be recorded within core MB6, although not for as long a duration.

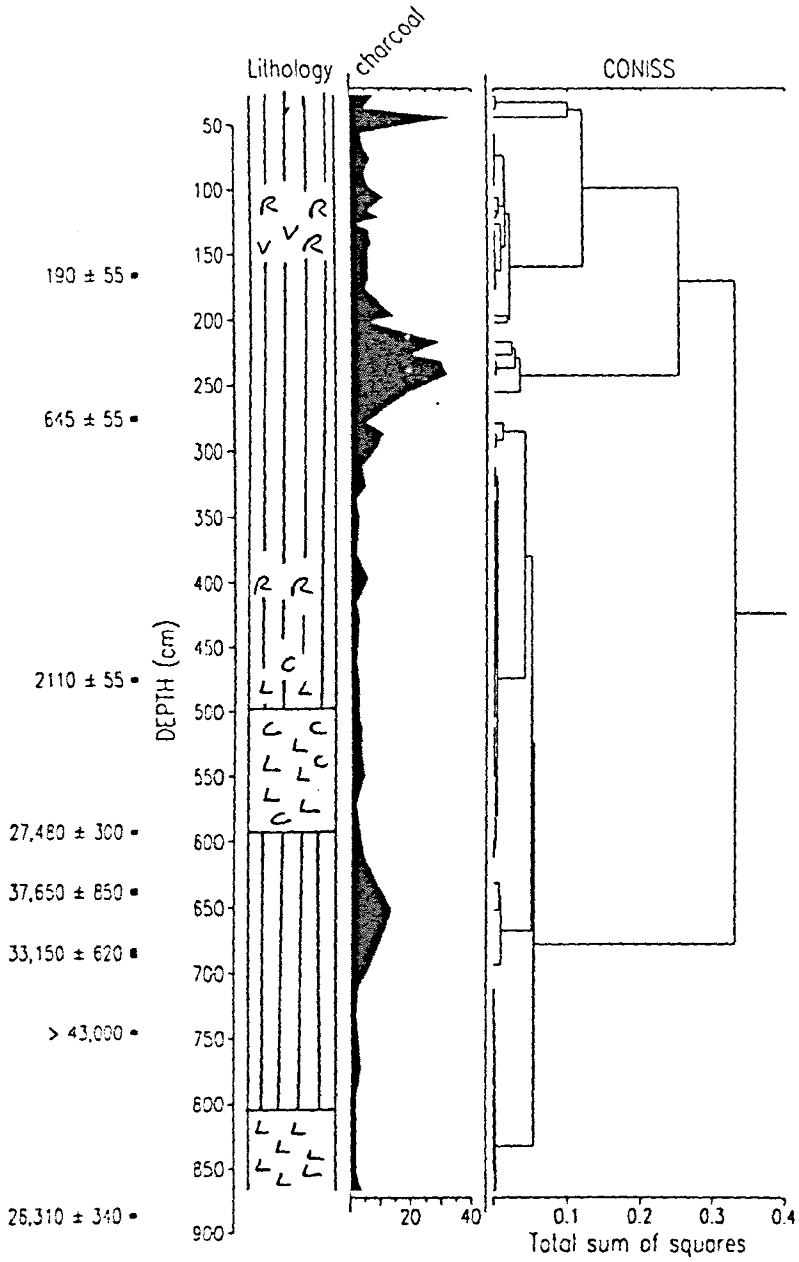


Figure 7.5 Core MB6: zonation of the charcoal record

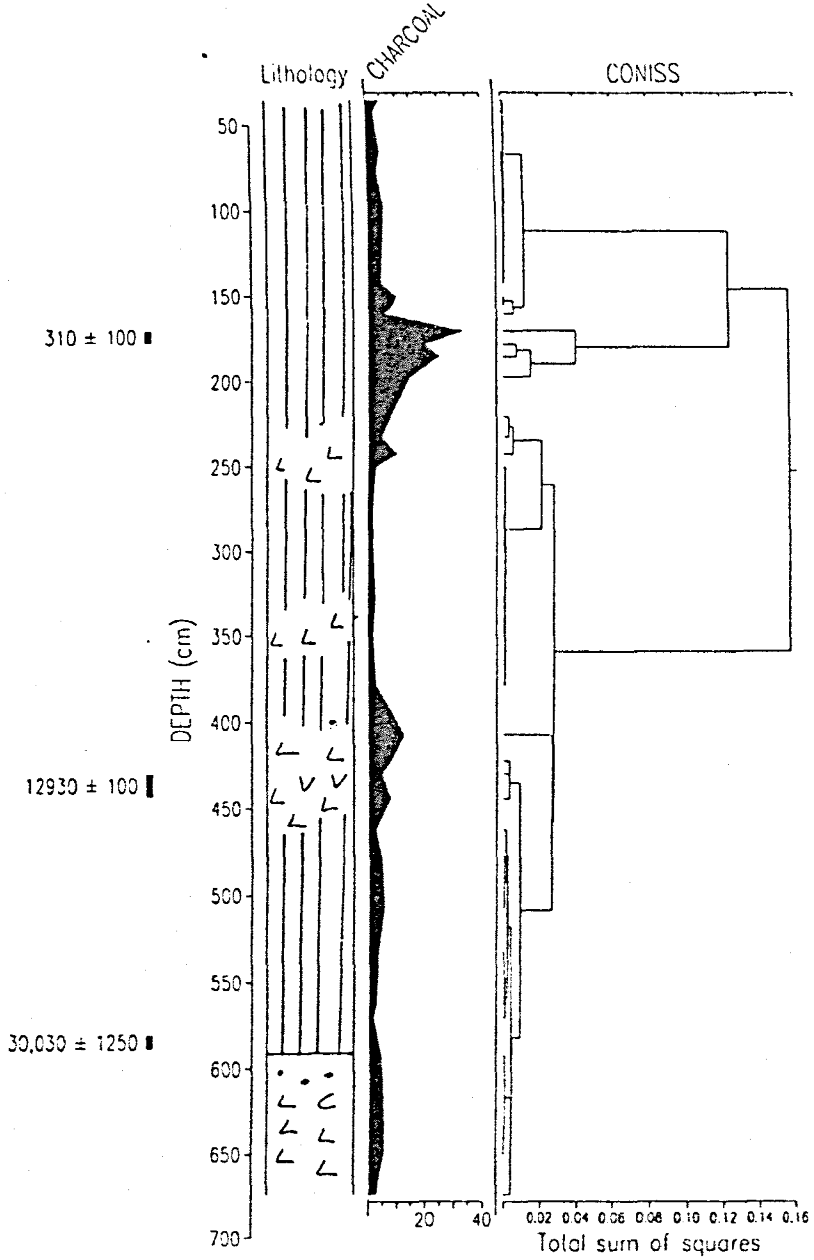


Figure 7.6 Core MB3: zonation of the charcoal record

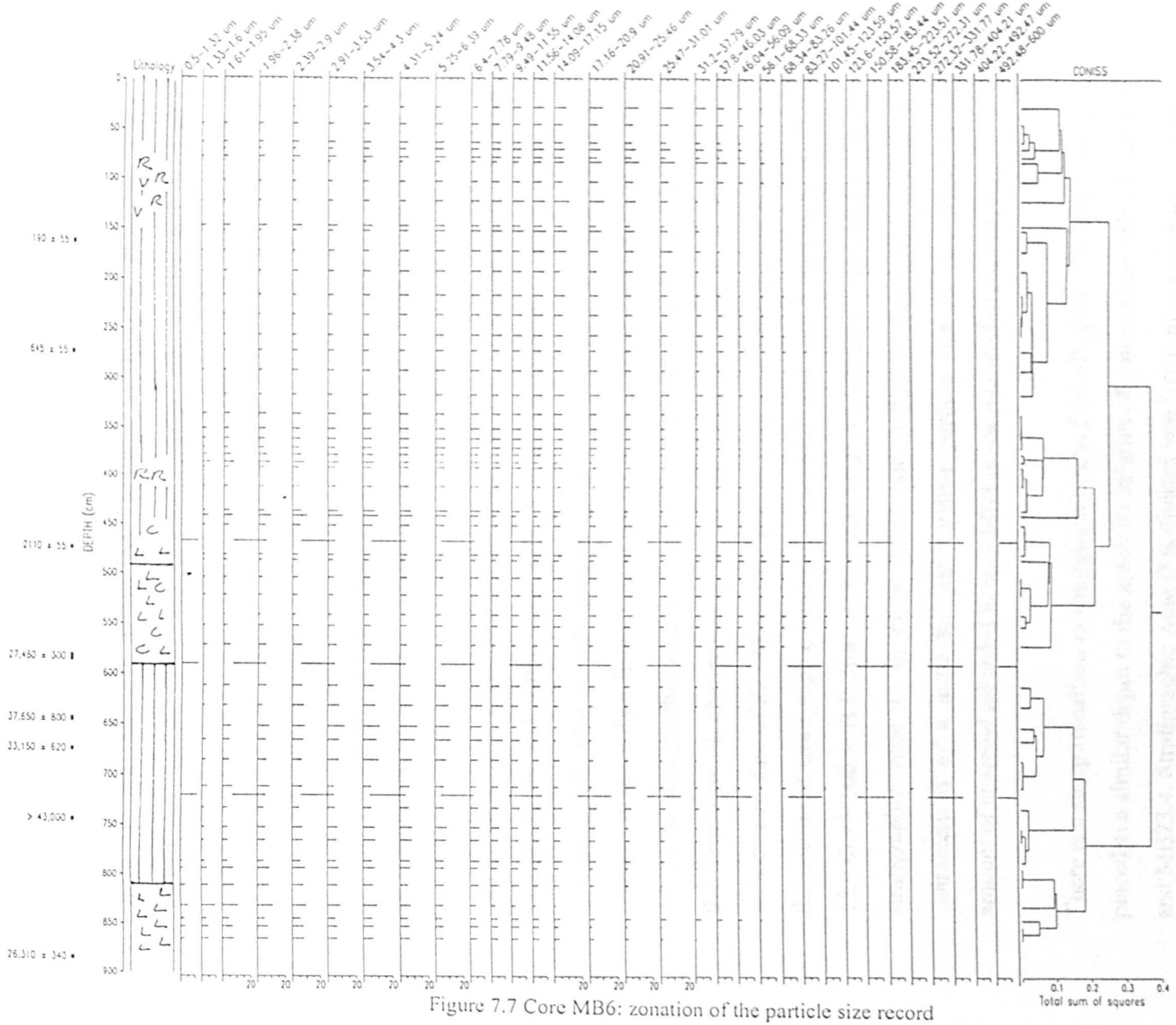


Figure 7.7 Core MB6: zonation of the particle size record

Stratigraphic zone B contains the top of pollen zones MB3.1, MB6.1 and MB23.1, the whole of pollen sub-zones MB3.2a, MB6.2a and MB23.2a and the lower part of pollen sub-zones MB3.2b. MB6.2b and MB23.2b. This collection of pollen zones within a single stratigraphic zone suggests changes recorded in the pollen flora are not mirrored within the sediment stratigraphy. However, there are significant changes within the inorganic particle size spectra and charcoal data from core MB6. At the transition to pollen sub-zone MB6.2b, there is a significant decrease in inorganic matter particle size. This is mirrored by the rapid increase in the amount of charcoal (Chapter 5). As this is not recorded in core MB3 it is thought to result from local hydrological changes within the Mubwindi Swamp catchment that has affected the sediments of core MB3, but not core MB6.

Stratigraphic zone C contains the upper part of pollen sub-zones MB3.2b, MB6.2b and MB23.2b, and pollen zones MB3.3, MB6.3 and MB23.3. Again, sedimentary changes at the base of stratigraphic zone C operate at a different time scale to changes in the pollen flora. This is not the case at the top of stratigraphic zone C where the stratigraphic zone and pollen zone boundaries are synchronous. Due to the sequence of change recorded in the separate cores, it is suggested the radiocarbon date of 27,480 +/- 300 yr B.P. from core MB6 can be extrapolated to the bottom of stratigraphic zone C in cores MB3 and MB23. Similarly, the date of 12,930 +/- 100 yr B.P. from pollen zone MB3.3 could be extrapolated to the top of stratigraphic zone C in cores MB3 and MB23.3. Stratigraphic zone C is characterised by a large inorganic matter particle size in core MB6. A large amount of charcoal recorded in core MB3 is not recorded in core MB6.

There is a sharp transition to stratigraphic zone D in all cores. This transition is placed at a similar depth to the lower boundaries of pollen zones MB3.4, MB6.4 and MB23.4. Stratigraphic zone D is divided into five pollen sub-zones in cores MB6 and MB23, and three in core MB3. The fluctuations of charcoal (Figure 5.10), and inorganic matter particle size (Figure 7.7), over this time period suggests these divisions are also recorded within the sediment stratigraphy. Pollen sub-zones MB3.4a, MB6.4a and MB6.4b all have very low levels of charcoal. Within pollen sub-zone MB6.4c there is a considerable rise in the amount of charcoal from the gravimetric and particle size methods (Figure 5.10). This rise is also recorded in pollen sub-zone MB3.3b, further evidence to suggest correlation of these two pollen zones. The amount of charcoal tails off within pollen sub-zones MB3.4c and MB6.4d, with a noticeable increase towards the top of the cores.

Stratigraphic zone D is characterised by relatively minor fluctuations in particle size in core MB6. The depths were the changes in particle size do occur, do not directly correspond to the boundaries identified for the pollen sub-zones. However, similarly to the pollen sub-zonation, there are also five identified changes in particle size (Figure 7.7) and charcoal (Section 5.7). This similarity indicates recorded changes in the pollen spectra are also recorded by changes in the sediment composition, but at different stratigraphic positions. This suggests different response times of vegetation and sedimentary change within the Mubwindi Swamp catchment.

The two short cores (MB3 and MB23) record the same number of stratigraphic and pollen zones as the longest core (MB6). Although the pollen zones in the lower part of the two short cores are notably compressed. This compression factor is less pronounced towards the top of the cores. The identification of the same number of stratigraphic zones, pollen zones and the close relationship between the depths at which the boundaries change suggests there has been synchronous sediment accumulation throughout the north-eastern part Mubwindi Swamp, and that the dating control recorded in cores MB3 and MB6 could be extrapolated between the cores analysed.

CHAPTER 8

Interpretation of the pollen and spores retained within the Mubwindi Swamp sediments

8.1 Introduction

Within this chapter pollen diagrams will be described individually for each core. The inferred composition of the vegetation within the Mubwindi Swamp is described during the time periods covered by the cored sediments, as indicated by the radiocarbon control (Chapter 4).

8.2 Construction of the pollen diagrams

The pollen diagrams presented in this thesis are drafted using the software packages Tilia and Tilia Graph (Grimm, 1991). In these diagrams, the 'X' axis represents pollen percentage, in terms of relative percentage with a separate scale for each taxon. The 'Y' axis represents depth, in centimetres down-core. On each diagram the stratigraphy is plotted, the available radiocarbon dates and the number of pollen grains that comprise the pollen sum for each level is indicated. The results from the numerical zonation (Chapter 7) are extended to pollen diagrams based on the local pollen and spore and the non-dominant local pollen and spore sums.

The most important information for reconstruction of within catchment changes in vegetation composition and distribution is derived from the non local pollen data (Section 7.2). Within the non-local pollen sum, five categories were used to collate the pollen types into broad ecological groups; montane forest, high altitude forest, degraded forest, swamp forest and forest shrubs. The assigning of pollen taxa to one of the groups was based on published work to date (Bonnefille and Riolett, 1988; Taylor, 1990; Hamilton, 1972; 1982), and the information presented in Chapters 2, 3 and 6. For example, the swamp forest category contained taxa (*Anthocleista*, Myrtaceae and *Rapanea*) that presently were recorded most commonly in close proximity to Mubwindi Swamp, with occasional representation at higher altitudes. *Cyathea* and *Myrica*, although recorded in a similar position, were also found to be growing on the Mubwindi Swamp surface. These taxa were also over-represented by their spores and pollen respectively in surface sediments (Chapter 6). Hence, *Cyathea* and *Myrica* were assigned to the local pollen and spores sum. The division of pollen data within these categories is further indicated by a DCA biplot of the pollen taxa derived from core MB6 (Figure 8.1). This biplot clearly separates out high altitude taxa, Ericaceous Belt taxa from the altitudinally lower, montane forest taxa (Section 2.4). Within the montane forest group, sub-divisions into 'primary' montane forest, upper montane forest, degraded montane forest, forest shrubs and swamp forest taxa are also visible. It should be stressed that these categories were used purely an aid for interpretation of the pollen data and had no influence on the percentage calculation or subsequent zonation of the data, stratigraphically constrained, or unconstrained.

8.3 Presentation and description of pollen and spores from core MB6

The non-local pollen record for core MB6 is shown in Figure 8.2. The pollen diagrams resulting from the other two pollen sums used, local pollen and spores and local non-dominant pollen and spores (Chapter 7), can be seen in Figures 8.3 and 8.4 respectively. To enable the pollen zones to be described in terms of the radiocarbon data, the pollen zone boundaries have been attached to the age-depth curve (Figure 8.5). This Figure provided the template to describe the pollen zones in terms of stratigraphic depth and age. However, it must be emphasised that the age-depth curve can only provide a very approximate age due to the relatively poor dating control in places (Chapter 4).

Five pollen sub-zones have been identified within zone MB6.4 by the stratigraphically constrained clustering technique within Tilia (Figure 8.2), and to a degree with the DCA plot (Figure 7.3), although the distinction between these groups is not so apparent in the latter. This is not surprising due to the relatively short time-scale incorporated within the pollen zone, i.e. approximately 2000 years and the lack of total forest clearance as recorded in other parts of the Rukiga highlands (Taylor, 1990). Hence, it is suggested over this time-period there have been relatively subtle changes in the pollen record, and thus, the composition of vegetation. It was decided to investigate the nature of these sub-zones highlighting

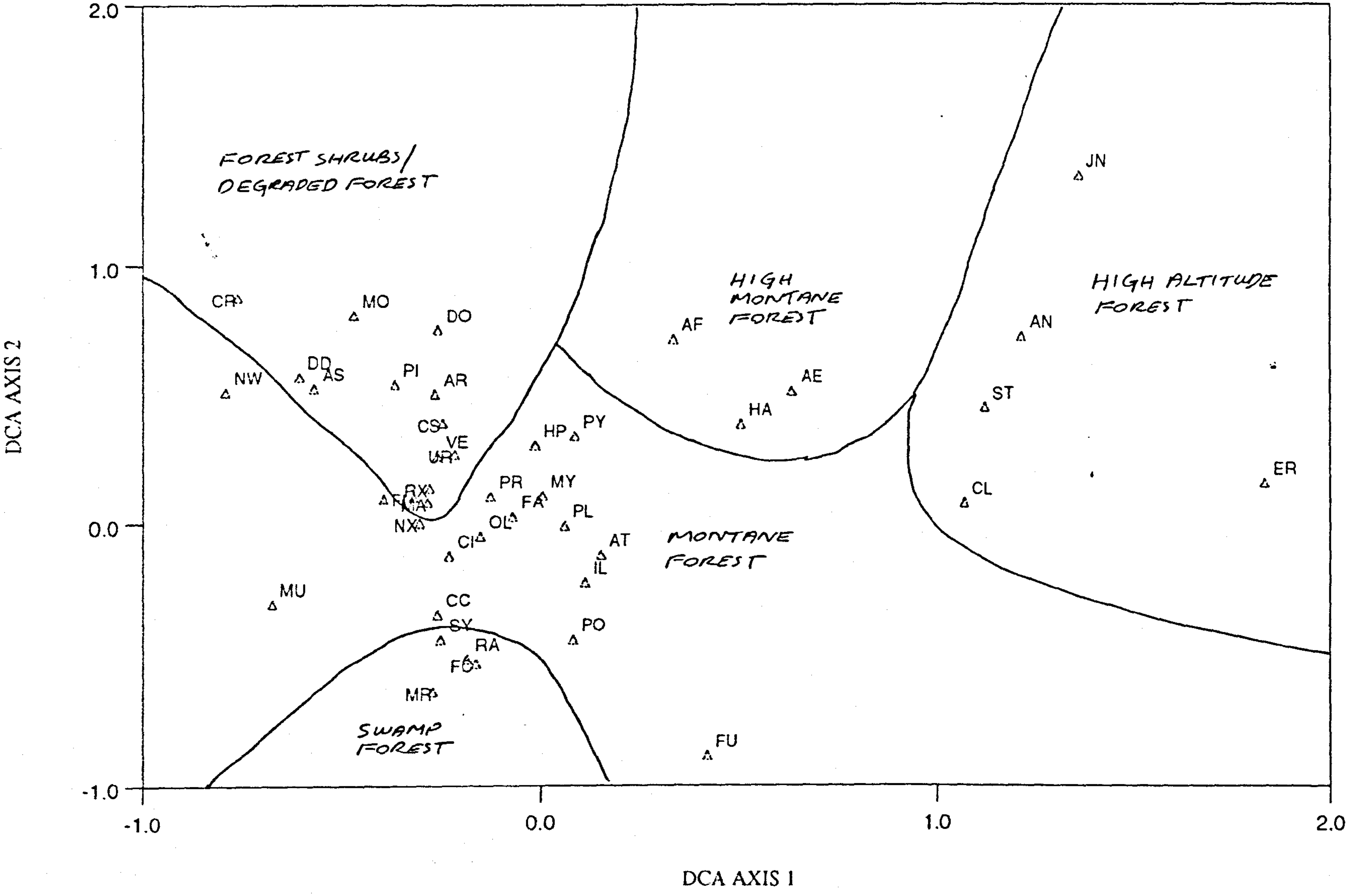


Figure 8.1 DCA plot of the pollen taxa for the non-local pollen sum of core MB6

Figure 8.2 Core MB6: non-local pollen diagram

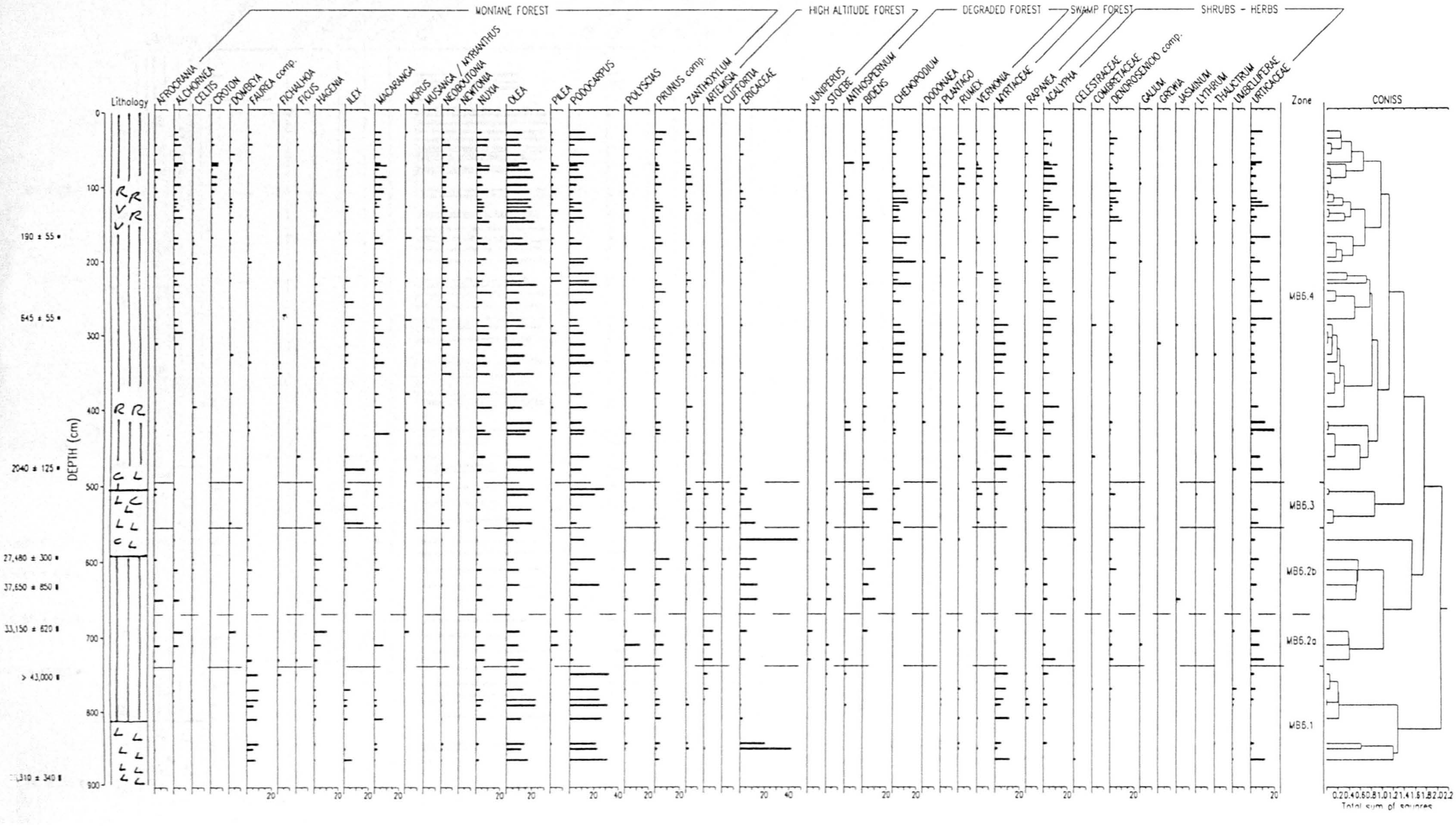
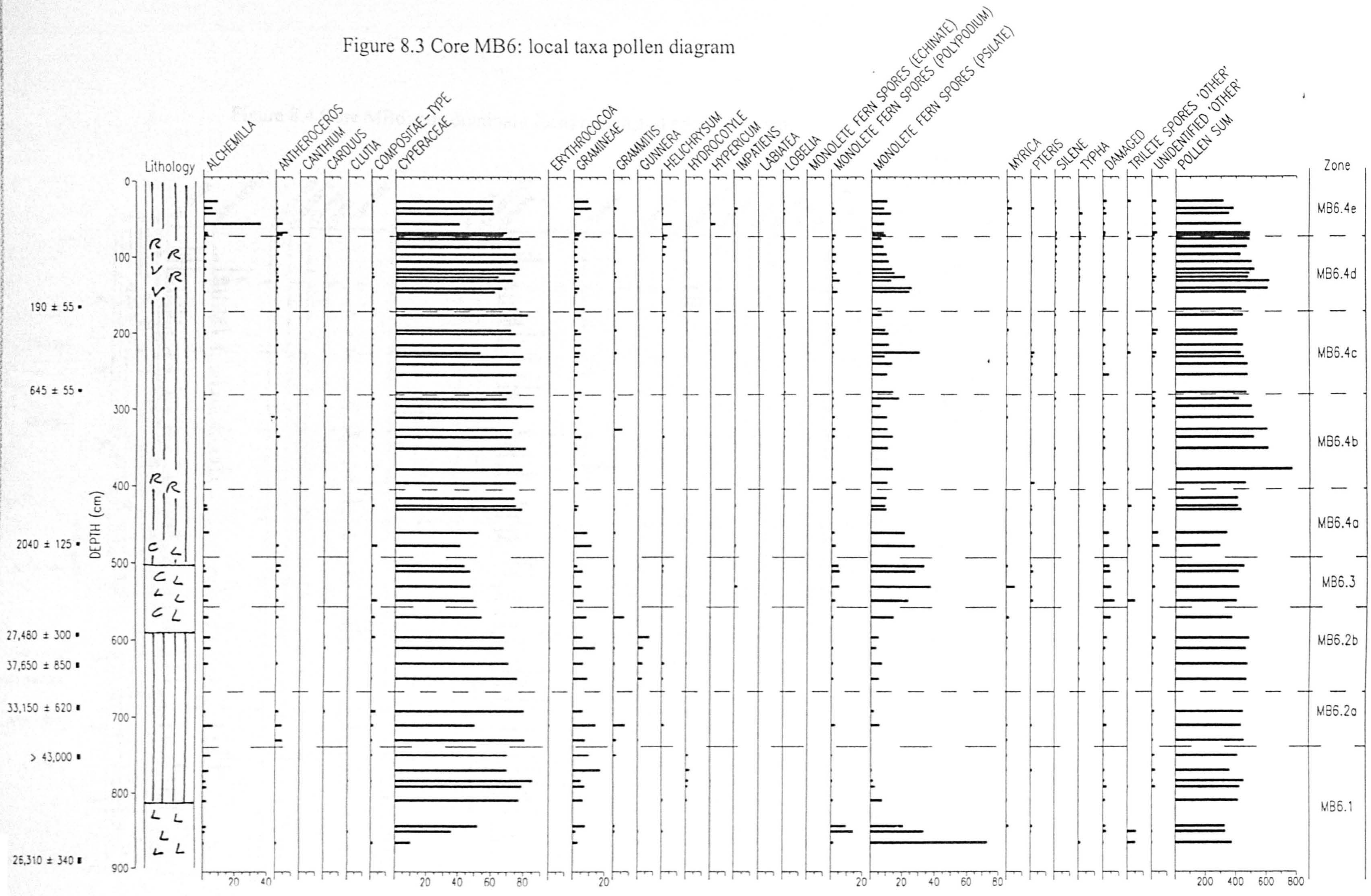


Figure 8.3 Core MB6: local taxa pollen diagram



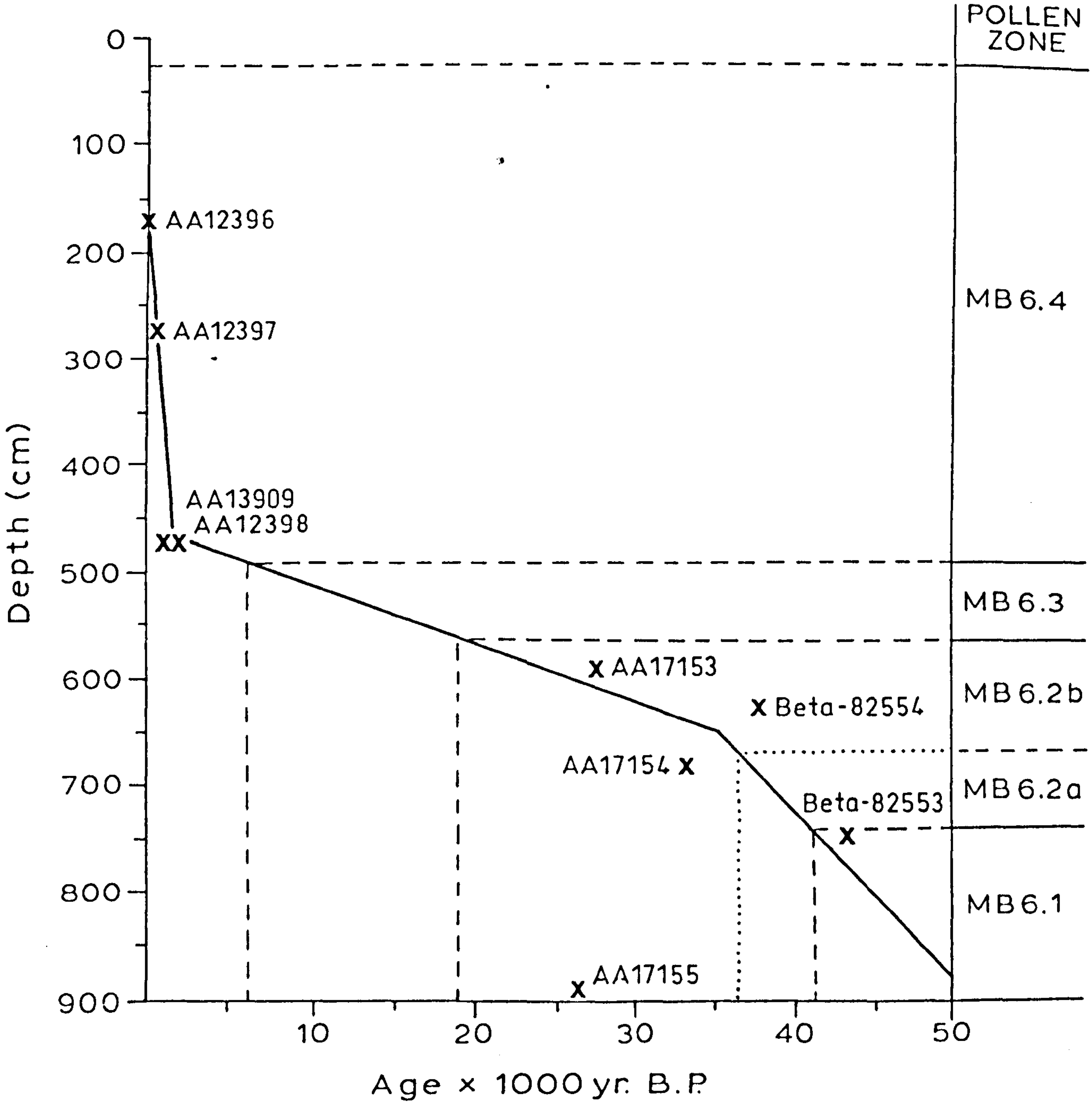
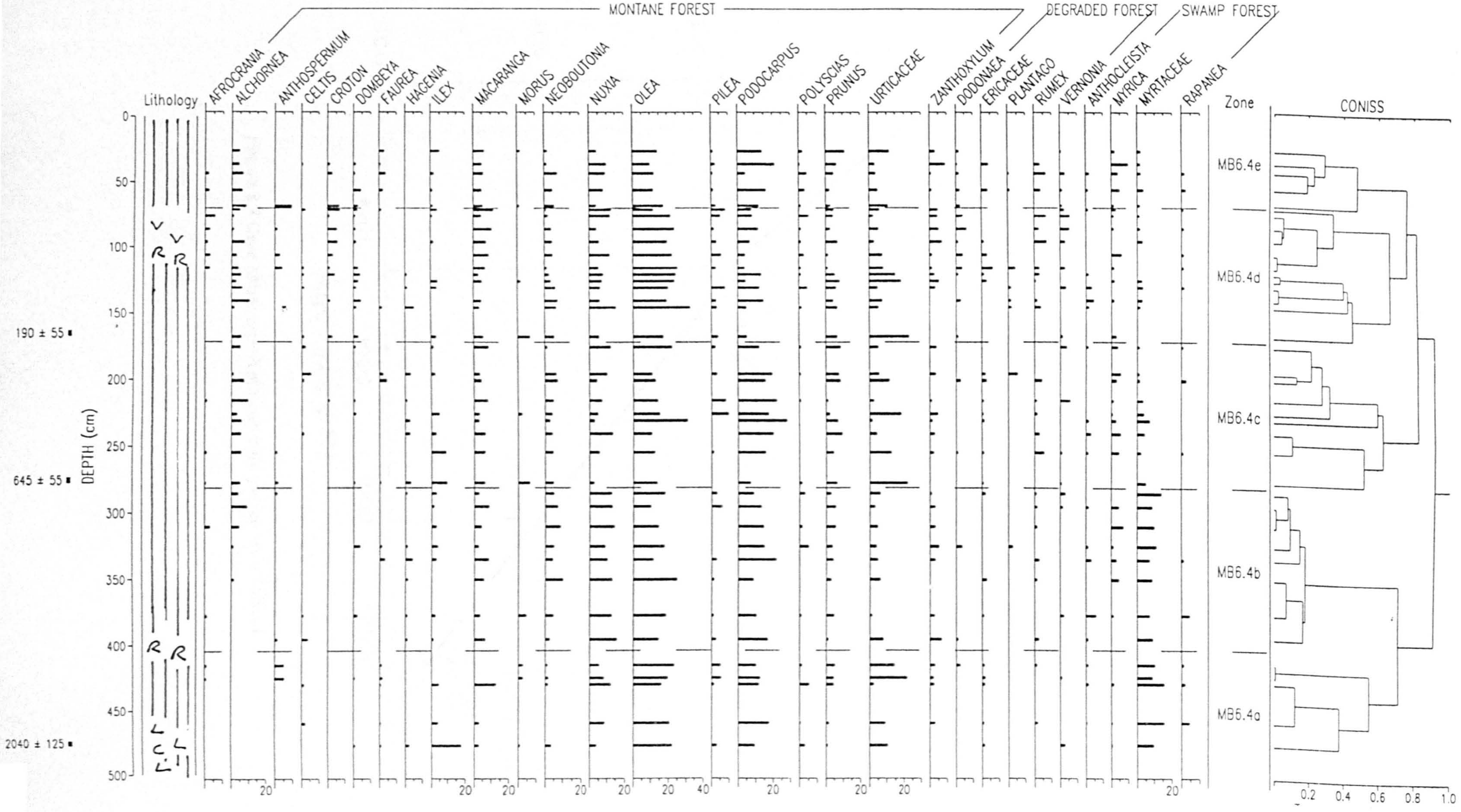


Figure 8.5 MB6: age-depth curve with fitted pollen zones

Figure 8.6 Core MB6: non-local pollen record for pollen zone MB6.4



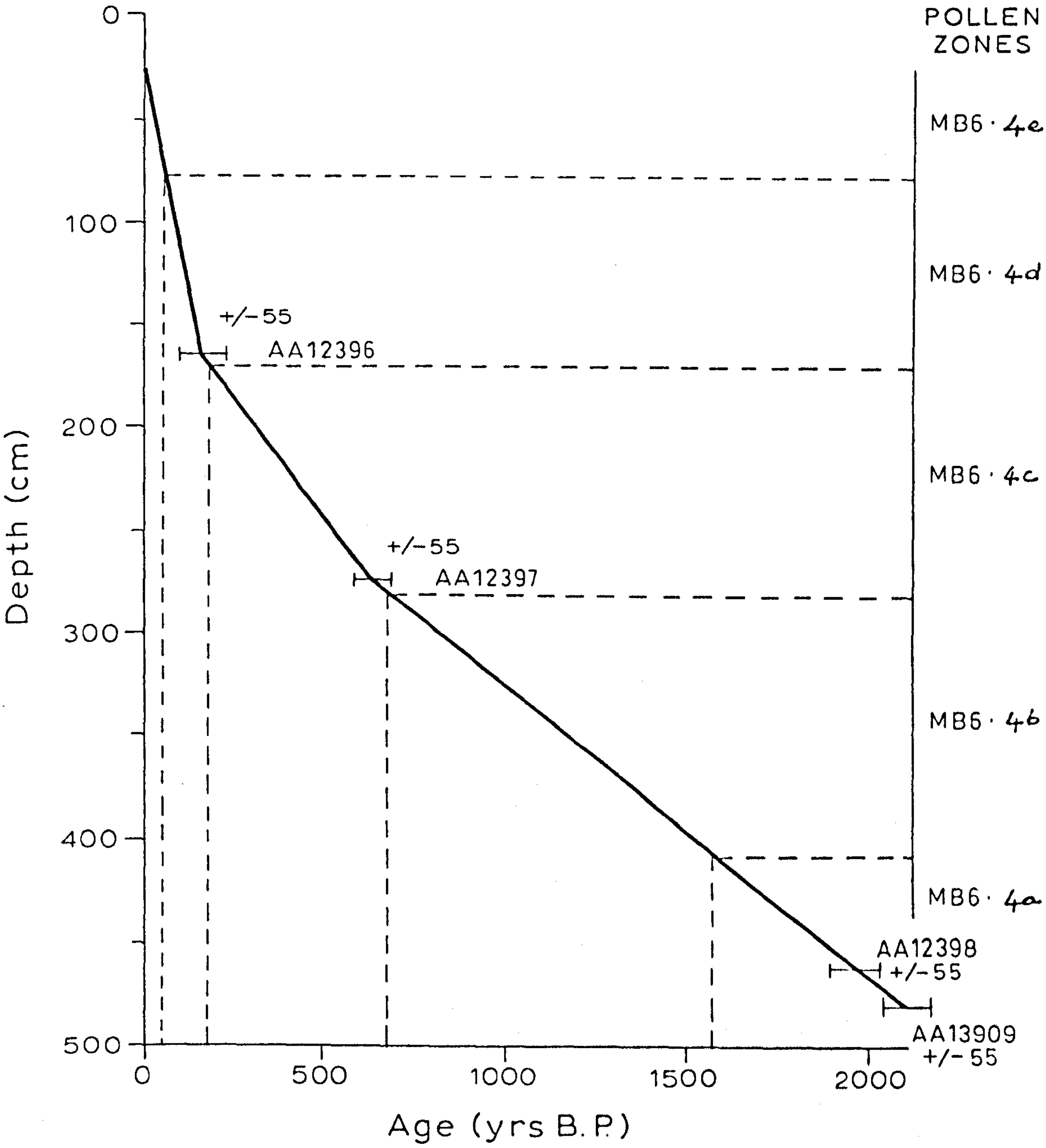


Figure 8.7 Core MB6: age-depth curve for pollen zone MB6.4

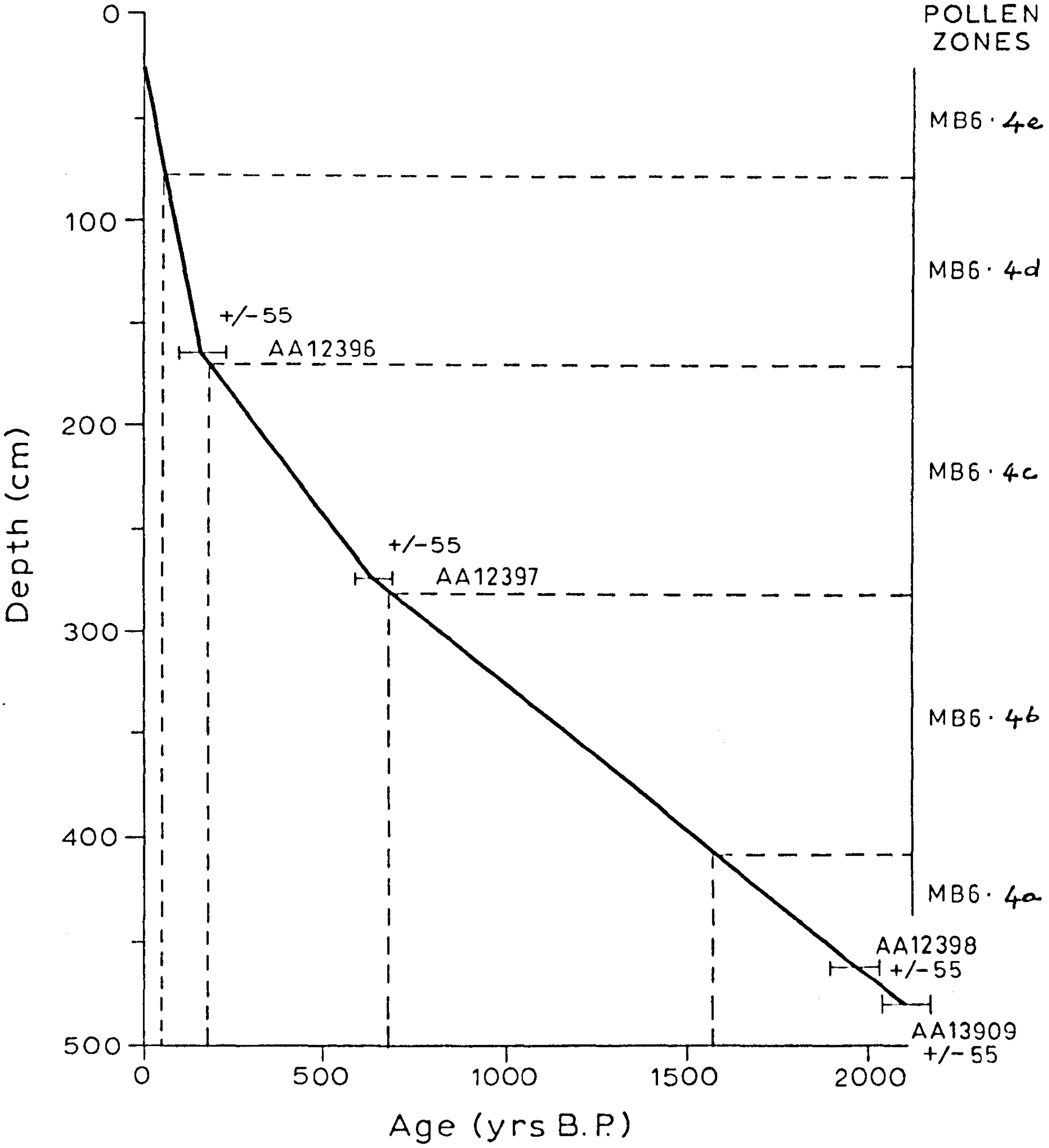


Figure 8.7 Core MB6: age-depth curve for pollen zone MB6.4

changes in pollen from these Late Holocene sediments (Figure 8.6). The format for describing the data will remain the same as for the rest of the core. Due to the increased resolution of the radiocarbon data for this part of the core, and the inadequate age scale in Figure 8.5, a new age-depth curve was constructed (Figure 8.7). This has allowed for the temporal delimiting of the pollen sub-zones in this part of the core and a calculation of the sedimentation rates for each sub-zone

Pollen zone MB6.1 extends from the base of the core at 884 cm to 740 cm, and includes the radiocarbon dates of 26,310 +/- 340 yr B.P. from 886 to 894 cm (AA-17155) and > 43,000 yr B.P. (Beta-82553) from 748 to 755 cm. On extrapolation of the age-depth curve (Figure 8.5) the upper date of this pollen zone is thought to be very close to 43,000 yr B.P. The lowermost sediments are thought to be in excess of 50,000 years old.

Within the montane forest category pollen zone MB6.1 is characterised by high proportions of *Faurea*, *Olea* and *Podocarpus* pollen types. *Hagenia*, *Ilex*, *Macaranga*, *Nuxia*, *Prunus* and Urticaceae pollen are all present in relatively low amounts. *Afrocrania*, *Anthospermum*, *Celtis*, *Neoboutonia*, *Pilea*, *Polyscias* and *Zanthoxylum* pollen are all present but at low sporadic percentages, and never reach a quantity of greater than 5 % of the non-local pollen sum. The high altitude forest category is dominated by Ericaceae pollen at the base of pollen zone MB6.1, although this rapidly declines to a low, constant level. Towards the top of the pollen zone, *Artemisia* and *Stoebe* pollen are present, albeit in low amounts. Taxa from the degraded forest category are noticeably absent during this zone, never reaching more than 5 % of the non-local pollen sum. Notable within pollen zone MB6.1 from the swamp forest category is the large amount of Myrtaceae pollen, with *Anthocleista* and *Rapanea* pollen recorded at low percentages. There is an increase in *Anthocleista* pollen towards the top of the pollen zone. Pollen from the forest shrub category is also present at very low levels.

In the pollen sum from the local pollen and spores (Figure 8.3), Cyperaceae and *Psilate* Fern spores are dominant. At the base of pollen zone MB6.1 *Psilate* Fern spores dominate with Cyperaceae at low levels. Throughout the pollen zone there is a decrease in the percentage of *Psilate* Fern spores and an increase in the percentage of Cyperaceae pollen. *Alchemilla* and Gramineae pollen steadily increase throughout pollen zone MB6.1. As with the *Psilate* Fern spores, the percentage of *Polypodium* Fern spores rapidly decrease throughout the pollen zone. Pollen from non-dominant local sources (Figure 8.4) show considerable percentage variation within this pollen zone: *Alchemilla* pollen and *Cyathea* spores dominate throughout pollen zone MB6.1, with occasional occurrences of *Clutia*, *Helichrysum*, *Hydrocotyle* and *Myrica* pollen, and Trilete spores.

Pollen zone boundary The boundary between pollen zones MB6.1 and MB6.2 is placed at 740 cm, as a result of changes in the percentages of *Acalypha*, *Artemisia*, Ericaceae, *Faurea*, *Juniperus*, Myrtaceae, *Podocarpus*, *Stoebe* and Urticaceae pollen. However, *Hagenia*, *Nuxia* and *Olea* pollen curves remain at near constant levels about this zone boundary. Within the local pollen (Figure 8.3) there is a rapid fall in *Alchemilla* pollen, Anthoceros spores and Compositae pollen. However, many of the other pollen types show no major change about the pollen zone boundary.

Pollen zone MB6.2 is placed between 740 cm and 555 cm and includes the radiocarbon dates of 33,150 +/- 620 yr B.P. from 748 to 755 cm (AA-17154), 37,650 +/- 850 yr B.P. from 683 to 690 cm (Beta-82554) and 27,480 +/- 200 yr B.P. from 590 to 595 cm (AA-17153). Extrapolating the age-depth curve (Figure 8.5), the lower zone boundary is placed at 43,000 yr B.P., the upper boundary being placed at about 18,000 yr B.P. However, as suggested in chapters 4, 5 and 7, the sedimentary record is characterised by two main sedimentary hiati. The first is present towards the top of pollen zone MB6.2.

Due to the changes in pollen percentages the pollen zone has been divided into two sub-zones - MB6.2a and MB6.2b. The pollen sub-zone boundary is placed at 675 cm, corresponding to an inferred date of approximately 37,000 yr B.P. This sub-division is required mainly due to mid-zonal changes in *Bidens*, Ericaceae, *Hagenia*, *Olea*, *Podocarpus* and *Stoebe* pollen. These two sub-zones will be described as a single zone with the differences in pollen percentages being highlighted.

Within both sub-zones the montane forest category is characterised by high levels of *Afrocrania*, *Alchornea*, *Hagenia*, *Nuxia*, *Olea*, *Prunus* and Urticaceae pollen. There are low, but sustained levels of *Faurea* and *Polyscias* pollen throughout the pollen zone. In sub-zone MB6.2a, there are low amounts of *Ilex*, *Macaranga*, *Podocarpus* and *Zanthoxylum* pollen that increase in pollen sub-zone MB6.2b. From the high altitude forest category there are relatively high amounts of *Artemisia*, Ericaceae and *Juniperus* pollen in pollen sub-zone MB6.2a, with a low but consistent amount of *Stoebe* pollen. In pollen sub-zone MB6.2b, there is an increase in the amount of Ericaceae and *Stoebe* pollen. Noticeable throughout pollen zone MB6.2 is the low percentage of pollen derived from the degraded and swamp forest categories. Within the forest shrub category there is an increase in Urticaceae pollen percentages recorded.

Within pollen zone MB6.2 the local pollen (Figure 8.3) is dominated by Cyperaceae pollen. This dominance is reflected by the low percentages of other pollen and spores present in this zone. The pollen derived from the non-dominant local taxa (Figure 8.4) shows two interesting patterns. Most noticeable is the dominance of *Alchemilla* and Gramineae pollen in pollen sub-zone MB6.2b and dominance of Compositae pollen in sub-zone MB6.2a. There is a very rapid increase in *Gunnera* pollen to approximately 20 % of the non-dominant local pollen sum. These local changes in pollen spectra emphasises the requirement for the pollen sub-zone division: within catchment changes in pollen also being recorded at a local level. Many other local pollen types are present only in isolated amounts without significant trends. Gramineae pollen remains at about 40 % of the non dominant local pollen sum throughout the pollen zone.

Pollen zone boundary The MB6.2 and MB6.3 pollen zone boundary is placed at 555 cm as a result of changes in the percentages of *Chenopodium*, *Cliffortia*, Ericaceae, *Hagenia*, *Ilex*, *Neoboutonia*, *Olea*, *Podocarpus*, *Vernonia* and Urticaceae pollen. Grammitis, Monolete Fern and *Pteris* spore percentages also change significantly about this pollen zone boundary. There is also a significant rise in the amount of damaged pollen grains.

Pollen zone MB6.3 contains sediments between 555 cm and 495 cm. Extrapolation of pollen and sedimentary data from core MB3 (Chapter 7), indicates pollen zone MB6.3 would contain the radiocarbon date of 12,930 +/- 1250 yr B.P. from 430 to 443 cm in core MB3 (Beta-60065). Extrapolating the age-depth curve (Figure 8.5), the lower zone boundary is placed at 18,000 yr B.P., the upper boundary being placed at about 6000 yr B.P. However, as suggested within chapters 4, 5 and 7, the sedimentary record is characterised by two main sedimentary hiati. The second is present towards the top of pollen zone MB6.3. Therefore, respectively the lower and upper boundaries to this pollen zone are thought to age considerably younger and older than suggested from the age-depth curve. The ages possibly equate to about 14,000 and 11,000 yr B.P. for the lower and upper boundaries of the pollen zone.

Pollen zone MB6.3 is characterised by high levels of *Ilex*, *Olea* and *Podocarpus* pollen and to a lesser extent *Hagenia*, *Macaranga*, *Neoboutonia*, *Nuxia*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen from the montane forest category. Within pollen zone MB6.3, relative to pollen zone MB6.2, there is a decline in *Artemisia*, *Juniperus* and *Stoebe* pollen from the high altitude forest category. However, there is a notable peak in *Cliffortia* pollen relative to pollen zone MB6.2. Within this category, Ericaceae pollen still dominates. There is an increase in *Bidens*, *Chenopodium* and *Vernonia* pollen from the degraded forest category. Pollen from the swamp forest category are present, albeit at very low levels.

Pollen from local taxa (Figure 8.3) are dominated by Cyperaceae and *Psilate* Fern spores. As one moves up the pollen zone, Cyperaceae pollen percentages gradually increase although Psilate Fern spores still remain at a relatively high level. Non-dominant local pollen types (Figure 8.4) are dominated by *Alchemilla* pollen, Anthoceros, Grammitis, *Polypodium* and Trilete fern spores. There is also an increase in the amount of damaged grains. Gramineae pollen are present at low, constant levels, throughout the pollen zone.

Pollen zone boundary The boundary between pollen zones MB6.3 and MB6.4 is at 495 cm, largely as a result of changes in the percentages of *Ilex*, Myrtaceae *Podocarpus* and Urticaceae pollen.

Pollen sub-zone MB6.4 contains sediments between 495 and 23 cm (the top sample collected). Pollen zone MB6.4 contains the radiocarbon dates of 2110 +/- 55 yr B.P. (AA-12308) and 1970 +/- 55 yr B.P. (AA-13909) from 473 to 477 cm, 645 +/- 55 years from 273 to 277 cm (AA-12397) and 190 +/- 55 yr B.P. from 163-167 cm (AA-12396).

Pollen sub-zone MB6.4a spans from 495 to 405 cm and includes the radiocarbon dates of 2110 +/- 55 yr B.P. (AA-12308) and 1970 +/- 55 yr B.P. (AA-13909) from 473 to 477 cm. Extrapolating the age-depth curve (Figure 8.7), the lower and upper boundary of the pollen sub-zone can be dated to approximately 2100 and 1575 yr B.P. respectively. This corresponds to a sedimentation rate of 0.158 cm yr^{-1}. The pollen sub-zone is characterised by high amounts of *Nuxia*, *Olea* and *Podocarpus* pollen from the montane forest category, and *Acalypha* and Urticaceae pollen from the forest shrub category. There are fluctuating amounts of *Ilex* and *Macaranga* pollen. *Faurea*, *Neoboutonia*, *Pilea*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen remain at low levels throughout the pollen sub-zone. All the other pollen types, apart from *Alchornea* and *Plantago*, are present at low quantities. Local pollen (Figure 8.3) is dominated by Cyperaceae, particularly as the levels of *Psilate* Fern spores decreases. Non-dominant local pollen (Figure 8.4) is dominated by Gramineae pollen. There are increasing amounts of *Alchemilla* pollen, all other pollen types are present at low quantities.

Pollen sub-zone boundary The MB6.4a and MB6.4b pollen sub-zone boundary is placed at 405 cm as a result of changes in *Acalypha*, *Bidens*, *Macaranga*, *Nuxia*, *Olea*, Urticaceae and *Zanthoxylum* pollen percentages. *Alchemilla* pollen and Trilete spores also change about this pollen sub-zone.

Pollen sub-zone MB6.4b spans from 405 to 280 cm. Although there are no radiocarbon dates included in this pollen zone, extrapolation of the age-depth curve (Figure 8.7) indicates the lower and upper boundaries can be dated at approximately 1575 and 680 yr B.P. respectively. This corresponds to a sedimentation rate of 0.144 cm yr $^{-1}$. Similarly to pollen sub-zone MB6.4a, *Olea* and *Podocarpus* pollen still dominate the pollen sub-zone. However, *Macaranga*, *Neoboutonia*, *Nuxia*, *Prunus* and *Zanthoxylum* pollen increase in comparison to pollen sub-zone MB6.4a. Myrtaceae and Urticaceae pollen, although still important components of the pollen flora, are reduced in comparison to the previous sub-zone. Towards the top of pollen sub-zone MB6.4b there is an increase in *Alchornea*, *Bidens*, *Chenopodium* and *Neoboutonia* pollen, with a concomitant decrease in *Olea* and *Podocarpus* pollen. Local pollen is increasingly dominated by Cyperaceae pollen with all other types present at low quantities. Non-dominant local pollen is dominated by Gramineae pollen with *Lobelia*, *Polypodium* Fern spores, *Myrica* and *Silene* pollen becoming increasingly common components of the pollen sub-zone.

Pollen sub-zone boundary The pollen sub-zone boundary is placed at 280 cm due to changes in *Acalypha*, *Chenopodium,* Ericaceae, *Ilex*, Myrtaceae, *Nuxia*, *Pilea* and Urticaceae pollen percentages. There are also changes in Gramineae pollen, Grammitis, *Polypodium* Fern and *Pteris* spores from the local pollen.

Pollen sub-zone MB6.4c spans from 280 cm to 170 cm and includes the radiocarbon date of 645 +/- 55 years from 273 to 277 cm (AA-12397). Extrapolating the age-depth curve (Figure 8.7) the lower and upper boundaries can be dated to approximately 680 and 200 yr B.P. respectively. This corresponds to a sedimentation rate of 0.217 cm yr $^{-1}$. *Alchornea*, *Ilex*, *Rumex*, Ericaceae and *Prunus* pollen increases relative to pollen sub-zone MB6.4b. Conversely, Myrtaceae pollen shows a significant decrease. The most notable characteristic of pollen sub-zone MB6.4c is the widely fluctuating amounts of *Acalypha*, *Chenopodium*, *Nuxia*, *Olea*, *Pilea*, *Podocarpus* and Urticaceae pollen, whereas amounts of *Macaranga*, *Neoboutonia*, *Polyscias*, Myrtaceae and *Zanthoxylum* pollen remain at, or near, constant percentages. Pollen from local sources is dominated by Cyperaceae, with *Psilate* Fern spores still an important component of the local pollen sum. Gramineae pollen still dominates the non-dominant local pollen and spores (Figure 8.4). There is an increase in the amount of *Cyathea* spores, *Myrica* pollen, *Pteris* and *Selaginella* spores towards the top of the pollen sub-zone.

Pollen sub-zone boundary The pollen sub-zone boundary is placed at 170 cm due to changes in *Acalypha*, *Croton*, *Dodonaea*, *Dombeya*, *Macaranga*, *Neoboutonia*, *Nuxia*, *Plantago*, *Podocarpus* and Urticaceae pollen. Cyperaceae, Gramineae, *Helichrysum* pollen and Fern spore percentages also change across this sub-zone boundary.

Pollen sub-zone MB6.4d spans from 170 cm to 75 cm, and includes the radiocarbon date of 190 +/- 55 yr B.P. from 163 to 167 cm (AA-12396). On the basis of the age-depth curve (Figure 8.7), the lower and upper boundaries date to approximately 200 and 50 yr B.P. respectively. However, caution must be applied to these dates due to the relatively high standard deviation attributed to the young date. The age-depth relationship indicates a sedimentation rate of 0.76 cm yr^{-1} for the sub-zone. *Croton*, *Dendrosenecio*, *Dodonaea*, *Dombeya*, Ericaceae, *Macaranga*, *Olea*, *Plantago*, *Polyscias*, *Rumex* and *Vernonia* pollen all increase relative to pollen sub-zone MB6.4c, with *Olea* being the dominant pollen type. *Podocarpus* pollen decreases, whereas *Alchornea*, *Ilex*, *Neoboutonia*, *Nuxia*, *Pilea*, *Prunus* and *Zanthoxylum* pollen remain at similar levels relative to the previous pollen sub-zone. Pollen from local sources indicate an increasing presence of *Alchemilla*, *Anthoceros*, *Dendroscencio*, *Helichrysum* and latterly *Typha* pollen. Following an initial increase in *Psilate* Fern spores, there is gradual increase in Cyperaceae pollen (Figure 8.3).

Pollen sub-zone boundary. The sub-zone boundary is placed at 75 cm due to changes in the amount of *Acalypha*, *Alchornea*, *Bidens*, *Croton*, *Faurea*, *Macaranga*, *Olea*, *Rumex*, Urticaceae and *Vernonia* pollen. The local pollen shows a very sharp decline in Cyperaceae, probably because of an over-representation of *Alchemilla* pollen in this sample.

Pollen sub-zone MB6.4e spans from 75 cm to 23 cm (the top of the core). It includes no radiocarbon dates, but, on interpolation of the age-depth curve (Figure 8.7), it probably represents the most recent 50 years or so, and accumulated at a rate of 1.04 cm yr^{-1}. *Alchornea*, *Bidens*, *Faurea*, *Neoboutonia*, *Podocarpus*, *Prunus* and Urticaceae pollen all increase relative to pollen sub-zone MB6.4d. *Acalypha*, *Afrocrania*, *Macaranga*, *Nuxia*, *Olea*, *Pilea*, *Vernonia* and *Zanthoxylum* pollen all decrease relative to the previous pollen sub-zone. *Croton*, *Dombeya*, *Olea* and *Polyscias* pollen remain at similar levels. *Dodonaea* and *Rumex* pollen percentages decrease, although only slightly. The dominant local pollen and spores remain at similar levels to the previous zone. Pollen from non-dominant local sources are dominated by *Alchemilla* and Gramineae pollen with *Cyathea*, *Silene*, *Lobelia* and *Helichrysum* pollen also present. There is also a marked increase in the percentage of *Typha* pollen towards the top of the pollen sub-zone.

8.4 Presentation and description of pollen and spores from core MB3

In terms of pollen sums used, categories assigned and the numerical techniques applied, the process for the construction of pollen diagrams for core MB3 is identical to that used for core MB6. The recorded changes in the non-local pollen percentages down-core are presented in Figure 8.8. Core MB3 is divided into four pollen zones; MB3.1, MB3.2, MB3.3 and MB3.4. with MB3.2 and MB3.4 being divided into sub-zones. The pollen diagrams that result from the local pollen and spores and local non-dominant pollen and spores pollen sums are presented in Figures 8.9 and 8.10 respectively. So that these data can complement those used from the non-local pollen sum, the pollen zone boundaries are placed in the same position as in Figure 8.8.

The following is a description of the pollen and spores occurring in each pollen zone in core MB3 and the nature of the pollen zone boundary.

Pollen zone MB3.1 ranges from the base of the core at 674 cm to 610 cm. This zone is placed below the radiocarbon date of 30,000 +/- 1250 yr B.P. from 580 to 588 cm (Beta-60066). *Faurea*, *Ilex*, *Olea*, Myrtaceae, *Podocarpus* and Urticaceae pollen dominate pollen zone MB3.1. Ericaceae, *Hagenia*, *Macaranga* and *Neoboutonia* pollen are present, albeit at relatively low percentages. Pollen derived from other taxa within the high altitude, degraded and swamp forest

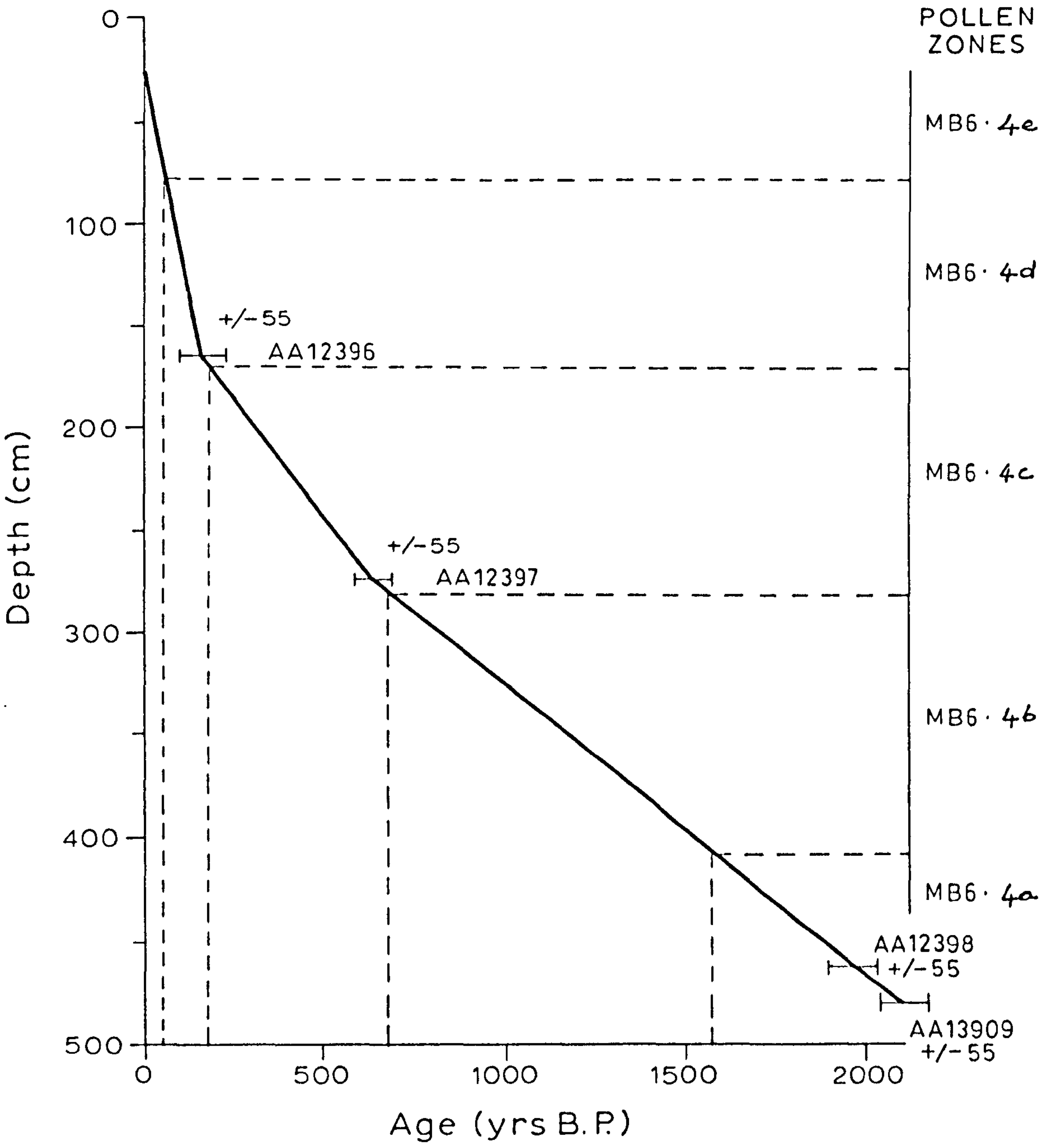


Figure 8.7 Core MB6: age-depth curve for pollen zone MB6.4

Figure 8.8 Core MB3: non-local pollen diagram

Figure 8.9 Core MB3: local pollen and spore diagram

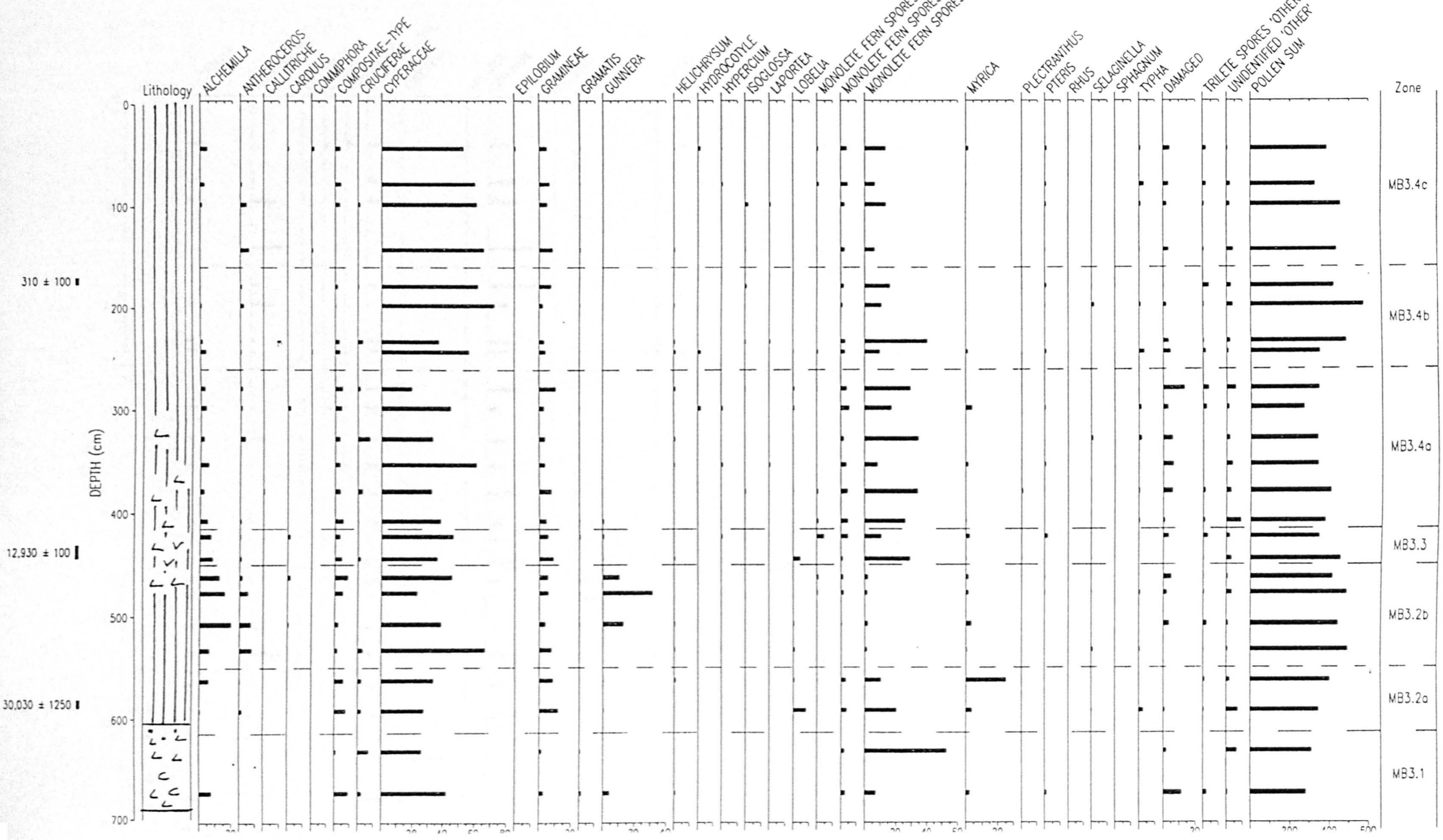


Figure 8.10 Core MB3: non dominant local pollen and spore diagram

categories are only present in low quantities, if at all. Similarly, apart from Urticaceae pollen, the forest shrub category is not represented within this pollen zone. Cyperaceae and *Psilate* Fern spores are dominant in pollen zone MB3.1. Fern spores dominate in the lowermost part of the pollen zone whereas in the upper of the pollen zone Fern spores and Cyperaceae become co-dominant. Gramineae pollen is present throughout the pollen zone albeit in very low levels. Within the local non-dominant pollen and spore sum *Alchemilla*, Crucifereae pollen and *Grammitis* spores co-dominate the pollen spectra.

Pollen zone boundary The MB3.1 and MB3.2 pollen zone boundary is placed at 610 cm. It is placed here due to changes in the quantities of *Artemisia*, *Hagenia*, Myrtaceae, *Nuxia*, *Olea*, *Podocarpus* and Urticaceae pollen. The amount of Crucifereae, Gramineae, *Lobelia* and *Myrica* pollen also changes about the pollen zone boundary.

Pollen zone MB3.2 spans from 610 to 450 cm and includes the radiocarbon date of 30,030 +/- 1250 yr B.P. from 580 to 588 cm (Beta-60066). On the basis of the numerical analysis this pollen zone is divided into two pollen sub-zones.

Pollen sub-zone MB3.2a spans from 610 to 550 cm. *Alchornea*, *Hagenia*, *Nuxia*, *Olea* and *Prunus* pollen from the montane forest category increase relative to pollen zone MB3.1. *Faurea* and *Podocarpus* pollen decrease relative to pollen zone MB3.1, whereas *Ilex* pollen percentages remain at a similar level. The pollen from the high altitudinal forest category is completely dominated by *Artemisia* pollen, with low percentages of Ericaceae pollen present. The swamp forest category is dominated by Myrtaceae pollen, although this is present at a relatively low level. The only pollen to originate from the forest shrub category is Urticaceae pollen. The local pollen shows an increase in Cyperaceae, and a large increase in Gramineae pollen to approximately 20 % of the local pollen. There is a notable rise in the amount of *Myrica* pollen.

Pollen sub-zone boundary The MB3.2a to MB3.2b pollen sub-zone boundary is placed at 550 cm. It is placed here due to changes in the pollen percentage of *Alchornea*, *Artemisia*, *Cliffortia*, Ericaceae, Myrtaceae, *Olea*, *Pilea*, *Podocarpus*, *Stoebe* and Urticaceae pollen. *Alchemilla*, *Anthoceros* spores, Cyperaceae, Gramineae, *Myrica* pollen and *Psilate* Fern spores percentages also change notably about the pollen sub-zone boundary.

Pollen sub-zone MB3.2b spans from 550 to 455 cm and predates the radiocarbon date of 12,930 +/- 100 yr B.P. from 443 to 447 cm (Beta-60665). *Artemisia*, *Cliffortia*, Ericaceae and *Stoebe* pollen from the high altitude forest category all increase relative to pollen sub-zone MB3.2a. *Ilex*, *Faurea*, *Hagenia*, *Olea* and *Podocarpus* pollen from the montane forest category decrease relative to pollen sub-zone MB3.2b, whereas *Nuxia*, *Pilea* and *Polyscias* pollen stay at similar levels to the previous sub-zone. In the swamp forest category, *Rapanea* pollen increases relative to pollen sub-zone MB3.2b, whereas Myrtaceae pollen decreases. *Bidens* and *Chenopodium* pollen form the degraded forest category increase relative to the previous pollen sub-zone. Pollen from the local non-dominant pollen and spores (Figure 8.10) is dominated by *Alchemilla*, *Gunnera* and Gramineae pollen. *Gunnera* pollen is a particularly important component of the pollen sum towards the top of the pollen sub-zone.

Pollen zone boundary The MB3.2 to MB3.3 pollen zone boundary is placed at 455 cm. It is placed here due to changes in the percentages of *Alchornea*, *Artemisia*, *Chenopodium*, Ericaceae, *Faurea*, *Hagenia*, *Ilex*, *Juniperus*, *Macaranga*, *Neoboutonia*, *Nuxia*, *Podocarpus*, *Polyscias*, *Prunus* and *Rapanea* pollen. The amount of Cyperaceae, *Gunnera*, Gramineae pollen and *Psilate* Fern spores also changes dramatically about the pollen zone boundary.

Pollen zone MB3.3 is located between 455 and 415 cm. *Celtis*, *Hagenia*, *Ilex*, *Neoboutonia*, *Nuxia*, *Olea*, *Podocarpus*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen from the montane forest category increase in abundance relative to pollen sub-zone MB3.2b. *Artemisia*, *Cliffortia*, Ericaceae, and *Stoebe* pollen from the high altitudinal forest category decrease relative to pollen sub-zone MB3.2b. Myrtaceae and *Rapanea* pollen from the swamp forest category decrease relative to pollen sub-zone MB3.2b. Pollen from local sources (Figure 8.9) show a marked decrease in Cyperaceae pollen, with a large increase in *Psilate* Fern spores, other pollen and spores remain at similar levels to the previous pollen sub-zone. The non-dominant local pollen sum (Figure 8.10) is dominated by *Alchemilla* and Gramineae pollen with a large decrease in the amount of *Gunnera* pollen present.

Pollen zone boundary The MB3.3 to MB3.4 pollen zone boundary is placed at 415 cm. It is placed here due to changes in the percentages of *Acalypha*, *Anthocleista*, *Dendroscencio*, Ericaceae, *Juniperus*, Myrtaceae, *Podocarpus*, *Rapanea* and Urticaceae pollen. *Alchemilla* and Psilate Fern spores also change about the pollen zone boundary.

Pollen zone MB3.4 The boundaries for this pollen zone are placed at 415 cm and 45 cm (the core surface). Pollen zone MB3.4 contains the radiocarbon date of 310 +/- 100 yr B.P. from 173 to 177 cm (Beta-61809). Based on extrapolation of the pollen and sediment data from core MB6, this zone is analogous to pollen zone MB6.4 (Chapter 7). Therefore, in a similar manner to core MB6, pollen zone MB3.4 is thought to cover the period shortly before 2000 yr B.P. through to the present day. According to the constrained numerical zonation, the pollen zone consists of three major sub-zones (MB3.4a, MB3.4b and MB3.4c).

Pollen sub-zone MB3.4a extends from 415 to 260 cm. From the montane forest group category *Alchornea*, *Ilex*, *Olea*, *Pilea*, *Podocarpus*, *Prunus* and *Zanthoxylum* pollen all increase in abundance relative to the previous pollen zone. *Macaranga*, *Neoboutonia* and *Polyscias* pollen all remain at low levels. *Cliffortia* and Ericaceae pollen from the high altitude forest category decrease in abundance relative to pollen zone MB3.3. *Anthocleista* and Myrtaceae pollen from the swamp forest category increase in abundance relative to the previous pollen zone. *Acalypha* and Urticaceae pollen both increase relative to the previous pollen zone. Cyperaceae pollen and *Psilate* Fern spores co-dominate the local pollen sum (Figure 8.9), although they both fluctuate markedly throughout this pollen sub-zone. *Alchemilla* and Gramineae pollen co-dominate the non-dominant local pollen sum (Figure 8.10), other pollen types are present at low percentages.

Pollen sub-zone boundary The MB3.4a to MB3.4b pollen sub-zone boundary is placed at 260 cm. It is placed here due to changes in the quantities of *Alchornea*, *Croton*, *Dodonaea*, *Dombeya*, Ericaceae, *Macaranga*, Myrtaceae, *Neoboutonia*, Urticaceae and *Vernonia* pollen. There are significant changes in the amount of Cyperaceae pollen, *Psilate* Fern spores and Gramineae pollen about the pollen sub-zone boundary.

Pollen sub-zone MB3.4b The boundaries for pollen sub-zone MB3.4b are placed at 260 cm and 160 cm. It contains the radiocarbon date of 310 +/- 100 yr B.P. from 170 to 173 cm (Beta-61809). *Afrocrania*, *Alchornea*, *Croton*, *Dombeya*, *Macaranga*, *Neoboutonia*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen from the montane forest category all increase relative to the previous zone, whereas *Ilex* and *Nuxia* pollen decrease. Ericaceae pollen continues to increase, although none of the other pollen types from the high altitude forest category are present in significant quantities. *Dodonaea*, *Chenopodium*, *Plantago*, *Rumex* and *Vernonia* pollen from the degraded forest category all increase relative to pollen sub-zone MB3.4a. *Anthocleista* and Myrtaceae pollen, from the swamp forest category, decrease relative to pollen sub-zone MB3.4a. *Acalypha*, Umbelliferae and Urticaceae pollen all increase relative to the previous pollen sub-zone. Pollen percentages from local taxa (Figure 8.9) are dominated by Cyperaceae, with *Psilate* Fern spores present at decreasing levels throughout the sub-zone. The non-dominant pollen types (Figure 8.10) are increasingly represented by Gramineae pollen up the pollen sub-zone. Other local pollen types are present at fluctuating levels.

Pollen sub-zone boundary The MB3.4a to MB3.4b pollen sub-zone boundary is placed at 260 cm. It is placed here due to changes in the quantities of *Alchornea*, *Croton*, *Dodonaea*, *Dombeya*, Ericaceae, *Macaranga*, Myrtaceae, *Neoboutonia*, Urticaceae and *Vernonia* pollen. There are significant changes in the amount of Cyperaceae pollen, Fern spores and Gramineae pollen about the pollen sub-zone boundary.

Pollen sub-zone MB3.4c The boundaries for pollen sub-zone MB3.4c are placed at 160 cm and 45 cm (the uppermost sample collected). *Alchornea*, *Bidens*, *Faurea*, *Neoboutonia*, *Podocarpus*, *Prunus* and Urticaceae pollen all increase relative to pollen sub-zone MB3.4b. *Acalypha*, *Afrocrania*, *Macaranga*, *Nuxia*, *Olea*, *Pilea*, *Vernonia* and *Zanthoxylum* pollen all decrease relative to the previous pollen sub-zone. *Croton*, *Dombeya*, *Olea* and *Polyscias* pollen remain at similar levels. *Dodonaea* and *Rumex* pollen percentages decrease, although only slightly. Local pollen and spores (Figure 8.9) remain at similar levels to the previous sub-zone. Pollen from non-dominant local sources (Figure 8.10) are dominated by *Alchemilla* and Gramineae pollen with *Cyathea* spores, *Helichrysum*, *Lobelia* and *Silene* pollen sub-dominant. There is a marked increase in the amount of *Typha* pollen towards the top of the pollen sub-zone.

8.5 Presentation and description of pollen and spores from core MB23

In terms of the pollen sums used, and categories assigned to the pollen data the construction of pollen diagrams for core MB23 is identical to that used for cores MB6 and MB3. Changes in the pollen percentages down-core are presented in Figure 8.11. Core MB23 is divided into four pollen zones, MB23.1, MB23.2, MB23.3 and MB23.4. Pollen zone MB23.2 is sub-divided into pollen sub-zones MB23.2a and MB23.2b. Pollen zone MB23.4 is divided into five sub-zones; MB23.4a, MB23.4b, MB23.4c, MB23.4d and MB23.4e. These sub-zones are numbered in accordance with equivalent pollen assemblages in the other cores. The pollen diagrams that result from the local pollen and spores and the local non-dominant local pollen and spores pollen sums (Section 8.2) are portrayed in Figures 8.12 and 8.13 respectively.

Pollen zone MB23.1 ranges from the base of the core at 595 cm to 540 cm. *Faurea*, Myrtaceae, *Olea* and *Podocarpus* pollen from the montane forest category dominate this pollen zone. *Hagenia*, *Ilex*, *Macaranga*, *Neoboutonia*, *Nuxia* and *Prunus* pollen are also present, albeit at relatively low levels. Pollen derived from the high altitude forest category is dominated by Ericaceae pollen, although *Artemisia* and *Stoebe* pollen are also well represented. Myrtaceae pollen dominates the swamp forest category. The degraded forest category is dominated by *Anthospermum* pollen. Very little pollen is present from any other taxa within this category. Forest shrubs are poorly represented by their pollen, with *Acalypha*, Umbellifereae and Urticaceae pollen being present at the bottom of the pollen zone.

Figure 8.11 Core MB23: non-local pollen diagram

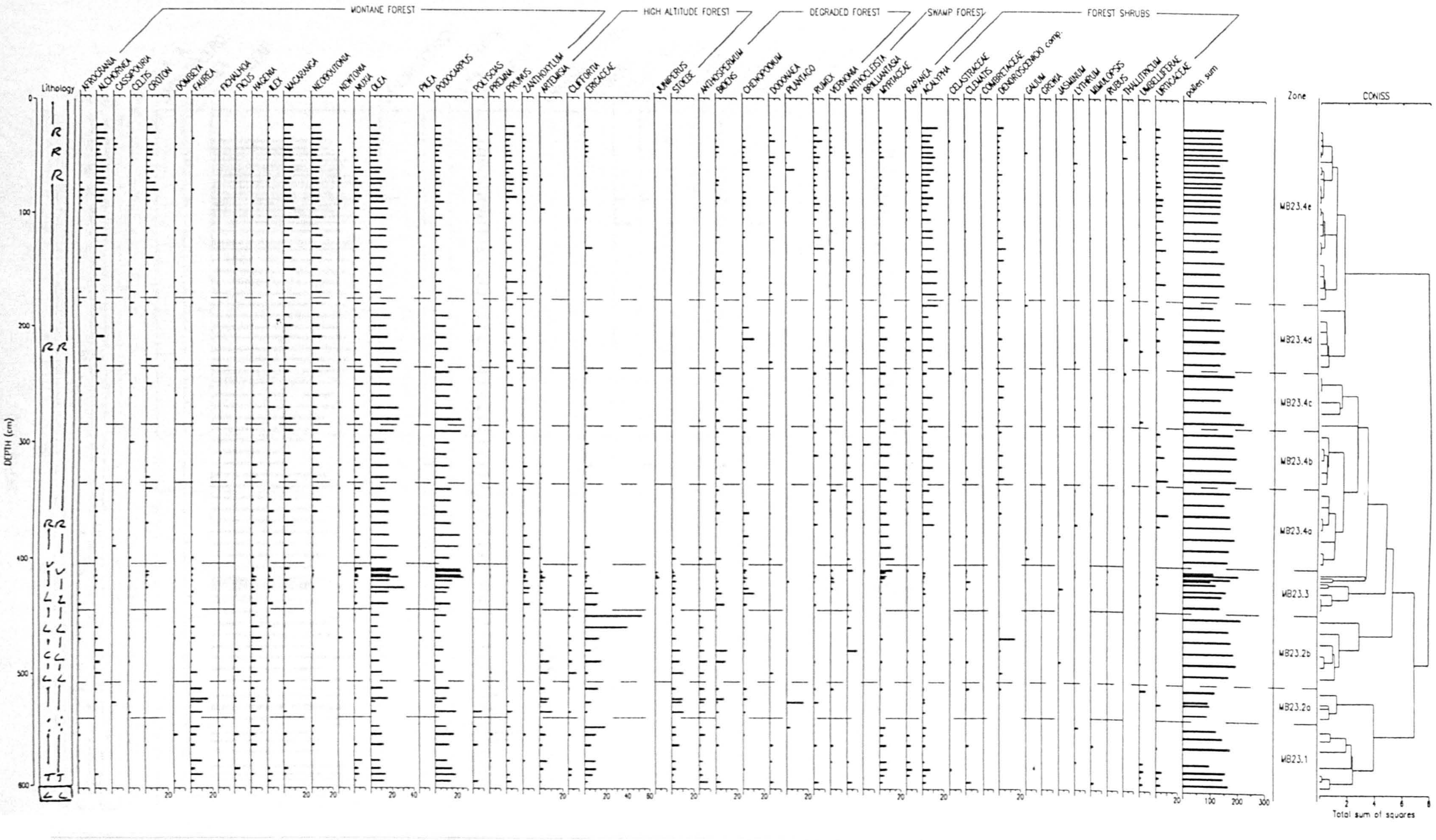


Figure 8.12 Core MB23: local pollen and spore diagram

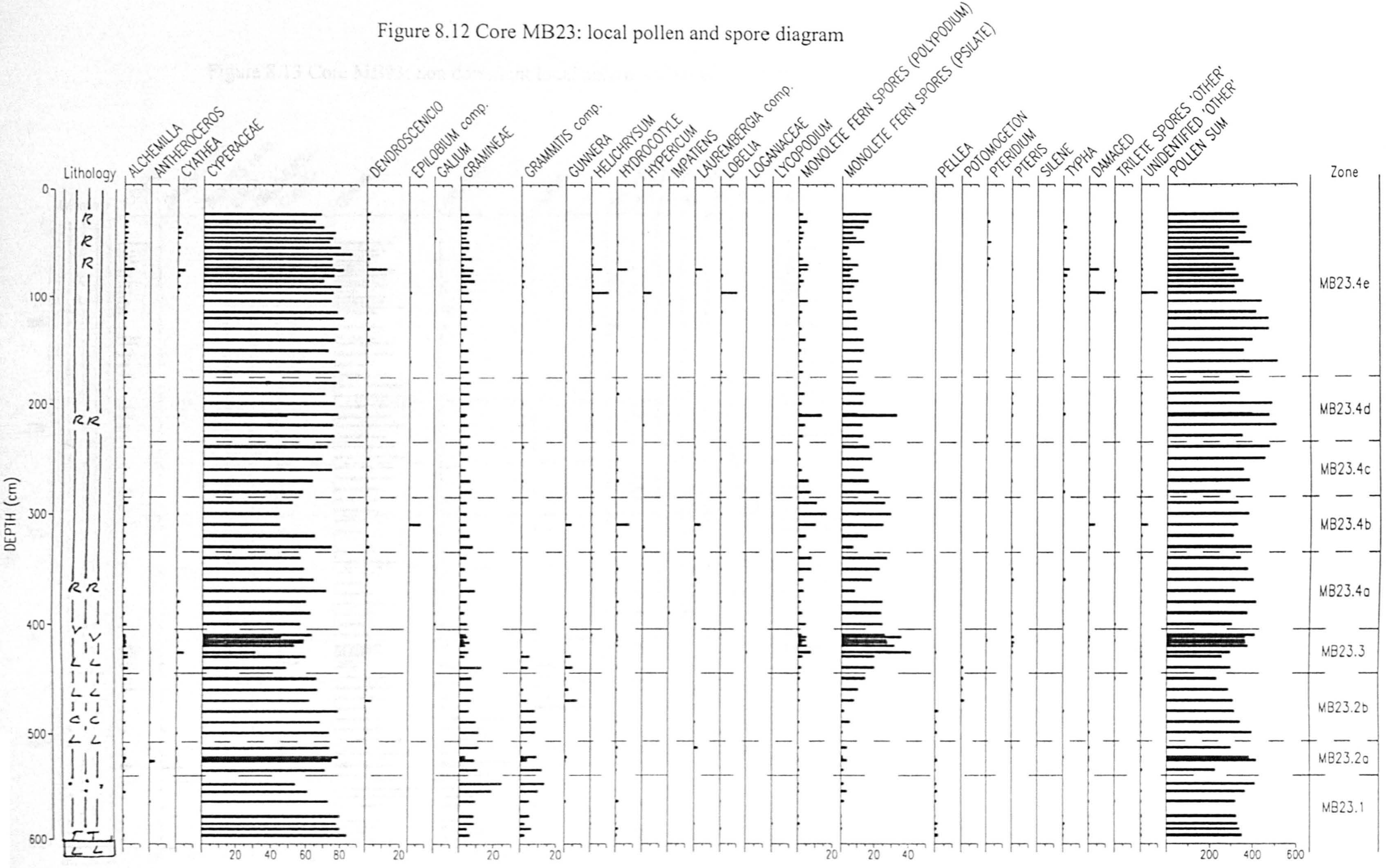
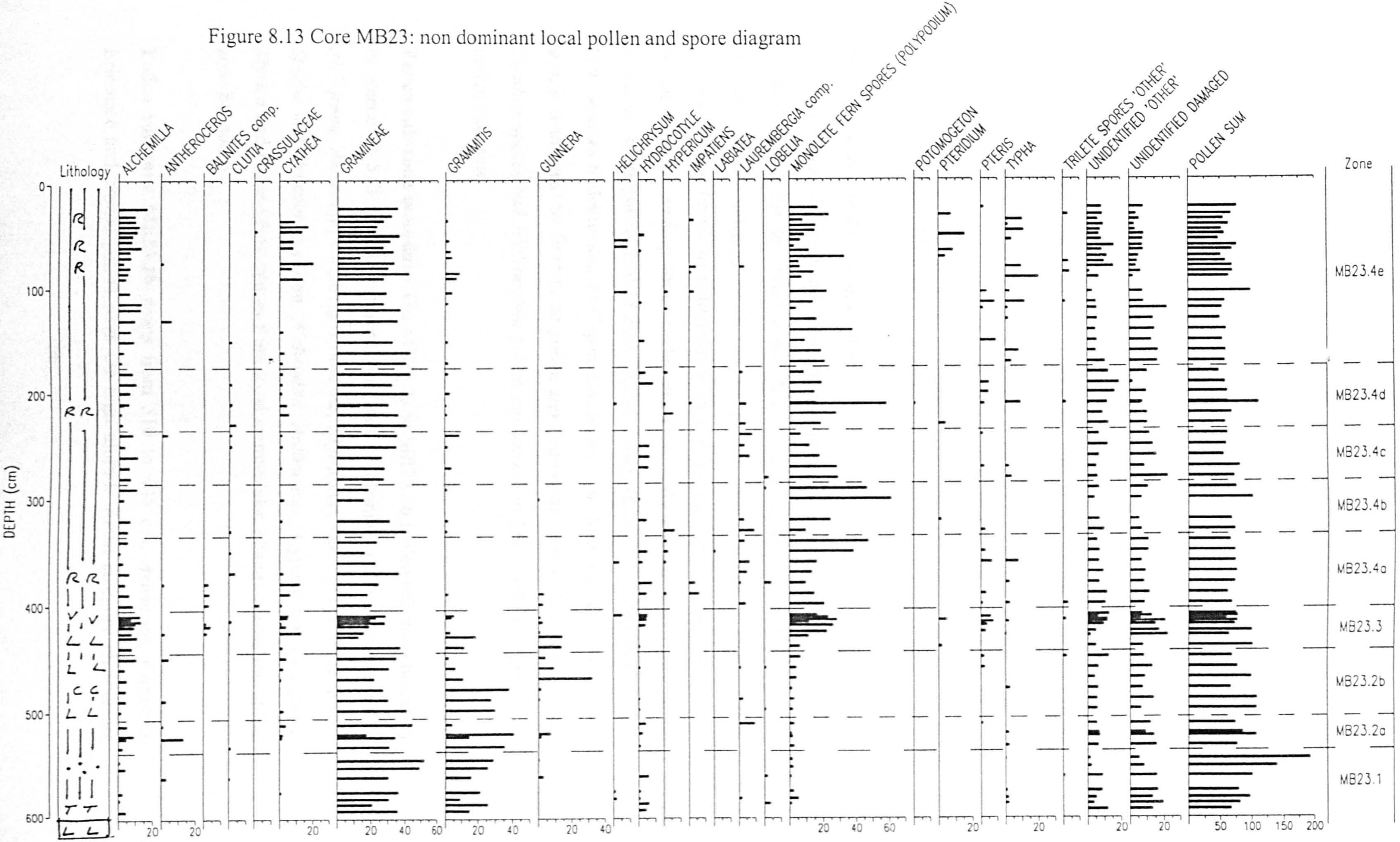


Figure 8.13 Core MB23: non dominant local pollen and spore diagram



Locally produced pollen is dominated by Cyperaceae pollen at the base of the pollen zone. Gramineae pollen and *Grammitis* spores are co-dominant when Cyperaceae and *Psilate* Fern spores are removed from the pollen sum (Figure 8.13). There are fluctuating amounts of *Alchemilla*, *Hydrocotyle*, *Typha* pollen and Trilete spores.

Pollen zone boundary The MB23.1 to MB23.2 pollen zone boundary is placed at 540 cm. It is placed here due to changes in the percentages of *Artemisia*, Ericaceae, *Faurea*, Myrtaceae, *Olea*, *Podocarpus* and *Stoebe* pollen.

Pollen zone MB23.2 spans from 540 to 445 cm. It is sub-divided into two pollen sub-zones: MB23.2a and MB23.2b.

Pollen sub-zone MB23.2a spans from 540 cm to 510 cm. Within this pollen sub-zone *Artemisia*, *Cliffortia* and *Stoebe* pollen from the high altitude forest category all increase relative to pollen zone MB23.1, as does *Faurea* pollen from the montane forest category. Relative to pollen zone MB23.1, *Olea*, *Pilea*, *Podocarpus* and *Polyscias* pollen stay at similar levels, whereas *Prunus* and *Nuxia* pollen decrease. Swamp forest pollen are very rarely present within this pollen sub-zone, as are pollen derived from degraded forest taxa. The pollen spectra from local sources is dominated by Cyperaceae pollen. The local non-dominant pollen sum is dominated by Gramineae pollen and *Grammitis* spores. *Alchemilla* pollen, *Cyathea* spores and *Hydrocotyle* pollen are present at low levels throughout the pollen sub-zone.

Pollen sub-zone boundary The MB23.2a to MB23.2b pollen sub-zone boundary is placed at 510 cm. It is placed here due to changes in the percentages of *Alchornea*, *Artemisia*, *Cliffortia*, Ericaceae, Myrtaceae, *Olea*, *Pilea*, *Podocarpus*, *Stoebe* and Urticaceae pollen. *Alchemilla*, *Anthoceros*, Cyperaceae, Gramineae, *Myrica* and *Psilate* Fern spores from local sources also change across the pollen zone boundary.

Pollen sub-zone MB23.2b spans from 510 to 445 cm. *Artemisia*, *Cliffortia*, Ericaceae and *Stoebe* pollen from the high altitude forest category all increase relative to pollen sub-zone MB23.2a. *Ilex*, *Faurea*, *Hagenia*, *Olea* and *Podocarpus* pollen from the montane forest category decrease relative to pollen sub-zone MB23.2b, whereas *Nuxia*, *Pilea* and *Polyscias* pollen stay at similar levels to the previous sub-zone. In the swamp forest category, *Rapanea* pollen increases relative to pollen sub-zone MB23.2a, whereas Myrtaceae pollen decreases. *Bidens* and *Chenopodium* pollen form the degraded forest category increase relative to the previous pollen sub-zone. The pollen spectra from local sources is dominated by *Alchemilla*, *Gunnera* and Gramineae pollen. Pollen from the local non-dominant pollen and spores (Figure 8.13) is dominated by *Alchemilla*, *Gunnera* and Gramineae pollen. *Gunnera* pollen is particularly important toward the top of the pollen sub-zone.

Pollen zone boundary The pollen zone boundary between MB23.2 and MB23.3 is placed at 445 cm. It is placed here due to changes in the quantities of *Artemisia*, *Bidens*, *Chenopodium*, Ericaceae, *Macaranga*, *Nuxia*, *Olea*, *Podocarpus* and *Zanthoxylum* pollen. The amount of *Cyathea*, Cyperaceae and *Psilate* Fern spores also change abruptly across the pollen zone boundary.

Pollen zone MB23.3 is located between 445 and 365 cm. Throughout the pollen zone *Celtis*, *Croton*, *Ilex*, *Macaranga*, *Neoboutonia*, *Nuxia*, *Olea*, *Podocarpus*, *Polyscias* and *Zanthoxylum* pollen from the montane forest category increase in abundance relative to pollen sub-zone MB23.2b, whereas *Hagenia* pollen decreases. *Cliffortia*, Ericaceae and *Stoebe* pollen from the high altitude forest category decrease relative to pollen zone MB23.2, although there is an increase in *Artemisia* and *Juniperus* pollen. Myrtaceae pollen from the swamp forest category increases relative to pollen sub-zone MB23.2b. *Bidens*, *Chenopodium*, *Rumex* and *Vernonia* pollen from the degraded forest category all increase relative to the previous pollen sub-zone. Pollen from local sources is dominated by Cyperaceae, with a large increase in *Psilate* Fern spores, particularly towards the top of the pollen zone. Non-dominant local pollen are represented by Gramineae pollen and latterly *Polypodium* Fern spores. *Alchemilla*, *Cyathea*, *Gunnera* pollen and *Pteris* spores are also present throughout the pollen zone.

Pollen zone boundary The MB23.3 and MB23.4 pollen zone boundary is placed at 365 cm. It is placed here due to changes in the quantities of *Alchornea*, *Anthocleista*, *Artemisia*, *Macaranga*, *Myrica*, Myrtaceae, *Neoboutonia*, *Podocarpus*, *Rapanea*, *Rumex*, Urticaceae, *Vernonia* and *Zanthoxylum* pollen. Pollen from local sources remains at similar levels either side of the pollen zone boundary.

Pollen zone MB23.4 extends from 395 to 23 cm (the core surface). MB23.4 contains five pollen sub-zones with the boundaries being placed at 325, 290, 235 and 185 cm. The five pollen sub-zones will be described separately.

Pollen sub-zone MB23.4a contains sediments between 395 and 295 cm. From the montane forest category *Ilex*, *Macaranga*, *Neoboutonia*, *Nuxia* pollen all increase in abundance relative to the previous pollen zone. *Olea*, *Pilea*, *Podocarpus*, *Polyscias* and *Prunus* pollen all remain at similar levels. *Anthocleista* and Myrtaceae pollen from the swamp forest category increase in abundance relative to the previous pollen zone. All pollen types from the high altitude forest category decrease relative to pollen zone MB23.3. *Bidens*, *Chenopodium*, *Rumex* and *Vernonia* pollen from the degraded forest category increase relative to the previous pollen zone. *Acalypha*, *Dendroscencio* and Urticaceae pollen dominate the forest shrub category. Pollen derived from local pollen taxa fluctuates markedly throughout this pollen sub-zone (Figure 8.12), with Cyperaceae pollen and *Psilate* Fern spores dominant. Similarly, the pollen from non-dominant local sources (Figure 8.13) fluctuate markedly throughout this pollen sub-zone. *Alchemilla*, Gramineae, *Hydrocotyle*, *Laurembergia* and *Lobelia* pollen, *Pteris* spores and *Typha* pollen are all well represented within the pollen sub-zone, indicative of a relatively diverse local flora.

Pollen sub-zone boundary The MB23.4a and MB23.4b pollen sub-zone boundary is placed at 325 cm. It is placed here due to changes in the quantities of *Alchornea*, *Anthocleista*, *Celtis*, *Dendroscenicio*, *Ilex*, Myrtaceae, *Olea*, *Podocarpus*, *Vernonia*, Urticaceae and *Zanthoxylum* pollen. From the local taxa there are large changes in the amount of Cyperaceae and Gramineae pollen, Fern spores and *Laurembergia* pollen.

Pollen sub-zone MB23.4b contains sediments between 325 and 290 cm. *Hagenia*, *Neoboutonia*, *Prunus* and *Zanthoxylum* pollen from the montane forest category all increase relative to the previous pollen sub-zone. *Olea* and *Podocarpus* pollen both initially increase, and then decrease. There is little change in the amount and type of pollen from the degraded, high altitude forest, and forest shrub categories compared to the previous pollen sub-zone. Pollen from *Anthocleista*, Myrtaceae and *Rapanea* pollen remains at similar percentages relative to the previous pollen sub-zone. Pollen from local sources (Figure 8.12) is dominated by Cyperaceae pollen. The importance of this pollen type decreases dramatically through the pollen sub-zone as the number of *Psilate* Fern spores steadily increases. Similarly, the abundance of Gramineae pollen decreases as the amount of *Polypodium* Fern spores increases up the pollen sub-zone. In comparison to pollen sub-zone MB23.4a the local pollen flora (Figure 8.13) is not very diverse.

Pollen sub-zone boundary The MB23.4b and MB23.4c pollen sub-zone boundary is placed at 290 cm. It is placed here due to changes in the quantities of *Faurea*, *Ilex*, Myrtaceae, *Neoboutonia*, *Olea*, *Podocarpus*, *Prunus* and Urticaceae pollen. Levels of *Alchemilla*, Cyperaceae, Gramineae and Fern spores from the local taxa also change about the pollen sub-zone boundary.

Pollen sub-zone MB23.4c contains sediments between 290 cm and 235 cm (the uppermost sample collected). *Afrocrania*, *Alchornea*, *Celtis*, *Ilex*, *Nuxia*, *Polyscias* and *Prunus* pollen from the montane forest group all increase relative to the previous sub-zone, whereas *Macaranga*, *Neoboutonia*, *Olea* and *Podocarpus* pollen all decrease. Pollen types from the high altitude forest category are not present in significant quantities. There is a slight increase in the amount of *Chenopodium* pollen, although *Dodonaea*, *Plantago*, *Rumex* and *Vernonia* pollen from the degraded forest category, all show no change relative to pollen sub-zone MB23.4b. The swamp forest category pollen spectra remains very similar to pollen sub-zone MB23.4b. Similarly, the forest shrub taxa are still dominated by *Acalypha*, *Dendroscencio* and Urticaceae pollen. Pollen from local taxa is increasingly dominated by Cyperaceae, whereas *Psilate* Fern spores decrease throughout the sub-zone. Gramineae dominates the non-dominate local taxa (Figure 8.12) as the presence of Fern Spores decreases. *Alchemilla*, *Grammitis*, *Hydrocotyle* and *Typha* pollen are present in sporadic amounts.

Pollen sub-zone boundary The MB23.4c and MB23.4d pollen sub-zone boundary is placed at 235 cm. It is placed here due to changes in the quantities of *Acalypha*, *Alchornea*, *Croton*, *Dodonaea*, *Macaranga*, *Olea*, *Podocarpus*, *Prunus* and Urticaceae pollen. The levels of pollen from local taxa are relatively stable about the pollen sub-zone boundary.

Pollen sub-zone MB23.4d contains sediments between 235 and 185 cm. *Alchornea*, *Celtis*, *Croton*, *Macaranga*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen from the montane forest group all increase relative to the previous sub-zone, whereas *Ilex*, *Nuxia*, *Olea* and *Podocarpus* pollen decrease. Pollen types from the high altitude forest category are not present in significant quantities. *Bidens*, *Chenopodium*, *Rumex* and *Vernonia* pollen are recorded at low percentages throughout the pollen sub-zone. *Anthocleista*, Myrtaceae and *Rapanea* pollen, from the swamp forest category increase slightly relative to pollen sub-zone MB23.4c. *Acalypha* and Urticaceae pollen increase dramatically from the previous pollen sub-zone. Pollen percentages from local taxa (Figure 8.12) are dominated by Cyperaceae pollen, with *Gramineae* pollen and *Psilate* Fern spores at near constant levels throughout the sub-zone. Towards the sub-zone boundary, there is a slight increase in *Alchemilla*, *Clutia* pollen, *Cyathea* and *Pteris* Fern spores.

Pollen sub-zone boundary The MB23.4d to MB23.4e pollen sub-zone boundary is placed at 185 cm. It is placed here due to changes in the quantities of *Alchornea*, *Celtis*, *Croton*, *Dodonaea*, *Dombeya*, *Faurea*, *Macaranga*, *Olea*, *Plantago*, *Polyscias*, *Prunus* and *Zanthoxylum* pollen. The local pollen taxa do not change in significant quantities about the pollen sub-zone boundary.

Pollen sub-zone MB23.4e contains sediments between 185 cm and 23 cm (the uppermost sample collected). *Afrocrania*, *Alchornea*, *Celtis*, *Croton*, *Macaranga*, *Neoboutonia*, *Nuxia* and *Polyscias* pollen from the montane forest category all

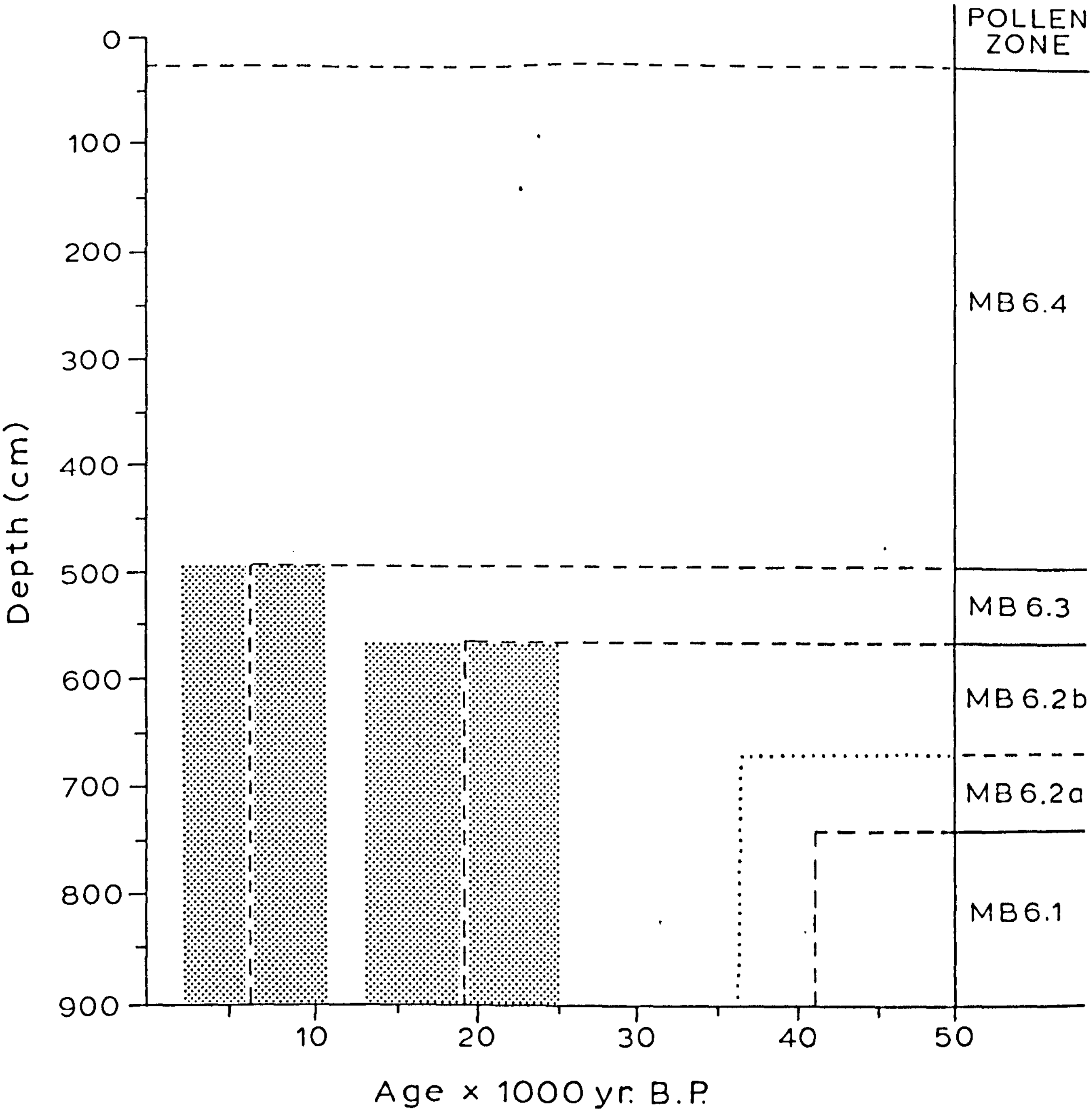


Figure 8.14 Adjusted age-depth curve for MB6 highlighting timing of sedimentary hiati within the Mubwindi Swamp sediments

increase relative to the previous pollen sub-zone, whereas *Ilex*, *Olea* and *Podocarpus* pollen all decrease. Ericaceae pollen increases relatively to the previous pollen sub-zone, although the other pollen types from the high altitude forest category are not present in significant quantities. *Bidens*, *Chenopodium*, *Dodonaea*, *Plantago*, *Rumex* and *Vernonia*, from the degraded forest category, increase relative to pollen sub-zone MB23.4d. Myrtaceae pollen, from the swamp forest category, decreases relative to pollen sub-zone MB23.4d, whereas *Anthocleista* pollen increases. *Acalypha*, *Dendroscencio* and Urticaceae pollen from the forest shrub category increase relative to the previous pollen sub-zone. Pollen percentages from local taxa are dominated by Cyperaceae pollen. Towards the core surface there is a slight increase in *Psilate* Fern spores, with an associated decrease in the dominance of Cyperaceae pollen. Non-dominant local sources (Figure 8.13) are dominated by Gramineae pollen. *Alchemilla* and *Typha* pollen are sub-dominant. The amount of *Cyathea*, *Pteridium* and *Typha* pollen increases significantly towards the top of the pollen sub-zone.

8.6 Vegetation reconstruction and summary of the pollen data

Reconstruction of the vegetation within the Mubwindi Swamp catchment is based on the combined pollen results presented for cores MB3, MB6 and MB23 (Figure 7.1). This evidence is interpreted in the light of the evidence presented in previous chapters. Changes in the composition and distribution of vegetation within the Mubwindi Swamp catchment will be considered as four local assemblage zones. These correspond to the pollen zones and are representative of periods when there has been a significant change in the composition and distribution of the vegetation within the Mubwindi Swamp catchment.. The temporal boundaries of these local pollen assemblage zones are presented in Figure 8.14. This also indicates the position, and duration of, sedimentary hiati.

Local pollen assemblage zone one: prior to 41,000 yr B.P.

The lower part of cores MB3, MB6 and MB23 are all thought to occur below the radiocarbon date of > 43,000 yr B.P. (Beta-82553) from 748 to 755 cm in core MB6 and cover a period not covered to any great extent by the palaeoecological records from other sites in the Rukiga highlands (Muchoya Swamp's oldest radiocarbon date recording an age of 42,000 +/- 1700 yr B.P.). The large quantities of *Faurea* pollen, even though it is shown to be a well dispersed pollen type, indicate that the parent taxon (*F. saligna*) was the dominant taxon growing on the hillsides adjacent to Mubwindi Swamp. Today *F. saligna* forms almost pure stands near Ruhiija, at an altitude of approximately 2450 m. The pollen spectra indicates that species of the Ericaceae were also significant components of the surrounding vegetation. Due to large number of species that produce this pollen type (Section 2.4), it is not possible to determine the precise source of Ericaceae pollen. Species of *Nuxia*, *Olea* and *Podocarpus* were also present. The probable source of *Nuxia* pollen was *N. congesta*; at present this is growing close to Ruhiija, at a similar altitude to *Faurea saligna*. *Olea* and *Podocarpus* pollen are likely to have been produced by taxa that can presently be found within the Mubwindi Swamp catchment (Chapter 6). However, some of the *Podocarpus* pollen may have been released by *P. falcatus*. Although not recorded within Bwindi-Impenetrable Forest at present, this species does occur in the more arid areas along the Western Rift (Melville, 1958). The large amount of Myrtaceae pollen is thought to have originated from two species of *Syzygium; S. cordatum* and *S. guineense*, the former is recorded throughout the Mubwindi Swamp catchment at present, the latter being recorded from a similar altitude in other parts of Bwindi-Impenetrable Forest (Kakuru, 1993). The high percentage of Myrtaceae pollen suggests that the parent taxa were present at high densities within the Mubwindi Swamp catchment, probably close to the margins of Mubwindi Swamp.

The pollen spectra indicate that minor components of the surrounding forest were species of *Hagenia*, *Ilex*, *Macaranga*, *Polyscias* and *Prunus*. The parent taxa thought responsible for these pollen types are *Hagenia abyssinica*, *Ilex mitis*, *Macaranga kilimandscharica*, *Polyscias fulva* and *Prunus africana* respectively. *Hagenia abyssinica* has a broad ecology (Dale, 1940; Bentjee, 1994). Due to its known high pollen production (Hamilton, 1972), its presence in local pollen assemblage zone one is thought to indicate an infrequent occurrence within the surrounding vegetation. Similarly, *Ilex mitis* has a broad ecological range; it is found across a range of altitudes and in dry and water-logged soil conditions (Langdale-Brown *et al*, 1961; Lind and Morrison, 1974). However, the pollen, type being representative of the density of the parent taxa within the surrounding vegetation (Chapter 6) indicates that *Ilex mitis* was a significant component of the vegetation, possibly sub-dominant within the surrounding catchment. *Prunus africana* is a characteristic tree of upper montane forest and moist lower montane forest (White, 1983), although it is only locally common within Bwindi-Impenetrable Forest (Cahusac, 1958). Due to the moderate to high export ability of the pollen, it is suggested that the parent taxa were only locally present within the vegetation surrounding Mubwindi Swamp. *P. africana* became increasingly scarce towards the upper boundary of local pollen assemblage zone one. Indeed, except for *Nuxia* there is a decrease in the amount of pollen derived from all the sub-dominant forest taxa towards the top of local pollen assemblage zone one. The persistence of pollen derived from *Nuxia* spp. within the sediments can possibly be explained by the relatively high export ability of this pollen type (Chapter 6). In association with *Polyscias fulva*, and to a lesser extent *Neoboutonia macrocalyx*, *Macaranga kilimandscharica* is a coloniser of forest gaps (Chapter 6). The pollen types derived from these taxa are present at low levels throughout local pollen assemblage zone one, thus indicating that they were relatively insignificant components of the surrounding vegetation. An exception to this is *Neoboutonia macrocalyx* which, due to its poor pollen dispersal (Chapter 6), could have been relatively common within the surrounding vegetation.

Due to some similarities between pollen from local pollen assemblage zone one, and that found within the surface sediment samples, it would seem likely the range of montane forest taxa recorded in Chapter 6 would have been present within the Mubwindi Swamp catchment. These taxa would have been associated with taxa from a slightly higher altitude than present to form a type of high montane forest. Pollen from other montane forest taxa may well have been deposited as a result of long distance transport; this could have been particularly so for well dispersed pollen types such as *Celtis*. Towards the top of local pollen assemblage zone one, and the radiocarbon date of > 43,000 yr B.P. (Beta-82553) from 748 to 755 cm, the vegetation composition changes to a higher altitudinal nature. *Artemisia* and *Stoebe* pollen became increasingly important components within the Mubwindi Swamp sediments as the presence of high montane forest taxa decreased. *Artemisia afra* and *Stoebe kilimandscharica*, probable sources of *Artemisia* and

Stoebe pollen respectively are unrecorded within the Rukiga highlands today (Taylor, 1990). The plants are, however, characteristic of the Ericaceous Belt on drier mountains in eastern Africa (Hedberg, 1951); for instance they are common between 3200 m and 3660 m on Mount Elgon (Hamilton and Perrot, 1981).

Pollen derived from the local taxa indicate a mixed local vegetation complex throughout the period represented by local pollen assemblage zone one. There was an increase in *Alchemilla*, with a steady decrease in *Carduus*. The isolated peaks of the other local pollen types are thought to reflect a combination of differential local pollen export and changes in the vegetation on the swamp surface. This is further supported by the lack of trends through the local pollen data. Fern spores and Cyperaceae pollen indicate a distinct transgressive period of change in local vegetation. This change may be a facet of differential preservation; Fern spores being more resistant to decay (Taylor, 1988) are likely to be over-represented in the older, clay-rich basal sediments. Alternatively it may represent a period of initial swamp development, following the initial damming of the valleys that make up Mubwindi Swamp, as suggested in Chapter 5. The vegetation change follows the sequence of ferns dominating the vegetation, then ferns and sedges are co-dominant, and lastly, sedges becoming dominant towards the top of local pollen assemblage zone one. This pattern of change is also been recorded in core MC2 at Muchoya Swamp where initial high levels of Fern spores rapidly tail off as Cyperaceae pollen dominates. As suggested previously, this further indicates that the basal sediments from Mubwindi Swamp predate those from Muchoya Swamp, assuming that the two basins originated for the same period of tectonic dislocation (Chapter 3).

The combined pollen flora from zones MB3.1, MB6.1 and MB23.1 indicate an association of high montane forest with an increasing component of ericaceous belt vegetation was present within the Mubwindi Swamp catchment prior to about 41,000 yr B.P.

HIATUS

Due to the rapid changes in Myrtaceae, *Podocarpus*, *Prunus* and Urticaceae pollen about the local pollen assemblage zone one to two boundary there is further evidence for the sedimentary hiatus suggested in Chapter 5 and 7. However this is recorded as a gradual increase core MB23, rather than the rapid change in cores MB3 and MB6. Extrapolating the radiocarbon data (Chapter 4) this hiatus is thought to be of a relatively short duration in core MB6, if present at all. On the strength of the radiocarbon dates of > 43,000 yr B.P. (Beta-82553) and 33,150 +/- 620 yr B.P. (AA-17154) from core MB6 it is thought this hiatus records a break of a few thousand years in core MB6, possibly with longer hiati in cores MB3 and MB23 (Chapter 7).

Local pollen assemblage zone two: approximately 40,000 to 25,000 yr B.P.

Local pollen assemblage zone two comprises two main vegetation associations with a mid zonal change. Initially, pollen derived from *Artemisia afra* and members of the Ericaceae were present with relatively high densities of *Hagenia abyssinica*, *Nuxia* spp., *Olea* spp. and *Prunus africana*, and more occasional occurrences of *Alchornea* spp. and *Afrocrania* spp. The composition of this vegetation within the Mubwindi Swamp catchment may comprise a three layered structure. At the highest altitudes *Artemisia afra* would form a scrub, possibly with members of Gramineae and occasional high montane forest trees such as *Faurea saligna* and *Hagenia abyssinica* present. On mid and lower slopes *Olea capensis* ssp. and *Podocarpus* spp. dominated the forest with. *Faurea saligna*, *Ilex mitis*, *Nuxia* spp., *Polyscias fulva* and *Prunus africana* also present. At the lowest altitudes surrounding Mubwindi Swamp, *Syzygium* spp. grew with a small amount of *Alchornea* spp. also present.

Towards the upper Section of local pollen assemblage zone two the pollen spectra indicate a change in the composition of the ericaceous belt vegetation to an *Artemisia afra*, *Cliffortia* spp. and *Stoebe kilimandscharica* association with increased dominance from members of the Ericaceae. It is thought a proportion of *Alchemilla* and Gramineae pollen were likely to have been produced from taxa associated with the high altitudinal arboreal scrub, rather than from the local vegetation on the Mubwindi Swamp surface. Members of the Ericaceae were also present throughout this zone, although it is not possible to determine the originators of this pollen type due to the large number of genera within this family (Section 2.4). Notably there was a peak in *Cliffortia* pollen, this is thought to have originated from *Cliffortia nitidula*, this species does not occur in south-west Uganda at present, but it appears the plant could have been formerly much more widely distributed than today (Taylor, 1988). This change is concomitant with an increase in pollen derived from *Faurea saligna*, *Ilex mitis*, *Macaranga kilimandscharica*, *Podocarpus* spp., *Prunus africana* and *Zanthoxylum* spp., and a decrease in pollen from *Alchornea* spp., *Hagenia abyssinica* and *Olea* spp.

There is an inferred change in environmental conditions to those that supported an increased amount of montane forest taxa, concomitant with a diverse ericaceous belt association. This mid zonal change is also recorded by the local taxa, specifically by the massive increase in *Gunnera* pollen. This is thought to have originated from the aquatic herb *G. perpensa*. A possible explanation could have been the local growth of *G. perpensa* and hence the presence of the pollen type not being relative to the concentration within the surrounding vegetation. The vegetation on Mubwindi Swamp surface is still dominated by members of the Cyperaceae. Thus, conditions on the Mubwindi Swamp surface appear to have remained relatively moist with *Gunnera perpensa* and members of Cyperaceae dominating in the vegetation. This suggestion is also supported by increase in *Myrica* spp., likely to have been growing on Mubwindi Swamp surface, as it does during the present day.

Thus, local pollen assemblage zone two contains an association of high montane forest with ericaceous belt vegetation within the Mubwindi Swamp catchment. It is suggested there may have been compression of the limits of the 'classical vegetation zonation' now found within east and central Africa (Section 2.4). Alternatively, there may have been an ecotone between montane forest and higher altitudinal vegetation types. The possible environmental controls responsible for these situations will be discussed in part three.

HIATUS

On the basis of a change in the age-depth curve (Chapter 4), and the rapid changes in the percentages of the pollen and spore flora (specifically Cyperaceae, Ericaceae, Fern spores, *Hagenia*, *Ilex*, *Olea*, *Podocarpus* and *Vernonia*), there is thought to be a large sedimentary hiatus centred on the boundary between local pollen assemblage zones two and three (Chapter 7). This rapid change in micro-fossil distribution about the zonal boundary is also accompanied by sedimentary change (Chapters 4 and 5). Extrapolating the age-depth curve (Chapter 4) the sedimentary hiatus falls between the radiocarbon dates of 27,480 +/- 300 yr B.P. (AA-17153) for 590 to 595 cm from core MB6, and 12,930 +/- 100 yr B.P. (Beta-60065) for 430 to 443 cm from core MB3. This break in sedimentation is thought to have spanned from approximately 25,000 yr B.P. through to about 13,000 yr B.P. (Figure 8.14). However, these temporal boundaries can only be determined by the available radiocarbon data and should not be deemed as precise.

Local pollen assemblage zone three: approximately 13,000 to 11,000 yr B.P.

Within local pollen assemblage zone three, lower altitudinal vegetation types were more important components of the vegetation within the Mubwindi Swamp catchment in comparison to local pollen assemblage zone two. However, there was still a significant presence of ericaceous belt vegetation present within the Mubwindi Swamp catchment. There was an increase in pollen derived from *Cliffortia nitidula*. Interestingly, *Juniperus* pollen is present in small amounts. *Juniperus* pollen is likely to originate from *Juniperus procera*, a tree associated with high altitudinal, dry conditions (White, 1983). It seems probable that *J. procera* was present, either as isolated specimens at the highest altitudes surrounding Mubwindi Swamp, or at higher altitudes within the region. Due to the relatively low record of their pollen types within the Mubwindi Swamp sediments it is likely *Artemisia afra*, *Cliffortia nitidula*, Ericaceae spp. and *Stoebe kilimandscharica* were only present as isolated specimens on the highest slopes surrounding Mubwindi Swamp. At lower altitudes, this vegetation type was replaced by *Ilex*, *Olea* and *Podocarpus* dominated forest. Other trees present were *Hagenia abyssinica*, *Macaranga kilimandscharica*, *Neoboutonia macrocalyx*, *Nuxia* spp., *Polyscias fulva*, *Prunus africana* and *Zanthoxylum* spp. Combined, these taxa formed a type of dry montane forest. Towards the top of local pollen assemblage zone three there is an increase in the pollen grains derived from montane forest, concomitant with a decrease in pollen from high altitude sources. Ericaceae pollen percentages tail-off gently, although the *Podocarpus* curves rise sharply.

The increase in Fern spores and associated decrease of Cyperaceae percentage may indicate a rapid expansion of ferns on the Mubwindi Swamp surface. Alternatively, this rise in Fern spores may result from an increase in inorganic material, and hence be an artefact of differential preservation. This indicates differential preservation may account for the high amount of Fern spores within local pollen assemblage zone one.

Due to the increased sampling resolution within core MB23 (eight samples analysed for zone two in comparison with two and four samples from cores MB3 and MB6 respectively), it is possible to determine more precisely the nature of vegetation transition. The previous suggestion of a mix of ericaceous belt taxa and montane vegetation present within the Mubwindi Swamp catchment during this pollen zone still holds true. However, from the record in pollen zone MB23.3 it is suggested that the change in the structure of the vegetation was characterised by development stages. These led to a relatively open type of moist lower montane forest as suggested by the pollen derived from *Croton macrostachys* pollen in core MB23 and *Dombeya* spp., *Macaranga kilimandscharica* and *Neoboutonia macrocalyx* in all three cores; combined with relatively high levels of pollen derived from taxa of the degraded forest category. This decline is similarly associated with the rise in swamp forest taxa. The increase in *Syzygium* spp., which is recorded across Mubwindi Swamp, occurs earlier within cores MB3 and MB23 compared to core MB6. The relatively local position to the parent taxa of these cores, being located closer to the swamp margin, could explain why pollen type is recorded earlier in these cores.

Thus, within local pollen assemblage zone three there was a transition from a predominantly ericaceous belt vegetation to a relatively open stand of moist lower turn pollen sub-zone MB6.4b is thought to correspond to pollen sub-zones MB23.4b and MB23.4c. These between-core differences are thought to either represent localised differences in the vegetation relative to the position of the individual cores. Alternatively, the different number of pollen sub-zones may result from the different sampling intervals used in the different cores. It seems likely that the different sub-zone notation result from a combination of the factors outline above. Overall it is thought there were four main shifts in the composition of the late Holocene vegetation within the Mubwindi Swamp catchment. This corresponds to the four main shifts in sedimentary environment highlighted in Chapter 7.

A dynamic community of moist lower montane forest with a similar composition to that of the more remote areas of Bwindi-Impenetrable Forest (Chapter 3) was present within the Mubwindi Swamp catchment between approximately 2500 and 1575 yr B.P. *Olea capensis* ssp. and *Podocarpus* spp. dominated this moist lower montane forest with an under-story comprising fluctuating amounts of *Ilex mitis*, *Macaranga kilimandscharica*, and *Nuxia* spp. *Syzygium* spp. were likely to have formed a fringing band of vegetation close to the Mubwindi Swamp margins, as *Syzygium cordatum* does today (Chapter 6). Members of the Urticaceae were present in relatively high amounts, indicative of a well developed ground flora. This is not accompanied by high amounts of pollen from other arboreal taxa known to indicate an open forest, therefore it is suggested Urticaceae can form a significant component of the ground flora within a relatively dense forest. Pollen from local sources indicates an increased growth of species of Cyperaceae on the Mubwindi Swamp surface, as the importance of Ferns decline.

Due to the long hiatus in sedimentation it is not possible to say when the forest type was established within Mubwindi Swamp catchment. Based on the range of taxa present, it is suggested the forest described above was thought to have been well established, and therefore likely to have been in existence within the catchment prior to the date of 2110 +/- 55 yr B.P. from core MB6. However, the pollen spectra from core MB23 records an increase in the amount of *Croton macrostachyus*, *Neoboutonia macrocalyx*, *Rumex* spp. and *Vernonia* spp. and species of the Urticaceae. The presence of these taxa within montane forest today indicates some form of disturbance, this disturbance was not sustained, nor constant, through the time period. Indeed, this may have been attributed to a period of increased natural disturbance, such as that presently attributed to elephant activity.

From approximately 1575 yr B.P. through to 680 yr B.P. the forest within the Mubwindi Swamp catchment became more mixed, with *Hagenia abyssinica*, *Ilex mitis*, *Macaranga kilimandscharica*, *Neoboutonia macrocalyx*, *Prunus africana* and *Zanthoxylum* spp. being more important than previously. Latterly the densities of *Alchornea* spp., Ericaceae spp, *Macaranga kilimandscharica* and *Rumex* spp. increased. This change is concomitant with a decrease in *Olea* spp. and *Podocarpus* spp.; this suggests a possible opening up of the forest. Gaps where present, were quickly colonised by fast growing tree species. Disturbance of the vegetation within the Mubwindi Swamp catchment is also indicated by the rapidly fluctuating amounts of *Nuxia congesta*, *Olea* spp., *Pilea spp.*, *Podocarpus* spp. and members of Urticaceae. However, *Macaranga kilimandscharica*, *Neoboutonia macrocalyx* and *Polyscias fulva* remain at almost constant levels throughout this period. Similarly, other taxa indicative of disturbance do not show an increased density within the Mubwindi Swamp catchment, as would be expected if the proposed disturbance was catchment-wide. A possible explanation of this vegetation reconstruction could be a mosaic type of growth pattern within the Mubwindi Swamp catchment as a result of localised disturbance.

At approximately 750 yr B.P. there was a massive reduction in *Syzygium* spp. and the expansion of the *Alchornea* under-story; this change is thought to have been associated with the moister land adjacent to Mubwindi Swamp. Possibly the wetter, riparian habitats, previously occupied by *Syzygium* spp., had been occupied by moist lower montane forest, specifically *Alchornea hirtella* thicket, as this is present today. However, identified at a similar time, is a very significant increase in the amount of charcoal (Chapter 5). Thus, these changes in vegetation composition may result from localised burning within the Mubwindi Swamp catchment.

Between 680 and 75 yr B.P. the pollen spectra indicate a continuation of the type of forest described previously, with some subtle differences. There is an increase in arboreal taxa indicative of secondary forest within the Mubwindi Swamp catchment. Due to the presence within the Mubwindi swamp catchment at present, these are thought to include *Croton macrostachys*, *Dombeya goetzenii*, *Macaranga kilimandscharica* and *Polyscias fulva*. The pollen curves from *Macaranga* and *Neoboutonia* highlight a steady increase in the former and concomitant decrease in the latter. A similar pattern is apparent for *Dombeya* and *Croton* respectively. This may highlight the individual ecological roles within disturbed forest that the parent taxa of these pollen types take, as is the case at present (Chapter 6). This indication of increased disturbance is further supported by a marked increase in pollen derived from taxa of a ruderal habit, such as *Chenopodium* spp., *Dodonaea* spp., *Plantago* spp., *Rumex* spp. and *Vernonia* spp. The pollen from taxa that presently fringe Mubwindi Swamp, such as *Alchornea hirtella* and *Syzygium* spp., remain similar to the previous pollen zone. Thus, it is thought disturbance was concentrated within the surrounding forest, rather than around the swamp margins. Further evidence for within catchment disturbance is apparent from the sedimentary data, particularly the increases in charcoal (Chapter 5) recorded during this period. There are some notable differences in the pollen spectra of the comparable sub-zones of the different cores. *Croton* and *Neoboutonia* appear over-represented in core MB23, at around 10 % of the non-local pollen sum, whereas these taxa commonly reach only 5 % in the other cores. It is suggested these differences primarily result from the position of core MB23, being closer the Mubwindi Swamp margin, and the parent taxa, compared to other cores.

The main montane forest tree to have reduced its pollen input is that of *Podocarpus* spp. Once in decline, *Olea* pollen dominated the pollen sum, as is the case at present (Chapter 6). After this initial domination *Olea* pollen also starts shows a percentage decrease. The decline in the parent taxa of these pollen types allowed for the further expansion of taxa indicative of disturbed areas. These changes in the composition of the vegetation are also recorded by pronounced changes in sediment composition during this period (Chapter 4). Pollen from local sources indicate there was an increasing presence of *Alchemilla*, *Helichrysum*, and latterly *Typha* species within the local vegetation. Following an initial increase in Ferns there was a gradual replacement by members of the Cyperaceae.

In summary a type of degraded moist lower montane forest was present in the Mubwindi Swamp catchment from approximately 680 to 75 yr B.P. Whatever the driving mechanisms responsible for creating the degraded forest, these appear to be more prevalent towards the top of local pollen assemblage four. When comparing the pollen data several interesting observations can be made. Firstly, there is a steady decline in *Podocarpus* pollen noted in all cores; this is closely followed by an increase in *Polyscias* and *Prunus* pollen. Although this result could indicate a direct replacement of the niche previously occupied by *Podocarpus* spp. by these taxa, due to the highly dispersed nature of *Podocarpus* pollen, this pattern probably results from regional clearance of *Podocarpus* spp. and a relatively localised increase of *Polyscias fulva* and *Prunus africana*. Additional support for the presence of more recent disturbance within the Mubwindi Swamp catchment comes from the relatively high amount of large-sized inorganic material and charcoal (Chapter 5). These are suggestive of increased in-wash of allochthonous sediment, possibly as a result of decreased slope stability within the Mubwindi Swamp catchment.

Relative to the previous period, the pollen retained in the top of the cores indicates a period of relative stability within the Mubwindi Swamp catchment. This is recorded as a rise in previously sub-dominant taxa and no increased fall in the favoured timber species (Section 3.7) or increased rise in the taxa from disturbed forest. The trees that in 'primary forest' would occur as specimens in the under-story become relatively more common. *Prunus africana*, *Zanthoxylum* spp. and latterly *Ilex mitis* are good examples of tree species that follow this pattern. The increased dominance by these taxa suggests gaps in the forest suggested to previously are becoming closed. This is further supported by the slight decrease in taxa indicative of degraded forest. At the top of the cores there are increases in the amount of pollen derived from *Olea capensis* ssp. and *Podocarpus* spp. There is also a decrease in the amount of charcoal and inorganic material recorded from these top sediments in core MB6 (Chapter 5). With the proposed stability only recorded in the top samples, it is not possible to indicate with any certainty this is indicative of increased within catchment stability. Furthermore, this 'recovery' is only recorded from core MB6, and is not recorded so strongly by the pollen data from cores MB3 and MB23. Thus, it is thought this is either an anomaly of the MB6 record or it is so recent it has yet to be recorded fully by the Mubwindi Swamp sediments.

An interesting facet of the structure of the pollen curves in MB23 is the pattern of increases and decreases in the percentages of pollen; this is also recorded in core MB6 (although not so strongly) and is not apparent in core MB3. This pattern is thought to result from the increased sampling resolution of sediments from core MB23, and is also thought to be ecologically significant. The possible cause of this cyclical change could be a mosaic type of moist lower montane forest growth within the Mubwindi Swamp catchment as suggested at an earlier period for *Faurea saligina*. This mosaic growth pattern would provide a high amount of pollen to the sediments when the parent taxa was growing relatively close to the location of the coring site. Subsequently, as new taxa become established, these will dominate the pollen spectra.. For all of the pollen curves that exhibit this harmonic form, the changes recorded in the pollen percentages indicate that vegetation change is a cyclical process. Due to the smooth nature of the pollen curves, the phenomenon is thought to result from natural rather than human induced changes, such as timber cropping cycles.

These harmonic curves are only apparent at a high sampling resolution. In the case of the Late Holocene sediments from core MB23, the 1 cm sample slices equates to approximately 5 years of sediment accumulation. Thus, when this resolution is achieved changes in the pollen percentages present in the sediments are thought to operate at a similar frequency to changes within the surrounding vegetation. The harmonic nature of the pollen curves from some of the montane forest category can also be applied to the pollen from the degraded forest category as these become numerically important components of the vegetation in the upper Section of the core.

To summarise, vegetation within the Mubwindi Swamp catchment has not remained stable during the Late Pleistocene and Late Holocene periods. During the earliest part of the cored record, high montane forest was replaced by ericaceous belt taxa, although some taxa from lower altitudinal forest persisted, albeit at a reduced extent. It seems likely that a precursor of today's Bwindi-Impenetrable Forest survived the last glacial period of northern latitudes, albeit at a much reduced extent as it was mixed with taxa from higher altitudes. Following reinstation of sediment accumulation after 2500 yr. B.P., the pollen record suggests the Mubwindi Swamp catchment was surrounded by moist lower montane forest similar to that found in parts of Bwindi-Impenetrable Forest today. There has been time-transgressive disturbance, possibly attributed to human activity that culminated in the selective deforestation of the more favoured species within the Mubwindi Swamp catchment.

PART 3 DISCUSSIONS AND CONCLUSIONS FROM THE THESIS

CHAPTER 9

A discussion of Late Quaternary sediment and vegetation dynamics within the Rukiga highlands

9.1 Introduction

Within this Chapter the processes that determined the composition of the Mubwindi Swamp sediments will be discussed. The discussion will then focus on the composition and distribution of the vegetation within the Rukiga highlands. The possible forcing mechanisms for sedimentary and vegetation change within the Mubwindi Swamp catchment will be highlighted within a regional framework in Section 9.3.

9.2 The origin and development of Mubwindi Swamp - the sedimentary record

Before the environmental information recorded within swamp sediments can be deciphered it is imperative to comprehend the controls on sediment accumulation: the cornerstone upon which 'more sophisticated' environmental reconstructions are based. There are several developmental stages to permit swamp sediments to accumulate (Foster and Fritz, 1987). First, a sedimentary basin must form; this is followed by colonisation by swamp vegetation under favourable hydrological conditions to allow for partial decomposition and resultant infilling of the basin. The development of a swamp ecosystem is controlled by several factors, the most important being climate, geomorphology, and the composition of the subjacent strata (Franzen, 1994). The roles these factors have played, and the influence on the type and rate of sediment accumulation within Mubwindi Swamp, will be discussed in context of the radiocarbon dating control (Chapter 4). The discussion will then focus on the controls responsible for determining the rate and type of sediment accumulation.

Based on the radiocarbon date of > 43,000 yr B.P. (Beta-82553), Mubwindi Swamp sediments contain a record from approximately 50,000 yr B.P. This is slightly older than those sediments at Muchoya Swamp (Taylor, 1990), or Kashiru Swamp (Bonnefille and Riolett, 1988), previously the two oldest swamp sediment cores from central Africa.

In stratigraphic zone A of core MB6 the high amount of charcoal, not recorded in core MB3, is thought to be derived from catchment instability; the record from core MB6 extends further into the Late Quaternary than cores MB3 and MB23. The onset of sediment accumulation at Mubwindi Swamp is thought to be temporally related to the formation of Muchoya Swamp (Taylor, 1990), the bi-directional drainage observable at Ahakagyezi Swamp today (Taylor, 1993), and possibly the formation of Kashiru, Kamiranzovu and Rusaka swamps towards the south of the central African region. Similar ages for the basal sediments of these swamps indicate a common formative mechanism was responsible for initiating sedimentation. This formative mechanism was possibly a period of major tectonic dislocation recorded throughout the Western Rift Valley. This tectonic dislocation could also provide the mechanism for the incorporation of volcanic material within some of the cores.

Specifically for the Mubwindi Swamp catchment this tectonic dislocation is thought to have resulted in the damming of the southern end of the basin by a landslide. The landslide is thought to have originated from the hillside to the south-east of the catchment. The debris associated with this slip presently separates the main body of Mubwindi Swamp from the small swamp annex, from which core MB22 was extracted (Chapter 4). Once the landslide had dammed the southern part of the basin a head of water developed. This build up of water was responsible for the production of stratigraphic zone A.

The slipped land, and resultant dam, was lowest at the south-west of the catchment, at the present position of the river (Section 3.9). Once the water level had reached the top of the dam, rapid down-cutting of the unconsolidated slumped sediments would be likely. This erosional activity would provide a changing base level for the river that the drainage would have to adjust to. This would result in headward erosion back through the Mubwindi Swamp sediments. This process of headward erosion is evident during the present-day: the confluence of the rivers entering Mubwindi Swamp resulting in a drop of swamp level by approximately 2 m (Section 3.9). Headward erosion will continue in a northward direction until a state of equilibrium is reached between the river's hydrological budget, the base level and the sediments within the Mubwindi Swamp catchment.

A characteristic feature of stratigraphic zone B is that it attains different lengths in different cores - attaining its greatest length in core MB6. The different lengths of stratigraphic zone B suggests the presence of an erosional hiatus. This was recorded as a longer break at the relatively marginal location of cores MB3 and MB23, in comparison to core MB6. Noticeable from cores MB3 and MB6 are changes in the amount of charcoal (Chapter 5). One such change recorded at 700 cm in core MB6 corresponds to an increase in the particle size of the inorganic fraction. This change in sediment composition is thought to reiterate the presence of a sedimentary hiatus between the radiocarbon dates of > 43,000 yr B.P. (Beta-82553) from 748 to 755 cm and 33,150 +/- 620 from 683 to 690 cm (AA-17154) in core MB6. It is thought a common forcing mechanism was responsible for creating these sedimentary hiatus, and that the forcing mechanism operated at a catchment-wide level. The inclusion of sand in the basal deposits of cores MB3 and MB23, and a rapid increase in sediment size in core MB6, suggests the presence of migrating rivers of some considerable force were responsible for these deposits and associated hiati in sedimentation. The hiatus is thought to be shortest in core MB6, longer in core MB3 and longest of all in core MB23.

Within this period there is a regional record of sedimentary hiati spanning from approximately 40,000 to 30,000 yr B.P. The placement of a hiatus at Muchoya casts doubt on the suggestion by Taylor (1990) that this period is recorded by continuous sedimentation. Indeed, a radiocarbon date of 42,000 +/- 1700 yr B.P. (Pta-4195) from 1860 to 1920 cm is followed immediately by a date of 30,550 +/- 290 yr B.P. from 1800 to 1860 cm (SRR-2963) in core MC2. Further evidence of a sedimentary hiatus is apparent from a layer of lake mud being deposited. Further south, sand deposits at Kashiru Swamp (Bonnefille and Riolett, 1988) indicate two periods of in-wash of allocthonous sediments into the swamp basins dated to around 40,000 yr B.P. and 31,000 yr B.P. Again these are thought to be due to the fluvial nature of the environment within the catchment during this time. The stratigraphy from Kamiranzovu Swamp (Hamilton, 1982) appears much more complicated, suggesting there were lacustrine periods resulting in the clay deposition; these alternated with shallower water when detrital material was deposited. These deposits suggests Kamiranzovu Swamp 'developed' from a lake, to a sedge dominated swamp, to a swamp forest during this period. The transition from herbaceous/amorphous to amorphous/wood peat is centred at approximately 31,000 yr. B.P., precisely when the records at Muchoya Swamp changed from a lacustrine to a peat accumulating swamp. Therefore it is thought an increase in hydrological budgets operated at a regional rather than catchment scale. As this period corresponds to a time when temperatures were thought to be reduced relative to the present day regime (Bonnefille *et al*, 1992), an increase in the hydrological budget is thought to result from reduced evaporation.

The second hiatus in sedimentation suggested from the radiocarbon data (Chapter 4) is placed at about 590 cm in core MB6 and 480 cm in core MB3. The hiatus is again thought to exist throughout the Mubwindi Swamp catchment and result from a synchronous change in the hydrological budget. The temporal placement of this is contemporaneous with the development of lacustrine conditions within the Muchoya Swamp catchment (Taylor, 1990). The presence of a sedimentary hiatus at Rusaka Swamp (Bonnefille *et al*, 1995), an age-depth anomaly and sand layer deposit at Kashiru Swamp (Bonnefille and Riolett, 1988) are temporally synchronous with the sedimentary change at Mubwindi Swamp. The wide spatial spread of synchronous sedimentary changes indicate that these result from regional climatic change leading to full glacial conditions, rather than catchment specific responses to fluctuations in hydrological budgets.

All the Ugandan sites, apart from Ahakagyezi Swamp, have some sediments of volcanic origin, which are most likely to be derived from activity in the Virunga Volcano field. At Muchoya Swamp three volcanic ash bands are radiocarbon dated to between 21,540 yr B.P. and 16,260 yr B.P. (Taylor, 1992). Interestingly, these dates correspond to a sand layer at Ahakagyezi Swamp; this is thought to have been derived from catchment instability. The sediment records from Katenga and Butongo Swamps are both underlain by volcanic sediments. This reiterates the earlier suggestion (Chapter 3) that the sedimentary records from Butongo and Katenga swamps date back about 17,000 years. This is considerably older than the 8000 years proposed by Morrison and Hamilton (1974), and the 11,000 years proposed by Taylor (1988).

The different sediment characteristics of stratigraphic zones A and C indicate a different mechanism was responsible for their deposition. The differences are so marked it is suggested that stratigraphic zone A was either deposited under lacustrine conditions, or as a result of paludification. Both mechanisms would result from the damming of the Mubwindi Swamp catchment by the proposed landslide. The possibility of a lacustrine origin for this basal clay was not supported by diatom analysis, no frustrules being found within eight basal clay samples investigated. However, this result could be explained by a lake not being present for long enough for a diatom flora to develop, it seems more likely the basal clay results from paludification of the extant soils. Stratigraphic zone C resulted from inorganic material being washed in from the surrounding catchment. Specifically, this is thought to be associated with an increase in hydrological budget within the Mubwindi Swamp catchment.

On the basis of changes in the amount of inorganic sediment, inorganic sediment size distribution, charcoal fragment size and amount (Chapter 5) and the radiocarbon dates of 12,930 +/- 1250 yr B.P. from 430 to 443 cm (Beta-60065) from core MB3, and 2110 +/- 55 yr B.P. (AA-12398) and 1970 +/- 55 yr B.P. from 473 to 477 cm (AA-13909) from core MB6 it is suggested a sedimentary hiatus spans approximately 8000 years, covering the early to late Holocene periods. Again, it is thought that changes in the hydrological budget were responsible for causing the break in sedimentation. During this period it is suggested there was erosion of sediments from the southern part of Mubwindi Swamp, the area where erosive power resulting from hydrological budget changes would have been concentrated, as they are today. This suggestion is reiterated by the complex stratigraphies recorded within the short cores abstracted from the southern part of Mubwindi Swamp. These highlight erosion and subsequent fluvial deposition, resulting from transverse river migration (Chapter 4).

At Butongo Swamp the transition from fine swamp peat/mud to a banded swamp peat/mud indicates a significant change in type of sediment accumulated, and therefore hydrological budget. At Katenga Swamp the transition from fine swamp peat/mud to fine swamp peat/mud with wood peat is thought to record a similar response to a changing hydrological budget. Similarly to Mubwindi Swamp, the record at Kashiru Swamp (Aucour *et al*, 1993; Bonnefille and Riolett, 1988) contains a sedimentary break dating from the late Pleistocene-Holocene transition, as do Kamiranzovu and Kuwasenkoko swamps (Hamilton, 1982). At Muchoya Swamp there is a five metre deposit of clay associated with the upper part of this time period, followed by a sedimentary break of approximately 4000 years duration. A deposit of sand at Ahakagyezi Swamp and the ensuing sedimentary hiatus lasts from between 11,000 to 9,000 yr B.P.

This period of sedimentary change marks the transition from late glacial conditions, and resultant relatively rapid climatic change. The sedimentary records indicate that the climatic ameriolation was not a uni-directional, nor a constant process. It is possible that a significant factor in causing these hiati was increased levels of effective precipitation due to the reinstating of the south-west monsoonal circulation (Kutzbach and Bliesner, 1982; Kutzbach and Street-Perrot, 1985; Street-Perrot and Perrot, 1990; Rossignol-Stick, 1983). In the case of Mubwindi Swamp, where the sedimentary hiatus is the longest recorded by any of the swamps in central Africa, I suggest the steep-sided nature of the catchment has 'magnified' the influence of an increased hydrological budget, subsequently leading to a longer hiatus.

Apparent from the Mubwindi Swamp sediments are two significant, and one relatively minor, hiati in sedimentation. These appear to be a response to regionally recorded climatic and tectonic changes. Hiati in sedimentation are often regarded as a lack of information that should be simply delimited and negated. I suggest the presence of a sedimentary hiatus is one of the strongest palaeoenvironmental indicators within a sedimentary sequence. The main problems sedimentary hiati raise is do they result from a lack of sediment accumulation, or do they result from post-depositional erosion of the sediment?

(David Thomas; pers. comm.). In the case of Mubwindi Swamp, the hiati are thought to result from erosion, particularly as sediment erosion can be observed at present within the southern part of Mubwindi Swamp (Section 3.9). The temporal placements of the hiati at Mubwindi Swamp reiterates this suggestion as they occur during periods of increased effective moisture availability throughout the region (Bonnefille, 1993), thus providing the mechanism necessary to erode in situ sediments, i.e. an increase in the hydrological budget. The shallowest sediments are recorded at the southern end of Mubwindi Swamp; these result from erosion of formerly accumulated sediments. A fluctuating hydrological regime is reiterated by the distinct changes in inorganic particle size recorded in core MB6 (Chapter 5). These suggestions will be discussed in more detail in Section 9.3 within the wider context of the vegetation reconstruction.

Due to the long hiatus in sedimentation it is not possible to say when sediments that comprise stratigraphic zone D began to accumulate, but it was certainly before the date of 2110 +/- 55 yr B.P. from core MB6. It is possible that re-initiation of peat accumulation during the late Holocene at Mubwindi Swamp does not indicate a sudden transition from a humid to a less humid climate approximately 2000 yr B.P., but is a consequence of a more gradual process of aridification or increased seasonality, which may have commenced 4000 yr B.P. Sediment accumulation within Mubwindi Swamp only re-commenced once the hydrological budget fell during the late Holocene. This is thought to be related to a period of regional climatic change (Section 9.3). During the late Holocene, there was rapid sedimentation recorded in those swamps without sedimentary hiati. This was thought to be due to warm, wet climatic conditions (Bonnefille, 1993) resulting in rapid accumulation and slow decay within stratigraphic zone D. This rapidity of accumulation could result from either environmental change, restricting the decomposition of organic material, or a more rapid and luxuriant growth of vegetation on the Mubwindi Swamp surface, or as would seem likely some combination of the two.

Throughout central Africa, there is slow, but sustained increase in the depth of sediment accumulated down the altitudinal sequence. There is no peat formed at Kuwasenkoko Swamp (Hamilton, 1982) and maximum depth of accumulation recorded at Ahakagyezi Swamp (Taylor, 1990). This is thought to highlight a common response by peat formation throughout central Africa, the rate of peat accumulation is determined by increased moisture and temperature at lower altitudes, thus facilitating increased growth rates and/or decreased decomposition. This altitudinal gradient reiterates the responsive nature of the sediment stratigraphies in isolating the forcing mechanisms responsible for environmental change in central Africa.

The composition of late Holocene sediments at Mubwindi Swamp has changed dramatically with different types of peat, coarse inorganic sediment, and charcoal present. Indeed, results from the range of analytical techniques applied to the Mubwindi Swamp sediments in part two indicate the magnitude of the allocthonous and autochthonous inputs have varied considerably over the cored record. These variations are thought to result from late Holocene changes in the hydrological budget within the Mubwindi Swamp catchment. When the results from the charcoal analysis are standardised against inorganic matter content, there is a very notable increase in charcoal recorded from approximately 800 yr B.P. This is not associated with an increase in the size of the inorganic fraction, and hence is thought to be associated with an increase in the intensity / frequency of burning within the Mubwindi Swamp catchment, rather than an increased mobility of charcoal fragments. When standardised against time, the results for core MB6 indicate there was an additional period of increased burning during the past few centuries. This could result from an increase in the intensity / frequency of burning, related to pit-sawing activity (Section 3.7). Within the uppermost samples, particularly from core MB6, there is a decline in the amount of charcoal and size of the inorganic sediment. This possibly indicates a very recent (sub-century) reduction in the amount of fire-induced disturbance. This change is only recorded from the top two samples from core MB6, and therefore cannot be applied with any significance throughout the Mubwindi Swamp catchment.

The techniques of charcoal determination applied to cores MB3 and MB6 highlight similarities in the sediment composition between the two cores. The major similarities indicate contemporaneity of sediment accumulation throughout Mubwindi Swamp. Hence, the sedimentary data from the two cores are individual, providing a complimentary record of environmental controls responsible for sediment accumulation within the Mubwindi Swamp catchment. Within this record, some of the problems associated with determination of the origin of individual sediment constituent have been negated. It is apparent from the proposed development of Mubwindi Swamp that the accumulated sediments closely reflect changes in the hydrological budget. In the case of Mubwindi Swamp this is thought to be particularly so due to the steep-sided nature of the surrounding catchment, and the resultant rapid transfer of rainfall to the swamp surface. However, the sedimentary, and therefore hydrological budget changes recorded at Mubwindi Swamp, have been widely felt across the central African region.

The outlined complexities of sediment accumulation and ultimate composition within tropical swamps is exemplified by the wide range, both in type and extent, of sediments found within Mubwindi Swamp. The results indicate that the hydrological budget (Figure 9.1) of the Mubwindi Swamp catchment is ultimately responsible for the composition and distribution of the accumulated sediments within the basin. Indeed, for further studies of tropical swamps before a full interpretation of the information held within a sedimentary record is attempted it is imperative that the swamps catchment, and its hydrological regime be described in full. This is a facet that has been missing from previous palaeoecological studies within central Africa and further afield. This omission has diluted the interpretations from peat accumulating systems in the tropics so far.

9.3 Late Quaternary composition and distribution of montane vegetation within the Rukiga highlands, and beyond.

Nonwithstanding the exceptions outlined in chapter 6, the results from the vegetation surveys and surface sediment analysis indicate that pollen accumulations in the sediments at Mubwindi Swamp generally reflect the vegetation growing within the immediate catchment. This is particularly so as the modern samples were taken from a location and environment similar to those from where the fossil sequences were collected. This finding supports further the suggestion by Taylor (1993) that the tightly constrained catchments of the swamps

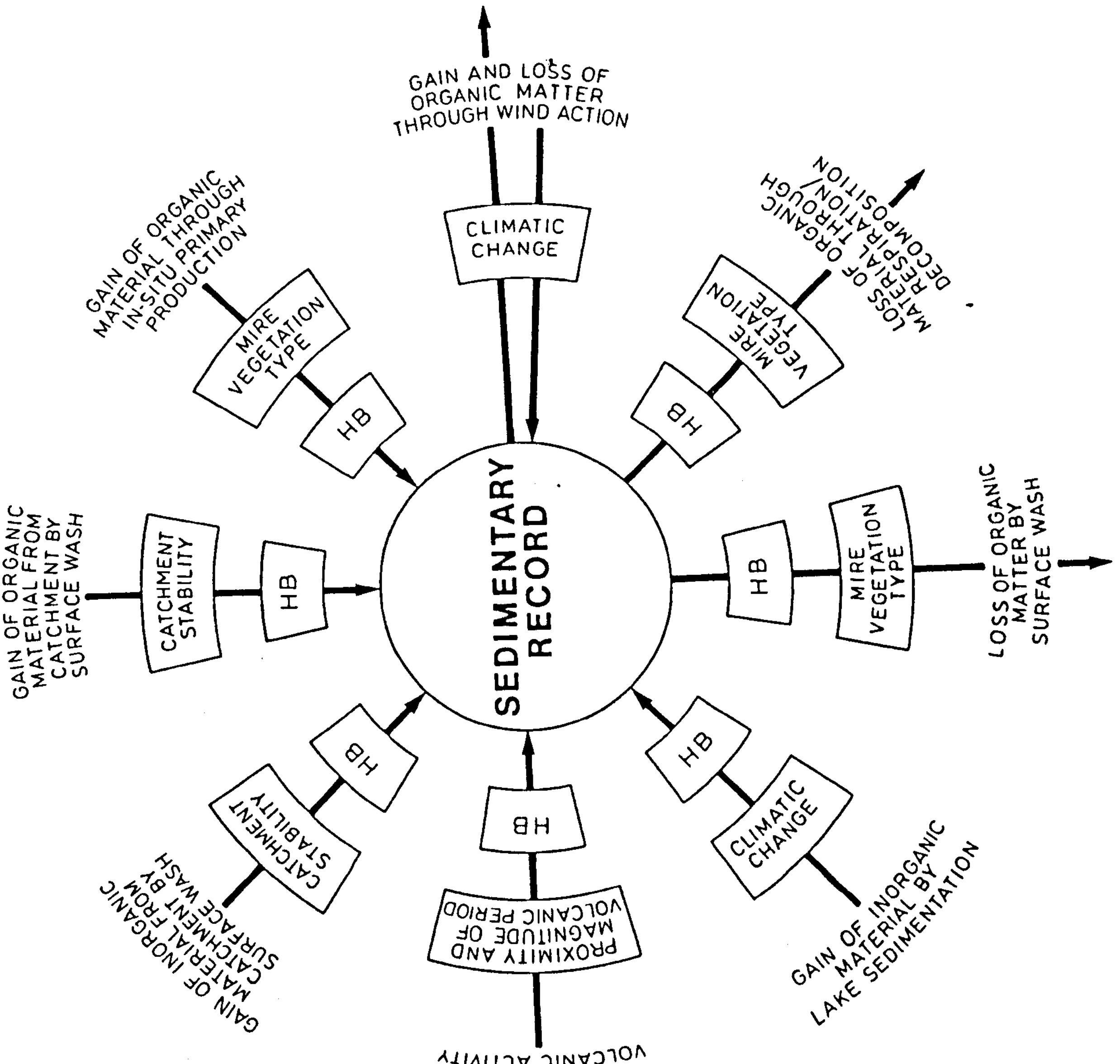


Figure 9.1 The influence of hydrological budget on sediment accumulation

within the Rukiga highlands makes them ideal locations for palynological study. However, the pollen-vegetation relationship recorded for the Mubwindi Swamp sediments should not be directly applied to the other swamps within the Rukiga highlands due to a whole range of factors determining this relationship (Section 6.1), some of which are specific to the Mubwindi Swamp catchment.

Within the Rukiga highlands, the altitudinal range, spatial distribution, swamp topographies and different time periods covered by the sedimentary records from the peat-accumulating swamps allow for the isolation of the various forcing mechanisms (e.g. climatic, geomorphic, human and vegetation succession) that have been responsible for fluctuations in the composition and distribution of montane vegetation. This record can be extrapolated further afield within central Africa. The difficulty in isolating these forcing mechanisms from a regionally incomplete record can be highlighted by an earlier suggestion that the record from Ahakagyezi Swamp represented human-induced forest clearance dating back in excess of 4000 years (Hamilton *et al*, 1986), subsequent analysis showed the palynological changes represented a change to a drier vegetation type as a result of climate change, rather than human-induced forest clearance (Taylor, 1990).

The sedimentary and pollen records from the Rukiga highlands described in Section 2.6 will be interpreted in a series of time periods: before 43,000 yr B.P., 43,000 to 22,000 yr B.P., 22,000 to 14,000 yr B.P., 14,000 to 10,000 yr B.P., 10,000 to 4000 yr B.P., 4000 to 2000 yr B.P., and 2000 yr B.P. to present. These periods have been chosen as to highlight major changes within the sedimentary environment and vegetation composition. As with all temporal divisions, the boundaries between these periods should be viewed as 'fluid' as they are imposed only to aid in the discussion of changes in vegetation composition and distribution. It is possible to indicate what the composition and distribution of the vegetation was within the Rukiga highlands at any point throughout the past 50,000 years.

For each time period, a map of the Rukiga highlands has been produced for a spot time. These maps indicate the type of vegetation typical of the era within six broad categories: derived vegetation, regenerating forest, dry grassland scrub, montane forest, ericaceous scrub and swamp vegetation.

Derived vegetation includes all the land that is actively managed and includes farmed land and forest plantations. The main agricultural crops of the region are bananas, beans, Irish and sweet potatoes, millet, sorghum and wheat. Within the Rukiga highlands hill-slope terracing is the most common form of agricultural land; allowing for agricultural production on the steep slopes (Plate 10.1).

Regenerating forest includes degraded and regenerating forest. It also includes bamboo forest dominated by *Synarundinaria alpina*. It is most likely that, in the context of the Rukiga highlands that bamboo forest represents a form of regenerating forest (Hamilton, 1982). Broad-leaved species within this category are *Dombeya goetzenii*, *Macaranga kilimandscharica* and *Neoboutonia macrocalyx*. Other common taxa associated with regenerating communities are species of *Dodonaea*, *Plantago* and *Rumex*.

Dry grassland scrub comprises a mix of grasses interspersed with patches of broad-leaved woodland and scrub. There is no modern analogue of this vegetation type today within of the Rukiga highlands. It is likely this vegetation type is similar to the 'dry transitional montane forest' as described by White (1983) within which Afromontane and non-Afromontane species occur together. Within the pollen record, the vegetation category is characterised by high levels of Ericaceae and *Hagenia* in conjunction with large amounts of Gramineae pollen.

Montane forest includes broadleaf, hardwood trees together with some conifers. At present the vegetation type is found in central Africa at altitudes between 1000 and 3000 m. Key taxa are *Celtis*, *Chrysophyllum*, *Croton*, *Drypetes*, *Faurea*, *Hagenia*, *Ilex*, *Nuxia*, *Olea*, *Podocarpus* and *Prunus*. Specifically within the Rukiga highlands it is the dominant type of vegetation found at present within Bwindi-Impenetrable Forest (Section 3.5). As suggested in Section 2.4 montane forest is divided into upper and lower altitudinal zones with the adjectives moist and dry being used where appropriate.

Ericaceous scrub comprises of high altitudinal vegetation types found at present in central Africa between 3000 and 3500 m. There are no modern analogues of this vegetation type at present within the Rukiga highlands although it can be found on the nearby Virunga volcanoes. Key species include a range of the members of the Ericaceae such as *Erica arborea*, *Philippia* spp. and *Vaccinium* spp. Also present are *Artemisia afra* and *Stoebe kilimandscharica.* Ericaceous scrub is known to burn readily, it is then usually replaced by secondary grassland (White, 1983). Therefore, large amounts of Gramineae pollen may be present in the fossil record.

Swamp vegetation of tropical mires varies considerably in composition, depending on altitude, climate and the nature of the catchment (Hamilton and Taylor, 1986). At present in the Rukiga highlands uncultivated swamps can be dominated by forest, sedges, grasses and even *Sphagnum* spp.

Combining the symbols assigned to each category it is possible to produce the mosaic of vegetation types represented by the pollen data. However, there is considerable within category variation in the vegetation composition, and this will be highlighted in the text. To place the reconstructed vegetation in context, the present-day composition and distribution of the vegetation within the Rukiga highlands will be described. As outlined in Section 1.3, the past reconstructions will be used to highlight how the present-day vegetation pattern has arisen; this in turn is used to aid in the reconstruction of past vegetation composition and distribution.

Present-day vegetation

Present-day vegetation in the Rukiga highlands (Figure 9.2) is largely derived vegetation, being the product of intense human activity. However, there are three large blocks of forested land remaining, in addition there are also several, smaller patches of secondary forest, particularly close to Bwindi-Impenetrable Forest. The most important of the three forest blocks is Bwindi-Impenetrable Forest; this represents the largest fragment of what is believed to be the dominant vegetation type for much of the area in the absence of intense human activity (Hamilton, 1969; 1974). However, much of this prime site of montane forest has been heavily

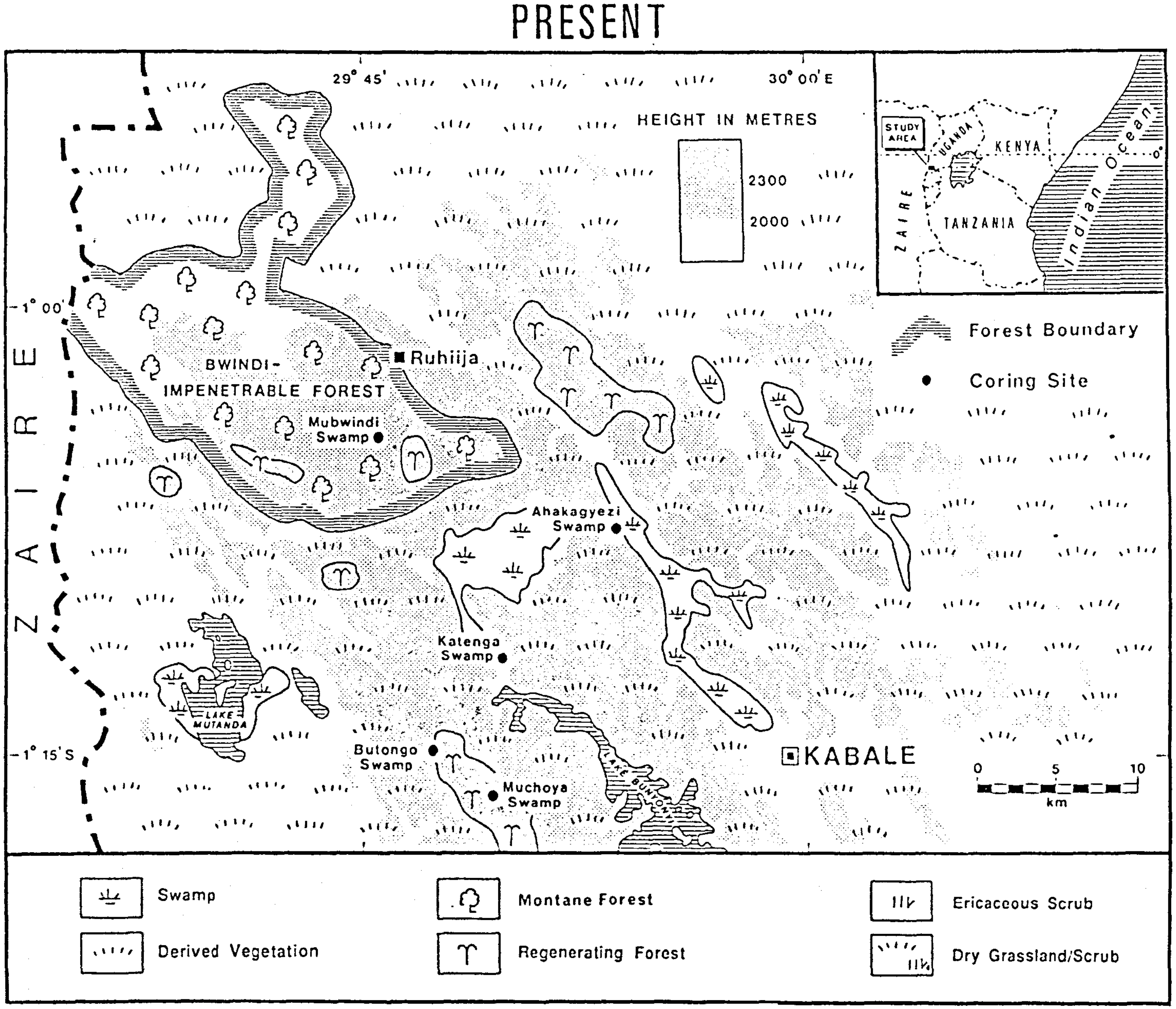


Figure 9.2 Vegetation composition and distribution at present

degraded as a result of human activity (Chapter 6). The composition and distribution of montane vegetation is a mosaic composed of several different associations, some of these are driven by local climatic and edaphic conditions, others result from altitudinal and of past human-induced disturbance. Superimposed on these are the ecological constraints of forest regeneration and niche occupation. Ecological factors will become more important in the future with a cessation of human-induced disturbance resulting from protective National Park legislation (Plate 9.2).

There are several areas of regenerating forest, one of the areas is Mafuga Forest (Hamilton, 1969); small seedlings and trees of the type of species present in Bwindi-Impenetrable Forest are found at Mafuga Forest (Hamilton, 1969). Another area of regenerating forest is Euchoya Forest, this is dominated by bamboo (*Synarundinaria alpina*). The only other place *Synarundinaria alpina* is present is in two discrete fragments within the south-east corner of the Bwindi-Impenetrable Forest. The most common broadleaf species within the bamboo forest are *Neoboutonia macrocalyx* and *Alchornea hirtella*. In smaller openings *Croton macrostachyus*, *Dombeya goetzenii* and *Macaranga kilimandscharica* are also present as isolated individuals. The distribution of these specimens indicate that the colonising trees within the surrounding vegetation have very specific roles, being able to occupy a range of niches. Other species present include *Bersama abyssinica*, *Maesa lanceolata*, *Nuxia* spp. and *Polyscias fulva* (Hamilton, 1969; Morrison, 1968).

By far the most common type of land-cover during the present-day is derived vegetation. Hill-terraces cover the majority of the land within the Rukiga highlands (Plate 9.3). More recently, due to land shortage many of the swamps have been drained for agricultural production to support population density increases. Elsewhere patches of degraded and regenerating forest are restricted to areas most unfavourable to agriculture, these increase in size and density toward the Bwindi-Impenetrable Forest although never individually attaining a large size.

Plate 9.1. Mists linger within incised valleys.

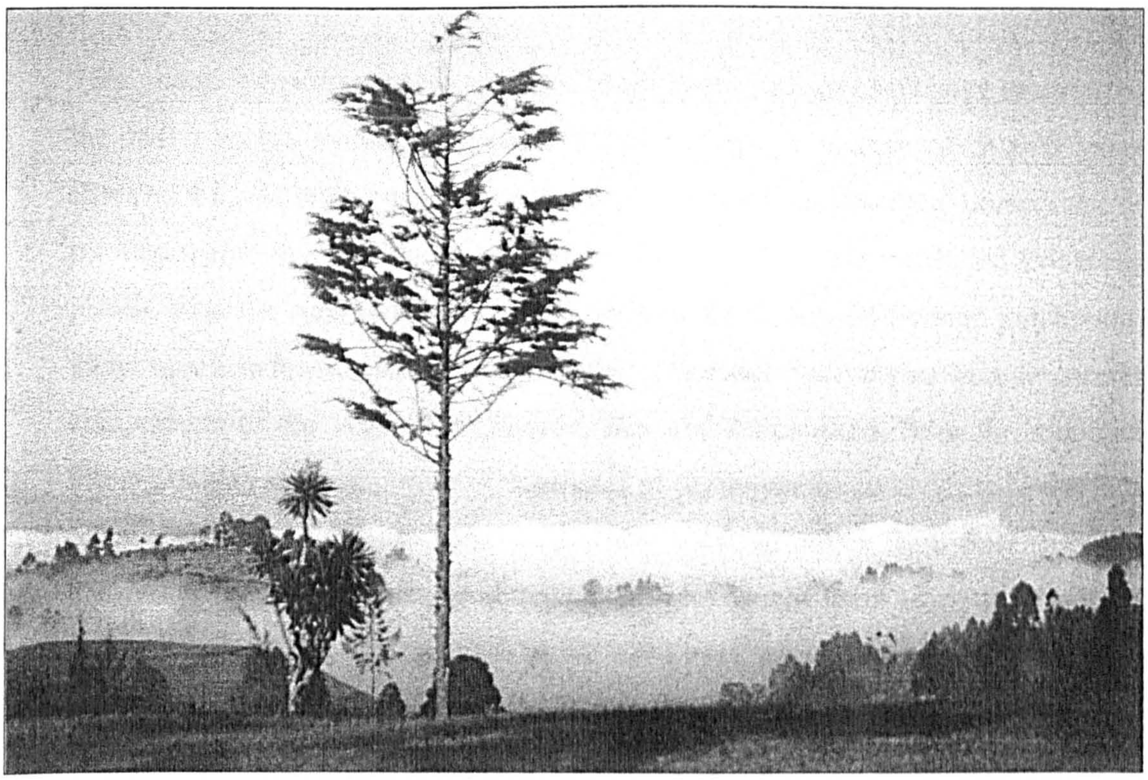


Plate 9.2. The boundary of Bwindi - Impenetrable Forest National Park.

> 43,000 yr B.P.

This period is represented by sediments from Mubwindi and Muchoya swamps, at the first site the record is thought to extend back in excess of 50,000 years (Section 9.2). At both these sites, ericaceous scrub was an important component of the vegetation, more so than suggested by Taylor (1990) who excluded Ericaceae pollen from the non-local pollen sum. Within the Muchoya Swamp catchment, upper montane forest taxa, such as *Hagenia*, *Olea* and *Podocarpus* were important components of the vegetation. *Faurea*, *Ilex* and *Macaranga*, from the montane forest category were important components of the vegetation within the Mubwindi Swamp catchment. Due to some similarities between pollen from this zone and that found within the surface sediment samples it would seem likely the range of parent taxa recorded in Chapter 6 would have been present within the Mubwindi Swamp catchment, although at reduced quantities than previously recorded. The high percentage of Myrtaceae pollen suggests that the parent taxa were present at high densities within the catchments, probably close to the swamp margins, particularly given that *Faurea saligna* is a productive pollen producer (Chapter 6) and therefore pollen from this taxa likely to dominate the pollen record. Relatively hydrophytic taxa, such as *Cyathea*, *Myrica* and *Syzygium* were present within the Mubwindi and Muchoya swamp catchments.

With high altitudinal montane forest dominating the vegetation within the surrounding catchments and wet swamp forest fringing Mubwindi and Muchoya swamps there is an anomaly, given present-day species distributions (Section 2.4). In the same way 'occult' precipitation can encourage tree growth at higher altitudes (Coe, 1967), the presence of a lake, or water-logged soil in the present location of Mubwindi Swamp (Section 9.2) it is thought to have allowed species of *Syzygium* and *Myrica* to be important components of the vegetation around the swamp margins. It is quite likely a similar situation at Muchoya Swamp allowed *Cyathea* spp. to dominate at Muchoya Swamp catchment. Thus, locally wet edaphic conditions are thought to have provided a buffering influence against the ambient dry, cool climate.

This vegetation composition and distribution indicates that temperature and moisture levels were slightly reduced within Rukiga highlands relative to the present-day climatic regime. Although there are very few palaeoecological records that date to this period within central Africa a similar reconstruction of slightly cooler than present climatic conditions between 43,000 and 53,000 yr B.P. have been reconstructed from northern Botswana (Holmgren *et al*, 1996).

The vegetation distribution within the Rukiga highlands at 45,000 yr B.P. is highlighted in Figure 9.3. Throughout the region there was mixed ericaceous belt and upper montane forest vegetation at the highest altitudes within the Rukiga highlands. Although there are no records from swamps at altitudes lower than Mubwindi Swamp, it is thought that montane forest taxa were increasingly important at lower altitudes, and towards the base of the valleys. Where there were water courses, moist types of vegetation would develop. There was a transition to a drier forest type at around 43,000 yr B.P. The vegetation composition changes to a higher altitudinal nature. *Artemisia afra* members of the Ericaceae and *Stoebe kilimandscharica* became increasingly important components of the vegetation at the highest altitudes as the presence of high montane forest taxa decreases. This in turn is thought to have become an increasing component of the vegetation at lower altitudes.

43,000 to 22,000 yr B.P.

Within the Rukiga highlands this period is represented by pollen records from Mubwindi and Muchoya swamps, and latterly Ahakagyezi Swamp. However, this period contains sedimentary hiati (Section 9.2). During the first half of this period within the Mubwindi Swamp catchment there was montane forest mixed with ericaceous scrub. This contained *Artemisia*, Ericaceae, *Ilex*, *Olea*, *Podocarpus* and *Stoebe*, and was present until approximately 35,000 yr B.P. Ericaceous belt vegetation was also present within the Muchoya Swamp catchment. Similarly, the vegetation was composed of *Artemisia*, *Cliffortia*, Ericaceae and *Stoebe*. Although the dominant vegetation types were similar, there was a higher percentage of montane forest taxa within the Mubwindi Swamp catchment. Although the time period covered synchronously by the sediments from two sites is relatively short,

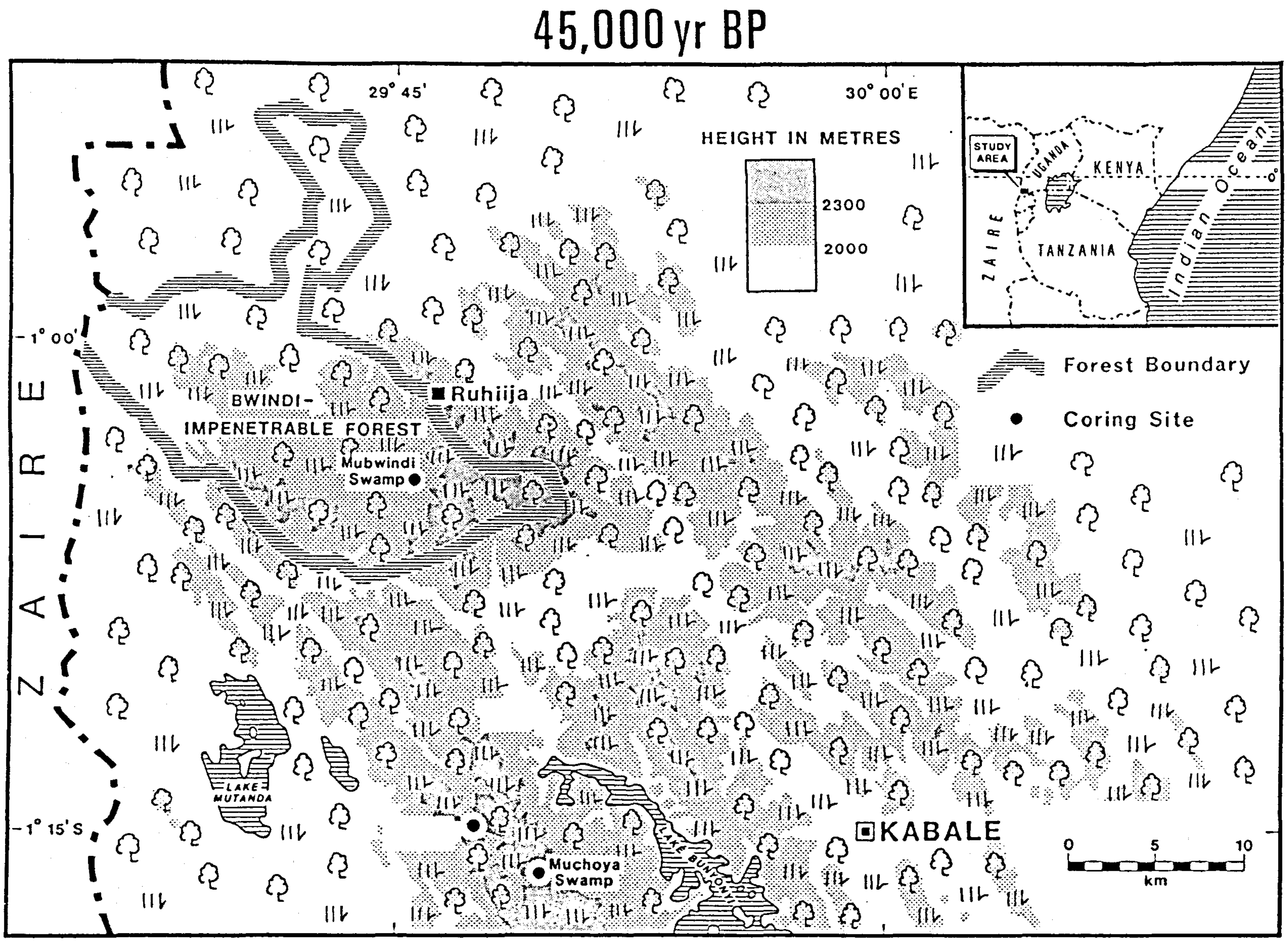


Figure 9.3 Vegetation composition and distribution at 45,000 yr B.P.

the recorded vegetation adheres to the altitduinal sequence outline in Section 2.4, and can therefore be extrapolated throughout the Rukiga highlands. At the lowest altitudes, such as those surrounding Ahakagyezi Swamp catchment, the vegetation would have been composed of a mixed upper montane forest and moist lower montane forest association, of a similar composition to that found in the highest parts of the southern sector of Bwindi-Impenetrable Forest today (Section 3.5).

Further south, a mix of high montane forest dominated by *Olea* and *Podocarpus* in association with *Cliffortia* and Ericaceae was recorded at Kashiru Swamp (Bonnefille and Riollet, 1988) and Rusaka Swamp (Bonnefille *et al*, 1995). However, the radiocarbon dating of these sections of the core is very poor and cannot be temporally correlated with the Rukiga highland data with any great precision.

Within the Muchoya Swamp catchment, vegetation was dominated by *Hagenia* from about 30,000 yr B.P. The total dominance of this pollen type (c. 80%) means the other pollen types are under-represented. However, there was a relative increase in the amount of *Ilex*, *Podocarpus* and *Zanthoxylum* within the catchment, this suggests a shift in vegetation to that of a lower altitudinal nature from about 30,000 yr B.P. At about a similar time there was a change in the structure of the ericaceous vegetation and montane forest within the Mubwindi Swamp catchment. Due to the conflicting dating control (Section 4.4) the timing of this change cannot be determined specifically although it is thought to be synchronous with the change recorded at 32,000 yr B.P. at Muchoya Swamp (Taylor, 1990). Towards the upper Section of this time period the pollen spectra indicate a change in the composition of the ericaceous belt vegetation to an *Artemisia afra*, *Cliffortia* spp. and *Stoebe kilimandscharica* association with increased dominance from members of the Ericaceae. It is thought a proportion of *Alchemilla* and Gramineae pollen are likely to have been produced from taxa associated with the high altitudinal arboreal scrub, rather than from the local vegetation on the Mubwindi Swamp surface. Within the Mubwindi and Muchoya swamp catchments vegetation characteristic of moist conditions, such as *Myrica* and *Syzygium*, were at a minimum

Thus, during the short time when both Muchoya and Mubwindi swamps are accumulating sediments there was considerably more pollen derived from montane forest within the Mubwindi Swamp catchment. It is thought this component of montane vegetation would have increased towards lower altitudes. However, at Ahakagyezi Swamp pollen in the lowermost sediments indicate only Ericaceae, *Hagenia* and *Myrica* were present within the catchment towards the end of this time period. During the same period trees such as *Macaranga*, *Myrica*, *Olea*, *Podocarpus*, *Rapanea* and *Syzygium* also supplied pollen to sediments accumulating at Kashiru and Kamaranzovu swamps in Burundi and Rwanda (Bonnefille and Riolett, 1988; Hamilton, 1982). Thus, montane forest appear to have been more common in areas where topographic and edaphic conditions were favourable, such as the steep sided, relatively enclosed catchment, that contains Mubwindi Swamp.

At lower altitudes in central Africa the sediments from Lake Mobutu Sese Seko dated to between 29,500 and 25,350 yr B.P. contain pollen derived from forest, presently at higher altitudes than the lake (Sowunmi, 1991). Further south, Zambezian woodland pollen from sediments of Lake Tanganyika have been dated between 35,000 and 15,000 yr B.P. These are also indicative of drier conditions (Vincens, 1993). The pollen data suggests relative to present day, there was a shift to cooler and drier climatic conditions throughout central from about 43,000 yr B.P. A similar rapid shift to a cooler climate has been reconstructed for northern Botswana (Holmgren *et al*, 1996). This change can be correlated with a downward trend in southern hemisphere insolation (Street-Perrot, 1994).

However, the sedimentary data indicate an increase in hydrological budgets at about 40,000 yr B.P. at Mubwindi, Muchoya and Kashiru swamps. A regionally recorded increase in the hydrological budget is also indicated by an overflow of Lake Mobutu Sese Seko between 28,000 and 25,000 yr B.P. (Harvey, 1976). Similarly, the buried palaeosols on the saddle between Visoke (3711 m) and Karisimbi (4507 m) indicate intense weathering (reflective of relatively warm conditions) took place between 35,000 and 25,000 yr B.P. (Mahaney, 1990). To explain this anomaly between vegetation composition and palaeohydrological indicators is thought the continued presence of cooler than present temperatures led to decreased evaporation levels resulting in an increase in hydrological budgets.

The vegetation distribution within the Rukiga highlands at 30,000 yr B.P. is highlighted in Figure 9.3. Throughout the region there was a mix of ericaceous vegetation and montane forest, grassland scrub becoming more important at lower altitudes. Montane forest was densest within topographically enclosed areas, such as the location of the southern sector of Bwindi-Impenetrable Forest. Altitudinal gradients of vegetation distribution (Section 2.4) appear to have been compressed relative to the present-day. It is possible this compression was due to high adiabatic lapse rates arising from reduced atmospheric moisture levels and mean annual temperatures (Section 2.3). Indeed, Bonnefille (1993) calculated falls in temperature of up to 6 °C and reduction in atmospheric moisture by 40 % in equatorial Africa towards the late glacial maximum.

22,000 to 14,000 yr B.P.

This period is represented by sediments from Ahakagyezi and Muchoya swamps and latterly Butongo and Katenga swamps. During this time period pollen derived from ericaceous vegetation and dry grassland scrub dominated within the Rukiga highlands. At the highest altitudes these taxa were combined with *Artemisia* and *Stoebe*, although these taxa never colonised the lowest altitudes within the Rukiga highlands. Even during the last glacial maximum it is thought that ericaceous vegetation did not occur within the Rukiga highlands as a distinct vegetation type (Section 2.4). Elements of montane forest were present during this time period; Ahakagyezi and Muchoya swamps recorded *Hagenia*, *Olea* and *Podocarpus*. Other montane forest taxa were present at very low levels, although *Alchornea* was quite common within the Ahakagyezi Swamp catchment. Both swamps supported the growth of swamp forest within their catchments, this included taxa such as *Myrica* and members of the Myrtaceae, probably *Syzygium*.

The presence of montane forest taxa throughout the Rukiga highlands, albeit at varying levels during this time period, indicate the suggestions by Sosef (1994) for Mini Refugia, and Maeve and Kelman (1994) for Riparian Refugia appears to be

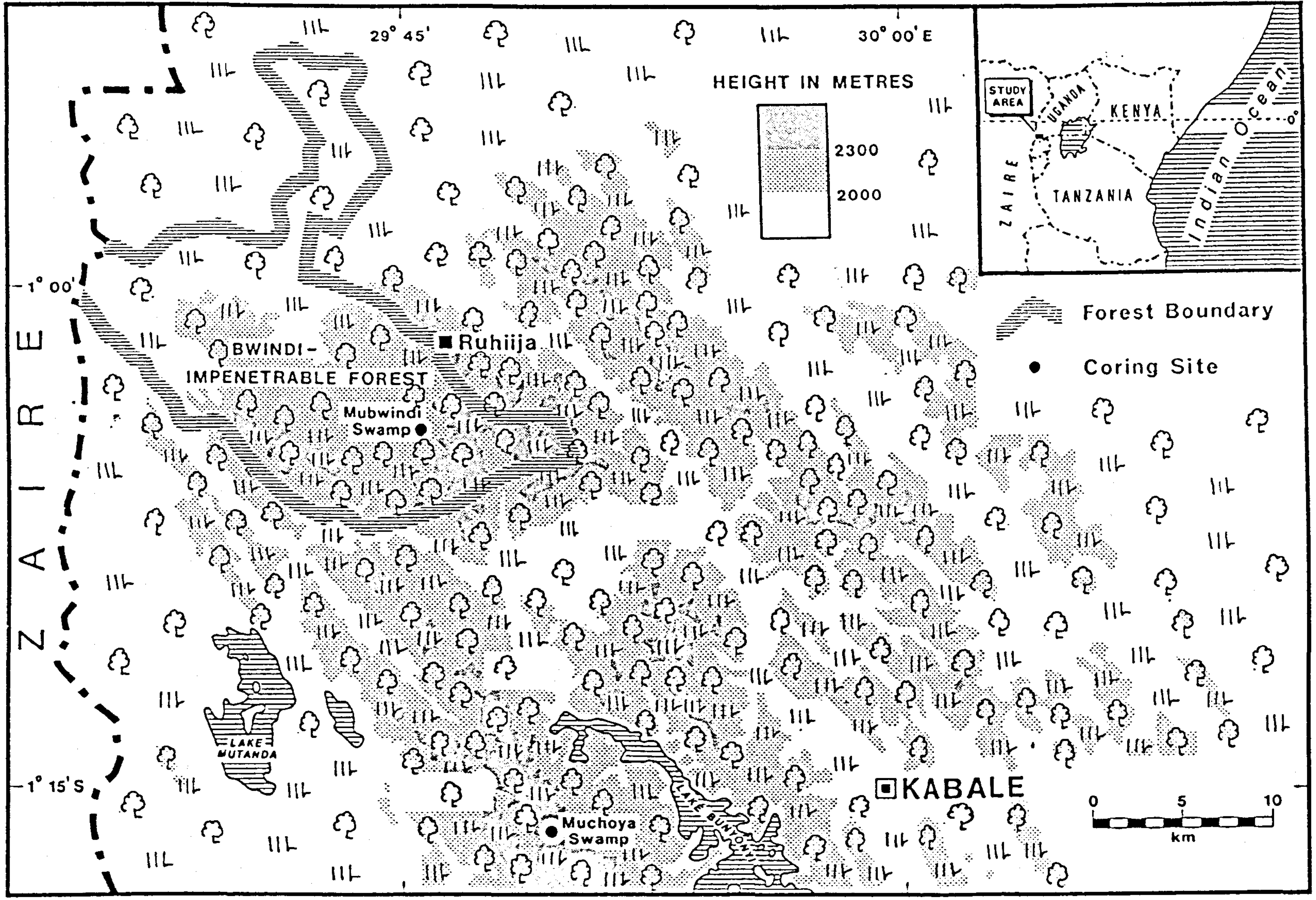

30,000 yr BP

Figure 9.4 Vegetation composition and distribution at 30,000 yr B.P.

attractive models that could be applied to the Rukiga highlands. In view of the generally arid nature of the last glacial period (Bonnefille *et al*, 1992; Bonnefille, 1993), the majority of the Rukiga highlands supported grassland, intermixed with forest patches. The forest patches would act as 'stepping stones' for the subsequent migration of flora and fauna following climatic ameriolation, the forest patches acting as a series of mini-refugia. The degree to which the flora and fauna were able to expand from the forest blocks depends on the nature of the gap and the dispersal capabilities of the taxa concerned.

Forest refugia provide a means of explaining large scale survival and, as a consequence present-day composition and distribution of forest species (Raup, 1993). In conjunction with the question of where forest refugia were located ? is the question of what was the reason for their persistence? (Section 2.5). The influence of precipitation, frequency of clouds and mist and the local topography (Plate 9.1) are all thought to have been crucial in sustaining the presence of montane forest species during periods when the regional climate was relatively cool and dry. Indeed, the importance of local moisture and edaphic conditions is important at present, montane forest being recorded up to 4000 m along stream courses on Mount Kenya (Coe, 1967). The importance of temperature in determining the upper limits of species range is supported by a number of observations. Hedberg (1959), found eighteen species which attain their highest recorded altitudes on Mount Elgon adjacent to a hot spring, included within these is *Hagenia abyssinica* (Hamilton, 1982). Inversion of whole vegetation zones has been recorded in valleys which are relatively enclosed topographically, thus liable to strong temperature inversion (Coe, 1967; Hamilton, 1982).

The area covered by Bwindi-Impenetrable Forest is more rugged and dissected than other areas of the Rukiga highlands (Section 3.2). The distribution of the present-day rainfall for the Rukiga highlands (Section 3.3) highlights the considerable variation in the present-day distribution, being highest over the area covered by Bwindi-Impenetrable Forest. The concentration of the isohyets are related to the passage of the rain-bearing weather systems being 'funnelled' into the area, presently covered by Bwindi-Impenetrable Forest, by the sharply rising high ground of the Virunga Volcanoes to the south-west. These factors are thought to have been important in maintaining patches of montane forest during full glacial conditions. Thus, although this period is covered by a sedimentary hiatus at Mubwindi Swamp, these possible mini refugia of montane forest are thought to have been densest towards the location of the southern sector of Bwindi-Impenetrable Forest, as a result of higher moisture conditions and the relatively dissected topography.

Overall during this period lake levels were reduced throughout central Africa (Butzer *et al*, 1972; Haberyan and Hecky, 1987; Livingstone, 1975; Street and Grove, 1979; Talbot *et al*, 1984; Williamson *et al*, 1991). This is at odds with the lacustrine phases recorded at Muchoya Swamp about 20,200 yr B.P. (Taylor, 1990), at Kashiru Swamp about 21,500 yr B.P. (Bonnefille and Riolett, 1988) and at Kamiranzovu Swamp about 20,000 yr B.P. (Hamilton, 1982) and the sedimentary hiati recorded at Mubwindi Swamp (Marchant *et al*, in press) and Rusaka Swamp (Bonnefille *et al*, 1995). The most likely cause for these lakes and sedimentary hiati was an increased hydrological budget within the swamp catchments, prior to full glacial conditions; the most likely cause being a fall in the temperature and hence reduced evaporation. The cool, arid nature of this period is further demonstrated by the presence of glacially crushed quartz grains on the Virunga Volcanoes (Mahaney, 1990), and expansion in firn lines on the Ruwenzori (Livingstone, 1967) and Mount Kilimanjaro (Osmaston, 1989). The palaeoclimatic estimates for Africa suggested by Roeland *et al* (1988) indicated a decrease of 4 ^{oC} +/- 2 ^{oC}, these estimates were subsequently modified to 4 ^{oC} +/- 1 ^{oC} (Bonnefille *et al*, 1992) for the period of full glacial conditions, both estimates being derived from the transfer function approach on pollen derived from the Kashiru Swamp sequence.

The vegetation distribution within the Rukiga highlands at 18,000 yr B.P. is highlighted in Figure 9.4. Throughout the region ericaceous vegetation dominated with isolated patches of montane forest. Grassland scrub was the dominant type of vegetation at lower altitudes. Montane forest was densest within relatively moist areas, and/or within topographically dissected valleys, such as found within the southern sector of Bwindi-Impenetrable Forest.

18,000 yr BP

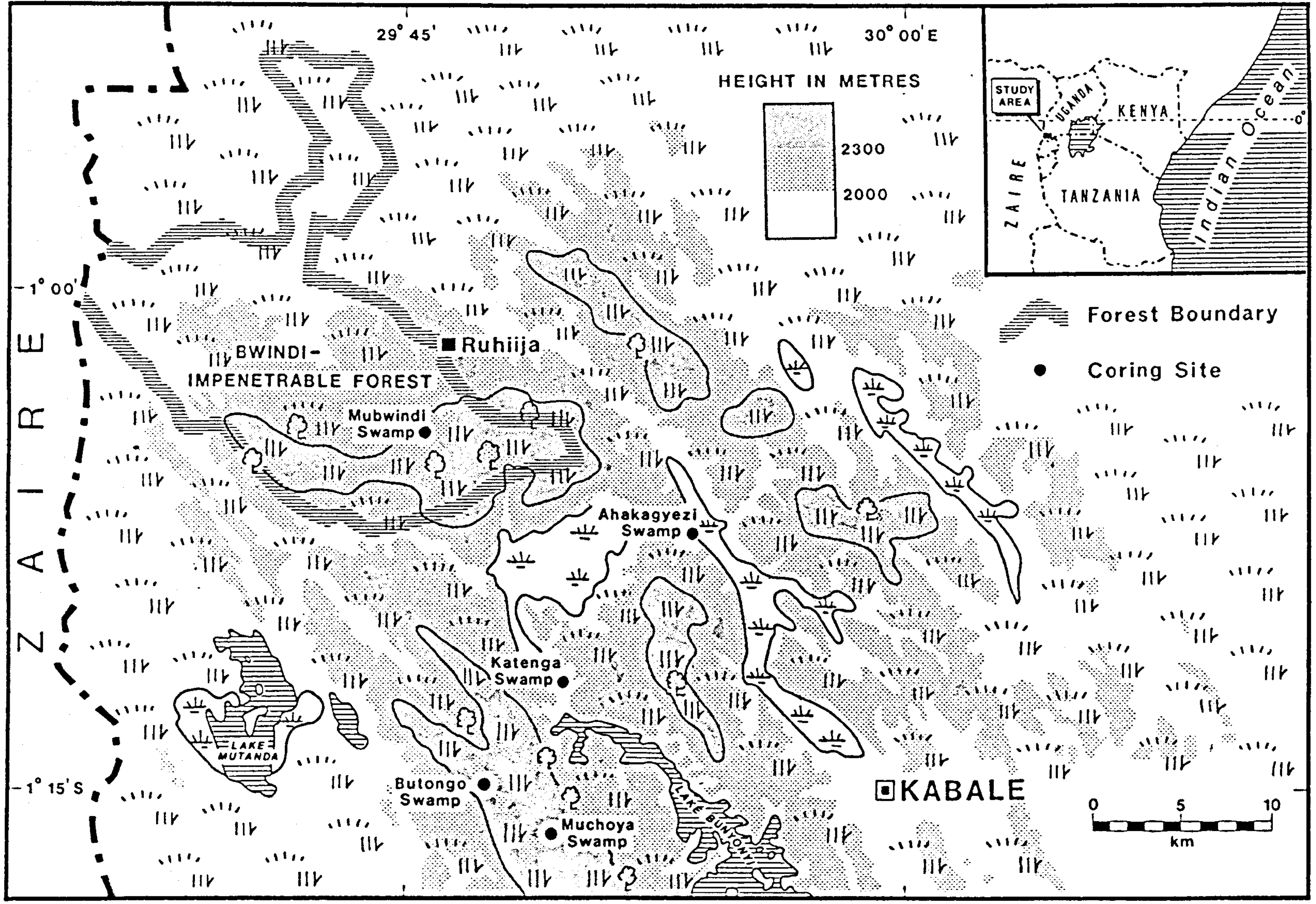


Figure 9.5 Vegetation composition and distribution at 18,000 yr B.P.

14,000 to 10,000 yr B.P.

This period is covered at some point by sediments from all the swamp sites in the Rukiga highlands (Section 9.2). During the first part of this time period at all the sites within the Rukiga highlands (apart from Mubwindi Swamp) there was an increased dominance of *Hagenia*, reaching maximum levels at about 11,000 yr B.P. The lack of a '*Hagenia* rise' at Mubwindi Swamp may result from the late glacial hiatus extending through the early part of this period. Alternatively, it may result from the montane vegetation being of a more mixed type within the catchment At Ahakagyezi, Butongo and Katenga swamps *Hagenia* was associated with *Faurea* and *Olea*. The montane forest at Muchoya Swamp appears to have been of quite an open composition, with relatively high levels of *Alchornea*, *Dombeya* and *Macaranga* present.

Following reinstatement of sediment accumulation at Mubwindi Swamp no one taxa dominates the upper part of this time period, with a mix of ericaceous scrub and montane forest present. The relatively high diversity of montane forest trees present within the Mubwindi Swamp catchment further indicates that the forest was relatively dense during the upper part of this time period. The dense structure of this forest within the Mubwindi Swamp catchment is corroborated by the almost absent levels of heliophytic taxa such as *Alchornea, Croton, Dombeya* and *Macaranga*. A relatively dense forest is also supported by the low levels of charcoal identified for stratigraphic zone C. The presence of fluctuating hydrological budgets within the swamp catchments (Section 9.2) is further reiterated by the levels of the Cyperaceae changing markedly throughout this time period.

Further to the south changes in the pollen spectra are not recorded at Kashiru Swamp until after 13,000 yr B.P. The Kashiru Swamp sequence records an increase, and co-dominance *of Alchornea, Fichalhoa, Hagenia, Macaranga, Podocarpus* and *Syzygium*. At Kuruyange Swamp there was a replacement of *Hagenia* by *Olea, Macaranga* and *Syzygium* (Jolly and Bonnefille, 1991). Similarly at Rusaka Swamp, where sediments accumulated from 12,000 yr B.P., there was a decrease in Gramineae pollen associated with an increased presence of

Afrocrania, *Cliffortia*, *Ilex* and *Myrica*. There followed a rise in *Hagenia* and *Macaranga* from approximately 11,500 yr B.P. Further north, the increase in montane forest did not occur until much later; 12,500 yr B.P. at Lake Mahoma, and 9500 yr B.P. at Lake Cheranganni (Livingstone 1967). As within the Rukiga highlands these records indicate an increase in the amount of montane forest taxa previously present following late glacial conditions.

The transition from late glacial conditions throughout central Africa has been widely felt by 14,700 yr B.P. when the glaciers started to retreat (Osmaston, 1989; Rosquist, 1990). At Lake Mobutu Sese Seko pollen from lower altitudinal vegetation is recorded from 14,700 yr B.P., increasing in abundance until 12,500 yr B.P. (Ssemmanda and Vincens, 1993). At Lake Kivu, water levels rose at about 12,500 yr B.P., a transitory low stand being recorded from 11,000 to 10000 yr B.P. before the lake overflowed into Lake Tanganyika at 9500 yr B.P. (Hamilton, 1982). The was a rise in water level of Lake Tanganyika has been dated to approximately 13,000 yr B.P. (Williamson *et al*, 1991). Abrupt changes in the levels of effective precipitation between 11,000 and 10,000 yr B.P. have been recorded from lake level evidence in Africa (Gasse *et al*, 1990; Roberts, 1990; Roberts *et al*, 1993). Thus, geomorphic, lake-level and vegetation changes, although recording a slightly different response times, all mark the transition from late glacial conditions through climatic ameriolation.

The palaeoecological evidence suggests there was spread of montane forest taxa in central Africa from about 13,500 yr B.P. A re-interpretation of the radiocarbon data places this change approximately 1500 years before the 12,000 yr B.P. suggested by Taylor (1990); but agrees with the suggestion by Taylor (1988) that there was a slight expansion of montane forest between 13,800 and 14,200 yr B.P. It is thought this early expansion phase was significant throughout the Rukiga highlands. The spread of lower altitudinal forest types is some 1500 to 2000 years earlier in south-west Uganda, than that recorded in Burundi. Also, the precursor is *Hagenia* dominated forest rather than the steady increase in mixed montane forest recorded to the south, and on the Ruwenzori. The early expansion of montane forest within the Rukiga highlands may have been attributed to the forcing mechanism responsible for the maintenance of forest patches suggested during full glacial conditions, i.e. that of the rain bearing clouds being funnelled into the Rukiga highlands by the topography; and a deeply dissected topography. These local conditions allowed for montane forest expansion earlier than that to the southern and northern parts of central Africa.

The precursor of the Holocene moist lower montane forest was isolated patches of montane forest that persisted in central Africa, although these patches do not appear to have attained a significant size. It is suggested montane forest expansion appears to have taken place from a number of isolated foci, rather than as a broad front from a single source (Jolly *et al*, in press). The presence of moist lower montane forest taxa at some locations, and not at others, further supports the earlier suggestion of mini forest refugia resulting from the influence of local factors, such as soil conditions and topography. A more recent analogue for such an occurrence is documented for the patchy spread of vegetation in the Sahel during the mid Holocene (Ballouche and Newmann, 1995). One such location where soil conditions and topography is thought to have been favourable for persistence of montane vegetation within the Rukiga highlands was within the Mubwindi Swamp catchment. From such locations the forest was able to spread out relatively quickly as climatic conditions improved.

Montane forest spread was most likely facilitated by climatic change following the last glacial, when levels of atmospheric CO_2, temperature and monsoonal activity in tropical Africa are believed to have been reduced relative to the present (COHMAP, 1988; van Campo and Gasse, 1993; Gasse and van Campo, 1994). Due to the differential timing of this montane forest spread it is suggested climatic change, and its influence on the vegetation composition and distribution was complex. Furthermore, evidence is beginning to emerge in the neotropics that suggest rain forest spread was not a smooth process during the late glacial (Hooghiemstra and van der Hammen, 1993). It is possible that variations in glacial-interglacial boundary conditions at northern latitudes influenced monsoonal activity over tropical Africa during the late glacial, but that the level of influence imparted to the vegetation depends upon local conditions (Jolly *et al*, in press).

The vegetation distribution within the Rukiga highlands at 12,000 yr B.P. is highlighted in Figure 9.5. Throughout the region ericaceous vegetation mixed with montane forest and grassland scrub was still present. Montane forest was densest within topographically enclosed areas, such as the southern sector of Bwindi-Impenetrable Forest.

10,000 to 4000 yr B.P.

This time period is covered by sediments from all the swamps in the Rukiga highlands apart from Mubwindi Swamp. Although all sites with a radiocarbon chronology reflect a hiatus in sedimentation from the early Holocene. This hiatus in sedimentation was shortest at Ahakagyezi Swamp, where it only lasted approximately 1000 years; at Mubwindi Swamp it last approximately 9000 years, at Muchoya Swamp approximately 4000 years.

Within the Ahakagyezi Swamp catchment during this time period the montane forest was dominated by *Alchornea* with *Ilex*, *Macaranga*, *Olea*, *Podocarpus* and *Zanthoxylum* also present. The vegetation within the Muchoya Swamp catchment was quite different from the other sites, particularly there was a significant presence of members of the Ericaceae. Although much of the Ericaceous pollen may have resulted from locally present parent taxa it is thought some must have originated from vegetation with a non-local position. This is further supported by occasional presence of *Artemisia*. *Alchornea*, *Celtis*, *Ilex*, *Macaranga*, *Olea*, and *Podocarpus* were also present within the catchment. Within the Katenga Swamp catchment the pollen spectra indicate an *Olea* dominated montane forest that was relatively open with high amounts of *Macaranga*, *Neoboutonia* and *Polyscias* also present. The openness of the montane forest is further supported by the time-transgressive increase in *Alchornea* throughout the period. Although there was a similarly large amount of *Alchornea* present, the vegetation was quite different within the Butongo Swamp catchment. The record highlights two major changes; firstly a rapid rise in *Polyscias* and secondly, a large increase in Gramineae. The rise in *Polyscias* is not recorded at any other site within the Rukiga highlands. Due to its sustained presence within the Butongo Swamp catchment, it is suggested it resulted from localised growth rather than regional vegetation change. Why the

12,000 yr BP

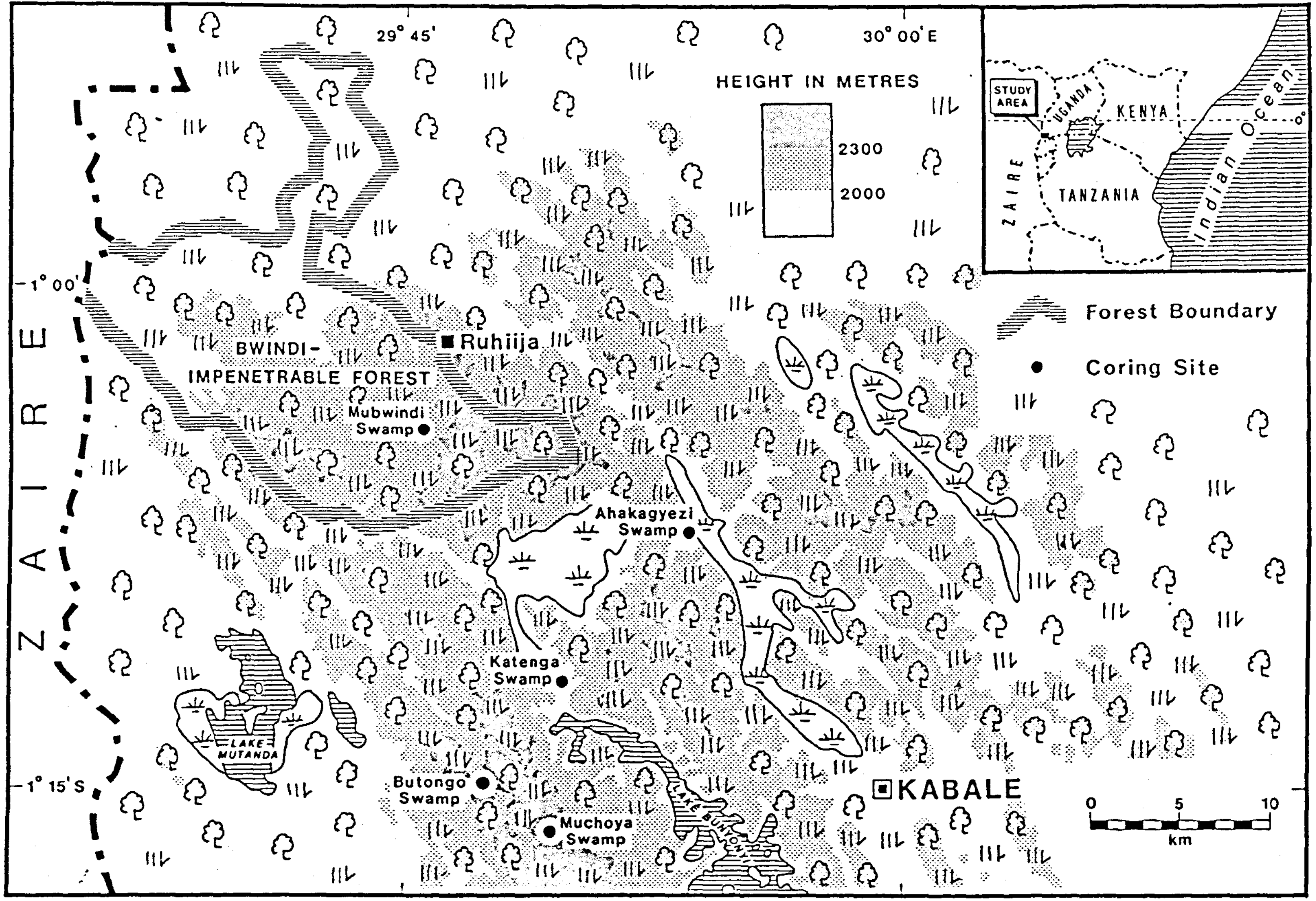


Figure 9.6 Vegetation composition and distribution at 12,000 yr B.P.

Butongo Swamp catchment sustained *Polyscias* is unknown; it could result from localised disturbance, or favourable edaphic conditions for this taxa. According to evidence derived from all the swamps in the Rukiga highlands, *Alchornea* was common in forests in the Rukiga Highlands during the early Holocene, when it appears to have been an important component of colonising forest (Taylor, 1993; Jolly *et al*, in press).

Thus, there was a relatively high proportion of ericaceous taxa at the highest altitudes within the Rukiga highlands, these are indicative of a slightly drier forest type likely to be related to the higher altitude, and consequently a cooler, drier climate. This is something of an anomaly as reconstructions of precipitation and temperature levels (Bonnefille, 1993) indicate warmer and wetter conditions. An early Holocene humid climate has also been suggested by pollen (Kendall, 1969) and diatoms (Stager *et al*, 1997) from Lake Victoria. The climate of this period is thought to have been derived from enhancement of southerly monsoons at this time (Sirocko *et al*, 1996). This had the effect of high lake levels throughout east and central Africa (Roberts, 1990; Roberts *et al,* 1993; Talbot and Johannessen, 1992). Some of these spatial differences in forest composition during the early to mid Holocene may result from endogenic differences, such as differential soil moisture and slope characteristics. Others may result fro a relatively diverse palaeoclimate. Indeed African rainfall patterns are very patchy today, with the influence of lakes and topographic variation being very important (Nicholson, 1994). With these factors taken into consideration some geographic variation in the composition and distribution of montane vegetation would be expected. If this is the case the transfer function approach, which assumes that changes in vegetation are principally climatically controlled, may not be appropriate for tropical Africa. Similarly this regional variation suggests that caution should be applied to the use of regional biomes to investigate climate-vegetation feedback (Prentice and Thompson-Webb, 1994). Nonetheless, additional data will be need to confirm or refute this apparent temporal and spatial variation (Stager *et al*, 1997).

Towards the end of this period, from approximately 6000 yr B.P., the composition and distribution of the vegetation surrounding the Ahakagyezi Swamp catchment changed to a drier type of montane forest. This change was also recorded by the vegetation on Ahakagyezi Swamp surface by the development of swamp forest. At Butongo Swamp an increase in *Ilex* may correlate with the increase in *Ilex* recorded at Muchoya Swamp from about 5500 yr B.P. The spread of drier forest types than previously present was widespread after about 6500, probably in response to greater seasonality (Stager *et al*, 1997), possibly resulting in pole-ward extension of the migration of the ITCZ (Nicholson and Flohn, 1980).

Because of the absence of sediments dating to the early Holocene (Section 9.2), it is not possible to indicate when moist lower montane rain forest became widely established within the Mubwindi Swamp catchment, following the last glacial period. However, a date slightly before or similar to the establishment of lower montane forest around Ahakagyezi Swamp (i.e. around 10,000 yr BP) (Jolly *et al* in press) seems probable.

The vegetation distribution within the Rukiga highlands at 8000 yr B.P. is highlighted in Figure 9.6. This suggests montane forest was present throughout this period. The composition of the montane forest varied according to differences in altitude, micro-climate and topography. Montane forest reached its maximum extent in the Rukiga highlands prior to the period of increased seasonality at approximately 6500 yr B.P.

4000 to 2000 yr B.P.

This time period is recorded by all the swamp sediments in the Rukiga highlands, although only latterly by those at Mubwindi Swamp.

At Ahakagyezi Swamp there was a continued increase in the extent of swamp forest colonisation. Within the catchment there was continued presence of *Celtis*, *Olea* and *Podocarpus*. Due to the increased dominance of the pollen spectra by Myrtaceae pollen, *Celtis*, *Olea* and *Podocarpus* are thought to have been more important components of the non-local vegetation than within the previous time period, forming a type of dry montane forest within the catchment. Similarly, at Katenga Swamp *Olea* and *Podocarpus* dominated the surrounding vegetation.

8,000 yr BP

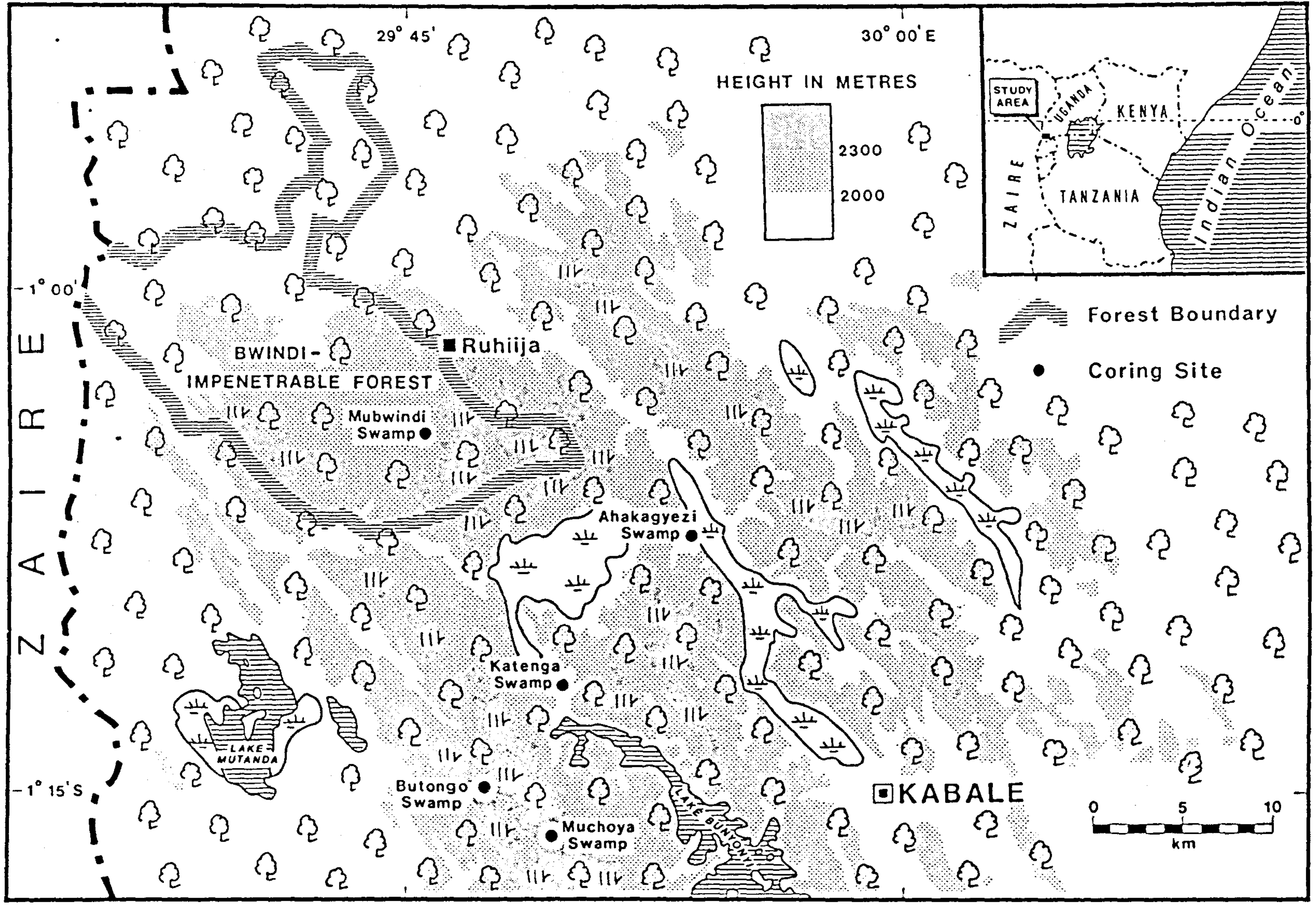


Figure 9.7 Vegetation composition and distribution at 8000 yr B.P.

However, unlike at Ahakagyezi Swamp there was no expansion of swamp forest. *Macaranga* and *Polyscias* were much more important components of the vegetation around Butongo Swamp than elsewhere in the Rukiga highlands. The vegetation on the swamp surface then changes to one dominated by *Sphagnum.* According to Lind (1956), in the normal case of swamp seral succession *Sphagnum* eventually ousts the swamp grass *Miscanthus*, this may explain the dominance of *Sphagnum* at his site today.

From approximately 2500 yr B.P., following the re-instating of sedimentation at Mubwindi Swamp, Myrtaceae was present within the catchment. This was associated with a dynamic community of moist lower montane forest with a similar composition to that of the more remote areas of Bwindi-Impenetrable Forest was present. At Muchoya Swamp this time period was dominated by *Myrica*: on the basis of the dominance of this taxa, and a decrease in members of the Cyperaceae, it is suggested this growth of *Myrica* was restricted to Muchoya Swamp surface. Within the catchment there was a more mixed type of montane forest than previously present. Towards the top of the time period there was a sharp rise in the amount of pollen from *Podocarpus*. At Ahakagyezi and Muchoya swamps these changes can be correlated with a decline in *Alchornea*, *Celtis*, *Ilex* and *Macaranga*. Thus, from approximately 4000 yr B.P. there was a significant change in the composition of vegetation within the Rukiga highlands to a drier type of forest. This facilitated the growth of swamp forest on swamp surfaces and allowed sediments to accumulate again at Mubwindi Swamp.

From about 5000 yr B.P., at Lake Mobutu Sese Seko there was an increase in the pollen derived from semi-deciduous forest, particularly in *Celtis* spp. and establishment of swamp forest around the lake; dominated by *Phoenix reclinata* and *Anthocliesta* spp. (Ssemmanda and Vincens, 1993). This is the oldest record of a late Holocene transition to arid conditions. Further south the outflow from Lake Kivu to Lake Tanganyika was interrupted from about 3500 yr B.P., (Haberyan and Hecky, 1987). Similarly, the Lake Tanganyika outflow was closed from about 4000 yr B.P. with lake levels lowered by about 75 m (Vincens *et al*, 1993). Further afield, this period of climatic aridity has been suggested at sites from Madagascar (Burney, 1993), across equatorial Africa (Scott, 1982; Scott *et* *al*, 1991; Street and Grove, 1979; Stager, 1982; Vincens, 1989; Vincens *et al*, 1994) to Zaire and Congo (Elenga *et al*, 1994; 1996; Maley, 1989). Sedimentary data from Cameroon (Giresse *et al*, 1994) and Ethiopia (Bonnefille and Mohammed, 1994) also indicate the onset of drier conditions in the late Holocene. Evidence from the River Nile and a high resolution diatom record from Lake Victoria indicate the onset of more arid conditions in central Africa dates to the end of this time period, i.e. from around 2500 to 2000 yr BP (Butzer 1984, Stager *et al.* 1997).

Low lake-level events and a transition to a drier type of vegetation appear to result from continental aridiity attributed to temporary weakening of the monsoonal circulation. The mechanism behind such a change may result from decreased efficiency of thermohaline conveyor belts (Street-Perrot and Perrot, 1990), or from changes in tropical land conditions and related feedback processes (Gasse and van Campo, 1994). Additional evidence for a change in oceanic circulation patterns comes from Morocco, this suggests reduced oceanic heat transfer was responsible for the late Holocene climatic aridity (Lamb *et al*, 1995).

Therefore, it appears that at least one period of late Holocene climatic change has been recorded throughout Africa, thus, implying distinct, sub-Milankovitch climatic change rather than a continued progression of Holocene warming. Although the changes in montane vegetation composition cannot be attributed to an early phase of human impact, as earlier suggested for the Muchoya Swamp catchment (Hamilton *et al*, 1986), these late Holocene changes in vegetation composition and distribution are synchronous with a rise in agricultural activity Indeed, the rate and direction of the Pastoral Neolithic spread (Section 2.8) are thought to be partly determined by Late Holocene shrinkage of the Rift Valley lakes (Butzer *et al*, 1972; Richardson and Richardson, 1972), this exposed large areas of previously inundated grazing land. It is also suggested this change allowed increased livestock levels from about 3000 yr B.P. (Bower, 1988; Schoenburn, 1993), probably as a result of a transition to a more intensive and established pastoral system. Indeed the effectiveness of late Holocene human population at modifying their environment in central Africa is still an unknown quantity.

2000 yr B.P. to the present

This time period is recorded by sediments from all the swamps in the Rukiga highlands although there is an undated sedimentary hiatus at Butongo Swamp. On the strength of the similarly high amounts of pollen from degraded forest and derived vegetation with the other sites in the Rukiga highlands, and the lack of stratigraphic change, it is suggested the 550 cm core from Lake Bunyoni stems from this time period. The presence of *Alchornea*, *Dombeya*, Ericaceae and *Hagenia* suggest degraded forest was present within the Lake Bunyoni catchment throughout the period represented by the sediments.

The pollen spectra from Ahakagyezi Swamp indicate from 2000 yr B.P. until approximately 800 yr B.P. indicate there was continued expansion of swamp forest, however this was of a more mixed nature than previously recorded. Within the catchment there was a dense covering of montane forest. The pollen record from the Mubwindi Swamp catchment indicate *Olea* and *Podocarpus* dominated the surrounding montane forest until approximately 1000 yr B.P. This montane forest was relatively closed with little sign of disturbance, a fringing band of *Syzygium* was present around the Mubwindi Swamp margins. The record from Butongo Swamp also shows indication of forest disturbance with increases in *Alchornea*, *Macaranga*, *Neoboutonia* and *Polyscias* with concomitant decreases in *Ilex* and *Olea*. Soon after these fluctuations there is a rapid change in the vegetation composition on the swamp surface to one dominated by *Sphagnum* spp. Human activity could have been responsible initiating *Sphagnum* peat development. The possible impetus for such a change in local vegetation is likely to result from a change in the nutrient status of the swamp, possibly due to catchment deforestation. This is thought to indicate a change to more ombrotrophic conditions at the swamp (Hamilton and Taylor, 1986). An anthropogenic cause of peat growth has been suggested for the initiation of peat formation in the British Isles (Moore, 1973; 1975; Moore and Bellamy, 1974) and Scandinavia (Hafsten and Solem, 1976).

Within the Muchoya Swamp catchment there was a time-transgressive decrease in *Celtis*, Ericaceae, *Ilex*, *Olea* and *Podocarpus* stemming from approximately 2200 yr B.P. This decrease is mirrored by increases in taxa that are present within disturbed, open habitats such as *Dodonaea*, *Dombeya*, *Hagenia*, *Macaranga*, *Nuxia*, *Rumex* and *Vernonia*. This has been linked with a rising charcoal concentrations and human-induced clearance (Taylor, 1992). This period within the Rukiga highlands is characterised by forest clearance. The initial focus of this was concentrated at the highest altitudes. Higher altitude sites in the Rukiga highlands may have been favoured initially for agriculture because: (a) the land would be easier to prepare as forest growing on ridge-top locations is less dense than at lower altitudes, (b) the incidence of disease, such as malaria is much less, and (c) the hill top locations would offer natural protection from potentially hostile neighbouring clans. The higher altitude sites in the Rukiga highlands were eventually abandoned with land at lower altitudes increasingly being the focus of agricultural activity.

From approximately 1000 yr B.P. there was an altitude change in the focus of vegetation degradation. Within the Ahakagyezi Swamp catchment there was a decline in the established forest components such as *Celtis*, *Olea*, and *Podocarpus*. This was associated within the Mubwindi Swamp catchment with an increase in taxa from a more open habit such as *Dodonaea*, Ericaceae, *Polyscias* and *Vernonia*. Although the forest around Mubwindi Swamp has retained intact there is an indication of disturbance in close proximity, specifically the increases in the amount of *Dodonaea* and *Vernonia* pollen (Chapter 8) and charcoal (Chapter 5). As there are not the dramatic changes in vegetation, recorded at the other sites in the Rukiga highlands, this disturbance is not thought to have occurred within the immediate catchment but was likely to have stemmed from a location in close proximity. Possible locations of this disturbance are thought to be the areas now vegetated by patches of bamboo forest. As highlighted in Section 2.4, these patches indicate an advanced stage of forest regeneration, supporting the suggestion of earlier clearance.

The decline in the *Syzygium* dominated swamp forest, at Ahakagyezi Swamp may be significant in the proposed model of a transition of agricultural activity to lower altitudes. Schmidt (1980), notes that the wood of *Syzygium* is favoured as a source of charcoal for smelting in north-west Tanzania today. In the context of the Rukiga highlands, this *Syzygium* decline may correspond to a need to seek out new resources in order to maintain the developing iron industry (Taylor and Marchant, 1996). The shift of agricultural populations to lower altitudes has also been documented for the Rakai district further to the west (MacLean, 1996), which similarly may have been caused by soil degradation at the highest altitudes combined with a period of technological innovation. A movement of settlement and farming from highland areas to the more subdued topography of lake shore areas may be why the Mubwindi Swamp catchment has managed to retain forest cover virtually intact (Jolly *et al*, in press).

As was apparent for the previous period of late Holocene climatic change, increases in aridity or seasonality, may also have played a role in changing forest composition. Stager *et al* (1997) provide more precisely dated evidence than the record from Mubwindi Swamp for a sharp decrease in the Precipitation:Evaporation ratio effecting Lake Victoria from around 600 years ago. It is possible that reduced levels of effective precipitation may have favoured taxa - such as *Podocarpus* and *Celtis* - which presently favour drier soils or more seasonal types of forest in western Uganda (Marchant and Taylor, in press). Indeed an estimated cooling of 2°C has been suggested for the Ethiopian highlands that is thought to be contemporaneous with the little Ice Age (Bonnefille and Mohammed, 1994). The timing of this change corresponds with a peak in the amount of *Podocarpus*, and taxa that favour drier soils, and a very noticeable peak in charcoal. These changes are thought to be responses to a further period of late Holocene increased aridity. Nevertheless, the very dramatic changes in vegetation at Ahakagyezi Swamp are likely to result from human activity.

Conversely to the previous period, the changes in montane forest composition within the Mubwindi Swamp catchment dated at approximately 200 yr B.P. may represent the onset of marginally more humid climates: Nicholson (1996) and Stager *et al* (1997) suggest that levels of effective precipitation in central Africa increased from around 200 years ago. These climatic induced changes on the vegetation are not recorded elsewhere in the Rukiga highlands as a result of forest clearance. However, timber from *Podocarpus* is presently a favoured target of pit-sawyers in the area (Section 3.7). In view of this, and the increased abundance of taxa representing gappy and regenerating forest and degraded soils, together with the relatively recent radiocarbon date, perhaps the most likely cause of changes in pollen spectra was the selective felling of trees for timber. Significantly, this time period includes the period of the first World War, when Uganda Forest Department data record a heightened interest in *Podocarpus* in Bwindi-Impenetrable Forest as a source of wood for rifle stocks (Marchant and Taylor, in press).

There are tentative signs from the recent fossil record of montane forest re-growth within the Mubwindi and Muchoya swamp catchments, these are recorded as a decrease in *Dodonaea*, *Dombeya* and *Vernonia* with a concomitant increase in *Ilex*, *Macaranga*, *Neoboutonia* and *Podocarpus*. Within the Mubwindi Swamp catchment the date of the recovery roughly coincides with the gazetting of Bwindi-Impenetrable Forest as a Forest Reserve. It is thus possible that increased regulation of the activities of pit sawyers and other users, following gazetting of the forest, has allowed for some recovery of timber trees, such as *Podocarpus*.

The area around the Mubwindi Swamp catchment did not experience the wide-scale clearance recorded at the other sites within the Rukiga highlands, and further afield, although there has been a degree of disturbance. It is suggested one possible cause of the disturbance is the increased disturbance imparted on the vegetation by elephant (*Loxidonta loxidonta africana*). The influence of elephant on the surrounding vegetation can be a significant factor in determining vegetation composition (Buechner and Dawkins, 1961; Butynski, 1986; Plumtree, 1994). This influence may have been magnified due to the increased concentration of the animals into the Mubwindi Swamp catchment (where the animals are concentrated at present during the two dry seasons) by regional forest clearance. Alternatively, the floristic change could represent an increased input of pollen from a wide range of degraded habitats within the Rukiga highlands, this input would possibly dilute the input from within the Mubwindi Swamp catchment. More recently it would seem feasible that the driving force was one of human activity operating within Bwindi-Impenetrable Forest. Indeed, the main control has been the activities of pit-sawyers which commenced around 100 years ago (Section 3.7). As outlined from the present-day vegetation survey (Chapter 6) pit-sawing has been the main control on the present-day forest composition. Although there is now a ban on pit-sawing within Bwindi-Impenetrable Forest, the gaps originally opened up in the forest appear to be maintained by the activities of elephant and other, more vigorous grazing animals.

Despite these relatively minor perturbations the forest within the Mubwindi Swamp catchment has remained intact (Plate 9.2). There are a number of possible causes responsible for the 'protection' afforded to Bwindi-Impenetrable Forest: (a) the ground is more dissected and potentially less favourable to agriculture, (b) there has been some degree of protection afforded by the (until recently) resident indigenous pygmy population against the colonising agriculturists, and/or (c) the area presently covered by the Bwindi-Impenetrable Forest was furthest from the main influx of agriculturists and simply therefore the last area to be reached. It is suggested that there has been some degree of protection afforded by the BaTwa, against the colonising agriculturists, although the degree of this protection cannot be quantified by this research. Indeed, one of the prominent BaTwa often laments that they were once mortal enemies of the pioneering agriculturists, keeping all strangers out of the forest (Kingdon, 1990). Indeed, a series of bitter wars with the BaTwa were quelled by the British administration in 1912. A precursor of Bwindi-Impenetrable Forest may have corresponded to some form of disputed border between territories, the associated economic and political instability would have placed severe limitations on the development of sedentary agriculture. A second possibility is related to the development of what are believed to have been highly centralised societies in the Great Lakes Region between Lake Victoria and the Western Rift Valley (or what is now the eastern border of Zaire). The development of central African ‘kingdoms’ or precolonial ‘states’ commenced during the early part of the present millennium (Sutton, 1990; Robertshaw, 1994), and it is possible that any forests which were intact at the time of state formation and were located towards the outer-limits of the kingdoms’ sphere of influence, were ‘protected’ as a natural deterrent to potential invaders.

The vegetation distribution characteristic at 2000 and 800 yr B.P. within the Rukiga highlands are highlighted in Figures 9.7 and 9.8 respectively. These highlight the spread of forest clearance throughout the Rukiga highlands initially from the hill-top sites to lower altitudes. These proposed changes reiterate the present-day vegetation composition and distribution within the Rukiga highlands (Figure 9.2).

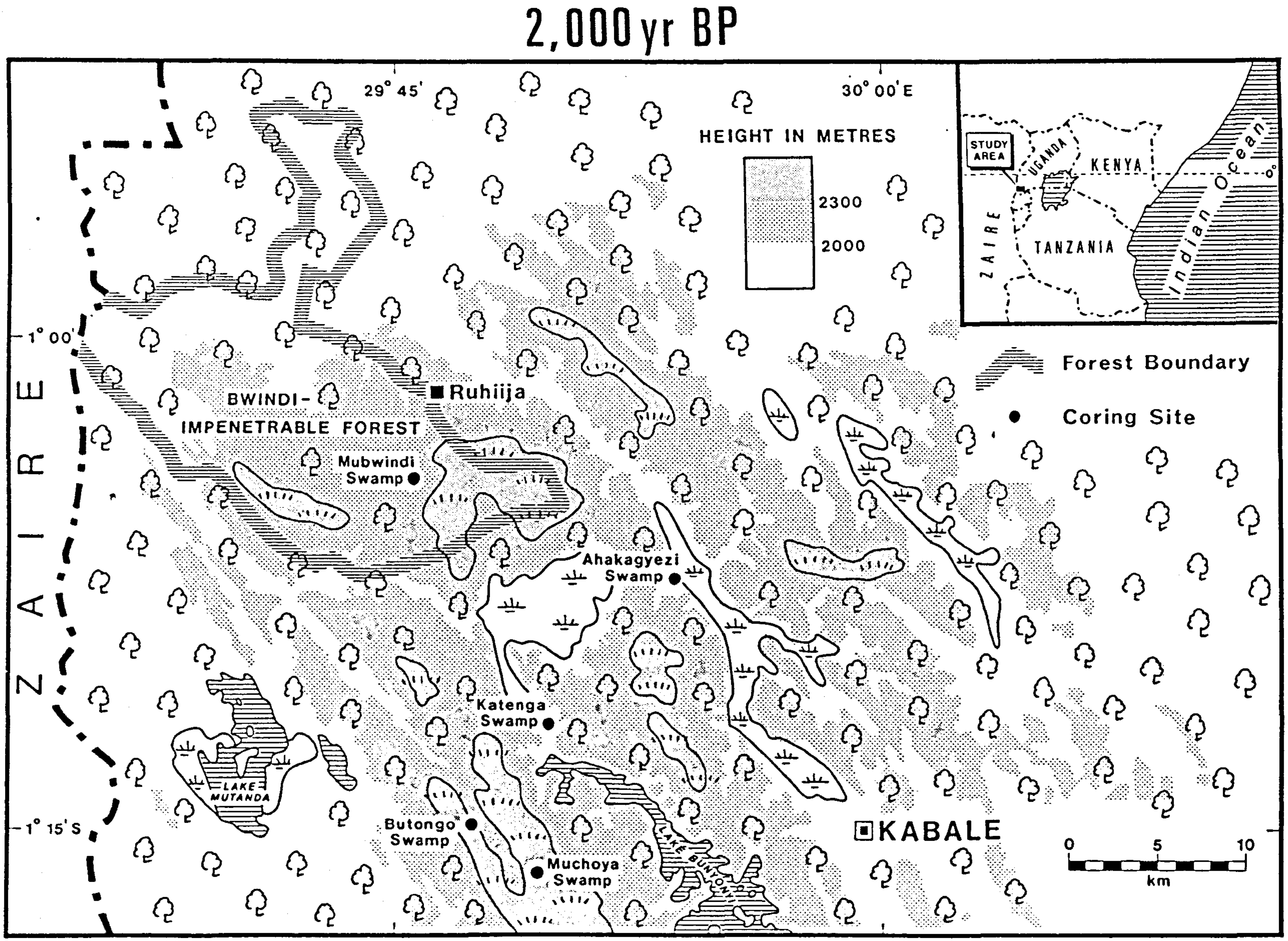

2,000 yr BP

Figure 9.8 Vegetation composition and distribution at 2000 yr B.P.

800 yr BP

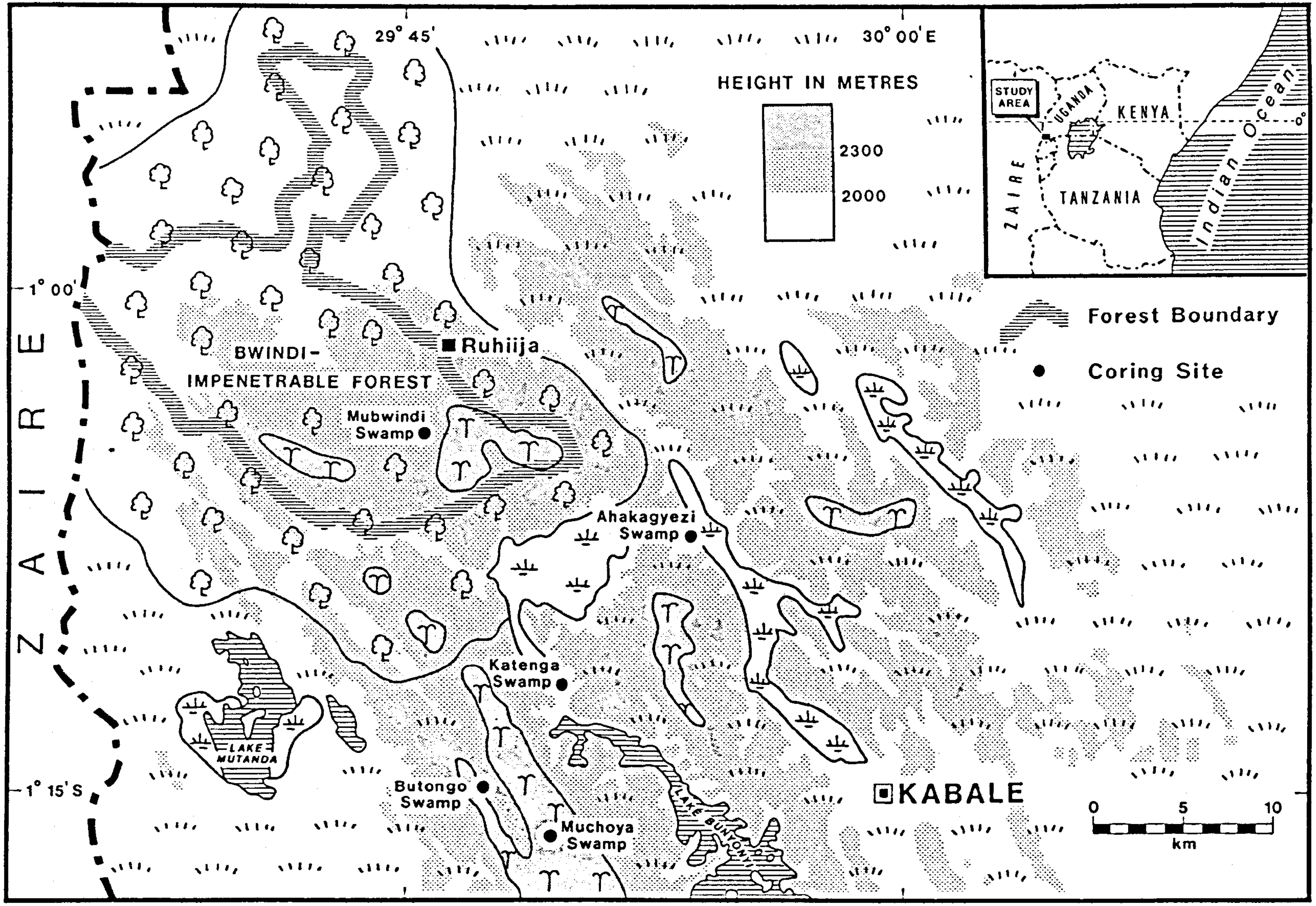


Figure 9.9 Vegetation composition and distribution at 800 yr B.P.

CHAPTER 10 Conclusions from the thesis and future research possibilities

10.1 Introduction

In this Chapter the findings from the thesis will be summarised. Areas where the results from the present research contribute to the fields of archaeology and conservation will be highlighted. Where the foci of future research lie within Uganda, and further afield within the study of tropical palaeoecology will be discussed.

10.2 A summary of montane forest dynamics within the Mubwindi Swamp catchment

There are six main findings that have arisen from the research within the Mubwindi Swamp catchment.

1. Pollen and spores recorded within the surface sediments comes largely from plants growing within the immediate catchment. This further supports the suggestion by Taylor (1993) that the swamps in the Rukiga highlands are highly suitable for palynological study of changes in vegetation and climate. The modern pollen - vegetation relationship determined within Chpater 6 is thought to be unique to the Mubwindi Swamp catchment due to the unique catchment characteristics, and should be extended to other catchments with caution.

2. An important influence on the present composition and distribution of montane forest within the Mubwindi Swamp catchment has been pit-sawing activity in the past, and the recovery time lapsed since pit-sawyers ceased to operate. Indeed, the majority of the forest within the Mubwindi Swamp catchment can be described as secondary; the only site suggested not to have been influenced by pit-sawing activity is the small island. Gaps within the montane forest, and the forest shrub complex found therein, once produced by human activity, are maintained by elephants and more general mammal-induced grazing pressure. All the differences in vegetation composition and distribution cannot be explained purely by past human activity and the activities of forest dwelling mammals. The composition

and distribution of the vegetation are partly driven by local climatic and edaphic conditions. Superimposed on these are the ecological constraints of forest regeneration and niche occupation.

3. Sedimentary hiati have been inferred from the radiocarbon dating and analysis of the extracted sedimentary sequences. The delimitation of these hiati in sedimentation has been crucial to understanding vegetation changes within the Mubwindi Swamp catchment, and to allow placement of these within the temporal framework. These sedimentary hiati have provided information regarding the palaeohydrology of the Mubwindi Swamp catchment.

4. Sediments from three separate cores, abstracted from different locations on Mubwindi Swamp are shown to highlight similar records of vegetation change. Thus, sediments within the Mubwindi Swamp catchment reflect catchment-wide changes in montane vegetation composition and distribution. The vegetation that produced the pollen and spores retained within the Mubwindi Swamp sediments has changed considerably over the Late Quaternary. These variations in past vegetation composition demonstrate there have been some elements, sometimes at a much reduced level, of montane forest taxa during past climatically cooler, and drier periods than present. A precursor of the present Bwindi-Impenetrable Forest may have survived this period due to steeper ecological gradients than present, and locally favourable edaphic and climatic conditions.

5. A re-initiation of peat formation at Mubwindi Swamp during the late Holocene may have been climatically motivated. The peat deposits contain evidence for the presence of a dynamic community of lower montane forest throughout the last 2000 years or so. Fluctuations in composition appear to have been caused by both exogenic (e.g. climate, human) and endogenic (e.g. successional) processes. This record of late Holocene vegetation change covers the period when there is human-induced forest clearance well documented at other sites throughout central Africa. Superimposed upon what appears to have been continuous variation are three relatively important changes in the composition of lower montane forest. The first, around 680 yr B.P., could have been caused either by a low level of human activity, a shift to a less humid climate, or some combination of the two. The

second, from 200 yr B.P., appears to be due to selective utilisation of timber trees within the forest by humans. The third, beginning 50 yr B.P., may represent some recovery of forest, as a result of a reduction in the activities of pit-sawyers

6. The record of vegetation history supplied by sediments from Mubwindi Swamp indicates that a precursor of the present Bwindi-Impenetrable Forest has been in existence throughout the late Holocene, and has been - at most - only moderately influenced by human activity during the same period. According to pollen data from a number of sites in the Rukiga Highlands, other areas of lower montane forest have not fared so well. Taken together, the evidence indicates that the onset of clearance of forest in western Uganda during the late Holocene was catchment specific. The evidence from the Rukiga Highlands thus serves as a warning against attempts to extrapolate evidence of the timing of forest clearance from one - or a limited number - of pollen based studies across broad expanses of central Africa.

10.3 A summary of montane forest dynamics in the Rukiga highlands

Before summarising vegetation changes during the Late Quaternary the value of stratigraphic information in tracing swamp development and changes in hydrological budgets of swamps should be reiterated. Both sediment type and the rate of sediment accumulation have been shown to vary significantly within the Rukiga highlands. The sediment type and rate of accumulation is ultimately going to be a result of the catchments hydrological budget, therefore I suggest there is a strong requirement to accurately record the present catchment topography and hydrological dynamics of any new site to be investigated. Indeed, an interpretation of sedimentary changes (and the fossils retained within those sediments) at any particular site can only be achieved with a thorough understanding of the catchment controls on the hydrological, and hence sedimentary regime.

Regionally, this importance of sediment characteristics is further reiterated as contemporaneous sedimentary changes have been shown to be indicative of contemporaneous periods of environmental change. To further increase the effectiveness of macro-scale sedimentary studies there is a urgent requirement to standardise the method for logging sediments; I suggest ubiquitous use of the

Tröels-Smith (1955) method as it operates on a classified scale, has become something of standard in temperate stratigraphic studies, is incorporated into the latest version of TiliaGraph (Grimm, 1995). This approach is particularly valid as sediment stratigraphy in the tropics is much more diverse than is, for example, the case with swamp deposits in more temperate latitudes, partly due to the much longer records. As has been shown at all the swamps with more than a single core, there are marked between-core variations in stratigraphy. Therefore, I emphasise the requirement to extract multiple cores from a swamp basin to understand the factors that determine sediment composition.

Prior to 43,000 yr B.P. a mixed ericaceous belt and upper montane forest vegetation was present at the highest altitudes and moist lower montane forest at the lower altitudes within the Rukiga highlands. Close to water courses, moist types of vegetation developed. There was a rapid transition to a drier forest type around 43,000 yr B.P. when a mix of ericaceous vegetation and high montane forest colonised the highest altitudes, grassland scrub being more important at lower altitudes. Montane forest was denser within topographically enclosed areas such as the location of the southern sector of Bwindi-Impenetrable Forest. There was a relatively subtle change to a moister type of forest from approximately 30,000 yr B.P. with components of montane forest becoming more important prior to full glacial conditions of northern latitudes. Towards the maximum period of aridity and reduced temperatures at 18,000 yr B.P., ericaceous vegetation dominated; isolated patches of montane forest persisting in areas that were buffered from the ambient climate by the dissected topography and diverse edaphic conditions. Grassland scrub was the dominant type of vegetation at lower altitudes.

Following full glacial conditions ericaceous vegetation mixed with montane forest. Grassland scrub was still present throughout the Rukiga highlands. Within the early and mid Holocene, montane forest was present throughout the Rukiga highlands although the composition varied considerable according to differences in altitude, micro-climate and topography. The wetter and warmer climatic conditions facilitated the spread of montane forest which reached its maximum extent in the Rukiga highlands around 6000 years ago. From between 4000 to

3000 yr B.P. there was a significant change in the composition of the montane forest within the Rukiga highlands to an overall drier type of forest. This facilitated the growth of swamp forest on some of the swamps and expansion of taxa previously restricted to lower altitudes. From approximately 2000 yr B.P. montane forest clearance by a growing agricultural population was initially focused at the highest altitudes, as the density of the agricultural and pastoral communities increased and agricultural technology developed there was a transition to the lower altitudes. These population movements led to the highly developed system of agricultural terracing practiced within much of the Rukiga highlands (Plate 10.1). Despite this regional spread of agriculture, the forest within the Mubwindi Swamp catchment has remained intact. However, there have been relatively subtle fluctuations in the composition of the montane forest that are centred around 680, 200 yr B.P and within the last century. These changes are thought to stem from a combination of regionally recorded climatic change, selective deforestation as a result of pit sawing activity and most recently the controls imparted due to gazetting of Bwindi-Impenetrable Forest.

10.4 Wider implications of montane forest dynamics in central Africa; conservation, archaeology and palaeoecology.

The records discussed from the Rukiga highlands highlight the prominence of the Rukiga highlands as providing one of the best-dated, and most complete records of Late Quaternary environmental change within the tropics. Sediment accumulating ecosystems in the tropics contain long-term records, hence have been subjected to a range of different environmental changes including climatic, anthropogenic and ecological succession. More recently, the time-transgressive nature of montane forest clearance highlights the need for additional sources of evidence.

One area of future collaboration is with the field of archaeology, which would add considerably to understanding more recent changes in montane forest composition and distribution in central Africa. For example, from approximately 800 yr B.P. (the Early Iron Age to Late Iron Age transition), significant changes in land-use and settlement patterns occurred in central Africa. Specifically, environmental change, including climatic change and human-induced soil erosion and forest clearance have been detected (Marchant and Taylor, in press). However, the evidence for archaeological and environmental change have come from different catchments. It has therefore been difficult to link archaeological with palaeoenvironmental evidence. Therefore, there is an urgent requirement to work closely within the archaeological field to independently derive data from the same location and for the same period on the nature, timing and rate of archaeological with vegetation change.

It has been concluded by IPCC (1995) that increased concentrations of various greenhouse gases will lead to major global climatic change over the coming decade. Although there are significant uncertainties regarding the IPCC approach (Singer, 1996), it is expected that climatic change will not be a smooth, or linear process (Vitousek, 1994). In the same token, as in the past montane forest will not be likely to respond to future climatic variations as independent units; but will be influenced by individual responses of species. Predictions of how species will react will depend on understanding long-term population dynamics as a function of climatic change, such as can be provided by the high resolution palaeoecological data provided in Part 2. An understanding of these changes, and likely response of montane vegetation, is crucial given the present-day boundary that restricts the ability of the flora (and fauna) to adjust to future climatic change (Figure 10.1)

On a large scale general circulation models (GCMs) are presently of little value in predicting future climates at regional scales (Sulzman *et al*, 1995). A recent approach to estimating the magnitude of climatic changes incorporates the influence that biophysical feedback has on the ambient climate system, particularly as energy and water fluxes across the land-atmosphere interface are mediated by the composition and distribution of vegetation (Prentice, 1995). To understand the biophysical feedback influence one particular model, BIOME 6000, documents the vegetation cover at 6000 yr B.P. and links this into existing climatic models (Prentice, 1995; Prentice and Webb, 1994). Although at the preliminary stages, this approach is starting to realise the potential of the palynological data within research into global environmental change by developing a new generation of coupled climatic models that are sensitive, and more realistic to the natural systems under observation. If these new generation models are to fulfil their potential they must have high quality, well dated pollen records, such as available from the Rukiga highlands. On a cautionary note, the differences recorded in the vegetation composition and distribution within the Rukiga highlands at any particular time in the past (Section 9.3) indicates that on a small scale it is very difficult to assess a single biophysical feed-back component that can be incorporated within models. This is particularly so as these models operate on the basis of 50 km^2 pixel. This thesis has highlighted the considerable within pixel differences in vegetation composition. This variation needs to be accounted for within these coupled models if the biophysical feedback is to be accurately incorporated.

The composition and distribution of montane vegetation along altitudinal gradients is the cornerstone of vegetation reconstruction in montane environments, particularly as vegetation is often regarded as one of the best indicators of the general environment (Hamilton, 1982). Therefore, the application of the vegetation scheme outlined in Section 2.4 must be investigated as to its robustness. Are floristically critical altitudes present within montane vegetation? Are changes in vegetation distribution on different mountains synchronous, if so was this the case in the past? Indeed, further surveying of present-day vegetation distribution and the relationship of this to the pollen commuted to sedimentary records is necessary for more objective interpretation of palaeoecological records.

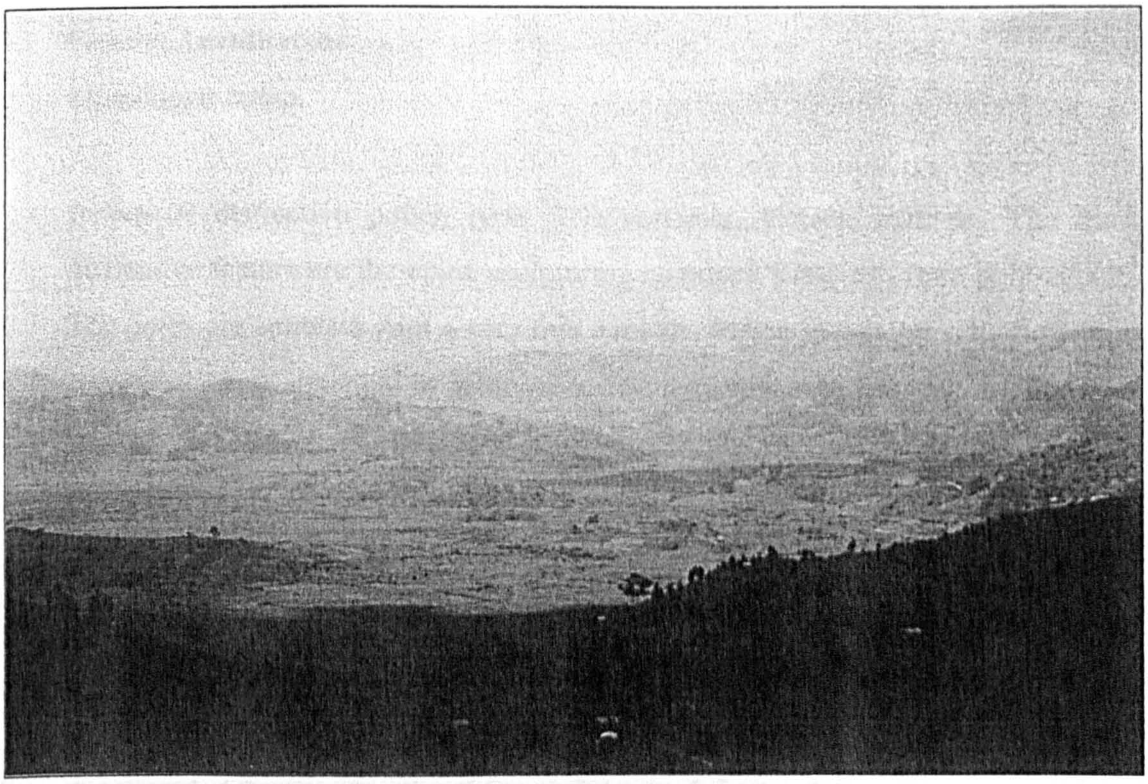
On a regional scale, or over a longer temporal scale, the different floristic belts and zones outlined in Section 2.4 will occur at different altitudes. The reconstructed vegetation composition and distribution within the Rukiga highlands indicates that taxa behave individually, rather than as *en masse* communities which rigidly adhere to the forest types outlined in Section 2.4. Therefore, montane vegetation forms an disjointed altitudinal continuum, reflecting ambient environmental conditions. Within this large scale zonation there are anomalies that result from local topographic and edaphic conditions, climatic regime and human influence. These distribution anomalies in the composition and distribution of montane vegetation emphasises the need to be flexible in the uniformitarian approach when reconstructing past vegetation communities from pollen analysis, and the requirement to fully understand present-day catchment controls on the vegetation composition and distribution and how these are commuted to the sedimentary recorded

Although the palynological record is 'complete' for the Rukiga highlands, this should be viewed as a launch pad to provide other proxy-environmental data throughout central Africa. If we are to truly understand how swamp ecosystems operate, there is a need to increase the available number of sites in central Africa before the at-surface agricultural activity destroys the below surface-sedimentary records. There exists a number of infilled lake basins within the Rukiga highlands. These could potentially provide a long term record of environmental change and information on the influence of tectonic activity along the Western Rift Valley. The latter has been suggested as being instrumental in forming some of the swamps in central Africa. One such lake basin (Plate 10.2), this is equidistant between Ahakagyezi and Mubwindi Swamps and at an altitude of 1950 m. These basins could yield complimentary information, particularly that from fossilised flora and fauna concentrations and sedimentary analysis.

From the Mubwindi Swamp pollen and vegetation survey data it appears that selective logging has played an important role in determining the present-day composition of Bwindi-Impenetrable Forest only since the latter stages of the last century. Just why Bwindi-Impenetrable Forest was retained during some 2000 years of extensive and seemingly often unreversed clearance elsewhere within the Rukiga highlands remains to be determined (Taylor and Marchant, 1996). However, it appears that cultural protection from the BaTwa may have had some bearing on the distribution and influence of forest clearance and on the current structure of the montane forest. As suggested for the requirement of archaeological research, there is also an urgent need for anthropogenic research within the Rukiga highlands which may provide answers to the questions regarding the altitude and site-specific nature of human impact and determine the underlying cause of why Bwindi-Impenetrable Forest has been retained as an island of montane forest surrounding by a high population densities and intensive agricultural practice.

Plate 10·1. Intercropping within the Rukiga highlands.

Plate 10·2. An infilled lake within the Rukiga highlands.



Appendix

The following descriptions of pollen type and potential sources of these includes taxa found at present within the Mubwindi Swamp catchment, or taxa that have been important components in the past. These descriptions are based on the work of Bentjee (1994) Hamilton (1991) and my own observations in the field. Identification of the pollen was aided by a range of publications (Bonnefille and Riolett, 1971; Bonnefille and Guiot, 1990; Hamilton, 1976; 1982; Kingham, 1976; Salgado-Labouriau, 1982; Scott, 1982; Taylor, 1988). The description of the pollen grains follows that of Punt *et al* (1994). It must be stressed that the following are only brief profiles of the fossil grains encountered during the count, and are not definitive descriptions. The descriptions are arranged alphabetically according to family. Pollen identification is to the lowest taxonomic level available (commonly generic). Following the taxon type there is an indication of the accuracy at which the pollen type was identified. This scheme is on a scale of increasing accuracy of identification (similar - comparative - identical). Where possible, the parent taxa thought responsible for the pollen type are described, and an ecological interpretation suggested. These pollen types are also documented in a series of Plates.

Family: **Acanthaceae**

Mimulopsis comp.

Pollen A distinctive pollen type. Trizonoporate, tectate, scabrate. The most distinctive feature are the exine sculpturing elements, these run from pole to pole. The pores are annulate with a very thin annulus. Pollen grains are semi-prolate in equatorial view, spherical in polar view. The long axis measures 60 µm, the short axis 35 µm. The exine is thick and clearly stratified; ectexine = endexine. Plate 1.
Potential sources The pollen could have been derived from *Mimulopsis alpina*, *M. arborescens* or *M. solmsii*. This latter species is dominant within the Mubwindi Swamp catchment in open forest where it can form a blanket covering. *M. solmsii* is a common ground story shrub up to 3 m tall. The stem is ribbed and ridged, with branching opposite, leaves are thin and toothed; 9 * 5 cm. When well developed, *Mimulopsis solmsii* has a 'hummock-hollow' growth pattern. Due to

the large grain size, lack of dispersal aids, and the low height of the parent taxa, the pollen is poorly dispersed (Hamilton, 1972). Thus, the parent taxa is grossly under-represented within pollen spectra.

Family: **Alangiaceae**

Alangium id.

Pollen A very distinctive pollen type. Tricolporate, clavate, a conspicuous feature are the truncated clavate elements. Colpi are very small and inconspicuous, almost absent. Semi-oblate in equatorial view. The long axis measures up to 50 µm, the short axis 35 µm. The exine is thick and clearly stratified; ectexine > endexine. Plate 2.

Potential sources There is only one species of *Alangium* present within Bwindi-Impenetrable Forest: *Alangium chinense* (Kakuru, 1993). This is a tree up to 25 m tall, shorter at lower altitudes. The trunk is straight and cylindrical with branches a right angles and a layered crown. Small buttresses are sometimes present. The grey-green bark is thin and smooth, and sometimes vertically fissured. The leaves are broadly elliptic, measuring approximately 12 * 6.5 cm. The yellow or white flowers are a conspicuous feature, they are highly fragrant. *Alangium chinense* is a wide spread species found on forest edges (Bentjee, 1994). A fast growing semi-deciduous tree common in secondary and open types of forest. Although not recorded within the Mubwindi Swamp catchment, it was growing at 2450 m near Ruhiija. The pollen is classed as poorly dispersed (Hamilton, 1972), hence, the parent taxa is under-represented within pollen spectra.

Family: **Apocynacae**

Tabernaemontana comp.

Pollen Not an easily identifiable pollen type. Trizonocolporate, psilate. The pollen grain is thin walled and easily folded, prolate in equatorial view. The long axis measures 32 µm, the short axis 24 µm. The polar area is small with indented colpi. The exine is stratified; endexine = ectexine. Columellae are present although not clear.

Potential sources There are three species of *Tabernaemontana* presently recorded within Bwindi-Impenetrable Forest; *T. pachysiphon*, *T. odoratissima* and *T. ventricosa* (Kakuru, 1993). *T. pachysiphon* was the only species present recorded within the Mubwindi Swamp catchment (Chapter 6). This is a tree up to 20 m tall, commonly between 9 and 15 m. The stem is relatively thick with thick, brown-black, vertically fissured bark. The waxy dark green leaves measure approximately 20 * 5 cm, with entire margins and a drip tip. *T. pachysiphon* is a wide spread under-story tree found between lower to mid altitudes within the Mubwindi Swamp catchment. *T. pachysiphon* can take the role of a pioneer species, particularly on forest edges (Bentjee, 1994). Results from Chapter 6 indicate the pollen is very poorly dispersed, hence the parent taxa are grossly under-represented within pollen spectra.

Family: **Aquifoliaceae**
Ilex id.

Pollen A very distinctive pollen type. Trizonocolporate, clavate, intectate. Clavate elements are very distinctive, being up to 3 μm long. The pollen grain is prolate in equatorial view, circular with open furrows in polar view. The long axis measures 30 μm, the short axis 25 μm. The exine is clearly stratified; ectexine > endexine. Plates 3 and 4.

Potential sources Only *Ilex mitis* is presently recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This is an under-story tree of dry evergreen forest and derived thicket (Bentjee, 1994). *I. mitis* is common beneath *Olea-Podocarpus* forest between 3100 and 1500 m (Hamilton, 1982). However, it was recorded rarely within the Mubwindi Swamp catchment (Chapter 6). Hamilton (1972) suggests the pollen has a low to poor dispersal capability. However, results from Chapter 6 indicate that representation within pollen spectra reflects densities of the parent taxa within surrounding vegetation.

Family: **Araliacea**

Cussonia / Scheffleri comp.

Pollen A distinctive pollen type. Trizonocolporate, tectate, reticulate. Prolate in equatorial view, slightly rhomboid, angular in polar view. The long axis measures 20 µm, the short axis 15 µm (wider at the equator). In equatorial view the pores are transversely elongated, almost appearing as a 'secondary colpi'. The exine is clearly stratified; ectexine = endexine, apart from near the pore where the endexine > ectexine. Plates 5 and 6.

Potential sources This pollen originates from a wide group of trees and shrubs and lianas. *Cussonia* spp. tend to have a paw-paw like habit while *Scheffleri* spp. have a more spreading habit. Members of the two genera occur over a wide altitudinal range, from disturbed to primary forest, from semi-evergreen bushland to upland dry evergreen forest (Tennant, 1968). Neither genera were recorded at present within the Mubwindi Swamp catchment, although they are present in Bwindi-Impenetrable Forest. The pollen has low export ability (Hamilton, 1972), consequently the parent taxa is under-represented within pollen spectra.

Polyscias comp.

Pollen A pollen type that has some similarity to *Cussonia / Scheffleri*, particularly in polar view, the bulging outline is more prominent than in *Cussonia / Scheffleri*. Trizonocolporate, psilate, microreticulate, tectate. Prolate in equatorial view. The long axis measures 18 µm, the short axis 15 µm. In polar view the grains have a triangular appearance. The exine is stratified; ectexine > endexine, stratification is clearer at the poles. Columellae are present and very clearly defined. Plates 7 and 8.

Potential sources *Polyscias fulva* is the only species of *Polyscias* presently recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This is a tree up to 25 m tall. The trunk is straight and cylindrical, ending abruptly and dividing into a number of main branches. The grey-yellow bark is thin and smooth with lentils, flaking on older trees. The cream coloured slash is soft, sometimes with orange spots, turning rapidly darker, with a resinous and colourless sap. The leaves are pinnate, up to 1 m long with 12 to 15 leaflets that measure approximately 11 * 4.5.

The yellow flowers have a cinnamon-like odour. *Polyscias fulva* is an abundant tree in secondary forest, fast growing and short lived (30 to 40 years), occasionally a large tree (25 m) in mature forest (Bentjee, 1994). The species has a wide distribution throughout central and south-west Africa (Tennant, 1968). A light requiring species, ascending to 2500 m on wetter mountains (Hamilton, 1982). Recorded within the Mubwindi Swamp catchment, although not common. Results from Chapter 6 indicate that the pollen reflects a similar percentage of the parent taxa within the surrounding vegetation.

Family: **Compositae**

Artemisia id.

Pollen Care must be taken to distinguish this pollen from that of *Stoebe*. Trizonocolporate (pores are very inconspicuous), microechinate. Depressed prolate in equatorial view, circular in polar view with intruded colpi. The long axis measure 25μm, the short axis 22μm. The exine is stratified; ectexine > endexine, particularly between the colpi. Columellae are conspicuous. Plates 9, 10 and 11.

Potential sources No species of *Artemisia* are found within Bwindi-Impenetrable Forest at present. The genus is presently restricted to altitudes higher than those within the Rukiga highlands. At present the nearest potential source of this pollen type is the higher ground of the Virunga Volcanoes. *Artemisia afra* is a thorny, close growing shrub, occasionally growing to a small tree. *Artemisia afra* is an important constituent of Ericaceous and Afroalpine vegetation, here it can tolerate drier conditions than many other taxa present (Lind and Morrison, 1974). *Artemisia afra* is a coloniser of burnt areas, this can lead to local dominance (Bentjee, 1994). A moderately well dispersed pollen type (Hamilton, 1972), hence the density of the parent taxa is accurately represented within pollen spectra.

Bidens comp.

Pollen Can be confused with other Compositae types, apart from *Carduus*, from which it can be easily distinguished due to the large size of *Carduus*. One of the characteristic features of *Bidens* are the spines, which are sometimes absent. The pollen grain is trizonocolporate, echinate with approximately 15 spines, 3 to 5 µm long, arranged equally between the colpi. Spherical, in polar view with deeply intruding colpi, 20 to 25 µm in diameter. The exine is stratified, particularly between the colpi; ectexine > endexine. Plates 12 and 13.

Potential sources The pollen is derived from a varied group of shrubs and herbs. Many of the taxa are found on forest edges and within *Erica*- dominated bush-land (Bentjee, 1994). The parent taxa can be indicative of relatively dry conditions. The taxa was not recorded within the Mubwindi Swamp at present. The pollen of *Bidens* is relatively locally dispersed (Hamilton, 1982). Therefore, if the taxa is growing close to the site of sediment accumulation the taxa can be over-represented within pollen spectra.

Dendrosenecio (Senecio) comp.

Pollen Can be separated from other Compositae pollen types by its relatively large size. The pollen grain is spherical in equatorial view, diameter 35 µm. The spines are relatively short and truncated. Circular in polar view with deeply intruding colpi. The exine is not stratified. Plate 14.

Potential sources The pollen is derived from a wide range of Giant Groundsels (*Scenico*, subgenus *Dendroscenicio*), being a conspicuous element of Afroalpine vegetation (Lind and Morrison, 1974). The taxa are not recorded within the Mubwindi Swamp catchment, or Bwindi-Impenetrable Forest at present. The taxa can be a dominant component of high altitude vegetation on the wettest mountains. The pollen is of moderate to high export ability (Hamilton, 1972). Therefore, the parent taxa can be over-represented within pollen spectra.

Stoebe id.

Pollen Care must be taken to distinguish this pollen from that of *Artemisia*. Trizonocolporate, microechinate, scabrate (sculpturing is thinner than in *Artemisia*). Pores are inconspicuous but easier to see than in *Artemisia*. Sub-spherical in polar view with intruding colpi. The long axis measures 25 µm, the short axis 22 µm. The exine is stratified; ectexine > endexine, exine up to 3 µm thick between the colpi. Columellae are present, although not as conspicuous as in *Artemisia*. Plates 15 and 16.

Potential sources The pollen is thought to have been derived from *Stoebe kilimandscharica*. This is a small, wiry shrub up to 5 m (heath-like). The foliage is very small, silvery grey-green. *Stoebe kilimandscharica* is a prominent member of the Ericaceous and Afroalpine Belts, favouring relatively dry conditions (Hamilton, 1982). Found between 2750 and 3750 m, it is a common under-story shrub of *Philippia* thicket (Hamilton, 1982). It can be a conspicuous shrub of grassland, where it sometimes forms thickets itself (Bentjee, 1994). Occasionally it grows in open places within dry upper montane forest (Hamilton, 1982). Not recorded within the Mubwindi Swamp catchment, or Bwindi-Impenetrable Forest at present. The pollen is moderately well dispersed (Hamilton, 1972). Similarly to *Artemisia*, the parent taxa is accurately represented within pollen spectra.

Crepis, *Latuca*, *Sonchus* and *Vernonia* (*Vernonia* comp.)

Pollen A very distinctive pollen of Liguliflorae type. Trizonocolporate (pores are very inconspicuous), echinate, fenestrate. The pollen grain is spherical; the size is variable with diameters ranging from 25 to 35 µm. There is much within group variation in morphology. Divisions on size, features or shape made during pollen counting were not significantly consistent to warrant sub-divisions within the final pollen data set. Plates 17, 18 and 19.

Potential sources Due to the wide range of potential sources I will concentrate on *Vernonia*. *Vernonia* is a common taxa found within secondary or disturbed forest (Bentjee, 1994). It was present within the Mubwindi Swamp catchment, being the dominant herb in moister locations. The pollen type is produced by a large number of taxa, ranging from moderate to poor export ability (Hamilton, 1972). The pollen grains are easily damaged. Consequently, the parent taxa are suggested to be under-represented within pollen spectra.

Family: **Cornaceae**

Afrocrania id.

Pollen A very distinctive pollen type. Trizonocolporate, echinate, spines approximately 1 μm long, although these can be easily damaged and missing. The pollen grain is spherical to subprolate in equatorial view, 25 μm in diameter. Sub-angular to semi-oblate in polar view with open colpi that extend the length of the grain. The exine is faintly stratified; endexine > ectexine. Plate 20.

Potential sources No species of *Afrocrania* have been recorded within Bwindi-Impenetrable Forest at present. The pollen is likely to have been derived from *Afrocrania volkensii*. This is a tree up to 25 m tall. with a straight trunk. The grey to black bark is slightly granular with vertically elongated lenticles. The leaves are pale green, measuring approximately 11 * 4 cm, the petiole is up to 0.8 cm long. If the leaf is gently pulled in two, the two parts remain attached by the extended veins (Hamilton, 1991). The flowers are small and greenish. *Afrocrania volkensii* is present within montane forest between 2400 and 3100 m, as a localised tree and within disturbed patches of bamboo (Dale, 1940). The pollen type is poorly dispersed (Hamilton, 1972). Thus, the parent taxa is thought to be under-represented within pollen spectra.

Family: **Cupressaceae**

Juniperus id.

Pollen A very distinctive pollen type. Inaperturate, tectate, micro reticulate. The long axis measures 30 μm, the short axis 18 μm. The exine is clearly stratified; endexine = ectexine, columellae are absent. Plate 21.

Potential sources No species of *Juniperus* have been recorded within Bwindi-Impenetrable Forest at present. The pollen is likely to have been derived from *Juniperus procera*. This is a tree up to 40 m tall. The trunk has low branches, and a pyramidal crown, spreading with age. The pale brown bark peels off in rectangular flakes. The leaves are very small and scale like, paired. *Juniperus procera* is present between 2000 and 2750 m in drier Montane Forest (Lind and Morrison, 1974). The pollen has a low export ability (Hamilton, 1972), consequently the parent taxa is under-represented within pollen spectra.

Family: **Cyatheaceae**

Cyathea id.

Spore A distinctive Trilete spore. Spore wall is 1.5 μm thick. The Trilete furrows are very delicate, tapering to a fine point. The long axis of the spore varies between 25 and 30 μm. Plates 6.22, 6.23.

Potential sources There are two main sources of the spore recorded within Bwindi-Impenetrable Forest; *Cyathea camerooniana* and *C. maniana* (Kakuru, 1993). Due to the dominance of *Cyathea maniana* within the Mubwindi Swamp catchment during the present-day it is thought this species the most likely source. *Cyathea maniana* is a tree fern, up to 8 m tall. The trunk is un-branched, bearing a crown of un-branched long leaves. The lower part of the petiole is very prickly. Spore are borne on the underside of the fonds. *Cyathea maniana* is common in valleys in wetter areas between 1500 and 2500 m where it can dominate the vegetation (Lind and Morrison, 1974). This species is less dominant in more open forest (Bentjee, 1994). Present within the Mubwindi Swamp catchment as fringing pockets of vegetation. The spores are poorly dispersed (Chapter 6), consequently the parent taxa is under-represented within pollen spectra.

Family: **Cyperaceae** id.

Pollen A very distinctive pollen type. Inaperturate, lozenge shape. The long axis varies from 20 to 50 μm. Although thought to originate from different parent plants, or correspond to some physiological aspect, there was no significant division on size characteristics. Thus, different pollen morphologies were not separated into distinct groups. Plates 24, 25 and 26.

Potential sources The parent taxa often forms the dominant swamp vegetation. Usually indicative of a sedge, peat-forming swamp. There are a large number of taxa within this family, some of the more common are *Cyperus denudatus*, *C. latifolium*, *Carex monostachya*, *C. papyrus*, *C. platycaulis*, *C. runssoroensis* and *Pycreus nigricans*. At present within Mubwindi Swamp, *Cyperus latifolium* tends to favour the drier, more elevated parts of Mubwindi Swamp whereas *Cyperus denudatus* favours the wetter areas. Due to the local nature of the parent vegetation Cyperaceae pollen usually dominates the pollen sum. Respective to the amount and proximity of parent taxa to the site of sediment abstraction the pollen type is not necessarily over-represented within pollen spectra.

Family: **Ericaceae** id.

Pollen A distinctive pollen type. Inaperturate, psilate, tetrad. No significant divisions were apparent between the different morphologies of pollen grains within this family.

Potential sources The pollen is produced by three main genera; *Agauria*, *Erica* and *Phillipia*. Within this family there are a wide range of growth forms, from trees to shrubs. These plants are most abundant within the Ericaceous Belt, where they dominate the vegetation (Bentjee, 1994). However, members of the family can be found down to 1000 m, where they colonise disturbed ground (Hamilton, 1982). *Erica arborea* was occasionally seen within the Mubwindi Swamp catchment. Pollen has moderate dispersal ability (Hamilton, 1972). Thus, the pollen in sediments is thought to be slightly over-representative of the parent taxa within the surrounding vegetation. If present in large contiguous quantities, the pollen type is representative of parent taxa from Ericaceous Belt vegetation (Hamilton, 1982), if not, one must look for a more individual source.

Family: **Euphorbiaceae**

Acalypha comp.

Pollen Not an easily distinguishable pollen type from other small porate grains. Care must be taken for correct identification. Usually tri or tetrazonoporate, faintly scabrate under * 1000 (appears psilate under * 400), tectate. The shape is dependent on the number of pores; circular in bizonoporate types, angular in tetrazonoporate types. Size varies from 12 to 20 µm in diameter. The exine is stratified under * 1000; ectexine = endexine. The ectexine is raised at the pores, particularly in the tetrazonoporate types although this may be a facet of the slit-like pores. Plates 27, 28 and 29.

Potential sources The pollen is derived from a wide range of annual or perennial shrubs, herbs and occasionally trees of varying habit (Hamilton, 1972). There are thirty species of *Acalypha* within East and central Africa, two of these being cultivated (Smith, 1987). The genus does not occur at high altitudes, being most common within Moist Lower Montane Forest, particularly secondary vegetation (Lind and Morrison, 1974). Very well dispersed pollen type (Hamilton, 1972) (almost to exclusion from pollen sum). Therefore, the parent taxa is likely to be over-represented within pollen spectra.

Alchornea comp.

Pollen A distinctive pollen type, particularly in polar view. However, it can be confused with a range of pollen types, particularly *Macaranga*, in equatorial view. Trizonocolporate, operculate (operculum obvious in polar view), tectate, faintly microreticulate under * 1000. The pollen grain is a depressed oblate shape in equatorial view, the diameter measures approximately 18 to 20 µm. Circular to semi-angular in polar view with intruding colpi. The exine is 2 µm thick, being thicker around the colpi, stratified under * 1000; ectexine = endexine. Plates 30 and 31.

Potential sources There are three main sources of the pollen; *Alchornea cordifolia*, *A. hirtella* and *A. floribunda*. Due to the dominance of *Alchornea hirtella* within the Mubwindi Swamp catchment during the present-day it is thought this is the most likely source. *Alchornea hirtella* is an under-story shrub, or tree up to 8 m tall with numerous branches at all heights. The light brown bark is thin, fairly smooth with a red-brown slash. The leaves are dark green and waxy, tending to be clustered at the ends of branches with an acute apex. *Alchornea hirtella* is a moisture loving taxa, common along forest edges and within clearings (Bentjee, 1994). Found as an under-story tree around disturbed areas, suggested to have a similar ecology to *Corylus* (Taylor, 1993). *Alchornea hirtella* coppices readily and can form dense thickets, as it does within the Mubwindi Swamp catchment. The pollen is moderately well dispersed (Hamilton, 1972), if the parent taxa is locally present (as it often is), it can be over-represented within pollen spectra. However the results from Chapter 6 indicate the density of the parent taxa is accurately represented within pollen spectra.

Croton id.

Pollen A distinctive pollen type that can be separated principally on size from *Dobera*, *Jatropha* and *Neoboutonia* pollen, with which it has been grouped in the past (Punt, 1962). The pollen grain is inaperturate, gemmate (gemmae in rosettes), intectate. The pollen grain is spherical, very large, up to 50 µm in diameter. Plates 32 and 33.

Potential sources There are two sources of this pollen type recorded at present within Bwindi-Impenetrable Forest: *Croton sylvaticus* and *C. macrostachyus* (Kakuru, 1993). *C. macrostachyus* is presently found within the Mubwindi Swamp catchment. This is a tree up to 25 m tall with a wavy trunk and a thin crown. The dark brown or grey bark is hard and thick, generally smooth becoming granular and fissured on old trees. The leaves measure 12 * 9 cm, the margins are entire or with very small teeth. The yellow-white flowers are sweet scented. *C. macrostachyus* is a widespread tree, common within secondary forest and on forest edges (Smith, 1987). Growing up to 2300 m, it can be found in valleys at higher altitudes (Lind and Morrison, 1974). Hamilton (1972) classed this as a very poorly dispersed pollen type, although results from Chapter 6 indicate pollen within the surface sediments provide an accurate reflection of the parent taxa within surrounding vegetation.

Drypetes comp.

Pollen A distinctive pollen type. The main features are the relatively large size and thin exine. Trizonocolporate, reticulate, sculpturing elements are heavy. The pollen grain is semi-oblate in equatorial view, circular to sub-angular in polar view. The long axis measures 33 µm, the short axis 28 µm. The exine is thin, unstratified with columellae faintly visible.

Potential sources There are three species of *Drypetes* currently recorded within Bwindi-Impenetrable Forest; *Drypetes bipindensis, D. gerrardii* and *D. ugandensis* (Kakuru, 1993). *Drypetes gerrardii* and *D. ugandensis* were recorded at present within the Mubwindi Swamp catchment, *D. gerrardii* being more common although both were recorded in similar habitats. *Drypetes gerrardii* is an under-story tree, up to 20 m tall with a dense crown, often branching from near the base. The brown bark is thin and smooth. The leaves are small, measuring approximately 6.5 * 2.5 cm, the leaf margin is almost entire, occasionally toothed. *D. gerrardii* is an abundant species in many forests, ascending to 2400 m, found on drier sites at lower altitudes (Lind and Morrison, 1974). *Drypetes gerrardii* and *D. ugandensis* were common under-story trees within the Mubwindi Swamp catchment, particularly at higher altitudes. The pollen has a very low dispersal capability (Chapter 6), consequently the parent taxa is under-represented within pollen spectra.

Macaranga id.

Pollen Not the most easily distinguishable pollen type, the main features are the colpi; in equatorial view these are thick and have an 'angular' orientation. Trizonocolporate, the pores are elongated transversely, tectate. Sub-oblate in equatorial view, subangular in polar view. The long axis measures 18 µm, the short axis 14 µm. The exine is 1 µm thick (thicker around colpi), and stratified; ectexine = endexine, columellae are present but faint. Plate 34.

Potential sources There are five species of *Macaranga* presently recorded within Bwindi-Impenetrable Forest; *M. capensis, M. kilimandscharica, M. lancifolia, M. monandra* and *M. schweinfurthii* (Kakuru, 1993). *Macaranga kilimandscharica* was recorded at present within the Mubwindi Swamp catchment in open areas. *Macaranga kilimandscharica* is an under-story tree reaching 20 m tall. The straight trunk has a thin crown, which is shinny when viewed from below. The trunk is fluted on older trees. The bark is thin and smooth, with a reddish colouring. A conspicuous feature are the spines on the trunk, which easily break off. The heart shaped leaves measure approximately 13 * 8 cm, with a long pointed tip. *Macaranga kilimandscharica* is abundant in wetter montane forests between 1400 and 2500 m, often being associated with secondary forest where it is a very quick growing gap coloniser, as is *M. lancifolia* (Smith, 1987). Hamilton (1972) classifies *Macaranga* as being a well dispersed pollen type. However, results from Chapter 6 indicate the density of parent taxa is accurately represented within pollen spectra.

Neoboutonia id.

Pollen A very distinctive pollen type, morphologically similar to *Croton* but smaller. Inaperturate, gemmate (gemmae in rosettes), intectate. The spherical pollen grain measures up to 30 μm in diameter. The sculpturing is thick and easily damaged. Plates 35, 36 and 37.

Potential sources Only *Neoboutonia macrocalyx* is presently recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This is a tree up to 15 m tall with a short stem and spreading crown. The whitish bark is very thin and smooth. The slash is off-white to pale brown, sometimes mottled. The large, often insect damaged leaves measure approximately 30 * 30 cm, with 5 to 9 main veins spreading from the base, these can be covered in hairs on the under-surface, particularly in younger trees. The whitish flowers are up to 0.5 cm in diameter. *Neoboutonia macrocalyx* is a common species of wetter montane forest between 1400 and 2500 m (Hamilton, 1982), often growing in open areas of the forest, particularly in wetter areas (Smith, 1987). *Neoboutonia macrocalyx* was commonly recorded within the Mubwindi Swamp catchment in open areas, never being present as a sub-canopy species. The pollen has a moderate to low export ability (Chapter 6), consequently the parent taxa is under-represented within pollen spectra.

Family: **Gramineae** id.

Pollen A very distinctive pollen type. Large, spherical, monoporate pollen grain up to 40 μm in diameter. Although it was not possible to distinguish between the different genera in this family there was considerable variation in the size of the pollen grains. Plates 38 and 39.

Potential sources This pollen type is produced from a wide range of grasses, from swamp grass to Montane Bamboo (*Synarundinaria alpina*). *Synarundinaria alpina* grows up to 20 m tall. Between 15 and 40 years in age, it flowers irregularly. Bamboo can cover large areas and often dominants between 2300 to 3200 m. It is thought of as a seral stage in montane forest development (Hamilton, 1982). However, as the pollen originates from a wide range of habitats, in its own right there is little ecological indication. The pollen type is generally well dispersed, consequently the parent taxa can be over-represented within pollen spectra.

Family: **Guttifferae**

Symphonia sim.

Pollen Not the most distinctive pollen type. Trizonoporate, reticulate, tectate. Sculpturing elements are relatively thin, particularly around the colpi. Prolate in equatorial view. The long axis measures 36 μm, the short axis 22 μm. The colpi are elongated, within these, the pores are clearly visible. The exine is stratified; ectexine = endexine.

Potential sources The only species of this genus present recorded within Bwindi-Impenetrable Forest is *Symphonia globulifera* (Kakuru, 1993). This is a tree up to 40 m tall with a straight trunk and a small crown. A characteristic feature are the branches, being short and at right angles to the trunk. The yellow-brown bark is thin and smooth. The leaves are simple, opposite, these measure 8 * 2 cm. The bright red flowers are waxy. *Symphonia globulifera* is a common tree up to 2500 m (Lind and Morrison, 1974). It is present near water courses, or on the margins of Swamp Forest, where it can dominate (Bamps *et al*, 1978). *Symphonia globulifera* was rarely recorded within the Mubwindi Swamp catchment. *Symphonia* is a poorly dispersed pollen type (Hamilton, 1972), this is corroborated by results from Chapter 6. Consequently, the pollen type is under-represented within pollen spectra.

Family: **Haloragaceae**

Gunnera id.

Pollen A very distinctive pollen type, particularly in polar view. Trizonocolporate, scabrate, tectate. Semi-oblate in equatorial view with long colpi, tapering towards the pore. The pollen grain is characteristic in polar view, with very indented colpi. The exine is clearly stratified; ectexine = endexine with clear columellae. Plates 40, 41 and 42.

Potential sources The pollen is thought to have been derived from *Gunnera perpensa*, this has been recorded on the Mubwindi Swamp surface at present (Katende, 1984). *Gunnera perpensa* is a semi-aquatic herb. The plant can be submerged, apart from the inflorescence. *Gunnera perpensa* grows on the edge of swamps, and in drier locations within swamps between 1560 and 3800 m (Boutique and Verdcourt, 1973). The parent taxa is possibly very responsive to changes in the hydrological budget (Hamilton, 1982). The parent taxa is thought to be over-represented within pollen spectra, particularly if it is growing near the site of sediment accumulation.

Family: **Lauraceae**

Ocotea comp.

Pollen Not the most distinctive pollen type, trizonoporate, reticulate, tectate. Oblate to semi-oblate in equatorial view with indented colpi in polar view. The long axis measures 25 μm, the short axis 20 μm. The exine is clearly stratified; ectexine = endexine.

Potential sources The only species of this genus recorded within Bwindi-Impenetrable Forest is *Ocotea kenyensis* (Kakuru, 1993). This was also recorded within the Mubwindi Swamp catchment on an island, where it grew adjacent to the swamp. *Ocotea kenyensis* is a tree up to 20 m tall with a much branched, small buttressed, crooked trunk. The greyish-brown bark is lightly fissured. The slash is very characteristic, being fibrous, pink and smelling of menthol. The leaves measure 9 * 4.5 cm, these are alternate, ovate, and whitish underneath. *Ocotea* *kenyensis* is a very slow growing tree, although it can form dominant associations, e.g. *Ocotea - Olea* forest (Bentjee, 1994). The pollen has a very low export ability (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is under-represented within pollen spectra.

Family: **Leguminosae**

Newtonia id.

Pollen A very distinctive pollen type. Trizonocolporate, reticulate. Semi-oblate in equatorial view. The long axis measures 35 μm, the short axis 30 μm. There is a small polar area with indented colpi. The pores are elongated along the colpi, these run the full length of the grain. The exine is stratified; ectexine > endexine, particularly between the colpi, columellae are clear. Plates 43 and 44.
Potential sources Only *Newtonia buchananii* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993), this was also recorded within the Mubwindi Swamp catchment. *Newtonia buchananii* is a tree up to 50 m tall. The trunk is stout and buttressed. The crown is dense and widely spread. The thin, light grey bark has lenticles with a characteristic red latex. *Newtonia buchananii* is a characteristic tree of mature Moist Lower Montane Forest, found up to 2200 m, usually being recorded as isolated specimens (Lind and Morrison, 1974). The species is usually found by streams, ground water or within riverine forest (Brenan, 1959). The pollen is poorly dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxon is grossly under-represented within pollen spectra.

Family: **Loganiaceae**

Anthocleista id.

Pollen A very distinctive pollen type. Trizonoporate, microreticulate, spherical with diameter ranging from 30 to 35 μm. The exine is approximately 2 μm thick, stratified; ectexine < endexine. A very characteristic feature are the large concentric, annulate pores (granulate); these measure approximately 4 µm in diameter. Plates 45 and 46.

Potential sources *Anthocleista zambesiaca* and *A. schweinfurthii* have been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). *Anthocleista zambesiaca* was recorded as isolated specimens within the Mubwindi Swamp catchment. *Anthocleista zambesiaca* is a tree up to 25 m tall with a straight and cylindrical trunk, with few branches. The thin and spreading crown has very large leaves. The greenish to brown bark is thin, fairly smooth, with small vertical fissures approximately 2 cm apart. The leaves measure approximately 45 * 25 cm, these are spongy and resemble a cabbage leaf. *Anthocleista* spp. are frequently found around swamps, forest edges, valley forests and within damp secondary forest (Lind and Morrison, 1974). The species is particularly present where the surrounding forest has been destroyed (Bruce and Lewis, 1960). The pollen type is moderately well dispersed (Hamilton, 1972), this is confirmed by the results from Chapter 6. Consequently, the parent taxa can be over-represented within pollen spectra.

Nuxia id.

Pollen A very distinctive pollen type. Trizonocolporate, psilate, tectate. Semi-oblate in equatorial view. The long axis measures 12 µm, the short axis 9 µm. The pollen grain is circular in polar view with intruding colpi; these are relatively thick and taper towards the poles. The exine is thin and stratified; ectexine = endexine. Plates 50, 51 and 52.

Potential sources *Nuxia congesta* and *N. floribunda* have been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). Neither species were recorded within the Mubwindi Swamp catchment, but are common in other parts of Bwindi-Impenetrable Forest, *Nuxia congesta* is the most abundant of these. *Nuxia congesta* is a tree up to 15 m tall with an irregular trunk that has thick, rough, gnarled bark. The leaves are usually borne in whorls of three, these measure approximately 9 * 4 cm and are glabrous. The fragrant, white flowers are compact and borne in great profusion. *Nuxia congesta* is found between 1500 and 2800 m. *Nuxia floribunda* is common up to approximately 2000 m (Bruce and Lewis, 1960). *Nuxia congesta* is a mountain forest species, it is particularly found in secondary forest and derived woodland where it can form a significant component of the vegetation (Bentjee, 1994). The pollen is classified as being well dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is over-represented within pollen spectra.

Family: **Moraceae**

Ficus id.

Pollen An easily distinguishable pollen from other porate types, but care must be taken within the Moraceae. Bizonoporate, faintly scabrate under * 1000 (psilate under * 400). The pores are slightly operculate and located at the poles. Sub-oblate in equatorial view, tapering towards the poles. The long axis measures 15 µm, the short axis 11 µm. The exine is thin and not stratified. Plates 53 and 54.

Potential sources Ten species of *Ficus* have been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). Although no Ficus species were recorded by the vegetation survey (Chapter 6), *Ficus* spp. were noted, primarily as lianas. The genus has many species with Fig trees being common in a range of habitats. Growth form varies widely within the genus from parasitic vines to free standing trees. *Ficus* spp. can increase soil moisture in their immediate vicinity; often forming associations with hygrophylous plants (Lind and Morrison, 1974). The highly specialised pollination procedure common to this genus would preclude, except under abnormal circumstances, the incorporation of *Ficus* pollen into pollen spectra (Hamilton, 1982).

Musanga comp.

Pollen An easily distinguished pollen type from other members of Moraceae, apart from *Myrianthus*. The pollen grain is bizonoporate, psilate. The slightly operculate pores are found at the equator. The pollen grain is sub-oblate in equatorial view. The long axis measures 16 µm, the short axis 9 µm. The exine is thin and not stratified. Plates 55 and 56.

Potential sources Two species of *Musanga* have been recorded within the Bwindi Forest; *Musanaga cecropioides* and *M. leo-errerae* (Kakuru, 1993). *Musanaga* *cecropioides* is the most common species. This is a tree up to 30 m tall with a straight trunk, bearing a spreading, umbrella shaped crown. The grey to brown bark is very thin with ring marks and corky outgrowths. The slash is pink and fleshy. Leaves are palmately compound, with 11 to 25 segments. *Musanaga cecropioides* is a common tree in secondary or swamp forest (Lind and Morrison, 1974). A light requiring species, it is sometimes locally dominant (Bentjee, 1994). Similarly to *Ficus*, due to specialised insect pollination, the parent taxa are under-represented within pollen spectra.

Myrianthus comp.

Pollen Very difficult to distinguish the pollen from *Musanga*. Pollen type is bizonoporate, with the pores at the equator. Sub-oblate in equatorial view. The long axis measures 16 µm, the short axis 14 µm (slightly larger than *Musanga*). The exine is thin and not stratified. Plates 57 and 58.
Potential sources There are two species of *Myrianthus* present within Bwindi-Impenetrable Forest; *Myrianthus arboeus* and *M. holstii* (Kakuru, 1993). *M. holstii* was rarely recorded within the Mubwindi Swamp catchment. This species is an under-story tree up to 20 m tall. The brown bark is smooth with a pink slash, turning red. *Myrianthus holstii* is found above 1300 m as an under-story tree (Lind and Morrison, 1974). The pollen has a low export ability (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxon is under-represented within pollen spectra.

Family: **Myricaceae**

Myrica id.

Pollen A very distinctive pollen type. Trizonoporate, occasionally tetrazonoporate, scabrate. Sub-oblate to oblate in equatorial view; sub-triangular in polar view, up to 35 µm in diameter. The pores lack operculum and are elongated towards the poles. The ectexine protrudes around the pore, this is stratified; ectexine = endexine. Plates 59 and 60.

Potential sources Two species of *Myrica* have been recorded within Bwindi-Impenetrable Forest; *Myrica kanditiana* and *M. salicifolia* (Kakuru, 1993). Only *Myrica kanditana* was present within the Mubwindi Swamp catchment. Locally common on the swamp surface, *Myrica kanditana* is a bushy tree up to 5 m tall with a dense crown. The trunk is crooked and slightly oblate. The brown bark is roughly fissured. The greenish-yellow flowers are small and compact. *Myrica salicifolia* is a characteristic tree of swamp habit, recorded up to 2260 m (Taylor, 1990). The pollen is moderately well dispersed (Hamilton, 1972), this is supported by the results from Chapter 6. As the parent taxon inhabits swamps, pollen from such a local source can be over-represented within pollen spectra.

Family: **Myrsinaceae**

Rapanea id.

Pollen A very distinctive pollen type. Trizonocolporate, occasionally tetrazonocolporate. Subprolate in equatorial view. The long axis measures 17 µm, the short axis 15 µm. Circular in polar view with intruding colpi. A distinguishing feature are the colpi which are truncated. The rounded pores within these are very difficult to see. The exine is 2µm thick and stratified; ectexine = endexine. Plates 61 and 62.

Potential sources Previously six species within this genus have been recorded although these are now thought to be variants of *Rapanea melanophloeos* (Bentjee, 1994). *Rapanea melanophloeos* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This was only rarely recorded within the Mubwindi Swamp catchment. *Rapanea melanophloeos* is a tree up to 20 m tall with a cylindrical trunk. The whitish bark has small fissures, the pink slash has brown lines. The obviate leaves are rhododendron-like, clustered at the end of the branches, measuring approximately 12 * 5 cm. The mid-rib is red with numerous translucent streaks. *Rapanea melanophloeos* has a wide ecological range; it can dominate in high montane forest; also it is present at lower altitudes in swamp forest (Lind and Morrison, 1974). The pollen is a moderately well dispersed type (Hamilton, 1972). Results from Chapter 6 indicate that the parent taxa is accurately represented within pollen spectra.

Family: **Myrtaceae**

Syzygium id.

Pollen A very distinctive pollen type. Trizonocolporate, can be tetrazonocolporate, tectate, psilate. Subprolate in equatorial view, subangular in polar view depending on the number of colpi. Colpi in the trizonocolporate type form a tri-radiate mark. The exine is approximately 1 µm thick and clearly stratified; ectexine = endexine. Plates 63 and 64.

Potential sources Two species of *Syzygium* are recorded within Bwindi-Impenetrable Forest; *Syzygium cordatum* and *S. guinense* (Kakuru, 1993). *Syzygium cordatum* is common within the Mubwindi Swamp catchment, where it fringes the swamp. This a tree up to 30 m tall with an irregular trunk. The dark brown, thin bark is vertically fissured with a pink to red slash. The leaves are opposite, these measure 5 * 3 cm, are gland-dotted and fragrant when crushed. The white flowers are fragrant. *Syzygium cordatum* is found in wetter areas up to approximately 2300 m (Lind and Morrison, 1974). The pollen is likely to originate from *Syzygium cordatum* or *S. guinense*. However, recently within the Rukiga highlands there has been widespread planting of *Eucalyptus* spp. for fuel, and as an aid for swamp drainage. Therefore, pollen in the most recent sediments may be derived from this exotic taxa, care is needed to differentiate between the two forms of Myrtaceae. The pollen is moderately well dispersed (Hamilton, 1972). The results from Chapter 7 indicate the density of the parent taxa is accurately reflected within pollen spectra.

Family: **Olacaceae**

Strombosia comp.

Pollen It is difficult to separate the pollen from other members of the Olacaceae (Hamilton, 1972). Trizonoporate, reticulate, the sculpturing elements are very faint. The colpi are truncated and do not run the full length of the pollen grain. the pollen grain is sub-oblate, the long axis measures 25 µm, the short axis 20 µm. The exine is stratified; ectexine = endexine.

Potential sources Two species of *Strombosia* are recorded within Bwindi-Impenetrable Forest; *Strombosia scheffleri* and *S. tetranda* (Kakuru, 1993). *Strombosia scheffleri* is presently found as a locally occurring sub-canopy tree within the Mubwindi Swamp catchment. *Strombosia scheffleri* is a tree up to 30 m tall with a sometimes fluted straight trunk, , branches are high up on the trunk which ends in a short, condensed crown. The yellow-green bark is thin and smooth, flaking off in small pieces, this gives the trunk a mottled appearance. The leaves are large, measuring 23 * 9 cm, and are deeply channelled. The flowers are small and white. The tree ascends down to 2500 m (Lind and Morrison, 1974). The pollen is poorly dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is grossly under-represented within pollen spectra.

Family: **Oleaceae**

Olea id.

Pollen A very distinctive pollen type. Trizonocolpate, occasionally tatrazonocolpate, reticulate, the reticulum is dense and heavy, tectate. The pollen grain is oblate in equatorial view, circular in polar view with intruding colpi, these run the full length of the pollen grain. The long axis measures 20 µm, the short axis 16 µm. The exine is 2 µm thick, stratified; ectexine = endexine, columellae are clear. The separation of *Olea europa* spp. *capensis* (formally *O. africana*) and *O. capensis* ssp. was possible on the width of the reticulum. However, the resultant groupings were not found to be significant. Consequently, the pollen type is portrayed as a single *Olea* group. It was not possible to separate out the sub-species of *O. capensis*. Plates 65, 66 and 67.

Potential sources Two sub-species of *Olea capensis* spp. have been recorded within Bwindi-Impenetrable Forest: *Olea capensis* spp. *hochstetteri* and *O. capensis* spp. *welwitschii* (Kakuru, 1993). Both sub-species of *Olea* were recorded within the Mubwindi Swamp catchment, although they were not common, and the specimens were relatively young. The former sub-species is a large tree up to 45 m tall, with straight or wavy cylindrical trunk, bearing large ascending branches, and a large but fairly open crown. Large buttresses are usually present. The brown bark is thick and rough with deep vertical fissures. The leaves are long and thin, these measure approximately 13 * 4 cm. *O. capensis* spp. *welwitschii* is a smaller tree, up to 25 m tall. The cylindrical trunk bears a dense crown, buttresses are usually absent. The grey to whitish bark is smooth, becoming slightly vertically fissured on older trees. The slash is off-white with brown or orange markings, granular. Both sub-species can be the principle canopy former (Hamilton, 1982). *Olea* species are generally found between 1500 and 2500 m (2900 m on drier mountains) (Lind and Morrison, 1974). The genus prefers dry sites, or the drier northern and eastern slopes where it can become dominant (Bentjee, 1994). *O. europea* spp. *capensis* can be abundant between 2000 and 3000 m in dry forest, although it is now absent from Kigezi. The pollen type is well dispersed (Hamilton, 1972). Similarly, the results from Chapter 6 indicate the parent taxa is significantly over-represented within pollen spectra.

Family: **Podocarpaceae**

Podocarpus id.

Pollen A very distinctive pollen type. Saccate. There is considerable morphological variation within the group, particularly on the size of the pollen grain, and the angle that the saccus join the saddle. Differentiation of these different morphologies was not significant and are hence grouped together. The long axis of the pollen grain measures between 35 and 60 μm. Plates 68, 69 and 70.

Potential sources Two species of *Podocarpus* have been recorded within Bwindi-Impenetrable Forest; *Podocarpus flacatus* and *P. latifolius* (Kakuru, 1993). Both species of *Podocarpus* were recorded within the Mubwindi Swamp catchment, although they were not common, and the specimens were relatively young. *Podocarpus latifolius* is a tree up to 30 m tall with a straight trunk and small crown. In more open situations the trunk is branched lower down and has a spreading crown. The canopy has a blue tinge when viewed from below. The brown bark is fairly thin, rough and fibrous, peeling off in narrow strips, with a pink slash. The leaves are finger-like, these measure 9 * 1 cm. The seeds are blue-green, two forming on a fleshy red receptacle. *Podocarpus flacatus* is a tree up to 35 m tall. The trunk has a wide diameter and branches lower down than *P. latifolius*. The brown bark is fissured, with a pink slash. Mature leaves measure 5 * 0.3 cm. The blue-green fruit is single, without the red receptacle. Both species are found between 2000 and 3000 m (Lind and Morrison, 1974). *Podocarpus flacatus* is generally present in drier forest than *P. latifolius* (Hamilton, 1982). The pollen is very well dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is grossly over-represented within pollen spectra.

Family: **Polygonaceae**

Rumex id.

Pollen A very distinctive pollen type. Trizonocolporate, micro-reticulate under * 1000, tectate. The pollen grain is spherical; the diameter measures approximately 20 µm. The colpi are entire, in polar view these intrude over the whole grain, appearing as small notches (a very distinctive feature). The exine is approximately 1 µm thick, stratified under * 1000; ectexine = endexine. Columellae are present but not obvious. Plates 71 and 72.

Potential sources The pollen is derived from a wide range of fleshy herbs and small shrubs. Plants of this genus are common on disturbed or open ground (Bentjee, 1994). Due to this ruderal habitat the parent taxa are often associated with agricultural land. The pollen is of moderate export ability (Hamilton, 1972), consequently the parent taxa can be slightly over-represented within pollen spectra.

Family: **Proteaceae**

Faurea comp.

Pollen An easily distinguishable pollen type. Trizonoporate, micro-reticulate under * 1000, tectate. A triangular shaped pollen grain with convex walls in polar view. The long axis measures 25 µm, the short axis 15 µm. The exine is approximately 1.5 µm thick, but thinner and more constricted towards the pore, the pores are elliptical. The exine is stratified under * 1000; ectexine = endexine. Plates 73, 74 and 75.

Potential sources Only *Faurea saligna* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This is a tree up to 20 m tall. The trunk is usually straight with thick and rough, dark brown to almost black bark. The pink slash is fibrous. The leaves are thick and leathery with red veins, long and narrow (Willow-like), these measure approximately 12 * 2.25 cm,. The white flowers form on inflorescence, these occur in spikes. *Faurea saligna* can form pure stands on ridge tops (Hamilton, 1982). *Faurea saligna* is found between 1200 and 3200 m, although not being common in the lower part of this range (Lind and Morrison, 1974). *Faurea saligna* is fire tolerant (Jon Lovett, pers. comm.), this possibly accounts for local dominance. Favoured as a location for bee hives, and used for charcoal production (Rob Wild, pers. comm.). Not recorded within the Mubwindi Swamp catchment (Chapter 6) although noted to dominate the vegetation at higher altitudes. The pollen can be separated from *Allophyllous* pollen, but this division was not significant, thus pollen were grouped to form *Faurea* comp. According to Hamilton (1972) *Faurea* is a poorly dispersed pollen type, although analysis from Chapter 6 indicate the pollen is more moderately well dispersed. Thus, the parent taxa are thought to be over-represented within pollen spectra.

Family: **Rhizophoraceae**

Cassipourea sim.

Pollen Not an easily distinguishable pollen type. Trizonocolporate, reticulate, width of lumen 1 µm. Oblate in equatorial view, tapering towards the poles. The long axis measures 35 µm, the short axis 28 µm. The colpi run the full length of the grain, curving in towards the pore, the pores are very distinct. The exine is stratified; ectexine = endexine. Plate 76.

Potential sources Three species of *Cassipourea* have been recorded within Bwindi-Impenetrable Forest; *C. congoensis*, *C. gummiflua* and *C. ruwensorensis* (Kakuru, 1993). *Cassipourea ruwensorensis* was the dominant of these within the

Mubwindi Swamp catchment, often being the dominant under-story tree. This is a tree up to 20 m tall with a straight trunk, branching at right angles. The brown bark is very thin and smooth, with ring marks. The leaves measure approximately 15 * 5.5 cm, with yellow hairs on the underside. The green flowers with orange centres are fragrant. *Cassipourea ruwensorensis* is a wide spread species found up to 2400 m (Lind and Morrison, 1974). The pollen is very poorly dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa are grossly under-represented within pollen spectra.

Family: **Rosaceae**

Alchemilla id.

Pollen A very distinctive pollen type. Trizonocolpate, psilate, tectate. Prolate in equatorial view with rounded ends. The long axis measures 20 μm, the short axis 12 μm. Circular to angular in polar view with intruded colpi. The exine is approximately 2 μm thick and stratified; ectexine = endexine, columellae are clear. Plates 77 and 78.

Potential sources *Alchemilla* is a widely distributed genus of herbs characterised by a *Geranium*-type leave (Katende, 1984). *Alchemilla* is often found in association with swamp vegetation, where it can be locally dominant. Shrubby species of *Alchemilla* are also common within Afroalpine vegetation (Hedberg, 1951). The pollen is poorly dispersed (Hamilton, 1972). Consequently, the parent taxa can be under-represented within pollen spectra.

Cliffortia id.

Pollen An easily identifiable pollen type. Trizonoporate, rugulate, tectate. Sub-oblate to circular in equatorial view. The long axis measures 25 μm, the short axis 20 μm. Circular in polar view where the pores are distinctive; annulate and operculate. The exine measures 1.5 μm thick, increasing to 3 μm at the pores, it is stratified; ectexine = endexine. Plates 79 and 80.

Potential sources No species of *Cliffortia* have been recorded within Bwindi-Impenetrable Forest. The pollen is thought to be derived from *Cliffortia nintidula*; this is much branched tree, 4 to 5 m tall, becoming larger at lower altitudes. It is a conspicuous element of Ericaceous Belt vegetation, where it can be locally dominant (White, 1983). Depending on the local conditions, it can extend down to Upper Montane Forest (Hamilton, 1982). At lower altitudes it has been recorded within Bamboo thicket and along river banks (Graham, 1960). The pollen has poor to moderate export ability (Hamilton, 1972), consequently the parent taxa are slightly under-represented within pollen spectra.

Hagenia id.

Pollen A very distinctive pollen type. Trizonocolporate, faintly rugulate under * 1000, tectate. Oblate in equatorial view. The long axis measures 26 μm, the short axis 22 μm. Pores are operculate, widely transverse, and appear to bulge. The exine is 1.5 μm thick, increasing to 4 μm at the pore. The exine is stratified; ectexine > endexine. Plates 81 and 82.

Potential sources Only *Hagenia abyssinica* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993), although this was not recorded within the Mubwindi Swamp catchment. *Hagenia abyssinica* is a tree up to 20 m tall with a crooked, often gnarled trunk, branching in whorls with a spreading crown. The red-brown bark is rough, flaking raggedly. The branchlets are covered with yellow hairs. The leaves are imparipinnate, with 11 to 13 leaflets, these measure approximately 9 * 3 cm, with numerous teeth. The inflorescence are very large, pendulous, reddish. *Hagenia abyssinica* is a common member of the Upper Moist Montane Forest, up to 3300 m, although it has been recorded down to 1800 m on the western slopes of Mount Elgon (Dale, 1940). It is a gregarious species, often forming pure stands, usually around 3200 m, where low night temperatures exclude many other trees and competition is low (Hamilton, 1982). *Hagenia abyssinica* can extend into the Ericaceous Belt as dwarf specimens in sheltered places, or amongst *Erica* and *Stoebe* spp., possibly aided by a dense covering of epiphytes (Coe, 1967). *Hagenia abyssinica* can grow as a colonising tree in disturbed areas at lower altitudes (Hamilton, 1982). The pollen is moderately well dispersed (Hamilton, 1972), this is corroborated from the results of Chapter 6. Consequently, the parent taxa can be over-represented within pollen spectra.

Prunus comp.

Pollen Care is needed for correct identification of this pollen type; it can be confused with *Rubus* type. Trizonocolporate, psilate under * 400, faintly striate under * 1000. The pollen grain is small, oblate in equatorial view. The long axis measures 20 µm, the short axis 15 µm (although considerable size variation within the genus). The pollen grain is very distinctive in polar view where the colpi are deeply intruded, with only a small polar area. The exine is 1 to 1.5 µm thick and stratified; ectexine = endexine. Plates 83 and 84.
Potential sources Only *Prunus africana* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993), this was also recorded within the Mubwindi Swamp catchment. *Prunus africana* is a tree up to 35 m tall. The trunk is usually straight, bearing a few large branches and spreading crown. The dark brown to black bark is thick and rough, flaking in pieces. The slash is very characteristic; pink, turning darker, smelling of almonds. The leaves measure 15 * 5 cm and are hairy. *Prunus africana* is a widely distributed tree ascending to 3200 m (Coe, 1967). At lower altitudinal limits (1500 m) it is found on forest edges, often in remnants of riverine forest (Bentjee, 1994). Within the mid altitudinal range *Prunus africana* is found within mature forests where it can dominate (Hamilton, 1982). The pollen is moderately well dispersed (Hamilton, 1972), this is corroborated by results from Chapter 7. Consequently, the parent taxa is thought to be representatively recorded within pollen spectra.

Family: **Rubiaceae**

Anthospermum id.

Pollen A very distinctive pollen type. Trizonocolporate, scabrate (under * 1000), tectate. Oblate in equatorial view, the diameter measures approximately 25 µm. The pollen grain is circular in polar view with wide open furrows. The pores are distinctly elongated, transversely widened within the short colpi. The exine is stratified; ectexine = endexine, columellae are obvious. Plates 85 and 86.

Potential sources *Anthospermum* is a genus of 40 species, mostly these are shrubs although it can be represented as a ruderal species (*Anthospermum herbaceum*). *Anthospermum usambarense* is the most common species of the genus in east and central Africa. It is a prominent member of the Ericaceous Belt, particularly within exposed upland grasslands where it can be locally dominant (Verdcourt, 1976). The pollen type is moderately well dispersed (Hamilton, 1972). Consequently, the parent taxa is thought to be accurately represented within pollen spectra.

Psychotria sim.

Pollen Not an easily distinguishable pollen type. Trizonocolporate, reticulate (reticulum is very faint), tectate. Oblate in equatorial view with rounded poles. The long axis measures 20 μm, the short axis 16 μm. The pores are difficult to see. The exine is stratified; ectexine = endexine, columellae are present but faint.

Potential sources A very large genus, 200 species have been recorded within tropical Africa (Verdcourt, 1976). Only *Psychotria megistosticta* has been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993). This was recorded within the Mubwindi Swamp catchment as isolated specimens. *Psychotria megistosticta* is an under-story tree up to 15 m tall. The trunk is irregular with moderately rough bark, tending to split into squares. The leaves measure approximately 13 * 6 cm, sometimes with tufts of hairs on the underside. The midrib and veins on the underside are reddish in colour. *Psychotria megistosticta* is common as an under-story tree in Kigezi between 1900 m and 2600 m (Lind and Morrison, 1974). The pollen is very poorly dispersed (Hamilton, 1972), this is supported by the results from Chapter 6. Consequently, the parent taxa is under-represented within pollen spectra.

Family: **Rutaceae**

Zanthoxylum id.

Pollen A distinctive pollen type. Trizonocolporate, reticulate, irregular lumen, tectate. Subprolate to oblate in equatorial view, circular to semi-angular in polar view with open colpi and a small polar area. The long axis measures 20 µm, the short axis 16 µm. The exine is 1 to 1.5 µm thick, stratified; ectexine = endexine with obvious columellae. Plates 87 and 88.

Potential sources. Four species of *Zanthoxylum* have been recorded within Bwindi-Impenetrable Forest (Kakuru, 1993); *Z. gilleti*, *Z. leprieurii*, *Z. mildbraedii* and *Z. rubescens*, *Z. gilleti* being the most common. This was recorded within the Mubwindi Swamp catchment as isolated specimens. *Zanthoxylum gilleti* is a large tree up to 35 m tall. The thick trunk is armed with conical woody bosses, the branches are easily rotted. The crown is deciduous and well spread. The brown bark is thin and smooth, with small vertical fissures. The leaves are imparipinnate, these measure 25 to 100 cm long with 5 to 27 alternate leaflets, these are strongly aromatic when crushed. The red fruits have black seeds. The flowers are creamy white. *Zanthoxylum gilleti* is a common component of Lower Moist Montane Forest, where sometimes it is part of the intervening stage between colonising and climax forest (Hamilton, 1982). The pollen is moderately well dispersed (Hamilton, 1972), this is supported by the results from Chapter 6. The concentration within pollen spectra is thought to be an accurate reflection of the parent taxa within surrounding vegetation.

Teclea sim.

Pollen Not the most distinguishable pollen type. Trizoncolporate, striate, tectate. Prolate in equatorial view, semi-angular in polar view with intruding colpi. The long axis measures 20 µm, the short axis 14 µm. The exine is 1.5 µm thick, stratified; ectexine = endexine, columellae are clear.

Potential sources Two species of *Teclea* have been recorded within Bwindi-Impenetrable Forest: *Teclea grandifolia* and *T. noblis* (Kakuru, 1993). *Teclea noblis* was present within the Mubwindi Swamp catchment, although always as young specimens. This is an under-story tree up to 20 m tall. The trunk is crooked, often branched near the base. The light grey bark is thin, smooth, with a off-white slash having a green tinge. The leaves are dark green, usually trifoliate, these measure 14 * 4 cm. *Teclea noblis* is an under-story tree found in Dry Lower

Montane Forest up to 2500 m (Lind and Morrison, 1974). The pollen is of low export ability (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa are under-represented within pollen spectra.

Family: **Sapindaceae**

Allophylus comp.

Pollen An easily identifiable pollen type. Principally on shape it is possible to separate from *Faurea* and *Protea* pollen. Trizonoporate, microreticulate under * 1000, tectate. The pollen grain is triangular with concave walls, angular in polar view with elliptical pores. The long axis measures 25 µm, the short axis 15 µm. The exine measures 1.5 µm thick but thinner and more constricted towards the pores; stratified under * 1000; ectexine = endexine. Plate 89.

Potential sources Two species of *Allophylus* have been recorded within Bwindi-Impenetrable Forest: *Allophylus abyssinicus* and *A. ferrugineus* (Kakuru, 1993). Neither were present within the Mubwindi Swamp catchment. The trees of this genus are found in Lower Moist Montane Forest between 1400 to 2500 m (Lind and Morrison, 1974). *Allophylus ferrugineus* can be abundant in raised swamp forest from 2000 to 2500 m (Bentjee, 1994). The pollen has a low export ability (Hamilton, 1972), consequently the parent taxa is thought to be under-represented within pollen spectra.

Dodonaea id.

Pollen A very distinctive pollen type. Trizoncolporate, psilate, tectate. Subprolate in equatorial view. The long axis measures 25 µm, the short axis 22 µm. Circular in polar view, diameter 16 µm. Pores bulge at the apertures, being rectangular and annulate. The exine is approximately 2 µm thick, stratified; ectexine < endexine, ectexine is thicker towards the pores. Plates 90 and 91.

Potential sources The pollen is thought to be derived from *Dodonaea viscosa*. This is a shrub or small tree, up to 5 m tall. *Dodonaea viscosa* is a key component of montane scrub in disturbed areas; used as an indicator of disturbance (Hamilton, 1972). The plant is fire tolerant and reproduces very quickly following fire induced disturbance (Lind and Morrison, 1974). A moderately well dispersed pollen type (Hamilton, 1972), consequently parent taxa are thought to be representatively recorded within pollen spectra.

Family: **Sapotaceae**

Chrysophyllum sim.

Pollen Not an easily identifiable pollen type. Tetrazonoporate, psilate. Prolate in equatorial view. The long axis measures 35 µm, the short axis 20 µm. Pores are inconspicuous. The exine is thin (1.5 µm), appearing stratified, although not clearly. Columellae faintly present.

Potential sources Two species of *Chrysophyllum* have been recorded within Bwindi-Impenetrable Forest: *Chrysophyllum albidum* and *C. gorungosanum* (Kakuru, 1993). Both species were present within the Mubwindi Swamp catchment, with *C. albidum*, being dominant. *Chrysophyllum albidum* is a tree up to 40 m tall. The long, straight trunk is fluted for much of the length with buttresses sometimes present. The light brown bark is thin with vertical fissures. The slash is fibrous, red-brown with white streaks, exuding white latex. There is a dense, small spreading crown. Leaves are 16 * 5 cm, the lower surface have red to silvery-brown hairs. *Chrysophyllum albidum* is a widespread lower altitudinal species, forming the dominant canopy type in absence of larger emergent trees (Lind and Morrison, 1974). The two species were found to take this role within the Mubwindi Swamp catchment, where they dominated at the highest altitudes. Pollen has a poor dispersal ability (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is grossly under-represented within pollen spectra.

Family: **Sterculiaceae**

Dombeya id.

Pollen A very distinctive pollen type, although it can be easily damaged. Trizonoporate, echinate, spines are large and conical in shape, these measure up to

5 µm long and 4 µm wide across at the base, tectate. Spherical grain, diameter approximately 40 to 50 µm. Pores are circular and annulate. The exine is stratified; ectexine = endexine with clear columellae. Plates 92 and 93.

Potential sources Two species of *Dombeya* have been recorded within Bwindi-Impenetrable Forest; *Dombeya torrida* and *D. kirkii* (Kakuru, 1993). Both species were present within the Mubwindi Swamp catchment, *Dombeya torrida* being the dominant. This is a tree up to 20 m tall. The trunk is crooked, sometimes fluted, bearing an open spreading crown. The brown bark is thick and rough, deeply vertically fissured, sometimes flaking. The leaves measure approximately 12 * 9 cm, although these are variable in shape, the margin is toothed or crenate with a long petiole, (approximately 4 cm long). The flowers are white. *Dombeya* is a widespread genus with an altitudinal range between 1800 and 3200 m (Lind and Morrison, 1974). *Dombeya* is found within secondary forest, open forest and on upper slopes of Moist Lower Montane Forest, sometimes present within stands of *Synarundinaria alpina* (Hamilton, 1982). Also recorded as a coloniser of bare ground (Bentjee, 1994). A very poorly dispersed pollen type (Hamilton, 1972), although results from Chapter 6 indicate the dispersal capability is more modest. Consequently, the parent taxa is thought to be representatively recorded within pollen spectra.

Family: **Theaceae**

Ficalhoa comp.

Pollen The appearance is similar to *Nuxia* pollen. The pollen grain is trizonocolporate, smooth, tectate. Prolate in equatorial view with tapered ends. The long axis measures 14 µm, the short axis 8 µm. Circular in polar view with open furrows. The exine is stratified; ectexine = endexine.

Potential sources Only one species of *Ficalhoa* has been recorded within Bwindi-Impenetrable Forest; *Ficalhoa laurifolia* (Kakuru, 1993), although this was not recorded within the Mubwindi Swamp catchment. *Ficalhoa laurifolia* is a tree up to 25 m tall with a straight trunk and cylindrical branches at right angles to the trunk, smaller branches drooping. Branchlets are covered with long yellow hairs. The leaves measure 8 * 2.5 cm with numerous small teeth along the margins.

Ficalhoa laurifolia is a widely dispersed tree common in Moist Lower Montane Forest between 2000 and 3500 m, often near ridges, it can occur within Ericaceous Belt vegetation (Lind and Morrison, 1974). The pollen is moderately well dispersed (Hamilton, 1972). Consequently, the parent taxa are thought to be accurately represented within pollen spectra.

Family: **Ulmaceae**

Celtis id.

Pollen A very distinctive pollen type, although *Chaetacme* and *Hymenocardia* also produce a similar pollen (Hamilton, 1972). Trizonoporate, scabrate, tectate. Spherical in equatorial view, circular in polar view, the diameter measures approximately 20 to 25 µm. Pores are round to elliptical, slightly annulate, operculate. The exine is measures 1 to 1.5 µm thick, stratified; ectexine = endexine, tectum is deep, columellae are visible under * 1000. Plates 94 and 95.
Potential sources Three species of *Celtis* have been recorded within Bwindi-Impenetrable Forest; *C. africana*, *C. gomphophylla* and *C. zenkeri* (Kakuru, 1993). However, no species were recorded within the Mubwindi Swamp catchment. *Celtis africana* is the most common species of the genus. It is a deciduous tree up to 30 m tall. The straight trunk is unbuttressed with a much branched spreading crown. The light brown or whitish bark is very thin and smooth. The leaves measure 5 * 2.25 cm with two-three main lateral veins on each side. The most likely source of pollen is *Celtis africana*, this is a widely distributed tree, occurring in various habitats (Lind and Morrison, 1974), usually found in colonising forest or on relatively dry sites, where it can be locally dominant (Bentjee, 1994). The pollen type is well dispersed (Hamilton, 1972), this is corroborated by the results from Chapter 6. Consequently, the parent taxa is over-represented within pollen spectra.

Trema comp.

Pollen Care must be taken to distinguish from other Moraceae pollen types. The pollen grain is bizonoporate, scabrate under * 1000, tectate. Spherical to subprolate in equatorial view. The long axis measures 20 μm, the short axis 16 μm. Pores are annulate, slightly operculate and protruding. The exine is approximately 1 μm thick and stratified; ectexine = endexine. Plate 96.

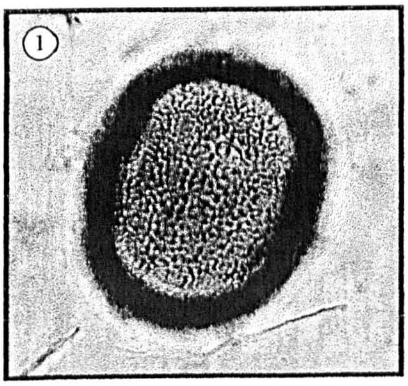
Potential sources Only one species of *Trema* has been recorded within Bwindi-Impenetrable Forest: *Trema orientalis* (Kakuru, 1993). *Trema orientalis* was only rarely recorded within the Mubwindi Swamp catchment as an under-story tree up to 15 m tall. The straight trunk, branches at right angles to the trunk. The light brown bark is thin and smooth. Leaves measure 11 * 4 cm, and have hair on the underside and toothed margins. *Trema orientalis* is common as an under-story tree in colonising forest (Lind and Morrison, 1974). *Trema orientalis* is often a pioneer in clearings and riverine forest (Polhill, 1966). The pollen is moderately well dispersed (Hamilton, 1972), consequently the parent taxa is thought to be representatively recorded within pollen spectra.

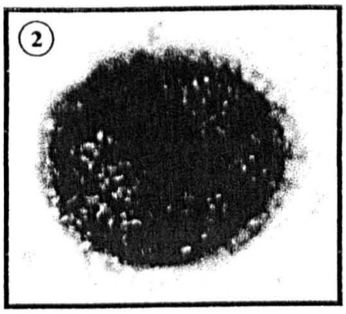
Family: **Urticaceae** id.

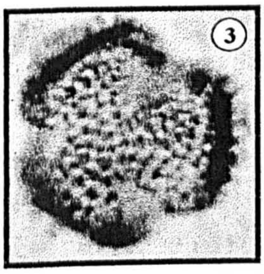
Pollen Determined only as far as family level due to the similar pollen morphology and poor preservation. Bi to perioporate, smooth, tectate. Spherical in equatorial view, diameter approximately 20 μm, although the grain is often crumpled. Pores are round, and readily visible. The exine is very thin and unstratified. Plates 97 and 98.

Potential sources Mostly the Urticaceae are herbs and small shrubs common between 2000 and 3000 m, particularly within moister areas (Hamilton, 1982). Urticaceae can be indicative of a regenerating forest with a developing herbaceous layer (Lind and Morrison, 1974). The pollen is very well dispersed, almost to the exclusion of the pollen sum. Consequently Urticaceae can be over-represented within pollen spectra.

Local vegetation In total, 123 pollen types were identified to the lowest taxonomic level possible using the pollen type-slide collection based at the University of Hull, Kew Gardens and CEREGE, identification keys and pollen floras available. Obviously this number is significantly greater than the pollen types already described. Many of the pollen types encountered originated from local vegetation. Therefore, they are of secondary interpretative value for the



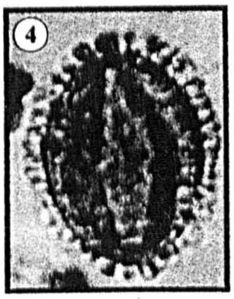


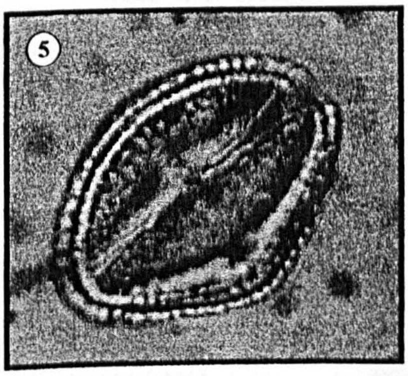


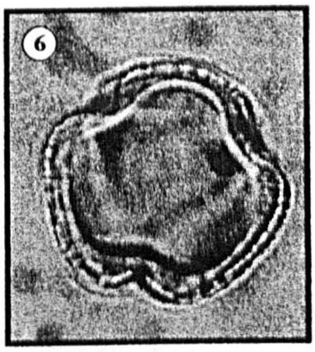
Magnification

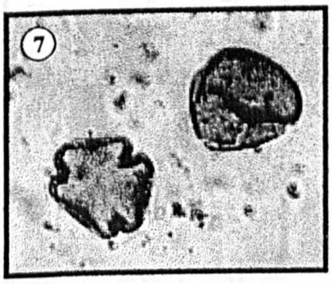
☐ x 400

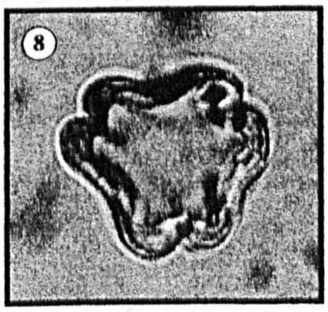
☐ x 1000

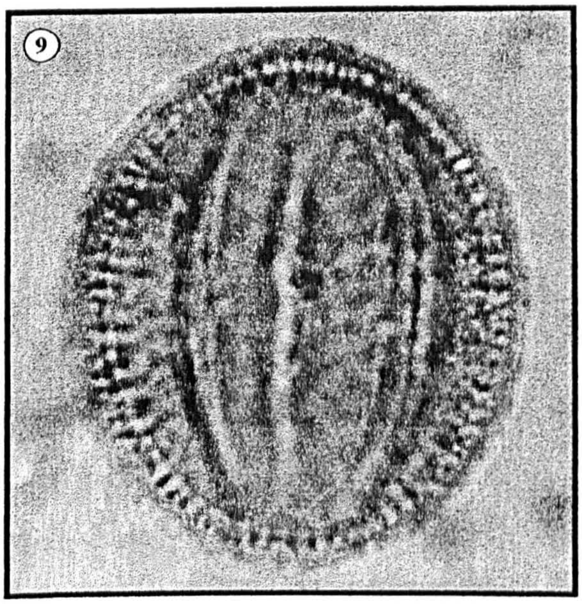


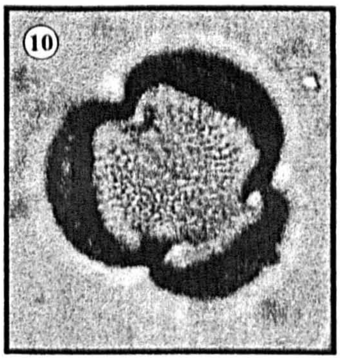


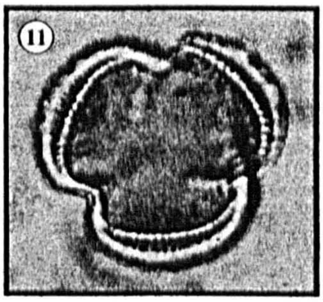


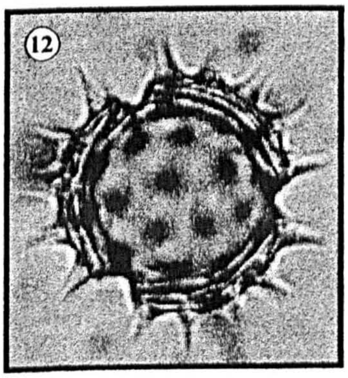


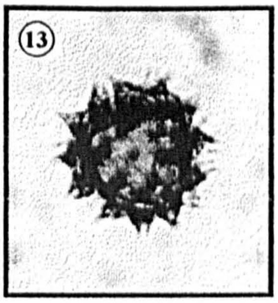



⑨

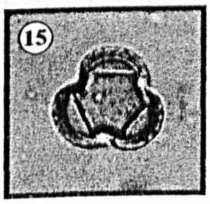

⑩

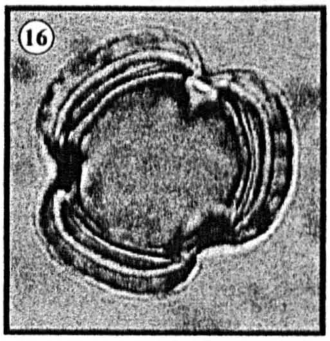

⑪

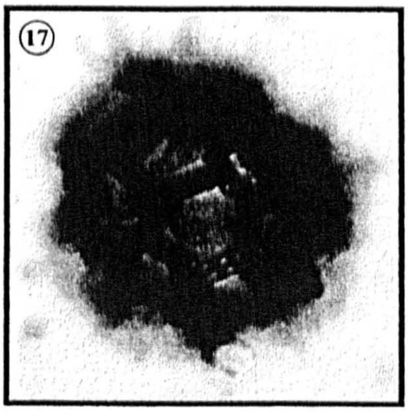

⑫

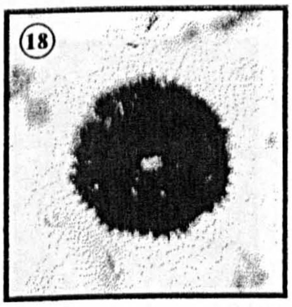

⑬

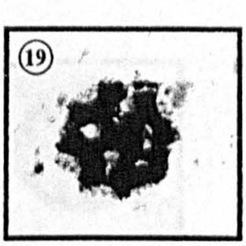

⑭

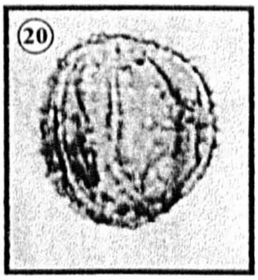

⑮

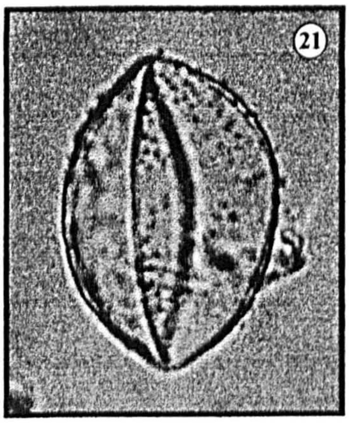

⑯

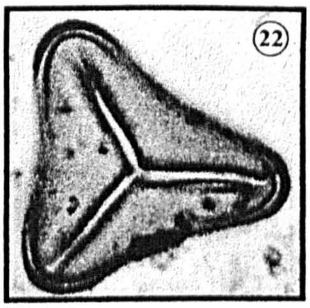

⑰

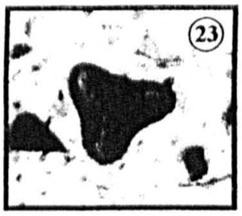

⑱


⑲

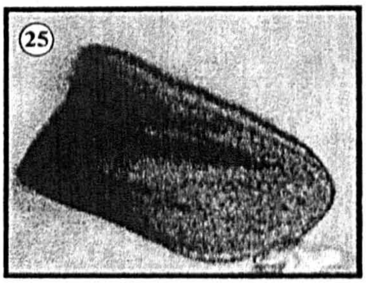

⑳

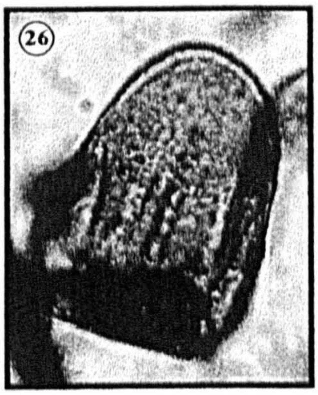

㉑

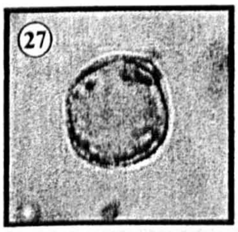

㉒

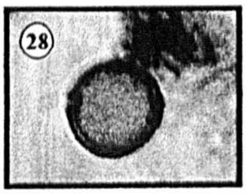

㉓

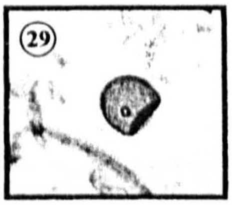

㉔

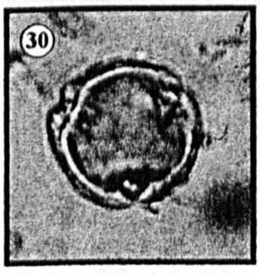

㉕

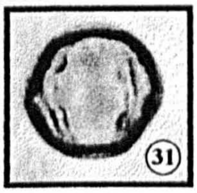

㉖

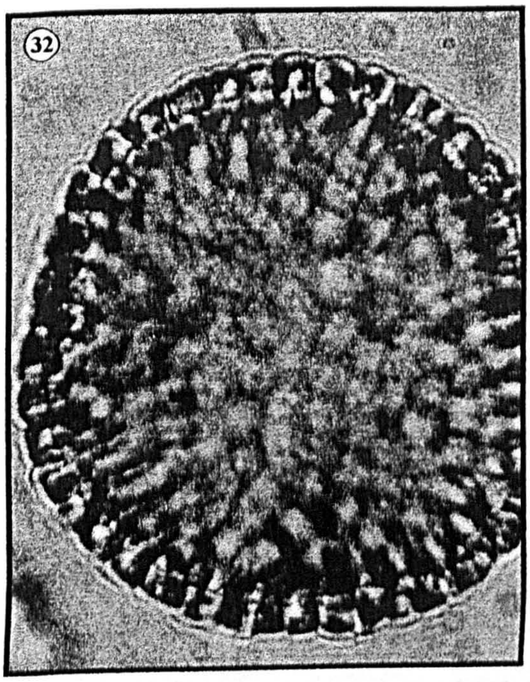

㉗

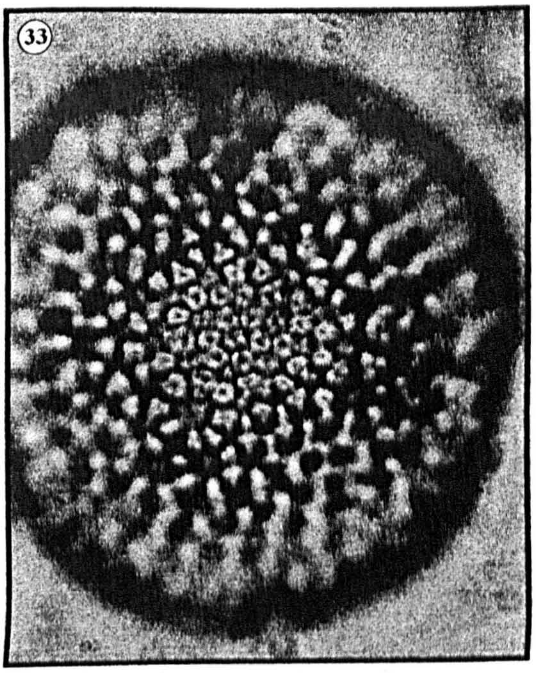

㉘

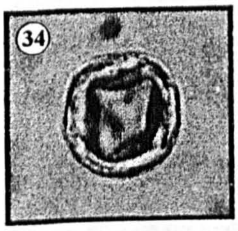

㉙


㉚

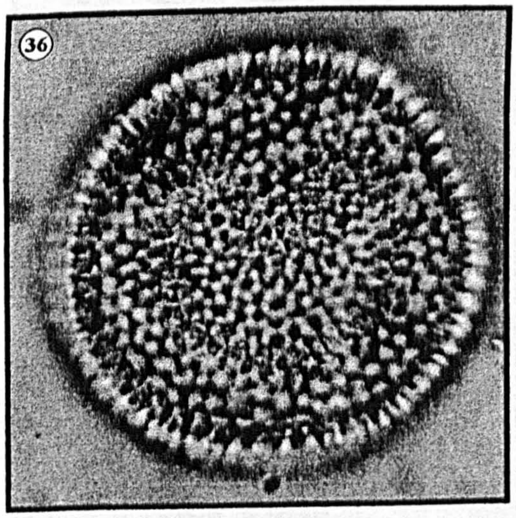

㉛

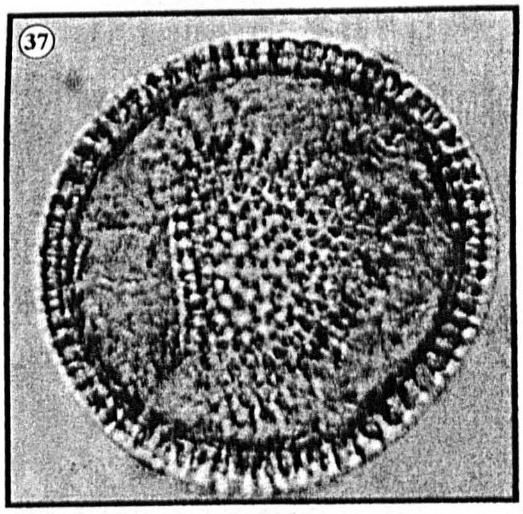

㉜

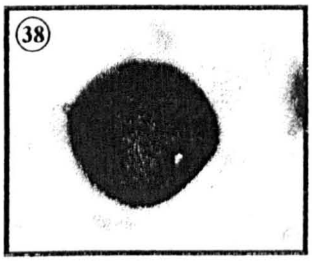

㉝

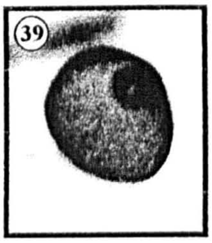

㉞

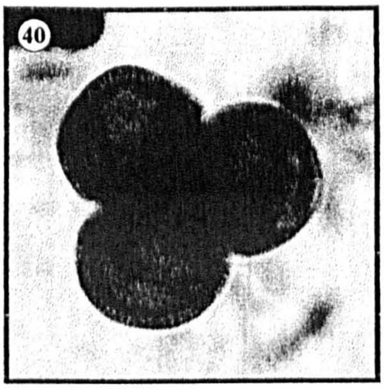

㉟

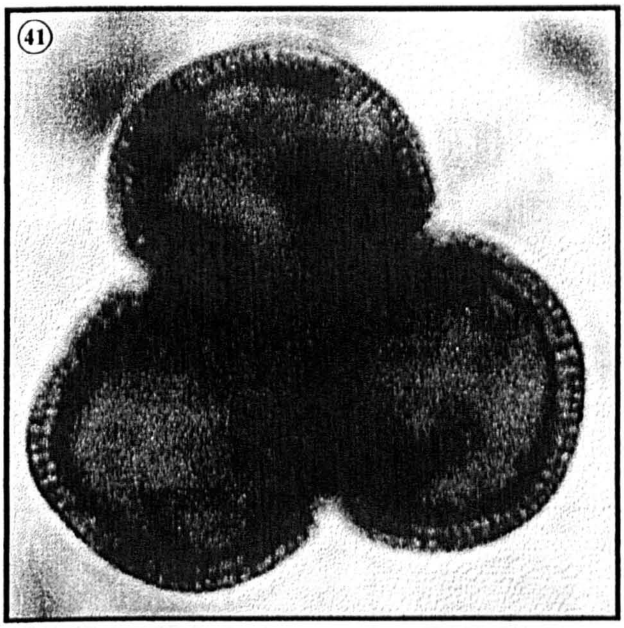

㊱

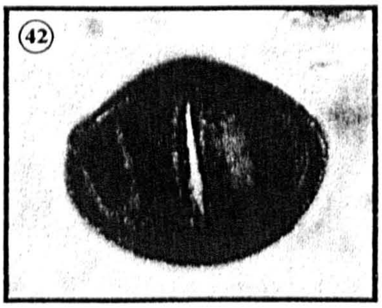

㊲

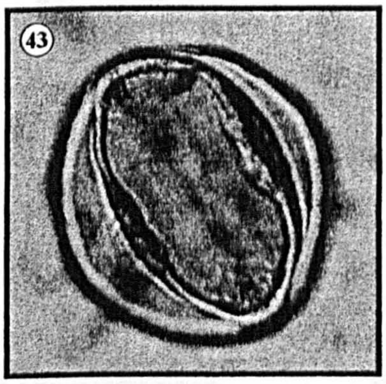
㊳


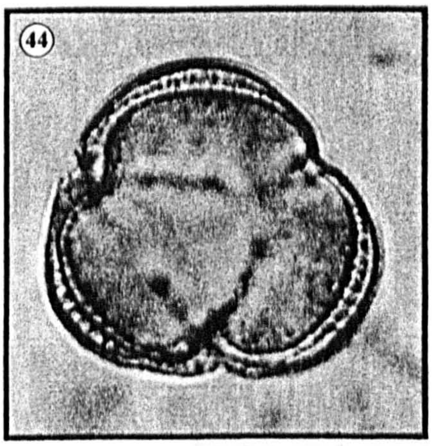
㊴


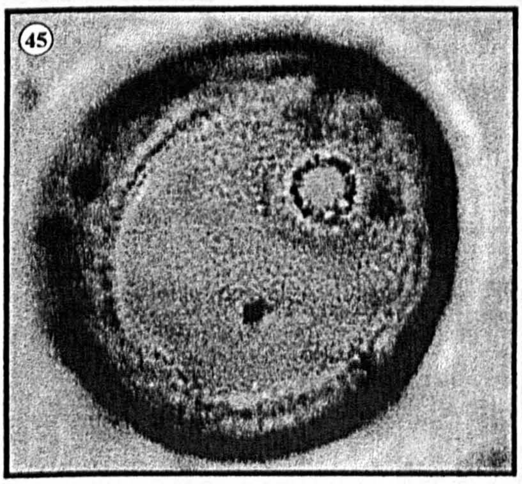
㊵


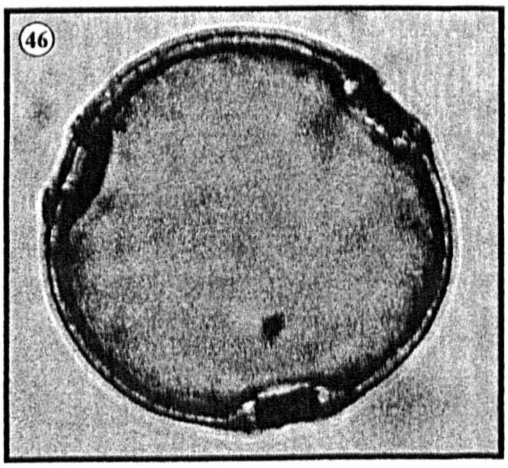
㊶


㊷


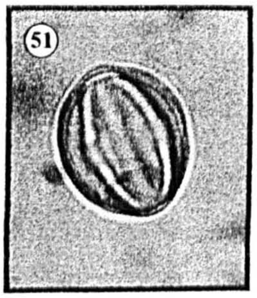
㊸


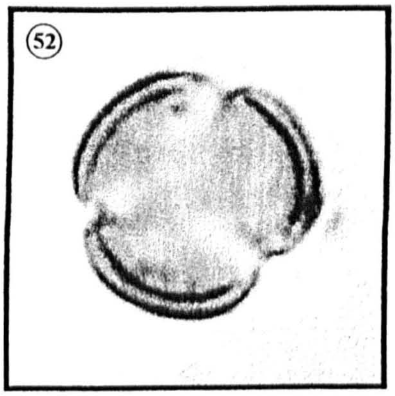
㊹


㊺


㊻


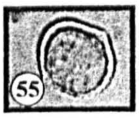

㊿

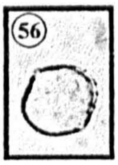

(51)

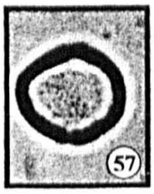

(52)


(53)

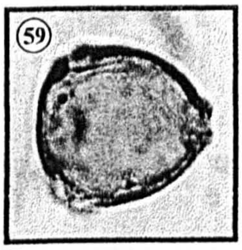

(54)

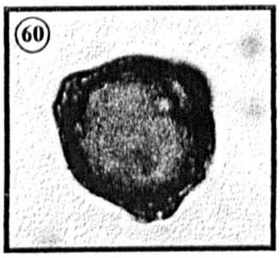

(55)

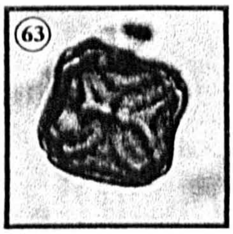

(56)


(57)


(58)


(59)


(60)

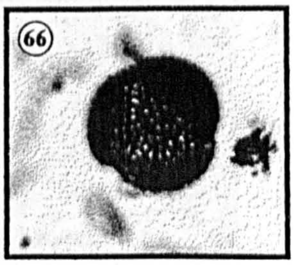

(63)

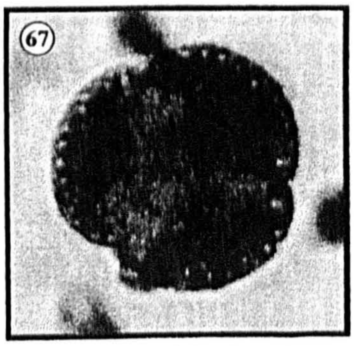

(61)

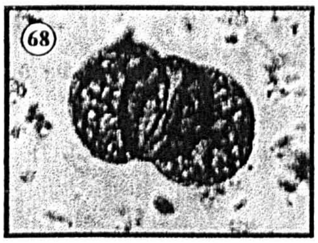

(62)

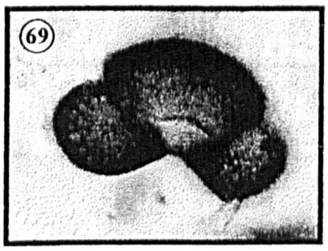

(64)

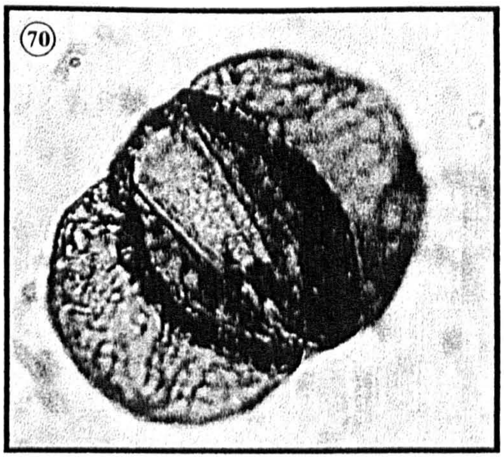

(65)

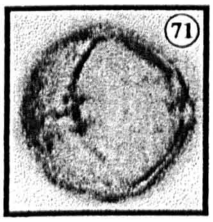

(66)


(67)


(68)

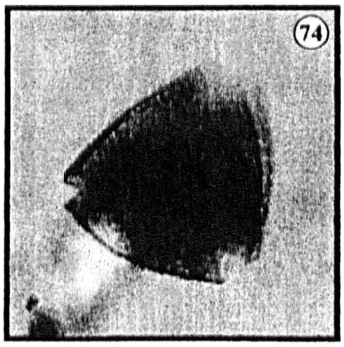

(69)

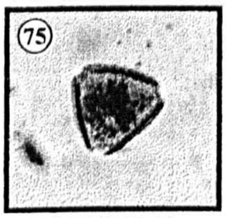

(70)

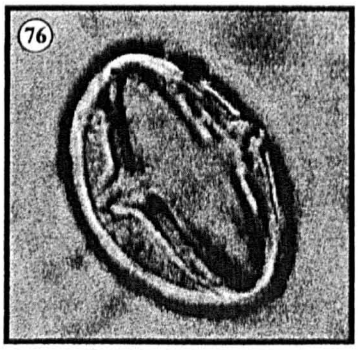

(71)

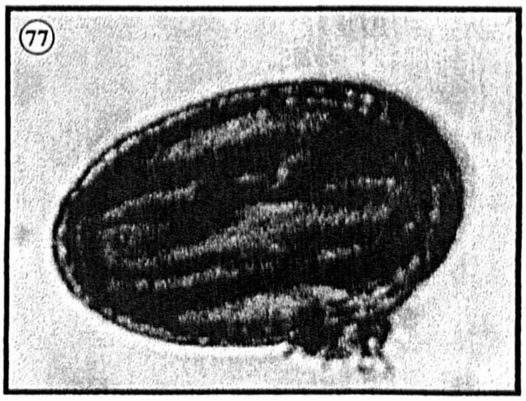

(72)

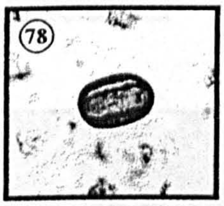

(73)

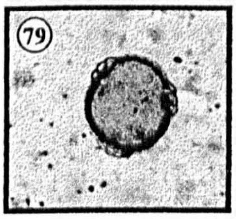

(74)

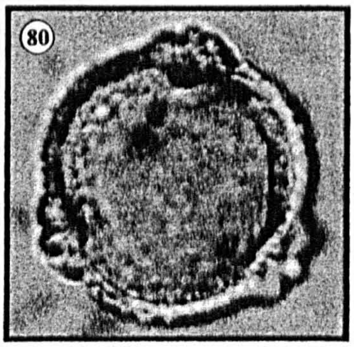

(75)

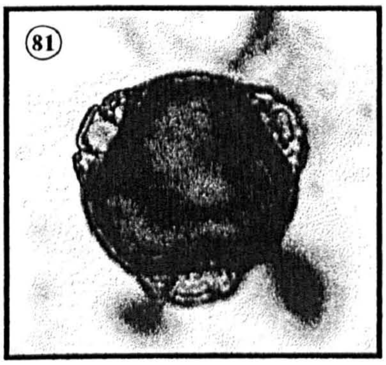

(76)

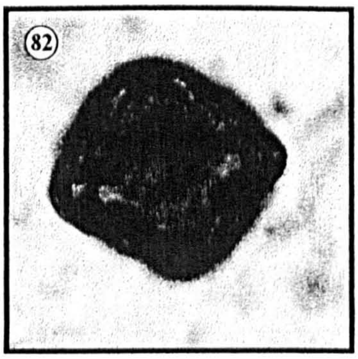

(77)

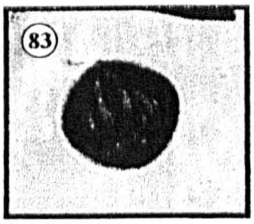

(78)

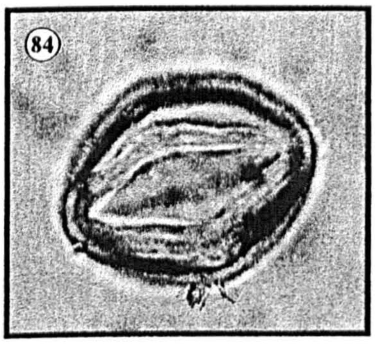

(79)

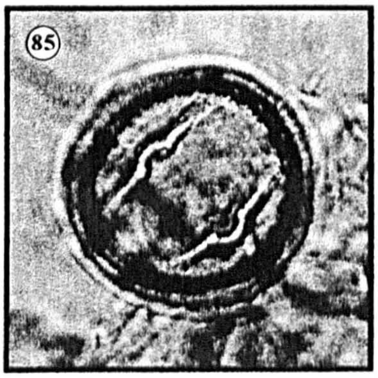

(80)

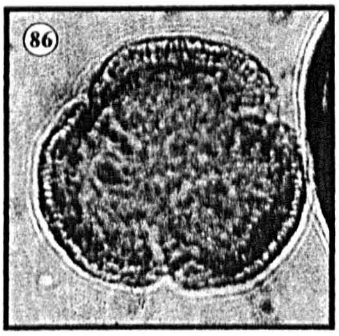

(81)


(82)


(83)

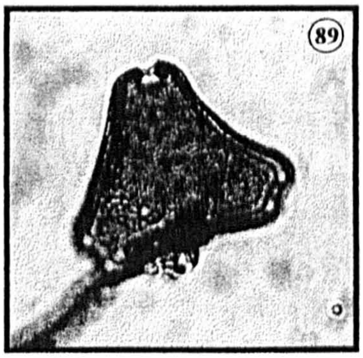

(84)

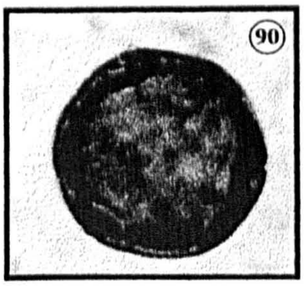

(85)

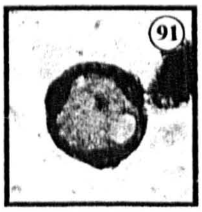

(86)


(87)


(88)

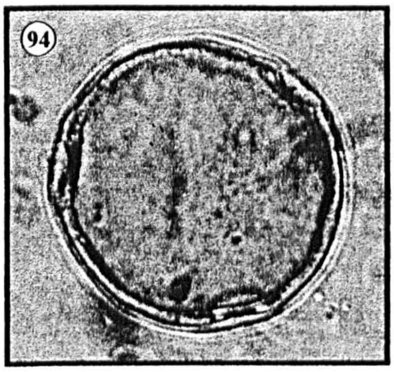

(89)

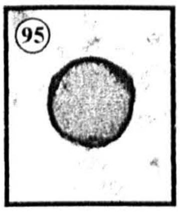

(90)

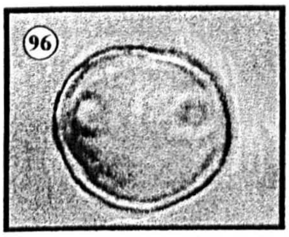

(91)

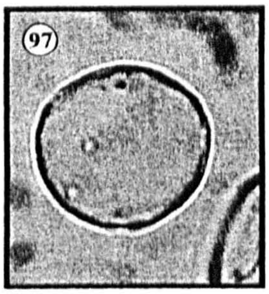

(92)

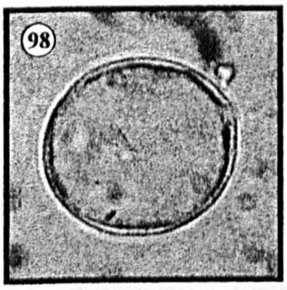

(93)

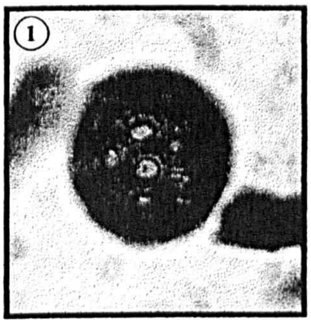

(94)

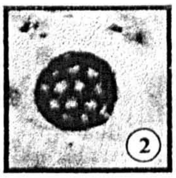

(95)

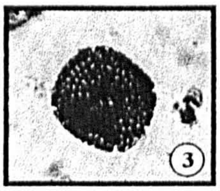

(96)

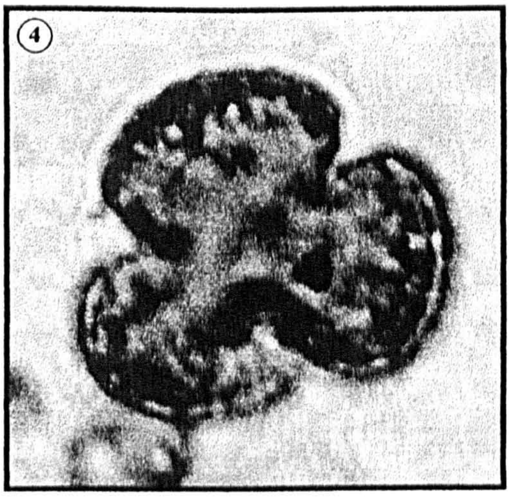

(97)

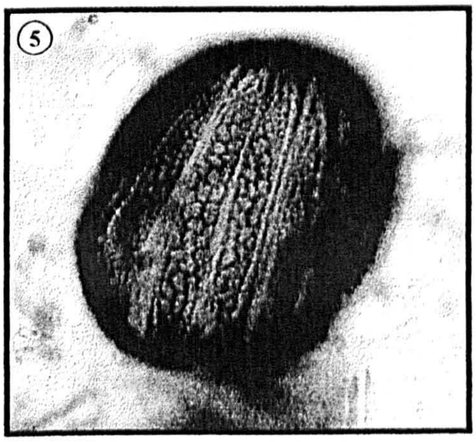

(98)


①


②

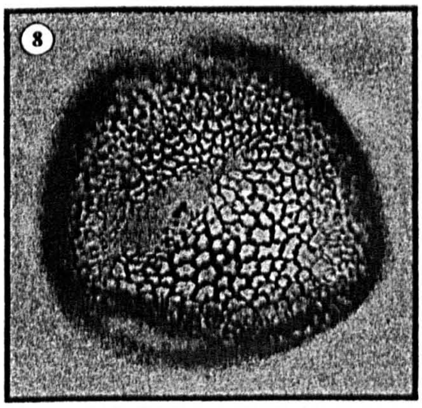

③

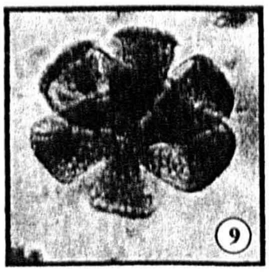

④


⑤


⑥

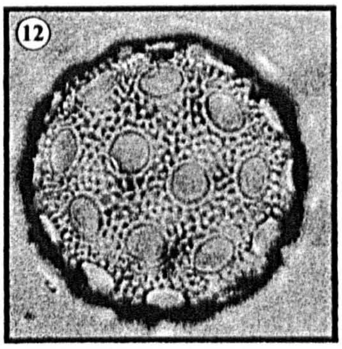

⑦

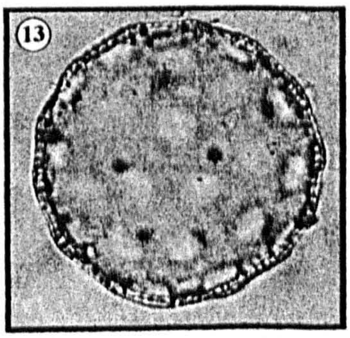

⑧


⑨

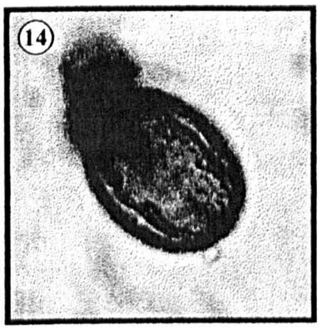

⑩


⑪

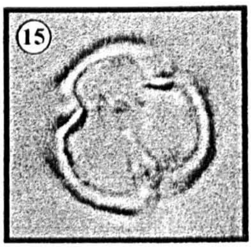

⑫


⑬

⑭

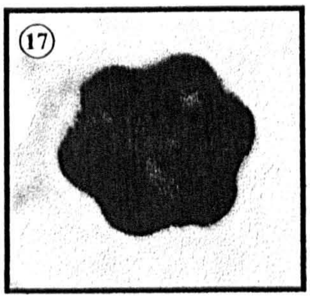


⑮

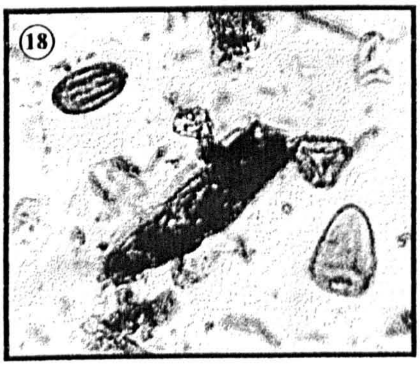


⑯

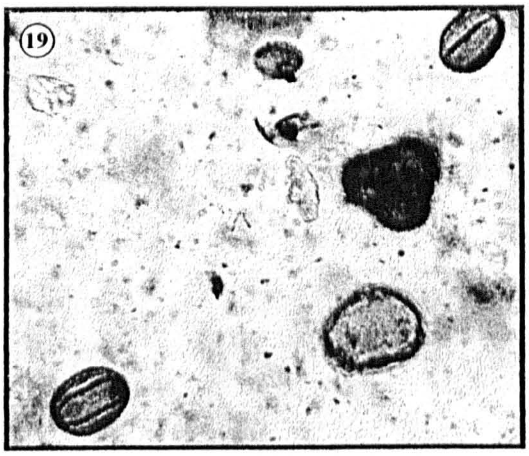
⑰



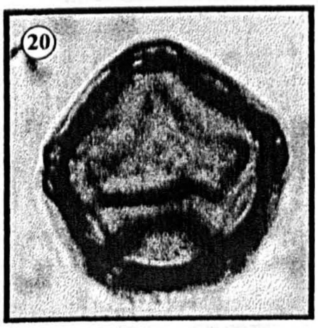
⑱

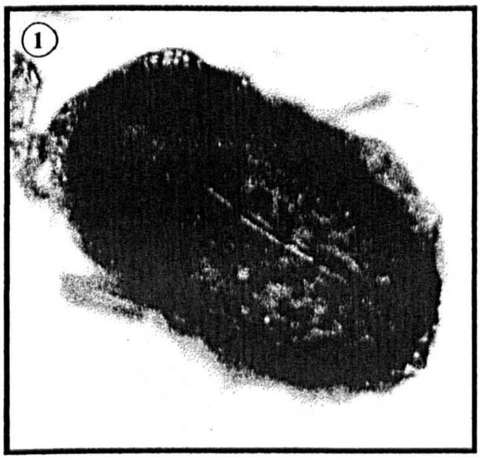


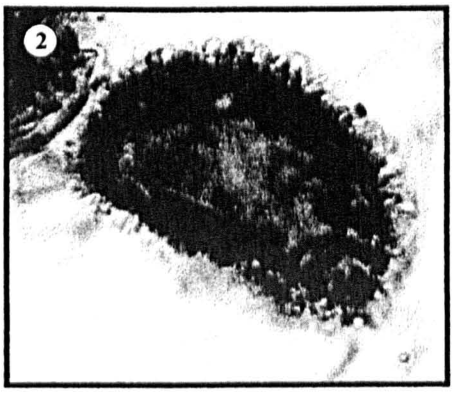
⑲

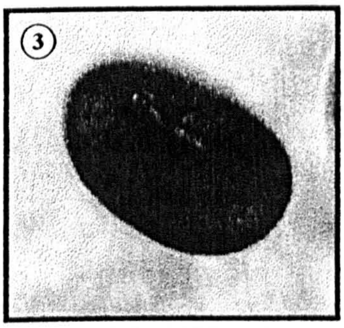


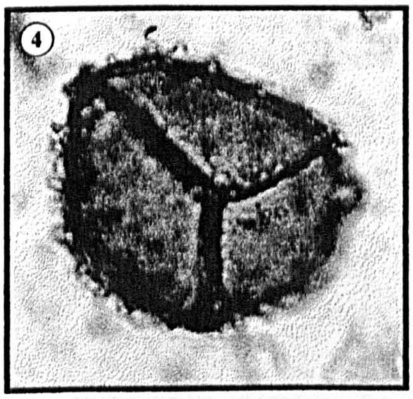
⑳

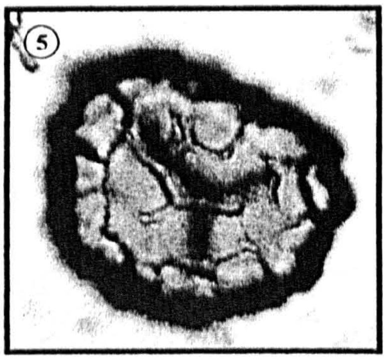


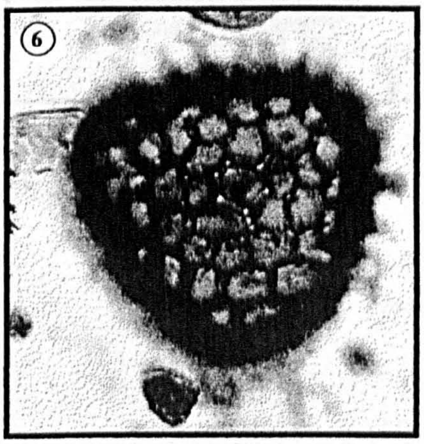

①

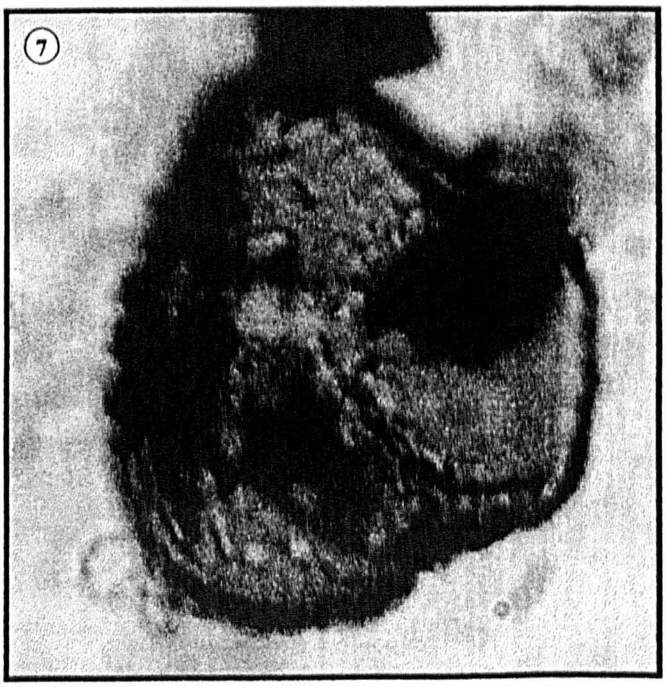

②

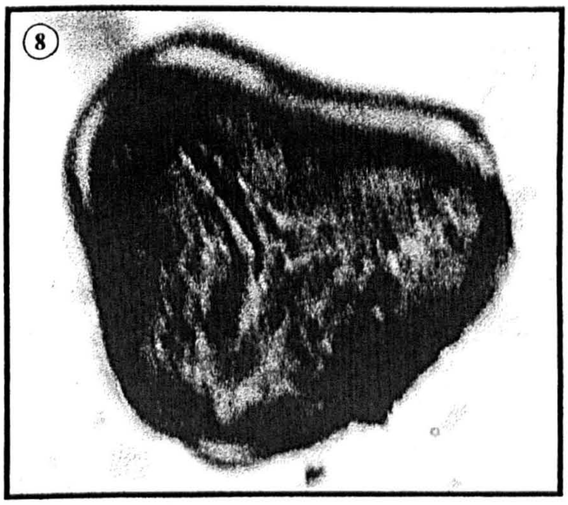

③

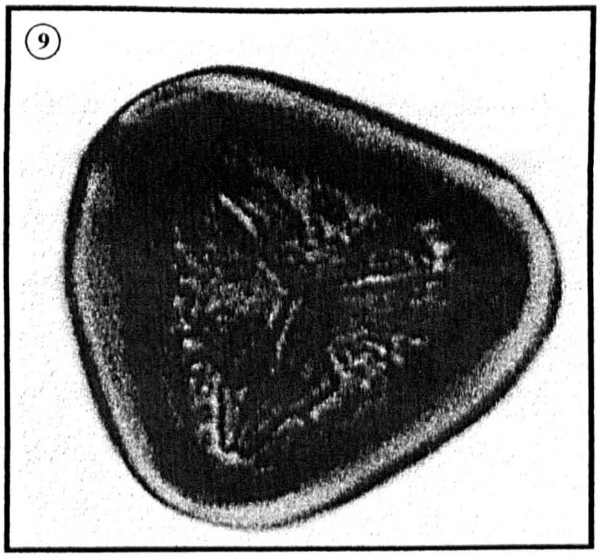

④

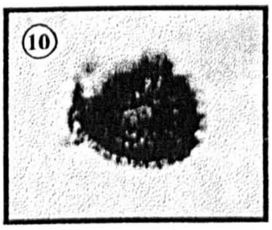

⑤

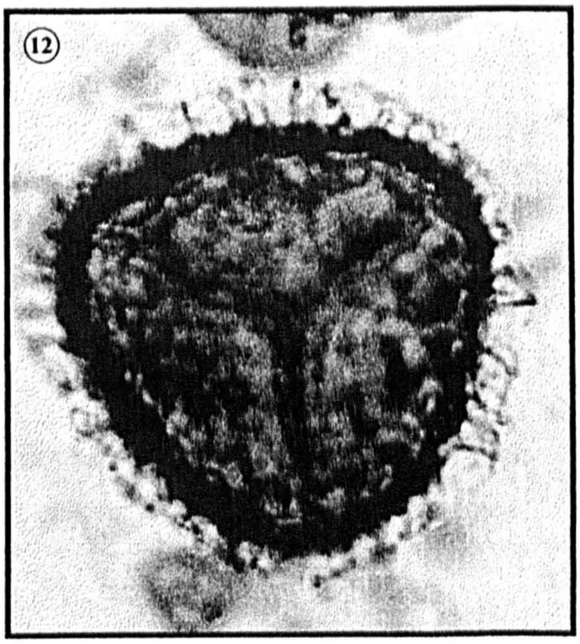

⑥

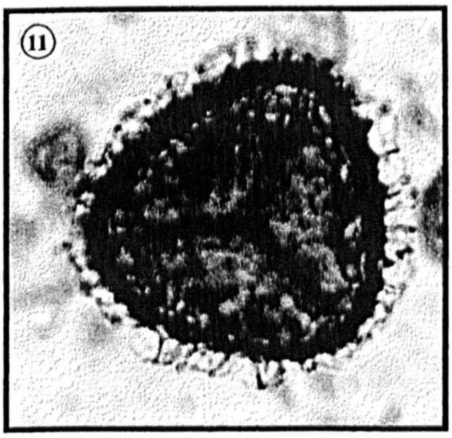

⑦


⑧


⑨


⑩


⑫


⑪

REFERENCES

Aaby, B. (1979). Characteristics of peat and lake deposits. In. *Palaeoecological change in the temperate zone in the last 15,000 years. Sub project B, lake and mire environments. Project Guide volume 1* (Berglund, B.E. ed.). Department of Quaternary Geology, Lund University. 1 - 140.

Aaby, B. and Digerfeldt, A. (1986). Sampling techniques for lakes and bogs. In. *Handbook of Holocene Palaeoecology and Palynology*. (Burglund, B. E. ed.) pp. 181 - 194. John Wiley and Sons. Chichester.

Ambrose, S. (1982). Archaeology and linguistic reconstruction's of history in east Africa. In. *The archaeological and linguistic reconstruction of African History* (Ehert, C. and Posansky, M. eds.). pp. 104 - 157. University of California Press, Berkeley.

Anfray, F. (1967). Matara. *Annales d'Ethiopie*. **7**, 33 - 53.

Atlas of Uganda (1967). Department of Lands and Survey, Kampala. 2nd. Edition.

Aubréville, A. (1949). Savanisation tropical et glaciations Quaternaires. *Adansonia*, 2, 16 - 84.

Aucour, A. M., Hillaire-Marcel, C. and Bonnefille, R. (1993). A 30,000 year record of ^{13}C and ^{18}O changes in organic matter from an equatorial peat bog. *Geophysical Monographs*. **78**, 343 - 351.

Aucour, A. M., Hillaire-Marcel, C. and Bonnefille, R. (1994). Late Quaternary changes from $\delta\ ^{13}C$ measurements from a highland peat bog from Equatorial Africa (Burundi). *Quaternary Research*. **41**, 225 - 233.

Baitwabobo, S. R. (1972a). Foundations of the Rujumbura society. In. *A history of Kigezi in south-west Uganda* (Denoon, D. ed.) pp. 36 - 48. National Trust, Kampala.

REFERENCES

Aaby, B. (1979). Characteristics of peat and lake deposits. In. *Palaeoecological change in the temperate zone in the last 15,000 years. Sub project B, lake and mire environments. Project Guide volume 1* (Berglund, B.E. ed.). Department of Quaternary Geology, Lund University. 1 - 140.

Aaby, B. and Digerfeldt, A. (1986). Sampling techniques for lakes and bogs. In. *Handbook of Holocene Palaeoecology and Palynology.* (Burglund, B. E. ed.) pp. 181 - 194. John Wiley and Sons. Chichester.

Ambrose, S. (1982). Archaeology and linguistic reconstruction's of history in east Africa. In. *The archaeological and linguistic reconstruction of African History* (Ehert, C. and Posansky, M. eds.). pp. 104 - 157. University of California Press, Berkeley.

Anfray, F. (1967). Matara. *Annales d'Ethiopie.* **7**, 33 - 53.

Atlas of Uganda (1967). Department of Lands and Survey, Kampala. 2nd. Edition.

Aubréville, A. (1949). Savanisation tropical et glaciations Quaternaires. *Adansonia*, 2, 16 - 84.

Aucour, A. M., Hillaire-Marcel, C. and Bonnefille, R. (1993). A 30,000 year record of ^{13}C and ^{18}O changes in organic matter from an equatorial peat bog. *Geophysical Monographs.* **78**, 343 - 351.

Aucour, A. M., Hillaire-Marcel, C. and Bonnefille, R. (1994). Late Quaternary changes from δ ^{13}C measurements from a highland peat bog from Equatorial Africa (Burundi). *Quaternary Research.* **41**, 225 - 233.

Baitwabobo, S. R. (1972a). Foundations of the Rujumbura society. In. *A history of Kigezi in south-west Uganda* (Denoon, D. ed.) pp. 36 - 48. National Trust, Kampala.

Baitwabobo, S. R. (1972b). Bashambo rule in Rujumbura. In *A history of Kigezi in south-west Uganda* (Denoon, D. ed.) pp. 54 - 71. National Trust, Kampala.

Baker, S. J. K. (1958). The geographical background of Western Uganda. *Ugandan Journal.* **22**, 1 - 9.

Ballouche, A. and Neumann, K. (1995). A new contribution to the Holocene vegetation history of the west African Sahel - pollen from Oursi, Bakina-Faso and charcoal from three sites in north eastern Nigeria. *Vegetation History and Archaeobotany.* **4 (1)**, 31 -39.

Bamps, P., Robson, N. and Verdcourt, B. (1978). Guttiferae. In *Flora Tropical East Africa.* (Polhill, E. R. ed.). Crown Agents, London.

Barry, P. and Chorley, L. (1990). *Mountain weather and climate.* Methuen. London and New York. 311 pp.

Bentjee, H. T. (1994). *Kenya trees, shrubs and lianas.* National Museums of Kenya, 568 pp.

Bennet, C. L., Beukens, R. P., Clover, M. R., Grove, H. E., Liebert, R. B., Litherland, A. E., Purser, K. H. and Sondheim, W. E. (1977). Radiocarbon dating using electrostatic accelerators: negative ions provide the key. *Science.* **198**, 508 - 510.

Birks, H. J. B. and Gordon, A. D. (1985). *Numerical methods in Quaternary pollen analysis.* Academic Press, London.

Birks, H. J. B. (1986). Numerical zonation, comparison and correlation of Quaternary pollen and stratigraphic data. In. *Handbook of Holocene Palaeoecology and Palaeohydrology.* (Berglund, B. E. ed.) pp. 734 - 774. John Wiley and Sons, Chichester.

Bonnefille, R. (1987). Évolution forestiere et climatique au Burundi durant les quarante derniers millers d'années. *C. R. Academie Science Paris,* **305 serie II,** 1021 - 1026.

Bonnefille, R. (1993). Afrique, paléoclimats et déforestation. *Sécheresse.* **4,** 221 - 231.

Bonnefille, R., Charlie, F., Guiot, J. and Vincens, A. (1992). Quantitative estimates of full glacial temperatures in equatorial Africa from palynological data. *Climate Dynamics.* **6,** 251 - 257.

Bonnefille, R. and Guiot, J. (1990). *Pollen dés Savanes d'Afrique Orientale.* Editions du Centre National de la Recherche Scientifique, Paris.

Bonnefille, R. and Mohammed, U. (1994). Pollen-inferred climatic fluctuations in Ethiopia during the last 3000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **109,** 331 - 343.

Bonnefille, R. and Riolett, G. (1971). Atlas dés pollen d' Ethiopie principales especes dés fôrets de môntagne. *Pollen et Spores.* **8,** 15 - 72.

Bonnefille, R. and Riollet, R. (1988). The Kashiru pollen sequence (Burundi). Palaeoclimatic implications for the last 40,000 years in tropical Africa. *Quaternary Research.* **30,** 19 - 35.

Bonnefille, R., Roeland, J. C. and Guiot, J. (1990). Temperature and rainfall estimates for the past 40,000 years in Equatorial Africa. *Nature.* **346,** 347 - 349.

Bonnefille, R., Riolett, G., Icole, M., Lafont, R., Arnold, M. and Jolly, D. (1995). Glacial - interglacial records from intertropical Africa, high resolution pollen and carbon data at Rusaka, Burundi. *Quaternary Science Reviews.* **14,** 917 - 936.

Booth, A. H. (1958). The zoogeography of west African primates: a review. *Bulletine Institute Africa noire, series A.* **20,** 587 - 622.

Boughey, A. S. (1955a). The vegetation of the mountains of Biafra. *Proceedings of the Linnean Society London.* **65**, 144 - 150.

Boughey, A. S. (1955b). The nomenclature of the vegetation of the mountains of Africa. *Webbia.* **11,** 413 - 423.

Boutique, R. and Verdcourt, B. (1973). Haloragaceae. In *Flora of Tropical East Africa*, (Polhill, E. R. ed.). Crown Agents London.

Bouxin, G. (1976). Ordination and classification in the upland Rugege Forest (Rwanda, Central Africa). *Vegetatio.* **32,** 97 - 115.

Bouxin, G. (1977). Structure de la strate arborescente dans un site de la fôret de Môntagne du Rwanda (Africqe centrale). *Vegetatio.* **33,** 65 - 78.

Bower, J. (1988). Evolution of Stone Age food producing cultures in east Africa. In. *Prehistoric cultures and environments the Late Quaternary of Africa* (Bower, J. and Lubell, D. eds.). Cambridge University Press.

Bower, J. and Lubell, D. (1988). (eds.) *Prehistoric cultures and environments in the Late Quaternary of Africa.* Cambridge University Press.

Bower, J. and Nelson, C. M. (1978). Early pottery and pastoral cultures of the central Rift Valley, Kenya. *Man.* **18,** 554 - 566.

Bradley, R. S. (1985). *Quaternary Palaeoclimatology - Methods of Palaeoclimatic Reconstruction.* Boston-Unwin Hyman. 472 pp.

Brenan, J. P. M. (1959). Leguminosae, sub family Mimosideae. In. *Flora Tropical East Africa.* (Hubbard, D. E. and Miln-Redhead, E. eds.). Crown Agents, London.

Brooks, D. and Thomas, K. W. (1967). The distribution of pollen grains on microscope slides, 1. The non-randomness of the distribution. *Pollen et Spores.* **9**, 621 - 629.

Bruce, E. A. and Lewis, J. (1960). Loganiaceae. In. *Flora Tropical East Africa.* (Hubbard, D. E. and Miln-Redhead, E. eds.). Crown Agents, London.

Buechner, H. K. and Dawkins, H. C. (1961). Vegetation change induced by elephants and fire in the Murchison Fall National Park, Uganda. *Journal of Ecology.* **42**, 752 - 766.

Burney, D. A. (1993). Late Holocene environmental change in arid south-west Madagascar. *Quaternary Research.* **40**, 98 - 106.

Burtt, B. D. (1934). A botanical reconnaissance in the Virunga Volcanoes of Kigezi, Rwanda, Kivu, *Kew Bulletin*, 145 - 165.

Butynski, T. M. (1984). *Ecological survey of the Impenetrable Forest and recommended actions for its management.* New York Zoological Society.

Butynski, T. M. (1986). Status of elephants in the Impenetrable Forest, Uganda. *African Journal of Ecology.* **23**, 189 - 193.

Butzer, K. W. (1984). Long-term Nile flood variation and political discontinuities in Pharaonic Egypt. In. *From Hunters to Farmers.* (Clark J.D. and Brandt S.A, eds.). pp. 102 - 112. Berkeley: University of California Press.

Butzer, K. W., Isaac, G. L., Richardson, J. L. and Washbourn-Kamou, C. (1972). Radiocarbon dating of east African lake levels. *Science.* **175**, 1069 - 1076.

Cahusac, A. B. (1958). *Forest type map of the Impenetrable Central Forest Reserve.* Technical Report. Uganda Forestry Department, Entebbe, Uganda.

Clacote, R. (1995). Pollen source area and pollen productivity, evidence from forest hollows. *Journal of Ecology*. **83**, 591 - 602.

Caratini, C., Bentaleb, I., Fontugne, M., Morzadec-Kerfourn, M. T., Pascal, J. P. and Tissot, C. (1994). A less humid climate since ca. 3500 yr B.P. evidence from marine cores off Karwar, western India. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **109**, 371 - 384.

Chaplin, J. H. (1974). The prehistoric rock art of the Lake Victoria Region. *Azania*. **9**, 1 - 50.

Chapman, J. D. and White, F. (1970). *The Evergreen forests of Malawi*. Commonwealth Forestry Institute. University of Oxford. 190 pp.

Clark, J. S. (1988a). Stratigraphic charcoal analysis on petrographic thin sections: application to fire history in north-western Minnesota. *Quaternary Research*. **30**, 81 - 91.

Clark, J. S. (1988b). Particle motion and the theory of charcoal analysis: Source area, transport, deposition and sampling. *Quaternary Research*. **30**, 67 - 80.

Clark, J. S. (1989). Ecological disturbance as a renewal process: theory and application to fire history. *Oikos*. **56**, 17 - 30.

Clark, J. S. and Hussey, T. C. (1996). Estimating the mass flux of charcoal from sedimentary records: effect of particle size, morphology and orientation. *The Holocene*. **6**, 129 - 144.

Clark, R. L. (1982). Point-count estimation of charcoal in pollen preparation and thin sections of sediments. *Pollen et Spores*. **24**, 523 - 535.

Clark, R. L. (1983). *Fire history from charcoal in lake and swamp sediments*. PhD Thesis, Australian National University, Canberra, Australia.

Clark, R. L. (1984). Effect on charcoal of pollen preparation studies. *Pollen et Spores*. **26**, 559 - 576.

Coe, M. J. (1967). The Ecology of the Alpine Zone of Mount Kenya. *Monographiae Biologicae*. **17**, 136 pp. W. Junk, The Hague.

Coetzee, J. A. (1964). Evidence for a considerable depression of the vegetation belts during the Upper Pleistocene of East African mountains. *Nature*. **204**, 564 - 566.

Coetzee, J. A. (1967). Pollen analytical studies in East and Southern Africa. *Palaeoecology of Africa*. **3**, 1 - 146.

COHMAP Members (1988). Climatic change of the last 18,000 years, observations and model simulations. *Science*. **241**, 1043 - 1053.

Colinvaux, P. (1989). *Ecology*. John Wiley and Sons. Chichester, 725 pp.

Colyn, M., Gautier-Hiern, A. and Verheten, W. (1991). A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography*. **18**, 403 - 407.

Coombe, A. D. and Simmons, W. C. (1933). *The volcanic area of Bufumbria. Part 1: The geology of the volcanic area of Bufumbria, south west Uganda.* Geological Survey of Uganda, Memoir no. 3 Government Printer Entebbe.

Costa, J. E. (1978). Holocene stratigraphy in flood frequency analysis. *Water Resources Research*. **14**, 626 - 632.

Cunningham, T. (1992). *People, Park and Plant Use research and recommendations for Multiple Use Zones and development alternatives around Bwindi-Impenetrable National Park, Uganda.* Report prepared for CARE-International (Kampala, Uganda).

Dale, I. R. (1940). The forest types of Mount Elgon. *Journal East Africa Natural History Society*. **45**, 74 - 82.

Davies, T. B., Bribgecombe, P. and Vincent, C. (1977). The daily cycle of weather on Mount Kenya. *Weather*. **32**, 406 - 417.

Davis, R. B. and Thompson-Webb III. (1975). The contemporary distribution of pollen in eastern North America: a comparison with the vegetation. *Quaternary Research*. **5**, 395 - 434.

Delcourt, H. R., Delcourt, D. A. and Thompson Webb III. (1984). Dynamic ecology: the spectrum of vegetation change in time and space. *Quaternary Science Reviews*. **1**, 153 - 173.

de-Marret, P. (1985). Recent archaeological research and dates from central Africa. *Journal of African History*. **26**, 129 - 148.

Denny, P. (1972). Lakes of south-western Uganda 1. Physical and chemical studies on Lake Bunyoni. *Freshwater Biology*. **2**, 143 - 158.

Diamond, A. W. and Hamilton, A. C. (1980). The distribution of forest passerine birds and Quaternary climatic change in tropical Africa. *Journal of Zoology, London*. **191**, 379 - 402.

Eggeling, W. J. and Dale, I. R. (1951). *The Indigenous Trees of the Ugandan Protectorate*. 2 ed. Entebbe Government printer. 491 pp.

Elenga, H., Schwartz, D., and Vincens, A. (1994). Pollen evidence for Late Quaternary vegetation and inferred climate changes in Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **109**, 345 - 346.

Elenga, H., Schwartz, D., Vincens, A., Bertaux, J., Denamur, C., Martin, L., Wirrmann, D. and Serrant, M. (1996). Holocene pollen data from Kitina Lake (Congo) Paleoclimatic and Paleobotanical changes in the Mayombe Forest area.

Comptes Réndus de l'Acàdemia des Sciences Serie II Fasicule A - Sciences de la Teire et des Plànetes, **323** (5), 403 - 410.

Everitt, B. S. (1978). *Graphical techniques for multivariate data.* Heinmann Educational Books Ltd. pp 5 - 41.

Faegri, K. and Iversen, J. (1989). *Textbook of pollen analysis.* Fourth edition, John Wiley, Chichester.

Finny, B. P. and Johnson, T. C. (1991). Sedimentation in Lake Malawi (East Africa) during the past 1000 years: a continuous record from the southern tropics. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **85**, 351 - 366.

Flenley, J. R. (1973). The use of modern pollen rain samples in the study of the vegetation history of tropical regions. In. *Quaternary Plant Ecology* (Birks, H. J. B and West, R. G. eds.). Blackwell, Oxford, 131 - 141.

Flenley, J. R. (1979). *The Equatorial Rain Forest, a geological history.* Butterworths, London and Boston. 162 pp.

Flenley, J. R. (1993). The origins of diversity in Tropical Rain Forests. *Tree.* **8**, 119 - 120.

Foster, D. R. and Fritz, S. C. (1987). Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. *Journal of Ecology.* **75**, 409 - 437.

Franzen, L. G. (1994). Are wetlands the Key to the Ice-age Cycle Enigma? *Ambio.* **23**, 300 - 308.

Gasse, F. and van Campo, E. (1994). Abrupt post-glacial climatic events in West Asian and North African monsoon domains. *Earth and Planetary Science Letters.* **26**, 435 - 456.

Gasse, F., Juggins, S., Khelifa, L. B. (1995). Diatom-based transfer functions for inferring past hydrochemical characteristics of African lakes. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **117,** 31 - 54.

Gasse, F., Ledee, V., Massault, M. and Fontes, J. C. (1989). Water level fluctuations of Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. *Nature.* **342,** 7 - 59.

Gasse, F., Téhet, R., Durant, A., Gilbert, E., and Fontes, J. C. (1990) The arid-humid transition in the Sahara and Sahel during the last deglaciation. *Nature.* **346,** 141 - 146.

Gauch, H. G., Whittaker, R. H. and Wentworth, T. R. (1977). A comparative study of reciprocal averaging and other ordination techniques. *Journal of Ecology.* **65,** 157 - 174.

Geraud, W. F. (1972). The settlement of the Bakiga. In. *A history of Kigezi in south-west Uganda.* (Denoon, D. ed.). National Trust. Adult Education Centre, Kampala.

Giresse, P., Maley, J. and Brenac, P. (1994). Late Quaternary palaeoenvironments in the Lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **107 (1-2),** 65 - 78.

Glagoleff, A. A. (1933). On the geometrical methods of quantitative mineralogical analysis of rocks. *Transactions of the Institute of Economic Mineralogy and Metallurgy, Moscow.* **59,** 475.

Goldberg, E. D. (1985). Refuges and dispersal in the speciation of African Forest Mammals. In. *Biological Diversification in the tropics* (Prance, G. T. ed.). Columbia University Press. 680 pp.

Gordon, A. D. (1982). Numerical methods in Quaternary palaeoecology, V. Simultaneous graphical representation of the levels and taxa. *Review of Palaeobotany and Palynology*. **37**, 155 - 188.

Gordon, A. D. and Birks, H. J. B. (1972). Numerical methods in Quaternary palaeoecology, 1. Zonation of pollen diagrams. *New Phytologist*. **73**, 221 - 249.

Goudie, A. (1996). Climate past and present. In. *The Physical Geography of Africa*. (Adams, W. M., Goudie, A. S. and Orme, A. R. eds.). Oxford University Press. 429 pp.

Graham, E. (1960). Rosaceae. In. *Flora Tropical East Africa*. (Hubbard, C. E. and Milne-Redhead, E. eds.). Crown Agents, London.

Grimm, E. C. (1991). *Tilia Graph 1.18*. Illinois State Museum, Springfield.

Grimm, E. C. (1995). *Tilia Graph 2*. Illinois State Museum, Springfield.

Grove, A. T. (1986). Geomorphology of the African Rift System. In. *Sedimentation in the African Rifts*. (Frostick, L. E., Renault, R. W., Reid, I. and Tiercelin, J. J. eds.), Geological Society Special Publication No. 25.

Grove, H. E. (1992). The history of AMS. In. *Radiocarbon After Four Decades, an Interdisciplinary Perspective*. (Taylor, R. E., Long, A. and Kra, R. S. eds.). Springer-Verlag, New York.

Grubb, P. J. (1971). Interpretation of the Massenerheberg effect on tropical mountains. *Nature*. **279**, 44 - 45.

Haaland, R. and Shinnie, P. (1985). (eds.). *African Iron Working, ancient and traditional*. Norwegian University Press. Bergen. 209 pp.

Haberyan, K. A. and Heckey, R. E. (1987). The Late Pleistocene and Holocene stratigraphy and palaeolimnology of lakes Kivu and Tanganyika. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **61**, 169 - 197.

Hafsten, U. N. and Solem, T. (1976). Age, origin and palaeoecological evidence of blanket bogs in Nord Trondelag. Norway. *Boreas*.. **5**, 119 - 141.

Hall, J. B. (1973). Vegetation zones on the southern slopes of Mount Cameroon. *Vegetatio*. **27**, 49 - 69.

Hamilton, A. C. (1969). The vegetation of south-west Kigezi. *Uganda Journal*. **33 pt. 2**, 175 - 199.

Hamilton, A. C. (1972). The interpretation of pollen diagrams from highland Uganda. *Palaeoecology of Africa*. **7**, 45 - 149.

Hamilton, A. C. (1974). Distribution patterns of forest trees in Uganda and their historical significance. *Vegetatio*. **29**, 21 - 35.

Hamilton, A. C. (1975b). A quantitative analysis of altitudinal zonation in the Uganda Forests. *Vegetatio*. **30**, 99 - 106.

Hamilton, A. C. (1976). Identification of East Africa Urticaceae pollen. *Pollen et Spores*. **18**, 27 - 66.

Hamilton, A. C. (1981). The Quaternary history of African forests: its relevance to conservation. *African Journal of Ecology*. **19**, 1 - 6.

Hamilton, A. C. (1982). *Environmental history of east Africa*. Academic Press, London and New York, 328 pp.

Hamilton, A. C. (1991). *A Field Guide to Uganda Forest Trees*. Makerere University Press. Kampala.

Hamilton, A. C. and Perrot, R. A. (1980). Modern pollen deposition on a tropical African mountain. *Pollen et Spores*. **22**, 437 - 468.

Hamilton, A. C. and Perrot, R. A. (1981). A study of altitudinal zonation within the Montane Forest Belt of Mount Elgon, Kenya-Uganda. *Vegetatio*. **45**, 107 - 115.

Hamilton, A. C. and Taylor, D. M. (1991). History of climate and forests in tropical Africa during the last 8 million years. *Climate Change*. **19**, 65 - 78.

Hamilton, A. C. and Taylor, D. M. (1986). Mire sediments in East Africa. In. *Sedimentation in the African Rifts*. (Frostick, L. E., Renault, R. W., Reid, I. and Tiercelin, J. J. eds.). Geological Society Special Publication. **25**, 211 - 217.

Hamilton, A. C., Taylor, D. M. and Vogal, J. C. (1986). Early forest clearance and environmental degradation in south west Uganda. *Nature*. **320**, 164 - 167.

Harcourt, A. H. (1981). Can Uganda's Gorillas survive? A survey of the Bwindi Forest Reserve. *Biological Conservation*. **19**, 269 - 282.

Harmsen, J., Spence, J. R. and Mahaney, W. C. (1991). Glacial-interglacial cycles and development of the Afroalpine ecosystem on east African mountains: II. Origins and development of the biotic component. *Journal of African Earth Sciences*. **12**, 513 - 523.

Harrop, J. F. (1960). *The soils of the western province of Uganda: A reconnaissance survey*. Memoir no. 6 of the Research Division of the Department of Agriculture, Uganda Series 1 - soils.

Hart, T. B., Hart, J. A., Deschamp, R., Fournier, M. and Atahols, M. (1996). Changes in forest composition over the last 4000 years in the Ituri basin, Zaire. In. The Biodiversity of African Plants (van der Maesen, L. J. G., van der Burgt, X. M. and van Medenback de Rooy, J. M. eds.). Kluver Academic Publishers. 859 pp.

Harvey, T. J. (1976). *The palaeolimnology of Lake Mobutu Sese Seko-Uganda-Zaire: the last 28,000 years*. PhD thesis, Duke University, North Carolina, U.S.A.

de Hastenrath, S. (1984a). Internal variability and annual cycle: Mechanisms of circulation and climate in the tropical Atlantic sector. *Monthly Weather Review*. **112**, 1097 - 1107.

de Hastenrath, S. (1984b). *The glaciers of Equatorial East Africa*. Reidel, Dordrecht, 353 pp.

Hedberg, O. (1951). Vegetation belts of the east African mountains. *Svensk-Botanisk Tidskerift*. **45**, 140 - 202.

Hedberg, O. (1954). A pollen analytical reconnaissance in Tropical Africa. *Oikos*. **5**, 137 - 166.

Hedberg, O. (1959). An 'open-air hothouse' on Mount Elgon, Tropical east Africa. *Svensk-Botanisk Tidskerift*. **53**, 160 - 166.

Hedberg, O. (1961). The phytogeographical position of the Afroalpine flora. *Recent advances in Botany Section*. **9**, 912 - 919.

Hedberg, O. (1963). Afroalpine floral elements. *Webbia*. **19**, 519 - 529.

de Heinzelin, J. (1952). Glacier recession and periglacial phenomena in the Ruwenzori range (Belgian Congo). *Journal of Glaciology*. **2**, 137 - 140.

Hiernaux, J. (1968). Bantu expansion: The evidence from physical anthropology confronted with linguistic and archaeological evidence. *Journal of African History*. **9**, 505 - 515.

Hill, M. O. and Gauch jn. H. C. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio*. **42**, 47 - 58

Hillaire-Marcel, C., Aucour, A. M., Bonnefille, R., Riolett, G., Vincens, A. and Williamson, D. (1989). Palynological evidence of differential residence times of organic carbon prior to its sedimentation in East African Rift lakes and peat bogs. *Quaternary Science Reviews*. **8**, 207 - 212.

Holmgren, K., Karlen, W. and Shaw, P. (1996). Paleoclimatic significance of the stable isotopic composition and petrology of a Late Pleistocene Stalagmite from Botswana. *Quaternary Research*. **43**, 320 - 328.

Hooghiemstra, H. and van der Hammen, T. (1993). Late Quaternary vegetation history and palaeoecology of Laguna Pedro Pala (Sub-Andean Forest Belt, East Corillera, Columbia). *Review of Palaeobotany and Palynology*. **77**, 235.

Howard, P. C. (1991). *Nature conservation in Uganda's Forest Reserves*. The I.U.C.N. Tropical Forest Program. Gland. Cambridge.

IPCC (1995). *Climate Change 1995: the science of climate change - summary for policy makers*. WMO/UNEP. Cambridge University Press, Cambridge (UK).

Jolly, D. and Bonnefille, R. (1992). Historie et dynàmique du marécage tropical de Ndurumu (Burundi), données polliniques. *Review of Palaebotany and Palynology*. **75**, 133 - 151.

Jolly, D. and Bonnefille, R. (1991). Diagramme pollinique d'un sondage Holocène de la Kuruyange (Burundi, Afrique Centrale). *Palaeoecology of Africa*. **22**, 265 - 286.

Jolly, D., Bonnefille, R. and Roux, M. (1994). Numerical interpretation of a high resolution Holocene pollen record from Burundi. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **109**, 357 - 370.

Jolly, D., Taylor, D., Marchant, R., Hamilton, A., Bonnefille, R., Buchet, G. and Riollet, G. (in press). Vegetation dynamics in central Africa since 18,000 yr BP:

pollen records from the interlacustrine highlands of Burundi, Rwanda and western Uganda. *Journal of Biogeography.*

Jones, C. B.(1987). Evidence supporting the Pleistocene Forest Refuge Hypothesis for Primates. *Biotropica.* **19**, 373 - 375.

Juggins, S. and ter Braak, C. (1994). *Calibrate - Software for Multivariate analysis and graphical exploration of species / environment data sets.*

Kagambirwe, E. R. (1972). *Causes and consequences of land shortage in Kigezi.* Occasional paper 23. Department of Geography, Makerere University.

Kakuru, W. (1993). *Distribution of trees with the Bwindi-Impenetrable Impenetrable National Park.* Unpublished MSc. thesis. Makerere University, Uganda.

Kamuhangire, R. (1975). The pre-colonial economic and social history of east Africa, with special reference to south-western Uganda salt lakes region. In. *Hadith 5 Economic and social history of east Africa,* (Ogot B. A. ed.). East African Literature Bureau.

Katende, A. B. (1984). *Omubwindi Swamp - report on vegetation and habitats.* Makerere University.

Kendall, R. L. (1969). An ecological history of the Lake Victoria basin. *Ecological Monographes.* **39**, 121 - 176.

Kenworthy, J. M. (1966). Temperature conditions in the tropical highland climates of east Africa. *East African Geographical Review.* **4**, 1 - 11.

Kent, P. and Coker, P. (1992). *Vegetation description and analysis.* Academic Press. 373 pp.

Kershaw, A. P. and Bullman, D. (1994). The relationship between modern pollen samples and environment in the humid tropic region of north-eastern Australia. *Review of Palaeoecology and Palynology.* **83**, 83 - 96.

Kingdon, J. (1971). *East African Mammals: an Atlas of Evolution in Africa.* Academic Press. London, New York.

Kingdon, J. (1987). *Endemic mammals and birds of western Uganda: Measuring Uganda's biological wealth a plea for supra-economic values.* Presidential Address.

Kingdon, J. (1990). *Island Africa: The evolution of Africa's rare animals* and *plants.* Collins London. 287 pp.

Kingham, D. L. (1976). A study of the pollen morphology of tropical African and certain other Vernoniaceae (Compositae). *Kew Bulletin.* **31**, 9 - 26.

Kochel, R. C., Baker, V. R. and Patton, P. C. (1982). Palaeohydrology of south-west Texas. *Water Resources Research.* **18**, 1165 - 1183.

Kutzbach, J. E. and Otto-Bliesner, B. L. (1982). The sensitivity of the African - Asian monsoonal climate to orbital parameter changes for 9,000 yr B.P. in a low resolution GCM. *Journal of Atmospheric Science.* **39**, 1177 - 1188.

Kutzback, J. E. and Street-Perrot, F. A. (1985). Milankovitch forcing of fluctuations in the level of tropical lakes from 18,000 to 0 yr B.P. *Nature.* **317**, 130 - 134.

Lamb, H. F., Gasse, F., Benkaddour, A. El Hamnuti, N., van der Kuars, S., Perkins, W. T., Pearce, N. J. and Roberts, C. N. Relationship between century scale Holocene arid intervals in tropical and temperate zones. *Nature.* **373**, 134 - 137.

Langdale-Brown, I., Osmaston, H. A. and Wilson, J. G. (1964). *The Vegetation of Uganda* and *its bearing on land use*. Government Printer, Entebbe, 159 pp.

Lanning, E. C. (1970). Ntusi: An ancient capital site of Western Uganda. *Azania*. **5**, 39 - 54.

Leakey, E. C. (1931). *The Stone Age culture of Kenya Colony*. Cambridge University Press.

Lebrun, J. (1935). Les essences foresteriers des regions montagneuses du Congo oriental. Publis. Inst. Agron. Congo-Belge, Sersci 1.

Leggart, G. J. and Osmaston, H. A. (1961). *Working plan for the Impenetrable Central Forest Reserve, Kigezi District*. Forestry Department. Uganda.

Lezine, A. M. and Casanova, J. (1989). Pollen and hydrological evidence for interpretation of past climates in tropical Africa during the Holocene. *Quaternary Science Review*. **8**, 45 - 55.

Lind, E. M. (1956). Studies in Ugandan Swamps. *Uganda Journal*. **20**, 166 - 176.

Lind, E. M. and Morrison, M. E. S. (1974). *East African vegetation*. Longman, London 257 pp.

Livingstone, D. A. (1967). Post-glacial vegetation of the Ruwenzori mountains in Equatorial Africa. *Ecological Monographs*. **37**, 25 - 32.

Livingstone, D. A. (1975). Late Quaternary change in Africa. *Annual Review of Ecology* and *Systematics*. **6**, 249 - 280.

Livingstone, D. A. (1980). Environmental change in the Nile Headwaters. In. *The Sahara and the Nile*. (Williams, M. A. J. and Faure, H. eds.). Balkema, Rotterdam. 336 - 360.

Livingstone, D. A. (1982). Quaternary geography of Africa and the refuge theory. In. *Biological Diversity in the Tropics.* (Prance, G. T. ed.). Columbia University Press, New York. 680 pp.

Livingstone, D. A. and Clayton, W. D. (1980). An altitudinal cline in tropical African grass floras and its palaeoecological significance. *Quaternary Research.* **13**, 392 - 402.

Lönnberg, E. (1929). The development and distribution of the African fauna in connection with, and depending on, climatic changes. *Arkiv for Zoologica.* **21A**, 1 - 33.

Lowe, J. and Walker, M. (1991). *Reconstructing Quaternary Environments.* Longman Scientific and Technical. 389 pp.

Lugan, B., Sirven, P. and Verin, P. (1979). Etúde de la grotte due de Rwabugiri, Parc Nátional de l'Akagera (Rwanda). *Azania.* **16**, 145 - 154.

MacLean, M. R. (1996). Late Stone Age and Early Iron Agriculture settlement patterns in Rakai District, south-western Uganda. In. *The growth of farming communities in Africa from the equator southwards.* (Sutton, J. ed.). The British Institute in Eastern Africa, 338 pp.

Maeve, J. and Kelman, M. (1994). Maintenance of rain forest diversity in riparian forests of tropical savannahs: implications for species conservation during Pleistocene drought. *Journal of Biogeography.* **21**, 121 - 135.

Mahaney, W. C. (1990). Glacially crushed quartz grains in Late Quaternary deposits in the Virunga Mountains, Rwanda - indictors of wind transport from the north ? *Boreas.* **9**, 81 - 89.

Mahaney, W. C., Harinsen, R. and Spence, J. R. (1991). Glacial-interglacial cycles and development of the Afroalpine ecosystem on east African mountains. *Journal of African Earth Sciences.* **12**, 505 - 512.

Maley, J. (1987). Fragmentation de la Forêt Dense Humide Africaine et extension des biotopes môntagnards au Quaternaire récent. Nouvelles données polliniqués et chronologiques. Implications paléoclimatiques et biogéographiques. *Palaeoecology of Africa.* **18**, 307 - 334.

Maley, J. (1989). Late Quaternary climatic changes in the African rainforest: the question of forest refugia and the major role of SST variations. In. *Palaeoclimatology and Palaeometerology: Modern and past patterns of global atmospheric transport.* (Leisen, M. and Sarntheim, M. eds.). NATO Advances in Science Institutes, SERC,-Maths and Physics. **282,** 585 - 616. Kluver Academic Publishers, Dordrecht.

Maley, J. (1991). The African Rainforest, vegetation and palaeoenvironments during the late Quaternary. *Climatic Change.* **19,** 79 - 98.

Maley, J. (1995a). Les fluctuations majeures de la Forêt Dense Humide Africaine au cours des vingt derniers millénaires. In. *L'alimentation en Forét Tropicale: interactions bioculturelles et applications au devlopement.* (Hladik, C. M. ed.). UNESCO Parthenon Publishers, Paris, 14 pp.

Maley, J. (1995b). The impact of Arid phases on the African Rainforest during its geological history. In. *African Rain Forest Ecology and Conservation.* (Weber, W., Vedder, A., Morland, H. S., White, L. and Hart, T. eds.). Yale University Press.

Maley, J. (1996). The African rain forest - main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proceedings of the Royal Society of Edinburgh.* **104 B,** 31 - 73.

Maley, J. and Elenga, H. (1993). The role of clouds in the evolution of tropical African Palaeoenvironments. *Veille Climatique Satellitaire.* **46,** 51 - 63.

Marchant, R. A., Taylor, D. M. and Hamilton, A. C. (in press). Late Pleistocene and Holocene history of Mubwindi Swamp, south-west Uganda. *Quaternary Research.*

Marchant , R. A. and Taylor, D. M. (in press). Dynamics of montane forest in central Africa during the late Holocene: a pollen-based record from south-west Uganda. *The Holocene.*

Meadows, M. E. (1984). Contemporary pollen spectra and vegetation of the Nyika Plateau, Malawi. *Journal of Biogeography.* **11**, 223 - 233.

Melville, B. (1958). Gymnospermae. In *Flora of Tropical East Africa.* (Polhill, E. R. ed.). Crown Agents, London.

Mitchell, P. (1988). Human adaptation in South Africa during the Late Glacial Maximum. In. *Prehistoric cultures* and *environments in the Late Quaternary of Africa* (Bower J. and Lubell D. eds.). Cambridge University Press.

Moore, P. D. (1973). The influence of Prehistoric cultures upon the initiation and spread of Blanket Bog in Upland Wales. *Nature.* **241**, 350 - 354.

Moore, P. D. (1975). Origin of blanket mires. *Nature.* **245**, 267 - 269.

Moore, P. D. and Bellamy, D. J. (1974). *Peatlands.* Elk Sciences London.

Moore, P. D., Webb, J. A. and Collinson, M. E. (1991). *Pollen analysis.* 2ed. Blackwell Scientific Publications. 216 pp.

Moreau, R. E. (1966a). *The bird faunas of Africa and it islands.* Academic Press. New York and London. 424 pp.

Moreau, R. E. (1966b). Climatic change and the distribution of forest vertebrates in West Africa. *Journal of Zoology London.* **158**, 39 - 61.

Morrison, M. E. S. (1961). Pollen analysis in Uganda. *Nature.* **190,** 483 - 386.

Morrison, M. E. S. (1966). Low latitude vegetation with special reference to Africa. In. *Proceedings of the International Symposium on World Climate from 8000 to 0 B P.* Imperial College Royal Meteorological Society.

Morrison, M. E. S. (1968). Vegetation and climate in the uplands of south-western Uganda during the Later Pleistocene Period, 1. Muchoya Swamp, Kigezi District. *Journal of Ecology.* **56,** 363 - 384.

Morrison, M. E. S. and Hamilton, A. C. (1974). Vegetation and climate in the uplands of south-west Uganda during the later Pleistocene Period, 2. Forest clearance and other vegetational changes in the Rukiga highlands during the past 8,000 years. *Journal of Ecology.* **62,** 1 - 31.

Nicholson, S. E. (1994). Recent rainfall fluctuations in Africa and their relationship to past conditions over the continent. *The Holocene.* **4,** 121 -131.

Nicholson, S. E. (1996). Environmental Change within the historical period. In W. M. Adams, A. S. Goudie and A. Orme, editors, *The Physical Geography of Africa.* Oxford: Oxford University Press, 60-87.

Nicholson, S. E. and Flohn, H. (1980). African environmental and climatic changes and the general atmospheric circulation in the late Pleistocene and Holocene. *Climatic Change.* **2,** 313 - 348.

Nilsson, E. (1931). Quaternary glaciation and pluvial lakes in British East Africa. *Geografiska. Annaler.* **13,** 249 - 349.

Nilsson, E. (1940). Ancient changes of climate in British East Africa and Abyssinica. *Geografiska. Annaler.* **22,** 1 - 79.

Oliver, R. and Fage, J. D. (1984). *A short history of Africa.* Pelican Books, Chaucer Press, Bungay.

Osmaston, H. A. (1989). Glaciers, glaciation and equilibrium line altitudes on Kilimanjaro. In. *Quaternary* and *Environmental Research on East African Mountains*, (Mahaney, W. C. ed.). pp. 7 - 30. AA Balkema, Rotterdam.

Patterson III, W. A., Edwards, V. J. and Maguire, D. J. (1987). Microscopic charcoal as an indicator of fire. *Quaternary Science Reviews*. **6**, 3 -23.
Petts, G. and Foster, I. (1991). *Rivers* and *Landscape*. Edward Arnold. 274 pp.

Pitman, C. R. S. (1937). *The gorillas of the Kayonza region, Western Kigezi, south-west Uganda*. Annual Report, Smithsonian Institution.

Phillipson, D. W. (1977). *The Later Prehistory of Eastern and Southern Africa* London.

Phillipson, D. W. (1986). Life in the Lake Victoria Basin. *Nature*. **320**, 110 - 111.

Phillipson, D. W. (1988). *African Archaeology*. Cambridge University Press.

Plumptree, A. J. (1994). The effects of trampling damage by herbivores on the vegetation on the Parc-National-Des-Volcans, Rwanda. *African Journal of Ecology*. **32 (2)**,115 - 129.

Polhill, E. R. (1966) Ulmaceae. In. *Flora Tropical East Africa*. (Hubbard, D. E. and Milne-Redhead, E. eds.). Crown Agents, London.

Porkras, E. M. and Mix, A. C. (1985). Aeolian evidence for the spatial variability of the Late Quaternary climates in tropical Africa. *Quaternary Research*. **24**, 137 - 149.

Prentice, I. C. (1995). Biome 6000: palynological data as a test for Earth System models. Palynologie et Changements Globaux. Paris

Prentice, I. C. and Thompson-Webb III. (1994). Biome 6000: towards a global palaeovegetation data set. *Global Change News letters*. **19**, 1 - 4.

Punt, W. (1962). Pollen morphology of the Euphorbiaceae with special reference to taxonomy. *Wentia*. **7**, 1 -116.

Punt, W., Blackmore, S., Nilsson, S. and Thomas, A. L. E. (1994). *Glossary of pollen and spore terminology*. LPP contributions series No. 1. LPP Foundation, Utrecht. 71 pp.

Purseglove, J. W. (1950). Kigezi resettlement. *Uganda Journal*. **14**, 139 - 152.

Raup, D. M. (1993). Diversity crises in the geological past. In. *Biodiversity*. (Wilson, E. O. ed.). National Academy Press. Washington D. C.

Richardson, J. L. and Richardson, A. E. (1972). History of an African Rift lake and its climatic implications. *Ecological Monographs*. **42**, 449 - 534.

Ritchie, J. C. (1974). Modern pollen assemblages near the arctic tree line, Mackenzie Delta region, Northwest Territories. *Canadian Journal of Botany*. **52**, 381 - 396.

Roberts, N. (1990). Ups and downs of east African Lakes. *Nature*. **346**, 107.

Roberts, N., Taied, M., Barker, P., Damnati, B., Icole, M. and Williams, D. (1993). Timing of the Younger Dryas climatic event in East Africa from lake level changes. *Nature*. **366**, 146 - 148.

Robertshaw, P. (1991). Gego falls: A complex site east of Lake Victoria. *Azania*. **26**, 63 - 195.

Robertshaw, P. (1994). Archaeological survey, ceramic analysis, and state formation in western Uganda. *The African Archaeological Review*. **12**, 105 - 131.

Robertshaw, P. (1996) The Interlacustrine Iron Age. Annual report 1995 - 1996 of the British Institute in East Africa.

Roeland, J. C., Guiot, J., and Bonnefille, R. (1988). Pollen et reconstruction quantitative du climat. Validation des donnees d'Afrique órientale. *C. R. Academie Scientifque Paris.* **307 ser 2,** 1735 - 1740.

Rosqvist, G. (1990). Quaternary glaciations in Africa. *Quaternary Science Reviews.* **9,** 281 - 297.

Rossignol-Strick, M. (1983). African monsoons, an immediate climatic response to orbital insulation. *Nature.* **30,** 46 - 49.

Runge, J. and Runge, F. (1996). *Late Quaternary palaeoenvironmental conditions in eastern Zaire (Kivu) deduced from remote sensing and morpho-pedological and sedimnetological studies.* Actes 2eme symposium de Palynologie Africaine, Tervirens, 19 pp.

Rwandusya, Z. (1972). The origin and settlement of the people of Bufumbria. In. *A history of Kigezi in south-west Uganda* (Denoon, D. ed.). National Trust, Kampala.

Salgado-Labouriau, M. L. (1982). Pollen morphology of the Compositae of the northern Andes. *Pollen et Spores.* **24,** 397 - 452.

Schmidt, P. R. (1980). Early Iron Age settlements and industrial locales in West Lake. *Tanzania Notes* and *Records.* **84 - 85,** 77 - 94.

Schroenbrun, D. L. (1992). The contours of vegetation change and human agency in Eastern Africa's Great Lakes region about 2,000 B.P. to about 1,000 A. D. Draft paper submitted to *Forest and conservation history.*

Schoenburn, D. L. (1993). We are what we eat. Ancient agriculture between the Great Lakes. *Journal of African History.* **34,** 1 - 31.

Schopf, J. M. (1975). Modes of fossil preservation. *Review of Palaeobotany and Palynology*. **20**, 27 - 53.

Schwartz, D. (1992). Asséchment climatique vers 3,000 B.P. et expansion Bantu én Afrique centrale atlantique: quelques réflexions. *Bulletin Sociéte Geologie France*. **163**, 353 - 361.

Scott, L. (1982). Late Quaternary fossil pollen grains from the Transvaal, south Africa. *Review of Palaeobotany and Palynology*. **36**, 241 - 278.

Scott, L., Cooremans, B., de Wet, J. S. and Vogel, J. C. (1991). Holocene environmental changes in Namibia inferred from pollen analysis of swamp lake deposits. *The Holocene*. **1**, 8 - 13.

Singer, S. F. (1996). A preliminary critique of IPCC's second assessment of climatic change. In. *The Global Warming Debate* (Elsley, J. ed.). The European Science and Environment Forum, London, UK.

Shinnie, P. L. (1967). *Meroe*. London

Sirocko, F., Garbe-Schönberg, D., McIntyre, A. and Molfine, B. (1996). Teleconnections between the subtropical monsoons and high latitude climates during the last deglaciation. *Science*. **272**, 526 - 529.

Smith, A. R. (1987). Euphorbiaceae (Pt 1). In. *Flora Tropical East Africa*. (Polhill, E. R. ed.). Balkema, Rotterdam-Boston.

Smith, B. N. and Epstien, S. (1971). Two categories of ^{13}C / ^{12}C ratio for higher plants. *Plant Physiology*. **47**, 380 - 384.

Snowden, J. D. (1933). A study in altitudinal zonation in south Kigezi and on Mounts Muhavura and Mgahinga, Uganda. *Journal of Ecology*. **21**, 7 - 27.

Snowden, J. D. (1953). *The grass communities* and *mountain vegetation of Uganda*. Crown Agents, London.

Soper, R. C. (1971a). A general review of the Early Iron Age for the southern half of Africa. *Azania*. **6**, 5 - 38.

Soper, R. C. (1971b). Iron Age archaeological sites of the Chabi Sector of Murchison Falls National Park, Uganda. *Azania*. **6**, 53 - 58.

Sosef, M. (1994). *A study of the Begoniaceae of Tropical Africa.* Wagenigen Agricultural University papers, 94 - 1.

Souwumi, M. A. (1991). Late Quaternary environment in equatorial Africa: palynological evidence. *Palaeoecology of Africa*. **22**, 213 - 238.

Spieksma, F. T. M., Nikkels, B. H. and Bottema, S. (1994). Relationship between recent pollen deposition and airborne pollen concentration. *Review of Palaeobotany and Palynology*. **82**, 141 - 145.

Ssemmanda, I. and Vincens, A. (1993). Végétation et climate dans le Bassin du lac Albert (Oganda, Zaïre) depuis 13,000 ans BP. Apport de la palynologie. *C. R. Academie Science. Paris* t, **316 (2)**, 561 - 567.

Stager, J. C. (1982). The diatom record of Lake Victoria: the last 17,000 years. *Proceedings of the 7th Diatom symposium*, 455 - 476.

Stager, J. C., Cumming, B. and Meeker, L. (1997) A high resolution 11,400-yr. diatom record from Lake Victoria. East Africa. Quaternary Research. **47**, 81 - 89.

Street-Perrot, A. F. (1994). Palaeo-perspectives: changes in terrestrial ecosystems. *Ambio*. **23**, 37 - 43.

Street, A. F. and Grove, A. T. (1979). Global Maps of lake-level fluctuations since 30,000 yr B.P. *Quaternary Research*. **12**, 83 - 118.

Street-Perrot, A. F. and Perrot, R. A. (1988). Holocene vegetation, lake levels and climate of Africa. In. *Global climates since the last glacial maximum.* (Wright, H. E., Kutzbach, J. E., Thomson Webb III, Ruddiman, W. F., Street-Perrot, F. A. and Bartlein, P. J. eds.). University of Minnesota Press.

Street-Perrot, A. F. and Perrot, R. A. (1990). Abrupt climatic fluctuations in the tropics, the influence of Atlantic Ocean circulation. *Nature.* **343**, 607 - 612.

Sulzman, E. W., Poiani, K. A. and Kittel, T. G. F. (1995). Modelling human-induced climatic change: a summary for environmental managers. *Environmental Management.* **19**, 197 - 224.

Summerfield, M. A. (1996). Tectonics, Geology and Long-term Landscape Development. In. *The Physical Geography of Africa.* (Adams, W. M., Goudie, A. S. and Orme, A. R. eds.). Oxford University Press. 429 pp.

Sutton, J. E. G. (1971). Temporal and spatial variability in African Iron Furnaces. In. *African Iron Working, ancient* and *traditional* (Haaland, K. and Shinnie, P. L. eds.). Norwegian University Press. Bergen. 209 pp.

Sutton, J. (1990). *A Thousand Years of East Africa.* Nairobi: British Institute in East Africa.

Sutton, J. E. G. (1993). The antecedents of the Interlacustrine Kingdoms. *Journal of African History.* **34**, 33 - 64.

Swain, A. M. (1973). A history of fire and vegetation in north-eastern Minnesota as recorded in lake sediments. *Quaternary Research.* **3**, 383 - 396.

Talbot, M. R. and Johannessen, T. (1992). A high resolution palaeoclimatic record for the last 27,500 years in tropical West Africa from the carbon and nitrogen isotopic composition of lacustrine organic matter. *Earth and Planetary Science Letters.* **100**, 23 - 37.

Talbot, M. R., Livingstone, D. A., Palmer, P. G., Maley, J., Melack, J. M., Delibrias, G. and Gullikson, S. (1984). Preliminary results from sediment cores from lake Bosumtwi, Ghana. *Palaeoecology of Africa*. **16**, 173 - 192.

Taylor, D. M. (1988). *The environmental history of south west Uganda*. Unpublished D. Phil thesis, University of Ulster, Colraine.

Taylor, D. M. (1990). Late Quaternary pollen records from two Ugandan mires: evidence for environmental change in the Rukiga highlands of south-west Uganda. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **80**, 283 - 300.

Taylor, D. M. (1992). Pollen evidence from Muchoya swamp, Rukiga highlands (Uganda). *Bulletin Science General France*. 163, 77 - 82.

Taylor, D. M. (1993). Environmental change in montane south-west Uganda: a pollen record for the Holocene from Ahakagyezi Swamp. *The Holocene*. **3**, 324 - 332.

Taylor, D. M. (1996). Mountains. In. *The Physical Geography of Africa*. (Adams, W. M., Goudie, A. S. and Orme, A. R. eds.). Oxford University Press. 429 pp.

Taylor, D. M. and Marchant, R. (1996). Human impact in the lacustrine region: long-term pollen records from the Rukiga highlands. In. *The growth of farming communities in Africa from the equator southwards*. (Sutton, J. ed.). The British Institute in Eastern Africa, 338 pp.

Taylor, K. C., Lamorey, G. W., Doyle, G. A., Alley, R. B., Grootes, P. M., Mayewski, P. A., White, J. W. C. and Barlow, L. K. (1993). The flickering switch of late Pleistocene climatic change. *Nature*. **361**, 432 - 435.

Tennant, J. R. (1968). Araliaceae. In. *Flora Tropical East Africa*. (Milne-Readhead, E. and Polhill, R. M. eds.). Crown Agents.

ter-Braak, C. J. F. (1988). *CANOCO - a FORTRAN program for Canonical Commnity Ordination by [Partial] [Detremded] [Canonical] Correspondence analysis (Version 2.0).* TNO Institute of Applied Computer Science - Wageningen.

Tröels-Smith, J. (1955). Karakterisering af lose jordarter. *Dan. Geol. Unders. IV Raekke.* **3**, 1 - 73.

Turnbill, C. (1961). *The Forest People*, New York.

Turnbill, C. (1965). The Mbuti pygmies of the Congo. In. *African Peoples* (Gibbs, J. D. ed.).

Turnbill, C. (1966). *Wayward Servants*, London.

Turyanhikayo-Rugyem, B. (1942). *The history of the Bakiga in south-west Uganda and northern Rwanda between about 1500 and 1930.* PhD thesis University of Michigan.

van Campo, E. (1986). Monsoon fluctuations in two 200,000 year oxygen isotope pollen records off south-west India. *Quaternary Research.* **26**, 376 - 388.

van Campo, E. and Gasse, F. (1993). Pollen and diatom inferred climatic and hydrological changes in Sunmxi Co Basin (western Tibet) since 13,000 yr B.P. *Quaternary Research.* **39**, 300 - 313.

van der Maarel, E. (1979). Transformations of cover - abundance values in phytosociology and its effect on community similarity. *Vegetatio.* **39**, 97 - 114.

van Norton, F. (1977). Excavations at Mtupi cave. *Antiquity.* **51**, 35 - 40.

van Norton, F. (1979). The Early Iron Age in the interlacustrine region. The diffusion of iron technology. *Azania.* **14**, 61 - 80.

van Riet-Lowe, C. (1952). *The Pleistocene geology and prehistory of Uganda, pt 2 Prehistory*. Geology society of Uganda memoirs no 6.

van Zindderen-Bakker, E. M. (1962). A late glacial and post glacial climatic correlation between east Africa and Europe. *Nature*. **194**, 201 - 203.

van Zindderen-Bakker, E. M. and Coetzee, J. A. (1972). A re-appraisal of the Late Quaternary climatic evidence from Tropical Africa. *Palaeoecology of Africa*. **7**, 151 - 181.

van Zindderen-Bakker, E. M. and Coetzee, J. A. (1988). A review of the Late Quaternary pollen studies in east and central Africa. *Review of Palaeobotany and Palynology*. **55**, 155 - 174.

Vansina, J.(1984). Western Bantu expansion. *Journal of African History*. **25**, 129 - 145.

Verdcourt, P. H. (1976) Rubiaceae. In. *Flora Tropical East Africa*. (Hubbard, D. E. and Milne-Redhead, E. eds.). Crown Agents, London.

Vincens, A. (1989). Paleoenvironements du bassin nord-Tanganyika (Zaire, Burundi, Tanzanie) au cours des 13 dérniers mille ans: ápport de la pálynologie. *Review of Palaeobotany and Palynology*. **61**, 69 - 88.

Vincens, A. (1993). Nouvelle séquence pollinique du Lac Tanganyika: 30,000 ans d'histoire botanique et climatique du Bassin Nord. *Review of Palaeobotany and Palynology*. **78**, 381 - 394.

Vincens, A., Buchet, G., Elenga, H., Fournier, M., Martin, L., de Namur, C., Schwartz, D., Servant, M. and Wirrmann, D. (1994). Changement majeur de la vegetation du lac Sinnda (vallee du Niari, Sud-Congo) consecutif a l'assechement climatique Hòlocene superieur: ápport de la pálynologie. *C.* R. *Acad. Sci. Paris*. **318 serie II**, 1521 - 1526.

Vitousek, P. M. (1994). Beyond global warming: ecology and global change. *Ecology* **75**, 1651 - 1655.

Waddington, J. C. B. (1969). A stratigraphic record of the pollen influx to a lake in the Big Woods of Minnesota. *Geology Society of America Special Papers*. **123**, 263 - 282.

Walling, D. E. (1996). Hydrology and Rivers. In. *The Physical Geography of Africa*. (Adams, W. M., Goudie, A. S. and Orme, A. R. eds.). Oxford University Press. 429 pp.

Wang, F. B., Lin, B. H. and Yan, G. (1993). Organic carbon. Stable isotopic composition from peat in Ruoergi Plateau, Eastern part of Qinghai-Xizang Plateau. *Chinese Science Bulletin*. **38**, 1114 - 1118.

Watt, A. W. M. (1956). *Working plan for the Euchoya Central Forest Reserve, Kigezi District, Uganda, 1956 - 1960.* Uganda Forest Department, Entebbe.

Wayland, E J (1921). Rifts, Rivers, Rains and early man in Uganda. *Journal of the Anthropology Institute*. **64**, 333 - 352.

Wayland, E. J. (1924). The Stone Age in Uganda. *Man*. **124**, 169 - 170.

Wendorf, F., Close A. E., Schild, R., Wasylikowa, K., Housley, R. A., Harlan, J. R. and Krolik, H. (1992). Saharan exploitation of plants from 8,000 yr. B.P. *Nature*. 359, 721 - 724

White, F. (1983). *The vegetation of Africa*. UNESCO, Switzerland. 356 pp.

White, R. G. (1969). Blacksmiths of Kigezi. *Uganda Journal*. **33**, 65 - 73.

Williamson, D., Thouveny, N., Hillaire-Marcel, C., Mondeguer, A., Taieb, M., Tiercelin, J. J. and Vincens, A. (1991). Chronological potential of palaeomagnetic oscillations recorded in Late Quaternary sediments from Lake Tanganyika. *Quaternary Science Reviews*. **9**, 351 - 361.

Winkler, M. G. (1985). Charcoal analysis for palaeoenvironmental interpretation. A chemical assay. *Quaternary Research*. **23**, 313 - 326.

Wright, J. R. and Wright J. E. (1967). The use of surface samples in Quaternary pollen analysis. *Review of Palaeobotany and Palynology*. **2**, 321 - 330.