Contemporary Pollen Spectra from the Natal Drakensberg and their Relation to Associated Vegetation Communities

THESIS

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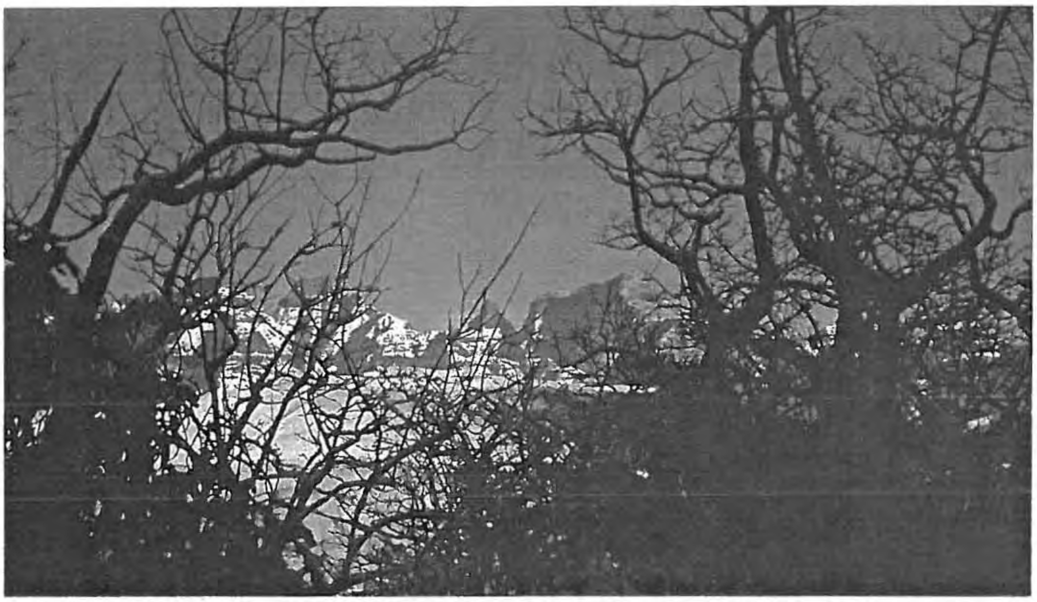

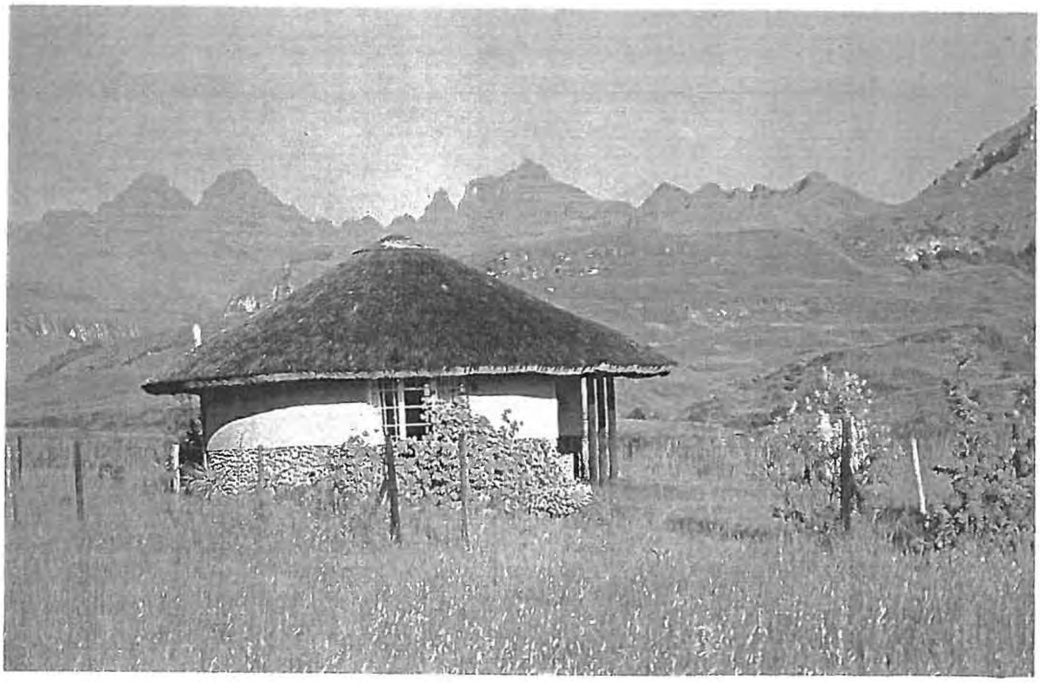

ABSTRACT

The research focuses on the contemporary pollen rain - vegetation relationship for vegetation communities within the Natal Drakensberg, a region which is recognized as having the potential for extensive palynological investigations. The objective was to investigate the fundamental assumption underlying palynology, viz: that the pollen rain of a particular region is indicative or representative of the existing vegetation of that region. If the modern pollen rain is indicative of and/or distinctive for a particular vegetation community then the principle of methodological uniformitarianism can be applied, which states that the present-day patterns and relationships can provide a factual basis for the reconstruction of the past through the extrapolation of modern analogues backwards in time.

A vegetation survey was conducted in thirteen communities identified as pertinent to the research and a two-year modern pollen rain sampling programme was carried out, using both surface soil and pollen trap samples as a means of recording and quantifying the pollen rain. Once the necessary sample preparation and pollen counts had been performed, descriptive and numerical/statistical methods were employed to determine and describe the existing pollen - vegetation relationship.

Descriptive analysis of the data sets was carried out with the aid of spectra depicted as rotated bar graphs and representing the relative percentage frequencies of the collected/counted taxa. Annual and seasonal pollen influx values were calculated and presented. Analysis of variance was applied to test various hypotheses related to sampling strategy and pollen influx variation. Statistical methods employed were two-way indicator species analysis (a classification analysis technique), detrended correspondence analysis and principal components analysis (ordination techniques), canonical correlation analysis (for data set association) and multiple discriminant analysis (for determination of vegetation zonal indices). The latter technique allowed for the probability of modern analogues to be assessed which are necessary for accurate interpretation of fossil pollen assemblages if the assumption under investigation is correct.

The findings of the study were that the modern pollen rain - vegetation assumption holds true. Recommendations are put forward regarding future contemporary pollen studies with regards to the number of soil and pollen trap samples required, the magnitude of the pollen count and the numerical/statistical techniques most appropriate to clearly interpret the results.

The conclusions are that future fossil pollen spectra can be expected to provide a good indication of former regional vegetation patterns for the study region. The study has extended the limited understanding of the contemporary pollen rain - vegetation relationship in South Africa and enables the interpretation of fossil pollen spectra to be carried out with greater confidence. This in turn lends greater credibility to possible Quaternary environmental change models required to help understand present and possible future environmental change.

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Frontispiece: Scenes from Cathedral Peak Forestry and Research Station. The upper photograph depicts the Cathedral Peak, The Bell and The Inner and Outer Horns along the Drakensberg Escarpment in winter. The lower photograph is of 'Home Sweet Home' at the Research Station.

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CHAPTER ONE
INTRODUCTION

The earth's climate is a dynamic system and climatic fluctuations during the last 2 million years have had a marked effect on the present environment (Hamilton, 1982). On a broad scale, geographical ranges of vegetation communities coincide with geographical patterns of climate which have led to the use of vegetation as an index of climate. The main objectives of the elucidation of palaeo-vegetation communities, and in turn, inferred palaeo-environments, is to determine and describe variations in the environment in the period beyond the range of meteorological records. The ultimate goal is to understand the physical causes of these variations. By applying principles established through present day research, it is possible to understand the mechanisms of change and the pattern of past environments in both time and space (Deacon and Lancaster, 1988).

These environmental change studies occupy a significant place within environmental sciences, particularly within the Quaternary, and are assumed to be reflected in vegetation patterns (Goudie, 1977). A number of techniques exist for the reconstruction of past vegetation patterns, but probably the most widely used and successful of these techniques, at the present, is the analysis of fossil pollen grains and spores present in a stratigraphical series of sediment.

Palynology, the analysis of pollen and spores, has been at the heart of Quaternary environmental reconstruction for the last three-quarters of a century (MacDonald and Edwards, 1991). As a tool in the elucidation of former environments, pollen analysis, coupled with radiocarbon dating of organic sediments within which pollen is preserved, is unequalled in the temperate regions. It has, however, been less widely applied in tropical (Flenley, 1979) and arid (Scott, 1984a) environments. The technique offers a perspective which can allow a detailed enough view of vegetation to study interactions between taxa and the cause, nature and rates of change in response to environmental change (Dodson, 1988). The principles of the technique provide a means of reconstructing past flora, past plant populations and the past vegetation. The reconstruction of past plant communities represents a major step towards the reconstruction of the past ecosystem, as the plant community is its most complex part. Once the community has been established, inferences can be deduced about the past environment, assuming the ecological requirements and tolerances of the species and the communities are known (Birks and Gordon, 1985).

Pollen analysis is a technique employed to elucidate certain problems, and therefore the application of the technique must be such as to solve the relevant problem. There is no one all-embracing method as methods and problems are interrelated. The medium of pollen production is the vegetation, and therefore an understanding of the vegetation surrounding a site is a paramount demand for utilization of pollen analytic data. Vegetation provides an invaluable expression of the limiting environmental factors, both physical and biological, of a particular region and it is this concept which forms the basis of pollen analysis and the resultant reconstruction of past environments (Scott, 1979).

The record of past vegetation change provides an important indication of how vegetation will respond to future climatic fluctuations, and this will in turn provide information as to the future agricultural and silvicultural potential of various regions. While the actual magnitude and duration of the response of vegetation to climatic change is not well understood, variations in the earth's climate are often deduced from changes in past vegetation recorded by fossil pollen. The sensitivity of pollen as an index of climatic change has been emphasized (Birks, 1981a; Davis and Botkin, 1985). Quaternary palynological data can be used to assess the relative importance of environmental change as opposed to independent human interference (for example grazing and man-induced fire regimes) in bringing about past changes in vegetation. This will in turn allow for assessment of the importance of various human activities in the context of global environmental change (Huntley, 1990).

The vegetation of a region is an expression of a complex of ecological variables, the most dominant of which is climate. Therefore, long term climatic fluctuations will be reflected in shifts or migration of particular vegetation communities, especially in areas adjacent to climatic and vegetation boundaries, such as ecotones. There is often a lag phase between climatic change and migration of species; this lag can, in some respects, be alleviated by studying environmental changes resulting from the effects of altitude in montane regions. These migrations are exaggerated in montane regions where altitude becomes an important ecological factor. Thus as the climate fluctuates over time, distinctive vegetation communities will ascend or descend depending on the optimum environmental conditions of the vegetation. Each plant species will react to climatic fluctuations according to its ecological adaptability, consequently many species with similar adaptability will occupy similar habitats. It is these habitats that migrate with climatic changes and not whole vegetation 'belts' as is often implied by oversimplification of the concept of taxa 'following' optimum conditions (van Zinderen Bakker and Coetzee, 1988). These migrations can be recorded if a site conducive to pollen entrapment and preservation, such as acidic anaerobic soils, lies within the region.

Underlying the science of palynology are two basic assumptions, firstly that the pollen rain provides some indication of the vegetation existing in an area and secondly, that the vegetation of the area in some way reflects the surrounding environment (Moore, Webb and Collinson, 1991). The latter assumption regarding whether or not past vegetation communities have been in equilibrium with climate has been thoroughly examined over the last 5-10 years, culminating in an extensive journal review (Vegetatio, 67, 1986). To date the question of degree of equilibrium between vegetation and climate is still unresolved and will continue to be a focus of attention as climatic models improve in both spatial and temporal resolution.

The former and more fundamental assumption underlying pollen analysis is that pollen provides some indication of the modern vegetation existing in the area. It is assumed that the pollen spectrum at a particular depth (or age) within a sequence in some way represents the contemporary, pollen-producing flora which was/is contributing to the pollen rain at that time. The relationship between pollen rain and vegetation is complex and modern pollen studies are an attempt to increase the present understanding and interpretation of this relationship.

To substantiate fossil pollen analysis, an investigation of the modern pollen rain of the study area is essential. Livingstone (1975) stressed that any imprecision in palaeo-environmental interpretation is not so much the fault of the pollen record as our own in failing to accurately model and estimate the pollen-vegetation relationship. From the fossil pollen record one cannot conclude with any degree of confidence that a particular community was present in the past on the basis of fossil pollen abundance of a particular species common or indicative of a vegetation community. One needs modern analogues or 'signatures' of present day communities, in the form of modern pollen spectra, which can be used as references against which fossil spectra can be compared. Thus a good understanding of the relationship is important, since it is this relationship between modern pollen rain and the pollen actually arriving at sites and becoming enmeshed and preserved that indicates the usefulness of the fossil pollen data.

The data available for South African contemporary pollen rain - vegetation relationships is minimal in comparison with Europe and North America where palynological studies have been conducted for over 80 years. In these regions, due to a large data base on the present-day relationship, a fossil pollen spectrum can be interpreted with a high degree of confidence. As the use of fossil pollen analysis increases in South Africa it is apparent that such a data base is sadly lacking and South Africa is still in the pioneering stage of this science. As a consequence, in order to substantiate conclusions drawn from previous pollen analyses in South Africa, it is necessary to carry out an extensive modern pollen rain programme. Although it is important to continue with palaeo-environment research, it is necessary to provide confidence levels by means of increasing the initial data base on which palaeo-environmental studies rely. The data base that this research has obtained for the Natal Drakensberg will allow for confident evaluation of future pollen analysis and possibly re-evaluation of existing research in this science.

A number of modern pollen studies have been performed at the few sites where fossil pollen studies have been conducted in South Africa (see Chapter 3). These relied to a large extent on the use of surface soil samples to obtain an indication of how representative the modern pollen is of the existing vegetation. However as modern pollen studies have not been the main focus of these investigations the studies give no indication of how many samples were required to gain a confident representation of the pollen rain. It is important therefore to determine the number of samples and the magnitude of the count required within distinct vegetation communities in those areas where fossil pollen analysis is viable, so as to enhance the understanding of the modern pollen rain - vegetation relationship in South Africa and in turn allow for more confident interpretation of fossil pollen analysis.

In South Africa, the xeric climate mitigates against the development of organic sediments and permanent natural lakes which traditionally have been the sites of palynological investigations. This site scarcity has inhibited the study of Quaternary change, although 'alternative' palynological sites have been discovered and used with a great deal of success. Organic sediments developed in association with hot springs have yielded pollen assemblages, such as Florisbad (van Zinderen Bakker, 1957), Wonderkrater (Scott, 1982a) and Aliwal North (Coetzee, 1967). At Groenvlei in the southern Cape Wilderness lakes region lacustrine sediments have preserved pollen from the late Quaternary period (Martin, 1968). Studies from high altitude headwater valleys, which form vleis, have been found to contain suites of stratified organic and inorganic sediments which have yielded pollen assemblages, for example the Drakensberg (van Zinderen Bakker, 1955), and more recently, the mountainous regions of the semi-arid karoo (Meadows and Meadows, 1988; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b). Meadows (1988a) points out that although these high altitude headwater vleis reveal a history of vegetation change through their fossil pollen remains, they also produce a history of environmental change within the clastic and organic sediments per se. Often palynological studies in South Africa have been conducted on 'alternative' fossiliferous materials, such as cave sediments (van Zinderen Bakker, 1982; Deacon *et al*, 1984; Opperman and Heydenrych, 1990), pan deposits (Horowitz *et al*, 1978), coprolites (Scott, 1987a) and hyrax middens (Scott and Bousman, 1990).

Since palynological reconstruction of Quaternary environments in South Africa is based primarily on comparisons of the fossil pollen spectra with recent spectra from different vegetation types and climatic regions (Scott, 1984b), it is necessary to obtain a knowledge about the relationship between pollen spectra and various vegetation communities. In this way pollen spectra of the modern vegetation can be constructed to provide a means of estimating the nature and extent of past conditions. In the absence of studies of modern pollen rain, Wright (1967) has suggested that the reconstruction of the former vegetation of an area becomes little more than speculation unless the fossil pollen assemblage can be related to a vegetation of known structure and composition. Therefore the need to strengthen the interpretation of the fossil record and the past climate, with the aid of modern analogues, cannot be overemphasized (Heusser, 1978).

At the Southern African Society for Quaternary Research International Symposium held in Swaziland in 1983 H.J. Deacon in his concluding address reviewed the palaeoclimatic data presented at the conference and noted the need for complementary lines of evidence in support of inferences from single sets of observations (Deacon, Lancaster and Scott, 1984). He stressed the necessity for critical evaluation of data and in the design of future research projects strongly recommended that modern analogues be used to model past climates and that biological data be used as checks against inference drawn from other lines of evidence. C.Heusser (in Deacon, Lancaster and Scott, 1984) in turn stressed the importance of quantifying pollen data and encouraged the search for long pollen sequences along the Drakensberg, where the vegetation would have been sensitive to temperate changes in the past.

1.1 RESEARCH OBJECTIVES

Whereas previously the contemporary pollen rain - vegetation relationship was a secondary consideration in what were primarily fossil pollen studies, this study has concentrated on the contemporary pollen rain - vegetation interaction. It was the intention of this study to critically assess the basic assumption underlying palynological investigations, namely that the pollen rain is indicative of the existing vegetation forming the vegetation community being studied.

The research focuses on the contemporary pollen rain - vegetation interaction for vegetation communities within a region which has been recognized as having the potential for extensive palynological investigations, the Natal Drakensberg (Deacon, Lancaster and Scott, 1984). The techniques involved are surface soil samples, a technique previously used in modern pollen work, and pollen traps, a technique which has yet to be developed to its full potential in southern Africa, a region where it is not always possible to obtain a good surface sample due to the aridity of the region.

The specific objectives of the study are to:

1) identify, describe and quantify the vegetation communities in the research area most likely to migrate or be affected by environmental change and therefore be of value in palynological studies;
2) construct a contemporary pollen reference collection of the pollen/spore producing flora of the region;
3) quantify the modern pollen rain of the identified vegetation communities by means of surface soil samples and pollen traps;
4) compare the two modern pollen sampling techniques;
5) compare the modern pollen spectra with the existing vegetation communities from which they were produced;
6) recommend a sampling strategy for future modern pollen rain studies in South Africa;
7) develop modern pollen spectra analogues which can be of use in future fossil pollen analysis.

The overall aim is to answer the question of whether the modern pollen rain is indicative of the vegetation community from which it was derived. Although the results relate to a specific, relatively small scale region, the Natal Drakensberg, this region has the potential to be an extremely important palynological research area. The observations will extend the limited understanding of the contemporary pollen rain - vegetation relationship in South Africa and will enable one to interpret South African fossil pollen spectra with more confidence and in turn give more credibility to possible Quaternary environmental change models.

CHAPTER TWO
THEORETICAL BACKGROUND

2.1 INTRODUCTION

Quaternary aged deposits have been studied more intensively than those of any other time span of comparable magnitude. Data to research and reconstruct this time period have been obtained from geomorphic and sedimentary sources and includes the use of biological and archaeological evidence. A large proportion of the evidence is obtained from the presence or absence and abundance of organisms that are found as fossils - foraminifers, mollusca, arthropods, vertebrates, algae, bryophytes and vascular plants, all of which contain compounds resistant to decay such as calcite, aragonite, chitin, silica, cutin, lignin and, in the case of pollen grains, sporopollenin (Birks and Birks, 1980; Shackley, 1981). Pollen grains and spores of vascular plants dominate the fossils preserved in terrestrial Quaternary sediments, consequently terrestrial Quaternary palaeoecology is predominantly investigated by the technique of stratigraphical pollen analysis (Cushing and Wright, 1967).

Interpretations of Quaternary deposits, particularly pollen rich sediments, are almost entirely from the extrapolation of present-day ecological observations backwards in time. Past communities, environments and ecosystems are reconstructed by analogy with present-day systems and with known ecological preferences of the taxa and communities involved. Implicit in all Quaternary pollen analytical studies, as in all palaeoecology, is the assumption and philosophical principle of methodological uniformitarianism, or actualism, which states that the nature of modern processes are the same as in the past and thus modern laws of nature can be extended backwards in time and used to reconstruct and explain past events. There is no way to prove or disprove the principle, as it is the basic logic and methodology of all historical sciences, including Quaternary palaeoecology (Rymer, 1978; Birks and Birks, 1980). All reconstructions of the past therefore require some application and extrapolation in time of modern ecological or geological knowledge.

The use of pollen data to reconstruct climate is based on certain assumptions arising from actualism: 1) species respond rapidly to climatic change and therefore 2) species' distributions and abundances are always in equilibrium with climate; 3) there are no other factors of importance that interfere with the way individual plant species react to climate, such as interaction between species and, 4) vegetation composition is accurately and consistently reflected by pollen assemblages.

2.2 EARLY HISTORY OF PALYNOLOGY

The year 1916, when Lennart von Post presented the first modern percentage pollen diagrams, is commonly heralded as the foundation of the science of palynology, although palynological history was initiated much further back in time. The study of pollen grains commenced with the improvement in construction of microscopes in the middle of the seventeenth century (Manten, 1967), since then pollen morphological studies have been closely associated with notable improvements in the development of the microscope. Nehemial Grew, in the eighteenth century, clearly established that, although pollen grains tend to be globular in form, they are of different size and form in different species, but those of the same species are all alike. Many botanist have contributed to the field of pollen morphology. Three 'early' researchers who stand out are H. von Mohl who, in 1834, published the first detailed descriptive classification of pollen form, C.J. Fritzsche who during the mid nineteenth century observed and accurately described the fine structure of the pollen wall and C.A.H. Fischer who made thorough studies of the pollen morphology of approximately 2 200 plant species (Manten, 1967).

By the late eighteen-nineties the basic principles of pollen analysis had been laid down and in 1905 Gustaf Lagerheim, from observations in Sweden, confirmed Harald Lindberg's discovery in Finland that the percentages of certain pollen grains can differ in successive layers. It was through Lagerheim, who made pollen and spore identifications from material collected by Lennart von Post, that von Post learned of the value of plant microfossils. Von Post first used pollen grains as stratigraphic indicators to solve the problem of whether or not stub horizons were synchronous or not during research carried out in 1908, and used the technique to validate distinctive geological Quaternary boundaries. Pollen analysis was now recognized as a new method for stratigraphic studies, the product being a pollen diagram. The first pollen diagrams were published in the Bulletin of the Geological Institute of Uppsala by von Post in 1916. Between 1916 and 1982 approximately 36 350 palynological papers have appeared worldwide (Edwards, 1986), proof of the importance and usefulness of pollen analysis as a stratigraphical tool.

2.3 PRINCIPLES

Pollen analysis was introduced by von Post (1916) as a geological tool, and it is therefore appropriate that it should adhere to geological principles. The greatest of these is Lyell's (1850 in Rymer, 1978) doctrine of uniformity-'The present is a key to the past'. In palynology this means that the pollen rain from existing plant communities should be used to interpret fossil pollen spectra in terms of the vegetation. A pollen diagram is a dynamic record of vegetation history (Moore, Webb and Collinson, 1991) and, on a large scale, vegetation change is the result of climatic change. Vegetation history, therefore, predominantly through the technique of pollen analysis, provides a chronological framework and a diary of climatic events (Walker, 1982). Early palynological work tended to place too great an importance on the effects of climate on vegetation change. It is now recognized that other factors such as edaphic and anthropogenic factors are also of significance to vegetation development, but have varying lag times which influence the rate of vegetation development (Sugden, 1990).

Pollen analysis depends on the fact that all angiosperms and gymnosperms produce pollen and pteridophytes spores, which are released or dispersed during reproduction. An important feature of pollen grains and spores are their sculptured outer casing or exine, which renders them easily recognizable and, due to species specificity, allows for identification, in theory, to species level. The exine is composed mainly of sporopollenin, a polymer of carotenoids and carotenoid esters, and is regarded as the most resistant organic material of direct biological origin found in nature (Brooks and Shaw, 1978). The resistance of sporopollenin to microbiological, chemical and physical degradation permits study of the morphology and microstructure of pollen grains and spores and is seen as the basis of the science of palynology. Under conditions of low microbiological activity, particularly in acidic anaerobic situations, sporopollenin decomposes extremely slowly; consequently pollen and spores are preserved or 'fossilized' under these conditions. These conditions include vleis, lake sediments, waterlogged acidic soils, marine sediments and peat bogs.

Within a stratified deposit, palynological studies show a successive sequence of pollen assemblages, which represent a broad overview of changing vegetation with time. The past vegetation is represented by the pollen spectra from that depth (time), which in turn is interpreted as an indication of the general environment of the catchment area. The catchment area can be defined from a continental scale, down to a regional and local scale, where mosaics of different communities may be established (Birks and Birks, 1980). Constructing the past environment on palynological evidence has associated problems and usually only a broad picture of major habitats can be determined. The incorporation of evidence from other macrofossil studies augments the palynological data and improves the accuracy of the picture.

The basic assumption underlying the interpretation of the fossil pollen assemblage is that the pollen falling within a particular region is indicative of the vegetation of that region (Moore, Webb and Collinson, 1991). By assuming that the same pollen-vegetation relationships exist today as existed in the past, it is possible to infer that the palaeo-vegetation that produced the fossil pollen assemblage is similar to the vegetation producing a similar modern pollen assemblage (modern analogue). The assumption is not only important in the use of fossil pollen records in palaeo-climatology, but is important to the interpretation of palynological data used in the research of plant migration, plant population change and plant community development. Central to the assumption is whether or not factors such as seed dispersal, soil development or intrinsic limitations on population growth rates can cause temporal lags between climatic change and vegetation response and whether anthropogenic interferences can alter or obscure the climate-vegetation relationship (MacDonald and Edwards, 1991).

The work of Davis and Botkin (1985) proved that species abundances are not always in equilibrium with climate and that biotic interactions can have a strong influence on climatic response and can obscure and delay the response. Also the environmental factors, particularly soil and disturbance, must be taken into account in reconstructing climate from vegetation and that the pollen record from sediments, even if vegetation is accurately recorded, cannot resolve climatic changes closer than to within one to two hundred years. The pollen record is unable to distinguish step changes from gradual changes, between larger, short-lived changes and small changes of longer duration and small fluctuations in temperature may leave no record in the pollen record. Pollen deposits can only record long-term climatic changes, providing a kind of running mean of climatic variation, rather than precise records of climatic change over a short time span.

The pollen rain never simply reflects the proportion of species present in the surrounding vegetation as individual plant species vary in the amount, frequency and periodicity of pollen production and in terms of their aerodynamic and dispersal capabilities. Consequently some species are always over- or under-represented in the pollen record (Stevenson, 1985).

Due to these many interacting variables palynologists have tended to look at the final outcome of these processes only, namely the modern pollen spectra. These spectra have been studied in relation to the surrounding vegetation communities without the consideration of the complicated intermediate processes that have produced the final spectra. Walker (1972) believes that the study of the modern pollen spectra represents the simplest, soundest and most repeatable approach to the reconstruction of past plant populations and communities as well as palaeoenvironments. Studies of the vegetation history of an area need to be informed by studies of modern pollen rain (Stevenson, 1985). Modern pollen rain studies are thus conducted to: 1) determine the relationship between pollen rain and vegetation, 2) compare modern and fossil pollen assemblages to trace patterns of palaeo-vegetation development and discover modern analogues for fossil pollen spectra, and 3) construct numerical transfer functions that use the empirical relationships between modern pollen rain and vegetation structure or climate to provide quantitative estimates of past vegetation or climate conditions (MacDonald and Ritchie, 1986).

If the fossil and modern assemblages are similar in their pollen composition and proportions, it is probable that the spectra were produced by similar vegetation communities. A modern vegetation analogue can thus be proposed for the fossil pollen assemblage. If similarities between modern and fossil pollen assemblages can be recognized in a stratigraphical and hence a temporal sequence of fossil pollen spectra, changes in past vegetation over time can be reconstructed in terms of present-day vegetation patterns in space. If no satisfactory comparison can be determined between the fossil and modern pollen assemblage and there is no independent evidence of sedimentary disturbance or reworking of the sediment, it can be concluded that the past vegetation has no geographically extensive modern analogue, or that the contemporary pollen data is incomplete and that modern analogues should be sought elsewhere. To exclude this last possibility an extensive modern pollen data set is required for the more dominant vegetation communities of the whole region.

Parsons and Prentice (1981) recognise two methods for the reconstruction of past vegetation from fossil pollen assemblages via the modern pollen-vegetation relationship. One method involves comparing each fossil spectrum with a range of modern pollen spectra from different vegetation regions so as to find a modern analogue for the former vegetation. The other involves applying pollen-vegetation conversion factors, estimated from modern pollen spectra in conjunction with quantitative descriptions of the vegetation surrounding the modern pollen sampling site. The first method, although widely used, lacks precision. Although it can be made more objective by numerical techniques (Birks, 1977; Ritchie and Yarranton, 1978; Liu and Lam, 1985; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b) it remains basically a qualitative method.

The modern pollen data are complex, quantitative and multivariate and, unlike fossil pollen, does not have a stratigraphical context. However they usually have some spatial context, be it either in terms of geographical location, ecological or vegetation setting, or position along vegetation or altitude gradients. So as to determine empirical modern pollen-vegetation relationships, surface samples need to be compared with the vegetation from which the modern pollen spectra originated. Such relationships are also complex and various numerical techniques to derive and describe this relationship have come to the fore within the last 20 years. These surface sample studies are an essential stage in the interpretation of fossil pollen assemblages. Although this factor was recognized by von Post in 1916 and later by Erdtman in 1943, it has only been comparatively recently that the full potential of surface samples has been explored. Birks and Birks (1980), Prentice (1982), and Birks and Gordon (1985) review the current approaches.

The nature of the pollen-vegetation relationship is a complex one and attempts at investigating the relationship have progressed primarily along two lines: 1) an assemblage approach with pollen assemblages interpreted in terms of the closest analogue in modern pollen spectra, and, consequently in modern vegetation, and 2) an 'individual taxon' approach dealing with the quantitative relationship of modern pollen production and dispersal from the plants that produced the pollen (Prentice, 1982).

With regards to the resultant pollen assemblage obtained via the modern pollen approach, the assumption is made that similar modern and fossil pollen assemblages reflect the same vegetation type. Previous applications of this approach have compared fossil pollen spectra to an array of modern pollen data from surface sediment samples (Davis and Webb, 1975). The best modern analogue of the past vegetation corresponds with the extant vegetation type mapped for the graphic area where the modern pollen sample corresponds favourably with the fossil pollen data.

In the 'individual taxon' approach, the modern pollen - vegetation relationship is isolated for a particular taxon, the pollen/vegetation calibration factors derived are applied to translate fossil pollen values into values of taxon abundance. Abundance values of the taxa are combined to 'reconstruct' past vegetation (Heide, 1981 in Liu and Lam, 1985). The pollen abundance, expressed as a percentage or influx value for each taxon, usually has been considered as proportional to it's abundance within the population surrounding the site of the pollen sampler (Delcourt *et al*, 1983a).

The quantitative reconstruction of palaeoclimatic variables from the palynological record has developed rapidly in recent years. Four distinct approaches have been developed and applied (Huntley, 1990): 1) an indicator-species approach, 2) an analogue-matching approach which takes into account the quantities of pollen of different taxa as well as of the qualitative composition of the pollen spectrum and is a natural progression from the first technique, 3) transfer-function techniques, using a multiple regression approach, have been developed and refined. These functions relate the value of an individual climatic variable to the pollen abundance-values for a series of pollen taxa, and 4) pollen-climate response surfaces which were first described by Bartlein *et al* (1986). These surfaces relate the pollen-abundance values for a particular taxon to the values of two or more climatic variables. This technique has a great potential for the reconstruction of palaeoclimates from fossil pollen and related data, as well as for the evaluation of independently-derived climatic scenarios in terms of their vegetation implications.

2.4 PROBLEMS ASSOCIATED WITH POLLEN ANALYSIS

As with all sciences there are basic assumptions and procedures which are followed and consequently exceptions to the norm occur creating problems. The basic assumptions of pollen analysis create difficulties which are further compounded by methodological and statistical problems. Faegri and Iversen (1975, pp. 168) point out "... in the long series of events between the release of the pollen from the anther to the final pollen diagram, much may happen to distort the record and make a diagram not only useless, but directly misleading unless the distortions can be compensated for." Errors will always occur in research, but with clear technical procedures and experience a number of these errors can be reduced or corrected.

Assemblages of pollen percentages reflect patterns in vegetation composition in both space and, by inference, in time (Prentice, 1985). However, pollen percentages do not correspond numerically with vegetation percentages, as in addition to random error, pollen percentages are systematically affected by production and dispersal bias. Production bias is the result of differential pollen production by taxa, while dispersal bias is due to the differential dispersal of pollen types. Production and dispersal bias combine to determine pollen representation, the extent to which pollen percentages under- or over-estimate the relative abundance of a taxon. Relative pollen representation of different taxa and the same taxa at different localities, is affected by pollen production, transport and dispersal mechanisms, deposition and preservation, as well as sampling and counting strategies (Heide and Bradshaw, 1982).

A quantitative relationship is assumed to exist between the number of pollen grains of a taxon deposited in the sediment at a site and the number of individuals of that taxon in the vegetation surrounding the site. Such a relationship is complex, being influenced by a large number of interacting variables. For example genetic, physiological, climatic and ecological factors controlling the flowering and pollen production of the species; the abundance of the taxon within the vegetation community; the structure of the community; the mode of pollen dispersal; the meteorological factors influencing pollen transportation; the physical, chemical, and biological conditions affecting pollen sedimentation and preservation at the site of deposition; the size and shape of the depositional catchment area; and the local site factors such as the presence or absence of surrounding vegetation (Birks and Gordon, 1985). The interactions of these factors are extremely complex and, as yet, poorly understood or studied. Existence of variation between taxa needs to be corrected, as taxa can depart from proportional representation by as much as an order of magnitude (Prentice, 1986a). The necessity to correct this variation has long been recognised and the use of explicit mathematical techniques is a recent development. No quantitative satisfactory explanatory models of pollen production, dispersal, sedimentation and preservation and therefore of modern pollen representation have yet been put forward.

The most common conversion factor is the R-value (Davis, 1963) which is a qualitative method which many researchers have followed (Parsons and Prentice, 1981). However there are both theoretical and practical problems with the method which have led other researchers (Faegri, 1966; Birks, 1973) to take a more pessimistic view. Parsons and Prentice (1981) review the R-value method and suggest that the main problems encountered with the method are attributable to the lack of (1) statistically adequate procedures and (2) suitable modern pollen and vegetation data sets. A method for estimating R-values needs to take into account the statistical procedures of ratios, site-to-site variability, and the effects of long-distance pollen dispersal. The R-value method met difficulties caused by statistical estimation problems (Parsons *et al*, 1983) and by failure to take account of the long-distance component of pollen spectra (Parsons and Prentice, 1981; Webb *et al*, 1981).

Prentice (1986b) has reviewed calibration techniques which show close consistency between the relative pollen representation of the same taxa in comparable sampling sites located in different areas. Von Post (1946) recognised that pollen percentages will misrepresent the percentages of the vegetation that produced the pollen. Pollen percentages are therefore a biased record of vegetation composition. If one assumes that the bias is constant, then the interpretation is straightforward. Correction factors for the bias can then be determined and, when applied to fossil data, yield an empirical calibration. Bradshaw and Webb (1985) have shown that the biases are not the same for all data sets, but vary in a predictable manner given variations in catchment size.

Some of the more common problems related to modern palynology studies are as follows:

2.4.1 POLLEN PRODUCTION

Individual plant species vary in the amount, frequency and periodicity of pollen production and the pollen grains themselves differ in terms of their aerodynamic and dispersal capabilities. Thus the pollen rain never simply reflects the proportion of species within the surrounding vegetation community and consequently some species are over- or under-represented in the pollen record. Seasonal and diurnal variation in the production of pollen adds to the complexity of the situation (Hawke and Meadows, 1989; Emberlin *et al*, 1990; Cadman, 1990). Thus it is imperative that an understanding of the modern pollen rain - vegetation relationship is obtained.

With regards to vlei or peat sites, it is often difficult to distinguish between local vlei elements and the more distant or extra-local pollen (Janssen, 1967). It is necessary to separate out the regional pollen which represents the vegetation surrounding the site and is therefore indicative of localized vegetation patterns. Modern pollen traps and surface soil samples are used, in conjunction with the fossil pollen analysis, to help create a better understanding of the existing relationship between local and regional influences (Meadows, 1984; Meadows and Meadows, 1988; Meadows and Sugden, 1991a,b; Meadows *et al*, 1987; Scott, 1982a, 1984a; Sugden, 1990). However this can become problematic as certain taxa, as was the case in this study, are produced both locally and regionally.

2.4.2 POLLEN DISPERSAL

The dispersal of pollen depends principally on atmospheric turbulence, windspeed and direction, weight and shape of pollen grains and the height and strength of the pollen source (Birks and Birks, 1980). The actual transfer of pollen grains from the anther to the atmosphere is essentially a physical process. The proportion of pollen emission that becomes airborne is a function of wind velocity, atmospheric turbulence, anther height above the surrounding surfaces and the density of the vegetation stand (Edmonds, 1979). The occurrence of long distance transport must also be accounted for, particularly when interpreting pollen assemblages from environments with a low local pollen production (Maher, 1963).

The nature of pollen dispersal creates problems. Since vegetation is not homogenous, one has to assume that the modern pollen spectra reflect the 'average vegetation' from the surrounding area. Heterogeneity is disregarded, although in theory the spatial pattern of vegetation within the study area would influence the pollen spectrum, because of the differential dispersal of different pollen types. Wind patterns can also cause directional biases in pollen representation. The most serious problem is long-distance transport of pollen from other vegetation types.

2.4.3 POLLEN PRESERVATION

Data describing the length of time a pollen grain remains viable in the atmosphere are limited, although there are indications that the atmospheric lifespan of anemophilous pollen may be quite short (Edmonds, 1979). The pollen viability is not important with regards to palynological studies, rather it is the rate of decay or decomposition of the exine which is of importance. Differential preservation, according to species and medium in which the pollen grains are preserved, vary (Havinga, 1984). Physical, chemical and biological processes affect pollen grains from the time they are liberated from the plant. Although the pollen exine is resistant to decay, due to it's sporopollenin content, it is still broken down with time by the processes of corrosion, degradation, breakage and crumpling. Badly preserved or deteriorated pollen are difficult to identify and affect the pollen sum.

2.4.4 IDENTIFICATION

The correct identification of the pollen grains is obviously of critical importance, because all further ecological interpretations depend upon accurate identification. Pollen grains are grouped into two main identification categories; determinable and indeterminable. Indeterminable means that the essential morphological features of a grain may be obscured and prevents assignment into a known pollen type. This may be as a result of concealment by extraneous matter, unsuitable orientation of the grain, deterioration of the exine and the presence of an 'unknown' pollen grain not described or represented in any available reference. It is necessary to record indeterminable pollen, as it affects accuracy of the total pollen count.

Determinable fossil pollen grains are matched with those of modern taxa of the lowest possible rank and the successful identification depends upon several factors; the range and reliability of the reference collection, the variability within the species, the grain morphology and preservation, and the experience of the analyst.

In South Africa (due to insufficient reference material) identification of grains can be problematic. Reference collections are slowly developing as researchers build-up collections for their own particular study areas. Scanning electron microscopy is a great advancement for solving identification problems, but if one is performing all counts with the aid of a light microscope, one needs to concentrate the reference material on light microscopy determinable morphological differences.

2.4.5 PREPARATION LOSS

Normal modern and fossil pollen processing involves various stages from sampling through to slide making and the final pollen count. Steps vary with individual preferences and the nature of the sample, although certain steps are common to most processing regimes. With the increasing emphasis on the method of fine resolution pollen analysis, especially in Quaternary studies, it becomes imperative to ensure that pollen spectra at the final stage of preparation (the slide) adequately reflect the initial sample (Jemmett and Owen, 1990).

When initiating a pollen study one normally follows a 'recipe' in pollen preparation work inherited from previous pollen workers, without much modification except for different lithologies and, with experience, adapts the recipe to ones own needs. Jemmett and Owen (1990) experimented with various recipes and point out that "... it is important to remember, at each stage of the preparation process, why we are doing it and possible effects on the final pollen spectrum." (pp. 211). Points of note in the methodology include: 1) differential loss of pollen during centrifugation and decanting of the supernatant, 2) lack of consistency between parallel samples; slides from a single sample are usually similar, but parallel samples had, according to Jemmett and Owen (1990) different pollen ratios, 3) plastic tubes retain pollen better than glass tubes, 4) pollen geometry can be an important factor in pollen loss, with large spherical grains lost in larger quantities during processing, and 5) problems of loss during sieving. All these factors can affect the pollen spectrum of the final slide and are important considerations for both qualitative and quantitative analysis.

A further source of error can be incurred during acetolysis as the composition and resistance of the exine to acetolysis differs between taxa, thereby possibly affecting the composition of the pollen spectra. Acetolysis can cause the total decay of the exines of some taxa, for example Juncaceae and Orchidaceae, and cause the enlargement or swelling of the exine in other taxa (J. Sugden *pers. comms.*, 1990).

The problem of preparation loss can be greatly reduced by applying caution, rather than strict adherence to a preparation recipe. With time one becomes familiar with one's own material and the various idiosyncrasies thereof. With initial checks at each stage of preparation it is possible to reduce preparation loss to a minimum and there is no substitute for experience.

An additional problem, although not a result of sample preparation, can occur as a result of slide preparation for counting. The assumption that the pollen and spores counted is a random sample (relative counts) is only valid if the whole slide is counted. If small counts are conducted, only a proportion of the slide is traversed and counted, thereby assuming that the grains are distributed at random over the whole preparation. This last assumption is not valid as the normal pollen analytical procedure is to prepare slides using coverslips, and as a result the main flow lines are outwards from a central zone. The edges of the preparation, particularly if precautions are taken to prevent the loss of glycerine jelly from under the coverslip and the corners, are not then representative of the whole (Brookes and Thomas, 1967). Therefore when performing relative counts it is more accurate to count the whole slide despite the fact that the pollen sum will exceed the predetermined number of counts. With experience one learns how much polliniferous silicone oil is required to obtain approximately the required number of pollen grains.

2.4.6 COUNT SIZE

Relative counts varying from 200 to approximately 1000 pollen grains per sample are usually conducted and the frequencies of the taxa expressed as a percentage of the pollen sum. There are inherent problems of proportionality involved with relative counts. Firstly, there is the question of how many pollen grains need to be counted to be representative of the sample and secondly, percentage increase in one particular taxon can 'mirror' a decrease in another. This decrease is not real, but as a result of relative counts as the taxa counts are dependent on each other.

Absolute pollen counts are more informative as pollen influx rates can be calculated and each taxon is independent and not influenced by fluctuations in the frequencies of associated taxa. Absolute counts can give influx values of grains/area/time period in the case of contemporary pollen on a seasonal and annual basis or, in the case of fossil pollen, over an extended time period determining rates of sedimentation.

2.4.7 STATISTICAL PROBLEMS

Pollen data is often analyzed using statistical techniques, and as such it is subject to the rules that govern all statistical relations (Faegri and Iversen, 1975). The data obtained from pollen analysis are estimates of the 'true' values. When decomposition occurs the pollen deposited within the sediment is a sample of the pollen produced in the catchment area, and the grains preserved until the time of investigation represent a sample of the original deposition. Furthermore, the core of sediment taken for analysis only represents a sample of the total deposit, so at least three sampling procedures have preceded analysis, all with inherent sampling errors.

The two types of statistical problems that are of principle interest to pollen analysts are: 1) sampling error and 2) irregular fluctuations of the pollen diagram curves, both of which interfere and can conceal the long-term fluctuations which are of interest in the research. Statistical errors arise with regards to the representativity of the pollen sample. It is obvious that the whole sediment cannot be studied, thus it is vital to concentrate on what is assumed to be representative which may involve a preliminary study to determine the heterogeneity of a sample site. As the representativity of a final pollen assemblage can be debatable, it is necessary to take modern pollen samples from the site and compare these spectra with the existing vegetation. This technique of determining modern analogues to help in fossil pollen analysis is extremely helpful (Liu and Lam, 1985; Meadows and Sugden, 1991a,b).

2.5 MODERN POLLEN SAMPLING AND ANALYSIS

In Europe and North America a large number of lake sites are used in fossil pollen analysis, therefore modern pollen collections are taken from either the lake surface by means of floating (Bonny, 1976) and/or submerged (Bonny, 1978) traps or from the lake sediments (Lamb, 1984; MacDonald and Ritchie, 1986; Burney, 1988). There is a discrepancy between surface and sediment samples much like that between soil and trap samples (discussed in Chapter 7 and 8). The lake surface pollen rain spectra are a true reflection of the pollen rain of the catchment, however due to factors such as surface winds, lake currents and depositional characteristics the pollen that is finally preserved in the lake sediments does not necessarily reflect the surface deposit. However it is from the sediments that fossil pollen cores are taken, therefore sediment pollen spectra prove to be better analogues than surface deposits.

Terrestrial based modern pollen samples are collected predominantly from river muds (Lézine and Edorh, 1991), surface soil samples (Markgraf *et al*, 1981; Pocknall, 1982; Stevenson, 1985) and moss polsters (Dodson and Myers, 1986; Kodela, 1990a; Randall, 1990). Probably the greatest advent to pollen rain - vegetation studies is the use of pollen traps, the most basic of which is a slide coated with vaseline placed into the open air for a specific time period. Recently more sophisticated traps have been applied and the most widely adopted designs include the Tauber trap (Crowder and Starling, 1980; Markgraf, 1980; Solomon and Silkworth, 1986; Hall, 1990; Kershaw and Strickland, 1990). These traps tend to be applied more to compare pollen rain with the regional vegetation and for determining modern analogues, while for a more intensive, shorter duration, volumetric pollen influx study the Burkard seven-day recording trap (Nilsson and Persson, 1981; Emberlin *et al*, 1990) and the Hirst-trap (Mandrioli *et al*, 1982; Spieksma, 1983) are the more popular. Other traps, employed to a lesser degree, include a ground level trap (Cundill, 1986), a Rotorod sampler lifted into the atmosphere by a tethered balloon (Mandrioli *et al*, 1982) and Cour's filter technique (Meiffren, 1988). All the pollen traps have proved to be successful in entrapping and preserving pollen grains and spores.

Generally pollen trap results are to be preferred to moss or lake sediment samples in that the time period over which the pollen is collected can be controlled and so values of cm^2/year can be calculated (Hicks, 1977). Not only can such values be compared directly with pollen influx values whenever absolute pollen frequency data is available, but, in some instances, these values are the only means of distinguishing two otherwise similar pollen assemblages. However, due to annual variations, trap results are only reliable if data is available for more than one year (Crowder and Starling, 1980).

Initial South African modern pollen studies used glass slides covered with vaseline (Coetzee and van Zinderen Bakker, 1952). More recently the pollen collecting techniques of surface soil samples (Scott, 1982a, 1989a; Meadows and Sugden, 1991a,b) and pollen traps (Meadows and Meadows, 1988; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b) have been used. These pollen traps are modifications on those described by Flenley (1973) and used with a great deal of success by Hamilton and Perrott (1980) and Meadows (1984) in East Africa and Malawi respectively. Other collecting techniques employed include Cour's filter method (van Zinderen Bakker and Müller, 1987; Cooremans, 1989) and hyrax middens (Scott and Bousman, 1990). Studies which have required a higher resolution of absolute pollen counts, for example for hayfever studies, have used the Burkard seven-day recording volumetric trap (Hawke and Meadows, 1989; Cadman, 1990, 1991). These techniques, in relation to South African work, are reviewed in chapter 3. The set-up and design of the pollen traps used in the present study are discussed in chapter five.

Modern pollen counts are compared to each other and the surrounding vegetation by descriptive and statistical means. Descriptive studies include Scott (1982a, 1989a), Meadows (1984), Newsome (1988) and Meadows and Sugden (1991a,b), while a number of statistical techniques have also been used. These techniques are reviewed by Birks and Gordon (1985) and Prentice (1986a), while Prentice (1980) reviews the multidimensional scaling (MDS) methods including principal components and co-ordinates analysis, canonical variates analysis and non-metric MDS, and Parsons and Prentice (1981) review the use of the R-values of Davis (1963). Other statistical data analysis methods include two-way indicator species and detrended correspondence analysis (Stevenson, 1985), principal components analysis (Birks, 1981b; Burney, 1987), principal components biplots (MacDonald and Ritchie, 1986), canonical variates analysis (Birks, 1977; Davis, 1980), canonical correlation analysis (Webb, 1974a), cluster analysis using various coefficients (Lamb, 1984; Kodela, 1990a), linear regression (Webb *et al*, 1981; Burney, 1988), factor analysis (Scott and Thackeray, 1987) and multiple discriminant analysis (Liu and Lam, 1985; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b). The statistical tests used in the context of this study are reviewed in chapter five.

2.6 CONCLUSION

Pollen analysis has proved to be an excellent tool for the reconstruction of past vegetation, especially for the Quaternary sediments. The method has been successfully applied to a wide range of vegetation types and climates. Reconstruction of past vegetation by means of pollen analysis is based upon the assumption that the present-day relationships between modern pollen spectra and the vegetation that produced them can be extrapolated back in time.This relationship needs to be documented in order to calibrate fossil pollen spectra in terms of vegetation patterns. This calibration cannot be established theoretically as the same taxon can be represented by different relative frequencies of it's pollen from one region to another. Therefore, for each regional palynological study the relationship of modern pollen rain to existing vegetation must first be determined and understood (Markgraf *et al*, 1981).

The palynological reconstruction of Quaternary environments in South Africa has, more recently, been based on comparisons of fossil pollen spectra with modern pollen spectra from different vegetation types and climatic regions. This relationship needs to be given priority as, this way, pollen spectra of the modern vegetation can be consulted to provide a means of determining the palaeo-environments (Sugden, 1990). Extensive contemporary pollen studies are required and are a necessity in any palynological investigation in South Africa. The fact that this has not been a priority in the past is a constraint on palaeo-ecologists attempting to reconstruct the Quaternary environment. A good understanding and knowledge of the contemporary pollen rain - vegetation relationship would reduce the problems and errors often encountered in palynology, viz. differential production, dispersal and preservation of pollen, and improve the confidence limits of interpretation of fossil pollen analysis.

CHAPTER THREE
SOUTH AFRICAN PALYNOLOGICAL RESEARCH

3.1 INTRODUCTION

South Africa, in contrast to Europe and North America has relatively few detailed palynological studies from which environmental fluctuations over time can be determined. Due to the paucity of available data and the large expanse of land that this data 'represents', it is not possible to accurately undertake a comparative study between the palynological data available, and consequently the patterns of environmental change are still relatively unclear in South Africa (Sugden, 1990).

Compared with Europe pollen analytical studies started relatively late in Africa, with the first publication, by Dubois and Dubois from West Africa, appearing in 1939 (van Zinderen Bakker and Coetzee, 1988). The development of palynology has been hampered by the scarcity of suitable deposits, the diverse flora with its wealth of sporomorph types and general lack of expertise. Pollen analysis was initiated in South Africa in 1947 by the Bloemfontein Centre of Palynology, Orange Free State. The Palaeoecology of Africa series which was started in 1966, and the earlier series Palynology in Africa edited by van Zinderen Bakker, and re-issued as Palaeoecology of Africa volume 1 in 1966 are as a consequence of the initial interest in South African palynology in the 1950's and 60's. The past decade has witnessed an increased awareness of environmental changes within South Africa, culminating in the publication of two edited volumes (Klein, 1984; Vogel, 1984), an extensive review by Tyson (1986), and a comprehensive account of late Quaternary palaeo-environments by Deacon and Lancaster (1988).

Pollen analysis in South Africa was developed during the 1950's by van Zinderen Bakker (1951, 1955, 1957 and 1962) and Coetzee (1967), although prior to this some pollen work had been performed with regards to hayfever (Ordman, 1947). In comparison with the temperate regions of the northern Hemisphere where numerous Quaternary pollen profiles have been produced, only a few have been studied in South Africa and, in general, this is also the case for the rest of Africa. The only exception is perhaps East Africa, where a number of long pollen profiles have been studied (Coetzee, 1967; Hamilton, 1982; Bonnefille and Riollet, 1988).

In the context of the study of Late Quaternary sediments in South Africa, spring and marsh (vlei) deposits from sub-humid regions have proved the most useful sources of fossil pollen (van Zinderen Bakker, 1955, 1957, 1982; Coetzee, 1967; Schalke, 1973; Scott, 1976, 1979, 1982a,b, 1983, 1984a, 1986a,b, 1987a,b, 1988a,b, 1989a,b; Scott and Vogel, 1983; Beaumont *et al*, 1984; Bousman *et al*, 1988; Meadows and Meadows, 1988; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b; Sugden, 1990). Cave sites from dry environments, where lack of moisture prevents the decay of fossil pollen by oxidation and microbial activity, have yielded fossil pollen of concentrations great enough to be considered, viz. Wonderwerk (van Zinderen Bakker, 1982), Boomplaas (Deacon *et al*, 1984), Equus Cave (Scott, 1987a) and Strathalan Cave B (Opperman and Heydenrych, 1990). Although lake deposits have proved to be the best source for fossil pollen in the temperate regions of the northern Hemisphere and East Africa, there are few such deposits which have been worked in South Africa other than a preliminary look at saline shallow water lake sediments from the Pretoria Saltpan (Scott, 1988a) and the work of Martin (1968) at the Wilderness Lakes system, southern Cape. A further source for palynological work has been artesian springs of groundwater reaching the surface in several of the drier parts of South Africa, allowing for the development of organic sediments and soils, for example at Aliwal North (Coetzee, 1967), Wonderkrater (Scott, 1982a), Moreletta River (Scott, 1984b), Florisbad (van Zinderen Bakker, 1957), Deelpan (Scott, 1988b) and Badsfontein (Scott and Cooremans, 1990). Other sources of fossil pollen from South Africa include hyena coprolites in cave deposits from Equus Cave (Scott, 1987a) and hyrax middens from Blydefontein Basin in the Karoo (Scott and Bousman, 1990).

Peat or vlei sediments are usually associated with cool, moist climates where decomposition of organic debris is retarded and hydrological conditions entail permanent water-logging and acidity. South Africa is generally regarded as too arid for such conditions to prevail, however at higher altitudes where precipitation is augmented and temperatures cooler, organic deposits, particularly in valley-bottoms and other topographical depressions, have developed. Such deposits have been identified from the Highland areas of the Drakensberg (van Zinderen Bakker and Werger, 1974), the Winterberg of the eastern Cape (Meadows and Meadows, 1988), the Outeniquas of the southern Cape, the Cedarberg of the western Cape and the Nuweveldberg of the central Karoo (Sugden and Meadows, 1989; Meadows and Sugden, 1988, 1990, 1991a,b).

Despite certain problems involved in the accurate dating of organic deposits in South Africa (Scott, 1982a; Scott and Vogel, 1983), an analysis of the radiocarbon-dating stratigraphy within the sediments can augment a palynological investigation for patterns in the environmental history of the Late Pleistocene and Holocene (Meadows, 1988b).

The fossil pollen analytical studies which have been carried out in South Africa have been extensively reviewed by Scott (in Klein, 1984), Deacon and Lancaster (1988), van Zinderen Bakker and Coetzee (1988), and Scott (1990). As the scope of this research lies within the modern pollen sphere of palynological investigations, this literature review concentrates on the modern pollen rain studies which have been conducted in South Africa. Since Scott (in Klein, 1984) reviewed South African modern pollen studies, a greater awareness of modern studies has become evident in palynological research (Meadows and Sugden, 1988, 1990, 1991a,b; Scott, 1986a, 1987a, 1988b, 1989b, 1990; Sugden and Meadows, 1989).

The present discussion divides South Africa into the ecozone regions described by Klein (1984) and Deacon and Lancaster (1988), to help clarify and to facilitate easier conceptualization of the research sites (Figure 3.1). With regards to Figure 3.1 the airspora work of Hawke and Meadows (1989) and Cadman (1990, 1991) are not represented, neither is the work of Cooremans (1989) and Scott and Cooremans (1992) as these studies were conducted over an extensive region and therefore cannot be represented by a single location on the map.

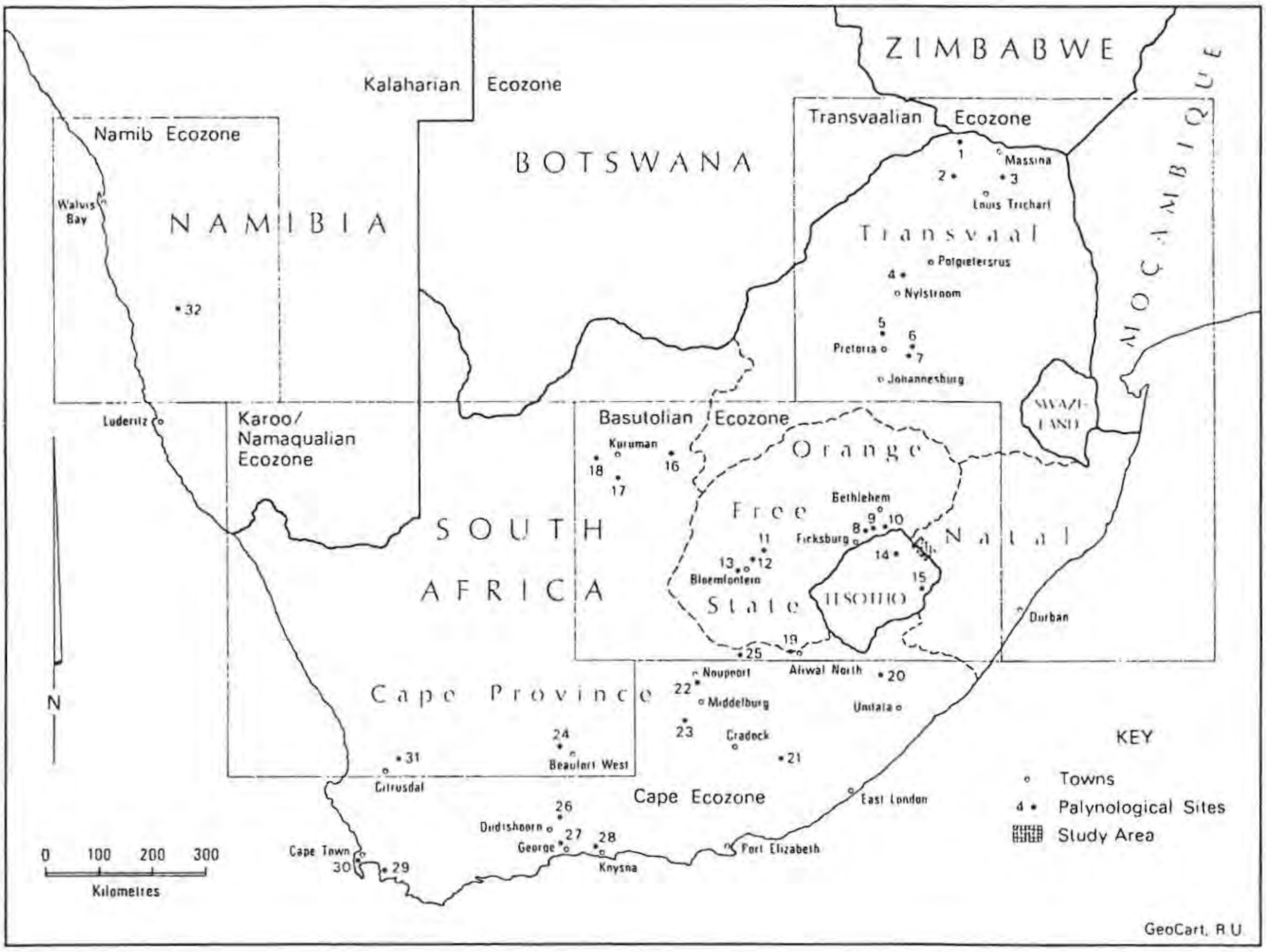


Figure 3.1 Map of South African palynological investigation sites where some form of modern pollen study has been undertaken. The region is divided into Ecozone regions described by Klein (1984); Deacon and Lancaster (1988).

1-Theuniskloof/Tugela (Scott, 1984b); 2-Scot (Scott, 1982a); 3-Tate Vondo (Scott, 1987b); 4-Wonderkrater (Scott, 1982a; Scott, 1983; Scott and Thackeray, 1987); 5-Soutpan, Pretoria (Scott, 1988a); 6-Moreletta River (Scott, 1984b); 7-Rietvlei (Scott and Vogel, 1983); 8- Elim (Scott, 1986a; 1989a); 9-Cornelia (Scott, 1986a; 1989a); 10-Craigrossie (Scott, 1986a; 1989a); 11-southern Middleveld (Coetzee and van Zinderen Bakker, 1952); 12-Florisbad deposits (van Zinderen Bakker, 1957); 13-Deelpan (Scott, 1988b); 14-Blue Mountain Pass (Scott, 1982a); 15-Maluti Mountains (van Zinderen Bakker, 1955); 16-Equus cave (Beaumont *et al*, 1984; Scott, 1987a); 17-Wonderwerk cave (van Zinderen Bakker, 1982); 18-Kathu Pan (Beaumont *et al*, 1984); 19-Aliwal North (Coetzee, 1967); 20-Strathalan Cave B (Opperman and Heydenrych, 1990); 21-Winterberg (Meadows *et al*, 1987; Meadows and Meadows, 1988); 22-Blydefontein Basin, Noupoort (Scott and Bousman, 1990); 23-Compassberg (Meadows and Sugden, 1988); 24-Nuweveldberg (Sugden and Meadows, 1989); 25-Badsfontein, Venterstad (Scott and Cooremans, 1990); 26-Boomplaas (Deacon *et al*, 1984); 27-Norga and Gwayang (Scholtz, 1986); 28-Groenvlei (Martin, 1968); 29-Cape Hangklip (Schalke, 1973; Scott, 1984b); 30-Noordehoek (Coetzee, 1986); 31-Cedarberg (Meadows and Sugden, 1990, 1991a,b); 32-Sassus vlei (van Zinderen Bakker and Müller, 1987).

3.2 CONTEMPORARY POLLEN STUDIES

Relatively few South African studies in Quaternary pollen analysis have included a systematic focus on the relationship between contemporary pollen rain and vegetation so as to contextualize the palaeo-vegetation reconstruction (Meadows, 1989). Scott (1979) makes a point of the fact that "...it is essential to assess the present pollen rain produced by different vegetation types and to establish ecological significance of the percentage values of each recorded fossil pollen taxon" (pp. 4-5). Due to the fact that "... very little information on the modern pollen rain produced by the different vegetation types for this vast region is available ..." (Scott, 1984b, pp.66), there has been inevitable interpretative problems regarding fossil pollen analysis. Most of the recent contemporary spectra which have been studied have come from the few areas from which fossil spectra have also been described and have not been the primary aim of the investigation.

3.2.1 BASUTOLIAN ECOZONE

The first published contemporary pollen rain study relating to palynological work is that of Coetzee and van Zinderen Bakker (1952) who collected atmospheric pollen, on vaseline coated slides, weekly for one year in the southern Middleveld of the Orange Free State (OFS). The resultant pollen counts were compared to those obtained by analyzing soil surface samples and the surrounding vegetation. The results obtained from both the atmosphere and the soil samples gave a similar spectrum with Poaceae pollen being the most prominent (90%) and Asteraceae (4%) the second most important grassland taxa (Coetzee and van Zinderen Bakker, 1952; van Zinderen Bakker, 1957). Three of these modern pollen spectra were used to elucidate the fossil pollen assemblage from Florisbad (van Zinderen Bakker, 1957). Comparable results are obtained by Scott (1976) and Horowitz *et al*, (1978) from sites in the western Orange Free State (OFS). A lower Poaceae:Asteraceae (71:12%) was obtained in the shrub karoo vegetation near Middelburg by Coetzee (1967), in comparison to the grasslands.

As expected for the OFS/Karoo region, the arboreal pollen percentages from the first contemporary pollen spectra of Coetzee and van Zinderen Bakker (1952) are low, with *Rhus* being the most important arboreal taxon with a value up to 9%. Scott (1982a) has recorded higher values on wooded koppies in the OFS (up to 25%). A mountain slope at 1 900 metres in *Cymbopogon-Themeda* veld in the eastern OFS (Ladybrand) also produced a high arboreal pollen content (Scott, 1982a), consisting mainly of *Celtis* (19-40%), *Rhus* (4-30%) and *Clutia* (2%) pollen. The non-arboreal pollen at this site consisted mainly of Poaceae (15-21%), Asteraceae (3-6%) and *Cliffortia* (0.5-11%).

Van Zinderen Bakker (1982) collected thirty surface samples, of which only seven contained pollen in large enough proportions to be counted, to augment the fossil pollen study at Wonderwerk. The study area is extremely hot and dry, thus pollen was easily oxidised on the soil surface and no moss cushions or stagnant water were available as recipients for pollen. Therefore it was only possible to collect surface samples which contained reasonable amounts of pollen shortly after the infrequent summer rains. The modern pollen spectra show over-representation of the taxa under which the samples were collected and low Poaceae counts as sampling was done before Poaceae had flowered that season. The remainder of the modern pollen spectra was in accordance with the scatter of low percentages of arboreal and non-arboreal pollen as reflected in the surrounding vegetation.

With regards to higher altitude sites, van Zinderen Bakker (1955) described a modern pollen spectrum for the highlands of Lesotho, in which four samples from a bog area at ± 3 000 metres were collected. The samples contained high numbers of Cyperaceae (43-50%), Poaceae (36-40%), Asteraceae (4-13%), Umbelliferae (now Apiaceae) (2-8%) and other unspecified herbs (13-37%). While a surface pollen sample from the Blue Mountain Pass in the Lesotho highlands (altitude 2700m, sample number 5890 of Scott, 1982a) provided a non-arboreal spectrum of 45% Ericaceae, 11% Poaceae, 11% Cyperaceae, 9% Asteraceae, 8% *Passerina*, 6% *Anthospermum*, 4% Aizoaceae-type and smaller percentages of various other pollen types (Scott, 1984b). Both studies were conducted in the austro-afromontane belt and concluded, albeit subjectively, that the contemporary pollen spectrum was indicative of the existing vegetation within the area of study.

The palynological work conducted by Scott (1986a) in sediment exposures near the Clarens area in the Little Caledon Valley, Orange Free State, produced no published modern pollen spectra. Unpublished material was cited to support the non-existence of fynbos pollen for a relatively high-lying (± 2100 m), dry north-facing slope in the Clarens area. Furthermore, an unpublished modern pollen spectrum from ± 2000 m on the Natal Drakensberg was used to rule out the possibility of long-distant dispersal of *Podocarpus* being relatively over-represented at zone CR1 as a result of low pollen production of other taxa (Scott, 1986a).

A subsequent palynological investigation of the area (Scott, 1989a) incorporated twelve contemporary pollen spectra to aid in the interpretation of fossil pollen assemblages of the Elim, the Cornelia, and the Craigrossie sequences from the Clarens area of the eastern OFS. The samples consisted of one hyrax dung sample and eleven surface scrapings of soil at different localities between ca. 1700 and 2700 metres in the Clarens, Natal and Lesotho regions. Although the surface spectra were useful, Scott points out that caution is necessary in the use of surface pollen spectra as a control for interpretations of fossil spectra, especially in areas where farming is practised.

Modern pollen spectra from habitats surrounding Deelpan, a well developed depression area in western Orange Free State, which is periodically filled with water during years of high rainfall, were used to facilitate a comparison with the pollen sequence from sediment taken at the Meriba site which forms an embayment in the southernmost part of Deelpan (Scott, 1988b). The modern pollen assemblages displayed a high degree of variability between the various sample sites around the pan, prompting Scott (1988b) to suggest that the fossil pollen sequences of the pan environment are "...likely to respond to local successional changes in vegetation rather than to climatic shifts..." (pp. 113) and therefore one should gain a better insight into the geomorphic changes in pan environments rather than rely on pollen analysis alone to determine possible palaeoclimates.

The majority of samples analysed by Cooremans (1989) in her assessment of modern pollen spectra in the central southern Africa were collected within the Basutolian ecozone. The assessment was carried out predominantly in the Kalahari thornveld of the northern Cape, in the grasslands of the western Orange Free State and in the northeastern Karoo. The modern pollen was sampled by means of surface soil samples and filter samples, similar to those developed by Cour (1974) and employed by van Zinderen Bakker and Müller (1987). Cooremans (1989) compared the modern pollen spectra to the vegetation communities from which they were collected and assessed the degree of variation in the resultant spectra collected by the two techniques. Overall the results conclude that the pollen spectra "... closely reflect..." (pp. 75) the vegetation types of the study area. Results of the comparison between the two collecting techniques displayed a higher grass pollen count from the filter method, while the soil samples displayed an over-representation of pollen from common trees and shrubs in those study areas dominated by woody vegetation.

A unique way of sampling contemporary pollen was attempted by Scott (1987a). He studied hyena coprolites preserved in a 2,5 metre deep sediment from Equus cave, near Taung in the southern Kalahari. The pollen percentages of hyena coprolites are affected by a complex variety of factors. However, as hyenas are predominantly carnivorous, their faeces can be interpreted as strongly representing the regional pollen. Analysis of modern hyena faeces from a compatible environment was required to support this view. Unfortunately hyenas have virtually been exterminated in the region and shelters with faeces of the survivors were difficult to locate. However, pollen in subrecent hyena coprolites from the O.F.S. grassland (± 2000 years BP) did not show the same composition as pollen in associated sediments. These coprolites contained a high proportion of Poaceae pollen (90%), whereas the sediment samples and surface samples from the same environment contained high proportions of local Asteraceae, Chenopodiaceae and Cyperaceae pollen and less regional Poaceae pollen (Scott and Klein, 1981). This supports the hypothesis that coprolites reflect dietary or regional pollen sources, or a combination of both, rather than local sources (Scott, 1987a).

A similar pollen source at Blydefontein was studied by Scott and Bousman (1990), who compared hyrax midden pollen spectra with pollen from Holocene alluvial sediments, near one of the hyrax middens, and modern surface pollen samples, including soil scrapings and fresh hyrax dung. Results indicated that the middens contain pollen which reflects local vegetation, and that diet of the hyrax probably does not have a major influence on the resultant pollen spectra. Results of the Scott and Cooremans (1992) study support the conclusions of Scott and Bousman, that the hyrax middens provide pollen spectra largely unaltered by diet as no distinct differences between dung and surface pollen spectra was observed.

Scott and Cooremans (1990) mention a modern pollen sample taken from Badsfontein, Venterstad near Aliwal North, which differed slightly to the fossil pollen spectra in that it contained prominent Aizoaceae pollen (35%). Scott and Cooremans concluded that, with minor exceptions, modern pollen surveys for the regional Karoo vegetation show slightly more Asteraceae than Poaceae pollen, but these data have, to date, not been published.

3.2.2 NAMIB ECOZONE

Although not truly a South African example, the van Zinderen Bakker and Müller (1987) study is a good example of the type of modern pollen research that can be performed in the more arid regions of the country. The technique of using surface samples in arid regions has the disadvantage of being a random sample over an extremely large area. In the van Zinderen Bakker and Müller study the filter-method, first described by Cour in 1974, was used in conjunction with owl pellets, animal excrement and coprolites. The technique requires the attachment of filters to the back of a vehicle which travels at 30-40 km/hour through the sample area. The authors don't compare the results to fossil work, but simply describe the modern pollen data. The data reflect the arid and hyper-arid conditions of the sampled area.

3.2.3 TRANSVAALIAN ECOZONE

As in the OFS grasslands, the Bankenveld of the northern parts of the highveld grassland plateau at Sterkfontein in the Transvaal show a high Poaceae:Asteraceae ratio of 38:2% (Horowitz, 1975). The woody component of the area produced relatively high arboreal pollen values consisting mainly of *Rhus* (34%) and *Olea* (5%).

Due to the disturbed nature of the vegetation surrounding the site of the Rietvlei fossil pollen sequence described by Scott and Vogel (1983), a corresponding contemporary pollen study of the region was not undertaken. As a control, however, one surface sample (No 6871) from the vlei margin was analyzed. The spectra showed that the arboreal pollen (other than the exotic elements) consisted of low percentages (6%) of Combretaceae type, *Rhus* and *Euclea*. The spectrum is dominated by Cyperaceae (66%) of local origin and a low Poaceae:Asteraceae ratio of 7.5:8.0%. (Scott, 1982a).

The woodlands of South Africa are poorly represented with regards to modern pollen spectra, with spectra restricted to the Transvaal and northwestern Cape (Scott, 1982a). Scott (1982a) collected twenty one samples from the Transvaal and four from outside the province and examined them in order to obtain data over a wide range of transitional vegetation zones. The zones sampled included: the austro-afromontane belt, the *Cymbopogon-Themeda* veld, the mountain forest belt, the Bankenveld, the northeastern mountain sourveld and sour bushveld, the sourish mixed bushveld, the Kalahari thornveld, the dry mountain Bushveld, the arid sweet bushveld and sandveld areas, and the Mopani veld. The arboreal pollen taxa become important in these areas and their distinction can be used to characterize and diagnose the various bushveld types (Scott, 1982a, 1983).

Scott and Thackeray (1987) use factor analysis on pollen spectra from the Wonderkrater peat deposit in the Transvaal (Scott, 1982a,b) to test previous inferences based on intuitive comparisons with modern spectra. The multivariate analysis provided a good resolution of the late Pleistocene and Holocene changes.

A single contemporary pollen spectra is recorded for research carried out in a mountainous area near Tate Vondo in Venda (Scott, 1987b). A surface pollen sample from north of Tzaneen near Duiwelskloof contained approximately 18% arboreal pollen belonging predominantly to Combretaceae. The spectra, in conjunction with fossilized pollen evidence from the region, is used to suggest that bush expansion in the area has taken place in recent years.

3.2.4 CAPE ECOZONE

Modern pollen spectra for the southern Cape have been described by Thiergart *et al*, (1962, in Klein, 1984), Martin (1968) and Schalke (1973). Due to the small number of spectra and conflicting results it is not possible to provide a clear picture of the pollen production of the area (Scott, 1984b). Results indicate that the arboreal pollen (*Podocarpus* and *Olea*) are important in regions with extensive indigenous forests and that, in some cases, the non-arboreal elements are also abundant in these forests, such as Knysna (Thiergart *et al*, 1962 in Klein, 1984).

During Martin's (1968) palynological investigation of Groenvlei in the Knysna region of the southern Cape, no modern pollen spectra were available for the Groenvlei area itself, thus four spectra in other Cape heath and temperate rainforest vegetation were used for comparison. The four sites were: Table Mountain, Cape Town with a treeless heath and bog environment; Deepwalls, Knysna with a forest vegetation; Grahamstown Nature Reserve, eastern Cape with approximately 20% forest and the rest heath; and the Knysna estuary, a muddy area surrounded by partly forested hill slopes. The Knysna estuary spectrum was the closest representation of the modern pollen rain of the Groenvlei region, while the spectra of B1 in the fossil spectra came closest to the Table Mountain spectrum. In contrast to the research undertaken in Knysna, Martin's (1968) spectra from the Macchia on Table Mountain shows no arboreal pollen despite the occurrence of forest patches on the lower slopes. The arboreal pollen is probably obscured by the high production of local macchia elements like Restionaceae, Asteraceae and Ericaceae (Scott, 1984b).

Schalke (1973) realized the importance of having "...an adequate knowledge of the relation between recent pollen spectra and the vegetation types in South Africa" (pp. 24). Again only four spectra are discussed, namely from the coastal macchia on Table Mountain, the evergreen Knysna forest and the coastal Knysna estuary spectra described by Martin (1968). Added to these is a fourth site of dune vegetation from Killarney. This spectra was dominated by *Myrica* and Myrtaceae in the arboreal pollen and Asteraceae, Chenopodiaceae and Euphorbiaceae in the non-arboreal pollen. Schalke (1973) points out similarities between the recent spectra and those of the fossil pollen diagram of Hangklip.

Coetzee (1976) has obtained spectra from sediments of some southwestern Cape river mouths, which have passed through Cape macchia vegetation. Results produced high non-arboreal pollen values consisting mainly of Asteraceae, Restionaceae, Ericaceae and *Cliffortia*; a few arboreal pollen types, mostly Proteaceae and *Podocarpus*, are also recorded.

3.3 POLLEN TRAPS

All the above modern pollen studies involved the use of surface soil samples or vaselined slides (Coetzee and van Zinderen Bakker, 1952), to obtain some indication of how representative the contemporary pollen was of the existing vegetation and no attempt was made to quantify any existing contemporary pollen - vegetation relationship. Recent work in the Cape Ecozone by Meadows *et al* (1987) and Meadows and Meadows (1988) in the Winterberg mountains of the eastern Cape, Sugden and Meadows (1989) in the Nuweveldberg of the central Karoo, Sugden (1990) in the Cedarberg, Nuweveldberg, Sneeuberg and Winterberg mountain ranges and Meadows and Sugden (1990, 1991a,b) in the Cedarberg mountain range of the southwestern Cape have placed more emphasis on studying any possible relationship between contemporary pollen and existing vegetation by creating modern analogues to determine past environments more objectively. The studies also bring into consideration the use of passive pollen traps reviewed by Meadows (1989) in order to ensure a close temporal relationship between the pollen sample and the vegetation survey, which is undertaken at one point in time (Bradshaw, 1981).

Meadows and Meadows (1988) describe the vegetation history of the Winterberg escarpment for the last 12 500 years by means of analyzing the pollen content of two organic cores from two large vleis, Dunedin and Salisbury. So as to check the accuracy and representativeness of the fossil pollen data, the contemporary pollen spectra of the area were constructed using surface soil samples and pollen traps left in the field for approximately one year. Results showed that, notwithstanding the under-representation of the arboreal pollen, pollen spectra from within the vleis, as a whole, presented an accurate picture of the Winterberg vegetation pattern (a complex mosaic of false thornveld, Dohne sourveld and Montane forest) and that the modern pollen rain is indicative of the vegetation communities which produced it (Meadows and Meadows, 1988).

Pollen analysis of organic sediment from the Nuweveldberg Mountains in the central Karoo yielded a 760 year vegetation history. Sugden and Meadows (1989) set up 17 pollen traps of a design used by Meadows (1984). These traps were placed at both 1 metre from the surface and at surface level. Traps were left in the field for two years and surface soil samples from the vicinity of the pollen traps were also analyzed. The contemporary pollen results were used to compare the modern spectra with the Holocene fossil pollen assemblages from the Nuweveldberg mountains by means of multiple discriminant analysis. Sugden (1990) also carried out an analysis of variance (ANOVA) on both trap and soil data to ascertain if there was any significant difference in the spectra for 1986 as opposed to 1987. A significant ($p < 0.05$) difference was found in 23% of the taxa represented in the trap samples, and in 43% of the taxa from soil samples. Multiple discriminant analysis was carried out on the Nuweveldberg modern pollen data to determine the contemporary pollen - vegetation relationship and to observe vegetation zonal indices and probability of a modern analogue which are used for an objective comparison to fossil pollen spectra. Multiple discriminant analysis compares fossil pollen assemblages to modern pollen assemblages collected from known vegetation regions (Liu and Lam, 1985; Meadows and Sugden, 1990, 1991a,b; Sugden, 1990; Sugden and Meadows, 1989).

A comparison was made between the trap and soil contemporary pollen data (Sugden, 1990). The pollen trap spectra had higher percentages of arboreal, wind pollinated taxa and a greater diversity of pollen types than the surface sample spectra. The modern pollen samples reflected the present vegetation patterns on the Nuweveldberg range, although several anomalies were revealed.

To ensure accuracy of the representativity of fossil pollen data derived from the Cedarberg range in south-western Cape, Meadows and Sugden (1990, 1991a,b) sampled the modern pollen rain using pollen traps and surface soil samples. Fifteen pollen traps were placed in the Cedarberg region for two consecutive years, while surface soil samples were collected from the top 5 cm of the soil at the base of seven pollen traps. Multiple discriminant analysis was performed on the data to derive any possible contemporary vegetation - pollen relationships and to enable modern analogue vegetation communities to be identified in the fossil spectra through multiple discriminant analysis and hence strengthen the conclusions of the fossil analysis.

Sugden (1990) concludes that the pollen traps located within the Cedarberg produced spectra which were a "...fair reflection..." (Sugden, 1990, pp. 239) of the surrounding vegetation. When comparing spectra from the 1 metre high traps to those at ground level, no marked differences were apparent, although the ground level traps had consistently higher percentages of local taxa, particularly Poaceae and Restionaceae, whereas traps at 1 metre had slightly higher percentages of arboreal and regional components. These trends are similar to the results from the Nuweveldberg (Sugden and Meadows, 1989). A comparison of the pollen trap spectra and the surface sample spectra was carried out to assess the representativity of the modern pollen spectra. This comparison gives some indication of the degree to which pollen preserved at the research site is representative of the fossil pollen data (Sugden, 1990).

The surface soil sample spectra were very similar to the pollen trap spectra from ground level. This suggested that the difference in representativity as compared to traps at 1 metre is not due to preservation anomalies of the pollen in the soil surface, but is probably due to the lifeforms, structure and stratification of the surrounding fynbos vegetation. From the comparisons it was evident that vlei elements are generally over-represented and arboreal elements under-represented within the surface sample spectra. Overall, the results from the pollen trap spectra, particularly those at 1 metre above the ground, proved to be a better reflection of the vegetation communities prevailing in the catchment area than the surface soil sample spectra (Sugden, 1990). The results suggest that the contemporary pollen rain, obtained from both modern pollen rain sampling techniques, are representative of the vegetation communities which produce it. This conclusion is supported by others in this field (Flenley, 1973; Hamilton and Perrott, 1980; Scott, 1984; Meadows, 1984; Meadows and Meadows, 1988; Meadows and Sugden, 1990, 1991a,b; Sugden and Meadows, 1989).

3.4 OTHER MODERN POLLEN STUDIES

Recently articles dealing with the study of contemporary pollen rain from the point of view of airspora spectra have been published. These papers deal with pollen 'forecasts' for public information with regards to allergies such as hayfever. Aeropalynological studies in South Africa were initiated in the 1940's and continued by Ordman (1947, 1955, 1961, 1963, 1972, in Hawke and Meadows, 1989) and Ordman and Etter (1956, in Hawke and Meadows, 1989) and contributed to the understanding of pollinosis and weather conditions in South Africa. Hawke and Meadows (1989) undertook a 5 week survey of the airspora spectrum of an industrial site central to the greater Cape Town region during the winter of 1987, focusing on the spectrum and it's relationship with selected meteorological factors. Cadman (1990) used two Burkard seven-day recording traps set-up in Johannesburg and Pretoria to determine pollen calenders for 1987 and 1988. This data was correlated to a number of meteorological factors (Cadman, 1991) and concluded that in Johannesburg rain and sunhours, while in Pretoria windspeed and minimum temperature were the most significant parameters with regards to particular pollen types. Presently a joint project between the universities of Cape Town and the Witwatersrand is monitoring pollen and spore in the major population centres of South Africa, namely Cape Town, Port Elizabeth, Bloemfontein, Durban, Pretoria and Johannesburg. Although these studies are not directly related to fossil pollen analysis, they do help to improve the understanding of present-day temporal and spatial pollen variation.

A contemporary pollen flow project has been carried out by Midgley (1989) on *Podocarpus falcatus*. The study used fruits from the female tree and the maximum distance from male to female trees to ascertain some indication of the distance and effectiveness of pollen flow. The study concluded that the maximum distance between seeded trees was 70 metres and that this distance was not sufficient to cause a drastic decline in seed set. This pollen flow is twice the distance previously suggested as a maximum and gives an indication of pollen dispersal of one of the forest dominants in South Africa. More such studies are required in South Africa, before modern pollen rain modelling can be considered.

3.5 CONCLUSION

In a review of contemporary pollen rain studies in southern Africa Meadows (1989) makes three recommendations concerning future Quaternary palynological research in the region: 1) all such analyses need to incorporate a systematic study of contemporary pollen rain. Both surface soil samples and pollen trap spectra should be obtained from the plant communities within the area of investigation, 2) detailed vegetation data is required from the study area, and 3) with the inclusion of a reliable contemporary pollen and vegetation analysis, statistical techniques, such as multiple discriminant analysis can be employed to elicit further information from the fossil pollen spectra. The concept of modern analogue vegetation (Liu and Lam, 1985; Sugden and Meadows, 1989; Meadows and Sugden, 1990, 1991a,b) needs to be implemented in South Africa, where plant communities may well be slight modifications of the natural vegetation and it is therefore likely that modern analogues for palaeo-vegetation communities still exist (Meadows, 1989).

With regard to general Quaternary vegetation reconstruction, undue weight is given to those few, better studied localities that are widely separated in time and space. Truswell and Harris (1982) in an Australian study point out that the generalisations from such varied and isolated data must be made with caution. What is needed is a broader contemporary pollen - vegetation data base. Meadows (1985) notes the difficulty of assessing the representativity of South African pollen on the basis of such few studies as are presently available. Replication of these data are necessary to eliminate variation over time, so that reliable modern palynological data, which can be used as modern analogues in statistical manipulations, is available.

From the palynological data alone a vegetation history of South Africa is slowly emerging. The results, despite some discrepancies, generally conform with reconstructions based on various other methods (Deacon and Lancaster, 1988). There are large gaps in the modern pollen surveys of South Africa, of which several early reports are summarized by Scott (1984b) and others described by van Zinderen Bakker (1982), Meadows and Meadows (1988), Scott (1982a, 1984b, 1986a, 1989b, 1990), van Zinderen Bakker and Muller (1987), Scott and Bonnefille (1986), and Scott and Bousman (1990).

This literature review concludes that more palynological data are required to refine the available picture and future research needs to use modern pollen spectra so as to establish objective transfer functions between fossil pollen spectra and palaeo-climatic conditions. Prospects of finding pollen sequences in the swampy basins and headwaters in under-researched regions such as Natal and the south-western Cape, are good (Scott, 1990). While despite polliniferous deposits being scarce in the arid regions of the country, midden sites and cave deposits remain a viable option.

Unless the contemporary relationships between pollen spectra and vegetation can be established reconstructions of former vegetation communities and their respective constraints remain little more than guesswork (Meadows, 1989). This review has shown that in most instances there is conclusive evidence of a close and direct association between the pollen rain characteristics and the vegetation which produces the pollen. However the evidence for such a relationship is sadly lacking for a greater proportion of the floristically diverse South Africa and thereby hampering palynological research into Quaternary environments.

CHAPTER FOUR
STUDY AREA

4.1 INTRODUCTION

The research was carried out at the Cathedral Peak Forestry and Research Station situated in the Bergville district of the Natal Drakensberg at latitude 29°00'S and longitude 29°15'E (2829 CC, CD and 2929 AA, AB) (Figure 4.1). Ongoing research at this station is directed at examining the influence of various veld management practices and water yield of the local mountain catchment area. This is being carried out on fifteen small gauged catchments, situated on the flat terrace, known as the Little 'Berg or foothills, which occurs below the main Drakensberg Escarpment (Schulze, 1983).

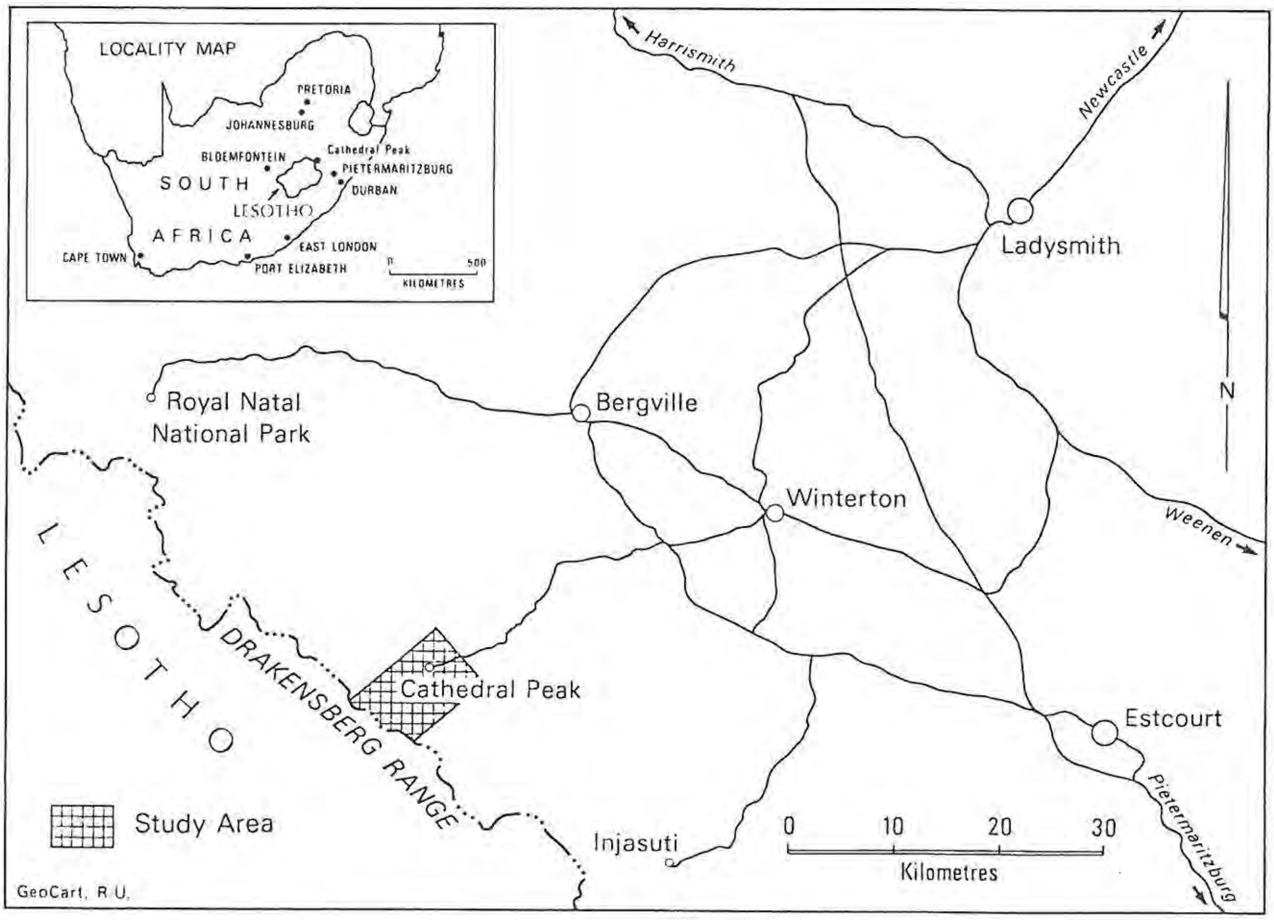


Figure 4.1 Situation of the Cathedral Peak Forestry and Research Station in the Bergville District of the Natal, Drakensberg.

The hydrological research station was established at the Cathedral Peak side of the Cathkin Peak Forest Reserve (proclaimed in terms of section 122 of the South African Act of 1909) following the fourth British Empire Forestry Conference in 1935. Subsequently J. Craib and S. St. Ballenden selected the site for the Cathedral Peak Forest Influences Research Station and this was approved in May 1938. The original research programme was drawn up by A. M. de Villiers in 1939 and had the following broad objectives:-

i) to investigate the effect of grassveld and exotic plantations on climate,
ii) to investigate the disposal of the atmospheric precipitation in the grassveld and plantations and to correlate this study with the investigation of the effects of the two plant formations on the soil moisture regime, on the erosion and on streamflow, and
iii) to study the influence of the vegetation, soil, climate, erosion and streamflow of a system of conservative veld utilization, of the veld exploitation and of the total protection of grassveld.

In the case of exotic plantations it was intended to afforest catchments with a number of different species (*Pinus* and *Eucalyptus*) under a regime of management practices and to examine these in terms of their effect on soil, climate, erosion and streamflow (Granger, 1976). Unfortunately the proposed research was thwarted by the intervention of World War II and only re-opened in 1945.

A geological survey was carried out in 1948 (Pike and de Villiers 1948) and in 1950 a botanical survey of the research area commenced, the field work of which was completed in 1953 (Killick, 1963). At this point in time the research area consisted of ten monitored catchments. By 1951 the weirs for catchments I, II and IV had been completed and with the exception of catchment VIII, which was instrumented in 1963, all the other 9 catchments were recording streamflow by 1954. Catchments II, III and VII were afforested with *Pinus patula* in 1951, 1956 and 1967 respectively.

In March 1972 it was decided that the original research questions regarding the influence of exotic afforestation on streamflow had been largely answered. With pressure being exerted on the Forestry Department to produce a sound, scientifically based management plan for the Natal Drakensberg Mountain Catchment Area, the research programme was modified. It was decided that no further exotic afforestation would take place and that the grazing in catchment I would be discontinued. The remaining six grassland catchments (this was increased to seven when catchment VII was burnt out in September 1972), together with five additional new catchments (XI-XV), all receive biennial spring burns, which form the nucleus of a number of burning experiments. The objective is to apply a different burning management treatment to each of the catchments. These treatments are to continue until such time as they have yielded their quota of useful data as regards the response of vegetation, soil, water and animal life to a particular treatment (Schulze, 1983).

Of the fifteen catchments monitored at Cathedral Peak, catchments I, VI, IX and X have been studied more intensively (Granger, 1976), while numerous comparisons have been made between the forested and grassed catchments (Nänni, 1972; Bosch, 1979; Schulze, 1979).

The choice of the Cathedral Peak Forestry and Research Station for the present study was based on four considerations. First, the effect of man (burning programmes, grazing and other agricultural practices) are controlled in the State Forest and Wilderness areas of the Natal Drakensberg thus enabling the research to be conducted within 'protected' areas. Secondly, the research station is well equipped (laboratory and computer facilities as well as a field herbarium), situated (good access to both the Little 'Berg and the main escarpment) and staffed, thus ensuring the task of conducting research more comfortable and the presence of the expertise most helpful. Thirdly, the montane environment gives one the opportunity to study dissimilar vegetation communities within a small region due to the effect of altitude and, fourthly, the Natal Drakensberg is one of the few regions in South Africa identified (van Zinderen Bakker, 1955; Heusser in Deacon, Lancaster and Scott, 1984) as having the potential for palynological studies due to the presence of environmental conditions favourable for the development of deposits. These vleis are poorly drained sunken areas where the soil is acidic, anaerobic and has a high organic content (up to 30%). It is under these conditions that pollen preservation is optimum.

4.2 GEOLOGY AND PHYSIOGRAPHY

The Cathedral Peak Research Station catchments all occur in the foothills of the Drakensberg escarpment known as the Little 'Berg between the altitudes of 1800 metres (5900 feet) and 2600 metres (8530 feet) and are therefore all immediately underlain by the basaltic lavas of the Stormberg Group, the youngest subdivision of the Karoo Supergroup. The basalts date from the Late Triassic period and reach a total thickness of 1500 metres in places. They poured out during a rapid succession of fissure-like eruptions with the superimposed conformal flows ranging from a few to approximately 50 metres in depth (Irwin *et al*, 1980; Willcox, 1989). The lava flows were originally horizontal, but now dip slightly due to isostatic adjustment. At Cathedral Peak the dip is 2° to the south.

In the research area both amygdaloidal and non-amygdaloidal basaltic flows occur (Pike and de Villiers, 1948). Two large dolerite dykes, part of the feeder system which produced the lavas, occur in the research area running almost parallel in an east-west direction from catchment XV across to catchment X.

4.3 CLIMATE

The climate of the region has been summarized by the schemes proposed by Köppen (1931, in Schulze, 1947), Thornthwaite (1948, in Schulze, 1947), Holdridge (1959, in Granger, 1976) and Phillips (1973, in Granger, 1976). Following Köppen's classification of climate, the Little 'Berg in the Cathedral Peak area may be classified as a Cwb type, that is a warm climate (mean temperatures of warmest month below 22°C) with a dry winter. The classification of Thornthwaite is possibly more specific in that it places the research area between the CCd and CBr climates where the former characterizes eastern Lesotho and the latter, Natal. The Ccd climate is described as being cool, subhumid with respectively insufficient or sufficient moisture in all seasons, while the Cbr climate is subhumid warm with sufficient moisture in all seasons (Schulze, 1947).

Several criticisms have been levelled at the above two systems of climate classification. In the case of the Köppen classification the major objection is that it fails to relate vegetation to broad climatic parameter values without adequate concern for such vegetation, while it has been pointed out by Schulze (1958, in Granger, 1976) that the Thornthwaite thermal regions, as defined by potential evapotranspiration intervals on an annual basis, leads to some anomalies. For example the system did not seem correct that the west coast of South Africa and the interior of Natal should fall in the same thermal efficiency region, as their respective climates differed markedly. Comparing the two classifications with reference to the Cathedral Peak region, it would seem that the Thornthwaite classification is the more sensitive as it brings out the fact that eastern Lesotho is cooler and receives less precipitation than the Natal side of the escarpment. However, the Thornthwaite classification does not, for any part of South Africa, distinguish between summer and winter rainfall climates (Killick, 1963).

Of the more recent attempts to classify vegetation and climate the works of Holdridge (Holdridge *et al*, 1971 in Granger, 1976) and Phillips (1973 in Granger, 1976) are of interest. The Holdridge system makes use of:

i) the mean annual bio-temperature,
ii) the mean annual precipitation and
iii) the potential evapotranspiration.

In this system the Cathedral Peak region falls into Life zone 2a defined as tropical, humid lower montane moist forest. This is in agreement with the more subjective classification of Phillips who allocated the same area to 5b of his Bio-climatic Potential Climax (BPC), where between altitudes of 1900 and 2900 metres the BPC is lower montane fynbos with evergreen short thicket in a humid to humid-subhumid climate. The area above 2900 metres (Drakensberg Escarpment) is designated 5a which has the same humidity and temperature description, but is defined as upper montane fynbos. Phillips (1973 in Granger, 1976) defines a bioclimatic region as one differentiated by an interplay of climatic factors and biotic phenomena, so integrated as to permit the development of natural vegetation and the associated animal life. Due to the lack of detailed knowledge and data, it is the predominant vegetation types and the prime climatological factors of rainfall, temperature and humidity that Phillips has used in his designation of bioclimatic regions. Within each bioclimatic region there may be a wide range of natural communities and also of disturbed or induced ones, resulting in bioclimatic subregions. Geological and physiographical features are intimately influential in contributing to the development of these regions and subregions. As a result of this interaction between vegetation, physiography and climate, bioclimatic regions have become a frequently used descriptor of the physical environment (Schulze, 1979).

In view of the fact that these last two classification schemes have been evolved on the basis of the distribution of natural vegetation in response to climate, the resultant delimitation of bioclimatic zones are of more use to a vegetation survey than the classifications of Köppen and Thornthwaite.

Average daily sunshine measured at 1854 metres on the Little 'Berg at the Cathedral Peak meteorological station varies between 8,3 hours during the wet summer month of December and 5,5 hours during the dry winter month of June, 30 and 82 per cent respectively of the possible sunshine. Temperature records show that air temperature is cool to mild, mean annual temperature of the region is approximately 16°C but both seasonal and diurnal variations are considerable (Irwin, *et al*, 1980).

The Drakensberg derives it's rain mainly from oceanic air-streams entering from east coast highs. At the beginning of summer most of the rainfall is orographic. Later, the frequency of thunderstorms increases and this form of precipitation provides approximately 50 per cent of the total rainfall. Most of the rain falls during the summer months of October to March, the proportion of which is about 85 per cent. The wettest months are January, February and March and the driest June and July (Killick, 1978). Edwards (1967) gives a mean annual rainfall of between 701 and 1500 mm.

In the Drakensberg there is a clearly defined correlation between precipitation and altitude, which is illustrated by the rainfall-topography transect (Figure 4.2). This transect passes through the Cathedral Peak Research Station, which displays the altitudinal rainfall pattern typical of that of other high mountain ranges. Figure 4.2 illustrates schematically the variations of mean annual rainfall (calender years) with altitude at six stations in the Cathedral Peak area, including one in Mokhotlong, Lesotho, 40 km southwest of Cathedral Peak.

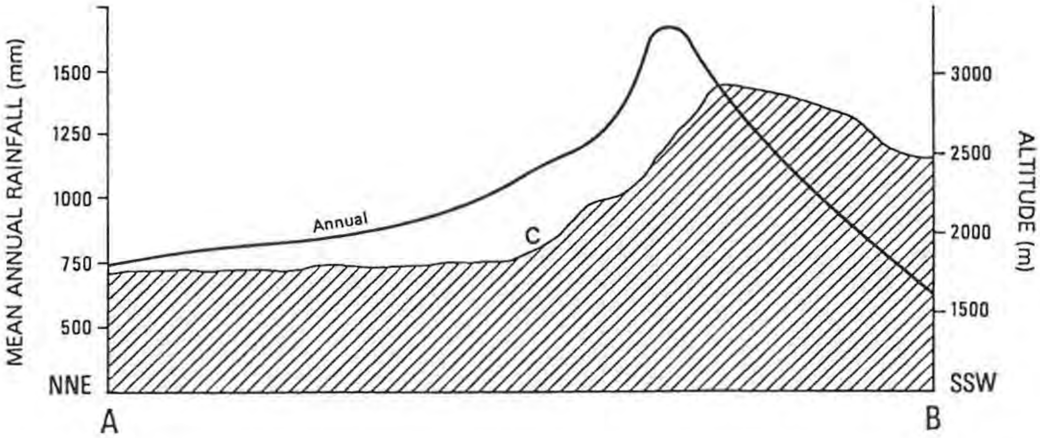


Figure 4.2 Rainfall-topographic transect from Bergville (A) to Methelsessane (B) (C represents the Mlambonja valley) showing correlation between precipitation and altitude (from Schulze, 1983).

Rainfall increases from 1240 mm in the Mlambonja valley (label C on Figure 4.2) of the montane belt to 1418 mm, near the edge of the Little 'Berg reaching a maximum of 2017 mm in the upper part of the sub-alpine belt and decreasing to 1609 mm on the summit of the Drakensberg in the alpine belt and 562 mm at Mokhotlong in Lesotho (Killick, 1978). Both mean annual precipitation (MAP) and mean January (highest monthly value) rainfalls peak before maximum altitudes are attained and then decrease rapidly in the lee of the high Drakensberg. It appears that rainfall is influenced by the distance from the escarpment, quite apart from altitude. This dependence of rainfall on distance from a physiographic barrier has been reported elsewhere by Wicht *et al*, (1969) in the south-western Cape. In addition to altitudinal influence, there is a superimposed and independent west to east directional decrease of precipitation in the Cathedral Peak area of the order of 3 per cent mean annual precipitation (MAP) per kilometre (Schulze, 1983).

Hail as an ecological factor seems of little significance in the area. According to Nänni (1956) hail can be expected once in every two years. Snow falls occur any time between April and September and are usually restricted to the summit and near-summit and only occasionally reach the lower limit of the sub-alpine belt. Summer fog occurs mainly on the Little 'Berg and the summit area. This fog is common and may be continuous for up to two weeks at a time. Evaporation, measured by a Symon's evaporation tank situated at 1854 metres, is highest between September and November. Mean annual evaporation is 1346 mm, which is close to the rainfall (1371 mm) recorded at the Cathedral Peak meteorological station (Schulze, 1983).

Wind is an important ecological factor in the Drakensberg. The 'bergwinds' which blow from the west during late winter and spring often attain great velocity. These winds, though not as hot and dry as at lower altitudes (they become heated as they descend), are important because they are generally accompanied by periods of low humidity and they blow at a time when soil moisture is at it's minimum. Winds are also important because they are prevalent during the dry season when fire hazard is at a maximum.

From the point of view of modern pollen analysis wind, associated with valley aspect, is possibly the most important meteorological phenomenon (Markgraf, 1980). Airborne pollen grains will be transported predominately in the direction of the prevailing wind. For example, as a result of localized valley winds, pollen grains will be deposited up-slope or up-valley from their source during the day, as most pollen is released during the morning. In the Natal Drakensberg the north facing slope of a valley will receive more direct insolation than that of the south facing slope, thus having a profound effect on the plant ecology. These effects are most obvious in the Little 'Berg but, except for the retention of snow for longer periods on south facing slopes and gullies, appear to have a minimum effect on the ecology of the Drakensberg Escarpment (Irwin, *et al*, 1980). Not all the slopes face directly north or south although most have a northerly or southerly component. Predominantly east- and west-facing slopes, although not showing the extremes mentioned above, are subject to morning-only or afternoon-only sun. This uneven heating/cooling of valley slopes produces two topographically induced wind systems viz: localized and regional wind systems.

Localized wind systems are set up by the rising (setting) sun warming (cooling) one slope, while the other is cooling (warming) resulting in uni-cellular overturning of air within a valley system (Figure 4.3). Anabatic winds will develop up both slopes and subsidence will occur over the central valley. Late in the morning, as an axial temperature gradient develops between the mouth and head of the valley, the up-slope winds begin to weaken as an up-valley wind is initiated. Above this an anti-valley wind will complete the circulation. In the late afternoon, as the slopes begin to cool, the valley wind weakens near the slopes and along the valley floor. A reverse helical circulation to that of the early morning begins to develop with descending katabatic flow down the valley slopes. Ascending motion occurs over the central valley. This phase is very transitory and is replaced by down-valley flow in the mountain-wind which blows in response to the now reversed temperature gradient between the head (cooler) and mouth (warmer) of the valley. To insure continuity the mountain wind has an anti-mountain wind as it's compensating return current (Preston-Whyte and Tyson, 1988).

These localized valley winds dominate and are strongest in summer when the heating effects will be greatest, while the mountain winds dominate and are strongest in winter when cooling effects are most pronounced.

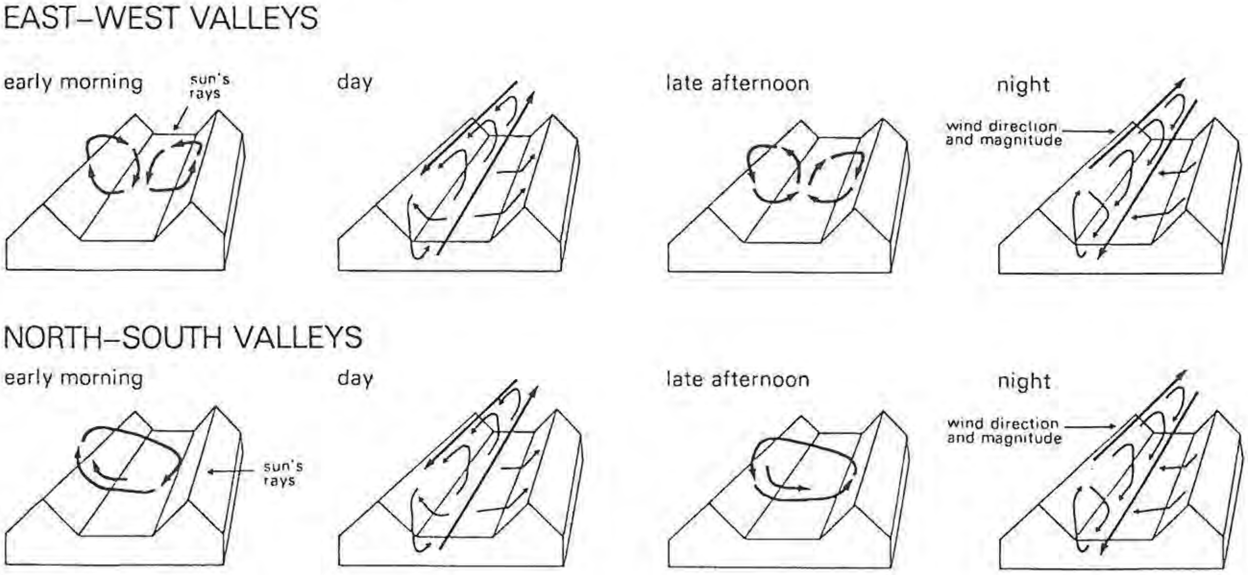


Figure 4.3 Diagrammatic model of the diurnal variation of local airflows in valleys (from Preston-Whyte and Tyson, 1988).

Associated with the mountain and valley winds are larger scale regional winds locally referred to as the uMzanzi and Minza winds. These regional winds are the result of the development of a temperature gradient between the mountains or escarpment and the plains or coastal region producing regional airflows on an appropriately larger scale. The mountain-plain (Minza) winds produce large-scale regional airflow between cooler mountains and warmer plains at night. Plain-mountain (uMzanzi) winds produce an opposite flow between cooler plains and warmer mountains by day. According to Preston-Whyte and Tyson (1988) both winds may have anti-wind counterparts, though these are seldom experienced, as they are weak and masked by gradient flows. Near the escarpment and in the Drakensberg foothills the combination of these two topographically induced airflows produce a characteristic layering of diurnal airflow in and above the valleys.

4.4 SOILS

Initial soil analysis from the area (van der Merwe, 1955 as cited in Nänni, 1956; van der Eyk *et al*, 1969) describe the soils as ferrallitic with a high degree of leaching, caused by high rainfall and relatively low temperatures of the area. Due to the prevailing moist conditions weathering is intense and, through percolation, the soils have been depleted of 'bases' such as calcium, magnesium, sodium and potassium as well as silica. Of the minerals originally found in the parent material only the un-weathered ones such as quartz are still present in the soil. These characteristics imply that the natural fertility of the soils is low, they are strongly acid and the small amounts of plant nutrients available are confined almost exclusively to the top soil which is relatively rich in organic matter.

A comprehensive survey of the soils of the Tugela Basin by van der Eyk *et al* (1969) did not consider the soils of the research area in much detail, other than describing the soils as stony and shallow which is in contrast to Killick's (1978) description, echoed by Irwin *et al*, (1980), of the soils of the Little 'Berg as having deep ill-defined horizons. The surface soil ranges in thickness from 17-30 cm and consists of dark brown to blackish brown, granular to crumbly clay-loam and clay permeated by grass roots. Soil reaction (pH values in KCl) in the upper A horizon varies, according to Killick (1978), from 3.9 under grassland to 5.9

under forest, with slightly lower (more acidic) pH values at depth. Organic content, as indicated by ignition loss, is high varying from 27% on the steep slopes at the summit of the higher catchments to nearly 50% on the flatter areas at the base of the catchments (Nänni, 1956). Considering the area is subject to regular burning these values are surprisingly high.

The next horizon down is a stratum varying from 45-120 cm and more in depth. It consists of granular brown clay loam to clay, dense and compact when moist, but badly cracked when dry. Then follows a stony loam with granular stones predominating and finally partly and slightly decomposed basalt. Soil pH varies from 5.6 to 6.6 and exchangeable base and total adsorbed base values are high. With the exception of potassium, higher cation values are to be found in the subsoil than in the surface soil. The clay mineral, montmorillonite, is present, weakly between 33-70 cm and definite at all layers below this (Killick, 1978).

A feature of the grass slopes of the sub-alpine belt are terracettes, horizontally arranged crescentic scars, which are formed largely by frost action on the soil (Killick, 1963).

4.5 VEGETATION

The vegetation of the Natal Drakensberg can be divided into altitudinal zones corresponding closely with the physiographic features. Killick (1963) identifies three such altitudinal zones in the Drakensberg, viz:

i) Montane Belt (1280-1829 metres)
ii) Sub-alpine Belt (1830-2865 metres)
iii) Alpine Belt (2866-3353 metres)

These belts coincide with the three terraces in the Drakensberg, namely the river valley system, the Little 'Berg or foothills and the summit areas respectively (Figure 4.4).

For the purpose of this research programme particular vegetation communities were selected from each of the three distinctive vegetation belts. The situation of each of the sampled communities in relation to each other and to altitude are shown in Figure 4.5. The *Themeda-*

dominated Highland Sourveld is not represented as it forms the dominant grassland community over extensive areas of the montane region and is observed in the areas not demarcated by the labelled vegetation communities.

i)	Montane Belt:	*Themeda* dominated Highland Sourveld (Acocks number 44a) (Acocks, 1988)
		Protea savanna or woodland
		Mountain *Podocarpus* forest
ii)	Sub-alpine Belt:	*Themeda-Festuca* sub-alpine grassland
		Leucosidea sericea scrubland
		Sub-alpine fynbos
		Rendlia altera grassland
		Hygrophilous herbaceous community (Low altitude vlei)
iii)	Alpine Belt:	*Erica-Helichrysum* alpine fynbos
		Merxmuellera-Pentaschistis-Festuca grassland
		Alpine sedge meadow (High altitude vlei)

The *Themeda-Festuca* sub-alpine grassland is further subdivided into three communities, viz. *Themeda triandra*, 'Mixed' and *Festuca costata* grassland.

Motivation for studying these particular vegetation communities was based on two criteria. Firstly, these are the dominant communities within each vegetation belt; thus if there has been or will be some form of environmental change it would be these communities which would be the most likely affected to an extent large enough to be recorded in the fossil pollen spectra. Secondly, the chosen communities follow either a successional pathway or a distinct topographic or geomorphological feature within the altitudinal vegetation belt.

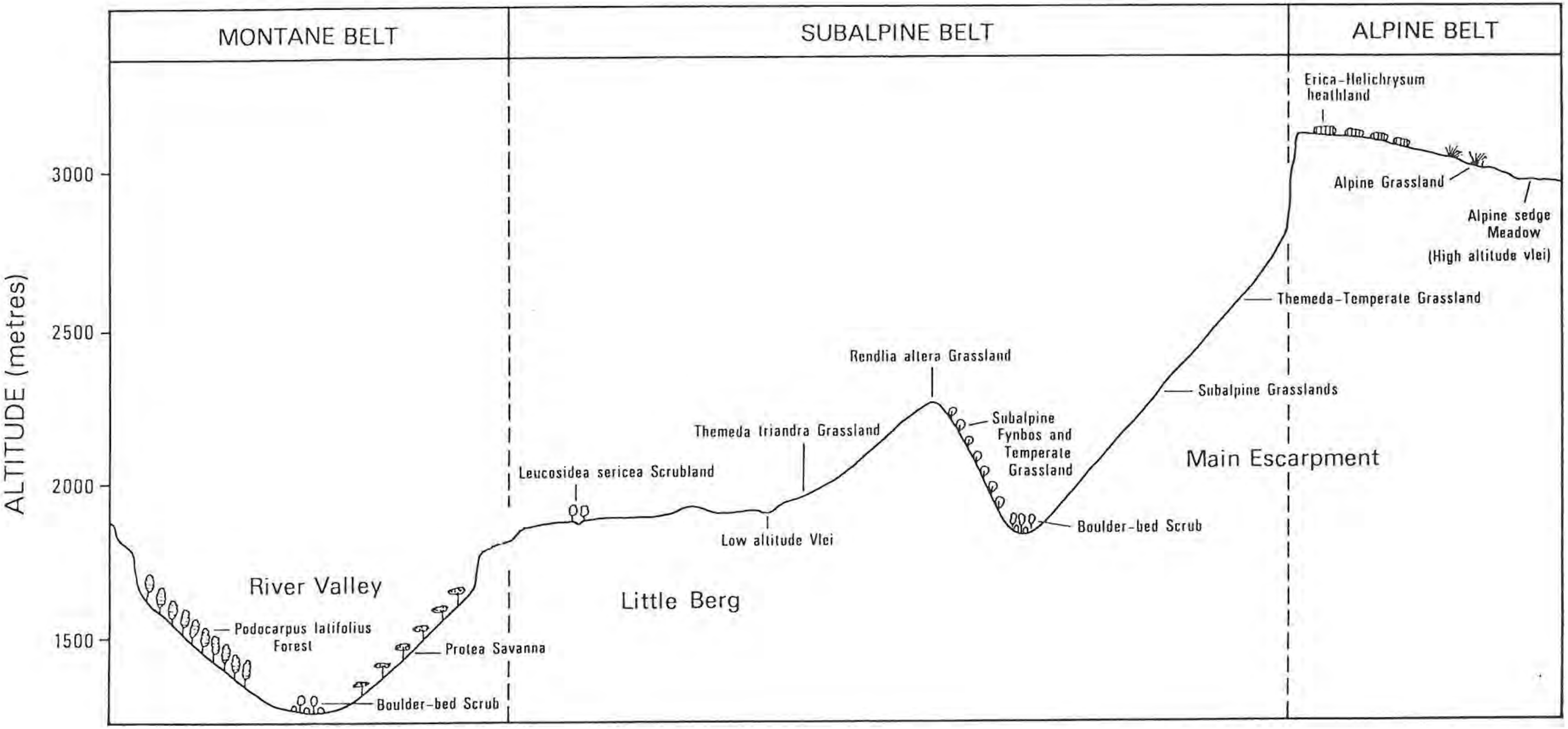


Figure 4.4 Cross-section through the Natal Drakensberg region displaying the vegetation belts and prominent vegetation communities (from Killick, 1963).

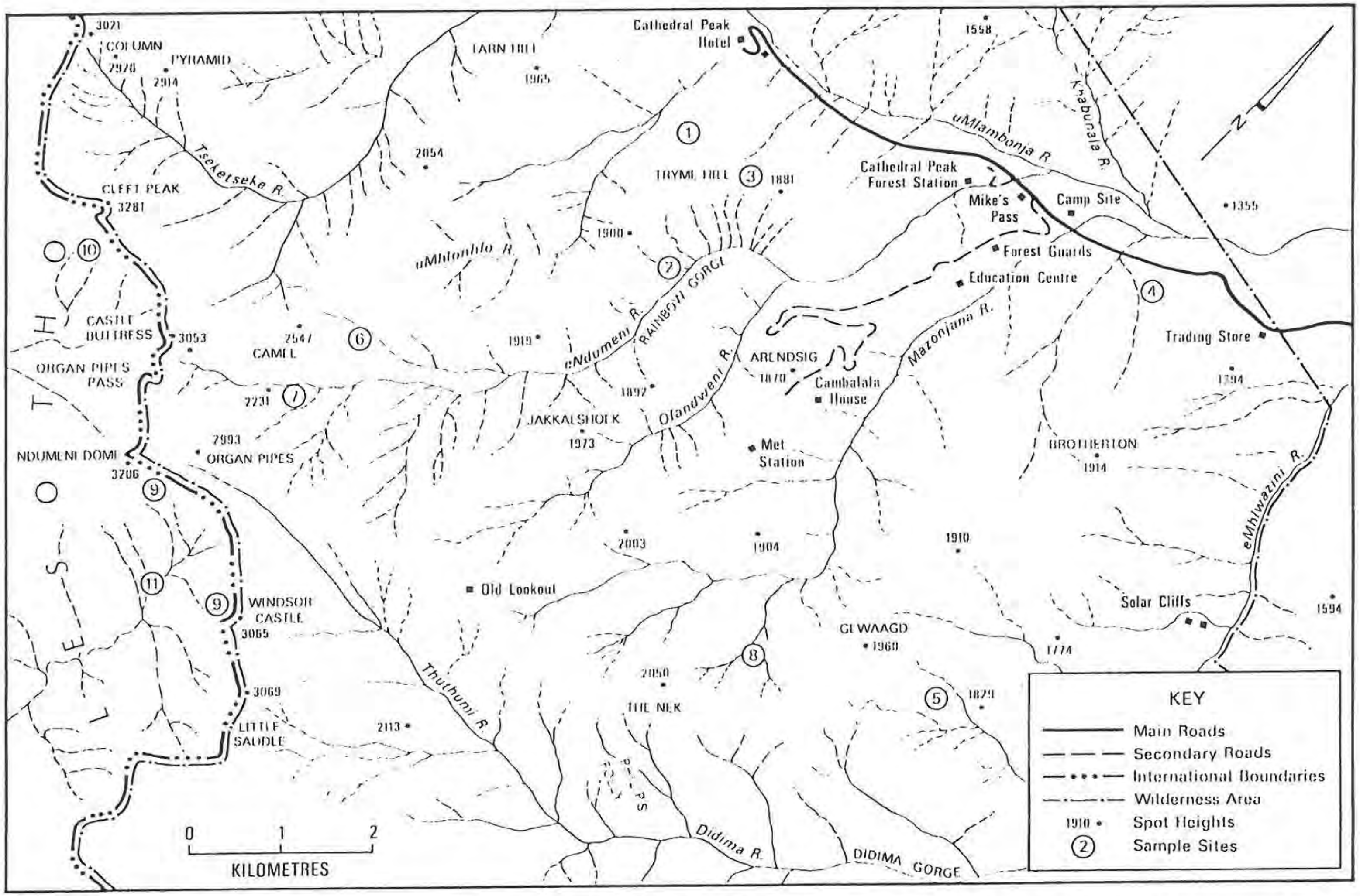


Figure 4.5 Situation of the sampled vegetation communities within the Cathedral Peak Research Station. 1-*Protea* savanna 2-*Podocarpus* forest 3-*Rendlia altera* grassland 4-Highland Sourveld 5-*Leucosidea sericea* scrubland 6-Sub-alpine temperate grasslands 7-Sub-alpine fynbos 8-Low altitude vlei 9-*Erica-Helichrysum* heathland 10-Alpine grassland 11-High altitude vlei

4.5.1 MONTANE BELT

The *Themeda*-dominated Highland Sourveld is dominated by relatively short bunch grass up to 1.5 metres high. An upper bunch grass stratum, from 1 to 1.5 metres high is discontinuous and represented by *Trachypogon spicatus*. The typical grassland character is given by the continuous, mid-grass stratum, 0.5 to 1.0 metres high, of predominantly *Themeda triandra* and *Tristachya hispida*. A lower stratum of short bunch, rhizomatous and stoloniferous grasses, less than 1.0 metres high, is discontinuous and common on shallow soil and as a result of disturbance. In common with other major moist grassland associations, this montane grassland type is a relatively stable community which is prevented from successional development by recurrent grass fires. In Clementsian terms it constitutes a fire subclimax since the community is several stages inferior to the climatic climax *Podocarpus latifolius* forest. Where fire is either absent or reduced in effect by topography or other factors, there is a development to mountain *Podocarpus latifolius* forest, especially along the steep slopes of the Drakensberg.

The mountain *Podocarpus* forest community (Plate 1) occurs in small patches of from less than one hectare to over ten hectares in extent, with occasional large stands of several hundred hectares. The generally small size of the forests means a high ratio of margin to edge, and a corresponding large 'edge effect'. Thus only towards the centres of the larger forest patches are climax forest conditions and climax forest species commonly found in addition to the dominant forest initials. This community extends from 1500 metres to 1820 metres and occurs on the streambank in deep kloofs and gorges on the southern, south-eastern and eastern aspects in the Cathedral Peak region (van Zinderen Bakker Jnr., 1973). The Indumeni forest along the eNdumeni river was selected as being representative of mountain *Podocarpus* forest in the Cathedral Peak Research area.

Plate 1 The Indumeni *Podocarpus* forest along the eNdumeni river.

Plate 2 *Protea* savanna community within the montane vegetation belt.

On steeper exposed slopes and ridges, within the montane vegetation belt, *Protea* savanna communities exist (Plate 2). These communities are composed of scattered, evergreen, compact *Protea* trees (*Protea caffra* and *P. roupelliae*) from 1 to 4 metres high. *P. caffra* and *P. roupelliae* savannas occur together although there is a segregation of the two communities on deeper and shallower soils respectively. The *Protea* savanna shows few tendencies to scrub formation, and scrub or woodland is rare (Killick, 1963). The grass stratum is principally the *Themeda*-dominated Highland Sourveld and, as a whole, *Protea* savanna is being replaced by pure grassland. The reason for the decline in *Protea* savanna is as a result of the damaging effects of veld fires as indicated by an examination of dead or dying *Protea* trees (Edwards, 1967). The presence of the dense grass cover in these communities results in the fires being both fierce and frequent. Although *P. caffra*, with its thick bark and growth from dormant buds is able to endure fires more successfully than the other species present, it is still adversely affected as a consequence of the intensity and frequency of the fires.

Another reason for the decline of *Protea* vegetation may be seen in the light of their ancient phytogeographical relationships. As expressed by Beard (1958), there is little doubt from the relics that occur in protected situations that the open *Protea* savannas are fire decimated remnants of a macchia-type floristically and physiognomically similar to the Cape fynbos.

4.5.2 SUB-ALPINE BELT

Within the sub-alpine belt the most extensive plant association is *Themeda-Festuca* subalpine grassland. Below 2700 metres consociations of *Themeda triandra* and *Festuca costata* occur on warm north-facing and on cool south-facing slopes respectively. In the lowest part of the sub-alpine belt, *Themeda* consociations resemble *Themeda*-dominated Highland Sourveld, but the temperate species are more prominent. In the absence of burning, development of sub-alpine *Themeda-Festuca* grassland is towards *Leucosidea* scrubland in the lower sub-alpine belt, and towards sub-alpine fynbos in the upper sub-alpine belt.

The *Leucosidea sericea* scrubland communities (Plate 3) occur in the lower subalpine belt, extending occasionally up protected gullies to below the main escarpment cliffs. They represent upward extensions into the sub-alpine belt of upland forest precursor communities, occurring locally along streams, on stream boulder beds and on gulley and slope talus. Although *Leucosidea* communities are commonly connected with plant succession along streams, the species also invade the lower sub-alpine grassland. *Leucosidea sericea* scrubland represents the principle climatic climax community in a zone of approximately 300 metres between the mountain *Podocarpus* forest climax and the main sub-alpine fynbos climax above 2300 metres.

The principle climax community of the sub-alpine region is what Killick (1978) describes as the *Erica-Philippia-Passerina* fynbos community. This study refers to this community simply as the sub-alpine fynbos, as the nomenclature of *Philippia evansii* has been changed to *Erica evansii* (De Wet *et al*, 1989). The sub-alpine fynbos or bushland is from 1 to 4 metres high, varying in density from an open scrub community, associated with grassland, to a dense scrub. The communities are best developed along streams, in gullies and on rock outcrops, situations where there is protection from fires. Sub-alpine fynbos is seral to forest at lower altitudes (Edwards, 1967).

Two other vegetation communities that were included in the research from the sub-alpine belt are related more to topographical features rather than being seen as part of the successional pathway. The *Rendlia altera* grassland is found between 1800 and 2400 metres on ridges of the spurs bounding the catchment areas on the Little 'Berg. The soil is thin, black, peaty, often covered with small stones and occasionally interrupted by basalt outcrops. The grasses are mostly short and characteristic of early stages in the grassland succession. The dominant is the grass *Rendlia altera*.

A further study site was set-up in a hygrophilous herbaceous community (Edwards, 1967) or low altitude vlei (Plate 4). In South Africa the word 'vlei' is used as a general term to cover most categories of seasonally or permanently damp, low lying, naturally formed areas such as swamps, marshes and fens (Downing, 1968; Noble, 1974). A vlei in the temperate grasslands can be defined as a naturally formed area on a level or sloping land surface which is sufficiently damp to have a hydromorphic soil capable of supporting a more hygrophilous vegetation than the surrounding area. The low altitude vlei under investigation in this research is defined as a headwater vlei (Downing, 1968; Begg, 1986).

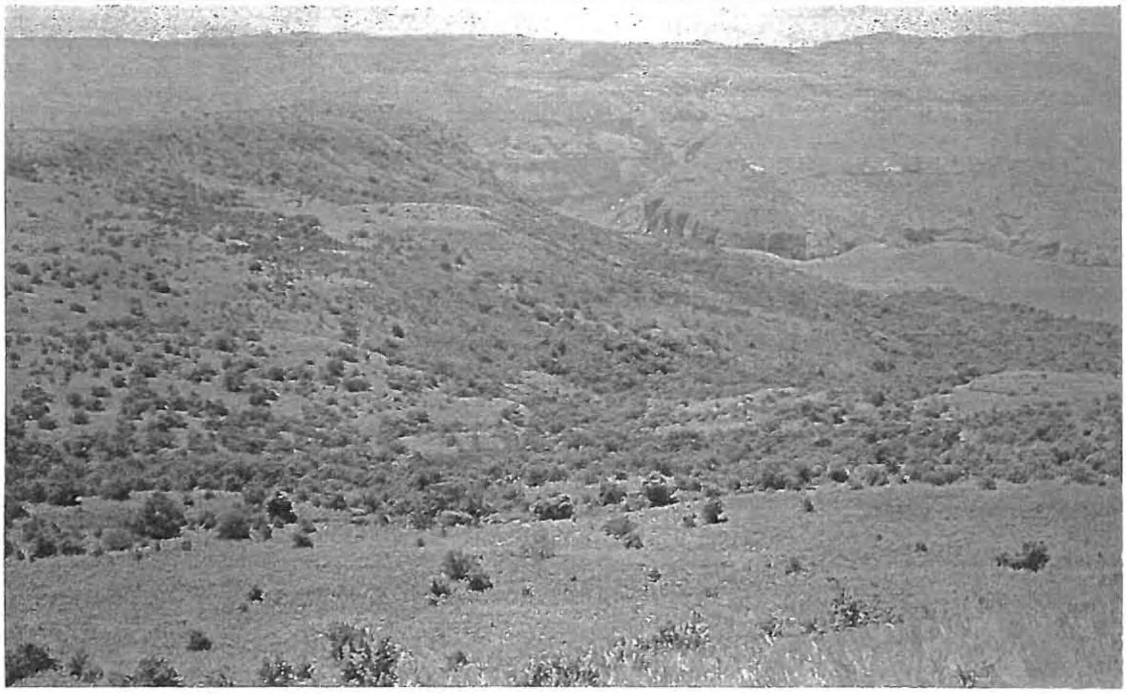


Plate 3 *Leucosidea sericea* scrubland in the 'protected' catchment IX, Cathedral Peak Research Station.

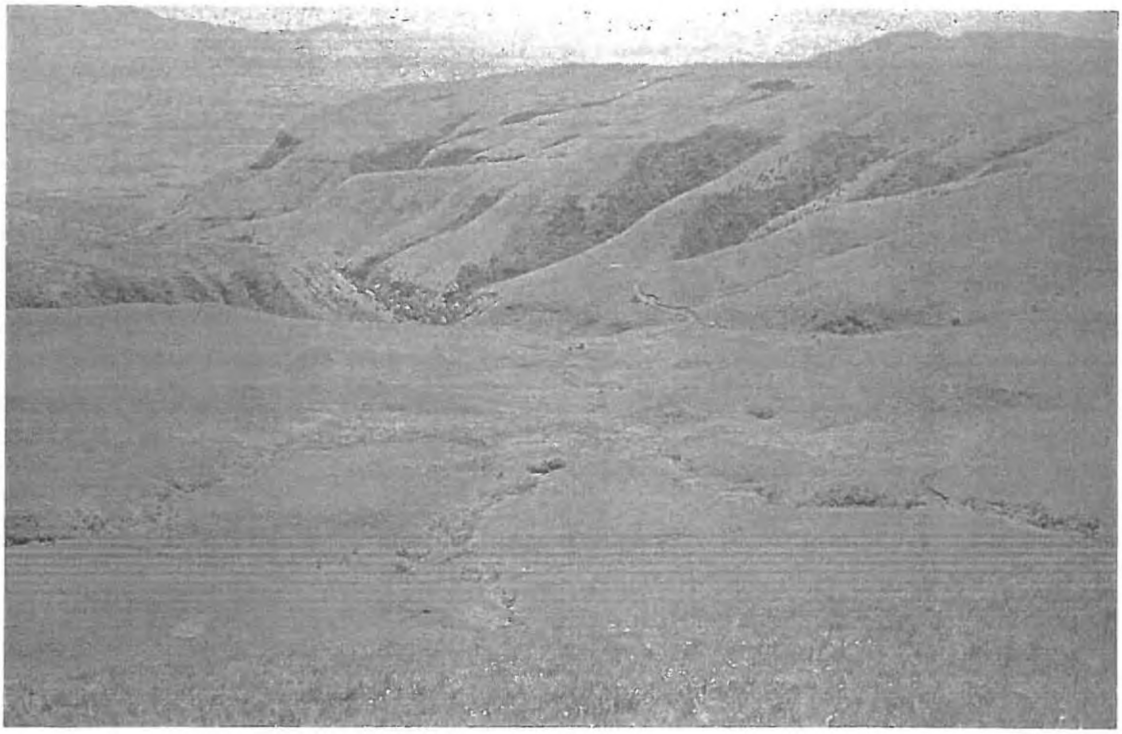


Plate 4 Low altitude headwater vlei at the convergence of a number of small streams, catchment VI, Cathedral Peak Research Station.

This vlei is characterised by streams traversing it, both as a single channel and as numerous small channels which frequently alter course. Most subalpine vleis are burned periodically, but owing to the moist nature of the soils, burning is usually limited to the upper portions of plants and fire damage is not severe. There is a close successional relationship between this community and grassland, the communities forming the beginning of fire deflected succession to grassland.

4.5.3 ALPINE BELT

The alpine belt extends in a narrow strip along the summit area of the high Drakensberg. The influence of the climatic conditions is seen in the xeromorphic character of the vegetation and in frost action on soils and vegetation. The principle plant communities are *Merxmuellera-Pentaschistis-Festuca* grassland and *Erica-Helichrysum* alpine fynbos or heathland (Killick, 1979) (Plate 5). Plants of temperate affinities are dominant in the vegetation. On the undulating summit areas of the Drakensberg Escarpment and stretching down into Lesotho are numerous headwater streams forming sponges or vleis. These communities are dominated by aquatic and hygrophilous vegetation forming alpine sedge meadows (Plate 6) (Edwards, 1967).

Present on the exposed buttresses and cliffs of the summit are open dwarf shrub communities, 0.2 to 1.0 metres in height, of *Erica* spp., *Helichrysum* spp. and other temperate species. The term 'alpine fynbos' is used to denote these communities. The term 'alpine' indicates the general physiognomic, xeromorphic and habitat features resulting from the montane climate and 'fynbos' or heathland indicates the affinities with vegetation, generally termed 'fynbos' found at lower altitudes in the south-western Cape. The climax community of the alpine belt is considered to be the *Erica* sp. (=DE 360)-*Helichrysum trilineatum* alpine fynbos/heathland, the species occurring in associations or consociations. Alpine heathland communities are interpreted as local edaphic or post-climax communities (Killick, 1963, 1979). Fires limit or deflect the alpine heathland plant succession, resulting in the development of *Merxmuellera-Pentaschistis-Festuca* alpine grassland.

The alpine grasslands are well developed on the summit area of the Drakensberg Escarpment, sometimes extending down gullies to 2700 metres. The communities range from local tussock grasslands to dense sward types. The principle plant association is *Merxmuellera-Pentaschistis-Festuca* grassland which forms a dense to relatively open sward, up to 0.8 metres high. This grassland is lightly grazed by Basuto owned horses, cattle and sheep. Burning, which seems to occur at least once every one to two years, has been observed, while little secondary modification of grassland is evident.

Numerous vleis and streams are also evident on the summit, they form the headwaters of the Tugela and Orange River systems. Killick (1963) divides the aquatic and hygrophilous vegetation associated with the communities into flushes, pools, streams, mud patches and sedge meadows. Alpine sedge meadows have a low continuous turf, 5 to 15 cm high, dominated by the sedges (Cyperaceae) *Carex monotropa* and *C. killickii*. The meadow is found on moist, but firm ground (due to the presence of a thick vegetation mat) on the summit area. The community occasionally exhibits a hummock structure as a result of trampling by Basuto owned cattle.

Plate 5 *Erica-Helichrysum* heathland dominating the exposed slopes of the Drakensberg summit alpine region.

Plate 6 Alpine sedge meadow on the summit area of the Drakensberg escarpment forming headwater high altitude vleis.

4.6 CONCLUSION

The vegetation of a region provides an invaluable expression of it's biological and physical controlling factors. The plant cover and abundance of recent as well as geological times can therefore reflect the most important factors such as climate. This concept forms the basis of pollen analysis and the reconstruction of past climates. Therefore it is important to obtain a good understanding of the present vegetation before a thorough modern pollen rain programme is instigated.

The Natal Drakensberg is an ideal region for a palynological investigation to be carried out. The presence of altitudinal related vegetation belts allows for a noticeable change in vegetation brought about by climatic fluctuations. These fluctuations can be observed in the abundance of particular pollen grains preserved in sediments. The sediments which facilitate pollen preservation are acidic, usually anaerobic, poorly drained soils, often associated with vlei-type conditions, these conditions are experienced in the Natal Drakensberg. The environmental conditions present in the research area echo Heusser's words that the Drakensberg has the potential for palynological research due to the presence of optimum pollen preservation sediments and where the vegetation would have and will be sensitive to climatic change (in Deacon, Lancaster and Scott, 1984).

CHAPTER FIVE
DATA COLLECTION AND METHODS OF ANALYSIS

5.1 INTRODUCTION

Modern pollen rain data were collected and analysed to investigate the assumption that pollen rain is indicative of the surrounding vegetation, thereby confirming and strengthening existing and/or future fossil pollen analysis and the resulting palaeo-environmental reconstruction. In the field a thorough vegetation analysis was conducted in vegetation communities recognized as pertinent to the proposed research. Thereafter an extensive two year pollen rain sampling programme was carried out, using both surface soil and pollen trap samples as a means of recording and quantifying the pollen rain. The methods, both descriptive and numerical, used to describe the pollen-vegetation relationship are described in this chapter.

5.2 VEGETATION ANALYSIS

5.2.1 INTRODUCTION

The medium of pollen production is vegetation, therefore knowledge of the vegetation is a "...paramount demand..." (Faegri, 1966, pp. 140). Before modern pollen rain - vegetation studies came to the fore Lichti-Federovich and Ritchie (1968) noted that one of the problems encountered in such studies was the lack of available adequate quantitative analysis of the surrounding vegetation. The first step involved in carrying out a modern pollen-vegetation analysis is therefore to quantify the present vegetation. For the delimitation of vegetation communities one needs to study the communities' stratification (canopy levels), species composition and some quantitative estimate of cover or abundance (Malmer and Regnéll, 1986). According to Birks and Gordon (1985) such vegetation data can take the form of tree counts, measurements of basal area, canopy area, or tree volume, or estimates of plant cover, density or frequency in plots around the sample site. Obviously the type and detail of vegetation sampling will depend on the specific aims of the investigation. If a detailed vegetation survey is conducted, the pollen and vegetation data can be classified independently, and the two classifications compared (Kershaw, 1973).

5.2.2 FIELD TECHNIQUES

A total of thirteen vegetation communities were selected from the three distinctive altitudinal zones described by Killick (1963) (see Chapter 4). Vegetation surveys was undertaken within each of the communities (Table 5.1) and species present and percentage aerial cover was recorded. The percentage aerial cover were deemed more appropriate than the more conventional basal cover (Bradshaw, 1981) for two reasons. Firstly, the aerial cover is an estimate of the dominance of a particular species within the community and secondly, as the pollen is produced from the upper, aerial part of the plant it was presumed that this measure would give a better representative value of the possible amount of pollen produced. Percentage aerial cover was measured as the proportion of the ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration (Kershaw and Looney, 1985).

The type of sampling technique employed was decided upon after consultation with personnel working within the research area (F. Smith, *pers. comm.*, 1988) and related literature (Killick, 1963; Edwards, 1967; Westfall *et al*, 1983; Westfall and Panagos, 1984; Everson and Clarke, 1987). Everson and Clarke (1987) evaluated sampling techniques on the Highland Sourveld within the research area using the quadrat, levy bridge, step point, wheel point, metric belt transect and 't Mannetje and Haydock methods. They conclude that the quadrat and wheel point techniques were most consistent. For the purpose of this study it was decided to use the quadrat as, although Everson and Clarke (1987) concluded that the wheel point method was the most suitable for determining grassland species composition within the research area, the wheel point method would not be suited to the sampling of species composition and abundance within the scrubland and forest vegetation. Therefore for the sake of standardization and consistency the quadrat sampling technique was employed.

Identification of species was predominantly done in the field with the assistance of a field herbarium. Unidentifiable species were labelled, collected and identified with the aid of keys and personnel at the Cathedral Peak Research Station or dried, pressed and identified at a later date at the Albany Herbarium (GRA).

Table 5.1 Number and size of quadrats recorded within the vegetation communities surveyed.

	Vegetation Community	Number of Quadrats	Size of Quadrats
MONTANE	Highland Sourveld	25	1m × 1m
	Protea Savanna	20	10m × 10m
	Mountain *Podocarpus* forest	20	10m × 10m
SUB-ALPINE	*Themeda triandra* grassland	20	1m × 1m
	'Mixed' grassland	20	1m × 1m
	Festuca costata grassland	20	1m × 1m
	Leucosidea sericea scrubland	20	10m × 10m
	Rendlia altera grassland	20	1m × 1m
	Low altitude vlei	25	1m × 1m
	Sub-alpine fynbos	20	10m × 10m
ALPINE	Alpine grassland	20	1m × 1m
	Erica-Helichrysum heathland	20	1m × 1m
	Alpine sedge meadow/high altitude vlei	20	1m × 1m

5.2.3 SAMPLE SIZE AND NUMBER

It is usually necessary to distribute a set of quadrats in an area in such a manner that the position of each quadrat is independent of all the other quadrats and is also independent of any prominent features of the area. A technique is required where conscious or unconscious prejudgment is eliminated, otherwise the final non-random sample will be of little use for further comparison as the use of statistics requires that the samples are random (Kershaw and Looney, 1985).

If the distribution of individuals in a population is completely random then the size of the quadrat is immaterial except from the standpoint of convenience. Any size convenient for the particular vegetation which is investigated can be used, however most individuals are not distributed at random and the size of the quadrat has a considerable effect on the variance of the data obtained. If there is a tendency for individuals to be grouped together, the measure of the variance of the data is at a maximum when the size of quadrat is approximately equal to the mean area of the groups of individuals (Kershaw and Looney, 1985). Since it is usually impossible to predetermine the scale of this pattern and since such patterns are often repeated on larger scales, the size of quadrat has to be chosen arbitrarily. The most suitable quadrat on theoretical grounds is the smallest possible, relative to the type of vegetation and to the practability of the enumeration of such a quadrat size.

The present study used 10m × 10m quadrats in the forest and scrubland communities. Similar vegetation studies conducted in the area have used 20m × 5m (Killick, 1963), which proved to be representative. It was decided, in consultation with forestry staff, to use the same quadrat area (100m^2), but use a 10m × 10m quadrat so as to reduce 'edge effect'. The grassland communities proved more of a problem as previous sampling strategies had employed either a Levy bridge or wheel point method (Everson and Clarke, 1987; Everson *et al*, 1989). For the sake of standardization and consistency it was decided to use quadrats within the grassland communities and to employ a 1m x 1m quadrat size.

For this study a random numbers table was used to determine sample sites. Firstly a peg was thrown into the vegetation community, from this starting point one moved parallel with the contour as many steps as the first two digits on the random numbers table indicated. One moved left for an even number and right for a odd number. Once the required number of paces was marked off, one then moved perpendicular up (even) or down (odd) according to the next two digits on the list. At this final point the lower right hand corner of the quadrat was placed.

The modern pollen rain collecting techniques of surface soil samples and pollen traps (see section 5.3.2) were positioned or collected in a similar, random, manner. Pollen traps were set-up and soil samples were taken from within the quadrat depending on the next two digits after those employed to position the quadrats. For example number 25 meant two metres along the horizontal and five metres up the vertical gradations on the 10m x 10m quadrats or 20 cm and 50 cm in a 1m x 1m quadrat. At this point a surface soil sample was collected and/or a pollen trap set-up.

The number of quadrats required was determined by drawing up a cumulative species versus quadrat number curve (Appendix 1). It is evident that in some communities, for example *Rendlia altera* grassland, alpine sedge meadow and *Erica-Helichrysum* heathland that fewer quadrats would have been representative, whereas communities such as alpine grassland, sub-alpine fynbos and *Festuca costata* grassland still show increases in cumulative species number at a sample size of fifteen to twenty quadrats. However as these increases are of the order of only one or two species over five quadrats, it was decided that twenty quadrats was sufficiently representative of the communities.

5.3 MODERN POLLEN ANALYSIS

5.3.1 INTRODUCTION

There are numerous techniques for sampling modern pollen, the instrumentation varying according to the objectives involved. Within the scope of this project the two approaches employed were: the analysis of surface soil samples and the 'trapping' of pollen grains and spores in pollen traps placed at one metre above the ground.

5.3.2 FIELD TECHNIQUES

5.3.2.1 Soil Samples

With regards to the number of soil samples required, a preliminary study was carried out in 1987 to determine just such a sample size (Hill, 1987). The results, in amalgamation with initial results obtained from the present study, indicated that, again depending on the vegetation community, approximately 18 to 20 samples were necessary to obtain a representative sample.

Twenty samples were taken randomly from within the vegetation survey quadrats. A sample of approximately 100 grams constituting the top 3-5 cm of the soil was taken, all overlying organic matter having been first removed. Samples were placed into paper bags, sealed and kept in a refrigerator to reduce bacteria and fungal growth, until the necessary laboratory techniques could be carried out (Hicks and Hyvärinen, 1986).

5.3.2.2 Pollen Traps

So as to replicate the conditions of pollen reception at a sediment surface, the active volumetric pollen and spore samplers (Hirst, 1952; Keynan *et al*, 1986) are inappropriate, and some kind of passive sampler which more accurately reflects the site of pollen deposition is necessary (Meadows, 1989). As these pollen traps were to be used in a number of vegetation communities covering an extensive mountainous area, they needed to be easy to construct, transport, install and re-collect. The 'Oldfield' pollen trap (Figure 5.1) used by Flenley (1973), Hamilton and Perrott (1980), Meadows (1984) and introduced to South Africa by Meadows *et al*, (1987) has proved to be just such a pollen rain sampler.

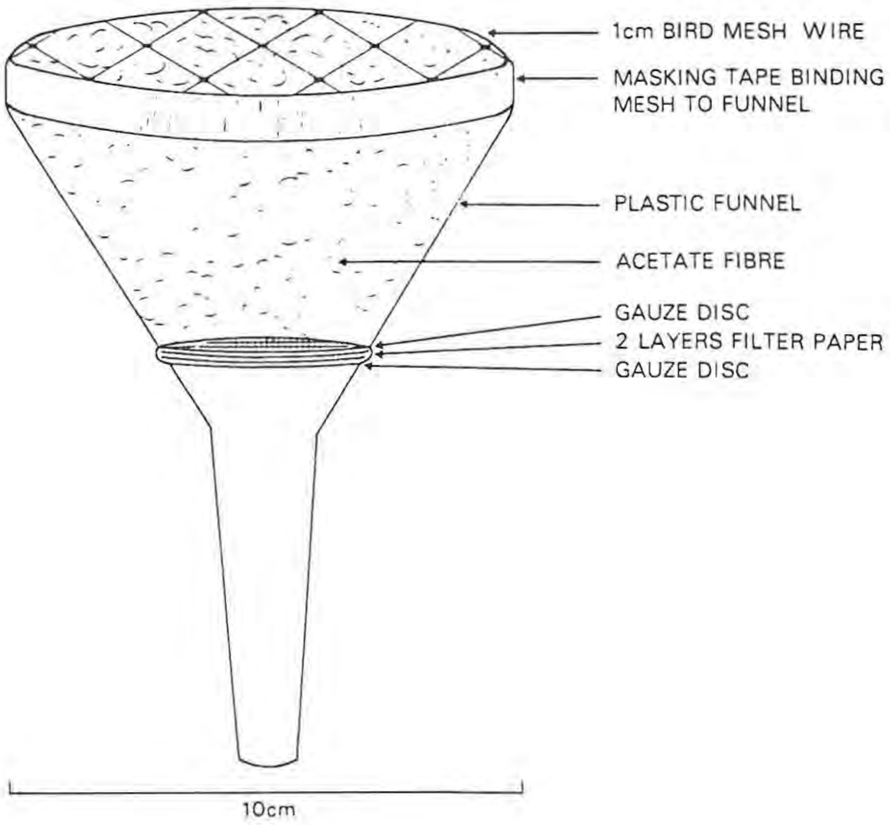


Figure 5.1 Schematic representation of a pollen trap. The trap was placed 1 metre above the ground on a metal stake.

The traps (Plates 7-9) consisted of a plastic funnel (area of 85.50 cm^2) with two discs of copper gauze placed within the base of the funnel. Sandwiched between the two discs were 2 microbiological filters with a pore size of 0.45μm. The filter allows for the passage of precipitation through the funnel, but retains the pollen grains. The funnel was filled with acetate fibre protected with a 0.5 cm bird netting fitted over the top of the funnel. Acetate fibre has become increasingly difficult to obtain and it has been suggested (Bush, 1992) that rayon be used as a substitute for the de-oiled acetate fibre. The funnels were placed on a one metre high metal stake with a ring welded onto the top into which the funnel was fitted, and was attached to the stake with masking tape. At the end of a sampling period the traps were removed, sealed in a plastic bag and kept in a cool place until such time as the necessary laboratory procedures could be carried out.

Plate 7 Pollen trap in the understorey vegetation in the *Podocarpus* forest.

Plate 8 Pollen trap and vegetation sampling quadrat in the *Protea* savanna community.

Plate 9 Pollen trap within a *Rendlia altera* grassland community on the plateau of the Little 'Berg.

These traps proved to be extremely efficient and, out of over 700 traps placed within the montane and sub-alpine vegetation communities, only 16 were lost or damaged to the extent that no representative pollen count was possible. Ten traps were also placed in each of the three alpine vegetation communities. All thirty traps (total of ninety) were stolen both after being placed there in June and September 1988 and again in December of 1989. These alpine communities are on the South African/Lesotho border and the area is used by the Basothos for domestic stock grazing. The traps, as a result of their design and their usage, are conspicuous on the short alpine heathland/grassland summit and consequently were misappropriated.

Sugden (1990) mentions contamination of the acetate fibre within the pollen traps due to defecation by birds being a concern. It has been suggested that this contamination can be accounted for by analyzing the 'bird-droppings' separately and assuming that the difference between the contaminated samples and the 'bird-droppings' represented the pollen rain from the surrounding vegetation. The present study found very few traps had been used as bird perches and any droppings found inside the traps were removed without any further analysis. The removal of acetate fibre from the pollen traps by birds and baboons was to a large extent, overcome by covering the traps with bird mesh.

The number of traps placed within each vegetation community varied (Table 5.2). Initially it was not known how many traps would be required to gain a good representation of the sample site. Preliminary results for the montane region of the Cedarberg (J. Sugden, *pers. comm.*, 1988) had shown that as few as five traps per community was sufficient to closely duplicate the results. Therefore it was decided to place as many traps as it was possible to carry to each of the sites with a minimum number of six.

Fieldwork was undertaken from June 1988 to June 1990, thereby gaining a full two years of modern pollen rain data. The traps were replaced on a tri-monthly basis until November-December 1989. A seventh sample of six months duration, December 1989 to June 1990, was performed to compare a six months sample with the usual tri-monthly samples. Two full years of data was not achieved for the sub-alpine fynbos and low altitude vlei communities. The tri-monthly sampling procedure allowed for the observation of any seasonal, as well as annual fluctuations.

Table 5.2 Number of traps placed within each vegetation community

Vegetation Community		Number of traps	Sample Numbers
MONTANE	*Protea* Savanna	18	1-18
	Podocarpus forest	18	19-36
	Highland Sourveld	6	43-48
SUB-ALPINE	*Rendlia altera* grassland	6	37-42
	Leucosidea sericea scrubland	9	49-57
	Themeda triandra grassland	9	58-66
	'Mixed' grassland	7	67-73
	Festuca costata grassland	9	74-82
	Sub-alpine fynbos	10	83-92
	Low altitude vlei	6	97-102

5.3.3 LABORATORY TECHNIQUES

The techniques used to chemically dissect out the pollen from both the soil and the pollen traps are adapted from Faegri and Iversen (1975), Faegri *et al*, (1989) and Doher (1980) and are based on the same principles applied to those for fossil pollen analysis. The aim of the sample preparation, purification, staining and mounting is to concentrate the pollen grains and spores making them more visible for identification and counting. The technique involves the removal of humic acids with sodium hydroxide (NaOH), removal of silica using hydrofluoric acid (HF), removing extraneous matter by acetolysis (9 parts acetic acid:1 part concentrated sulphuric acid), staining the pollen grains (with safranine) and then mounting or storing in silicone oil. Various steps are altered according to the material, these changes are discovered through experience and checking the state of the specimen at each stage of the procedure. For example, Orchidaceae and Juncaceae pollen grains are destroyed if acetolysis is allowed to occur for the full 5 minutes in a heated water bath.

The laboratory procedure of surface soil samples follows the above procedure (Appendix 2 for detailed procedure), but due to the greater proportion of sand in relation to organic matter present in the soil, digestion of silica by hydrofluoric acid requires longer than the specified three hours. The procedure for the pollen traps (Appendix 3) is adapted to separate the acetate fibre from the pollen grains (Meadows, 1984). The acetate fibre is dried and then dissolved in acetone for a period of 12 hours, after which the acetone is evaporated off before continuing with the standard techniques of purification and concentration of the pollen samples.

With regards to the surface soil samples, a relative count of 250, 500 and 1000 pollen grains and spores was undertaken. The exact number of grains counted ultimately depended on the volume of polliniferous oil placed onto the slide, as one cannot stop counting after 250, 500 or 1000 grains as the whole slide must be counted, due to unequal distribution of pollen grains on a slide (Brookes and Thomas, 1967). For the pollen traps, total counts of a measured volume of polliniferous silicone oil was conducted, so that pollen influx values per trap could be calculated.

All identification and counting was done using a Zeiss photomicroscope at a magnification of x400 and x630 (oil immersion). Pollen grains were identified from the reference collection housed at Rhodes University and the Albany Museum, from South African references (van Zinderen Bakker, 1953, 1956; van Zinderen Bakker and Coetzee, 1959; Welman, 1966; van Zinderen Bakker and Welman, 1970; Scott, 1982b, 1983) and from atlases of other countries (Heusser, 1971; Markgraf and D'Antoni, 1978).

Pollen counts are presented in the form of a graph prior to attempting interpretation (Birks and Gordon, 1985). For modern pollen data the graph is in the form of a rotated bar graph with taxa represented on the Y-axis and percentage occurrence on the X-axis. For comparative purposes it is necessary to use a relative percentage value as opposed to absolute values. Absolute values can and have been calculated for the modern pollen rain collected from the pollen traps, but it is not possible to do so for the soil samples. This is as a consequence of soil variation and lack of indication of sedimentation rates.

The use of relative pollen percentages introduces an inherent constraint into the data, namely the problem of proportionality: when one pollen type increases in relative frequency, some other type (s) must decrease as the sum of all proportions must always equal 1. Furthermore the expected correlation between the pollen types in a percentage data set is negative rather than 0, this may obscure real patterns among the different pollen types. Despite these drawbacks, for the sake of subjective comparison between the data sets (vegetation data are presented as percentages), relative percentage frequencies have been presented. Fossil pollen spectra are usually calculated as relative percentage frequencies, therefore for comparative purpose percentage values are more useful.

For percentage data, a critical decision is the specification of the taxa which will be included in the pollen sum. Birks and Birks (1980) argue that the choice should be based on the principle that all members of interest and under study should be included. In general, interest is usually concentrated on regional vegetation, in which case all pollen and spores which could originate from the surrounding vegetation should be included in the pollen sum (Janssen, 1970). Two exceptions have been made in this study, Bryophyta spores and the exotic taxa *Pinus* and *Acacia*. Certain Bryophyta spores were collected and identified within the high altitude vlei and *Podocarpus* forest communities, however the counts were low and the Bryophyta spores could not be identified further than the plant kingdom division, Bryophyta. Clarke and Duckett (1979) provide a good review of Bryophtya spore morphology and conclude that such studies are very much in the minority. No such work exists for South African species to an extent useful to palynologists.

Secondly, the taxa *Pinus* and *Acacia* have been excluded from the pollen sum. *Pinus patula* Schlechtd. and Cham. is an introduced exotic planted in the Cathedral Peak Research Area to study the effects of afforestation on water yield from particular montane catchments. Scanning electron microscopy work was performed on *Pinus* and *Podocarpus* pollen as they are morphologically similar. Once the differences were recorded and it was possible to distinguish between the two species under a light microscope the *Pinus* pollen was not counted or included in the pollen sum. A similar problem arose with the presence of *Acacia* pollen in the pollen spectra. The species *Acacia mearnsii* De Willd. is an exotic species prevalent in the surrounding farming area, however an indigenous species *Acacia sieberana* DC. has also been recorded in the region. It was decided to exclude *Acacia* pollen counts from the pollen sum as, although it was not possible to distinguish between the two species with the aid of a light microscope, there is only a single recording of *Acacia sieberana* from the area and it is doubtful if all the recorded *Acacia* pollen originated from this single specimen which is not located near any of the research sites. Both the exotic species are high pollen producers, as was evident by the presence of their pollen in all the pollen spectra including the presence of *Pinus* pollen in the alpine spectra. The addition of these species to the pollen sum would offset the relative percentage frequencies of the indigenous vegetation, affecting the resultant pollen rain spectra unique to a particular vegetation community.

Soil pH values were measured by adding 50 ml of 1M KCl to 20 grammes of soil. The solution is left standing for 50 minutes, then stirred and left to stand for another 10 minutes before measuring the pH value of the solution (Buys, 1980). All twenty surface soil samples collected for modern pollen rain analysis, per vegetation community, were measured.

5.3.4 OPTIMUM SAMPLE SIZE

Once the pollen counts of both the surface soil samples and pollen traps were completed a statistical test was performed on the data to determine the optimum sample size at a particular confidence limits. The test (described below) was applied at a 1%, 2%, 5% and 10% error. For ecological data these levels of error are deemed satisfactory. The formula used was:-

$$n = (z.s/d)^2$$

where:n = required size of sample

s = standard deviation of obtained results

d = tolerable margin of error at a specified level

z = value obtained from the z-table, depending on the confidence limit (Hammond and McCallagh, 1978).

The results allow for more confident recommendations to be made regarding the number of soil samples and pollen traps required within the studied vegetation communities to obtain a representative sample.

5.4 POLLEN INFLUX VALUES

The calculation of pollen influx (or annual/seasonal pollen deposition) was performed to remove possible inherent uncertainties in the interpretation and understanding of relative percentage frequency pollen analysis. The influx values are calculated as grains/cm^2/year (Berglund and Ralska-Jasiewiczowa, 1986) or, as in the case of seasonal data, grains/cm^2/90 days, 90 days being the average number of days per season, despite the fact that the idea of seasons or even years is artificial and the life-cycle of pollen and spore production does not follow the Julian calender (Mäkinen, 1977).

5.5 POLLEN REFERENCE COLLECTION

5.5.1 INTRODUCTION

During pollen analysis the principle problem is that of recognition of the pollen grains (Faegri *et al*, 1989). With regards to Quaternary palynology the analyst accepts a pre-existing modern taxonomy as a standard, and then must identify the fossil pollen by comparison with the standard. The research attempts to match the pollen grains with those of modern taxa of the lowest possible rank; this is rarely at the species level, more often at the generic or family level. Successful identification therefore depends to a large extent on the range and quality of reference material available. Monographic treatments of the pollen morphology of some individual plant families are available (Ladd, 1977; Salgado-Labouriau, 1982; Linder and Ferguson, 1985; Vincent and Getliffe Norris, 1989), but in addition to the problems of terminology and the use of highly developed apparatus, such as the scanning electron microscope, they also presume the possibility of identification to the family level, which is not always possible with the aid of only a light microscope.

A major limitation within the science of palynology in South Africa, be it fossil or modern pollen research, is the lack of reference collections and pollen atlases to aid in the identification of pollen grains and spores. Pollen atlases for South Africa include the series by van Zinderen Bakker (1953, 1956), van Zinderen Bakker and Coetzee (1959), Welman (1966) and van Zinderen Bakker and Welman (1970). Although these atlases make a valuable contribution to South African palynology, all pollen grains and spores are represented in diagrammatic form, which is not as satisfactory as photographic representations. Coetzee (1955) has produced a research paper on the basic structure of the *Acacia* pollen grain. More recently Scott (1982b, 1983) has produced some pollen photographs within his research papers and scanning electron microscope work has been done on the pollen grains of some South African taxa (Verhoeven and Venter, 1987; Vincent and Getliffe Norris, 1989, Balkwill and Getliffe Norris, 1985;) but to date no complete pollen reference collection exists for the South African flora. Consequently any palynological research undertaken in South Africa requires a regional reference collection to aid that particular study, as the task of establishing a pollen reference for the entire South African flora is enormous. At present, regional collections are housed at the University of the Orange Free State, the South African Museum in Cape Town, the University of Cape Town, Rhodes University and the Albany Museum, Grahamstown. Before any detailed palynological analysis could be carried out in the Natal Drakensberg, a detailed pollen microscope slide and photographic reference collection concentrating on the regional flora had to be established.

5.5.2 FIELD TECHNIQUES

At the time of the vegetation survey and on subsequent sampling trips, species that were either flowering or producing spores (Pteridophytes) were collected, identified and used to improve the existing pollen grain and spore reference collection housed at the Geography Department of Rhodes University. Further reference material was obtained by 'swopping' slides with the University of Cape Town.

A species list of the research area was obtained from the work of Killick (1963), Granger (1976) and unpublished records at the research station. These lists were used to identify and collect pollen reference material from flora not encountered in the present vegetation survey or as a result of the species being present in areas adjacent to the sampled vegetation communities. Pollen from these species was obtained from either the Rhodes University or Cathedral Peak Forestry and Research herbaria or, preferably, by collecting fresh specimens from the research area.

5.5.3 LABORATORY TECHNIQUES

The slide material of the pollen reference collection should correspond as closely as possible to the grains met within actual pollen analysis (Faegri, *et al*, 1989), which means that in most cases the extra-exinous waxes of entomophilous plants and the interior parts of the grains must be removed, leaving only the exines. The reason for the preparation, staining and mounting of a reference collection is to concentrate pollen grains and make them as visible as possible, while it is important to adopt the same preparation procedure for both reference and working material so as to facilitate comparison and identification.

For the preparation of the modern pollen samples, flowers or spore bearing pinnules were crushed, treated with 10% NaOH and heated in a water bath (50-60° Centigrade) for 5-10 minutes, stirring often. The residue was washed through a sieve (approximately 200 μm) and the humic acids removed by means of centrifugation. Next, extraneous matter was removed by the acetolysis process, washed and stained with safranine, before mounting the samples in glycerine jelly.

Preparation for making a mount embraces two processes: (1) washing out all reagents used during the preparation of samples, and (2) staining. A stain should be used that gives the maximum contrast during microphotography. Thus, a red or black stain is preferred, safranine being among the most useful in glycerol or glycerine-jelly preparations (Faegri, *et al*, 1989). Staining is required as it renders the pollen more recognisable in a preparation and it contributes to differentiation of grains. Overstaining of preparation can occur, this results in the loss of the finer structural details of the exine.

Glycerine jelly proved to be a good mounting medium although problems were encountered. Air bubbles which obscure detail within the slide develop when the glycerine jelly is overheated. With experimentation and experience it was discovered that air bubbles did not form if the jelly was heated to only 40-45°C. Recently, the use of an alternative mounting medium, DPX moutant, has been proposed (J. Sugden, *pers. comm.*, 1991). This method is being adopted in preference to the glycerine jelly method, as it is simpler, less time consuming, avoids problems relating to overheating and the slides have a longer life-span as they remain air-tight. Slides produced by the glycerine method have a limited life-span, as they are seldom air-tight after 10 years and therefore, the pollen grains are slowly destroyed by oxidation.

The basic procedure used to prepare and mount the reference slides is outlined in Appendix 4. Each slide is labelled with species number (Gibbs-Russell *et al*, 1984, 1987), family and species name, place of origin of the specimen and date on which mount was prepared. The slides were photographed, at a magnification of x630 and x1000, using a Zeiss photo-compound microscope with Kodak technical Pan black and white film 2415. Photographs were printed and placed onto labelled record cards. The photographs were taken at varying levels/depths of the pollen grains so as to show the various features. To date the Rhodes University Geography Department houses approximately 700 reference slides and photographs of pollen grains and spores, predominantly from the Natal Drakensberg as a consequence of the present study; others are from the montane areas of the Cedarberg and the Nuweveldberg.

When preparing modern pollen, contamination can occur. The pollen of some anemophilous species, for example Poaceae, is dispersed almost instantly when the anthers open, and must therefore be collected in the field when flowering occurs, or immediately before the anthers open. According to Faegri *et al*, (1989) herbarium material of such plants is not reliable and should be avoided where possible. Another contamination possibility is that the pollen of a particular species has already been dispersed and that the pollinator(s) that have visited the plant have deposited the pollen from another species. As long as the pollinator is constant there is little risk of contamination, but not all pollinators are constant. During laboratory work samples may be contaminated due to the laboratory being dirty, contaminated utensils or via the pollen present in the laboratory air. These laboratory problems can be avoided by proper laboratory care being upheld and performing checks for contamination by checking the final slide against the original, untreated, material.

5.6 SCANNING ELECTRON MICROSCOPY

5.6.1 INTRODUCTION

The scanning electron microscope (SEM) has added a new dimension to the study of pollen analysis (Birks and Birks, 1980) and has proved extremely useful as it enables more accurate identification of pollen grains. The increased popularity of SEM as a tool for studies of pollen morphology has focused attention on methods of preparation of pollen for observation. Initial studies used either acetolysis alone in preparation, or in comparisons of fresh and acetolysed pollen. These studies concluded that more fine detail was visible in the acetolysed material (Ridgeway and Skvarla, 1969; Hanks and Fairbrothers, 1970). Due probably to the influence of Erdtman (1960, 1969), the acetolysis method has become accepted as the standard procedure for preparing pollen for microscope observation. This palynological tradition appears to have arisen because earlier pollen studies were generally concerned with analysis of fossil pollen (Lynch and Webster, 1975).

There is at present a move towards developing new methods for SEM preparation as the acetolysis does have some marked disadvantages for the study of pollen of living taxa (Hesse and Waha, 1989; Smith and Tiedt, 1991). Most palynologists work with acetolysed material since this preparation removes waxes and other surface coatings from the fresh pollen and most closely approximates the process of fossilization (Hanks and Fairbrothers, 1970). Removal of the intine and other cellular contents during acetolysis renders grains liable to collapse in the vacuum chamber of the SEM (Nilsson *et al,* 1974). Rowley (1973) has pointed out that distortion due to shrinkage in acetolysed pollen may place a severe limitation on the amount of detail which can be observed at high magnifications. During the course of a comparative SEM survey of pollen morphology in the Euphorbiaceae, Lynch and Webster (1974) experimented with various published methods of preparation and concluded that none of them are completely satisfactory. The effect of various preparation techniques differ from taxon to taxon, as a consequence it is important to ascertain the amount of change in the material so that other researchers using the data can place it in its proper perspective for comparative interpretations.

Although SEM greatly enhances the morphological features of a pollen grain, its use is limited because it is not possible to count or obtain frequencies of taxa as one does using the light microscope. All identification and counts of pollen in this study were carried out with a Zeiss light photomicroscope. Some taxa are remarkably similar with respect to pollen morphology and SEM work was performed to augment the light microscope.

5.6.2 TECHNIQUES

It was proposed from the outset of this research that SEM work would not be attempted. Firstly, it was too costly and time consuming and secondly, all counting was to be done with a light microscope thus it was intended to concentrate the pollen reference slides and photographs on what would be visible under the light microscope. Once counting commenced, it was evident that *Pinus* and *Podocarpus* pollen types were similar, therefore SEM work was performed on a few specimens to try and help with the light microscope identification of the 'trouble' taxa.

The preparation procedure followed was the acetolysis method. Despite all the disadvantages (Hanks and Fairbrothers, 1970; Andersen and Bertelsen, 1972; Lynch and Webster, 1975; Hesse and Waha, 1989), it was felt that as the SEM work was being performed not as a separate morphological study, but rather to augment and help the light microscope work, that the pollen grains should be treated the same in both procedures. After acetolysis, the material was suspended in a drop of water and transferred to a brass stub onto which the pollen grains were adhered with an aqueous glue. The samples were coated with gold-palladium, and observations were made with a JEOL JSM-840 scanning electron microscope.

The SEM investigation was an exploratory study of the various techniques available and as a result, the less elaborate preparatory procedures were followed. The advantages and disadvantages of the different procedures are discussed by Echlin (1971), Köhler and Lange (1979), Lynch and Webster (1975), Ladd (1977), and Linder and Ferguson (1985).

5.7 STATISTICAL AND QUANTITATIVE ANALYSIS

5.7.1 INTRODUCTION

If modern pollen-vegetation relationships or 'corresponding patterns' (Webb, 1974b) can be determined, comparisons on the basis of overall similarity can then be made between fossil pollen spectra and modern pollen assemblages from known vegetation types. If similarities can be determined between modern and fossil assemblages it is likely that the spectra were produced by broadly similar vegetation, therefore a modern vegetational analogue can be proposed for the past vegetation. Such comparisons provide a factual and repeatable basis for vegetation reconstruction.

A recent direction for palynological investigations has been towards numerical and computation of the results (Birks and Gordon, 1985). The complexity of the statistical techniques vary and, to a large extent, depends on the type of data available and the problem being investigated. A variety of statistical techniques have been tried in an attempt to determine the most appropriate and meaningful results. This study has used some of these statistical techniques to help describe and elucidate the modern pollen rain - vegetation relationship. The techniques performed in the study are: analysis of variance, two-way indicator species analysis and detrended correspondence analysis, principal components analysis, canonical correlation analysis and multiple discriminant analysis. Each test was performed for a specific purpose which is explained below, together with a brief discussion of how the technique operates.

5.7.2 ANALYSIS OF VARIANCE (ANOVA)

Analysis of variance (ANOVA) techniques are used for a set of statistical problems in which one is interested in the effect of one or more non-metric variables on a single dependant variable, also called a response variable. Hinkle *et al*, (1979) describe an ANOVA as the technique to test for differences between the means of two or more groups of subpopulations. The underlying concept of an ANOVA is that sample values almost invariably differ and the question is whether the differences among the samples signify genuine population differences or whether they represent merely chance variations such as are to be expected among several random samples from the source population.

For an ANOVA, hypotheses are formulated about the means of the groups on the dependent variable and then tested for statistical significance (Hinkle *et al*, 1979). ANOVAs were undertaken to test whether the modern pollen data varied significantly from year to year or from season to season. A further ANOVA was carried out to determine if there was any significant difference between the mean of five and ten as opposed to the mean of twenty surface soil samples. This last ANOVA was performed to try and determine the least number of soil samples to obtain a representative sample number. A two-way ANOVA testing year and season against pollen data was tried, but a significant level (p-value) of less than 0.01 was calculated, therefore there was a significant interaction between seasonal and annual data. As a consequence, each variable was tested separately in a one-way ANOVA. A further ANOVA was performed on the soil pollen counts to determine whether there was any significant difference in performing counts of 250, 500 or 1000 pollen grains per sample.

The various hypotheses tested were as follows:

i) H_0: There is no significant difference between seasons for taxa represented in the pollen spectra.
   H_1: There is a significant difference between seasons for taxa represented in the pollen spectra.

ii) H_0: There is no significant difference between the two years for taxa represented in the pollen spectra.
   H_1: There is a significant difference between the two years for taxa represented in the pollen spectra.

iii) H_0: There is no significant difference in the means of the pollen counts from each vegetation community, from ten as opposed to twenty samples
   H_1: There is a significant difference in the means of the pollen counts from each vegetation community, from ten as opposed to twenty samples

iv) H_0: There is no significant difference in the means of the pollen counts from each vegetation community, with counts of 250, 500 or 1000 pollen grains and spores
   H_1: There is a significant difference in the means of the pollen counts from each vegetation community, with counts of 250, 500 or 1000 pollen grains and spores.

5.7.3 TWINSPAN AND DECORANA

The present study used both two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DECORANA), using the FORTRAN program for DECORANA and TWINSPAN stored on Rhodes University's mainframe computer, to classify and ordinate the vegetation communities under study. The techniques were also performed on the pollen spectra recorded from pollen traps and soil samples to investigate and subjectively compare both the classification and ordination of all three data sets (vegetation, soil and pollen trap data), seeking similarities or dissimilarities between them. With respect to palynological studies the multivariate classification and ordination procedures, TWINSPAN and DECORANA, have been used by Stevenson (1985) in a study of the vegetational history of south-western Spain and Ayyad *et al*, (1992) for the Nile Delta, Egypt.

According to Gauch (1982), results achieved by DECORANA are nearly ideal. DECORANA summarises a two-dimensional data structure efficiently and clearly, thereby implying that the underlying model matches the data structure to a considerable degree. DECORANA is most useful in the analysis of difficult data sets, and axis length for DECORANA sample ordinations have been found to be accurate to within 10-20% (Gauch, 1982), provided the data set for DECORANA satisfies two assumptions. The first is that the data set to be analyzed consists of records of the abundance of a set of attributes in a set of individuals. With ecological data, the attributes are ordinarily species and the individuals are ordinarily samples. The second assumption is that, at least in principle, the sample can be arranged along a gradient in such a way that species occupy only a limited extent of the gradient. In practice, the length of a gradient available for study may not be sufficient for any species to be strictly confined to a particular part of it. This does not matter; the assumption is that if the gradient were longer, species would be confined to particular parts of it. Hill (1979a) claims that for appropriate data, DECORANA is a more reliable method than reciprocal averaging or principal components analysis.

Gauch and Whittaker (1981) recommend this ordination technique for the positioning of sample points in a low-dimensional space. Successive partitions are then drawn in the ordination to generate a divisive, hierarchical classification. The partitions may be placed subjectively by drawing boundaries on ordination graphs by hand. Subjective partitioning can be particularly useful when:

1) divisions through sparse regions of the mass of sample points are desired,
2) field experience or previous analyses have provided a general understanding of the data that the researcher wants to incorporate into the analysis but cannot precisely specify, and
3) subjective clustering is often sufficient for the purposes of a given study.

All ordination techniques are best used in conjunction with a classification analysis, in this case two-way indicator species analysis (TWINSPAN). TWINSPAN is a polythetic divisive technique (Hill, 1979b; Gauch & Whittaker, 1981). The data is initially ordinated by reciprocal averaging, then those species that characterise the reciprocal averaging axis extremes are emphasised in order to polarize samples, and the samples are divided into two clusters by breaking the ordination axis near its middle. The sample division is refined by a reclassification using species with maximum value for indicating the poles of the ordination axis. The division process is then repeated on the two sample subsets to give four clusters, and so on, until each cluster has no more than a chosen minimum number of members or else the number of divisions (levels) is stipulated (Gauch, 1982).

TWINSPAN operates similar to the cluster analysis techniques performed on modern pollen spectra by Lamb (1984) using minimum-variance cluster analysis, Dodson (1983) who used clustering of surface soil samples based on a Bray and Curtis coefficient, and by Kodela (1990a) who performed a cluster analysis of surface pollen rain using Ward's method or the minimum sum-of-squares criterion and squared Euclidean distances as the measure of proximity. TWINSPAN results may be displayed as a dendrogram showing the resultant sample hierarchy, using the sequences of divisions as integral levels or computing the levels as the average distances between samples in ordination space (Gauch and Whittaker, 1981). TWINSPAN is recommended (Gauch, 1982) for hierarchical classification because of its effectiveness and robustness as a consequence of being polythetic and divisive. Further advantages of TWINSPAN are; (1) its use of the original data set, rather than a secondary dissimilarities matrix with information only on samples/species, (2) integrated classifications of both samples and species, and, consequently, (3) production of an arranged data matrix, (4) ordering of the sample sequence to place most similar samples together, making dendrograms clearer and (5) minimal computer requirements.

5.7.4 PRINCIPAL COMPONENTS ANALYSIS

There are two basic approaches to examining how clearly modern pollen spectra reflect the vegetation in which samples were collected (Birks *et al*, 1975). One approach is to utilise the information concerning the vegetation type from which the samples were collected in order to prove *a priori* groups of samples, and to compare and discriminate between these groups of samples on the basis of their pollen composition. If the between-group variation in pollen composition is greater than the within-group variation, then one can conclude that the initial classification of samples is valid and that the groups of samples, and hence the vegetation types in question, differ in their pollen spectra (Lichti-Federovich and Ritchie, 1968).

The second approach detects the prominent patterns or 'structures' within the data on the basis of the pollen composition of the samples without *a priori* reference to the vegetation. Once the groupings of samples derived from the similarities in pollen composition are established, maps of the vegetation can be constructed in order to examine how closely the structure of the modern pollen data resembles the structure of the vegetation. The second approach allows one to ask whether the vegetation plays any role in determining the internal structure of the pollen data. This question cannot be asked if the data are grouped according to the first approach, because this approach assumed a role for the vegetation *a priori*. Both approaches are useful in answering the basic question of the relationships between modern pollen and vegetation, but the second approach, implemented by means of principal components analysis (PCA), has been applied to this research due to the advantages mentioned below. The method has been extensively applied to pollen data (Adam, 1974; Webb, 1974a,b,c; Birks *et al*, 1975; Webb & McAndrews, 1976; Ritchie, 1977; Webb and Clarke, 1977; Caseldine and Gordon, 1978; Webb *et al*, 1978; Markgraf *et al*, 1981; Lamb, 1984).

PCA is an ordination technique for projecting a multi-dimensional group of points into a space of fewer dimensions, using rigid notation to derive orthogonal axes, which maximises distortion of distances between points when they have projected into fewer dimensions (Gauch, 1982). Compared to other ordination techniques (polar ordination, weighted averages), PCA is relatively objective, as the ordination calculations do not require subjective weights or end-points. Problems are encountered with some of the requirements of PCA, namely, the use of orthogonal axes, a property rarely found in ecological data, as environmental trends do not follow the linearity required by PCA (Kershaw and Looney, 1985). PCA is therefore only an approximation of the real world situation.

PCA enables the entire vegetation community to be used for the indication and indirect measurement of environmental complexes, in this case, modern pollen counts. PCA essentially involves the prediction of the values by statistical variables from a subset of more fundamental variables, or components. These components may vary in importance, therefore interest is attached to the most important, or principal, components. To be strictly applicable to the PCA model, the components of the data set must have a normal distribution and be non-correlated, a rarity in field data.

In classification studies, as with the use of PCA to analyze the research data, the aim is to examine a set of 'objects' in order to establish whether there is any group structure in the data; for example, do the objects fall naturally into a number of distinct groups so that objects within a group are in some sense 'similar' to one another? In the present study, the object is a pollen spectrum derived from either a pollen trap or surface soil sample, described by the proportion of the pollen count, and it is of interest to know (1) whether the samples can be divided into a certain number of (initially unknown) 'homogenous groups', and (2) if such groups do exist, whether they correspond to the vegetation categories from which the samples were taken. Cognizance must be taken of the fact that when pollen analysts speak of a collection of pollen spectra as 'homogenous', they usually have in mind a much less rigid definition of homogeneity than the usual statistical concept of samples from a multinominal distribution (Martin and Mosimann, 1965).

Principal components analysis was performed to find the principal components and thereby defining 'homogenous' groups for the soil and pollen trap contemporary pollen data and in turn correlate these groups to the vegetation categories also grouped as a result of PCA. PCA was performed to confirm the DECORANA and TWINSPAN results. To some extent it is a duplication of results, however PCA has been a common data analytical tool in previous modern pollen rain studies (Prentice, 1980; Birks, 1981b; Markgraf *et al*, 1981; Lamb, 1984; Burney, 1987) and it was decided to apply the various better used techniques to this studies' data set for comparative purposes. The PCA from the statistical graphics system, Statgraphics (Version 4.0), produced by Statistical Graphics Corporation (1989) was used to perform the statistical analysis.

5.7.5 CANONICAL CORRELATION ANALYSIS

Canonical correlation analysis is an eigen-analysis method applicable to a matrix of vegetation data (samples-by-species) and, simultaneously, a matrix of environmental data (samples-by-pollen counts). The object of the analysis is to find ordination axes that maximally reveal the joint, or common, structure of the two matrices (Austin and Greig-Smith, 1968). This goal is close to what ecologists would like, an objective mathematical tool to make the basic relationships between vegetation and environment emerge (Gauch, 1982).

Canonical correlation analysis of modern pollen and associated vegetation data (taxa) was performed by Webb (1974b). Results yielded high canonical correlation (0,93; 0,88; 0,83; 0,64; 0,59). Redundancy analysis indicated that 42% of the variance within the pollen data was covered by the first five canonical variables of the vegetation data, and that 50% of the vegetation variance is covered by the corresponding canonical variable of the pollen data. Although currently available significance tests for canonical correlations assume that the variables are multivariate normally distributed, the correlations obtained suggested that pollen-vegetation 'corresponding patterns' exist within the study area. Webb (1974b) reached a similar conclusion by comparing visually individual pollen and vegetation maps, and maps of principal component scores for the pollen and vegetation data sets.

The canonical correlation procedure was employed as it allowed for the simultaneous comparison of several variables, to determine a relationship (if any) between various data sets. Firstly, the modern pollen spectra obtained from soil samples and pollen traps were compared for each of the vegetation communities. Secondly, the soil and pollen trap spectra were compared to the taxa from the vegetation community in which the samples were taken. Thirdly, any relationship between seasons, for the pollen traps, was tested and fourthly, annual variations, for each vegetation community was tested. Canonical correlation analysis was performed using the statistical graphics system Statgraphics version 4.0 produced by Statistical Graphics Corporation (1989).

5.7.6 MULTIPLE DISCRIMINANT ANALYSIS

One of the primary tasks of palynologists is to construct past vegetation changes from pollen-stratigraphic evidence. This is usually done by comparing fossil pollen assemblages with modern pollen assemblages collected from known vegetation regions. Therefore, it assumes that the same pollen-vegetation relationship exists today as existed in the past and infers that the palaeo-vegetation that produced the fossil pollen is similar to the vegetation that produces the modern pollen analogue (Liu and Lam, 1985).

A numerical technique is required not only to quantitatively identify a pollen assemblage with a modern analogue from a known vegetation region, but also to obtain objectively, a fossil pollen assemblage without a modern analogue. Several numerical techniques have been employed to compare modern and fossil pollen spectra. The first attempts involved Spearman rank correlation analysis (King, 1973) and Pearson's product-moment correlation analysis (Davis and Webb 1975; Delcourt *et al,* 1983b in conjunction with geometric-mean linear regression analysis). These techniques directly compare a fossil pollen sample with the modern pollen spectra; the similarity of each pair of samples is measured by their correlation coefficient. Prentice (1980) points out that these correlation coefficients are unsuitable for comparing pollen spectra because they are not true measures of similarity.

Principal components analysis (Webb, 1974b; Ritchie, 1977; Birks and Berglund 1979) and canonical variate analysis (Birks, 1980) have been used to reduce the dimensionality of the pollen data. These multivariate numerical techniques summarize the variation within the data into linear combinations of variables (principal components or canonical variates) which allows for comparison between the modern and fossil pollen spectra in a multidimensional space. A scatter diagram of two dimensions or axes of the scores of the pollen is then plotted and the similarity between pollen spectra is measured by the distance between the two respective points. This is useful as a visual aid of comparison, but the spectra located between the two groups, fossil samples with no close modern analogue, may be placed spuriously close to a group of modern samples in the plots of the first few principle components of canonical analysis (Overpeck *et al,* 1985). An extension of canonical variate analysis may be useful; it provides for the possibility of a discriminant test based on Mahalanobis D^2 between a fossil sample and a set of modern samples.

With regards to discrimination and allocation, multiple discriminant analysis proves to perform the best. Although principal components analysis allows for comparison between fossil and modern pollen spectra in multidimensional space (Birks and Gordon, 1985; Scott and Thackeray, 1987), it does not provide a quantitative criterion value to discriminate between groups of samples or intermediate samples. As a consequence results can be influenced by subject decisions and prevent assigning group membership to new species of unknown identity (Liu and Lam, 1985). PCA allows for samples that fall within ecotones, whereas multidiscriminant analysis works only with *a priori* assemblages from defined communities. The advantage of multiple discriminant analysis (MDA) is that it can be used in both multivariate discrimination of present-day samples and the subsequent comparison of fossil and modern assemblages (Sugden, 1990).

Discriminant analysis derives linear combinations of variables, called discriminant functions, independent of each other. These functions ensure maximum separation among *a priori* groups. It is also used to classify new samples with unknown membership into one of the *a priori* groups. The discriminant function is a multivariate technique for sampling the extent to which different populations overlap one another or diverge from one another. The analysis has three principle uses:- 1) classification and diagnosis, 2) determining relations between populations and 3) as a multivariate generalisation of the t-test (Snedecor and Cochran, 1967). As a consequence discriminant analysis reveals: 1) whether and to what extent a fossil pollen assemblage has modern analogues based on the 'probability of modern analogue index' and 2) if a modern analogue exists, it relates the fossil assemblage to the modern pollen spectra representing its modern analogue, based on a 'probability of group membership' (Sugden and Meadows, 1989).

The application of discriminant analysis (DA) to palynological investigations of fossil and modern pollen data are constrained by a number of ecological and statistical assumptions. The ecological assumption is that the modern pollen samples adequately represent the palynological signature of the vegetation communities. This depends largely on the number and spatial distribution of modern pollen spectra used in the analysis in relation to spatial and statistical variability of the pollen rain in the vegetation communities.

The statistical assumptions for DA are:- 1) samples are randomly chosen; 2) probabilities of group membership are equal for all groups; 3) samples are correctly classified; 4) the variance-covariance matrices of groups are statistical equal and 5) the variables are normally distributed within each group. Assumption one, two and three hold. The fourth was tested statistically using Box's M statistic (Nie *et al,* 1975) and the fifth is tested by multivariate skewness and kurtosis measures (Nie *et al*, 1975; Jennrich and Sampson 1990). Despite the fact that the data sets did not meet all the assumptions of DA, this is not unusual for ecological data and the technique is robust enough to perform without all the required assumptions being fulfilled (Liu and Lam, 1985; MacDonald and Ritchie, 1986; Sugden, 1990).

The Biomedical Computer Program (BMDP) subprogram, DISCRIMINANT (B7M), was used to perform the analysis (Jennrich and Sampson, 1990). In the analysis the samples are divided into *a priori* groups and the analysis finds discriminant functions or linear combinations which best characterise the differences between the groups, so that the samples of unknown group identity may be assigned to one of the groups. The division of samples into *a priori* groups is critical, yet restrictive, as it does not allow for samples that fall within the ecotonal areas (Sugden, 1990). As all pollen rain samples were collected from distinct homogenous vegetation communities this disadvantage was not a restriction on the present study. The analysis can be explained by plotting each sample as a point in multidimensional space, where each variable represents a dimension. The points are projected onto a plane, which is selected so that the separation between groups is maximised. This plot of variables (function 1 versus function 2) forms part of the canonical variate analysis, which finds linear combinations of the dominant sets of variables in the classification function and permits comparison between modern and fossil spectra. The second set of variables is used to indicate group membership (Jennrich and Sampson, 1990). Discriminant functions are therefore derived to ensure maximum separation between *a priori* groups and to distinguish between pollen assemblages from known vegetation communities.

This study concentrates on modern pollen rain; as a consequence MDA was used to provide a vegetation zonal index and a probability of modern analogue from modern pollen only. However, the results are extremely useful not only in comparing a pollen assemblage with the 'palynological signature' of its assigned vegetation community, but also for future fossil pollen analysis from an area with great potential for the science.

The probabilities of group membership in the predicted and second most predictable groups of variables (function 1 and 2) are calculated from each modern pollen sample. The second most probable group is the vegetation assemblage that is geographically adjacent to the predicted assemblage. These probabilities reflect the zonal pattern of the vegetation along a gradient. As a result it is possible to convert the probabilities of the first two functions into a single vegetation zonal index for each sample. Modern pollen spectra typical of a vegetation region (100% probability of group membership) are assigned specific zonal indices, corresponding with the vegetation assemblages along the gradient (Liu and Lam, 1985; Sugden and Meadows, 1989). Samples classified as transitional between two vegetation communities are assigned intermediate zonal indices relative to the two probabilities of group membership.

Discriminant functions are derived which classify all modern pollen samples from sampled vegetation communities in the Natal Drakensberg into one of the ten (in the case of pollen traps) or thirteen (in the case of soil samples) *a priori* groups. The discriminant scores are plotted along the first two discriminant functions and this plot indicates how distinct the vegetation communities are from each other on the basis of their pollen rain characteristics.

The probability of a modern analogue index provides the probability that samples from the modern pollen group will be positioned in the vicinity of the fossil sample or the canonical variate axes. In palynological terms, it compares a pollen assemblage with the 'palynological signature' of it's assigned vegetation community, as represented by the group centroid (Sugden and Meadows, 1989).

Multiple discriminant analysis (MDA) with regards to palynology is beginning to have an impact with the studies of Liu and Lam (1985) in north-eastern North America, MacDonald and Ritchie (1986) in Canada, Dodson and Meyers (1986), and Kodela (1990a,b) in New South Wales, Australia coming to the fore. Palynological research in South Africa, particularly with regards to setting up modern analogues to aid fossil pollen analysis, is also applying MDA, with the papers of Sugden and Meadows (1989) and Meadows and Sugden (1990, 1991a,b) looking at modern/fossil pollen and pollen rain - vegetation relationship the most prominent.

With the use of MDA, made more accessible with the advent of good computer statistical packages, and the review of the technique with regards to palynological data (Liu and Lam, 1985; Sugden and Meadows, 1989) it appears that MDA has some advantages over the multivariate techniques usually applied, particularly in situations where good modern pollen rain data exists. Therefore it is essential to build-up a good modern pollen rain data base to complement MDA. Such a data set was completed for the Natal Drakensberg region with one of the reasons being that this region has a high potential for an extensive fossil pollen study to be conducted.

5.8 CONCLUSION

Data collection in any palynological investigation has many inherent difficulties, particularly due to the necessary sampling strategies and the laboratory and counting time required. The vegetation and pollen rain sampling techniques, were employed so as to allow for statistical analysis of the results for comparative purposes and to determine some sampling recommendations with regard to future modern pollen rain studies.

The preparation of a sample suitable for pollen counting follows a sequence of chemical procedures designed to concentrate the pollen sufficiently for counting. A pollen reference collection needs to be established to aid identification and scanning electron microscopy can augment the reference collection. Once pollen counts have been determined, be they absolute or relative, the results can be compared to the species composition of the vegetation community from whence they were collected. These comparisons are performed with the aid of various statistical techniques.

The statistical techniques used are: an analysis of variance to test for any significant differences between two samples, two-way indicator species and detrended correspondence analysis used to classify and ordinate the data, principal components analysis to determine group structure within the data sets, canonical correlation analysis to ordinate the data to determine joint or common data structures and multiple discriminate analysis to provide a vegetation zonal index and a probability of modern analogue to determine a 'palynological signature' for each vegetation community.

The success which has been achieved in the reconstruction and interpretations of vegetational history through the use of surface-sample data (Birks and Birks, 1980; Lamb, 1984; MacDonald and Ritchie, 1986; Sugden and Meadows, 1989) demonstrates the importance of studying contemporary assemblages in relation to vegetation. Contemporary pollen-vegetation relationships provide an accurate basis for the reconstruction of palaeo-vegetation through the extrapolation of modern analogues backwards in time, namely, methodological uniformitarianism. These studies also provide important insights into the accuracy with which pollen data reflect vegetation communities, they provide checks on the sensitivity of pollen analysis as a tool for characterising vegetation and show the potential sensitivity and resolution of pollen analysis when applied to specific palaeoecological problems. Thus studies and analysis of modern pollen spectra are an important means of testing some of the basic assumptions of the pollen analytical method (Birks and Gordon, 1985).

CHAPTER SIX
DATA DESCRIPTION AND ANALYSIS (1)

6.1 INTRODUCTION

Within this chapter the minimum number of samples required and the pollen count, at a given percentage of error, are described and analysed for each of the studied vegetation communities, thereby allowing for a modern pollen rain sampling strategy to be recommended. Soil pH values were measured and included for comparison with the observed pollen preservation. Modern pollen rain is quantified by the calculation and presentation of seasonal and annual pollen influx values, while analysis of variance (ANOVA) is used to determine if there are any significant annual or seasonal pollen influx value differences.

6.2 SOIL pH

For good pollen preservation within the soil, soil pH needs to be slightly acidic. Andersen (1986) states that in soils with a pH greater than 6 (KCl pH values) there is virtually no preservation of pollen and preservation is best achieved in soils with a pH value of less than 5.0, with associated low biological activity. The Ph values obtained from twenty soil samples for each vegetation community studied are tabulated (Table 6.1).

The results are in agreement with the studies of Killick (1963), Edwards (1967) and van Zinderen Bakker Jnr. (1973) that the soils from this region are generally acidic. The low pH values retard biological oxidation of the pollen grain exine by bacteria, fungi, yeasts and other biological agents, thereby facilitating good pollen preservation. Soils of the research area fall within a pH range of 4.0 to 4.6, except *Podocarpus* forest and sub-alpine fynbos, which had pH values of 5.40 and 5.23 respectively. The slightly higher values of these two communities could be as a consequence of the high proportion of decaying vegetation matter present within the surface organic 'O' soil horizon. The soils did produce good pollen preservation as was observed during surface soil sample counts.

Table 6.1 Soil pH values from the studied vegetation communities.

Vegetation Community	Mean pH Value	Standard Deviation
Highland Sourveld	4.10	0.141
Protea Savanna	4.27	0.173
Podocarpus Forest	5.40	0.486
Leucosidea sericea scrubland	4.53	0.180
Rendlia altera grassland	4.46	0.083
Themeda triandra grassland	4.35	0.058
'Mixed' grassland	4.56	0.112
Festuca costata grassland	4.38	0.079
Low altitude vlei	4.20	0.285
Sub-alpine fynbos	5.23	0.209
Alpine grassland	4.38	0.160
Erica-Helichrysum heathland	4.51	0.203
High altitude vlei	4.34	0.218

6.3 SAMPLE SIZE

Once soil sample and pollen trap counts had been completed, minimum soil and trap sample size was calculated, in retrospect, at an acceptable percentage of error. Soil sample results for the dominant taxa within each vegetation community are tabulated as Table 6.2 and those of the pollen traps as Table 6.4.

6.3.1 SURFACE SOIL SAMPLE SIZE

From a preliminary surface soil pollen study conducted in the Natal Drakensberg during 1987 it was proposed that twenty soil samples per vegetation community would suffice (Hill, 1987). The results of this study confirm this premise and a sample size of twenty was regarded as adequate to gain an acceptable representation of the dominant taxa with a 2% error in all the studied communities except the high altitude vlei and *Podocarpus* forest sites. For these sites a sample size of twenty allows for a, still ecologically acceptable, 5% error in representation of the dominant taxa.

Table 6.2 Calculated minimum sample size, at various percentages of error, for the dominant taxa within the soil samples from each community.

Vegetation Community	Taxa	Percentage Error		
		1%	2%	5%
Highland Sourveld	Poaceae	60	16	4
	Asteraceae	15	4	-
Protea Savanna	Poaceae	65	16	3
	Asteraceae	10	2	-
	Proteaceae	6	2	-
	Pteridophyta	14	4	-
	Cyperaceae	6	2	-
Podocarpus Forest	Poaceae	164	41	7
	Pteridophyta	57	15	4
	Podocarpaceae	55	14	4
	Ulmaceae	32	8	-
	Flacourtiaceae	22	6	-
Rendlia altera grassland	Poaceae	46	12	-
	Asteraceae	7	-	-
	Cyperaceae	4	-	-
Themeda triandra grassland	Poaceae	28	14	2
	Asteraceae	39	10	2
	Ericaceae	31	15	2
'Mixed' grassland	Poaceae	66	17	4
	Asteraceae	14	-	-
Festuca costata grassland	Poaceae	49	12	2
	Asteraceae	8	-	-
Low altitude vlei	Poaceae	75	19	3
	Cyperaceae	24	6	-
	Pteridophyta	64	16	3
	Asteraceae	14	4	-
Leucosidea sericea scrubland	Poaceae	32	16	2
	Asteraceae	22	6	-
	Leucosidea	5	-	-
	Rosaceae	36	9	-
	Pteridophyta	23	6	-
Sub-alpine fynbos	Poaceae	69	18	4
	Ericaceae	70	18	4
	Asteraceae	6	-	-
	Pteridophyta	59	15	4
	Liliaceae	10	-	-
Alpine grassland	Poaceae	31	7	-
	Cyperaceae	14	-	-
	Asteraceae	10	-	-
	Ericaceae	6	-	-
Erica-Helichrysum heathland	Ericaceae	250	125	20
	Poaceae	82	20	-
	Asteraceae	15	-	-
	Thymelaeaceae	139	68	5
High altitude vlei	Poaceae	508	127	20
	Cyperaceae	124	61	10
	Asteraceae	26	13	-
	Eriocaulaceae	10	-	-
	Juncaceae	19	-	-

An ANOVA was performed to investigate whether a soil sample size of five or ten as opposed to the originally sampled twenty, would be adequate. The ANOVA tested for any significant difference between the mean of the pollen taxa of five, ten and twenty samples. The hypothesis was that there is no significant difference between the mean of five, ten and twenty soil samples (Table 6.3). Only the results of the ANOVA between ten and twenty soil samples are presented as the results of five against ten soil samples proved that for all the communities there is a significant difference between the two sample sizes. Therefore a soil sample size of five is not recommended for any of the vegetation communities.

Table 6.3 Results of the ANOVA testing the significant difference between a sample size of ten and twenty soil samples.

Vegetation Community	Total taxa	Accept H_0	Reject H_0
Highland Sourveld	24	16 (67%)	8 (33%)
Protea savanna	32	13 (41%)	19 (59%)
Podocarpus forest	37	32 (86%)	4 (14%)
Rendlia altera grassland	32	32 (100%)	-
Leucosidea sericea scrubland	37	34 (92%)	3 (8%)
Themeda triandra grassland	32	32 (100%)	-
'Mixed' grassland	27	18 (67%)	9 (33%)
Festuca costata grassland	29	29 (100%)	-
Low altitude vlei	29	22 (75%)	7 (25%)
Sub-alpine fynbos	35	32 (91%)	3 (9%)
Alpine grassland	26	26 (100%)	-
Erica-Helichrysum heathland	23	14 (60%)	9 (40%)
High altitude vlei	28	28 (100%)	-

Results of the ANOVA on the two data sets allow one to conclude that a soil sample size of ten is adequate for the vegetation communities; *Rendlia altera, Festuca costata, Themeda triandra* and alpine grasslands, *Leucosidea sericea* scrubland, sub-alpine fynbos and high altitude vlei. A sample size of twenty is recommended for the remaining six communities. This result does not implicate the representativeness of a sample size, rather it determines that, for the above mentioned seven communities, a soil sample size of ten will achieve the dominant pollen taxa pollen proportions that are not significantly different to those calculated from a doubling of the sample size. An improved correlation between the two sample sizes was achieved when only taxa with relative pollen percentages greater than 1% or 0.5% of the total spectrum are considered. However with a reduced number of samples results become biased or misleading as, in some cases, only a few taxa could be considered. The results strengthen those of the minimum sample size calculation showing that overall at a percentage error of 2%, twenty surface soil samples suffice. Results of the ANOVA recommend that only ten samples are required within a number of the vegetation communities, but by comparing both the ANOVA and minimum sample size calculations it is recommended that a sample of twenty be applied within all the studied communities.

6.3.2 POLLEN TRAP SAMPLE SIZE

Taxa within both the surface and trap pollen spectra with a standard deviation of less than 0.61, although represented by a value greater than 2% of the pollen sum, were calculated to have an optimum sample size of one or less. This is because the lowest percentage error used is 1%. When calculating a minimum sample size it is important to consider the dominant taxa and the variation that these taxa display. For example, Ulmaceae, Pteridophyta and Sapindaceae arboreal taxa of the *Podocarpus* forest community, have a large standard deviation as the number of pollen grains 'caught' in the pollen traps varies between traps. Therefore a large number of traps would be required to reduce the error to 1%. On the other hand the dominant taxa of the 'Mixed' grassland have low standard deviations. For this community a greater resolution of error should be sought, but for the sake of consistency all the community samples sizes are calculated at the 1%, 2%, 5% and 10% error. Obviously one wishes to reduce the error to as low as feasible within the limits of possible sampling.

Table 6.4 Calculated minimum sample size, at various percentages of error, of the dominant taxa from the pollen traps.

Vegetation Community	Taxa	Percentage Error			
		1%	2%	5%	10%
Highland Sourveld	Poaceae	13	4	-	-
	Asteraceae	12	3	-	-
	Hypoxidaceae	6	-	-	-
	Pteridophyta	12	6	-	-
Protea Savanna	Poaceae	40	10	-	-
	Proteaceae	35	18	-	-
	Asteraceae	27	13	-	-
	Myriacaceae	9	-	-	-
	Scrophulariaceae	6	-	-	-
	Pteridophyta	6	-	-	-
Podocarpus Forest	Ulmaceae	258	65	10	-
	Poaceae	138	35	6	-
	Podocarpaceae	31	15	-	-
	Pteridophyta	199	50	8	-
	Sapindaceae	216	54	9	-
	Asteraceae	3	-	-	-
	Scrophulariaceae	9	-	-	-
	Flacourtiaceae	55	14	-	-
Rendlia altera grassland	Poaceae	58	14	2	-
	Asteraceae	49	12	2	-
	Cyperaceae	15	4	-	-
	Hypoxidaceae	24	6	-	-
	Pteridophyta	15	4	-	-
Leucosidea sericea scrubland	*Leucosidea sericea*	52	13	2	-
	Poaceae	26	7	-	-
	Asteraceae	-	-	-	-
Themeda triandra grassland	Poaceae	71	18	3	-
	Asteraceae	104	26	4	-
'Mixed' grassland	Poaceae	1	-	-	-
	Asteraceae	1	-	-	-
	Cyperaceae	1	-	-	-
Festuca costata grassland	Poaceae	50	12	2	-
	Asteraceae	39	9	-	-
	Ericaceae	5	-	-	-
Sub-alpine fynbos	Asteraceae	26	7	-	-
	Poaceae	71	17	3	-
	Proteaceae	32	8	-	-
	Scrophulariaceae	5	-	-	-
	Ericaceae	39	10	-	-
	Rosaceae	14	4	-	-
	Pteridophyta	53	13	3	-
	Crassulaceae	5	-	-	-
Low altitude vlei	Poaceae	368	92	37	2
	Asteraceae	39	10	2	-
	Cyperaceae	53	13	2	-

In most cases a 1% error has been obtained, for the number of pollen traps placed in the field (Table 5.2 in Chapter 5 for number of pollen traps per vegetation community), which is good for ecological data. A 5% and 10% error is still acceptable, particularly for the dominant taxa. These calculations of minimum sample size were performed in retrospect, therefore, if the percentage errors were at an unacceptable level then it may have been necessary to continue the pollen trap sampling programme for another year and/or collect more surface soil samples (possible inherent problems due to the fact that a full years modern pollen rain had 'landed' onto the soil surface - some of which could reach the sampling zone just below the surface covering vegetation).

Taxa of the *Protea* savanna community, with the exception of the dominants Poaceae, Proteaceae and Asteraceae, exhibit a 1% error for the 18 traps set-up in the community. These dominants have a 2% error for the number of pollen traps within the community. *Podocarpus* forest taxa Ulmaceae, Poaceae, Pteridophyta and Sapindaceae have a 5% error and Podocarpaceae a 2% error for the 18 traps set-up within the forest community. The *Themeda*-dominated Highland Sourveld has a 2% error for Poaceae and Asteraceae and a 1% error or less for the remaining taxa for a trap sample size of 6.

The sub-alpine grassland communities of *Themeda triandra*, 'Mixed' and *Festuca costata* have sufficient traps to obtain a less than 1% error, other than Poaceae and Asteraceae in the *Themeda triandra* grassland and Poaceae in the *Festuca costata* grassland. These taxa have a 5% error for the number of traps available, while Asteraceae of the *Festuca costata* grassland has a 2% error. The *Rendlia altera* grassland exhibits more variation within the dominant taxa. For the traps available (6) an error of 5% for Poaceae and Asteraceae and 2% for Cyperaceae, Hypoxidaceae and Pteridophyta was calculated.

Leucosidea sericea has a 5% and Poaceae a 2% error within the pollen trap spectrum of the *Leucosidea sericea* scrubland community with a trap sample size of ten. All the remaining taxa have errors of 1% or less. The sub-alpine fynbos community shows more variation with a 5% error for Poaceae and a 2% error for Asteraceae, Proteaceae, Ericaceae and Rosaceae for a trap size of ten. Due to seasonality, variation between traps and the low number of traps available (6), a 10% error in Poaceae and a 5% error in Asteraceae and Cyperaceae was calculated for the low altitude vlei community.

The pollen production of a particular taxon exhibits both seasonal and annual variation. In addition, the resultant pollen count from the pollen traps will vary according to trap situation. All these variations result in a reasonably high standard deviation for each taxon and consequently to obtain an error of less than 2% for all taxa within each community would require a sample size that is impracitible. The standard deviation varies both annually and seasonally, so the number of traps required to obtain a satisfactory representation would vary. However it was the intention of this study to recommend an overall sampling strategy (Chapter 9) and therefore the seasonal and annual variations must be incorporated. Overall the number of traps placed within each community were adequate, however to obtain a 1% improvement in the error would, in some cases, involve a tripling or quadrupling of the number of traps. However it is neither necessary (due to the nature of ecological data) or desirable (due to the number of samples required) to always obtain a 1% error.

6.4 POLLEN COUNT

As part of this modern pollen rain study it was decided to investigate the number of pollen grains counted per sample and determine what the lowest possible count could be. This test does not state how representative the count is of a particular community, but does show that if there is no significant difference between a count of 250, 500 or 1000 grains then a count of the lower numeral is sufficient (Table 6.5). The hypothesis tested was that there is no significant difference between a pollen count of 250, 500 and 1000 pollen grains per soil sample. Counts of 250, 500 and 1000 were chosen as they are the more popular count sizes undertaken in previous modern pollen studies. A 95% confidence limit was applied to this and all subsequent tests. For ecological data such a level of confidence is deemed satisfactory.

Table 6.5 Results of the ANOVA investigating any significant differences between counts of 250 and 1000 pollen grains from soil samples.

Vegetation Community	Total Taxa	Accept H_0	Reject H_0	Rejected Taxa
Highland Sourveld	24	22 (92%)	2 (8%)	Poaceae Valerianaceae
Protea Savanna	32	29 (91%)	3 (9%)	Gentiaceae Myricaceae Poaceae
Podocarpus Forest	37	37 (100%)	-	-
Rendlia altera scrubland	32	30 (94%)	2 (6%)	Illecebraceae Cornaceae
Leucosidea sericea scrubland	37	36 (97%)	1 (3%)	Poaceae
Themeda triandra grassland	32	30 (94%)	2 (6%)	Labiatae Rubiaceae
'Mixed' grassland	27	27 (100%)	-	-
Festuca costata grassland	29	29 (100%)	-	-
Low altitude vlei	29	28 (97%)	1 (3%)	Fabaceae
Sub-alpine fynbos	35	34 (97%)	1 (3%)	Boraginaceae
Alpine grassland	26	22 (85%)	4 (15%)	Aizoaceae Brassicaceae Dipsacaceae Droseraceae
Erica-Helichrysum heathland	23	23 (100%)	-	-
High altitude vlei	28	25 (89%)	3 (11%)	Caryophyllaceae Dipsacaceae Droseraceae

In most instances the ANOVA proved that a count of 250 was sufficient as there was no significant difference between counts of 250 and 1000 pollen grains. The larger number of rejected taxa in the alpine grassland, high altitude vlei and *Rendlia altera* grassland communities are of lesser importance within the context of the counts as these taxa represent a small proportion (less than 0.5%) of the pollen spectra. However the rejection of the Poaceae 250 count in *Themeda*-dominated Highland Sourveld, *Leucosidea sericea* scrubland and *Protea* savanna needs to be pointed out and indicate that a count greater than 250 is required for these three communities. The percentage acceptance of the hypothesis increased in the ANOVA between counts of 500 and 1000 grains (not shown in the form of a table).

The Highland Sourved Poaceae count was accepted for the ANOVA stating that there is no significant difference between counts of 500 and 1000, while the Poaceae counts of *Leucosidea sericea* scrubland and *Protea* savanna communities still reject the hypothesis at all levels of counts. Therefore to gain a 95% confidence in these two latter communities with regards to soil pollen a count in excess of 1000 grains is necessary to accurately represent the Poaceae count. Such a large count begins to become impractical and mistakes with regards to other taxa counts can develop. For the Highland Sourveld community a count of 500 is sufficient to gain a good Poaceae representation.

6.5 POLLEN INFLUX VALUES

Pollen influx values were calculated to investigate seasonal and annual fluctuations between the vegetation communities. It is well recorded that surface materials contain years of pollen accumulation, masking seasonal and annual variation, however research has not yet accurately established the number of years represented by surface soil content (Hall, 1990). Surface soil samples may give a better representation of the pollen rain as it allows for pollen production variation on both a seasonal and annual basis. However to understand this variation it must be recorded so as to help elucidate any possible variation and to obtain absolute values of pollen rain for a particular vegetation community. This pollen rain accumulation rate is the net number of grains accumulated per unit time, and is also referred to as pollen-deposition rates or pollen influx in units of grains cm^{-2} $year^{-1}$. This study uses the term pollen influx values and the measurement of grains cm^{-2} per unit time, bearing in mind Thompson's (1980) suggestion that the use of the term influx, with regards to palynology, is often inappropriate. He discusses what pollen analysts refer to as influx, namely, number of grains which have accumulated per unit area per unit time, and suggests that the term flux is more pertinent. Birks and Gordon (1985) prefer the term pollen-accumulation rate.

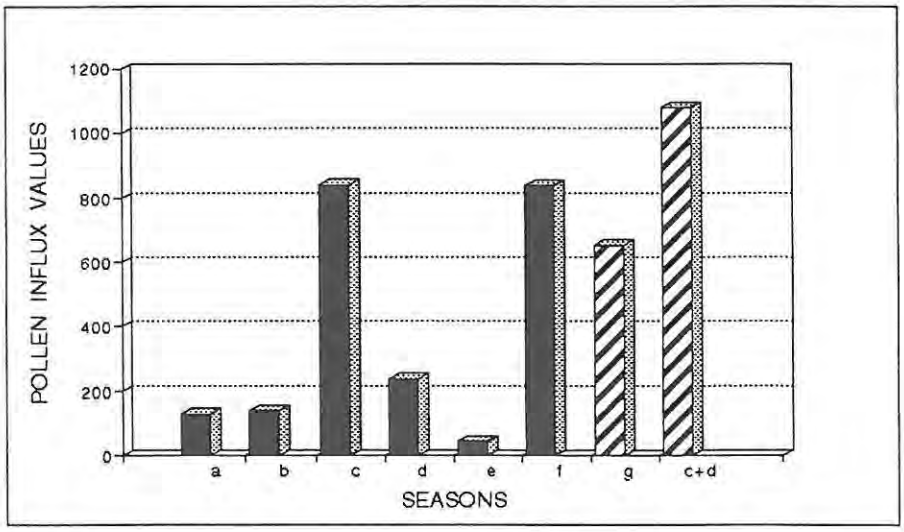
6.5.1 SEASONAL POLLEN INFLUX VALUES

The present study observed a distinct seasonality with regard to total pollen influx, particularly within the grassland communities, which was not observed within the relative percentage values from the soil/trap pollen spectra (discussed in Chapter 7). The pollen influx data is presented in the form of Table 6.6 and graphically by means of histograms (ref. Figures 6.1 a-j). The seasons are represented on the histograms (Figures 6.1 a-j) as winter (June-August), spring (September-November), summer (December-February) and autumn (March-May).

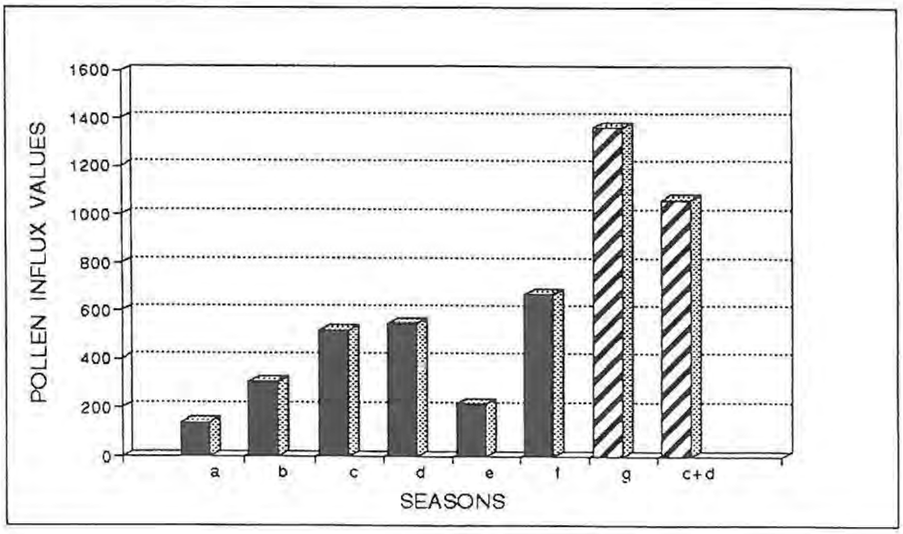
Table 6.6 Pollen influx values (grains/cm^2/90 days) for June 1988-90 for vegetation communities within the montane and sub-alpine regions of the Natal Drakensberg.

Vegetation Community	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990
Highland Sourveld	128.3	139.6	841.6	237.1	42.7	838.6	326.3
Protea savanna	138.1	306.2	516.1	546.2	219.5	670.3	681.1
Podocarpus forest	434.3	956.4	1 206.1	381.6	701.8	977.0	592.5
Rendlia altera grassland	79.7	178.6	901.8	204.3	126.9	928.0	470.6
Leucosidea sericea scrubland	383.4	358.7	239.7	156.3	362.6	123.1	746.8
Themeda triandra grassland	97.1	429.1	1 287.6	1 063.1	156.1	1 520.2	1 028.4
'Mixed' grassland	65.0	210.9	866.6	368.8	176.7	706.3	581.6
Festuca costata grassland	75.0	217.3	743.2	366.4	74.3	819.8	804.6
Low altitude vlei	-	1 283.6	1 055.2	558.0	82.1	393.4	602.6
Sub-alpine fynbos	-	-	-	208.1	513.2	913.9	779.1

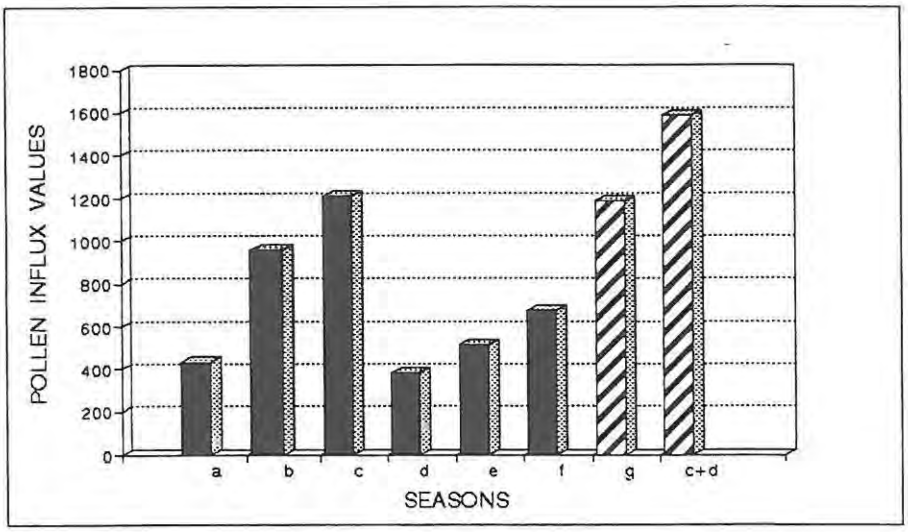
The grassland communities (Tables 6.6 and Figures 6.1 a,d,f-h) have low pollen influx values during the winter months, ranging from 65 grains/cm^2/90 days for 'Mixed' grassland to 128.3 grains/cm^2/90 days for *Themeda*-dominated Highland Sourveld, these values increase through spring to a maximum of approximately 700 - 1 300 grains/cm^2/90 days during the summer months. The influx values decline during autumn back to a winter low. In the following year (June 1989-90) once again these communities exhibit a rise in influx values towards summer. The group designated as '*g*' on the histograms represents both the summer and autumn months of 1989-90 and, as far as these grasslands are concerned, exhibits a decline in pollen influx following spring. This could be due to the low autumn influx 'pulling down' the summer value, which is reflected in a low six month average value. It can be assumed that if only a summer value was recorded during this second sampling year, the influx value would exceed that of spring.



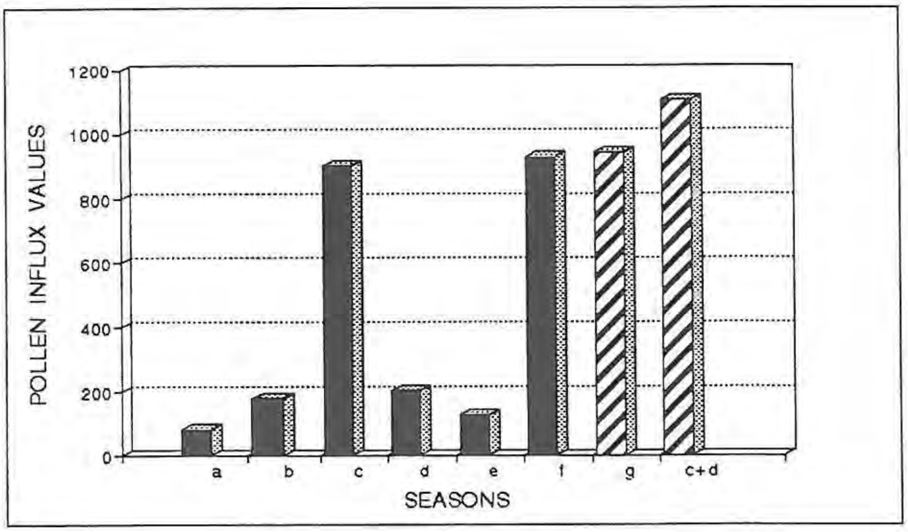
(a) Highland Sourveld



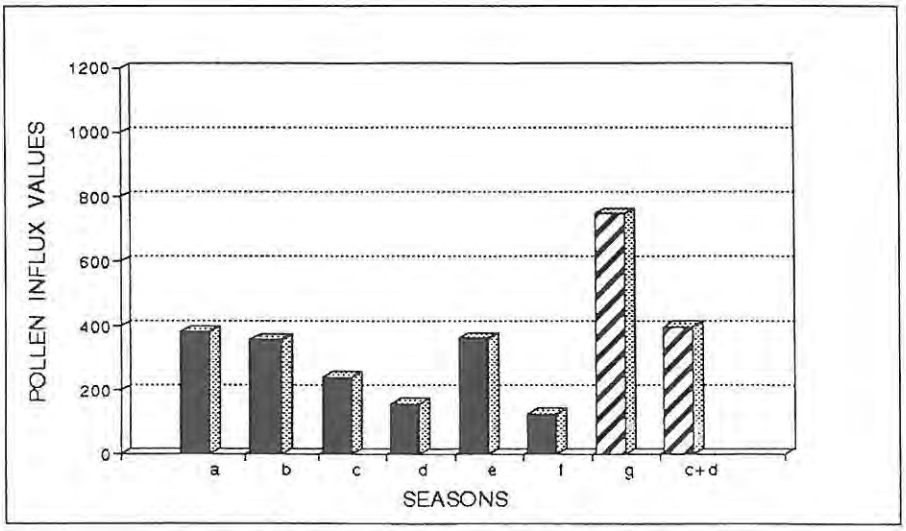
(b) *Protea* savanna



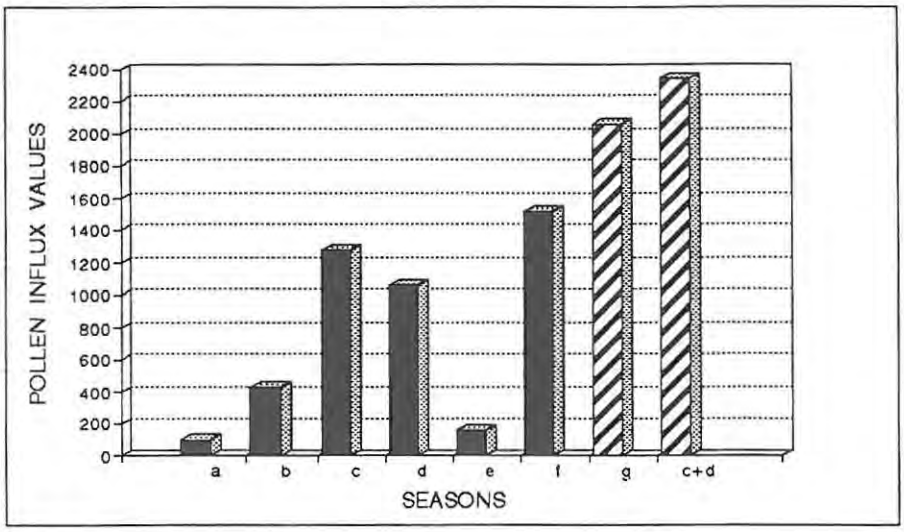
(c) *Podocarpus* forest



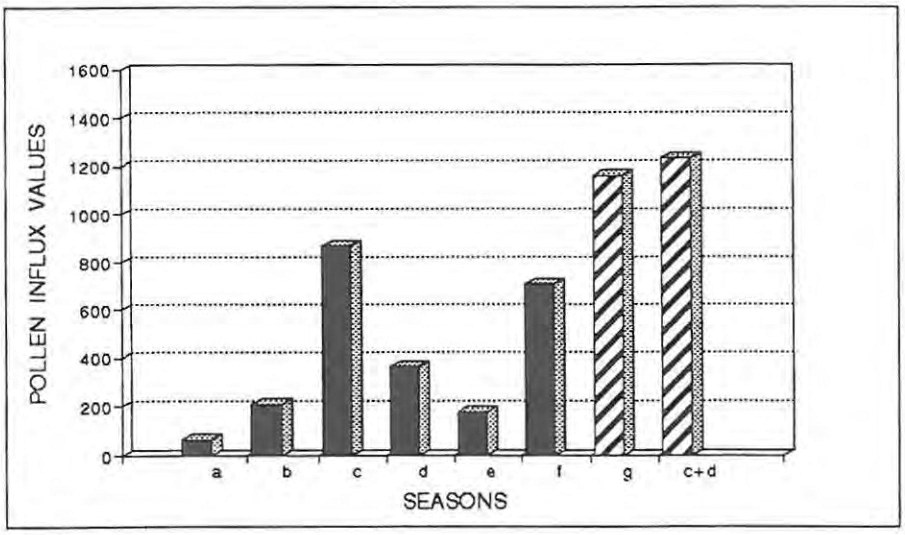
(d) *Rendlia altera* grassland



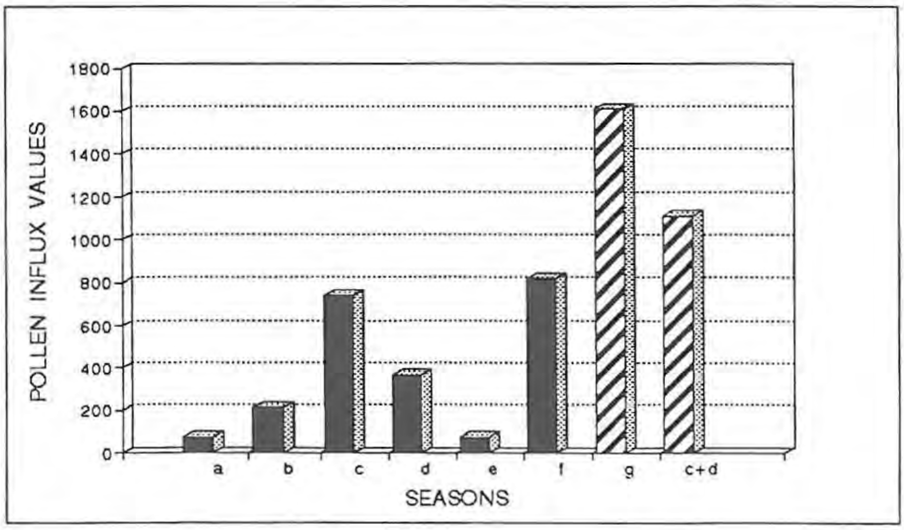
(e) *Leucosidea sericea* scrubland



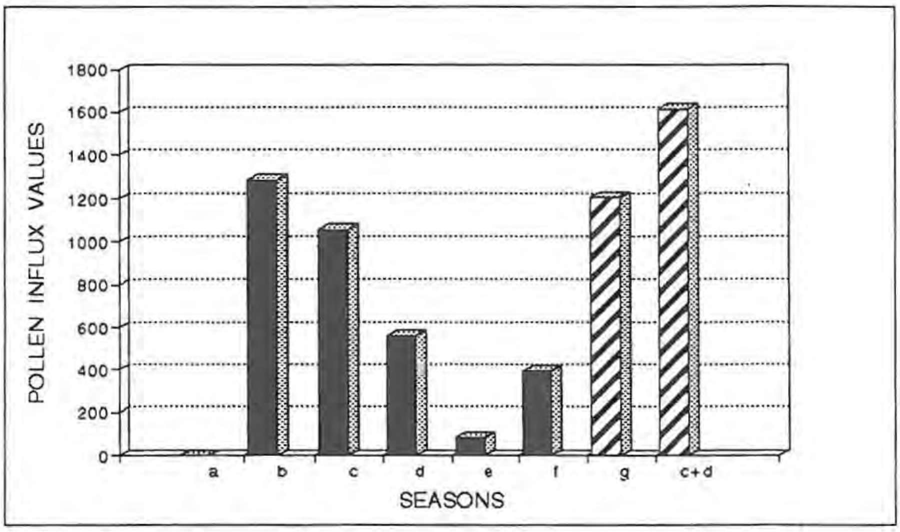
(f) *Themeda triandra* grassland



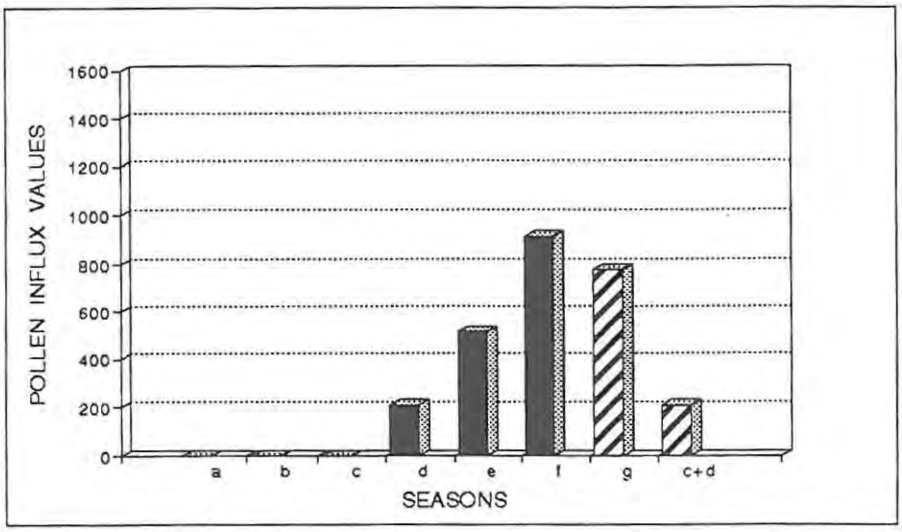
(g) 'Mixed' grassland



(h) *Festuca costata* grassland



(i) Low altitude vlei



(j) Sub-alpine fynbos

LEGEND: ■ grains/cm.cm/90day ▨ grains/cm.cm/180day

Figure 6.1 a-j: Seasonal pollen influx values (grains/cm^2/time unit) for the montane and sub-alpine vegetation communities studied. a=June-Aug 1988, b=Sept-Nov 1988, c=Dec-Feb 1989, d=March-May 1989, e=June-Aug 1989, f=Sept-Nov 1989, g=Dec-May 1990 and c+d=Dec-May 1989.

The summer and autumn pollen influx of 1990 was taken as a single sample to compare with the corresponding six months of the previous year. The results, from the *Themeda triandra* and 'Mixed' grassland communities are not dissimilar for the corresponding six monthly period. For the *Themeda*-dominated Highland Sourveld the periods do vary with 1988-89 recording an influx of 1078.7 grains/cm^2/180 days as opposed to 652.6 grains/cm^2/180 days for the 1989-90 period. The discrepancy can possibly be sought in the high pollen production (and resultant influx value) of the preceding tri-monthly September-November 1989 period. During the first week of September 1989, a serious fire swept through this sample site. The fire, as expected with early growing season burns, stimulated growth and thus the resultant pollen production for that season is high (838.6 grains/cm^2/90 days) compared to 139.6 grains/cm^2/90 days for the corresponding 1988 season. As a consequence of fire induced rapid early season growth, most pollen production during the 1989 season occurred during the spring months, thereby resulting in a lower summer influx value. This lower summer value added to the lower autumn value results in a six monthly influx value lower than the corresponding six months of the previous year.

A similar phenomenon is observed in the *Rendlia altera* grassland community (Figure 6.1d), where an early spring burn in 1989 resulted in the early flowering and pollen production of a large proportion of the species. Therefore there is a high (928 grains/cm^2/90 days) spring pollen influx value when compared to the 1988 spring influx value of 178.6 grains/cm^2/90 days.

Low altitude vlei pollen production (Figure 6.1i) is greatest during spring (1283.6 grains/cm^2/90 days), decreasing to 1055.2 grains/cm^2/90 days during the summer, to a low of 82.1 grains/cm^2/90 days during the winter months of 1988-89. The corresponding 1989-90 period produced lower pollen influx values. These lower pollen influx values could be as a consequence of unknown intrinsic factors and as no external variables such as fire or climatic variability were determined the author accepts the fact that there is posibly a random annual pollen influx variation as recorded by others (Bonny, 1980; Spieksma, 1983; Solomon and Silkworth, 1986; Hall, 1990). Further evidence of a large annual fluctuation is recorded in the six monthly comparison. The 1988-89 period recorded 1613.2 grains/cm^2/180 days and 1205.2 grains/cm^2/180 days for the corresponding 1989-90 period.

The influx values of *Protea* savanna increase from a winter low of 138.1 grains/cm²/90 days to an autumn high of 546.2 grains/cm²/90 days (Figure 6.1b). The autumn high value is due to the high pollen production of Poaceae and Asteraceae, constituting ± 60% of the pollen spectrum, during this season. In particular the grasses within the *Protea* savanna community seem to flower either in early spring or late summer. This is an actual event and not an anomaly caused by proportionality between *Protea* and Poaceae pollen as a consequence of percentage data. Pollen production declines during the winter of 1989, although the value (219.5 grains/cm²/90 days) is greater than the corresponding 1988 period (138.1 grains/cm²/90 days). The December-May six month period of 1988-89 records a value of 1062.3 grains/cm²/180 days as compared to 1362.2 grains/cm²/180 days for the 1989-90 period.

The other woody montane community, the *Podocarpus* forest, has a winter low of 434.3 grains/cm²/90 days, increasing to 1206.1 grains/cm²/90 days during the December-February summer months and declining to 381.6 grains/cm²/90 days during the autumn months of the 1988-89 season (Figure 6.1c). The increase in the winter months of 1989 are a consequence of high pollen production of *Celtis africana* (Ulmaceae). Values of between 200 and 1000 pollen grains of this species was collected during the winter months of 1989 and between 200 and 400 pollen grains for the corresponding 1988 season. All other species decrease in pollen production during the winter months, therefore the fact that *Celtis africana* produces pollen so late in the 'growing season' offsets the winter influx values. The same observation is witnessed in both years. The *Podocarpus* forest pollen influx value increases to 977.0 grains/cm²/90 days during the spring of 1989 and to 1185.0 grains/cm²/180 days for the summer and autumn of 1989-90. This six monthly period corresponds to the 1587.7 grains/cm²/180 days recorded during the corresponding 1988-89 period.

The *Leucosidea sericea* scrubland community of the lower sub-alpine region reflects a different seasonal variation (Figure 6.1e). The dominant of the community is *Leucosidea sericea* which flowers in August (Trauseld, 1969; and personal observations). As a result of the sampling period followed, the pollen production falls within the so-called winter months of June-August. Consequently, similar high influx values are recorded for the winter of 1988

(383.4 grains/cm²/90 days) and 1989 (362.6 grains/cm²/90 days). Thereafter, the values decline through spring and summer to an autumn low. An obvious anomaly within this data set is the large difference between the December-May influx values of 1988-89 (396.0 grains/cm²/180 days) and that of 1989-90 (746.8 grains/cm²/180 days). From the pollen trap counts (discussed in Chapter 7) a high Poaceae value is evident for the 1989-90 period which would result in some increase in influx value. However, overall, all the taxa producing pollen during this period produced considerably more pollen in 1989-90 than in 1988-89. This could be the result of some intrinsic seasonal variation or the consequence of an unmeasured climatic fluctuation within the region.

It is difficult to come to any firm conclusions with regards to the pollen influx values of the sub-alpine fynbos due to sampling commencing only in March of 1989 (Figure 6.1j). However, the data recorded does allow for a generalized description to be considered. Pollen production increases from an autumn low of 208.1 grains/cm²/90 days, to 513.2 grains/cm²/90 days in winter and to 913.9 grains/cm²/90 days during the spring months of 1989. The high June-August 1989 value is as a consequence of *Erica* species in the community producing large quantities of pollen, up to ± 740 grains/cm²/90 days. Ericaceae dominates (50%) the pollen spectrum during this time period. Thereafter the majority of the taxa produce more pollen, during the September-November spring period. The December-May 1989-90 sample cannot be compared to the corresponding six month period of the previous year as no samples were collected.

6.5.2 ANNUAL POLLEN INFLUX VALUES

The seasonal pollen influx values for the dominant vegetation communities of the montane and sub-alpine regions of the research area do show a marked seasonality over the two years. Furthermore, seasonal influx values fluctuate annually as has previously been described (Bonny, 1980; Hall, 1990). Despite this fluctuation the total annual pollen influx values do not significantly vary from year to year (Figure 6.2 and Table 6.7).

Table 6.7 Total pollen influx values (grains/cm²/year) for June 1988-90 for vegetation communities within the montane and sub-alpine regions of the Natal Drakensberg.

Vegetation Community	June 1988-May 1989	June 1989-May 1990	June 1988-May 1990
Highland Sourveld	1 346.6	1 207.9	1 277.3
Protea savanna	1 506.6	1 570.9	1 538.8
Podocarpus forest	2 978.4	2 271.3	2 624.9
Rendlia altera grassland	1 364.4	1 525.5	1 445.0
Leucosidea sericea scrubland	1 138.1	1 232.5	1 185.3
Themeda triandra grassland	2 867.9	2 704.7	2 786.3
'Mixed' grassland	1 511.3	1 464.6	1 488.0
Festuca costata grassland	1 401.9	1 698.7	1 550.3
Low altitude vlei	-	1 078.1	1 078.1
Sub-alpine fynbos	-	2 206.2	2 206.2

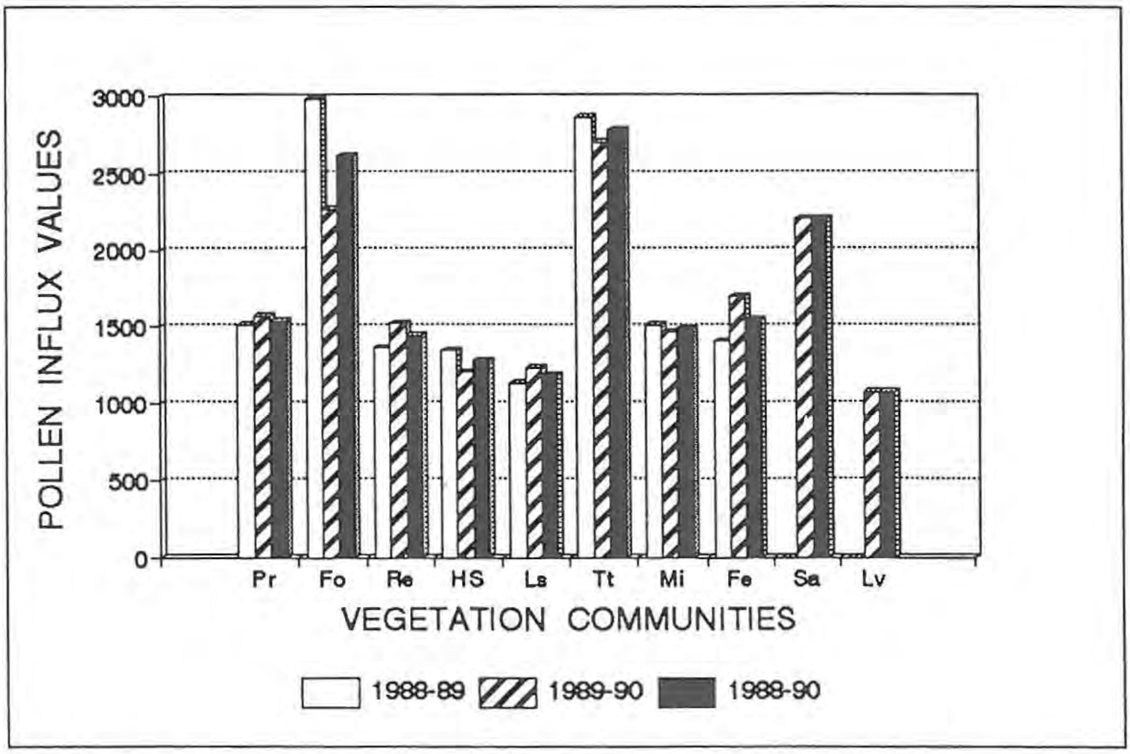


Figure 6.2 Total annual pollen influx values (grains/cm²/year) for the montane and sub-alpine vegetation communities. Pr=*Protea* savanna, Fo=*Podocarpus* forest, Re=*Rendlia altera* grassland, HS=Highland Sourveld, Ls=*Leucosidea sericea* scrubland, Tt=*Themeda triandra* grassland, Mi='Mixed' grassland, Fe=*Festuca costata* grassland, Sa=Sub-alpine fynbos and Lv=Low altitude vlei.

Protea savanna has an influx of 1506.6 grains/cm^2/year in 1988-89 and 1570.9 grains/cm^2/year in 1989-90, dominated by Poaceae (35%), Proteaceae (32%) and, to a lesser extent, Asteraceae (11%). *Podocarpus* forest has a high pollen production with a two year average of 2 624.9 grains/cm^2/year. As would be expected with such a large volume of pollen grains, the annual variation is large, ± 700 grains/cm^2/year. Within the forest community the family Ulmaceae (33%), Poaceae (19%), Podocarpaceae (12%), Sapindaceae (10%) and Pteridophyta (9%) are the dominant pollen or spore producing taxa.

For the *Rendlia altera* grassland influx values of 1364.4 grains/cm^2/year for 1988/89 and 1525.5 grains/cm^2/year for 1989-90 are recorded comprising mainly Poaceae (39%) and Asteraceae (27%). The grassland communities of *Themeda triandra*, 'Mixed', *Festuca costata* and *Themeda*-dominated Highland Sourveld all produce similar annual pollen influx values. *Themeda triandra* grassland has a high influx value of 2867.9 grains/cm^2/year for 1988-89 and 2704.7 grains/cm^2/year in 1989-90. These high values are largely due to high counts of Asteraceae and Poaceae which constitute 43% and 36% respectively, of the pollen trap spectrum.

Influx values of 1511.3 grains/cm^2/year during 1988-89 and 1464.6 grains/cm^2/year during 1989-90 were recorded for the 'Mixed' grassland community. The annual pollen trap spectrum is dominated by Poaceae (44%) and Asteraceae (34%) with the next dominant being a woody component - Anacardiaceae. Poaceae (49%) and Asteraceae (30%) also dominate the annual pollen trap spectrum of the *Festuca costata* grassland. The community had an annual pollen influx value of 1401.9 grains/cm^2/year for 1988-89 and 1698.7 grains/cm^2/year for 1989-90. The Highland Sourveld community records values of 1346.6 grains/cm^2/year for 1988-89 and 1207.9 grains/cm^2/year for 1989-90.

Despite the large pollen influx variation between December 1988 and May 1989 and the same period during 1989-90 recorded in the *Leucosidea sericea* scrubland, the annual pollen influx fluctuation is low. A value of 1138.1 grains/cm^2/year was recorded during the 1988-89 time period and 1232.5 grains/cm^2/year during 1989-90. The annual spectrum is dominated by *Leucosidea* (56%) and to a lesser degree by Poaceae (21%).

As no pollen influx values were recorded for the first half of the 1988-89 period within the low altitude vlei and sub-alpine fynbos communities it is not possible to compare two complete years of data. However, the annual pollen influx values for 1989-90 record a high influx value from the fynbos community (2206.2 grains/cm^2/year) and a somewhat lower value for the low altitude vlei (1078.1 grains/cm^2/year). The annual pollen trap spectrum for the sub-alpine fynbos community shows no one dominant taxon, although several do have significantly higher values than the rest, namely Poaceae (22%), Ericaceae (18%), Asteraceae (15%) and Proteaceae (12%), whereas the low altitude vlei is dominated by Poaceae (48%) and supported by Asteraceae (15%), Pteridophyta (13%) and Cyperaceae (9%).

Despite annual variation of the pollen influx values for the same season, the annual variation of the total pollen influx is low. The largest variation is recorded for the *Podocarpus* forest, where the discrepancy is 707.1 grains/cm^2/year. It is difficult to compare these influx values to other work as the European and North American research involves very different vegetation communities and species, furthermore the severe northern Hemisphere climate induces distinct growth and non-growth seasons. No eastern or southern African literature gives detailed pollen influx values. Work by Kershaw and Strickland (1990) who undertook a ten year pollen trapping programme in north-eastern Queensland, Australia have calculated pollen influx values as grains/cm^2/year for a lower montane or Simple Notophyll Vine forest. The average influx per trap was 907 grains/cm^2/year, with a range from 61 to 2029 grains/cm^2/year was recorded. The community in which their study was undertaken has similar family taxa as those of the *Podocarpus* forest, with an understorey dominated by Poaceae and Pteridophyta.

6.5.3 ANOVA OF SEASONAL AND ANNUAL VARIATION

ANOVAs were carried out to investigate the seasonal and annual variation in the relative percentages of pollen recorded from the pollen traps. The hypotheses tested were that: 1) there is no significant seasonal difference between the modern pollen spectra produced from vegetation communities and 2) there is no significant annual difference between the modern pollen spectra produced by the vegetation communities (Table 6.8).

Table 6.8 Results of ANOVA testing seasonal and annual pollen influx values for particular vegetation communities.

Vegetation Community	Total taxa	Seasonal		Annual	
		Accept H_0	Reject H_0	Accept H_0	Reject H_0
Highland Sourveld	28	10 (36%)	18 (64%)	10 (36%)	18 (64%)
Protea savanna	32	16 (50%)	16 (50%)	14 (44%)	18 (56%)
Podocarpus forest	33	9 (27)%	24 (73%)	10 (30%)	23 (70%)
Rendlia altera grassland	43	20 (47%)	23 (53%)	20 (47%)	23 (53%)
Leucosidea sericea scrubland	37	8 (22%)	29 (78%)	8 (22%)	29 (78%)
Themeda triandra grassland	37	12 (32%)	25 (68%)	16 (43%)	21 (57%)
'Mixed' grassland	32	11 (34%)	21 (66%)	-	32 (100%)
Festuca costata grassland	36	14 (39%)	22 (61%)	14 (39%)	22 (61%)
Low altitude vlei	34	19 (56%)	15 (44%)	11 (32%)	23 (68%)
Sub-alpine fynbos	38	13 (34%)	25 (66%)	13 (34%)	25 (66%)

The seasonal variation results are not conclusive either for seasonality or non-seasonality. Seasonality does occur in a number of taxa as was indicated from the seasonal pollen influx values derived from the pollen trap data. The *Leucosidea sericea* community has the greatest percentage with regards to rejecting the hypothesis, however one needs to be careful in how this is interpreted as percentage data are being applied. The distinct seasonality and high abundance values of the dominant *Leucosidea sericea* from this community can 'mask' the effect of other taxa and the high values can influence the ANOVA test. A similar picture emerges for the ANOVA data regarding annual pollen influx variation. In most instances the taxa of the vegetation communities do not show significant enough results either for or against annual variation. The exception is the 'Mixed' grassland community, taxa from within this community do not differ significantly on an annual basis. For the other communities some taxa show annual variation whilst others do not and the percentage of acceptance or rejection of the hypothesis range from 20 to 80%.

These two ANOVAs need to be studied in conjunction with the pollen spectrum and pollen influx values. The total pollen influx values show little to no significant annual variation with regards to the total pollen influx values per year. When this total value is broken down into the respective taxa it is evident that some individual taxa do exhibit annual variation. As it is the total spectrum or pollen signature that this study seeks it must be presented that there is little annual variation over the two study years with regards to the total pollen influx value from each vegetation community. However acknowledgement is given of the fact that annual variation does occur within some of the individual taxa.

6.6 SUMMARY

From these results a minimum soil and pollen trap sample size required, at a particular level of accuracy, has been calculated. The calculations, although determined in retrospect, confirm the pre-sampling decision regarding sample size. The calculations help to determine recommendations with regards to future modern pollen rain studies. The counts are also required for statistical tests, used to produce a more objective approach to the elucidation of a possible pollen rain - vegetation relationship and to describe a vegetation community's modern pollen spectrum and how distinctive or similar it is to other communities.

Absolute pollen influx values have been calculated to determine both seasonal and annual total pollen influx values for each of the vegetation communities. Despite an obvious seasonal fluctuation for a number of the dominant taxa within each of the studied communities, the annual influx fluctuation is not as marked. The results are used to augment the description of the pollen rain for the vegetation communities, in particular those communities which exhibit similar pollen spectra with regards to the percentage abundance of dominant taxa.

CHAPTER SEVEN
DATA DESCRIPTION AND ANALYSIS (2)

7.1 INTRODUCTION

This chapter describes the data and results of the descriptive and statistical analyses performed to investigate the modern pollen rain - vegetation relationship. Spectra, plotting relative percentage frequencies as rotated bar graphs, are presented to describe the relative abundance of taxa from each of the three data sets, namely vegetation composition and pollen counts from surface soil and pollen trap samples. The statistical techniques employed are: canonical correlation analysis (to determine the association between the data sets), two-way indicator species analysis (TWINSPAN) (a classification technique), detrended correspondence analysis (DECORANA) and principal components analysis (PCA) (used to determine ordination or 'grouping' of data), and multiple discriminant analysis (MDA) (to obtain a probability of modern analogue and vegetation zonal index). The motivation behind using each of these tests and the necessary procedures followed are outlined in Chapter 5. While the descriptive analysis allows one to obtain and subjectively compare the various data sets, the statistical analysis allows one to describe and quantify both the vegetation and pollen rain and therefore to make objective inferences about possible relationships between the two pollen rain collecting techniques and between modern pollen rain and the vegetation communities from which the pollen was collected.

7.2 VEGETATION AND POLLEN RAIN SPECTRA

7.2.1 INTRODUCTION

The spectra from each community have been placed together to facilitate easier comparative analyses between the vegetation, soil and pollen trap spectra. It was not possible to place the spectra onto a single diagram, as is often the case in such undertakings, due to the number of taxa involved from all the communities. Furthermore the initial emphasis, although not disregarding the inter-community spectra differences, is on similarities and/or differences between the vegetation and pollen rain spectra of a particular community. Therefore it was deemed more appropriate to place the spectra together as rotated bar-graphs representing the more dominant taxa within each spectrum. In most cases taxa with a representation of 0.5% or greater within a particular spectrum are graphically represented, however in some instances (mentioned in the figure descriptions) all the taxa are represented. A comprehensive list of the families recorded within each spectrum are presented as Appendix 5.

7.2.2 VEGETATION

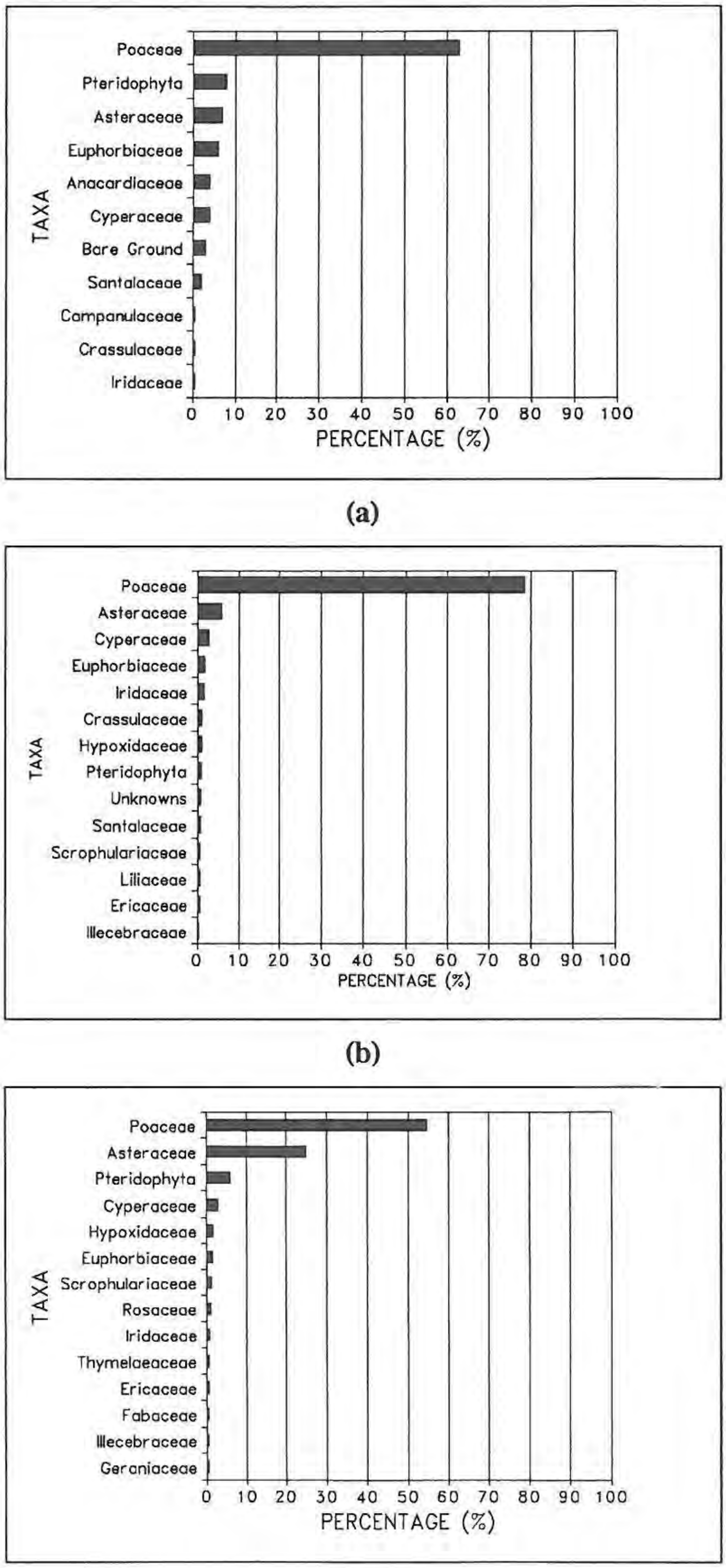
Initial quantification of the vegetation was carried out at species level, but as both the surface soil and pollen trap samples are recorded, predominantly, to the family level, the vegetation data was further analyzed at the family level. This reduces the resolution of the vegetation data, but is necessary for comparative purposes, which requires that all three data sets are presented at the level of the 'weakest set', in this case the family level of plant and pollen identification. The vegetation data are present as spectra (Figures 7.1a-7.11c), while species lists are presented as Appendix 6.

7.2.2.1 Montane Belt

The *Themeda*-dominated Highland Sourveld is dominated by Poaceae (63%) (Figure 7.1a). Everson and Clarke (1987) obtain a Poaceae value of 66% for the Highland Sourveld of the region during their comparative study of various grassland sampling techniques. The most conspicuous grasses are *Themeda triandra, Monocymbium ceresiiforme* and *Trachypogon spicatus*, although numerous other grass species are present in smaller quantities. *Pteridium aquilinum* (Pteridophyta - 8%), *Helichrysum* and *Aster* (Asteraceae - 7%), *Acalypha* (Euphorbiaceae - 6%), *Bulbostylis* and *Cyperus* (Cyperaceae - 4%) and *Rhus* (Anacardiaceae - 4%) are the other main contributing taxa.

The *Protea* savanna community is sub-divided into two distinct vegetation strata (Figure 7.2a). The upper stratum is dominated by the Proteaceae species *Protea caffra* and *P. roupelliae* (46%), and to a lesser extent *Diospyros austro-africana* (Ebenaceae), *Cussonia paniculata* (Araliaceae), *Halleria lucida* (Scrophulariaceae), *Rhus discolor*, *R. lucida* (Anacardiaceae) and *Myrica serrata* (Myricaceae). Although these latter species often covered 5-10% aerial cover of a single quadrat, the species rarely occurred in more than one or two of the twenty sampled quadrats. Species of the non-arboreal spectrum covered approximately 90% of the aerial ground cover and was dominated by the grasses (64%), with *Themeda triandra, Digitaria flaccida, Tristachya leucothrix, Elionurus muticus, Panicum natalense* and *Monocymbium ceresiiforme* being the most prevalent. Within the grassland stratum Cyperaceae, Pteridophyta, Asteraceae, Anacardiaceae, Rosaceae and Myricaceae occur with aerial cover values greater than 2% of the total spectrum.

The *Podocarpus* forest community was divided, similar to the *Protea* savanna community, into arboreal and non-arboreal taxa for the sake of analysis (Figure 7.3a), although the initial survey identified five strata, namely an upper, dominant, tree layer; a small tree layer; a shrub and herbaceous layer which included grasses and sedges; a ground and boulder layer; and, an epiphytic and climbers community. The arboreal spectrum was dominated by *Podocarpus latifolius* (Podocarpaceae - 34%), with Celestraceae, Flacourtiaceae, Sapindaceae, Apocynaceae, Rubiaceae, Rutaceae and Cornaceae representing the more abundant taxa. The non-arboreal spectrum comprised of a large percentage of Pteridophyta (27%), mostly large ground ferns of the species *Polystichum setiferum* var. *fuscopaleaceum, P. lucidum, P. luctuosum. Pteris captoptera, P. dentata* and *Blenchum punctulatum* var. *punctulatum*. Poaceae (22%) was the second most dominant non-arboreal taxa dominated by *Festuca africana, Stipa dregeana* var. *elongata*, *Oplismenus hirtellus* and *Ehrharta erecta* var *natalensis*. Other prominent non-arboreal taxa are Cyperaceae, Iridaceae, Rutaceae (herb and shrub forms of the family) and Liliaceae. This community displayed a high species diversity with a complex community structure and the total percentage aerial cover exceeded 100% due to stratification of the vegetation.

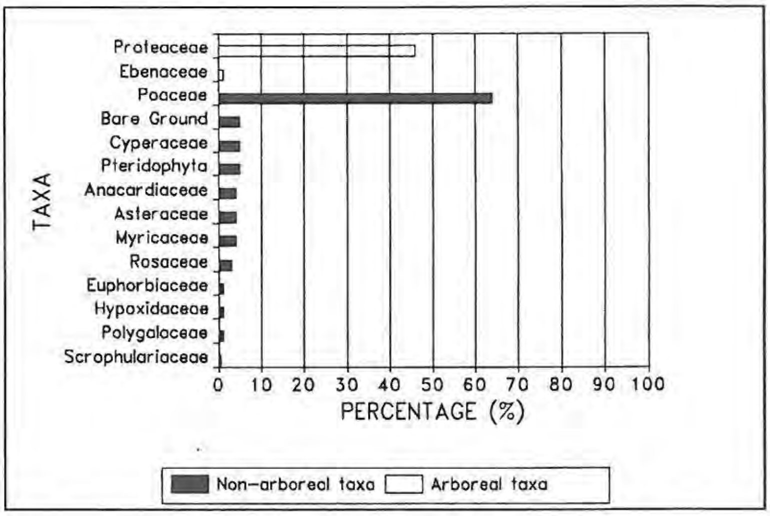


(a)

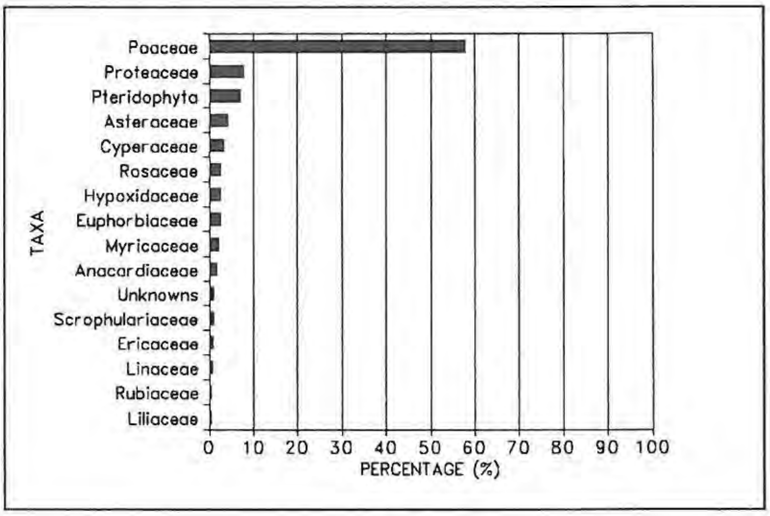
(b)

(c)

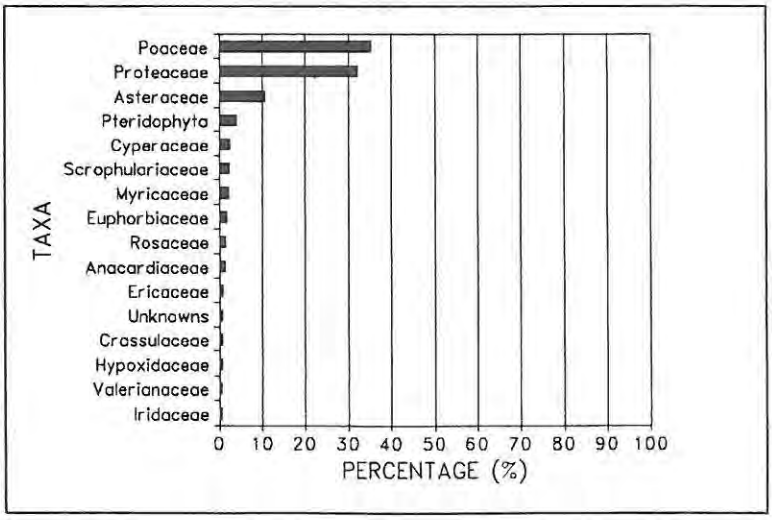
Figure 7.1 Highland Sourveld spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5 % of the total spectrum.



(a)

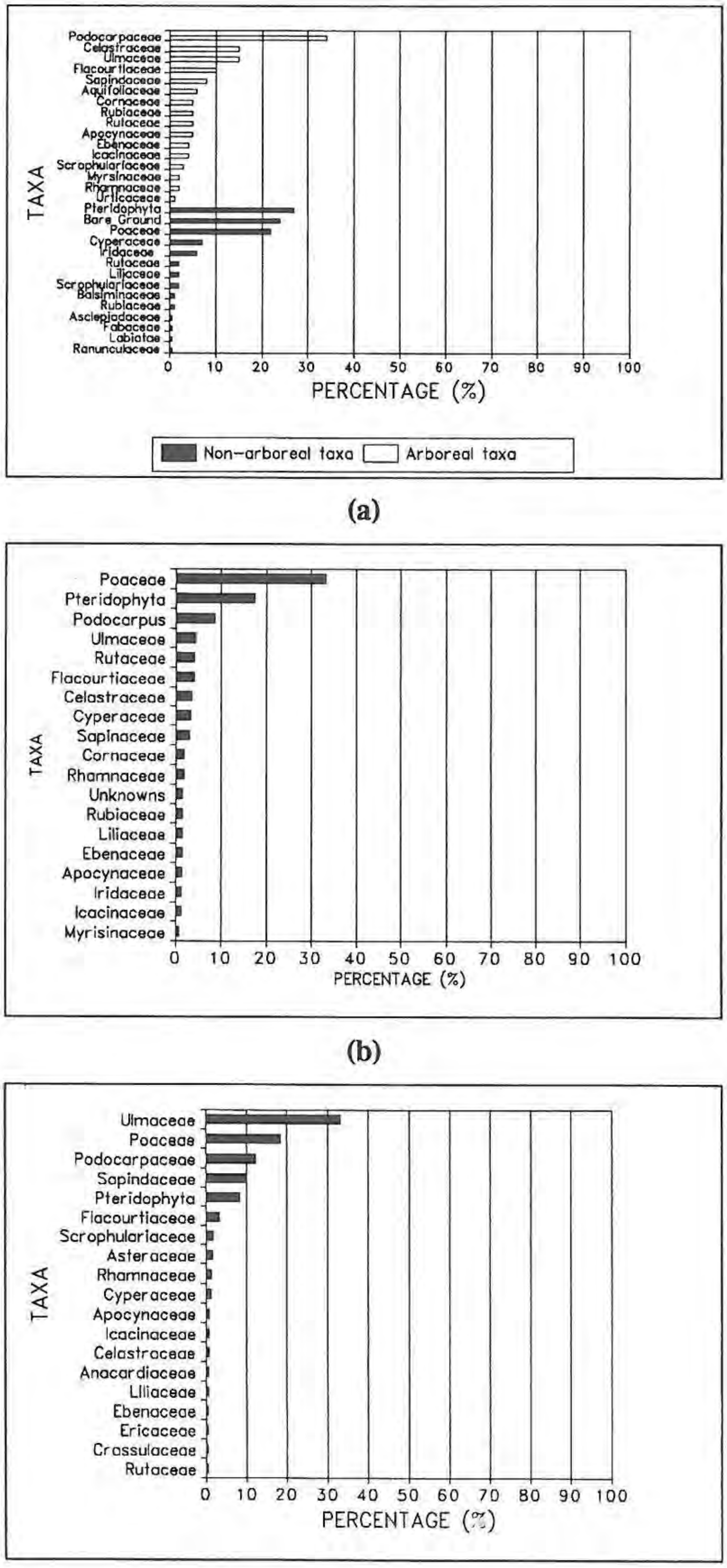


(b)



(c)

Figure 7.2 *Protea* savanna spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum. The vegetation spectrum is sub-divided into arboreal/non-arboreal taxa.



(c)

Figure 7.3 *Podocarpus* forest spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum. The vegetation spectrum is sub-divided into arboreal/non-arboreal taxa.

7.2.2.2 Sub-alpine Belt

The *Leucosidea sericea* scrubland has an aerial cover of approximately 60% in the arboreal stratum and up to 90% in the non-arboreal, ground stratum (Figure 7.4a). The arboreal stratum is dominated by *Leucosidea sericea* (Rosaceae) which constitutes ± 45% of the spectrum. Other arboreal families include Ebenaceae (*Diospyros austro-africana* and *Euclea crispa*) and Rhamnaceae (*Rhamnus prinoides*). The species *Erica evansii* (Ericaceae), *Buddleja salviifolia* (Loganiaceae), *Lithospermum afromontanum* (Boraginaceae), *Rhus dentata, R. lucida* (Anacardiaceae) and *Myrisine africana* (Myrsinaceae) are the other arboreal species.

Poaceae (32%) and Pteridophyta (30%) are the dominant components of the non-arboreal spectrum. The fern *Pteridium aquilinum* subsp. *aquilinum* was the only Pteridophyta observed, while the more obvious grasses include *Themeda triandra, Digitaria flaccida, Diheteropogon filiformis, Panicum ecklonii, Tristachya leucothrix* and *Miscanthus capensis*. The families Anacardiaceae, Cyperaceae, Ericaceae, Asteraceae, Boraginaceae, Euphorbiaceae, Lamiaceae, Liliaceae, Loganiaceae, Rubiaceae, Geraniaceae and Scrophalariaceae are represented in abundances greater than 0.99% of the non-arboreal spectrum.

The sub-alpine grasslands of the Drakensberg can be divided into five recognizable communities (Killick, 1978). Of these five, the *Rendlia altera* grassland on the plateau of the lower 'Berg and the Temperate grasslands which occur on the foothills of the Drakensberg escarpment were sampled.

The *Rendlia altera* grassland is dominated by the grass *Rendlia altera* supported by *Elionurus muticus, Alloteopsis semialata, Eragrostis racemosa, Harpochloa falx, Stiburus alopecuroides* and *Themeda triandra*. The Poaceae taxa comprise 55% of the total spectrum, while a further 14% comes from Cyperaceae species, predominantly *Bulbostylis schoenoides, B. humilis, Kyllinga pauciflora, Cyperus semitrifidus* and *C. obtusiflorus* var. *obtusiflorus* (Figure 7.5a). The herbs *Helichrysum* and *Aster* (Asteraceae) and *Hypoxis* and *Rhodohypoxis* (Hypoxidaceae) constitute a further 6% and 0.7% respectively.

The temperate grasslands are sub-divided according to topographic differences. A *Themeda triandra* grassland community dominates the warmer, north-facing slopes while a *Festuca costata* grassland community covers the cooler, south-facing slopes of this region. Both communities have a high proportion of Poaceae elements present, 61% and 76% respectively (Figures 7.6a and 7.7a). The *Themeda triandra* grassland is dominated by *Themeda triandra, Elionurus muticus, Alloteropsis semialata, Tristachya leucothrix*, and *Cymbopogon validus*. Genera of the Asteraceae family, *Helichrysum, Senecio, Vernonia* and *Aster* have a 15% representation, while shrub forms of Anacardiaceae (*Rhus* - 5%) and Ericaceae (*Erica* - 5%) contribute significantly to the spectrum. The *Festuca costata* community is dominated (± 50%) by the grass *Festuca costata*, while a diverse array of herbs, predominantly of the Asteraceae family, form the remainder of the more abundant taxa within this community.

Between the two grasslands, on the small plateaus and valleys, is an ecotone with elements from both grasslands invaded by a host of shrubs (predominantly *Rhus*) and tall herbs, of the genera *Helichrysum, Senecio* and *Kniphofia*. This community, described as Brackenveld by Killick (1978) and as 'Mixed' grassland in this study, is dominated by grass elements (62%), the most abundant being *Themeda triandra, Elionurus muticus* and *Festuca costata*, Anacardiaceae (16%) and Asteraceae (10%) (Figure 7.8a).

The hygrophilous herbaceous or low altitude vlei community is dominated by Cyperaceae (45%), the hygrophilous stemless rhizomatous herb *Gunnera perpensa* (Gunneraceae - 15%) and Poaceae (12%) (Figure 7.9a). Cyperaceae species diversity is high, the more dominant species being *Carex cognata, Cyperus schlechteri, C. semitrifidus*, and *Pycreus macranthus*. The more abundant grasses are *Stiberus alopecuroides* and *Harpochloa falx*. Within the sedge-grass community are a number of herbs, predominantly of the Brassiaceae, Ranunculaceae, Boraginaceae, Asteraceae, Dipsacaceae, Scrophulariaceae and Rosaceae families.

The sub-alpine fynbos arboreal spectrum is dominated by the plant families Rosaceae (21%), Thymelaeaceae (20%) and Ericaceae (18%) (Figure 7.10a). The family Rosaceae comprises of the species *Cliffortia linearifolia* and *C. spathulata*, Thymelaeaceae of *Passerina filiformis* and *P. montana* and Ericaceae of *Erica evansii* and *E. ebracteata*. The families, Ebenaceae, Proteaceae, Rhamnaceae, Myrsinaceae and Celastraceae are represented in the arboreal spectra with an aerial cover greater than 1%. The non-arboreal spectrum reflects the diversity of the community, with Poaceae (mostly *Cymbopogon validus, Themeda triandra* and *Festuca costata*) and Asteraceae (*Helichrysum*, *Senecio*, *Macrowania* and *Aster*) contributing the largest non-arboreal percentage cover values at 27% and 13% respectively. Thirteen other families have values of 1% or greater.

7.2.2.3 Alpine Belt

The summit or alpine grassland of the Natal Drakensberg escarpment is dominated by the xeromorphic grasses *Merxmuellera disticha, Festuca caprina* and *Pentaschistis oreodoxa.* Grass associates include *Merxmuellera drakensbergensis, Agrostis barbuligera, Koeleria capensis* and *Eragrostis caesia*. The grasses comprise 64% of the total community cover, while the sedges, in particular, *Scirpus falsus, S. ficinioides, Schoenoxiphium filiforme* and *Isolepis costata* contribute a further 16%. Asteraceae genera such as *Senecio, Berkheya* and *Helichrysum* contribute a further 11%, Ericaceae (2%) and Juncaceae (2%) make up the remaining families with an aerial cover value in excess of 1% (Figure 7.11a).

The dominants of the *Erica-Helichrysum* heathland are *Erica dominans* and *Helichrysum trilineatum*. Ericaceae (32%) and Asteraceae (30%) constitute the two dominant taxa, with Thymelaeaceae, Poaceae, Santalaceae, Rosaceae, Cyperaceae, Crassulaceae and Scrophulariaceae being the other taxa which contribute an aerial cover of 1% or greater (Figure 7.11b).

The high altitude vlei community is dominated by the sedges *Carex killickii, C. monotropha, Isolepis fluitans, S. ficinioides* and *Schoenoxiphium filiforme*, and the grasses *Argrostis barbuligera, Pentaschistis oreodaxa* and *Merxmuellera drakensbergensis*. *Ericaulon dregei* (Eriocaulaceae - 16%) and species of the families Asteraceae, Juncaceae, Ericaceae, Iridaceae, Scrophulariaceae, Aizoaceae, Hypoxidaceae and Fabaceae represent 1% or more of the aerial cover (Figure 7.11c).

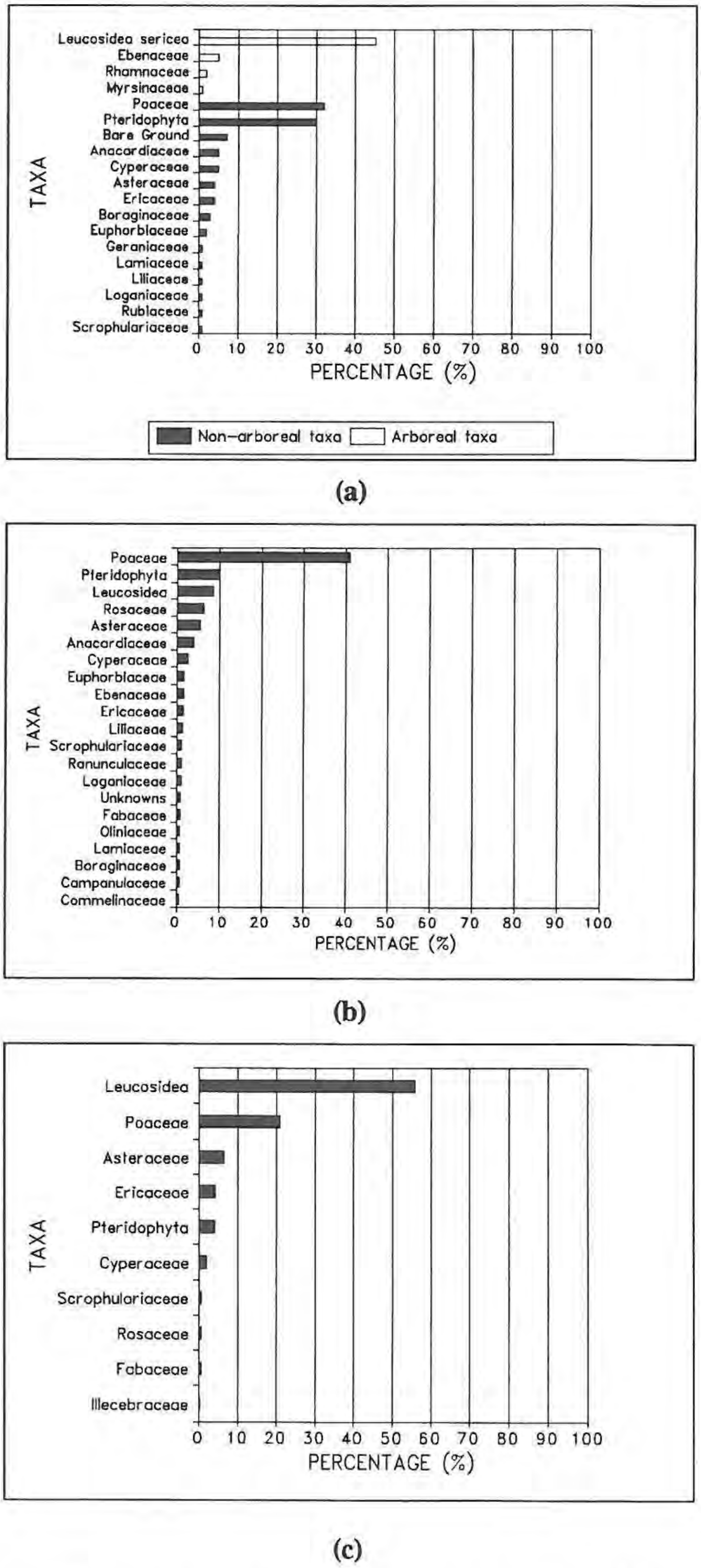
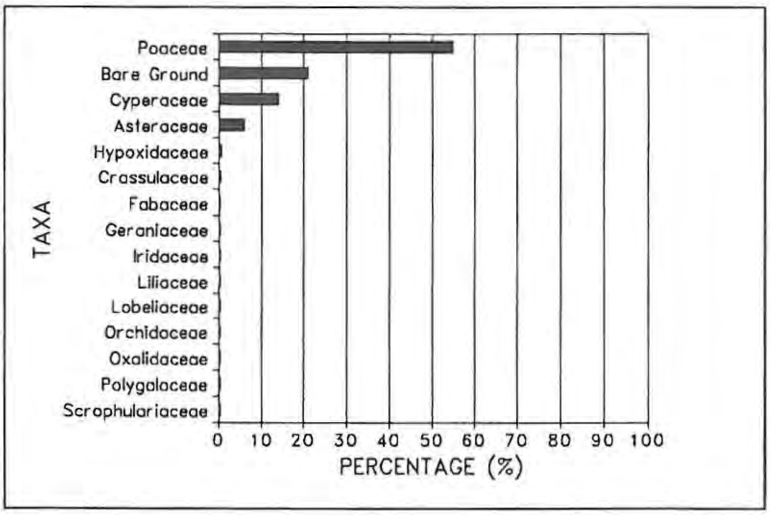
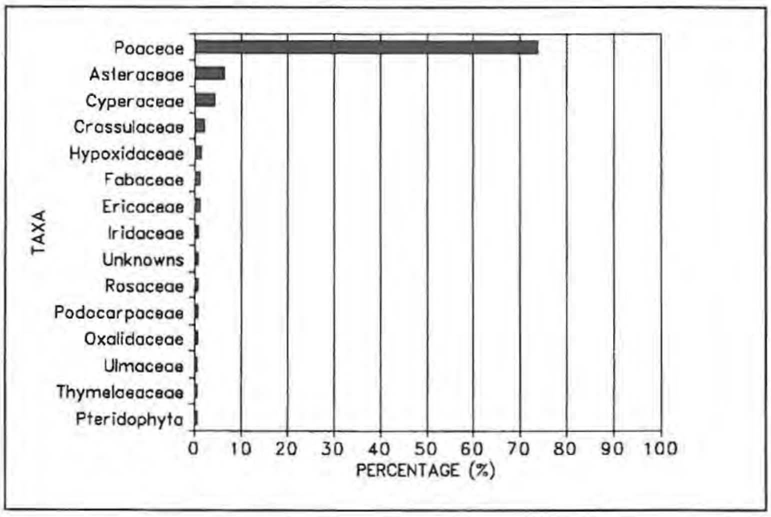


Figure 7.4 *Leucosidea sericea* scrubland spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5 % of the total spectra. The vegetation spectrum is divided into arboreal/non-arboreal taxa.



(a)



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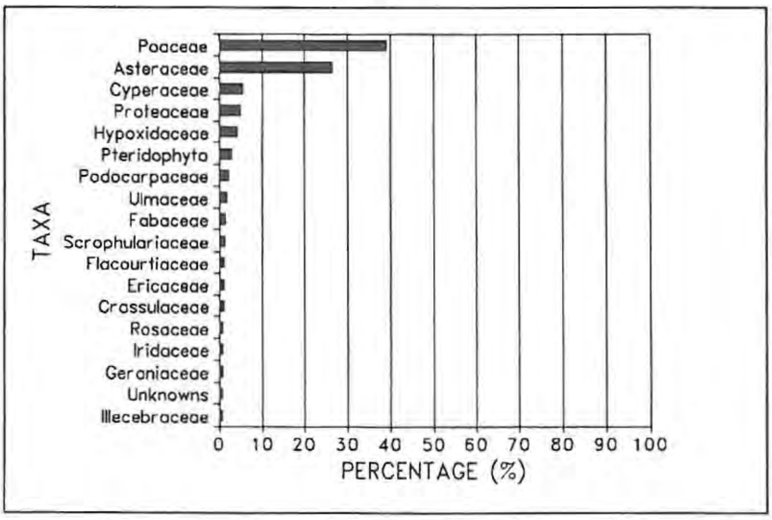


(c)

Figure 7.5 *Rendlia altera* grassland spectra: (a) vegetation, (b) soil and (c) pollen trap. All collected taxa recorded in the vegetation spectrum (a) and ≥ 0.5% for (b) and (c).

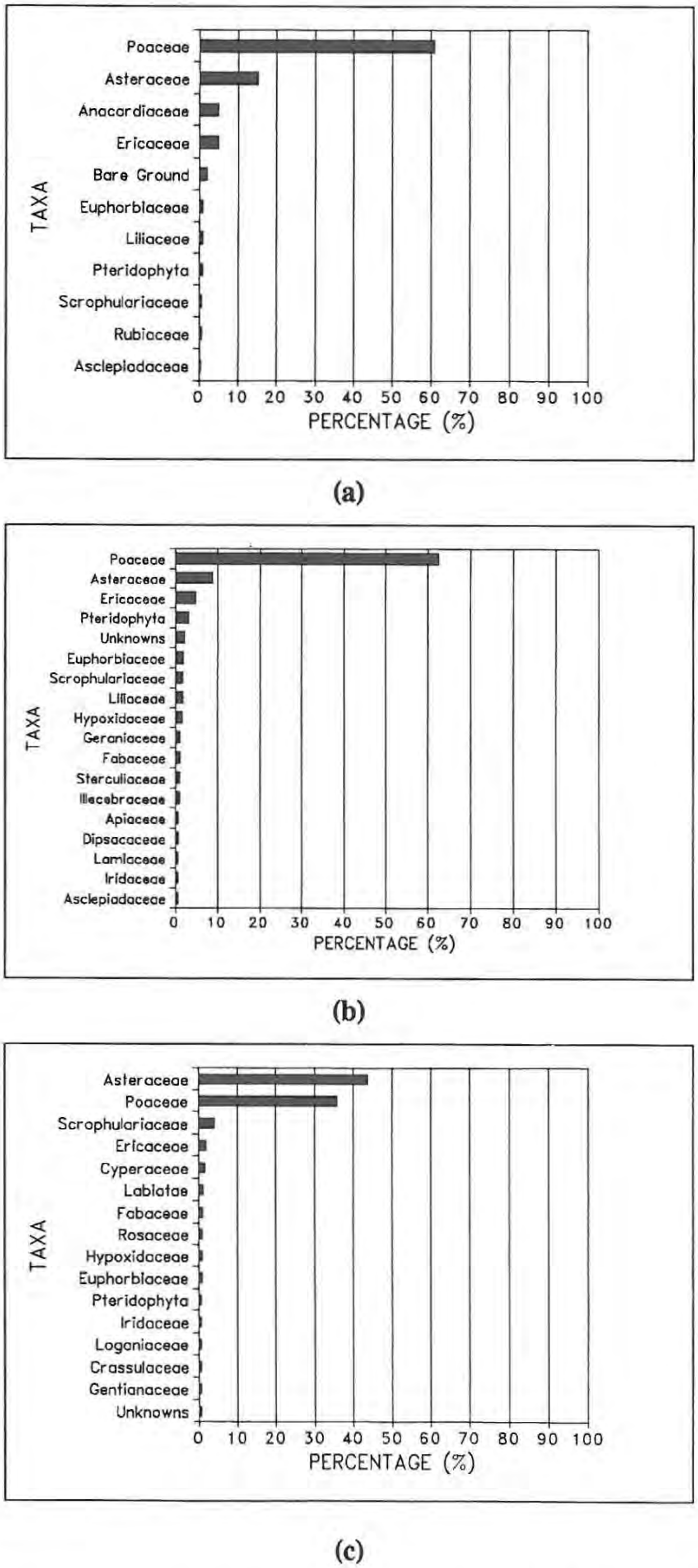


Figure 7.6 *Themeda triandra* grassland spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum.

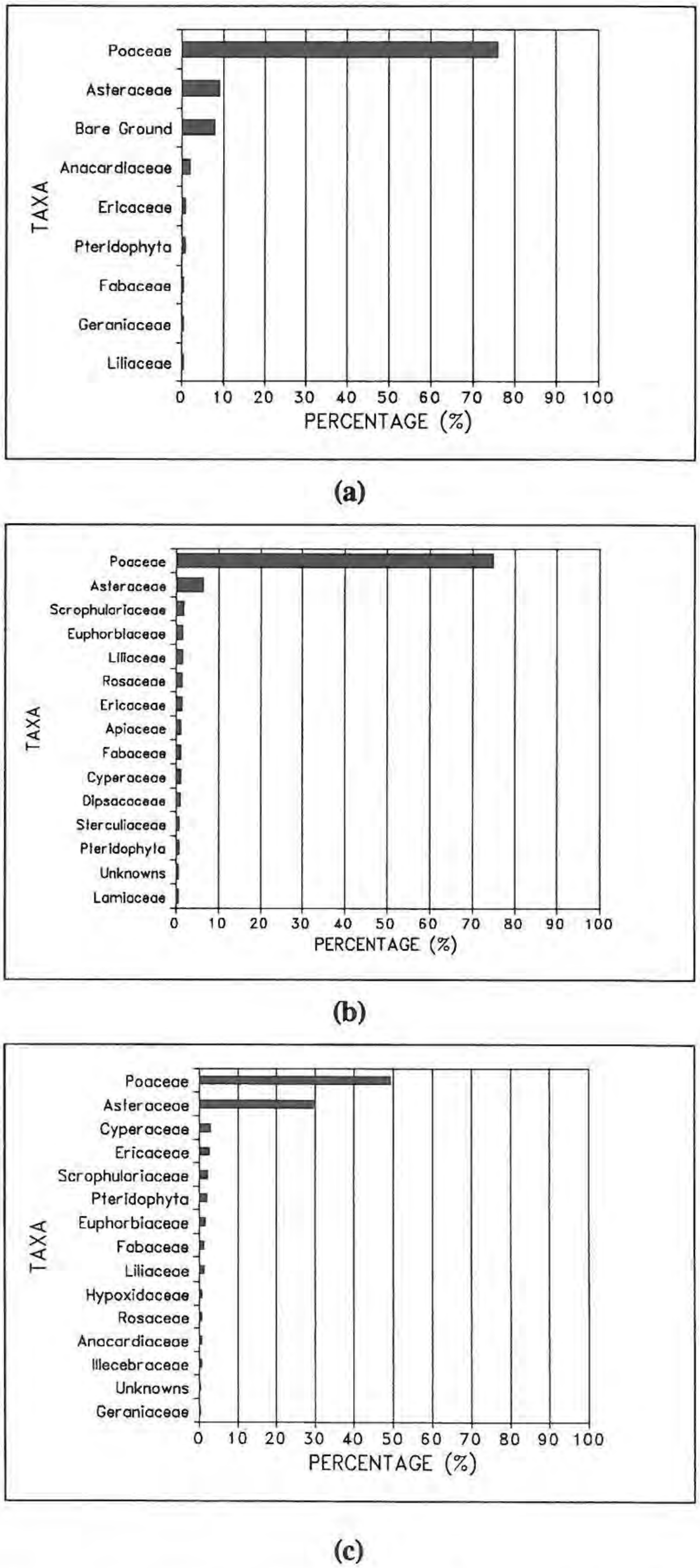
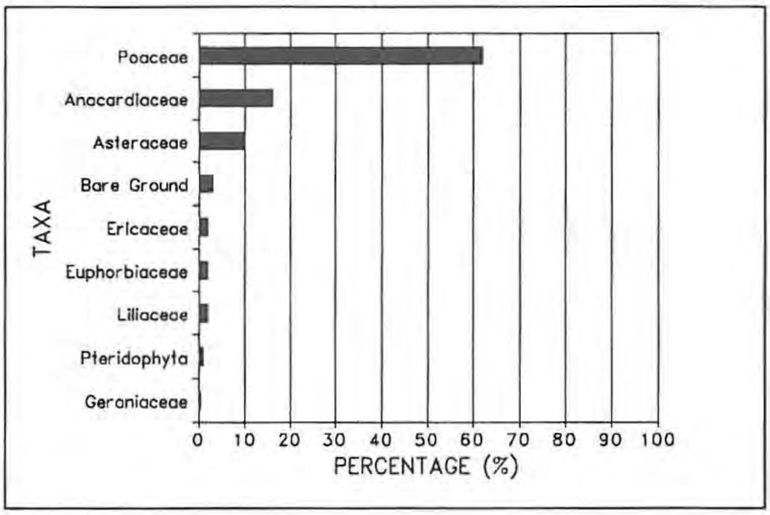
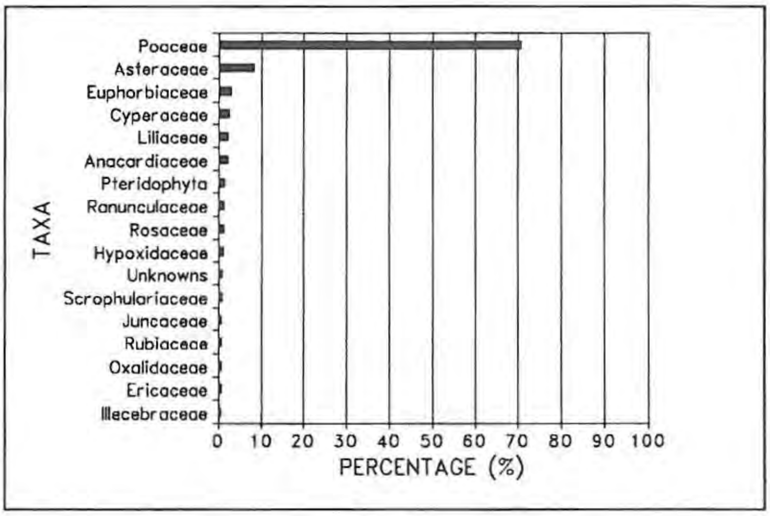


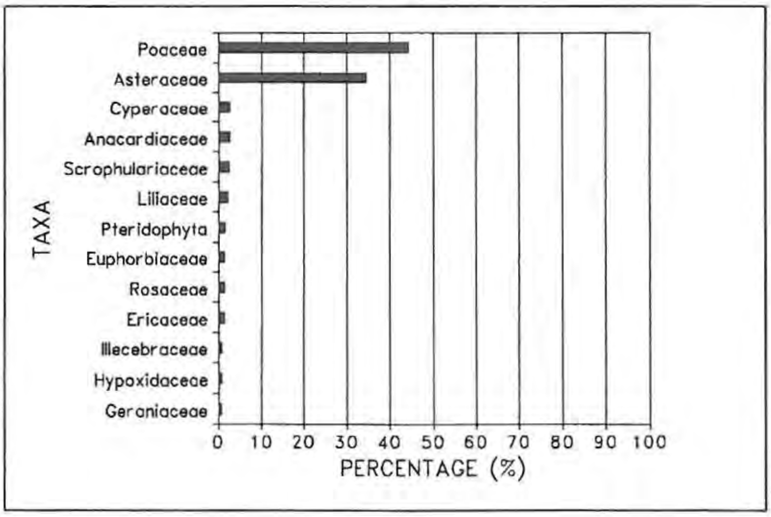
Figure 7.7 *Festuca costata* grassland spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum.



(a)

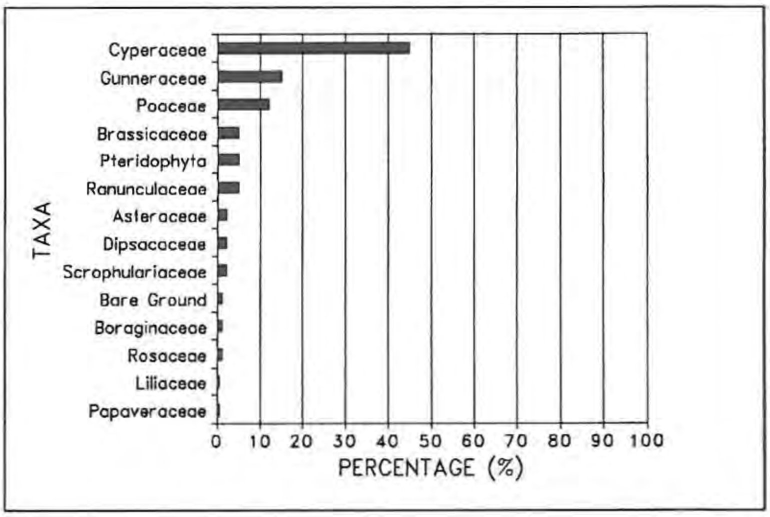


(b)

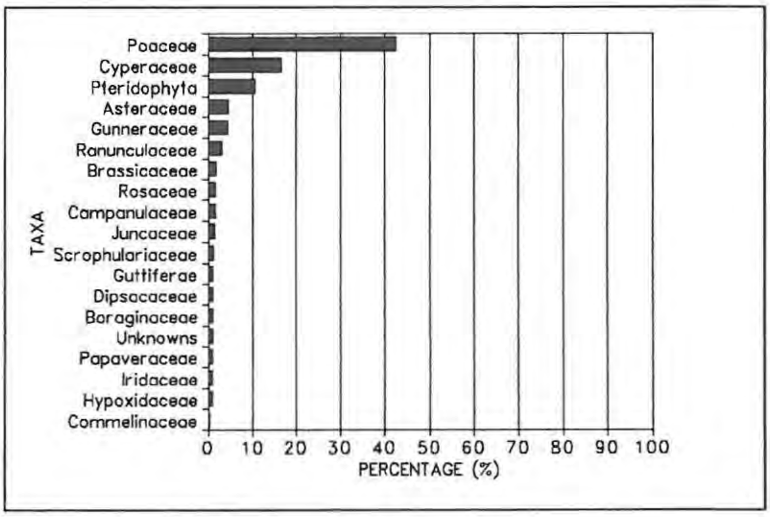


(c)

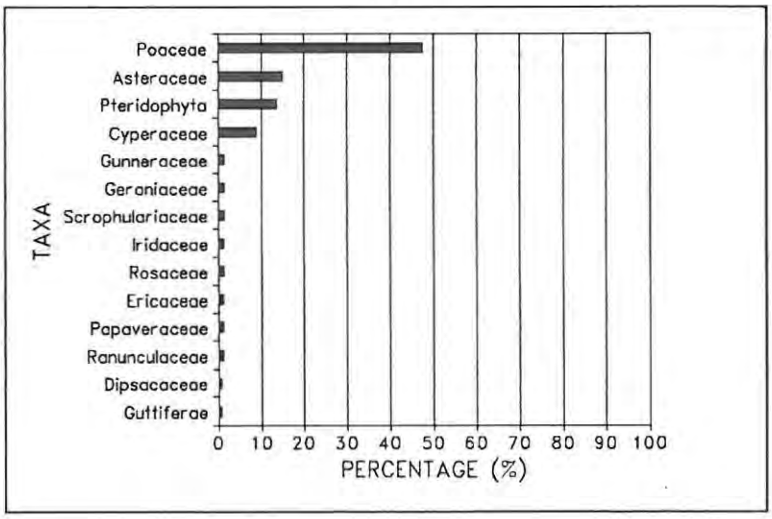
Figure 7.8 'Mixed' grassland spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum.



(a)

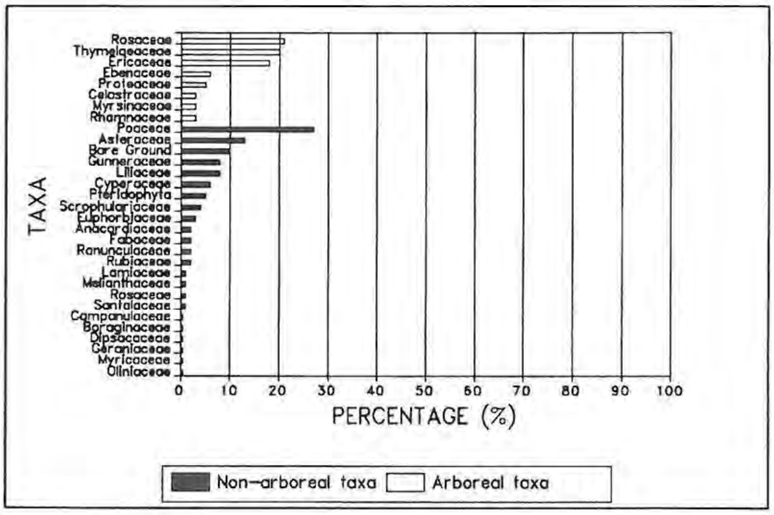


(b)

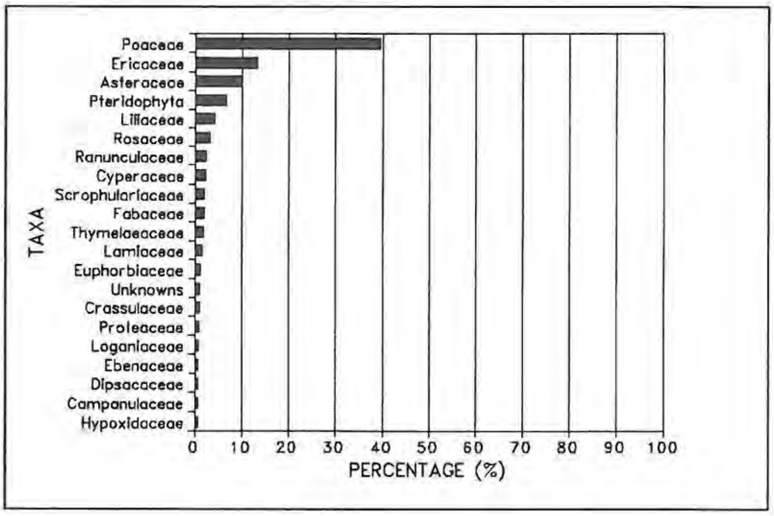


(c)

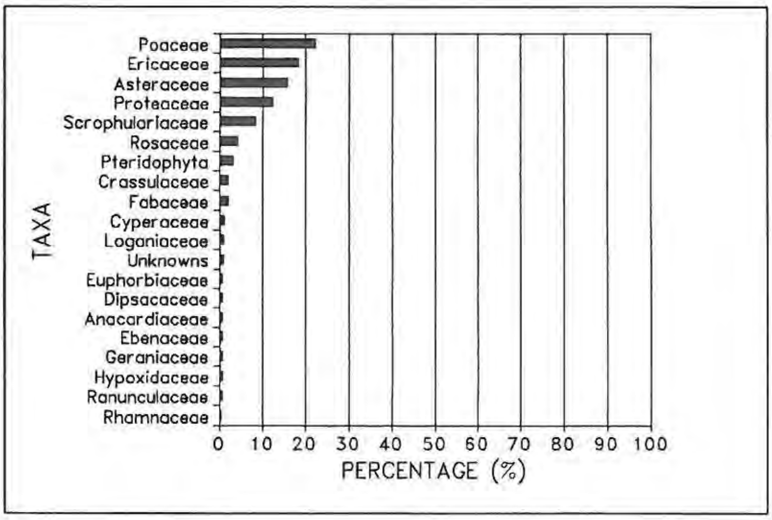
Figure 7.9 Low altitude vlei spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5% of the total spectrum.



(a)

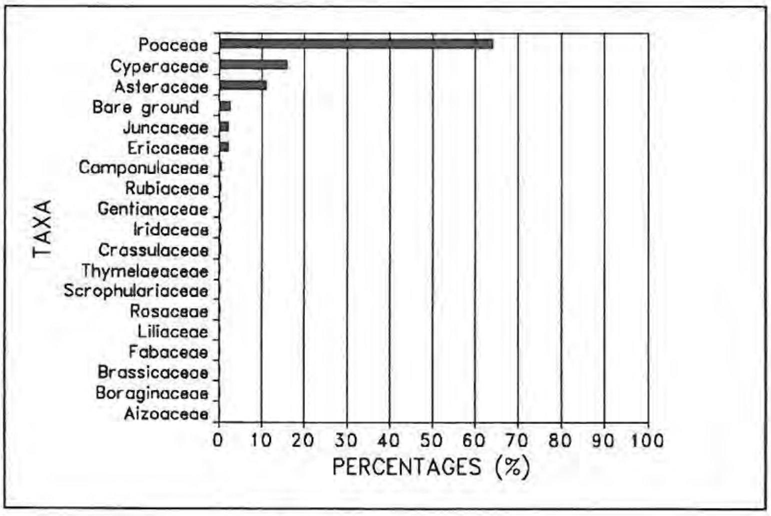


(b)

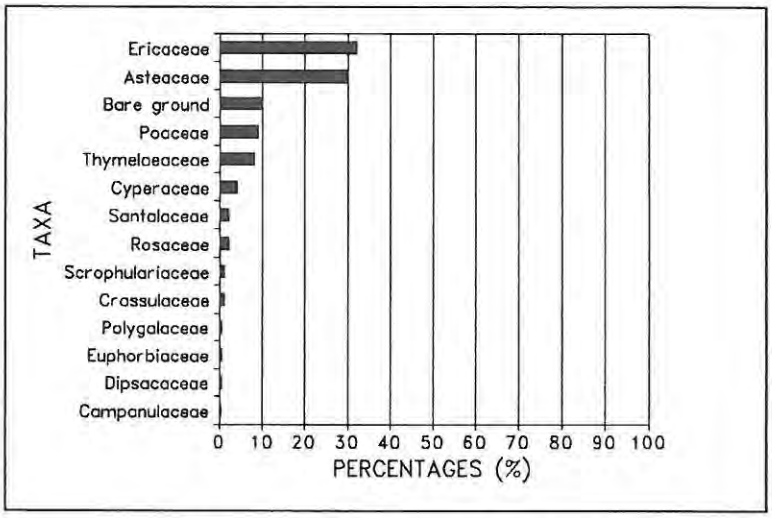


(c)

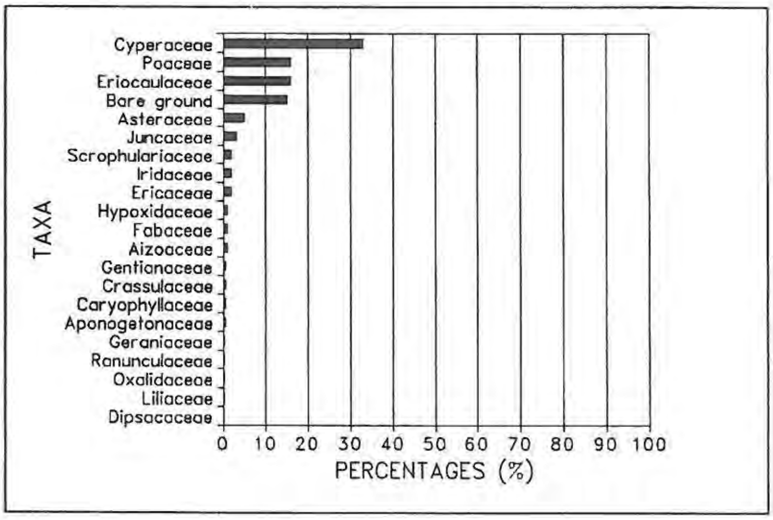
Figure 7.10 Sub-alpine fynbos spectra: (a) vegetation, (b) soil and (c) pollen trap. All taxa ≥ 0.5 % of the total spectrum. The vegetation spectrum is divided into arboreal/non-arboreal taxa.



(a) Alpine grassland

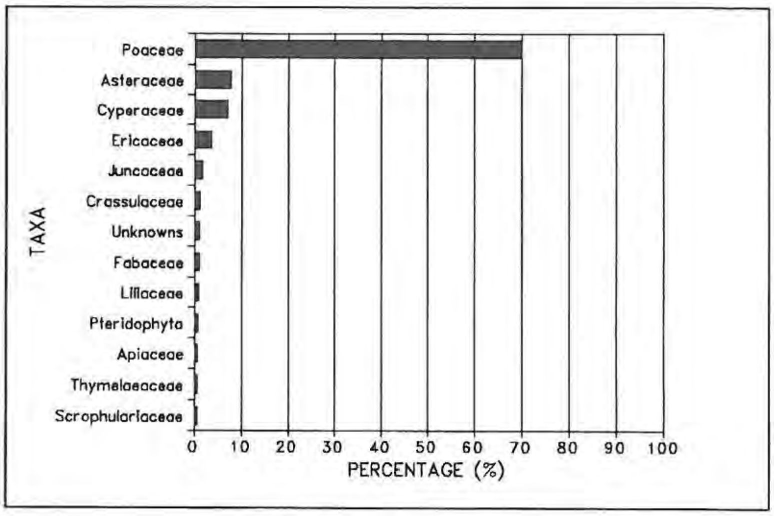


(b) *Erica-Helichrysum* heathland

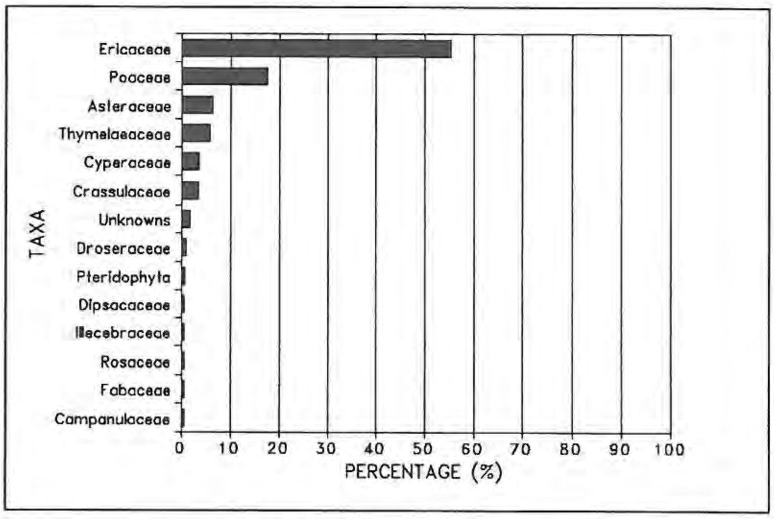


(c) High altitude vlei

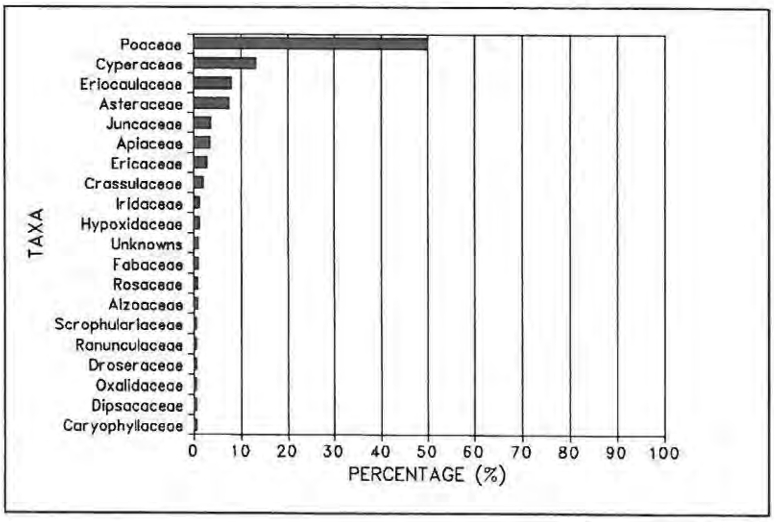
Figure 7.11 Vegetation spectra of the alpine vegetation communities. All taxa recorded are depicted in the spectra.



(a) Alpine grassland



(b) *Erica-Helichrysum* heathland



(c) High altitude vlei

Figure 7.12 Soil pollen spectra from the alpine vegetation communities. All taxa ≥ 0.5% of the total spectra.

7.2.2.4 Summary

Although an extensive and thorough vegetation analysis was performed, the results described above tend to be of a generalised nature, but as such give an overview of the dominant taxon within each of the studied communities. It is unfortunate that the pollen reference collection and the necessary technology is not readily available to allow for the identification of pollen samples to a species, rather than family level. If this was the case, an extensive, in-depth vegetation analysis would prove more useful. As it is the vegetation data used for modern pollen-vegetation relationship studies have to be generalised due to the nature of the pollen data. Despite using only a broad description of the vegetation it is necessary to carry out a thorough vegetation analysis to ensure accuracy of results and to allow more in-depth discussion if anomalies occur between pollen rain - vegetation comparisons.

7.2.3 SURFACE SOIL SAMPLES

Twenty surface soil samples were collected from each of the studied vegetation communities. The average pollen spectrum for each community is represented in the form of a rotated bar-graph (Figures 7.1b-7.10b, 7.12) and listed in Appendix 5.

7.2.3.1 Montane Belt

The *Themeda*-dominated Highland Sourveld is extensively dominated by Poaceae (79%) and, to a lesser degree, Asteraceae (5%) (Figure 7.1b). Other plant families with relative percentage abundance values of 1% or greater are Cyperaceae (2%), Euphorbiaceae (2%), Crassulaceae (1%) and Hypoxidaceae (1%). A total of 24 families are represented within this grassland community.

The *Protea* savanna community is dominated by Poaceae pollen (58%) and Proteaceae (8%) (Figure 7.2b). Spores of the Pteridophyta *Pteridium aquilinum* var. *aquilinum*, a dominant within the grass sward of the *Protea* community, contribute a significant proportion (7%). To a lesser extent Asteraceae (4%), Cyperaceae (3%), Rosaceae (3%), Euphorbiaceae (2%), Hypoxidaceae (2%) and Myricaceae (2%) contribute to the spectrum.

The climax community of the montane region, *Podocarpus* forest, has a high proportion of Poaceae pollen (33%) and Pteridophyta (18%) while the arboreal taxa Podocarpaceae (9%), Ulmaceae (4%), Flacourtiaceae (4%), Rutaceae (4%), Celastraceae (3%) and Sapindaceae (3%) are the next largest pollen contributors to the soil spectrum (Figure 7.3b). There are a total of 36 plant families represented in the soil pollen spectrum of this diverse community. Spores of the Bryophyta family were also observed but are not included in the pollen sum.

7.2.3.2 Sub-alpine Belt

The soil pollen spectrum of the *Leucosidea sericea* scrubland community similarly exhibits a high proportion of Poaceae (41%) and Pteridophyta (10%) pollen (Figure 7.4b). These high values are possibly an over-representation of the dominant grassland taxa due to the inherent problem of using soil samples to determine pollen spectra, namely; the soil samples are usually directly under or next to grass sward species, therefore the sample has an over-representation of locally produced pollen. *Leucosidea sericea* (9%), Rosaceae (other than *L. sericea* - 6%) and Asteraceae (5%) are the other families with pollen influx values greater than 5%. The community is diverse with pollen contributing species coming from 36 different plant families.

The surface soil spectra of the sub-alpine grassland communities all demonstrate a high proportion of Poaceae and Asteraceae pollen with the families Euphorbiaceae, Scrophulariaceae, Liliaceae, Cyperaceae, Pteridophyta, Fabaceae and Crassulaceae present in lower percentages. For *Rendlia altera* grassland, several arboreal taxa, namely Podocarpaceae, Ulmaceae, Flacourtiaceae, Celestraceae, Sapindaceae, Apocynaceae and Cornaceae are represented in the soil spectrum, albeit by values less than 1% (Figure 7.5b). The grassland communities, *Themeda triandra*, 'Mixed' grassland and *Festuca costata* (Figure 7.6b-7.8b) all display high Poaceae values and the remainder of the spectra comprise predominantly of sedges, herbs and annuals. The 'Mixed' grassland community has a relatively high proportion of Anacardiaceae (2%) possibly due to the presence of *Rhus* species in the community.

Poaceae (42%) and Cyperaceae (17%) dominate the low altitude vlei soil pollen spectrum (Figure 7.9b) with Pteridophyta (10%), Asteraceae (5%) and the hygrophilous species *Gunnera perpensa* (Gunneraceae - 4%) contributing significant percentages. Herb species from the Ranunculaceae and Brassicaceae families have pollen values in excess of 2% while a further 22 families produce values less than 2% of the total soil pollen count.

The soil pollen spectrum of the climax community of the sub-alpine region, the sub-alpine fynbos, has a relatively high proportion of the ubiquitous Poaceae pollen (39%) (Figure 7.10b). Next is Ericaceae (13%) principally *Erica ebracteata* and *E. evansii* pollen, and Asteraceae (9%) comprised of the herbs *Helichrysum, Senecio, Macowania, Euryops* and *Stoebe*. 35 plant families contribute to the soil pollen spectrum with, other than the three mentioned above, Pteridophyta (6%), Liliaceae (4%), Rosaceae (3%), and Ranunculaceae, Cyperaceae, Scrophulariaceae, Fabaceae and Thymelaeaceae contributing values of 2% or more of the total soil pollen count.

7.2.3.3 Alpine Belt

For the alpine *Erica-Helichrysum* heathland, *Merxmuellera-Pentaschistis-Festuca* alpine grassland and high altitude vlei communities soil samples are the only available modern pollen rain monitor (Figures 7.12a-c). The alpine grassland soil pollen spectrum, as expected, is dominated almost exclusively by Poaceae pollen (70%). Elements of Asteraceae (8%), Cyperaceae (7%) and Ericaceae (4%) complete the larger pollen influx contributors. The high altitude vlei community also exhibits a large Poaceae (50%) representation in the soil pollen spectrum, with the more hygrophilous Cyperaceae, Eriocaulaceae and Juncaceae taxa contributing 13%, 7% and 3% respectively. Asteraceae (7%) is the other major contributor. The *Erica-Helichrysum* heathland community has a dominance of Ericaceae (55%), Poaceae (18%), Asteraceae (8%), Thymelaeaceae (5%), Cyperaceae (3%) and Crassulaceae (3%) pollen.

7.2.3.4 Summary

What is noticeable from the soil pollen spectra from all the communities, with the possible exception of the *Erica-Helichrysum* heathland, is the dominance of the Poaceae taxon. This dominance is as a consequence of the over-representation of species which overlay the site from which the soil sample is taken. The sampling of a number of randomly distributed soil samples did not remove this over-representation as most soil samples had a grass covering. Therefore it is essential to view the surface soil sample results, not in isolation, but in conjunction with the pollen trap spectra. This over-representation is discussed in more detail in Chapter 8.

7.2.4 TRAP SPECTRA

Pollen trap data allows one to record seasonal or annual fluctuations and to obtain an accurate indication of rates of pollen influx (calculated as grains/cm^2/time unit). This calculation cannot be carried out with surface soil samples which are an average of the pollen influx for an unspecified number of years. The spectra presented and described below (Figures 7.1c-7.10c) are a two year average of the pollen trap data. The seasonal pollen influx (as a relative percentage) is presented in Appendix 7.

7.2.4.1 Annual Spectra

7.2.4.1.1 Montane Belt

The total pollen trap spectra for the two years of sampling display a dominance of Poaceae (50%) and Asteraceae (25%) in the *Themeda*-dominated Highland Sourveld grassland community (Figure 7.1c), while the *Protea* savanna community spectrum displays co-dominance of Poaceae (35%) and Proteaceae (32%) (Figure 7.2c). The increase in Proteaceae values relative to the soil samples is due to the pollen traps being placed above the ground vegetation stratum, and therefore receive more arboreal taxa pollen than soil samples. The relative percentage frequency of Asteraceae (11%) increases in the pollen trap spectrum in comparison to the soil samples. The *Podocarpus* forest trap spectrum (Figure 7.3c) is dominated by Ulmaceae (33%), Poaceae (19%), Podocarpaceae (12%), Sapindaceae (10%) and Pteridophyta (9%). This high Ulmaceae value is due to the high pollen production of *Celtis africana* (Ulmaceae). The dominant arboreal and non-arboreal taxa recorded from the vegetation analysis are reflected by relatively high percentage frequency values in the pollen trap spectra.

7.2.4.1.2 Sub-alpine Belt

The *Leucosidea sericea* scrubland displays an over-representation of the arboreal components, in particular *L. sericea* (56%) (Figure 7.4c). The ground dominant taxa Poaceae (21%) and Pteridophyta (4%) have much reduced values in comparison to the soil spectrum, this is as a consequence of low quantities of pollen being transported above the ground stratum and also due to the inherent problem of proportionality as a consequence of the high *L. sericea* value.

The *Rendlia altera* pollen trap spectrum is dominated by Poaceae (39%) and Asteraceae (27%), also recorded are the arboreal taxa Proteaceae (5%), Podocarpaceae (2%), Ulmaceae (2%), Flacourtiaceae (1%) and to a lesser extent Sapindaceae, Rhamnaceae, Icacinaceae, Celastraceae and Apocynaceae (Figure 7.5c). The *Rendlia altera* grassland community occurs on the Little 'Berg plateau, in this case with a *Protea* savanna on the north west facing slope and a *Podocarpus* forest along the south and south east slopes and valley. Consequently the plateau pollen rain spectrum records pollen grains blown up-valley; in the case of *Rendlia altera* grassland community the pollen from arboreal dominated taxa from both slopes have been recorded. The taxa involved are not represented in the vegetation of the *Rendlia altera* grassland. This phenomenon is discussed in Chapter 8.

The sub-alpine grasslands (Figures 7.6c-7.8c) are once again dominated by Poaceae and Asteraceae with *Themeda triandra* grassland recording values of Poaceae (36%) and Asteraceae (43%), *Festuca costata* grassland recording Poaceae (49%) and Asteraceae (30%) and 'Mixed' grassland recording Poaceae (44%) and Asteraceae (34%). The sub-alpine fynbos trap spectrum (Figure 7.10c) is dominated by Poaceae (22%), Ericaceae (18%), Asteraceae (15%) and Proteaceae (12%), which reflects the arboreal and non-arboreal dominant vegetation taxa. The low altitude vlei is dominated by Poaceae (48%) and to a lesser extent Asteraceae (15%), Pteridophyta (13%) and Cyperaceae (9%) (Figure 7.9c).

7.2.4.2 Seasonal Spectra

7.2.4.2.1 Montane Belt

Throughout the year, grass pollen either dominates or co-dominates the pollen trap spectra of the *Themeda*-dominated Highland Sourveld. During the December-February summer months Asteraceae (44%) species produce proportionally more pollen than Poaceae (35%). No taxa show any distinctive seasonality.

The *Protea* savanna pollen trap data does show some seasonality. Poaceae pollen dominated during the winter months, followed by the flowering of the *Protea* species (*Protea caffra*) from October onwards. This flowering is recorded in the high proportion of *Protea* pollen in the spring and summer spectra and declines during the autumn months when Poaceae and Asteraceae dominate. No other taxa show any distinct seasonality, with most taxa being present in all seasons. This is in contrast to the seasonality observed for some of the arboreal taxa within the *Podocarpus* forest community. *Celtis africana* of the family Ulmaceae flowers during early spring in the forest. This flowering is recorded by the high proportion (± 60-65%) of the total pollen sum during the corresponding sampling periods. During 1988 the species flowered in late August (personal observations) as the high pollen count was recorded in both the June-August and September-November spectra, while in 1989 the species flowered earlier and most of the pollen was recorded during the June-August period. *Allophylus africana* (Sapindaceae) also exhibited distinct seasonality, flowering in November to March (Palgrave, 1983). The flowering was slightly earlier in 1989 than 1988 as the Sapindaceae pollen influx value increased during the September to November spectrum of 1989 continuing into the December-June spectrum, while only the December to February spectrum of the 1988-89 sampling period recorded high Sapindaceae pollen. Generally the remaining taxa produce pollen throughout the year with no major peak periods. The slight variations in the proportion of the total pollen sum with seasons could be due to proportionality as a result of using relative percentage frequencies to calculate the pollen spectrum.

7.2.4.2.2 Sub-alpine Belt

The *Leucosidea sericea* community pollen trap data clearly displays the seasonality of *Leucosidea sericea* flowering. The species flowers during early spring and consequently dominates the June-August spectra of 1988 and 1989. The high proportion of *L. sericea* pollen 'masks' the presence of other taxa, so the Poaceae, Ericaceae and Asteraceae values of actual pollen production appear to be low due to the high proportion of *L. sericea*. The taxa Asteraceae and Pteridophyta show some seasonality, producing pollen/spores during late summer and autumn. Other taxa do not show distinct seasonality.

The *Rendlia altera* grassland community reflects the seasonality of pollen production of the arboreal taxon Ulmaceae originating from the *Podocarpus* forest below the grassland plateau. The proportion of Ulmaceae present during June-August in 1988 and 1989 increases and correlates to the increase observed in the *Podocarpus* forest. Another possible seasonal related value is that of *Protea*, which increases dramatically during September-November of 1988 and 1989. The *P. caffra* of the down-slope *Protea* savanna community flower during this period and with up-slope pollen movement, is recorded in the *Rendlia altera* grassland community trap spectrum. During the two years of study the dominants remain Poaceae and Asteraceae throughout the year with no local taxa displaying any marked seasonality. The high Hypoxidaceae (10.8%) value of December-February 1988-89 appears to be an anomaly.

The three sub-alpine grassland communities of *Themeda triandra*, 'Mixed' and *Festuca costata* show little seasonal variation with Poaceae and Asteraceae taxa dominating throughout and only Anacardiaceae displays some seasonality with increasing pollen influx during the summer December-February period.

Similar results were obtained for the low altitude vlei site, which is dominated by Poaceae and Cyperaceae pollen and Pteridophyta spores throughout the year. There are fluctuations in the proportion that each taxa represents of the total sum, but no distinct seasonality over the two years. The remaining taxa do fluctuate from season to season but in values too low to mark any significant variation.

The lack of seasonal data for sub-alpine fynbos renders it difficult to make any general conclusions, however a distinct rise in Proteaceae pollen during the autumn March-May months of 1989, which is present again in the six months sample of 1990, is observed. The Proteaceae within this community *Protea roupelliae* flower during late summer into autumn (Vogts, 1982) which is reflected in the pollen trap spectra. A further distinct seasonal rise is that of Ericaceae during the June-August 1989 period

7.2.4.3. SUMMARY

The trap spectra present a different picture to that obtained with the soil samples. The over-representation of Poaceae is reduced and the arboreal and Asteraceae taxa become more prominent. Asteraceae, although being predominantly a ground stratum taxa, have a greater pollen representation in the trap spectra especially in the sub-alpine grassland communities. These Asteraceae taxa must be wind transported and as a consequence of the morphology and weight of the pollen grains they are transported out of the ground vegetation stratum. The trap spectra presents arboreal taxa which are under-represented in the soil spectra due to the fact that the pollen is often wind transported some distance from the source and the dominance of Poaceae pollen 'masks' the presence of the taxa present in much lower relative percentage frequencies in the spectra. Seasonality is recorded for a number of taxa and the dominance of that particular taxon or taxa often masks the proportion of other taxa both during that sampling period and, to a lesser extent, in the two-year average pollen trap spectrum.

7.3 ASSOCIATION BETWEEN SPECTRA

7.3.1 INTRODUCTION

Canonical correlation was performed to obtain an objective quantitative value to show association between the two pollen collecting techniques and between the resultant pollen spectra and the vegetation spectra of the community from which they were collected.

7.3.2 CANONICAL CORRELATION ANALYSIS

The canonical correlations between the three data sets was high and confirms earlier studies (described in Chapters 3 and 4) recognizing the association between pollen rain and vegetation. Results are summarized in Table 7.1.

Table 7.1 Canonical correlation values of pollen trap, soil and vegetation spectra compared with one another.

Vegetation Community	Trap/Soil	Trap/Vegetation	Soil/Vegetation
Highland Sourveld	0.931	0.901	0.939
Protea savanna	0.683	0.872	0.588
Podocarpus forest	0.556	0.766	0.408
Rendlia altera grassland	0.859	0.856	0.919
Leucosidea sericea scrubland	0.476	0.882	0.625
Themeda triandra grassland	0.806	0.761	0.884
'Mixed' grassland	0.845	0.847	0.871
Festuca costata grassland	0.891	0.897	0.919
Sub-alpine fynbos	0.709	0.674	0.514
Low altitude vlei	0.954	0.701	0.797
Alpine grassland	-	-	0.692
Erica-Helichrysum heathland	-	-	0.748
High altitude vlei	-	-	0.939

Most communities display a strong correlation between vegetation and soil spectra. The *Podocarpus* forest, *Leucosidea sericea* scrubland, sub-alpine fynbos, *Protea* savanna and alpine grassland do not display as high a correlation. The two stratum vegetation communities do not produce a good vegetation-soil spectra correlation due to the over-representation of the ground taxa and the fact that possibly a large proportion of the arboreal pollen is wind transported and may be removed from the source region before reaching the ground. The 0.692 correlation of alpine grassland, although not a poor correlation, is not as strong as some of the other correlations possibly as a consequence of Asteraceae and Cyperaceae taxa not being well represented in the soil spectrum. The taxa Ericaceae, Juncaceae and Crassulaceae, although present in relatively small percentages in the vegetation spectrum, contribute significantly higher proportion of the soil pollen spectrum possibly as a consequence of being high pollen producers. Furthermore the soil pollen spectrum of the alpine grassland has a greater taxa diversity than the actual vegetation spectrum implying that the pollen source region is larger and that regional pollen plays an important role within the soil pollen spectrum of this community.

The correlation between pollen traps and vegetation spectra is also high, with the exceptions being sub-alpine fynbos and low altitude vlei. What is evident is that the stratified vegetation communities of *Podocarpus* forest, *Leucosidea sericea* scrubland, *Protea* savanna and sub-alpine fynbos have a better correlation between traps and vegetation, than between soil and vegetation as a consequence of the arboreal taxa pollen being collected by the traps. The over-representation of the ground taxa is reduced and the traps seem to reflect the surrounding vegetation more comprehensively. The reverse seems to be true for the montane and sub-alpine grassland communities which show higher soil/vegetation correlations than the trap/vegetation combination. Despite this the correlation values are high, suggesting that the pollen trap spectra are good indicators of the existing vegetation within a particular community.

The trap against soil pollen spectra correlation analysis provides a good indication of the usefulness of the modern pollen rain collecting techniques and allows for a comparison of the two techniques. There is a good correlation between the two techniques with regards to the grassland communities and slightly less so for the communities with a predominance of arboreal taxa. The weakest correlation (0.476) is obtained from the *Leucosidea sericea* scrubland, possibly due to the discrepancy between the soil and trap pollen spectra with regards the proportion of *Leucosidea sericea* pollen. The traps record values of up to 60%, while the soil has a value of less than 10% (Appendix 7).

An anomaly with regards to the low altitude vlei correlation values is recorded. Both the soil and trap spectra show weak correlations with the vegetation of the community, 0.797 and 0.701 respectively, while the correlation between the soil and trap spectra is high, 0.954. The soil and trap spectra display a high proportion of Poaceae, Asteraceae and Pteridophyta pollen grains and spores and lower Cyperaceae values, whereas the vegetation spectrum has high Cyperaceae and lower Poaceae, Asteraceae and Pteridophyta values. Therefore in this community the grasses are producing a high proportion of the pollen which is reflected in the pollen spectrum. The low *Protea* savanna (0.683), *Podocarpus* forest (0.556) and sub-alpine fynbos (0.709) correlations are a consequence of the discrepancy between the soil and trap spectra caused by the over-representation of ground taxa in the soil spectra of these communities.

Canonical correlations of the individual seasonal pollen trap spectra were calculated for each vegetation community (Appendix 8). There is a close association (>0.75) between seasons for the *Themeda*-dominated Highland Sourveld and the four sub-alpine grassland communities. With regards to the other communities, the *Protea* savanna displays some seasonality with a close correlation between the corresponding seasons over the two year sampling period. The winter and spring periods have correlation values of 0.93 and 0.95 for the corresponding months over the two years, while the correlation is as low as 0.55 between summer and winter of 1988-89. The autumn and winter periods have correlations of 0.63 and 0.62 respectively against the spring months.

Both the *Podocarpus* forest and *Leucosidea sericea* communities exhibit some seasonality with correlation values as low as 0.125 between certain seasons, whilst a correlation of 0.90 was calculated for the same season over the two years. In both communities the highest correlation is between the corresponding autumn and winter months when pollen production is at its lowest. During the spring and summer periods, when more pollen is produced and dispersed, the diversity is greater and will vary from year-to-year, therefore the correlations are not as strong (0.65-0.90). Correlation values for low altitude vlei are relatively good between all seasons, while the sub-alpine fynbos has low correlations between autumn and winter and winter and spring of 1989.

Canonical correlations were calculated to determine the association between the two years of study to aid in the understanding of the pollen influx values (Appendix 8). Results concluded that there was very little annual variation in pollen influx from all the communities despite large fluctuations in pollen influx values for corresponding seasons over the two years. All the correlations are of a value greater than 0.90 (other than *Podocarpus* forest) indicating a close association between the annual pollen trap spectra for all the montane and sub-alpine vegetation communities.

7.3.3 SUMMARY

A close correlation between the two pollen collecting techniques and between the techniques and the vegetation are obtained via canonical correlation analysis. The discrepancies or low association/correlation values can be related to the influence of the height and dispersal of, in particular, the pollen of arboreal taxa. No marked seasonality can be determined, with the use of canonical correlation analysis, for the montane and sub-alpine grasslands, possibly as a consequence of the all year dominance of Poaceae. The remaining communities all displayed some seasonality, in particular the *Podocarpus* forest and *Leucosidea sericea* scrubland. A high association (greater than 0.8) is obtained for all vegetation communities when correlating the annual pollen influx spectra, suggesting that overall there is a low annual pollen influx fluctuation for the studied communities.

7.4 COMMUNITY CLASSIFICATION - TWINSPAN

7.4.1 INTRODUCTION

The vegetation, soil and pollen trap samples were classified according to two-way indicator species analysis (TWINSPAN). This classification technique divides the complete data sets into distinct groups on the basis of differences between the various samples or groups of samples. This 'grouping' of samples allows one to observe the homogeneity of the samples and how distinctive are the samples to a particular grouping which in this case represents a vegetation community or a number of communities with similar taxa composition. The TWINSPAN division process was terminated at the six group level as additional variance, explained by subsequent divisions, was low and caused the division of particular communities into meaningless groups. The results of TWINSPAN are represented as dendrograms (Figures 7.13-7.15). If a sample size or 'grouping' of five (5) or greater was obtained within a split into a particular group then it was acknowledged in the dendrogram.

7.4.2 Vegetation

As sampling was performed in distinctive vegetation communities the final 'groups' should reflect this and a mixture of groups together at level six is indicative of communities with similar species composition. The vegetation TWINSPAN dendrogram (Figure 7.13) reflects the homogeneity of the studied vegetation communities with most quadrats from a community being representative of that community. The most heterogenous community, based on TWINSPAN output, is the *Themeda*-dominated Highland Sourveld with only twenty-two of the twenty-five quadrates distinctive of that community, while the remaining quadrats were dispersed between the groups of the other communities. The *Protea* savanna and *Themeda*-dominated Highland Sourveld remain grouped together after level 6. This is as a consequence of the understorey vegetation of the *Protea* community having a similar species composition as that of the *Themeda*-dominated Highland Sourveld. A similar situation arises with the *Themeda triandra* and 'Mixed' grassland communities which have a number of species common to both.

The *Podocarpus* forest community divides off at level 1 of the vegetation analysis dendrogram, as a consequence of it's species, mostly arboreal taxa, not being represented in any of the other vegetation communities. Level 2 divides the three alpine communities from the remaining communities. The *Erica-Helichrysum* heathland is split at level 3 and high altitude vlei and alpine grassland are divided at level 4. Of the remaining montane and sub-alpine communities the low altitude vlei is separated at level 3. Level 4 has the division of *Festuca costata* grassland and sub-alpine fynbos. These two communities are grouped together due to the species *Festuca costata* dominating the ground vegetation layer of both communities, albeit to a lesser extent in the fynbos. These two communities are divided at level 5. At level 5 the 'woody' *Protea* and *Leucosidea sericea* communities plus *Themeda*-dominated Highland Sourveld is split from the remaining sub-alpine grasslands. *Leucosidea sericea* community is divided at level 6 from the *Protea* and *Themeda*-dominated Highland Sourveld communities. The *Rendlia altera* grassland is divided from *Themeda triandra* and 'Mixed' grasslands at level 6.

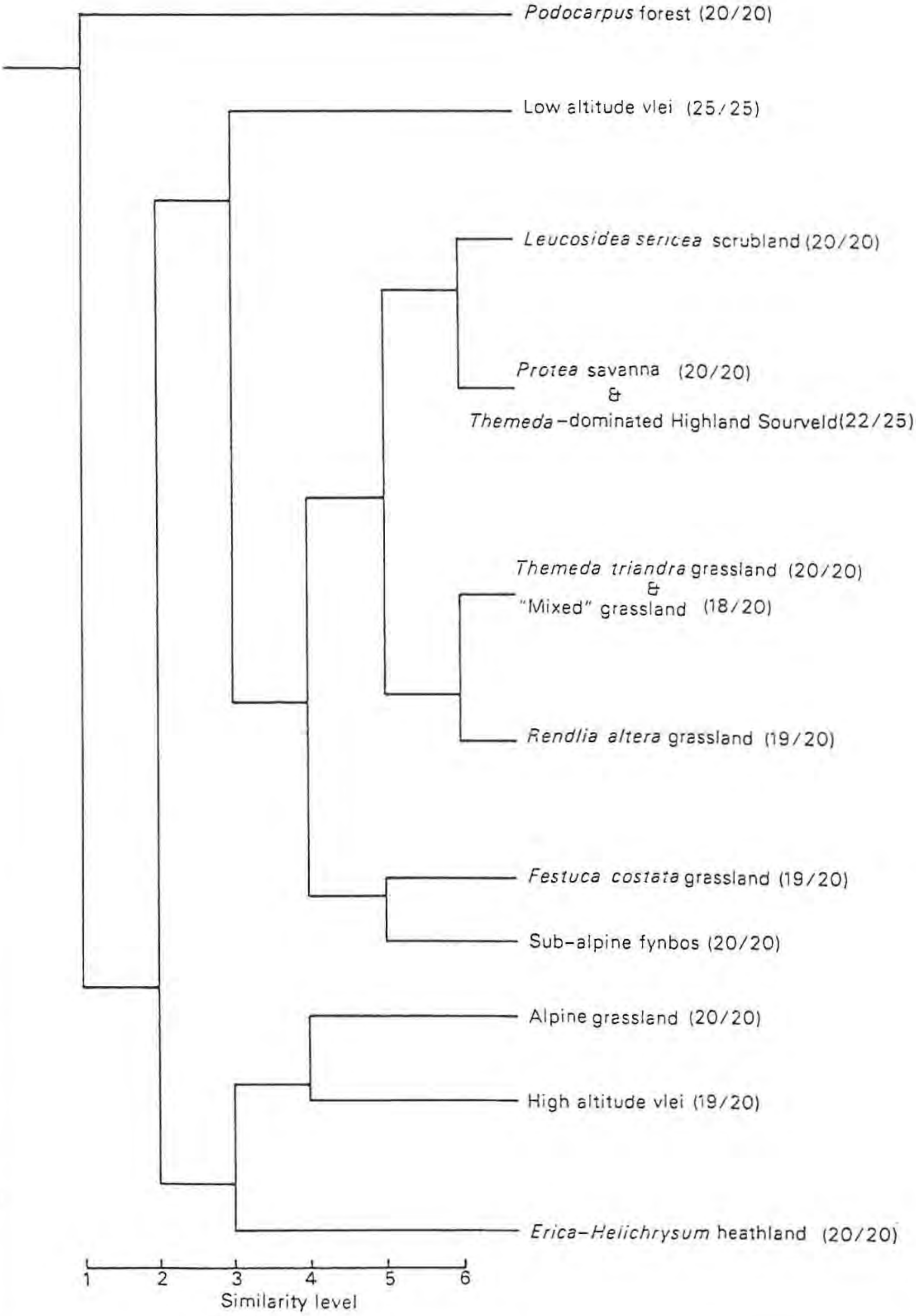


Figure 7.13 TWINSPAN dendrogram of the vegetation data. The bracketed values represent the number of samples out of the total sample size which are classified together at level 6.

7.4.3 Pollen Trap Data

For the pollen trap data (Figure 7.14) level 1 division is the *Podocarpus* forest split, while level 2 division results in the *Leucosidea sericea* and low altitude vlei communities being separated. Only nine out of a total of twenty-seven pollen trap spectra constitute the low altitude vlei within this grouping. This clustering is due to the presence of *Leucosidea sericea* pollen in the low altitude vlei pollen traps, which is derived from a few *Leucosidea sericea* trees which grow alongside the watercourse surrounding the south-east side of the vlei. As a result these pollen spectra are dominated by *Leucosidea sericea* pollen and therefore the relative percentage frequency classifies these samples with the *Leucosidea sericea* community. The two communities are separated at level 3. For the remaining communities level 3 division splits the 'fynbos' element from the grassland communities (including the rest of the low altitude vlei grouping). Both the sub-alpine and *Protea* communities have a relatively high proportion of Proteaceae, Ericaceae and Scrophulariaceae pollen which results in them being grouped together. They are divided at level 4. Level 4 also splits *Rendlia altera* grassland and the remaining low altitude vlei from the grassland communities. These low altitude vlei samples display high Cyperaceae and Poaceae relative percentage frequencies. The *Rendlia altera* and vlei sites both have Cyperaceae as a dominant pollen producer in the pollen trap spectra. The 'Mixed' and *Festuca costata* grassland pollen trap spectra are divided from *Themeda triandra* grassland, *Themeda*-dominated Highland Sourveld and a few (6/35) *Festuca costata* grassland pollen spectra. These grassland communities all exhibit very similar pollen trap spectra and rather than splitting these communities further (level 6) they could be classified together as the last division is based on the presence and/or absence of taxa present in low quantities in the spectra. This linking at level 6 is indicative or points towards the fact that the spectra of these communities are not distinctive enough to be used as indicators of particular vegetation communities based on the TWINSPAN analysis.

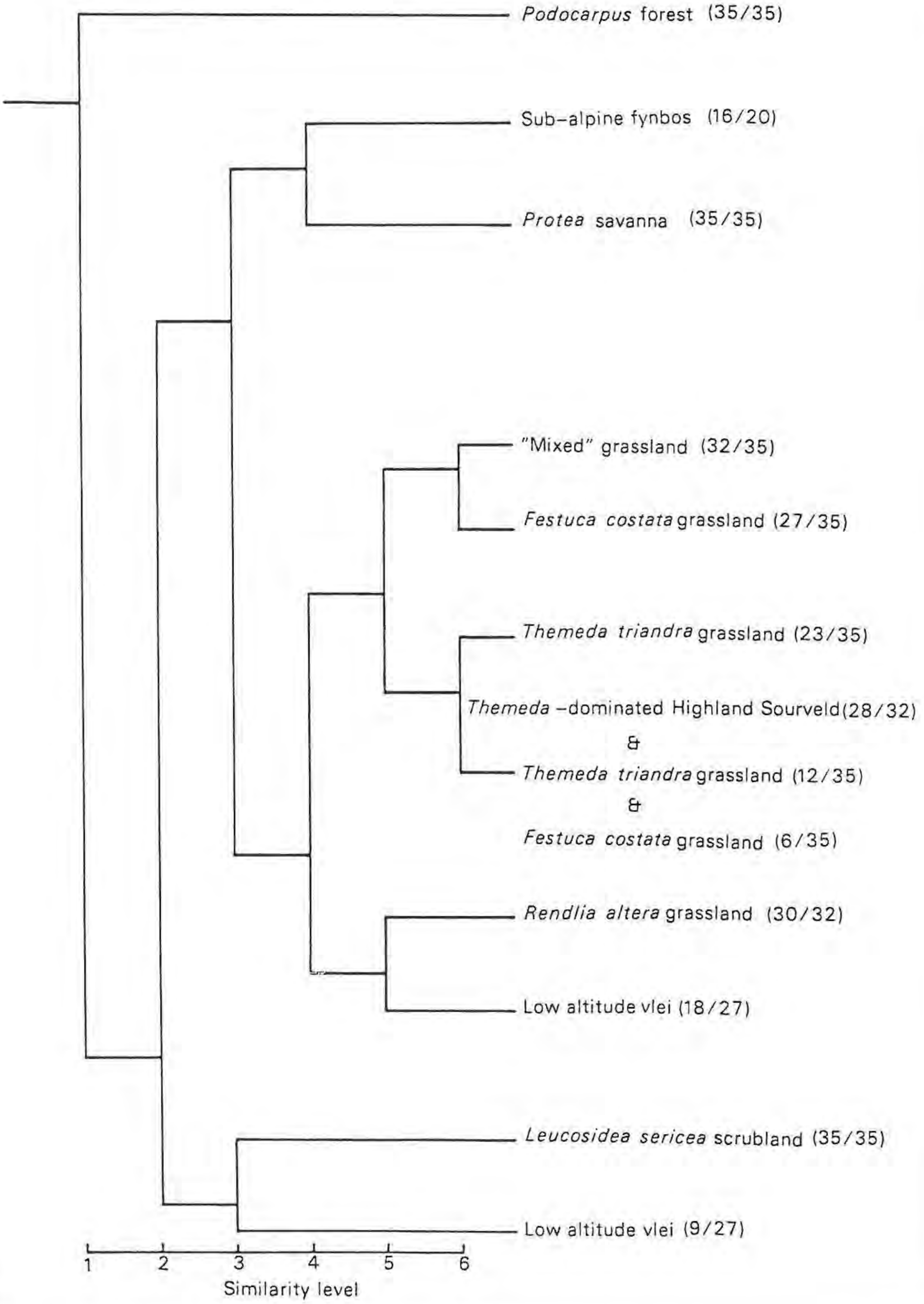


Figure 7.14 TWINSPAN dendrogram of the pollen trap data. The bracketed values represent the number of samples out of the total sample size which are classified together at level 6.

7.4.4 Surface Soil Data

As with both the vegetation and pollen trap dendrograms the *Podocarpus* forest community is the first group to be split away in the surface soil pollen sample TWINSPAN dendrogram (Figure 7.15). Level 2 division is not as distinct as in the two previous diagrams. The two resultant groups are a 'woody' component of *Leucosidea sericea, Protea* savanna and sub-alpine fynbos plus *Themeda triandra* and most (14/20) of the 'Mixed' grassland samples, while the other grouping is predominantly grass, sedge and herb communities. Dealing with the former group; the sub-alpine fynbos and *Leucosidea sericea* scrubland are grouped together at the level 3 split due to a similar Poaceae:Asteraceae ratio (4.1:1 for *Leucosidea* and 4.3:1 for fynbos) and Rosaceae, Pteridophyta, Cyperaceae, Euphorbiaceae and Scrophulariaceae pollen percentages. They are split at level 4.

The *Protea* community is grouped with *Themeda triandra* and 'Mixed' grassland due to the similarity of their soil pollen spectra particularly with regards to the Poaceae, Asteraceae and Pteridophyta taxa. The *Protea* community is split at level 4 by the high *Protea* pollen values and the two grassland communities are split at level 5.

The other half of the level 2 split has low altitude vlei, due to high Cyperaceae and Pteridophyta values, dividing from the remaining communities at level 3. Level 4 divides the alpine communities and *Festuca costata* grassland from the *Rendlia altera* grassland, *Themeda*-dominated Highland Sourveld and, a few samples (5/20) of 'Mixed' grassland. The latter grassland group is divided at levels 5 and 6. *Erica-Helichrysum* community is split from the other communities at level 5 due, in part, to high Ericaceae and Thymelaeaceae values and *Festuca costata* grassland is divided from alpine grassland and high altitude vlei at level 6. This is an instance were a seventh division could have been implemented to divide these two alpine communities. A comparison between the three dendrograms is discussed in Chapter 8.

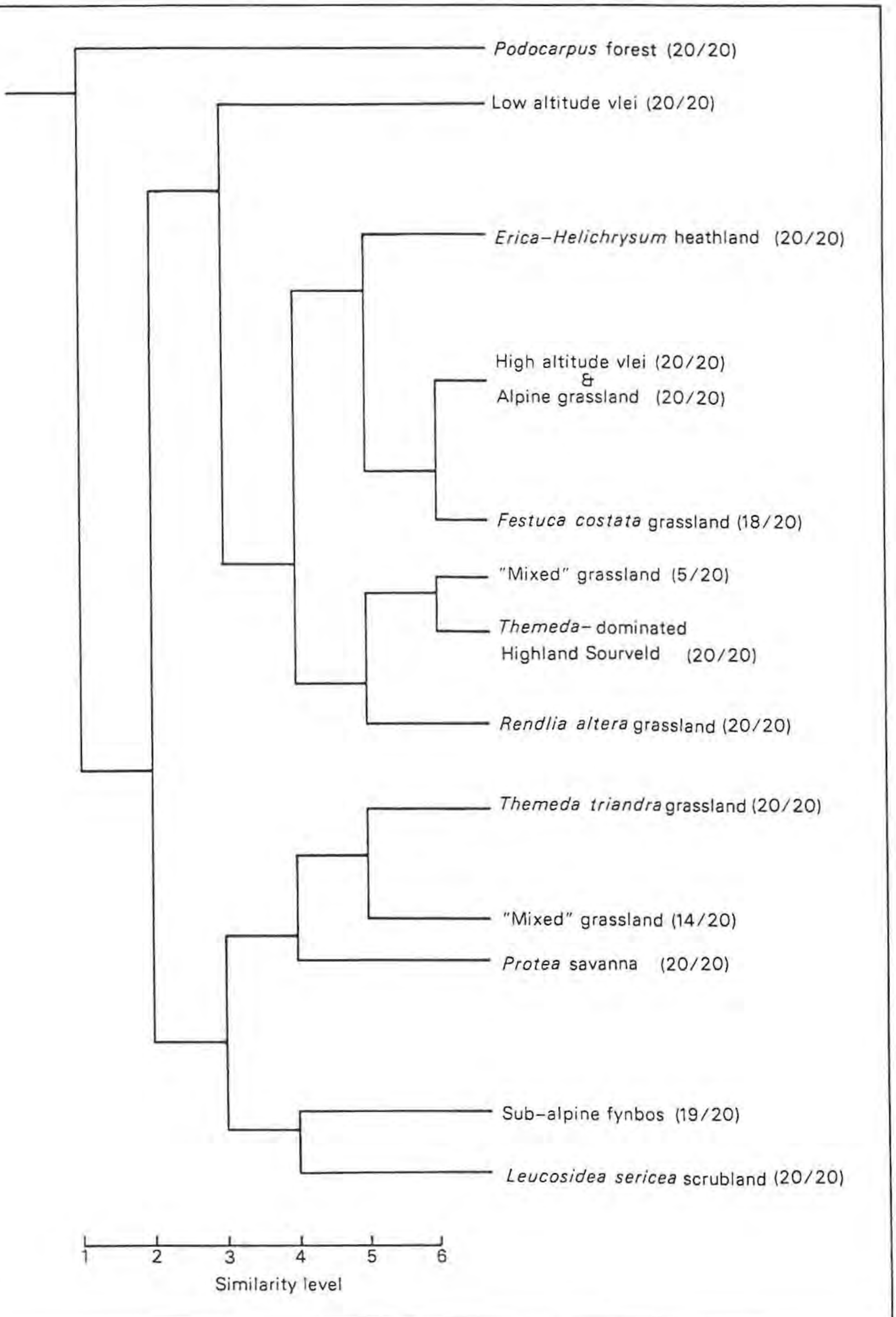


Figure 7.15 TWINSPAN dendrogram of the soil pollen data. The bracketed values represent the number of samples out of the total sample size which are classified together at level 6.

7.5 COMMUNITY ORDINATION

7.5.1 INTRODUCTION

The statistical tests of detrended correspondence analysis (DECORANA) and principal components analysis (PCA) were carried out to ordinate the data and to observe the resultant clustering of samples. Whereas the classification technique TWINSPAN divided the samples according to differences, the two ordination techniques tend to group or cluster samples according to their similarities. Therefore a clustering of samples is indicative of a similarity between them which can be related to the initial vegetation community from which the samples were collected. A clustering of the pollen spectra from a single vegetation community is indicative of the fact that all the spectra are distinctive and represent that community.

7.5.2 DECORANA

The ordination programme detrended correspondence analysis (DECORANA) was applied to compliment the TWINSPAN classification technique. The first two DECORANA components are plotted against each other allowing for a visual comparison of the various samples (Figures 7.16-7.18) and in each instance two graphs were plotted. The upper graph represents all the points of that particular data set, while the lower graph plots the centroid values of each community. The centroid value is not necessarily in the centre of most of that particular communities samples as a number of anomalies may exist which will 'shift' the centroid values. These anomalies have not been removed from the data sets. The three sets of results are subjectively compared to each other so as to observe grouping or clustering of samples, as it is not possible to overlay the three plots.

7.5.2.1 Vegetation

The vegetation analysis plot displays distinct grouping of most of the vegetation communities studied, however there is some overlap of the grassland dominated communities (Figure 7.16). The three alpine communities form a separate group from the rest of the communities, as does the 'woody' components *Podocarpus* forest, sub-alpine fynbos and *Leucosidea sericea* scrubland. The low altitude vlei community is also grouped as a separate entity. The communities which overlap and therefore have similar species compositions are the *Rendlia* *altera* grassland with *Themeda triandra* grassland, *Protea* savanna with *Themeda*-dominated Highland Sourveld, and *Festuca costata* grassland with 'Mixed' grassland. This grouping of communities do not reflect the same clustering pattern as the TWINSPAN. Whereas the TWINSPAN divides all the samples into units on the basis of distinct species, the DECORANA process combines samples depending on common species. Therefore the three above mentioned groups include vegetation communities which are closely associated on the basis of species/family taxa composition.

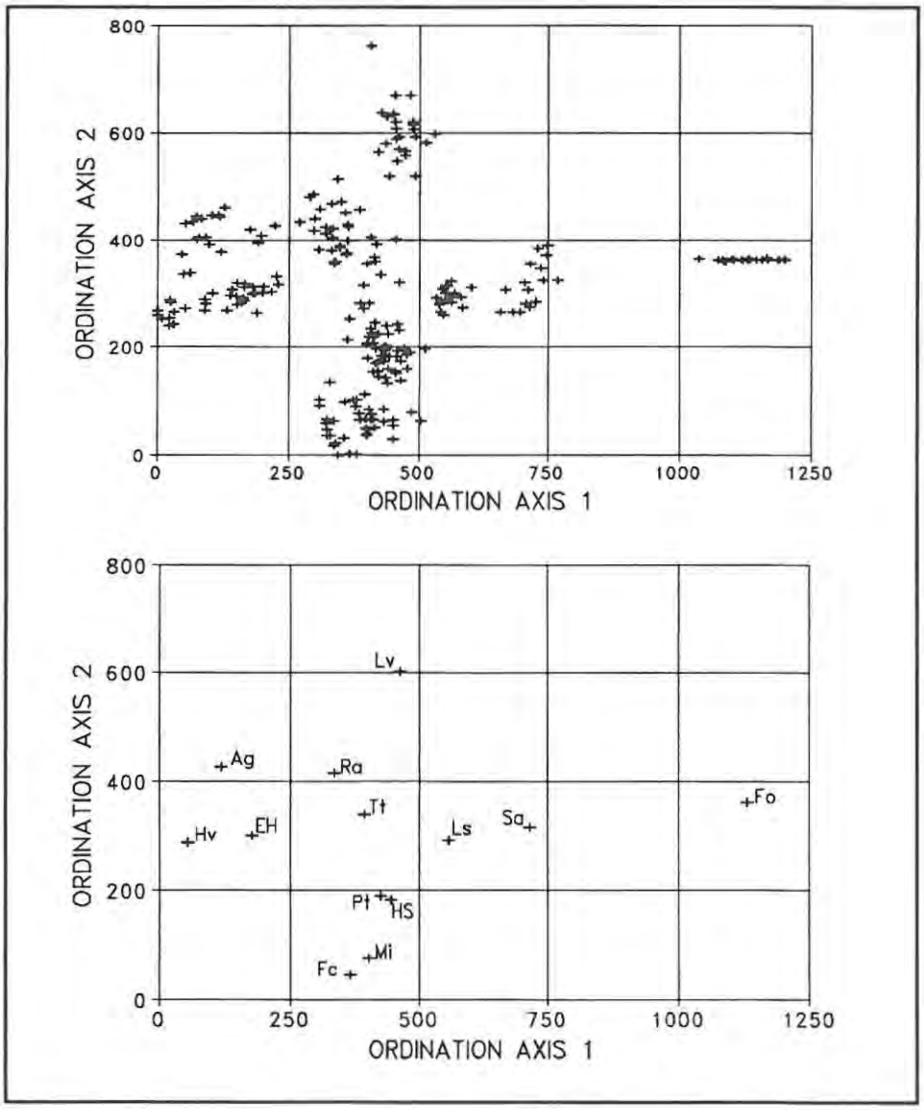


Figure 7.16 DECORANA plot of the vegetation data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos, Lv-Low altitude vlei, Ag-Alpine grassland, EH-*Erica-Helichrysum* heathland and Hv-High altitude vlei.

7.5.2.2 Surface Soil Data

The DECORANA plot of the surface soil data shows *Podocarpus* forest, *Leucosidea sericea*, sub-alpine fynbos and *Erica-Helichrysum heathland* communities as separate entities (Figure 7.17). All the remaining communities, based on their soil pollen spectra, are closely associated. The low altitude vlei community does show separate grouping possibly as a result of higher Cyperaceae and Gunneraceae pollen influx than the other communities. The alpine communities of high altitude vlei and alpine grassland, plus all the sub-alpine and montane grasslands and *Protea* savanna are associated as a consequence of the high proportion of Poaceae, Asteraceae and to a lesser extent the 'herb taxa' Euphorbiaceae, Scrophulariaceae, Fabaceae and Iridaceae pollen present in the soil spectra. These communities could be separated if the soil pollen was identified to species or even genera level, resulting in a plot not unlike the vegetation data. However the lack of South African pollen reference work and the fact that without the aid of a scanning electron microscope it is often not possible to distinguish between many Poaceae and Asteraceae genera has ensured that the modern pollen spectra have remained, predominantly, at the family taxa level.

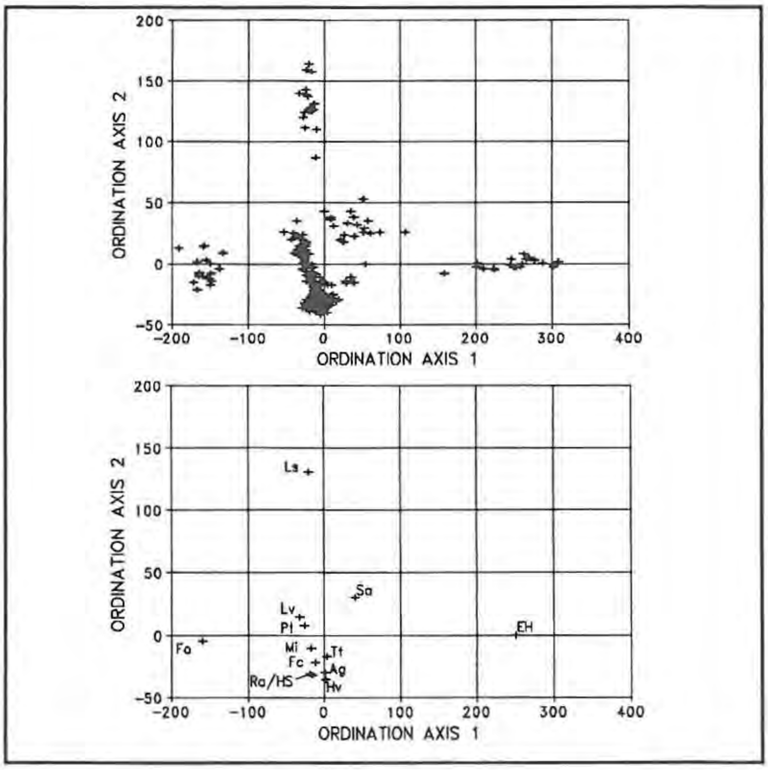


Figure 7.17 DECORANA plot of the soil pollen data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos, Lv-Low altitude vlei, Ag-Alpine grassland, EH-*Erica-Helichrysum* heathland and Hv-High altitude vlei.

7.5.2.3 Pollen Trap Data

A similar picture emerges for the pollen trap data (Figure 7.18) with the *Podocarpus* forest, *Protea* savanna, sub-alpine fynbos, low altitude vlei and *Leucosidea sericea* communities forming distinct groups. The *Leucosidea* community forms two groups due to the seasonal nature of it's pollen production. Two distinct pollen spectra obtained for the community per annum are a winter/spring grouping, caused by the high *Leucosidea sericea* pollen production during these seasons, and a summer/autumn grouping of the more 'usual' Poaceae/Asteraceae pollen influx. All the other communities are grouped together so as to make it impossible to observe any distinct groups. This large group is as a consequence of the large proportion of Poaceae dominating the spectrum, as was the case with the soil samples.

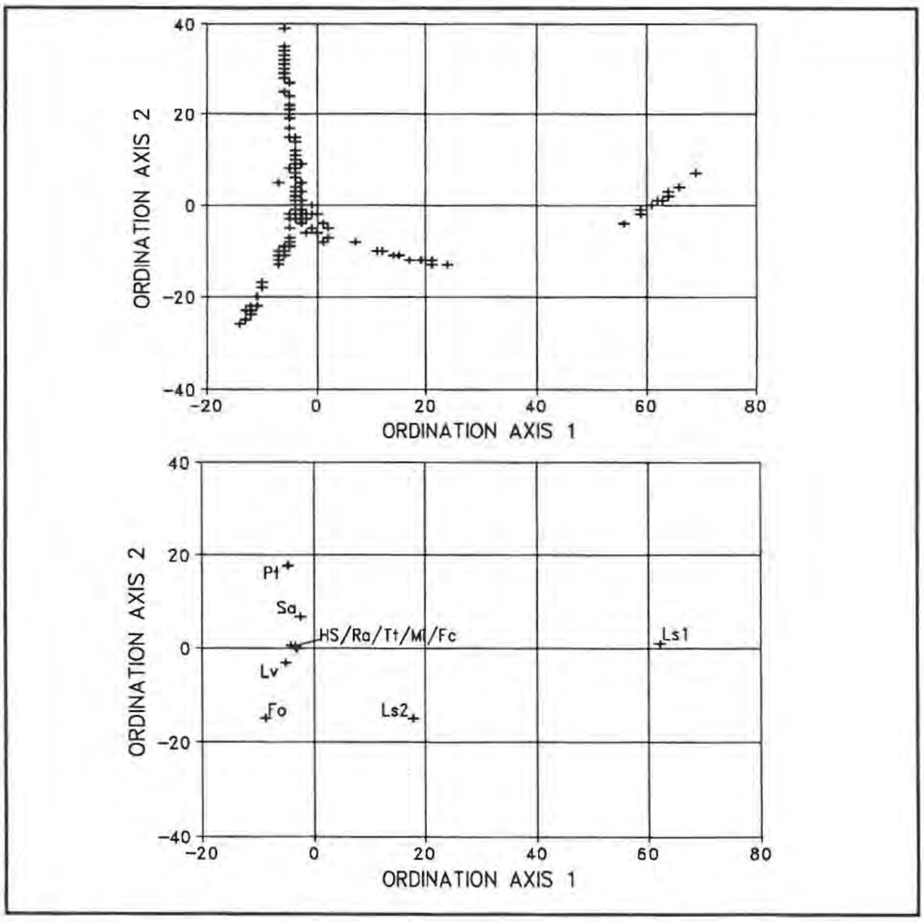


Figure 7.18 DECORANA plot of the pollen trap data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls1-*L.sericea* scrubland winter/spring samples, Ls2-*L. sericea* scrubland summer/autumn samples, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos and Lv-Low altitude vlei.

7.5.2.4 Summary

The DECORANA plots cluster samples together according to similarities, in particular the resultant plot of the vegetation data displays the homogeneity of the samples with particular communities formed by a cluster of samples taken from that community. The pollen plots are not as distinctive although the communities, *Podocarpus* forest, *Leucosidea sericea* scrubland, sub-alpine fynbos and *Erica-Helichrysum* heathland are distinctive, while the remaining communities, although retaining some individual identity are clustered close together as a consequence of the similarities between taxa composition and relative percentage values.

7.5.3 PRINCIPAL COMPONENTS ANALYSIS (PCA)

Principal components analysis (PCA) was performed on the vegetation, soil and pollen trap samples to establish whether there is any group structure in the data sets. The results are graphically represented (Figures 7.19-7.21) plotting the first two principal components. As with the DECORANA plots in each case all the data points were initially plotted and thereafter a further plot was constructed using only the centroid values for each community grouping.

7.5.3.1 Vegetation

The vegetation communities were identified prior to sampling as homogenous units and therefore are reflected as such in the PCA plot. The vegetation plot (Figure 7.19) has a distinct *Leucosidea sericea*, *Festuca costata* and 'Mixed' grassland grouping. The *Themeda triandra* grassland, *Protea* savanna, *Rendlia altera* grassland and *Themeda*-dominated Highland Sourveld communities can be grouped together, due to the presence of the grassland elements in the communities. This grouping is more obvious in the plot of all the vegetation data points than in the centroid plot graph. Despite the centroid values of these four communities being separated, there is an agglomeration of the individual data points which proves the close affinity between these communities based on species composition as produced by PCA. The vegetation PCA plot, although not exhibiting a similar pattern to the DECORANA vegetation plot, does show similar trends. Although the forest community samples are grouped close together they are in close association with the sub-alpine fynbos and alpine communities. The three alpine communities are grouped together and no distinction can be made between the samples. The centroid values of *Protea* savanna and the montane and sub-alpine grasslands are widely spaced, although the actual samples overlap each other, confirming the affinities between these communities on the basis of taxa composition.

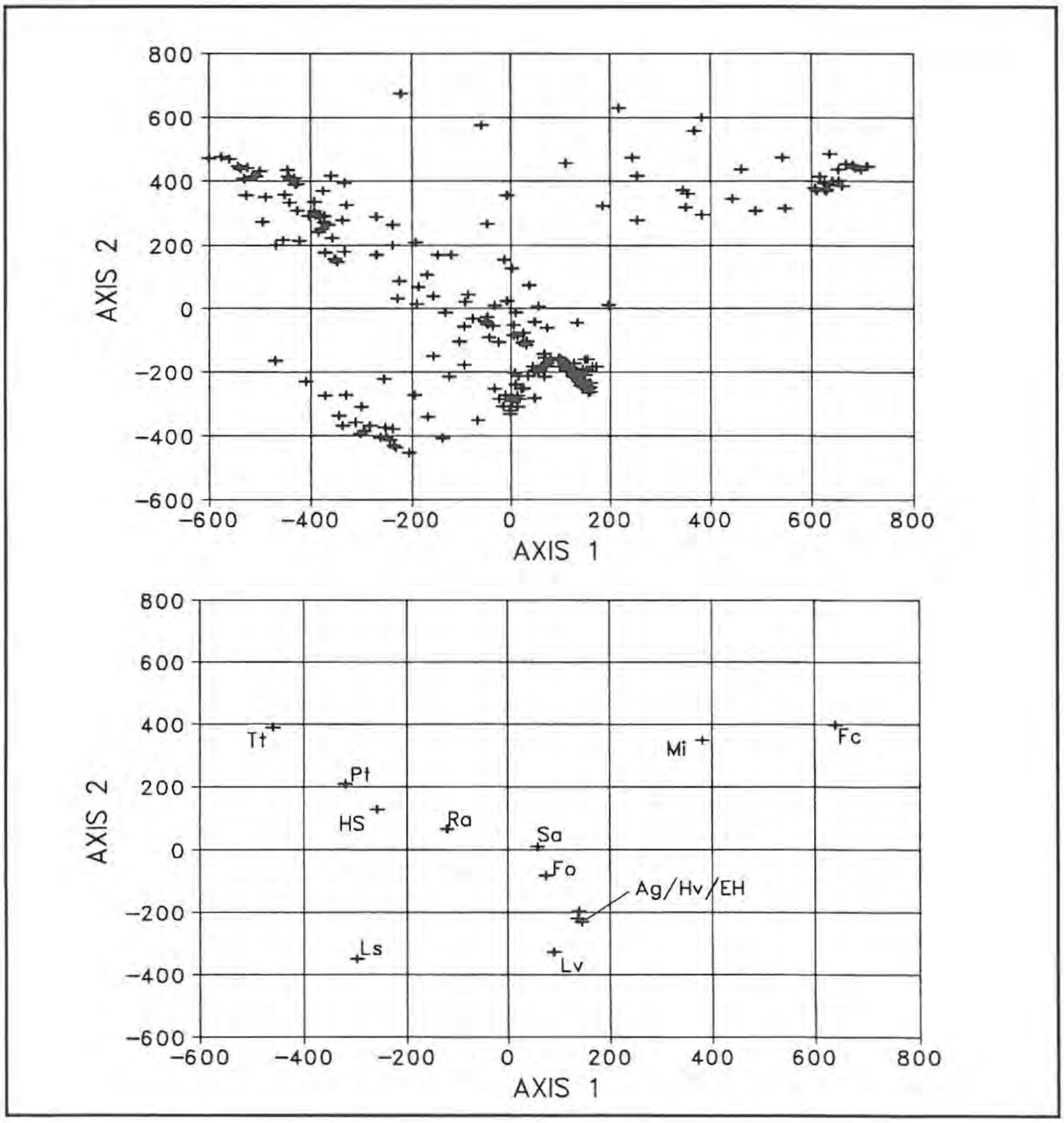


Figure 7.19 Principal components analysis plot of the vegetation data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos, Lv-Low altitude vlei, Ag-Alpine grassland, EH-*Erica-Helichrysum* heathland and Hv-High altitude vlei.

A group diversifying from this agglomeration and slightly less concentrated represents the low altitude vlei community. The vlei community shares Cyperaceae and some Poaceae elements with the alpine communities, but is distinct enough to warrant being classified as a separate homogenous unit. Most samples within a group have similar plot coordinates showing that these samples are closely associated. An anomaly to this observation is the 'Mixed' grassland community. Although all the samples within the defined group represent the community in question, they are not situated in close proximity to each other, indicating some heterogeneity of the community. The 'Mixed' grassland community has elements from both the *Themeda triandra* and *Festuca costata* grasslands with an invasion of woody species, for example *Rhus*. Therefore the samples are widely spaced on the PCA plot as some species exhibit more *Themeda* or more *Festuca* grassland affinities, although the 'Mixed' grassland community still represents a grouping and retains some distinctiveness from the other communities.

7.5.3.2 Surface Soil Data

The PCA plot of the soil pollen data (Figure 7.20) exhibits two homogenous units separated from the other communities, namely *Podocarpus* forest and low altitude vlei. All the other soil samples, on the basis of their soil pollen spectra, are clustered together. At the top of this grouping, albeit marginally, the high altitude vlei samples are concentrated. The vlei shares many pollen types with the rest of the grouping, however due to the relatively high percentage of Eriocaulaceae pollen the soil samples are set slightly apart. Below this grouping is a concentration of *Leucosidea sericea* community samples distinctive due to the high proportion of *Leucosidea sericea* pollen, but in close association with the other samples due to the presence of Poaceae and Asteraceae pollen from the understorey vegetation. Below this are the alpine region communities and sub-alpine fynbos. The fynbos community is present due to high Ericaceae pollen which the alpine communities display, particularly the *Erica-Helichrysum* heathland. Next is a concentration of the grassland communities; 'Mixed', *Festuca costata*, Highland Sourveld and *Rendlia altera* grasslands. Towards the lower end of the agglomeration of samples a group of soil pollen spectra representing the *Themeda triandra* grassland community are positioned. These spectra share the affinities with the above grasslands as well as with the *Protea* savanna community which forms a group at the base of the agglomeration. The *Protea* savanna community forms a separate group as a consequence of the high percentage of Proteaceae pollen and lower Poaceae values.

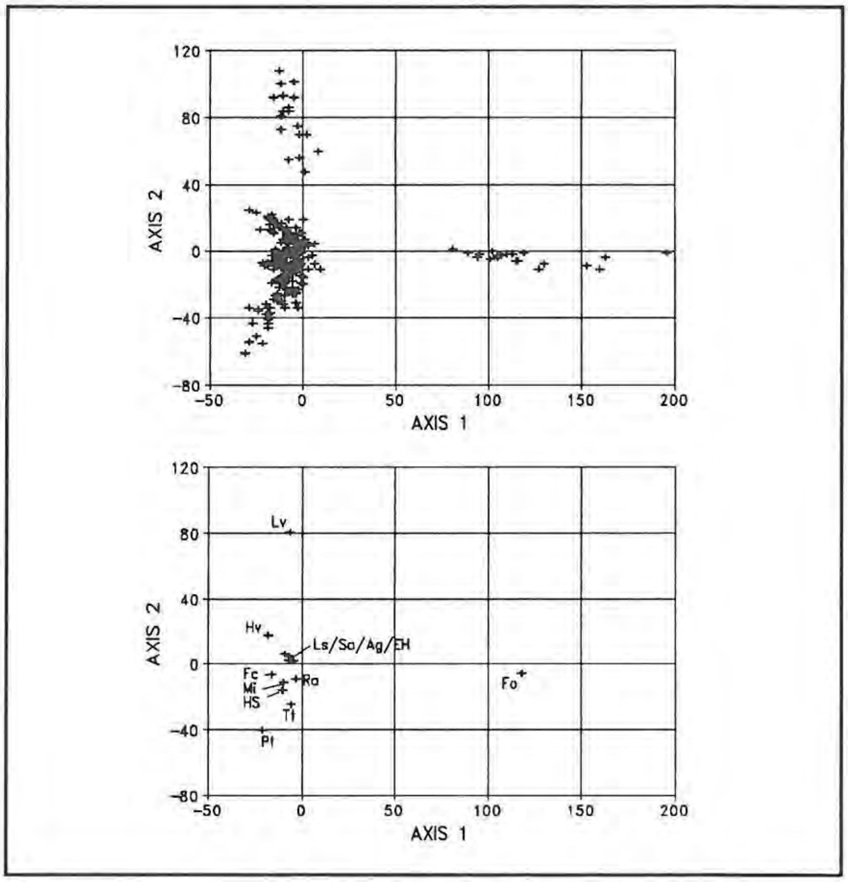


Figure 7.20 Principal components analysis plot of the soil pollen data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos, Lv-Low altitude vlei, Ag-Alpine grassland, EH-*Erica-Helichrysum* heathland and Hv-High altitude vlei.

7.5.3.3 Pollen Trap Data

The PCA plot of pollen trap data shows (Figure 7.21) a somewhat clearer picture than the soil data as the over-representation of Poaceae is removed. The *Podocarpus* forest forms a distinct unit due to the high proportion of arboreal pollen unique to this community. The *Leucosidea sericea* scrubland community does exhibit a disjunct distribution of trap samples which reflects the seasonality in pollen rain experienced, however this seasonality is not as exaggerated as was the case with the DECORANA analysis, therefore a single centroid value has been plotted. The plotting of a single value has 'shifted' the plot away from the greater *L. sericea* data point concentration and closer to the other data points. This 'shifting' is as a consequence of a number of *L. sericea* samples, during non-flowering of *L. sericea*, having closer affinities with the grassland communities. The ground stratum vegetation dominates these spectra and are not masked by a high *L. sericea* pollen value. The *Protea* savanna and *Leucosidea sericea* scrubland communities have a number of samples separated into an obvious group, however a few samples are present in the area of high concentration of samples. This group of samples represents the grassland communities. The five montane and sub-alpine grassland communities have samples grouped in this crescent shaped area and no obvious clustering of individual communities is evident. At the base of this concentration are a few low altitude vlei trap spectra which are separated due to their high Cyperaceae pollen percentages.

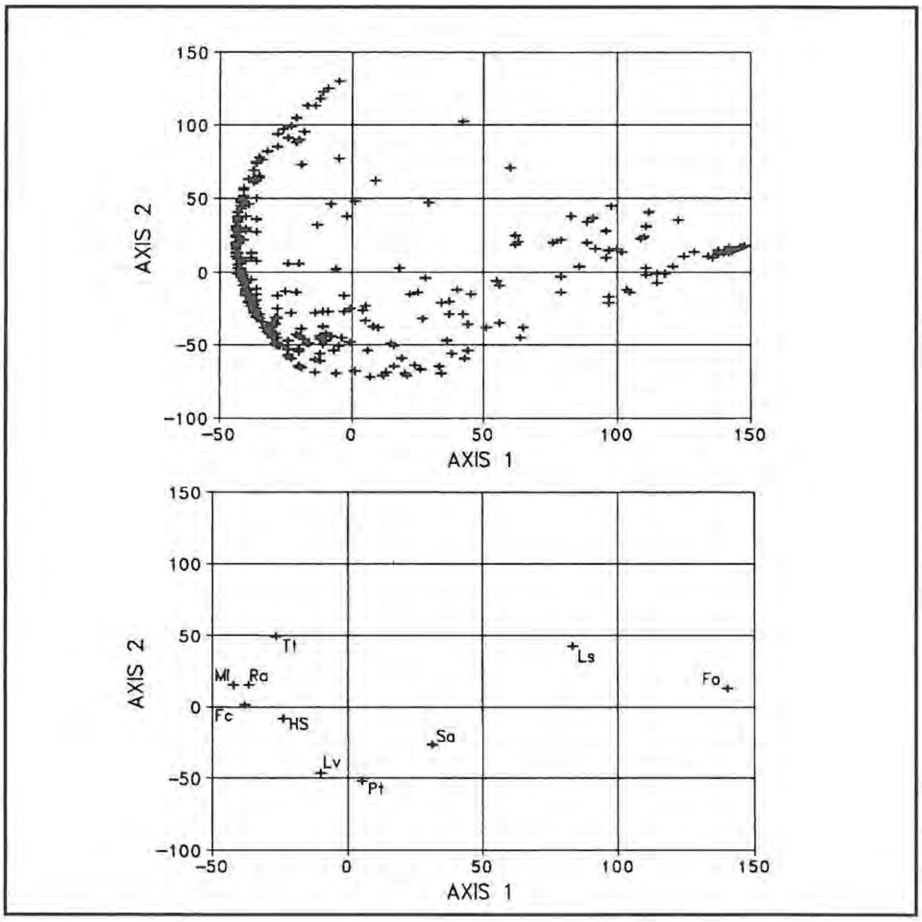


Figure 7.21 Principal components analysis plot of the pollen trap data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos and Lv-Low altitude vlei.

7.5.3.4 Summary

The PCA plots of vegetation, soil and trap samples do not provide clear visual distinctions to help elucidate the pollen-vegetation relationship. The vegetation plot shows that although the vegetation communities are homogenous, due to the closeness of the co-ordinates of samples from the same community, they are associated and often overlap each other due to similar species composition. Thus one would expect the pollen spectra to reflect the same trend. Both the soil and the pollen trap PCA plots do so. These plots can be interpreted as showing that the more dissimilar communities, such as *Podocarpus* forest, *Leucosidea sericea* scrubland and, to some extent, low altitude vlei and *Protea* savanna produce distinct pollen rain spectra. The grassland communities have similar pollen rain spectra with more subtle differences. The similarities and differences between the PCA plots and comparison with the other statistical tests are discussed in Chapter 8.

7.6 Multiple Discriminant Analysis

7.6.1 INTRODUCTION

The discriminant or canonical scores generated by multiple discriminant analysis (MDA) for the pollen traps and soil samples are plotted against the first two discriminant functions on the plots (Figures 7.22-7.23). Within the soil samples, the variation between pollen assemblages is accounted for by discriminant function 1 (99.85%), function 2 (0.109%) and function 3 (0.041%), while discriminant function 1 (98.81%), function 2 (0.692%) and function 3 (0.498%) account for the total variation within the pollen trap data. This shows that the discriminating power of the first two functions is high, although the BMDP programme performing this analysis uses the first four discriminant functions. As a consequence of the large number of plots the centroid values for each community are obscured, therefore the centroid values are plotted separately. The vegetation zonal and probability of modern analogue indices calculated from MDA are plotted as Figures 7.24 and 7.25.

7.6.2 POLLEN TRAPS

Both the pollen trap and soil sample scores show little variation about the centroid, indicative of little variation between the individual spectra within the same community. The pollen trap scores (Figure 7.22) show that the community centroids are clearly separated, although some communities are relatively close together and therefore exhibit some association. The *Podocarpus* forest, *Leucosidea sericea* scrubland and sub-alpine fynbos are well separated, and to some extent the *Protea* savanna and low altitude vlei centroids are separated, whereas the grassland communities are not as distinctly apart from one another, although each community still retains its individual identity.

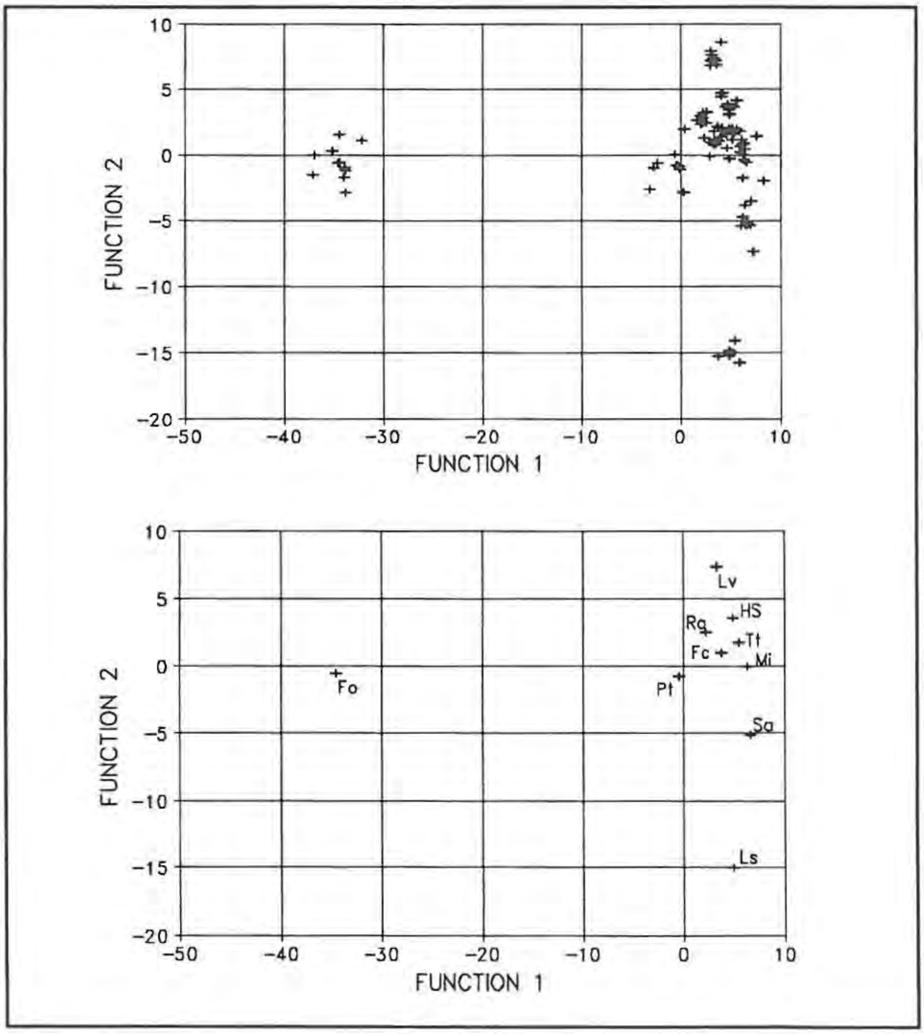


Figure 7.22 Multiple discriminant analysis plot of the pollen trap data. Top graph represents all the data points, while the lower graph the centroid values. HS-Highland Sourveld, Pt-*Protea* savanna, Fo-*Podocarpus* forest, Ls-*L.sericea* scrubland, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-Sub-alpine fynbos and Lv-Low altitude vlei.

7.6.3 SOIL SAMPLES

The surface soil samples are plotted in the same manner as the pollen trap samples but are slightly less well defined (Figure 7.23). Note that *Podocarpus* forest and *Leucosidea sericea* scrubland centroids are well separated from the other communities. Within the concentration of soil sample centroids the sub-alpine fynbos and low altitude vlei are set apart from the other centroids, indicating a similarity between the two and differences between the two pollen spectra and the rest. The *Erica-Helichrysum* heathland and *Protea* savanna centroids are separated, while all the grassland and high altitude vlei centroids are within close proximity of each other. In particular the sub-alpine grasslands, *Themeda triandra*, 'Mixed', *Festuca costata* and alpine grasslands centroids are close to each other as a consequence of the affinities between these communities. The *Rendlia altera* grassland and high altitude vlei centroids have almost identical co-ordinates (6.92 and 5.13 for *Rendlia* and 7.62 and 5.07 for the vlei), indicative of many similarities between the two soil pollen spectra, in particular percentages of the Poaceae, Asteraceae, Cyperaceae, Crassulaceae, Hypoxidaceae, Fabaceae, Ericaceae and Iridaceae taxa. The *Themeda*-dominated Highland Sourveld is slightly away from the other grassland communities, indicative of the uniqueness from the other grasslands.

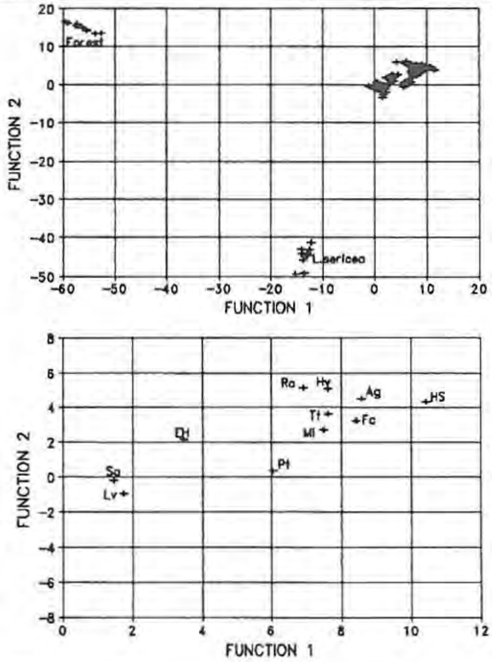


Figure 7.23 Multiple discriminant analysis plot of the soil pollen data. The lower graph is an enlargement of the concentration of centroids experienced in the first plot. HS-Highland Sourveld, Pt-*Protea* savanna, Ra-*Rendlia altera*, Tt-*Themeda triandra*, Mi-'Mixed', Fc-*Festuca costata* grasslands, Sa-sub-alpine fynbos, Lv-Low altitude vlei, Ag-Alpine grassland, EH-*Erica-Helichrysum* heathland and Hv-High altitude vlei.

Sugden (1990) suggests that to improve the definition of each assemblage a greater replication of the soil data is required. A larger sample size would possibly enhance the centroid position and strengthen the association between various soil pollen spectra due to affinities between various, closely associated, vegetation communities. The close clustering of the samples in this study, using twenty soil samples per community, suggests that the number of samples collected was sufficient.

7.6.4 VEGETATION ZONAL INDEX

The probabilities of group membership in the predicted and second most probable groups of variables, functions 1 and 2, are calculated for each modern pollen sample. A comparison of the objectively predicted group membership (which determines which groups the various samples represent) and the *a priori* group membership shows that 95.8% of pollen trap samples and 98.5% of the soil samples are correctly classified. This close association between the two methods of classification, subjective (undertaken in the field) and *a priori* (performed by MDA), is indicative of the modern pollen spectra being reliable contemporary data bases which may be used to determine analogue palaeo-vegetation assemblages. In most instances the second most probable group is the vegetation community that is geographically adjacent to the predicted community particularly with regards to the grasslands. These probabilities often reflect the zonal pattern of the vegetation along a temperature or, in this case mostly, an altitudinal gradient. Therefore it is possible to convert the probability values of the first two groups (functions 1 and 2) into a single 'vegetation zonal index' for each sample (Liu and Lam, 1985; Sugden and Meadows, 1989). Modern pollen spectra characteristic of a particular vegetation assemblage (100% probability of group membership) are assigned specific zonal indices which correspond with the vegetation communities along the predicted gradient, for example in the soil samples *Protea* savanna, sub-alpine fynbos and *Podocarpus* forest are the first three communities and are assigned indices of 1.0, 2.0 and 3.0 respectively. Intermediate zonal indices are assigned to samples which are transitional between two vegetation communities, therefore if two communities have close pollen spectra association the sample index values will fall between the two whole numbers representing the communities. For example, a trap sample classified as 80% *Protea* savanna and 20% *Podocarpus* forest would have a zonal index of 1.2.

The vegetation zonal indices for pollen trap spectra (Figure 7.24) and soil pollen spectra (Figure 7.25) nearly all approximate 100% as the samples are from known vegetation communities. However, some spectra do lie between two communities indicating that not all the spectra are distinctive of a particular vegetation community. Furthermore, although the pollen rain samples were collected from known vegetation communities it is important to recognize that the resultant spectra, of both pollen rain collecting techniques, do in fact represent the vegetation community from which they were taken.

The zonal indices for the soil pollen spectra are well defined with a few minor intermediate indices throughout the profile. Most of these discrepancies are a 90% representation of a particular community, for example *Rendlia altera* grassland, as opposed to 100%. A single soil sample from the high altitude vlei site is atypical of that community and more closely resembles the alpine grasslands, possibly as a consequence of over-representation of grass pollen from overlying vegetation. The pollen trap samples are also well defined, although the few discrepancies which do occur are large, thereby affecting the visuals of the figure. The low altitude vlei community has a single trap sample more closely allied to the *Rendlia altera* grassland, while both *Festuca costata* grassland and *Leucosidea sericea* scrubland have two samples associated with *Themeda*-dominated Highland Sourveld and *Festuca costata* grassland respectively.

7.6.5 PROBABILITY OF A MODERN ANALOGUE

This index is representative of the probability that modern pollen samples from a particular community, to which a fossil pollen sample could be assigned, will be positioned in the vicinity of the fossil sample on the canonical variate axes. In other words, it compares a pollen assemblage with the 'palynological signature' of its assigned vegetation community, as represented by the group centroid. The probability of a modern analogue is usually relatively high, falling between 0.6 and 1.0 for the majority of the samples. Lower values are as a consequence of samples having affinities with another community forming an ecotone between the two communities. In the case of this study, where ecotones were not considered in the sampling programme, a sample with a low probability of a modern analogue is more likely to be the result of some abnormality at that particular sampling site, for example over-representation of the overlying or surrounding vegetation.

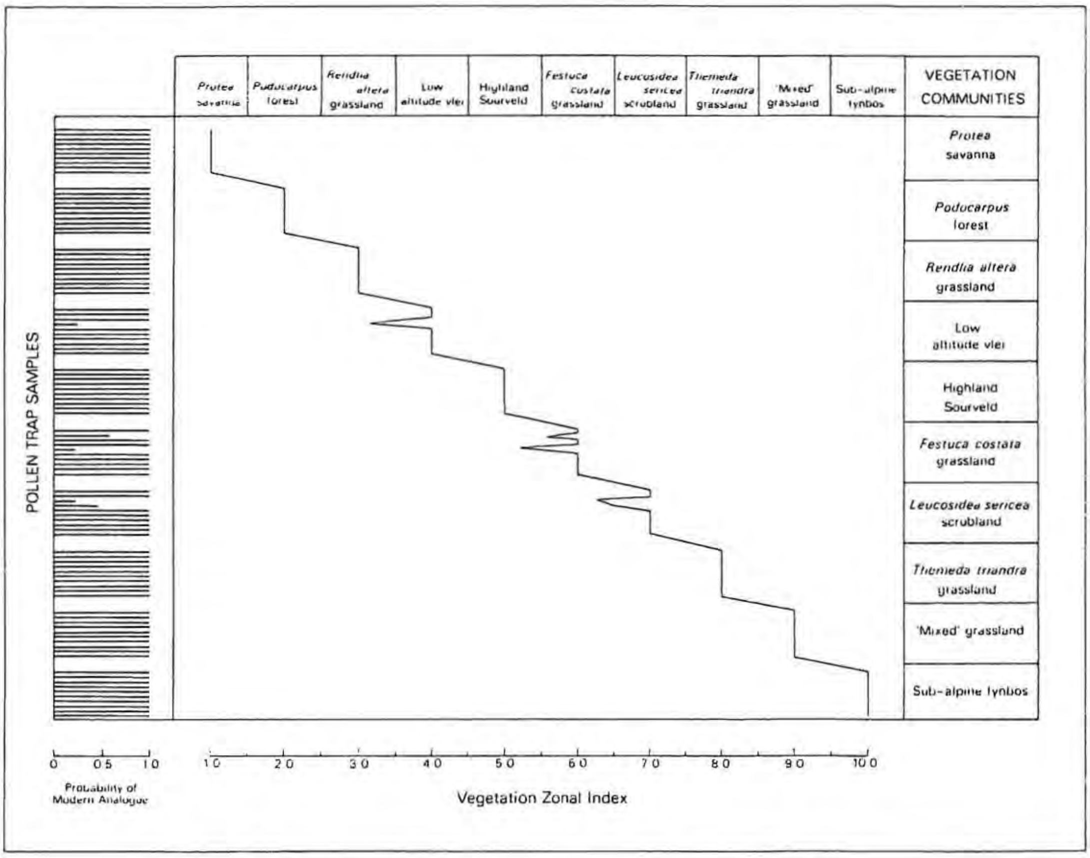


Figure 7.24 Results of the MDA for the pollen trap samples.

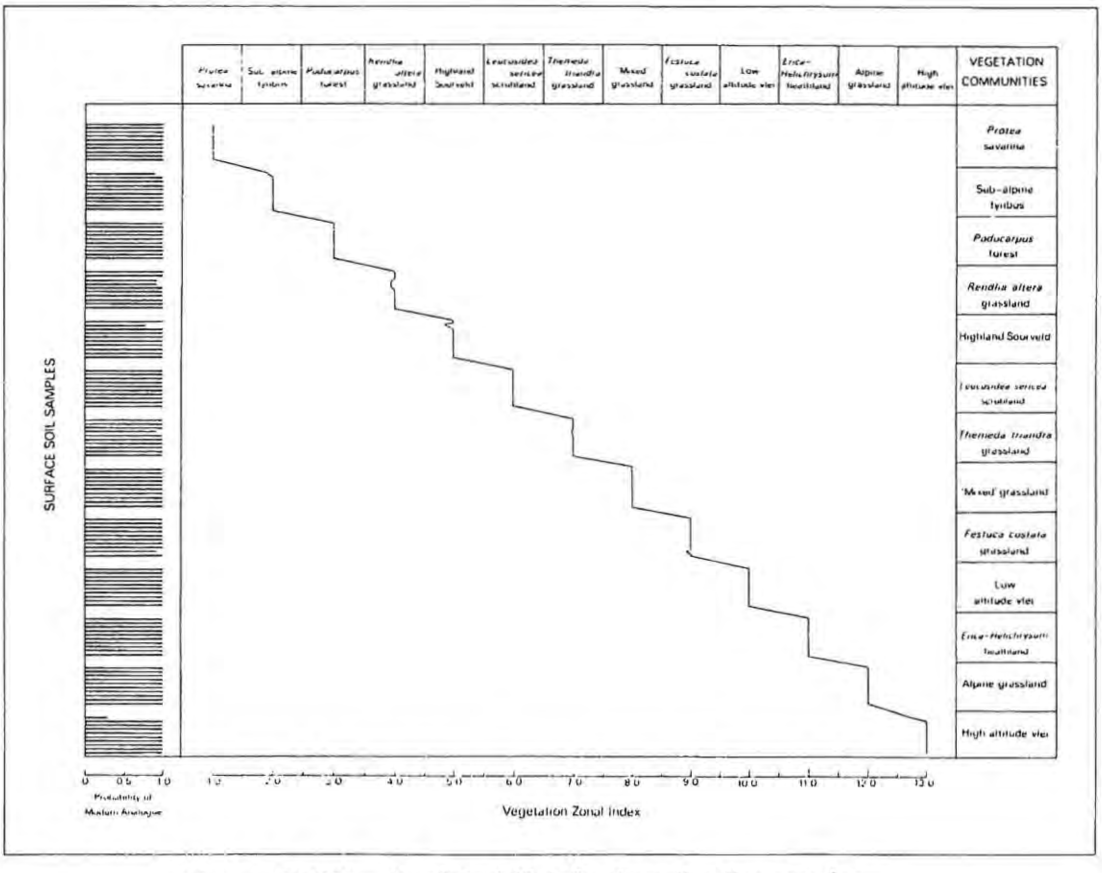


Figure 7.25 Results of the MDA for the soil pollen samples.

The probability of a modern analogue is high within all the communities for both the pollen trap and soil samples. A low of 0.40 is calculated for a single soil sample from the high altitude vlei site which is possibly as a result of over-representation of Poaceae. The pollen trap samples have a few low values; low altitude vlei has a single sample of 0.40, *Festuca costata* grassland has two at 0.65 and 0.40 and *Leucosidea sericea* has two at 0.40 and 0.55. Generally the modern analogue probabilities are high, which indicates that if a fossil pollen assemblage representing one of these samples was collected, it would be recognized as belonging to the corresponding vegetation community.

7.6.6 SUMMARY

Both the pollen trap and soil pollen spectra show that the vegetation communities can be separated into distinct vegetation assemblages on the basis of their pollen rain characteristics as determined by multiple discriminant analysis. The vegetation zonal indices for both pollen rain spectra types are well defined and show that each sample, within a community, is similar to each other and the composition of that community. The high probability of a modern analogue which both spectra types display is indicative of the fact that the chances of that particular spectra 'belonging' to the source vegetation community is high.

7.7 SUMMARY

Due to the number of both descriptive and statistical tests employed to investigate the modern pollen-vegetation relationship discrepancies between some of the results occur. However from the analysis of each data set, on an individual basis, it is evident that the *Podocarpus* forest, *Protea* savanna, *Leucosidea sericea* scrubland, low altitude vlei and *Erica-Helichrysum* heathland communities display very distinctive pollen rain spectra for both soil and trap spectra (other than the *Erica-Helichrysum* heathland for which no trap data exist). The grassland communities and high altitude vlei have a closer association. Generally a good correlation is calculated between the two pollen rain sampling techniques and between the techniques and the vegetation communities sampled. The soil spectra have an over-representation of the dominant ground taxon-Poaceae, while the trap spectra display a greater, and possibly more accurate representation, of the arboreal taxa.

The statistical analysis allows for the description and quantification of the modern pollen rain, which in turn enables comparisons to be made between the vegetation communities being studied. The tests ensure an objective approach to the relationship between the modern pollen rain and the source vegetation community. The results further allow one to describe the uniqueness of a particular pollen spectrum and the relationship between it and other spectra.

CHAPTER EIGHT
DISCUSSION

8.1 INTRODUCTION

To study modern pollen-vegetation relationships, the pollen data must be compared with the vegetation from which the modern pollen spectra originate (Birks and Gordon, 1985). This relationship is complex and the derivative thereof follows two processes; the first is a descriptive approach (Meadows, 1984; Meadows and Sugden, 1991a; Newsome, 1988; Salagado-Labouriau, 1979; Scott, 1989a) whereby modern pollen spectra are determined for described vegetation communities and the two data sets are subjectively compared. The second approach is more objective, involving numerical analysis which detects, summarizes and displays patterns of variation within modern pollen data. These methods compare modern pollen data and the vegetation types from which pollen rain samples were collected, and thereby characterize modern vegetation types in terms of contemporary pollen assemblages. Both approaches are used in this chapter to discuss the pollen-vegetation relationship for the studied communities. This chapter also includes a discussion on soil pH, optimum sample and pollen count size and pollen influx values.

8.2 SOIL pH

The soils of the studied vegetation communities are slightly acidic (mean pH values ranging between 4.1 and 5.4) and therefore the potential for pollen preservation is good. Observations made during surface soil pollen counts confirm this to be the case. The soil pollen was generally well preserved and little to no evidence of exine degradation was recorded. The soil pH measurements and state of pollen preservation observations confirm that the prevailing edaphic conditions are suitable for pollen preservation and possible fossilisation.

8.3 SAMPLE SIZE

8.3.1 VEGETATION

Standard 1m x 1m for grassland and 10m x 10m quadrats for the more complex stratified communities were employed and the resultant cumulative species versus sample size curves (Appendix 1) plotted to determine optimum sample size. Despite the range and varying degree of complexity of the vegetation communities, the study deemed that a quadrat sample size of approximately 15-20 samples would suffice for the sake of a modern pollen rain sampling programme. In most vegetation studies a larger sample size is required, but as it is only necessary to quantify the vegetation to family level, a smaller sample size proved to be accurate and sufficient enough.

8.3.2 SURFACE SOIL SAMPLES

The question of how many soil samples are required from each community was considered with the aid of an analysis of variance (ANOVA) and a minimum sample size calculation. Both techniques were carried out in retrospect. Two one-way ANOVAs were performed comparing the relative percentage frequencies of the taxa for 5, 10 and 20 soil samples (Section 6.3). The results comparing five against ten soil samples (not presented) determined that almost all taxa reject the hypothesis that there is no significant difference between the pollen counts sizes, with no community showing favourable results for reducing the soil sample size to five. In considering the results of an ANOVA between 10 and 20 samples a sample size of ten is sufficient for the *Rendlia altera*, *Festuca costata, Themeda triandra* and alpine grasslands, *L. sericea* scrubland, sub-alpine fynbos and high altitude vlei communities. The remaining communities require the larger (20) of the two sample sizes. However on closer examination of three of these communities; *Podocarpus* forest, low altitude vlei and *Erica-Helichrysum* heathland only one taxa from the top five dominant taxa of that community rejected the hypothesis. The taxa in question is Poaceae in the *Podocarpus* forest and *Erica-Helichrysum* heathland and Asteraceae in the low altitude vlei community. However as it is a dominant taxa that rejects the hypothesis it is recommended that a sample size of twenty be adhered to. For the Highland Sourveld, *Protea* savanna and 'Mixed' grasslands communities a number of the dominant taxa, which includes lesser represented taxa, reject the hypothesis. Therefore for these communities a soil sample size of twenty is recommended.

The results of the retrospective calculation to determine an optimum soil sample size at particular levels of confidence for the community's dominant taxa tended to suggest a sample size of twenty (Table 6.2). This sample size would allow one to produce pollen counts, of the more dominant taxa, to a high degree of confidence or small degree (1-5%) of error. Considering the results of the two techniques together it is suggested that a sample size of twenty be adhered to. The ANOVA results do suggest that a sample size of ten would suffice in some instances, but as the ANOVA does not allow for a varying degree of confidence to be considered (all ANOVAs were calculated at a 95% confidence limit) it is recommended that a surface soil sample size of twenty be applied for all the studied communities so as to obtain the least degree of error of the pollen count. A larger sample size was considered, however a preliminary study conducted by the author in 1987 (Hill, 1987) concluded that a soil sample size greater than twenty did not significantly improve the representation. A constraint of time against the possible benefits of a larger sample size was also considered. To obtain meaningful figures for a further ANOVA with regards to sample size a doubling or tripling of the sample size would be necessary and time would not allow for that. It is the authors subjective opinion, based on experience with the data set, that a doubling of the sample size would not improve the resultant spectra significantly enough to warrant such an undertaken.

8.3.3 POLLEN TRAP SAMPLES

The initial determinant of pollen trap sample size was based on conversations with Drs. J. Sugden and M. Meadows who have undertaken similar pollen rain sampling programmes in the montane regions of the Cederberg and Sneeuberg (Sugden, 1990) and on the number of traps that can be carried to each of the sites bearing in mind that a minimum sample size of five was suggested as being adequate (J. Sugden, *pers. comm.*, 1988) or as the "... absolute minimum..." (Moore *et al*, 1991, pp. 35). Once the initial pollen counts had been completed a retrospective calculation to determine the minimum sample size at varying degrees of confidence was carried out. Results of the calculation (Section 6.3.2) show that for all the montane and sub-alpine communities, in which pollen traps were placed, a confidence limit of 95% is obtained for all the dominant and more abundant taxa for the sample size applied. The taxon Poaceae in the low altitude vlei community requires a larger sample size (Table 6.4) to obtain a 95% confidence limit, although for the number of traps placed into the community (6) a 90% confidence is obtained. To improve the confidence limit a tripling or quadrupling of the number of traps placed in each community would have to be considered;

this was not possible due to the vastness of the region and the time required for sample preparation and counting. For the number of traps placed within each of the vegetation communities the obtained confidence limit of the pollen counts is high and sufficient.

8.4 POLLEN COUNT

To recommend an appropriate sampling strategy with regards to the number of pollen grains counted, two one-way ANOVAs were carried out. The first determined any significant differences between performing pollen counts of 250 and 1000 grains per soil sample. The ANOVA does not calculate or describe how representative this count is of the actual sample, but determines whether there is any significant difference, with regards to the relative percentage frequencies, between the counts. In other words if there is no significant difference between a count of 250 or 1000 for a particular community then the lower numeral count will suffice and save counting time and possible error. The results (Section 6.4) conclusively prove that for most vegetation communities a count of 250 pollen grains is sufficient and that a larger count will not produce a significantly different result. A large count of 500 or 1000 grains will ensure that some taxa with low (less than 0.5%) relative percentage frequencies will not be significantly different. For a count of 250 grains the taxa that rejected the hypothesis have, predominantly, low counts in the pollen sum. The exceptions to this are the Poaceae counts of the Highland Sourveld, *Protea* savanna and *L. sericea* scrubland communities. In these communities the co-dominant or dominant Poaceae taxa does show a significant difference between the three count sizes and as a consequence a count of 500 grains is recommended for the Highland Sourveld community and 1000 grains for the *Protea* savanna and *Leucosidea sericea* scrubland communities as determined by an ANOVA between counts of 500 and 1000 pollen grains. Of note is the fact that, for the obtained data set, a count of 250 will suffice within the diverse *Podocarpus* forest community.

8.5 POLLEN INFLUX VALUES

All the montane and sub-alpine communities exhibit seasonality with regards to pollen influx (Section 6.5.1). The grassland communities and the *Protea* savanna, which has a predominance of grasses in the ground stratum, show the more classical seasonality of low winter values increasing in spring to a summer high then decreasing again during the autumn-winter months. A similar trend develops during the 1989-90 season, although the influx values are greater during the spring of 1989 than the corresponding 1988 period. This marked anomaly between the corresponding seasons was not expected as the temperature figures from the Cathedral Peak Research area do not vary greatly between the two seasons. However South Africa experiences large temporal fluctuation in climatic conditions and this climatic variability is principally expressed in the unreliability of the rainfall (Cadman, 1990). Although there is no significant difference in the amount of rainfall received during the corresponding seasons, the spring of 1989 received more rain early on in the season. This could cause early flowering resulting in an earlier pollen influx peak when compared to 1988. However a detailed analysis of pollen rain and the possible meteorological factors which effects it needs to be carried out and several years of data would be required from a number of vegetation communities. Various meteorological factors have been associated with pollen influx values, but correlation does not necessary imply causality (Bringfelt *et al*, 1982).

Early flowering, as a consequence of fire, offsets the seasonality of pollen production as was observed in the Highland Sourveld and *Rendlia altera* grassland communities. Early spring burns resulted in the early seasonal flowering and resultant pollen production in these two communities. This early pollen production not only produces a high spring period pollen influx value but also lowers the subsequent summer influx value.

The *Podocarpus* forest and *Leucosidea sericea* scrubland communities exhibit marked seasonal pollen influx variation; however this is produced as a consequence of a single taxon, in the *L. sericea* case, or a few taxa (in the case of *Podocarpus* forest) producing large qualities of pollen during its flowering thereby dominating and 'masking' the presence of other taxa. *Leucosidea sericea* flowers during August-September and dominates the winter and spring trap spectra of 1988 and the winter spectra of 1989, when the species flowered slightly earlier. The *Podocarpus* forest influx values follow the more expectant high summer-low winter trend, but the winter values are dramatically increased by the flowering of *Celtis africana* (Ulmaceae) which occurs early in the growing season-August (Palgrave, 1983 and personal observations).

Neither the low altitude vlei nor the sub-alpine fynbos communities exhibit similar seasonal fluctuations. The vlei site has a spring high decreasing to winter in 1988-89 which is not reflected in 1989-90 and the data for the fynbos community is sparse and incomplete.

A similar two year pollen rain study was conducted by Hall (1990) in the Rocky Mountains and southwest Plains of the USA. The paper presents annual influx values for two 12-month samples. Although the vegetation composition is dissimilar to the present study, there are two worthwhile points to consider; firstly that pollen influx and pollen relative frequencies were directly related despite a high degree of variability and there was a "...dramatic difference..." (pp. 52) in the periodicity of high pollen production of different species in the two years of influx data, with trees showing greater variability than shrubs and grasses. A marked annual variation as recorded by Kershaw and Stickland (1990), Bonny (1980) and Cadman (1990) for total pollen influx values was not recorded for the vegetation communities studied. The greatest variation is recorded in the *Podocarpus* forest, as would be expected, due to the high pollen production and flora diversity. The communities dominated by one or two species, all except the forest community, do not show great annual variation, a phenomenon noted by Spieksma (1983). This is despite the fact that the individual taxa do display marked annual fluctuations as were evident from the seasonal trap spectra (Appendix 7).

The annual and seasonal pollen influx variation cannot be readily explained. Examination of the climatic variables of temperature, wind speed and direction from the meteorological station at Mike's Pass, Cathedral Peak, recorded no obvious major differences other than sunshine hours and rainfall on a seasonal basis. Kershaw and Strickland (1990) also conclude that a comparison between their data and regional climatic information revealed no obvious correlation. It is assumed that temperature and length of sunlight hours may affect the time of flowering and therefore pollen production, however flowering patterns are more complicated than that and individual species respond differently to various stimuli. The recorded influx variation in pollen influx is, according to Kershaw and Strickland (1990 pp. 286) "...simply a result of pollen production and dispersal capacities of those species that happen to be flowering in any particular year".

To reduce seasonal and annual variation which pollen traps record it is necessary to obtain results over an extended period of possibly 2-5 years. An alternative to such an extensive pollen sampling programme is to augment the pollen trap data with surface soil samples. Surface soil sampling was performed as it represents an average deposition of several years, and therefore minimizes annual and seasonal fluctuations (Salago-Labouriau, 1979).

The inherent problem of proportionality caused by the use of relative frequency data during pollen influx calculations was considered during analysis. The ANOVAs concentrating on seasonal and annual variation did not prove conclusive either for or against either seasonal or annual variation which is in contrast to the results of pollen influx values calculated. What are evident from the original data is that the dominants from each community reject the hypothesis that there is no significant difference between the seasons. If only the dominant taxa are considered (usually only two or three taxa) then seasonal variations are experienced in each community. However this result is masked when all the taxa are considered. The data for annual variation are more complex. The dominant taxa of the temperate grassland communities, Highland Sourveld and low altitude vlei do not exhibit an annual fluctuation, while the *Protea* savanna, *Podocarpus* forest, *Leucosidea sericea* scrubland and sub-alpine fynbos have taxa both for and against annual variation. In each of these above mentioned communities it is the arboreal taxa, for example Proteaceae, Podocarpaceae, Ulmaceae, *Leucosidea sericea* and the Ericaceae of the sub-alpine fynbos which reject the hypothesis that there is no significant difference between the two years of data. With regards to *Rendlia altera* grassland both the dominant taxa of the community and the arboreal pollen, which is deposited in this community, exhibit annual fluctuations.

Initially the ANOVA results do not show any clear indication for or against seasonal and annual pollen influx fluctuations. However a closer examination of the results show that both annual and seasonal variations do occur particularly in the dominants of each community. The high acceptance of the hypothesis comes mostly from the taxa with low representation within the spectra. With these lower values it is more difficult, using a test such as ANOVA, to discern fluctuations as they represent a small proportion of the spectra.

8.6 VEGETATION AND POLLEN SPECTRA

8.6.1 MONTANE BELT

The taxa recorded in the vegetation, soil and trap pollen spectra of the Highland Sourveld grassland community are similar although the relative frequency values vary. Both soil and trap spectra record taxa which were not recorded during the vegetation analysis of the community, while pollen of the taxa Rosaceae, Proteaceae, Myricaceae and Polygalaceae pollen are recorded from the pollen traps only. The pollen of these taxa are possibly wind-pollinated (anemophilous) and blown into the region from surrounding communities. Poaceae dominates all three spectra, with greater Poaceae pollen values recorded in the soil spectra (79%) than for the traps (54%). A larger proportion of Asteraceae pollen is recorded in the traps possibly as a consequence of wind transportation of the Asteraceae pollen. Both pollen spectra reflect the vegetation of the community, although the soil spectrum has a dominance of Poaceae which slightly 'masks' the other taxa while the pollen trap spectrum has a reduced Poaceae and an increased Asteraceae relative percentage frequency.

All *Protea* savanna taxa recorded in the vegetation community have pollen representation in the soil spectrum, while the taxa Araliaceae and Santalaceae are absent from the pollen trap spectrum. The soil and trap spectra show similar relative percentage frequencies, although a relatively low Proteaceae value is recorded in the soil spectrum. A high proportion of Proteaceae is recorded in the trap spectrum as a consequence of the traps being placed above the ground and more likely to 'catch' the arboreal *Protea* pollen, resulting in an over-representation of the Proteaceae pollen. A number of taxa are not recorded in the vegetation analysis, but have pollen values in either the soil or trap spectra, with low representation (approximately 0.5% of the total pollen sum); this pollen is possibly wind transported into the area from the surrounding vegetation communities.

A number of taxa which were identified in the *Podocarpus* forest, predominantly of herb and annual species, are not represented in the pollen spectra. A noticeable absentee is the arboreal Aquifoliaceae (*Ilex mitis*). No pollen was recorded for this species, either in the soil or traps samples, over the two years of sampling. The taxon Urticaceae is recorded in the soil spectra, but not within the traps. The species of these taxa could possibly be low pollen producers or poor pollen dispersers or, in the case of Urticaceae in particular, may not have flowered during the study period. Therefore no recent pollen production was recorded. Again pollen is recorded for taxa not represented in the vegetation spectra, mostly of low values; an exception is the Asteraceae pollen collected from the traps. The pollen has, in all probability, been washed into the area as a consequence of atmospheric washout (McDonald, 1962) as Asteraceae species are present in abundance on the surrounding hillslopes. The dominant taxa remain for all three spectra, with Pteridophyta and Poaceae being over-represented in the soil spectra as a consequence of these taxa dominating the ground vegetation cover above the soil sample sites.

8.6.2 SUB-ALPINE BELT

The *Rendlia altera* pollen spectra prove to be an excellent example of up-valley transportation of pollen, with the arboreal taxa of the *Podocarpus* forest and *Protea* savanna communities represented in the pollen spectra and not in the vegetation. The *Rendlia altera* grassland community occurs on the Little 'Berg plateau, in this case with a *Protea* savanna on the north west facing slope and a *Podocarpus* forest along the south and south east slopes and surrounding valley. Palynologists have recorded the phenomenon of up-slope deposition of arboreal species pollen in Europe (Markgraf, 1980), North America (Hall, 1990), New Zealand (Pocknall, 1982; Randall, 1990), Borneo (Flenley, 1973) and East Africa (Flenley, 1979; Hamilton and Perrott, 1980; Morrison and Hamilton, 1974). The uneven heating of the valley sides resulting in morning up-valley winds, coupled with the fact that most pollen is released during the morning, results in up-valley transportation of pollen. Some of this pollen will be deposited once it reaches an area out of the direct up-valley wind, for example on the plateau. Consequently the plateau pollen rain spectrum records these upward transported pollen grains. In the case of the *Rendlia altera* grassland community the pollen from arboreal dominated taxa from both slopes have been recorded. The taxa involved are not represented in the vegetation of the *Rendlia altera* grassland and are not present in large quantities in the pollen spectra, but enough to affect the total pollen sum. The *Rendlia altera* pollen spectra is very distinctive with a dominance of the grassland taxa, added to which is the presence of a diverse group of arboreal taxa. Pollen of Orchidaceae is not recorded in either the soil or trap samples as this pollen is destroyed during the acetolysis process which concentrates the pollen for the counting procedure. There is once again an over-representation of the high pollen producing Poaceae taxon.

The sub-alpine temperate grassland communities, *Themeda triandra*, 'Mixed', and *Festuca costata* all exhibit similar pollen spectra. The spectra are dominated by Poaceae and Asteraceae with Poaceae representing a greater proportion of the pollen sum in the soil samples and Asteraceae increasing in the trap samples. The Asteraceae species within these grassland communities must be predominantly wind-transported and therefore a higher proportion of pollen is recorded in the aerial pollen traps than at ground level. A number of taxa do occur in only one or other of the spectra, but these taxa are represented by low percentages. An exception is Cyperaceae which is recorded in the soil and trap spectra of both the *Themeda triandra* and 'Mixed' grassland communities, but not in the vegetation. The Cyperaceae pollen source is from the Cyperaceae communities, particularly *Bulbostylis* and *Carex* species, which were observed in the firebreaks surrounding these grassland communities. From a purely subjective comparison of the pollen spectra the soil pollen spectra seem to be a closer representation of the vegetation than the pollen trap spectra for these grassland communities.

Leucosidea sericea and Poaceae pollen dominate the trap spectrum of the *Leucosidea sericea* scrubland community. This high *L. sericea* value is not recorded in the soil spectrum. The high trap values are, to an extent, the result of pieces of *L. sericea* anthers being transported and entrapped in the pollen traps and due to the high pollen production of *L. sericea*. The high proportion of Poaceae and Pteridophyta from the vegetation analysis is recorded in the soil pollen spectrum, which also exhibits relatively high Asteraceae and Rosaceae (other than *L. sericea*) percentages. Overall both pollen spectra are indicative of the vegetation present within the community, although there is an over-representation of ground stratum species in the soil spectrum and of the arboreal *Leucosidea sericea* in the trap spectrum.

All the taxa represented in the low altitude vlei vegetation community are represented in the pollen spectra of both the soil and trap samples. The spectra reflect the fact that the Poaceae species are higher pollen producers than the Cyperaceae species and that the Asteraceae pollen is more prevalent in the trap spectrum, as has been observed in other communities. Pollen from taxa such as Geraniaceae, Ericaceae, Proteaceae and *Leucosidea sericea* are recorded in either of the two modern pollen spectra and originate from the surrounding vegetation, in particular the *Leucosidea sericea* pollen. It is often difficult to locate the source of regional pollen, but in the case of this *L. sericea* pollen it has it's origins in the *L. sericea* trees present along a main watercourse adjacent to the vlei site.

The more dominant taxa of the sub-alpine fynbos community appear as the dominants in both the soil and trap pollen spectra. Both pollen spectra are not as dominated by a single taxon as is the case, in particular, of the grassland communities. The Pteridophyta spores are more evident in the soil spectrum, while the arboreal Proteaceae species pollen increases in the trap spectrum. The spectra reflect the high diversity of the community and the co-dominance of Poaceae, Ericaceae and Asteraceae in the vegetation composition of the community. Rosaceae and Thymelaeaceae are not as obvious in the pollen spectra, possibly as a consequence of them being less abundant pollen producers or that the pollen is poorly dispersed.

8.6.3 ALPINE BELT

A similar picture emerges for the alpine vegetation communities. The dominant taxa in the vegetation communities are the main pollen producers recorded in the soil pollen spectra. A number of taxa are present in the pollen spectra which are not recorded within that particular vegetation community. These taxa are observed in the surrounding vegetation, therefore it is necessary to take cognizance of the regional vegetation with regards to the pollen rain. Within the alpine grassland the taxa Poaceae, Asteraceae and Cyperaceae dominate. Ericaceae is the most dominant pollen in the *Erica-Helichrysum* heathland. This high Ericaceae, in association with Asteraceae and Thymelaeaceae pollen relative frequencies, distinguishes this soil pollen spectrum from the other alpine spectra. The high altitude vlei soil spectrum is distinguishable by the Juncaceae and Eriocaulaceae pollen percentages.

8.6.4 GENERAL SPECTRA DISCUSSION

The possible deterioration of grains found in the pollen rain traps need to be considered, as Hamilton and Perrott (1980) point out that grain deterioration in surface soil and trap samples may not be due to adverse chemical conditions for preservation, but can result from the influx of a certain amount of older or recirculated pollen. This deterioration can effect resultant spectra. The recirculated pollen reaches a site predominantly by surface wash, having been stored for sometime in the catchment and only reaching the sample site once the process of deterioration has commenced or else has been deteriorating at the sample site. It can also reach the traps and soil samples via re-floatation into the atmosphere and then directly as part of the general pollen rain. Deteriorated pollen recovered from both the soil and pollen traps was extremely low in this study, possibly due to the short time period that the pollen was left in the traps and also due to soil acidity. The largest number of deteriorated grains was counted in the *Podocarpus* forest soil samples, however the number was low and contributed to the 'unknown' category rather than forming a separate group.

Since pollen traps do not receive surface washed pollen, while soil samples can, together with the fact that the two spectra are so similar, this would suggest that no 're-worked' or at least no significant values of 're-worked' pollen arrives at the soil sample via surface wash. A similar result is described by Meadows (1984) for work undertaken on the Nyika Plateau in Malawi. Meadows (1984) concludes, and this author accords, that the number of indeterminable pollen as a consequence of deterioration must be largely due to pollen which has been refloated into the atmosphere.

A pollen dispersal model described by Krzywinski (1977), albeit for northern Hemisphere tree species, helps to elucidate the pollen trap spectra dominated by a single taxon, in particular taxa that produce a large amount of pollen and dominate the pollen spectra for a single season, thereafter appearing at low values, for example *Celtis africana* (Ulmaceae) within the *Podocarpus* forest and *Leucosidea sericea* in the *Leucosidea sericea* scrubland communities. This model holds true particularly for high pollen producers that dominate a spectrum for a particular period of time. Directly under the species the pollen deposition is both high and complex, as one moves away from the species the complexity and deposition decreases. If it were possible to observe only direct deposition, during flowering without deposition of other species, a sharp peak of short duration at the time of flowering would be observed. During flowering, pollen is dispersed throughout the surroundings, including the canopy. From this canopy some of the pollen is wind-transported away, predominantly up-slope with the prevailing up-valley wind, therefore, in this case, Ulmaceae and other forest taxa are recorded in the pollen spectra of the *Rendlia altera* grassland on the plateau above the forest.

According to Krzywinski (1977) the subsequent removal of pollen from the vegetation is as follows; at the completion of flowering no more pollen is deposited on the canopy, so the depositional curve gradually declines as the pollen pool in the canopy decreases. Deposition at this time is dependent both on the amount of pollen detained by the vegetation and on the intensities of the removal agencies. Some pollen is not washed off but is deposited on the floor and into/onto the pollen rain samples by various objects. Some of this pollen is deposited when leaves are shed or via flowers, twigs, branches or bark. The resultant litter deposition curve consists of single peaks throughout the year which are usually not observed as such due to the nature of sampling, but the main peaks occur in periods of high pollen content in the community or in periods with a high deposition rate of litter (this high deposition of litter is not as evident in South Africa where marked stages of leaf senescence are not observed due to, comparatively, mild winter months). As would be expected, most litter of a particular species is deposited beneath that particular species, thus showing the importance of repetitive and random sampling to alleviate the over-representation of a single species, for example the taxa Ulmaceae in the *Podocarpus* forest and *Leucosidea sericea* in the *Leucosidea sericea* scrubland communities.

The pollen spectra are subjectively deemed to be representative of the vegetation communities from which they were collected and each spectra is distinct from the others, although in the temperate grassland communities it is the lower relative frequency taxa that need to be considered to distinguish between these communities. It is important to compare the pollen trap spectra with the soil spectra, since it is the relationship between present-day pollen rain and the pollen actually arriving at a site and becoming enmeshed and preserved which indicates the usefulness of fossil data (Meadows, 1984). The two data sets are similar, although the soil spectra tend to have a higher Poaceae value, while the trap spectra have higher Asteraceae and arboreal taxa relative percentage frequencies.

It is difficult to determine, for each vegetation community, which modern pollen spectrum is the more representative. The pollen trap spectra produce a more accurate representation of the arboreal taxa within and surrounding a particular community, whilst the soil pollen spectra are a culmination of a number of years of pollen rain. With regards to fossil pollen analysis it is possibly a fairer reflection to consider the soil pollen spectrum, as it is from the pollen rain collecting on the soil surface and becoming preserved that a fossil pollen assemblage originates. Despite the fact that both modern pollen rain collecting techniques produce distinctive and unique pollen spectra of the source vegetation community, in terms of fossil pollen analysis it is more appropriate to consider the soil pollen spectra. To improve upon the subjective opinion that the spectra of the three data sets are similar and therefore that the pollen rain is distinctive and unique for a particular vegetation community it is necessary to apply the more objective statistical analyses as discussed below.

8.7 ASSOCIATION BETWEEN SAMPLES

Canonical correlation analysis was carried out to compare a single overall or 'average' spectrum for each of the three data sets. This correlation allows for an objective comparison between the vegetation, soil and trap data sets. The canonical correlations are generally high, implying a strong relationship does exist between the spectra. There was a higher trap/vegetation correlation for the communities recognized as more distinctive by the PCA, MDA and DECORANA plots, in particular *Podocarpus* forest, *Protea* savanna and *L. sericea* scrubland than for the soil/vegetation correlation. The remaining communities exhibited a higher soil/vegetation correlation. The reason is possibly as a consequence of the arboreal taxa pollen being more important components of the pollen rain spectra in these communities and the Poaceae taxon is not as dominant.

Overall, the canonical correlation analysis shows that both the soil and trap spectra are representative of the vegetation community from which they were collected. The correlation makes no inferences about whether these spectra are distinctive or unique for any one particular community. The lower trap/soil spectra correlation of the forest and *L. sericea* scrubland communities is possibly due to the high pollen production of the arboreal species, for example *L. sericea*, Ulmaceae, Podocarpaceae and Sapindaceae which are recorded as a greater proportion in the trap samples than in the soil spectra which are dominated by Poaceae and Pteridophyta. The soil samples are usually overlain by species of the Poaceae family and therefore there is an over-representation of Poaceae pollen in the resultant surface soil spectrum.

8.8 SAMPLE CLASSIFICATION - TWINSPAN

All three TWINSPAN dendrogrames reflect the homogenous assemblages as a consequence of the sampling strategy employed. The TWINSPAN analysis divides the vegetation quadrats into their respective communities, although, due to similar species composition, the *Protea* savanna and Highland Sourveld communities and the *Themeda triandra* and 'Mixed' grassland communities are grouped together. The vegetation dendrogram displays the distinctiveness of the individual communities, that the communities can be separated as a consequence of their species composition and that the quadrats measured were representative of that particular community. The TWINSPAN technique is carried out by lumping all the samples together into the TWINSPAN programme, which then divides the samples according to their uniqueness or distinctiveness from each other. The final grouping is of a number of samples which are closely associated to each other but distinct from the other groupings. When the soil and pollen trap samples were put through this technique the resultant groups of samples were identified almost exclusively as belonging to one or, in some cases, two of the vegetation communities from which the samples originated. This implies that all the samples within the group have a close affinity to each other, they are distinct from the other groups of samples and that the samples are all representative of that particular group or in this case vegetation community.

Both the soil and trap TWINSPAN results show conclusively that the collected pollen rain samples are representative of particular vegetation communities and that, on the whole, these communities are distinctive, implying that each community has a distinctive soil or pollen trap spectrum. For the soil spectra the *Podocarpus* forest, low altitude vlei, sub-alpine fynbos and *L. sericea* scrubland communities are most distinctive. The remaining communities are more closely associated as a consequence of Poaceae dominating, to a lesser or greater degree, the soil spectra. Despite the presence of a high Poaceae value in all these communities they are distinctive on the basis of actual Poaceae relative percentage frequencies and the presence of other taxa specific to that community. The closest association is between the high altitude vlei and alpine grassland communities.

A similar dendrogram is obtained for the pollen trap samples with samples of the *Podocarpus* forest, sub-alpine fynbos, *Protea* savanna, *L. sericea* scrubland and low altitude vlei (a few samples) forming distinct groups. The grassland communities exhibit closer affinities based on their trap spectra. The trap spectra are not as distinctive as the soil spectra and it is difficult to separate the three sub-alpine temperate grasslands and Highland Sourveld communities based on trap spectra alone. A point of note is the separate grouping of *Rendlia altera* grassland from the other grassland communities, due to the presence of the arboreal taxa in the trap spectrum which is not as obvious in the soil spectrum. The *Protea* savanna trap spectrum is separated from the grassland communities which was not the case for the soil spectra. This is because the arboreal Proteaceae pollen has a higher proportional representation in the trap spectrum whereas there is an over-representation of Poaceae pollen in the soil spectrum, thereby grouping the Protea savanna community with the grasslands on the basis of soil pollen composition.

Both the pollen trap and soil sample dendrograms reflect the homogenous community assemblages that the vegetation analysis displays. The classification of the vegetation into recognizable communities was expected as homogenous vegetation communities were sought and sampled. However the TWINSPAN classification does allow one to observe the relationship or association between the communities. Both the pollen trap and soil dendrograms show similar classification trends. The initial division is that of the arboreal pollen dominated *Podocarpus* forest from the other communities. The next division is the 'scrubland' sub-alpine fynbos, *Protea* and *Leucosidea sericea* communities. This division is not as decisive because there are grass and herb elements present. Further divisions are on the basis of grass, sedge and herb percentages. The pollen rain dendrograms are similar with respect to the division of the various communities although the lack of pollen trap data for the alpine communities is unfortunate. The dendrograms show the similarity in the pollen rain obtained from the various grassland communities, but the fact that these communities are divided at level 5 or 6 into distinct groups, in most cases, is a good indication of the individuality of these communities.

8.9 SPECTRA ORDINATION

8.9.1 DECORANA

DECORANA, although traditionally performed in conjunction with the classification technique of TWINSPAN, does not produce similar results. Whereas TWINSPAN divides the samples from an original group according to dissimilarities, DECORANA groups samples according to their similarities. The DECORANA vegetation plot forms distinctive sample concentrations for low altitude vlei, *Podocarpus* forest, sub-alpine fynbos and *Leucosidea sericea* communities. The *Rendlia altera* and *Themeda triandra*, *Protea* savanna and Highland Sourveld, and *Festuca costata* and 'Mixed' grassland communities, having similar taxa composition, are also grouped together. The three alpine communities form a separate grouping. These alpine communities share some taxa and therefore the concentration of samples of the individual communities is not as obvious. There is a tentative altitudinal gradient along the axis from the alpine communities though the sub-alpine grasslands and other sub-alpine communities to the *Leucosidea sericea* and sub-alpine fynbos communities which are found predominantly in the river valleys to the *Podocarpus* forest which is situated in the river gorges of the montane belt.

The DECORANA plots of the soil and trap samples are more complex, predominantly as a result of the close affinities between the grassland communities. For the soil plot only *Leucosidea sericea* scrubland, *Podocarpus* forest, *Erica-Helichrysum* heathland and sub-alpine fynbos can be said to form distinct units, thereby displaying unique soil pollen spectra.

The remaining communities are closely aligned to each other; plotting the centroid value for each community confirms this close association. Similar conclusions are reached concerning the DECORANA plot of trap data with only *L. sericea* scrubland *Podocarpus* forest and *Protea* savanna forming distinct spectra. The DECORANA plots, of for example the pollen traps of *Podocarpus* forest, have similar coordinates and are therefore, graphically, close to each other. This is an indication that all the trap samples represent a single group and are representative of that community. This was observed for all the samples with the exception of the pollen trap data of *Leucosidea sericea* scrubland in which case two separate spectra concentrations are formed as a consequence of the influence of a strong seasonality of *L. sericea* flowering.

8.9.2 PRINCIPAL COMPONENT ANALYSIS (PCA)

Principal components analysis (PCA), like DECORANA, was carried out to establish whether there is any group structure in the samples. The results are plotted using the first two principal components, as a consequence the resultant plots and interpretation can be compared to that of the DECORANA (Section 8.9.1) and multiple discriminant analysis (MDA) (Section 8.11) plots. Performing both DECORANA and PCA is a duplication of results, but this study wished to apply as many of the more widely used modern pollen rain analyzing techniques as possible to determine the analytical technique most appropriate to a South African data set.

From the agglomeration or concentration of samples as a result of PCA no distinct community groupings is at first obvious. The more obvious concentrations are the *Festuca costata* grassland, the *Leucosidea sericea* scrubland and the three alpine communities clustered together. Although the centroid values display the *Themeda triandra* grassland, *Protea* savanna and Highland Sourveld communities as relatively far apart and therefore distinct from each other, the individual samples overlap each other due to the similar taxa composition of the three communities. The 'Mixed' grassland community samples display no recognizable clustering and the samples are widely spaced apart as these samples have affinities with a number of the other communities, in particular the *Themeda triandra* and *Festuca costata* grasslands. The three alpine communities display very similar taxa composition which is unique from the montane and sub-alpine communities, therefore these samples are concentrated together. Low altitude vlei samples, with high Cyperaceae values, do have some affinity to the alpine communities and a number of the samples overlap. The positioning of sub-alpine fynbos and *Podocarpus* forest samples, although forming some resemblance of a grouping, is unclear and unlike the DECORANA vegetation plot no obvious gradation between communities based on altitude or taxa relative percentage abundance is observed.

The PCA surface soil and pollen trap plots both exhibit the close affinity of the spectra of the various vegetation communities to each other with the exception of *Podocarpus* forest and low altitude vlei in the soil samples and *Leucosidea sericea* scrubland and *Podocarpus* forest (and to a lesser degree sub-alpine fynbos and *Protea* savanna) in the trap samples. This close spectra affinity is as a consequence of the dominance of Poaceae within the pollen rain spectra and to a lesser extent other ground stratum dominating taxa such as Asteraceae, Euphorbiaceae, Iridaceae and Fabaceae.

8.10 COMPARISON BETWEEN DECORANA AND PCA

A subjective comparison between the DECORANA and PCA plots reveal that the DECORANA plot has grouped the results 'better' than that of PCA, particularly with regards to the vegetation samples. However as the two techniques rely on different criteria to perform the analysis it is not appropriate to compare the plots against each other, rather the general trends of both plots need to be considered. From the vegetation data the DECORANA plot forms more distinctive groupings of the samples than does PCA. The two plots both display a concentration of the alpine communities, a close association of 'Mixed' and *Festuca costata* grassland, a concentration of *L. sericea* scrubland species and a mixing of the *Themeda triandra*, Highland Sourveld, *Rendlia altera* grasslands and *Protea* savanna on the basis of similar taxa composition. Generally the PCA plot shows the samples to be less representative of individual communities, while the DECORANA plot has the samples of a particular group more concentrated. The fact that the axis values are not the same does not affect this phenomenon to any great extent.

The soil plots reveal very different results with only the *Podocarpus* forest community separated from the other communities in both data sets. The DECORANA plot shows distinct grouping of the *L. sericea* scrubland, sub-alpine fynbos and *Erica-Helichrysum* heathland soil spectra, while the PCA plot displays, other than the *Podocarpus* forest community, the low altitude vlei soil spectra as being distinctive. Both plots show the close association of the grassland communities, *Protea* savanna and high altitude vlei on the basis of their soil spectra, although the DECORANA plot includes the low altitude vlei samples into this agglomeration and the PCA plot includes the alpine communities, *L. sericea* scrubland and sub-alpine fynbos.

The trap plots, although dissimilar with regards to centroid value orientation, both exhibit the same phenomenon. Samples plotting along a line such as is observed in the DECORANA plot is usually associated as being the effect of some environmental constraint such as altitude or water availability. In this case it is the result of the relative percentage frequencies of the various taxa present. For example the *Podocarpus* forest and *L. sericea* scrubland communities have lower Poaceae values than the other communities and are dominated by taxa other than Poaceae. They are plotted apart as they do not share the same dominant taxa. As the dominance of Poaceae increase in the samples an agglomeration of the samples occur as is evident by first the low altitude vlei then all the grassland samples. The sub-alpine fynbos, as a consequence of high Poaceae and Asteraceae values, are next followed by the *Protea* savanna samples which, although having a high Poaceae relative frequency, is co-dominated by Proteaceae, thus separating these samples from the rest. This trend is not as well established in the PCA plot, although the resemblance of it in the form of the crescent shaped concentration of samples is observed. All four principal components were plotted against each other for all the combinations possible, but the resultant plot was either a crescent or 'V' shaped plot. The PCA plot for trap spectra does show distinctive *Podocarpus* forest, *L. sericea* scrubland, sub-alpine fynbos and *Protea* savanna groups and a close association between the grasslands with each other and with the low altitude vlei community. The DECORANA plot formed two distinct concentrations of *Leucosidea sericea* samples due to the high *L. sericea* pollen production during the winter/spring collecting periods resulting in distinct seasonality. This phenomenon is not observed in the PCA plots.

Overall the DECORANA plots prove to be a better representation than the PCA plots. This subjective view takes into account the fact that the plot axis are not the same. It is not possible to objectively compare the two plots, for example by overlays, as the techniques use different techniques of analysis and such a comparison would be misleading. For the vegetation data distinct groups of samples which reflect particular vegetation communities or groups of communities are evident, while both the soil and trap plots for both techniques show that the more distinctive communities based on pollen rain are the *Podocarpus* forest, *L. sericea* scrubland, sub-alpine fynbos and to a lesser extent *Protea* savanna and the low altitude vlei communities. The alpine communities form a distinctive grouping while the grasslands show only subtle differences between the various communities. Furthermore it is evident from the clustering of spectra from any one particular vegetation community, that although there is a close association between some of the communities, all the spectra of a particular community are clustered together and therefore are similar and all represent the same community. For example despite the fact that the grassland spectra are closely associated to each other the spectra of a particular vegetation community still retain some individuality due to the abundance of the less dominant taxa and the relative percentage frequency of the dominant taxa.

8.11 MULTIPLE DISCRIMINANT ANALYSIS

Discriminant functions were determined for the modern pollen rain samples and classified into ten (for trap samples) or thirteen (soil samples) *a priori* groups which represented the studied vegetation communities. The resultant plots showed that all the samples from a particular community were closely associated and that all samples were concentrated around the centroid value with no anomalies existing. As a consequence it is not possible to display all the samples and the centroid values on the same plot, therefore separate graphs are presented (Section 7.6). The MDA plots generally confer with the DECORANA and PCA plots and display the close association between the grassland communities while the remaining communities display varying degrees of distinctiveness (Section 8.12 for comparison).

The vegetation zonal indices of both the soil and trap pollen spectra are well defined and only a few samples do not display a 100% representation of the community from which they were collected. The soil spectra discrepancies are in the order of a 0.1 (or 10%) discrepancy and are therefore of minor importance and are to be expected due to the close association between the various communities. However the trap spectra discrepancies, although few in number, have a greater effect on the resultant diagram (Figure 7.24). A single low altitude vlei sample and two samples each from the *Festuca costata* grassland and *L. sericea* scrubland more closely resemble the communities adjacent to them in the diagram. These variations are as a consequence of regional pollen inflow into the sampled communities. Regional pollen influx is the norm in such studies and possibly occur to some extent in this study region, but as the taxa composition is similar, at the family level, it is difficult to record this regional pollen flow.

The 'palynological signatures' or the probability of a modern analogue index is high for the majority of the pollen spectra. These high values imply that the pollen rain samples are indicative of the community from which they were collected and that if a fossil pollen spectra correlated with respect to taxa composition and relative percentage frequencies to a particular group of modern pollen spectra, then it is highly probable that the fossil pollen spectra is representative of the corresponding vegetation community from which the modern pollen spectra originated. The MDA diagram (Section 7.6.5) is analogous to the use of a modern pollen reference collection to help identify fossil pollen grains. Results of the study show that the probability of a modern analogue is high for all the studied vegetation communities including the closely associated grassland communities. Although the pollen trap spectra appear, from the subjective analysis of the DECORANA, PCA and MDA plots as well as the ordination technique of TWINSPAN, to produce more distinctive pollen spectra for a vegetation community, the soil spectra have the better probability of modern analogue scores. This is because the soil spectra showed less variation with regards to taxa and relative percentage frequencies between samples than was observed in the trap data. The soil spectra are the result of an accumulation of pollen rain over a number of seasons and years and therefore represents the 'average pollen rain' rather than particular time periods. Therefore the soil spectra, although not as distinctive between communities, tends to show less variation and as a consequence gives a better probability of modern analogue index. Furthermore the soil spectra will more closely resemble the fossil pollen spectra as the soil spectra is a reflection of the pollen rain which finally reaches the ground and is preserved, as opposed to the pollen trap spectra which is an indication of the general pollen rain of the area and not necessarily a reflection of the pollen which reaches the soil.

Overall, the modern analogue probability values are high, implying that if a fossil pollen assemblage displayed a spectra which correlated with the modern pollen spectra it would, in all probability, represent the corresponding vegetation community from which the modern pollen rain spectra originated. For a comparison between modern and fossil pollen assemblages it appears that the soil spectra would produce the best results, as the soil spectra display less variation within any one vegetation community, although the trap spectra are also closely associated.

8.12 COMPARISON BETWEEN MDA, DECORANA AND PCA

As a consequence of performing a multiple discriminant analysis (MDA) to obtain values of probability of a modern analogue and a vegetation zonal index the results can also be plotted using the first two discriminant functions (Section 7.6.2-3). The plots are compared with the results from DECORANA and PCA. Once again it must be noted that the axis scales are not the same, with the MDA functions being plotted on a much larger scale than the other two plots. It is possible to alter the MDA plot axis scale, but the resultant plot is no more meaningful as the comparison is subjective and it only makes it more difficult to discern the high concentration of the grassland samples.

Both the *Podocarpus* forest and *L. sericea* scrubland soil pollen spectra centroids are distinctive from the other communities in both the MDA and DECORANA plots, while only the forest community is distinctive in the PCA plot. In the MDA plot all the centroids are closely associated although sub-alpine fynbos and low altitude vlei are slightly separated, but closely related to each other, while *Erica-Helichrysum* heathland and *Protea* savanna are also slightly more distinctive than the grasslands and high altitude vlei communities. Although these centroids are all relatively close to each other, particularly when compared to the

DECORANA and PCA plots, these communities are distinct. It is not possible to correlate the distances between the centroids as meaningful when comparing two separate techniques as the distances are relative to that particular technique only. On closer inspection the MDA and DECORANA plots are very similar with, in both plots, the *Podocarpus* forest, *L. sericea* scrubland, sub-alpine fynbos, low altitude vlei, *Protea* savanna and *Erica-Helichrysum* heathland forming separate, more distinctive groups, while the grassland communities and high altitude vlei samples form a concentration of undistinguishable spectra.

There are general similarities in the trap spectra for all three plots. The *Podocarpus* forest, *L. sericea* scrubland, *Protea* savanna and to a lesser degree sub-alpine fynbos and low altitude vlei pollen trap spectra form distinctive communities. In all the plots the grassland communities are closely associated and the distinction between the communities, on the basis of pollen spectra, has to be determined from the presence or absence of the less prominent taxa.

8.13 SUMMARY

The question of number of soil samples was considered with the aid of an ANOVA and a minimum sample size calculation. The ANOVA results indicate that a soil sample size of ten would be sufficient in the *Rendlia altera*, *Festuca costata*, *Themeda triandra*, *Leucosidea sericea* scrubland, sub-alpine fynbos, alpine grassland and high altitude vlei. A sample of twenty is required in the Highland Sourveld, 'Mixed' grassland, low altitude vlei, *Protea* savanna, *Podocarpus* forest and *Erica-Helichrysum* heathland communities. These results are contrary to the calculation of minimum sample size which concluded that a sample of twenty was required for all the studied communities. The ANOVAs give an indication of the sample size and do not make any inferences about the representation of these sample sizes for a particular community. Similar calculations carried out on the pollen trap data revealed that the number of traps placed in each of the vegetation communities was sufficient to obtain a 1-5% degree of error which is acceptable for ecologically based data. To obtain as little as a 1% improvement would require a doubling or tripling of both the soil and/or pollen trap sample size which for the purposes of this study was impractible.

The use of absolute pollen influx values obtained from the pollen traps in the montane and sub-alpine vegetation communities give a good indication of mean annual and seasonal variation. To a greater or lesser extent all the communities exhibit seasonal pollen influx variation with the grassland and *Protea* savanna communities displaying the more 'normal' low winter - high summer trend. The *Podocarpus* forest and *Leucosidea sericea* scrubland communities seasonal variation is dominated by the seasonal flowering of certain species such as *Celtis africana* (Ulmaceae) and *Leucosidea sericea* respectively. The low altitude vlei site exhibits a spring high, while the data for sub-alpine fynbos is incomplete. The effect of burning culminating in the early flowering and resultant pollen production was observed in the Highland Sourveld and *Rendlia altera* grassland communities.

A marked annual pollen influx variation is not recorded although there are variations between the two sampled years, in particular within the high pollen producing *Podocarpus* forest. This is contrary to what was expected as individual taxa did display significant annual fluctuations when annual trap spectra were examined. The reason for calculating pollen influx values was to aid the descriptive analysis of the pollen rain for the vegetation communities as the absolute values allow one to compare pollen influx and possible production between communities as well as with other studies.

The ANOVAs performed served several functions; firstly they allowed for an improvement on the seasonal/annual pollen influx fluctuation question. The initial results were inconclusive, however by applying an ANOVA to only the more dominant taxa within each community the results showed conclusively that both annual and seasonal variation occurred based on individual taxa. These relative percentage frequency results enhance those of the absolute values applied to calculate the pollen influx values. Secondly ANOVAs were used to improve upon and make recommendations for a modern pollen rain sampling strategy. It was determined that a count of 250 pollen grains and spores was sufficient in all the studied vegetation communities except Highland Sourveld, *Protea* savanna and *Leucosidea sericea* scrubland. In these communities the dominant taxa were calculated to show a significant difference between the counts of 250, 500 and 1000 pollen grains and a count of 500 is recommended for the Highland Sourveld community and a count of 1000 for the *Protea* savanna and *L. sericea* scrubland communities.

The descriptive analysis of the pollen spectrum clearly show that there is a relationship between the pollen rain characteristics and the vegetation producing the pollen, and this is true for both pollen rain collecting techniques employed. On a broad scale there is an obvious division between the grasslands and the more complex communities. The *Rendlia altera* grassland is distinguishable by the presence of the arboreal taxa (in low relative percentage frequencies) from the surrounding down-wind communities. The three temperate grasslands have very similar spectra, although the presence of the woody invasive Anacardiaceae distinguishes the 'Mixed' grassland. The *Themeda triandra* and *Festuca costata* grasslands cannot be divided on the basis of their soil spectra alone, although a division can be made on the higher Asteraceae relative percentage frequency in the *Themeda triandra* trap spectra. The alpine grassland is distinguished by the presence of the hygrophilous Cyperaceae, Juncaceae and Crassulaceae taxa.

All the remaining communities are distinctive, with the dominant vegetation species of that particular community dominating the pollen rain spectra. Certain pollen types, in particular Poaceae and Ericaceae (except in high altitude vlei), appear in all the pollen spectra and can be regarded as well-dispersed. Both the exotic species from this area *Pinus patula* and *Acacia mearnsii* fall into this category, but have, for reasons already explained (Section 5.3.3), been excluded from the pollen sum.

The descriptive analysis will aid any fossil pollen analysis as it has been shown that the modern pollen rain is a good reflection of the existing vegetation and the spectra give a good indication of the regional vegetation, in particular the low and high altitude vlei sites on which any future palynological investigation would have to concentrate. Therefore any possible shifts which may occur or have occurred in the vegetation assemblage are likely to alter the pollen spectrum of these communities. As the pollen traps and soil samples provide a good indication of the regional, as well as local vegetation cover, it is expected the fossil pollen spectra would give a good indication of former regional vegetation patterns.

Canonical correlation results generally show a strong correlation between each of the three data sets and confirm the conclusions reached by Meadows (1984) who compared pollen trap and soil samples from the Nyika Plateau in Malawi and a similar study by Hamilton and Perrott (1980) from Mt. Elgon on the Kenya/Uganda border. There are a few anomalies with regards to this close correlation. Meadows (1984) obtains a much higher Cyperaceae pollen value for the soil samples of the dambo or vlei site (as was the case for the low altitude vlei site of this study) and despite Hamilton and Perrott's (1980) statement that "...the most striking feature is the similarity of the spectra..." (pp. 455) there was a consistent and obvious higher Urticaceae pollen value in the trap spectra of their study. Neither of these studies sampled the pollen rain in as many or varied vegetation communities as this study with similar conclusions being reached.

The canonical correlation analysis produces a high correlation between pollen trap spectra and the vegetation spectra of the more complex and stratified vegetation communities and the higher correlation or association of the surface soil spectra and vegetation of the grassland and single stratum dominated communities. The trap spectra are the truer representation of the taxa recorded in the more complex vegetation communities as the traps entrap the arboreal taxa pollen which is transported through the community but which may not reach the soil surface. Furthermore the arboreal pollen which does not reach the soil surface can be detained by the overlying vegetation and may be lost via refloatation. Also the arboreal taxa pollen which does become included in the soil profile can be 'lost' or 'masked' due to the proportionality high ground stratum pollen. Therefore the trap spectra of these communities, *Podocarpus* forest, sub-alpine fynbos, *Leucosidea sericea* scrubland and *Protea* savanna are a better representation of the taxa composition than the soil spectra. However, it needs to be borne in mind that the soil spectra become more important with regards to possible fossil pollen analysis as it is the pollen that reaches the soil and is preserved that will ultimately represent the vegetation community with regards to fossil pollen studies.

The soil/vegetation spectra correlation is conversely higher in the grassland and vlei communities due to the dominance of the ground stratum species. Despite these pollen spectra discrepancies the overall soil and pollen trap spectra correlation is high, thus indicating that the two pollen rain collecting techniques do display similar resultant spectra. The greatest variation was between the pollen spectra of the arboreal dominated *Podocarpus* forest and *Leucosidea sericea* scrubland communities where, despite having similar ground stratum taxa composition, the arboreal taxa dominate the pollen spectra, often (proportionality wise) to the detriment of the other taxa.

The TWINSPAN, DECORANA, PCA and MDA plots show that the vegetation samples group to form distinctive communities which reflect the sampled sites. The soil and trap spectra of the more complex, two strata vegetation communities where taxa other than Poaceae dominate or are in co-dominance (*Podocarpus* forest, *L. sericea* scrubland, sub-alpine fynbos, *Erica-Helichrysum* heathland, and to a lesser extent, *Protea* savanna and low altitude vlei) form distinctive groups. Therefore on the basis of both soil and trap spectra these communities can be identified and the resultant pollen rain spectra of these communities are unique and are distinctive from each other. In the case of the grassland communities and the high altitude vlei, is not possible to distinguish distinctive soil or trap spectra on the basis of PCA, DECORANA and MDA plots, as there are close associations between the communities on the basis of the pollen rain.

The problems encountered in identification below the family and, sometimes, genus level renders the use of multivariate statistical analysis in the identification and description of pollen assemblages, be they modern or fossil, important. By employing a comprehensive modern pollen sampling programme it proved possible, particularly with MDA, to recognize pollen 'signatures' for particular vegetation communities. These 'signatures' are extremely useful with regards to future fossil pollen analysis in the region. MDA facilitates the statistical comparison of a pollen spectrum and its corresponding vegetation community and enables modern analogues to be identified for comparison with fossil pollen spectra. The results of this study's MDA show a clear association of both the soil and trap spectra to the vegetation community from which they were collected.

With the aid of MDA palaeo-vegetation types can be inferred from fossil pollen assemblages and, without known modern analogues by computing the probability of a modern analogue. This probability is greatest when the zonal index approximates 100% similarity to a particular vegetation assemblage. This study identified and sampled ten (for pollen traps) and thirteen (in the case of soil samples) vegetation communities which could possibly be recognized or most likely occur within a fossil pollen assemblage. These communities were sampled and vegetation zonal indices and probability of a modern analogue values were calculated so as to enhance future fossil pollen analysis from this region and to develop a better insight into the pollen rain - vegetation relationship. Consequently good modern analogues are achieved which will prove extremely useful in aiding the correct identification of vegetation communities based on a fossil pollen assemblage collected from the Natal Drakensberg region.

CHAPTER NINE
CONCLUSIONS

9.1 INTRODUCTION

The objective of this study was to answer the question of whether or not the modern pollen rain of a particular vegetation community is indicative of and distinctive for that community. The study was carried out in a region with a high fossil pollen analysis potential, the Natal Drakensberg. If the above assumption is proved correct then the principle of methodological uniformitarianism can be applied, which states that present-day patterns and relationships can provide a factual basis for the reconstruction of the past through the extrapolation of modern analogues backwards in time. With respect to this study this implies that modern pollen spectra can be used to help determine and interpret palaeo-environments based on fossil analysis, if the modern and fossil pollen spectra are analogous.

Objectives set-up to study the basic assumption that the pollen rain is indicative of the vegetation community from which it originated (Moore *et al*, 1991) are outlined in Chapter 1. All of these objectives have been met within the limits of this study. The principle objectives were:-

- to identify, describe and quantify vegetation communities most likely to be effected by environmental change in the research region;
- construct a pollen reference collection for the region;
- quantify the contemporary pollen rain from the vegetation communities;
- compare the modern pollen spectra with the existing vegetation from the source habitats;
- compare the two modern pollen sampling techniques;
- set-up modern pollen spectra analogues which can be used to facilitate fossil pollen studies; and
- recommend a sampling strategy for future modern pollen rain studies in South Africa.

During the study, as a consequence of the techniques employed to describe the pollen spectra, it became evident that further discussions were necessary. These included comparing the various statistical techniques used to determine the distinctiveness of the individual pollen spectra and the annual and seasonal pollen influx fluctuations.

9.2 VEGETATION ANALYSIS

From the initial field survey thirteen vegetation communities were identified as being suitable in the context of the study's objectives. These communities either represented the dominant or climax communities within a particular altitudinal belt, were seral stages towards the climax community or developed/exist as a consequence of distinct topographical or geomorphological features. Environmental changes lead to altitudinal shifts or migration of vegetation communities and each species reacts to these changes according to its ecological adaptability. The consequence of such changes is that many species that have similar sensitivity to the environmental conditions occupy similar habitats and an altitudinal shift of such communities is an indication of changes in the environment that have taken place through time (van Zinderen Bakker and Coetzee, 1988). This principle is often oversimplified and it must be considered that, with environmental change, species will migrate but whole communities will not necessarily follow suit.

The vegetation communities were quantified by identifying and measuring the aerial cover of the species present within predetermined sized, marked quadrats. Quadrat size was determined by discussion with researchers in the area, while quadrat number was determined by plotting cumulative species/quadrat number curves for each community.

Although the pollen data were recorded to family level, the initial vegetation survey was conducted to species level. This ensured a more accurate representation for the descriptive analysis of the vegetation and it is possible to group the species into their respective families during analysis, while it is not possible to work the other way around. The communities are described with the aid of vegetation spectra which represents the species at a family level, to facilitate comparisons with the pollen spectra, and a species list (Appendix 6).

The statistical tests of two-way indicator species analysis (TWINSPAN), detrended correspondence analysis (DECORANA) and principal components analysis (PCA) were performed to help describe the distinctiveness or, in the case of the grassland communities, the close association between the various communities.

9.3 POLLEN REFERENCE COLLECTION

From the studied vegetation communities and the surrounding vegetation all flowering or spore producing species were collected and used to complement the pollen reference collection housed at Rhodes University. The reference collection has slides of approximately 700 species, most of which have been photographed to form a photographic reference collection. The photographic reference collection proved easy to use during the counting procedure, with the slide collection used as a check when morphologically similar pollen grains proved more difficult to identify. The presence and development of this reference collection is vital to ensure accurate identification of the pollen rain. A number of pollen atlases and pollen morphological references were also consulted, however they are poor substitutes for a local reference collection and experience. Despite the fact that scanning electron microscopy (SEM) of the pollen grains would greatly enhance the visual aspect it is not envisaged that SEM will become an important component of modern/fossil pollen analysis at this initial data collecting stage. SEM is a useful tool in helping identify morphologically similar pollen grains and spores, for example the genera *Podocarpus* and *Pinus*, but overall as the pollen counting procedure is performed at the light microscope level, SEM of all the pollen grains and spores would possible be of little value. The results of SEM are of too high a resolution to be used during the light microscope procedures and it is possibly more beneficial to obtain light micrographs of pollen at various depths of field and orientation as opposed to proceeding with SEM work.

9.4 MODERN POLLEN QUANTIFICATION

Modern pollen rain was collected with the aid of surface soil samples and pollen traps over a two year sampling period. The pollen traps were used to obtain an accurate measurement of the pollen influx both on an annual and seasonal basis, while the soil samples represent an 'average' pollen influx for an unspecified number of years. Both soil and trap pollen spectra are represented as rotated bar graphs (Chapter 7) and as lists (Appendix 5).

The soil pollen spectra display a dominance of the Poaceae taxon in all communities with the exception of *Erica-Helichrysum* heathland. This over-representation is in the order of 5-20% in comparison to the vegetation analysis and is possibly as a consequence of Poaceae often overlying the soil sample sites, being a high pollen producer, a good pollen disperser or more resistant to decay. Although this value is described as an over-representation it is only done so in comparison to the vegetation analysis values and could possibly be better described as a high representation. Despite the random sampling technique used, this high or over-representation could not be avoided (dispersal bias). The fact that the Poaceae relative percentage frequency is high has a proportionality effect upon the other, less dominant, taxa, which needs to be borne in mind during analysis. Arboreal taxa, for example in the *Leucosidea sericea* scrubland community, are under-represented in the soil spectra. These lower than expected arboreal relative percentage frequencies is possibly due to pollen of the arboreal taxa being wind-transported away from the source area or that some of the arboreal pollen which precipitates to the ground is detained by ground stratum vegetation and is 'refloated' into the atmosphere.

The high representation of the Poaceae taxon is reduced in the pollen trap spectra and the arboreal and Asteraceae taxa become more prominent. This prominence is possibly due to two reasons; firstly the dominance of Poaceae is reduced in the spectra and therefore the 'masking' effect of a high percentage of a single taxon is reduced and, secondly, the pollen traps receive proportionality more arboreal and Asteraceae pollen as this pollen is wind-transported above the ground vegetation stratum. The pollen trap spectra tend to bear a closer resemblance to the taxa present in the more complex stratified communities and also exhibit a regional pollen flow as a number of taxa collected in the traps are not recorded from the sampled vegetation community. Of particular interest is the pollen trap spectrum of the *Rendlia altera* grassland which displays pollen from both the down-wind and valley *Podocarpus* forest and *Protea* savanna communities. Due to uneven heating of the valley sides, which causes a day up-valley wind, pollen from the arboreal taxa of these communities are transported upwards and deposited on the plateau above. This phenomenon is more pronounced in the trap spectrum of the *Rendlia altera* grassland due to the fact that the traps are able to sample the atmospheric pollen that moves over the area, while the soil spectrum reflects only the pollen which settles on the surface of the samples area. The arboreal taxa are represented in the soil spectrum, but, due either to their normally low values or to the proportionality high Poaceae value, they have a low percentage relative frequency and go un-noticed, whilst they are more evident in the trap spectrum.

9.5 INFLUX VALUES

Seasonal and annual pollen influx variation is recorded in all the montane and sub-alpine vegetation communities. The grassland communities and *Protea* savanna display a low winter, high summer seasonal variation predominantly due to the seasonal fluctuation in Poaceae pollen production. The high *Protea* savanna summer value is further emphasized by the *Protea* species producing and dispersing pollen during this period. The remaining communities all display seasonal pollen influx variation governed by the pollen production time of the community dominants or co-dominants.

Annual pollen influx variation is not as obvious from the calculation of total pollen influx per year for the communities. Despite often large seasonal discrepancies between the two sample years, the total annual pollen influx values do vary, but not as significantly as recorded by previous studies (Bonny, 1980; Cadman, 1990; Hall, 1990).

The annual and seasonal fluctuations were further described by means of performing an analysis of variance (ANOVA) on the data sets. Initial results proved inconclusive, however when only the dominant taxa from each community are considered results supported the conclusion that both seasonal and annual fluctuations did occur.

Overall the *Themeda triandra* grassland (2786.3 grains/cm^2/year) and *Podocarpus* forest (2624.9 grains/cm^2/year) proved to be the highest pollen producers, while the low altitude vlei recorded a low value of 1078.1 grains/cm^2/year. A surprising result was the low *L.sericea* scrubland annual pollen influx value. High *L. sericea* absolute pollen values were recorded, but the other taxa produced low counts. This could be due to climatic variables such as less sunlight hours or cooler temperatures received by the community, the fact that the *L.sericea* scrub 'shades-out' a large proportion of the understorey and therefore the ground vegetation produces low pollen counts, or due to the fact that this community is in a protected catchment of the research region and has not been burnt either naturally or man-induced for approximately thirty years. A large proportion of the vegetation could be beyond the reproductive stage or simply produces less pollen as it is not stimulated by a regular fire which has the effect of increasing vegetation growth and reproduction.

9.6 COMPARISON OF SOIL AND TRAP SPECTRA

The pollen trap spectra, from traps situated at one metre above the ground, tended to be more representative of the regional vegetation than the surface soil samples. The trap spectra exhibited a truer reflection of the arboreal taxa present,whereas the soil spectra had an over-representation of the Poaceae taxon which 'masked' the proportion of the taxa present in lower percentages. The difference in representativity of the two sampling techniques is due, as recorded by Sugden (1990), to the life-forms and stratified structure of the vegetation and not due to differences in pollen preservation between the two techniques.

The soil samples tended to reflect an over-representation of Poaceae and an under-representation of the arboreal taxa, while the traps tended to produce a more representative spectra, making pollen trap data more reliable as modern pollen analogues. This causes a problem as although the trap spectra is more representative of the regional and local vegetation, it is the soil spectra which is a truer representation of the pollen rain which reaches the ground and has the potential, given the optimum environmental conditions, to become preserved. Therefore a fossil pollen spectrum is more likely to be similar to a soil as opposed to trap spectrum for any particular community. So although the trap spectra is a truer reflection of a communities pollen rain it is the soil spectra which will be a closer representation of the pollen which will be preserved to form the fossil pollen spectrum.

Canonical correlation analysis was generally high for both soil and trap spectra in relation to the vegetation. However the soil spectra of the Poaceae dominated communities showed a stronger correlation than the more complex structured communities, while the reverse is true for the trap spectra. This confirms the conclusions of the descriptive results regarding the over-representation of Poaceae and under-representation of the arboreal and Asteraceae taxa in the soil spectra, while the arboreal and Asteraceae counts are, proportionality, better represented in the trap spectra. Therefore the canonical correlation analysis is stronger between traps/vegetation as opposed to soil/vegetation for the stratified, vegetation communities where arboreal taxa have a greater representation.

There is a high correlation between the trap and soil spectra for all the communities with the exception of *L. sericea* scrubland and *Podocarpus* forest as was depicted by canonical correlation analysis and analysis of variance. These two weaker correlations are due to the under-representation of arboreal taxa in the soil spectra being exaggerated in these communities, which are dominated by arboreal taxa. A similar situation arises in the *Protea* savanna community although to a lesser degree due to the high proportion of Poaceae in the understorey vegetation.

Despite some obvious differences between the two pollen spectra, the overall results suggest that the modern pollen rain spectra from both sampling techniques is a good reflection of the vegetation communities which produced it. These results confirm the earlier conclusions of Hamilton and Perrott (1980), Meadows (1984), Scott (1982a, 1984b, 1989a), Meadows and Meadows (1988), Sugden and Meadows (1989), and Meadows and Sugden (1991a,b). This is an important comparison as it is the relationship between present-day pollen rain and the pollen actually arriving at the site of preservation (the soil) which is indicative of the usefulness of fossil pollen data (Meadows, 1984). Both pollen spectra prove to be good indicators of the existing vegetation. As a consequence, any fossil pollen spectra from the region, would be expected to be representative of the former regional vegetation patterns.

9.7 RELATIONSHIP BETWEEN POLLEN RAIN AND VEGETATION

The extensive contemporary pollen rain programme was undertaken to establish the existence of the pollen - vegetation relationship and to determine how closely the modern pollen relates to the vegetation of the study region. If a relationship exists then it is necessary to determine if this relationship is unique, for example does a community's modern pollen spectra represent that community and distinguish it from other communities. The descriptive analysis proves, albeit, subjectively, that there is a close and direct association between the pollen rain characteristics and the vegetation which produces the pollen. Both the soil and trap samples provide a good indication of the regional and local vegetation cover. Therefore one would expect any fossil pollen spectra from the region to yield a good indication of the former vegetation patterns.

The statistical tests of TWINSPAN, DECORANA, PCA and MDA were applied to the data sets and the results presented in the form of graphs. These graphs can be subjectively compared against each other, both for data sets from the same statistical test and between tests. Overall the plots show how similar samples of a particular spectra are to each other, so much so that often it was not possible to distinguish the centroid plot amongst the actual plots. This implies that all the spectra from a particular community closely resemble each other and any one of those spectra could be representative of the community. However exceptions do occur, such as the 'Mixed' grassland vegetation sample PCA plot (Figure 7.19). Here the samples are well dispersed in the plot as a consequence of the community sharing a number of taxa with the surrounding grassland communities, therefore the samples do not form a distinctive nucleus.

The plots of the various tests differ as a consequence of axis scales and the approach used in each test. Generally the DECORANA, and associated TWINSPAN, plots proved most effective for interpretation. The plots show that the more complex structured and stratified communities, where Poaceae did not dominate or was a co-dominant, displayed distinctive soil and trap spectra, for example in the *Podocarpus* forest, *Leucosidea sericea* scrubland, sub-alpine fynbos and, to some extent, low altitude vlei and *Protea* savanna communities. The *L. sericea* scrubland displayed two distinct trap spectra as a consequence of the strong seasonal influence of *L. sericea* flowering and pollen production on the rest of the relative percentage frequency spectrum. The grassland communities and those communities dominated by Poaceae are more closely associated and these communities retain their spectra distinctiveness based on the presence or absence and relative percentage frequencies of less prominent taxa.

Multiple discriminant analysis acts, in this study, much as a summary of both the descriptive and statistical conclusions. It allows firstly for a statistical comparison between a modern pollen spectrum and the vegetation community from which it originated and secondly allows for modern analogues to be displayed which are invaluable in analysing or interpreting fossil pollen spectrum. Both the soil and trap spectra produced high modern pollen probability analogue values implying that if a fossil pollen assemblage displayed a spectrum which correlated with the modern pollen spectrum it would, in all probability, represent the corresponding vegetation community from which the modern pollen rain spectra originated. Both the soil and trap spectra produce good modern analogues which can be used in future fossil pollen analysis. Despite the general over-representation of Poaceae and under-representation of Asteraceae and arboreal taxa it is recommended that the soil spectra analogues are more closely adhered to. Whereas the trap pollen spectra more closely represent the actual vegetation from which they were collected, thereby proving the assumption that there is a relationship between the pollen rain and the vegetation, it is the pollen which reaches the soil and is preserved which will be recorded in the fossil pollen assemblage. Therefore it is appropriate to use the soil samples despite the above mentioned discrepancies.

9.8 SAMPLING STRATEGY

It is not possible to set down any hard rules governing a sample programme of this nature as each situation presents itself differently. However, as a consequence of the extensive sampling programme followed in this study some guidelines are put forward. These guidelines are suggested as a result of the soil and trap sample size calculations, analysis of variance on the appropriate data and experience gained during this study.

Quadrat size, shape and number needs to be determined in the field. An initial sample size of ten proved inadequate for vegetation quadrats as a cumulative species/quadrat number plot proved. Therefore a further ten samples were taken; the resultant curve proved that twenty was an adequate sample size and thereafter new species were added at the rate of 1 or 2 per five quadrats, therefore approximately fifteen to twenty quadrats was deemed sufficient. It was assumed that the additional 1 or 2 species per five quadrats would not effect the final pollen spectrum sufficient enough to warrant a larger quadrat sample size.

A preliminary surface soil pollen survey concluded that a soil sample size of twenty was adequate to be representative of the soil pollen (Hill, 1987). Adam and Mehringer (1975) found that considerable variation existed in the pollen content of surface soil deposits even when samples where collected close together. They concluded that at least five samples are necessary to provide a representative mean value for the major constituents of the pollen spectrum, while Stevenson (1985) collected ten random samples of the surface litter and thoroughly mixed before sub-samples were taken. This procedure was considered to provide an adequate representation of the local pollen rain.

Once soil pollen counts had been completed, during the present study, a calculation was carried out to determine, in retrospect, the optimum soil sample size at a given percentage error. Only the dominant taxa were considered, as the remaining taxa are present in such low proportions in the pollen sum that a 1% error calculation is meaningless. Results indicate conclusively that a sample size of twenty is adequate for all the vegetation communities other than *Podocarpus* forest, *Erica-Helichrysum* heathland and high altitude vlei to obtain a 2% error (98% confidence limit). The dominants of these three communities reflect a relative percentage frequency with a 5% error (95% confidence limit) for the twenty collected soil samples, which with the total percentage frequency of these taxa is acceptable. Therefore for an extensive soil pollen programme a soil sample size of twenty proved adequate for all thirteen vegetation communities. The relatively low sample size is possibly due to the soil samples being an 'average' pollen influx value for a number of unspecified years. Thus the seasonal and annual fluctuations experienced with trap data is eliminated. An ANOVA was performed to compliment the results of this calculation. Results of the ANOVA proved that, for a number of communities, the sample size could be reduced to ten, whereas the remaining communities required a sample size of twenty. Using both sets of results as a guide it is recommended that twenty surface soil samples be collected for all the vegetation communities under investigation regardless of the complexity of the vegetation structure of the community.

Despite expected seasonal and annual variation the number of pollen traps required to obtain a 1-5% error is not large, this is possibly due to the efficiency of the traps. The number of traps used in this study proved to be sufficient for most communities, although in the more diverse communities, for example *Podocarpus* forest, to obtain relative percentage frequencies to within a 1 or 2% error would require an impractical number of traps. This is where the difference between the 'average' soil sample pollen influx and the absolute pollen trap influx values come into perspective. For example in the *Podocarpus* forest 15 soil samples are required to gain a 2% error of the Pteridophyta, whereas 50 traps are required to obtain the same representation in the forest community. For the number of traps employed in this study most dominant taxa are within a 5% or better error. To improve this error to 1% as was possible in the soil samples, is impractical as a large number of traps (50-200) would be required. Such a large number of traps would bring associated problems, such as the time required to transport and set-up so many traps and the laboratory and counting time with inherent problems.

This study recommends that a maximum of fifteen to twenty pollen traps be placed in each community. This is a large enough sample size to get within a 5% and sometimes 2% error and also is sufficient to allow for the loss of some traps. To reduce the error from 2% to 1% would require, often, a tripling or quadrupling of traps which is not possible due to time constraint and the results would not be any more meaningful at the level of modern pollen rain - vegetation studies.

The number of pollen grains counted per sample so as to gain a good (1-5%) error with regards to the percentage relative frequency was determined with the aid of an ANOVA. The results conclude that for most of the studied communities a count of 250 would suffice, whilst a count of 500 grains needed to be considered for the Highland Sourveld community and a count of 1000 for the *Leucosidea sericea* scrubland and *Protea* savanna communities. This suggests that a higher count is required in the more complex and taxonomically diverse communities despite the fact that, according to the data obtained in this study, a count of 250 is sufficient to obtain a good representation of the taxa within the diverse *Podocarpus* forest community.

9.9 FUTURE RESEARCH

The elucidation of environmental change in South Africa is, according to Meadows (1988b), regarded as an important scientific goal as it is only thorough the understanding of past environmental fluctuations that we can effectively manage the present environment. There has been a "...quantum jump..." (Butzer, 1984 pp. 259) in palaeo-environmental evidence from South Africa since 1970, however the emerging picture is still no more than a first approximation, due to the high diversity and variability in the South African environment. It is obvious that a great deal more palaeo-environmental evidence is necessary to allow for a second and thereafter possibly a third approximation of the temporal and spatial patterns of South African palaeo-climates. Such evidence depends a great deal on the advancement of the science of palynology which enhances other fields of evidence, particularly within the time scale of the last 25-30 000 years.

However, to ensure accurate evaluation and interpretation on the basis of fossil pollen analysis, more palynological data are essential to refine the present picture (Scott, 1990). Pollen analysis is no longer the "...occult art..." as once described by Ogden (1977 pp. 151), rather it is now firmly based on statistical analysis and consequently accurate objective interpretations are possible. This improvement has come about and will continue to come through the study of contemporary pollen - vegetation relationships, as to understand the past we need to understand the present and assume that the ecological processes in operation today did so in a similar fashion in the past. Once this is understood then it is possible to establish objective transfer functions between fossil pollen spectra and palaeo-climatic conditions. To do this we need to understand the contemporary pollen - vegetation relationship, then expand on this relationship to determine the effects of various environmental parameters from which detailed and objective transfer functions can be calculated.

Future palynological research needs to be directed towards obtaining a "...closer grid..." (Scott, 1990 pp. 266) of fossil pollen data in both space and time. However these studies must be backed by extensive modern pollen studies so as to ensure accurate evaluation of the resultant fossil pollen spectra. South Africa has a paucity of 'traditional' palynological sites, such as peat deposits, however there are a number of potentially good regions which have yet to be investigated. One such region is the vast Natal Drakensberg/Lesotho Highlands region. This study presents an extensive contemporary pollen - vegetation investigation for the Natal Drakensberg, concluding that the basic assumption of the present day pollen rain is indicative of the surrounding vegetation community is correct. Therefore the next step is a detailed and thorough fossil pollen analysis of the region. A feasibility study of the region was carried out by the author during this study and a number of pollen rich cores were obtained from suitable sites, two of which were used in the context of this study - described as low and high altitude vleis, at varying altitudes. A palynological study taking cores at various altitudes within the same region would be an ideal approach to investigating species, and possibly to some extent community, migration as a result of environmental changes and the enhanced effect of altitude.

Fossil pollen analysis in conjunction with modern pollen studies have come to the fore in South Africa in the recent years (Scott, 1982a, 1984a, 1986a,b, 1987b, 1988a,b, 1989a,b; Meadows and Meadows 1988; Sugden and Meadows 1989; Meadows and Sugden 1990, 1991a,b). These works have obtained good modern analogues to back-up and ensure accurate interpretation of resultant fossil pollen assemblages which is vital for accurate interpretation of palaeo-climates and environments. Future palynological research needs to continue along the same lines. It is of utmost importance to obtain accurate fossil pollen assemblages from as many regions of South and southern Africa as possible. This can only be achieved by on-site modern pollen studies and is necessary before any true palaeo-climatic modelling can be attempted due to the floristic and climatic diversity experienced in the region.

9.10 SUMMARY

This study undertook an extensive modern pollen rain sampling programme in the Natal Drakensberg, a region recognized as having the potential for fossil pollen analysis (van Zinderen Bakker, 1955; Heusser, in Deacon, Lancaster and Scott, 1984).The main objective was to study the basic assumption of pollen analysis that the contemporary pollen rain is indicative of the surrounding vegetation in the context of vegetation communities identified as most likely to be in some way influenced in terms of environmental change.

The findings of this study are that the surface soil and pollen trap spectra do reflect the vegetation communities from which they originated. There are, as expected, discrepancies in the data sets, but they can and have been explained in terms of the idiosyncrasies of that particular community. The spectra of the two modern pollen collecting techniques are similar and both annual and seasonal pollen influx values are recorded, with the annual variation not as large as expected or recorded in previous studies. Recommendations are made regarding future modern pollen studies with regards to number of soil samples and pollen traps required, the magnitude of the pollen count and the statistical techniques most appropriate to clearly interpret the results.

As a consequence of the close association between the contemporary pollen rain and vegetation the assumption that the modern pollen rain is indicative of the surrounding vegetation and that the resultant pollen spectra can be recognized as being distinctive for the vegetation community is proved correct. Therefore future fossil pollen spectra from this region can be expected to give a good indication of former regional vegetation patterns. The study has extended the limited understanding of the contemporary pollen rain - vegetation relationship in South Africa and enables the interpretation of fossil pollen spectra with more confidence. In turn it gives greater credibility to possible Quaternary environmental change models required to help understand present and possibly future environmental change.

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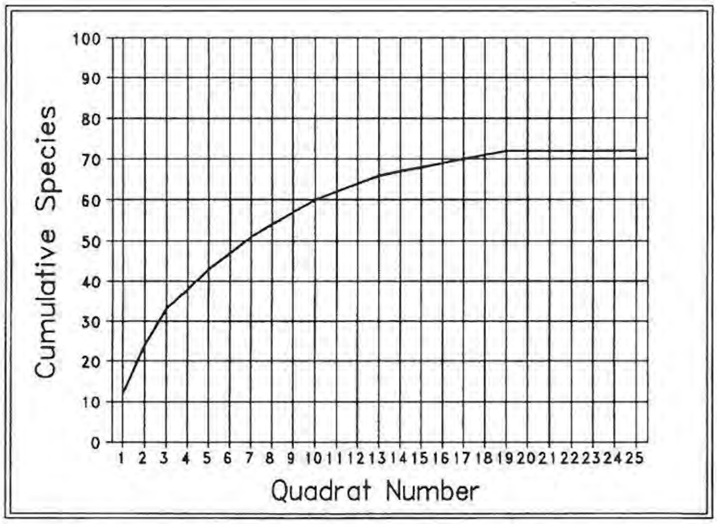
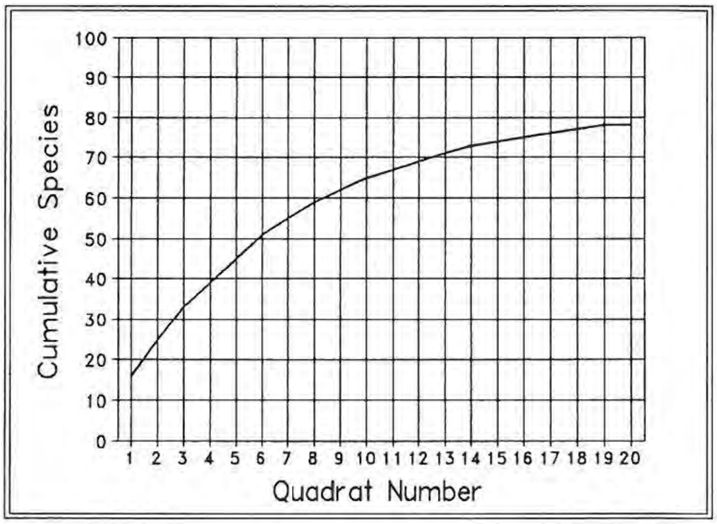
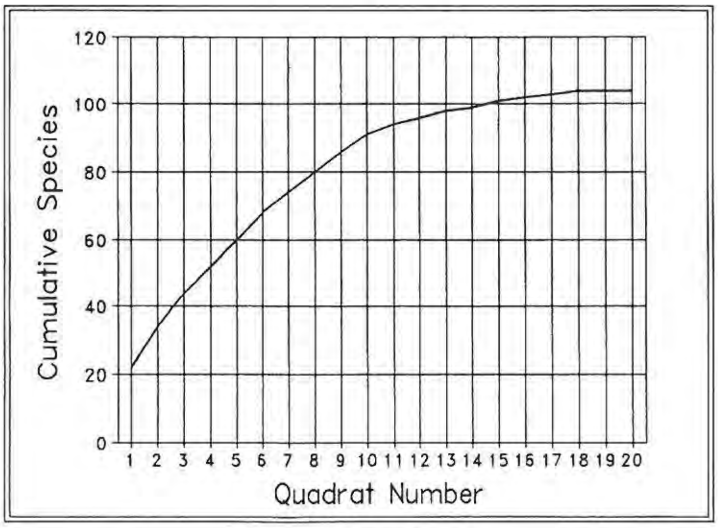
APPENDIX 1
CUMULATIVE SPECIES/QUADRAT NUMBER PLOTS



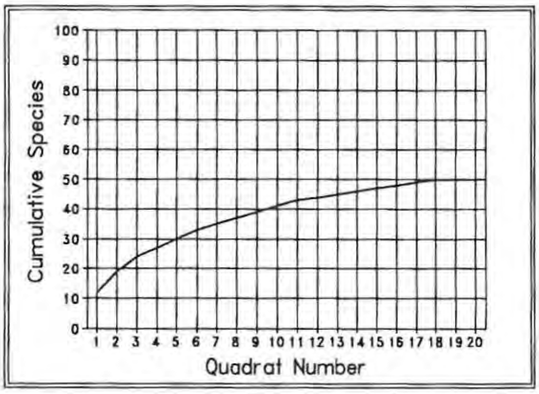
Themeda-dominanted Highland Sourveld



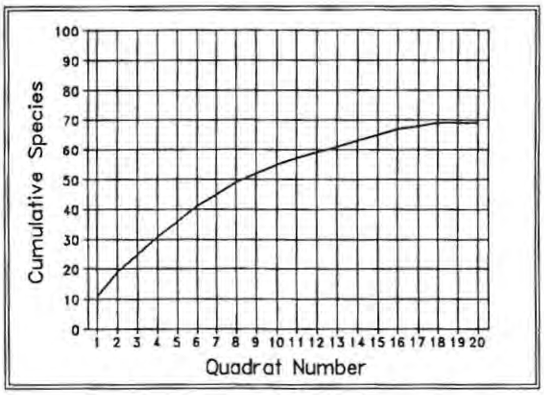
Protea savanna



Podocarpus forest



Rendlia altera grassland



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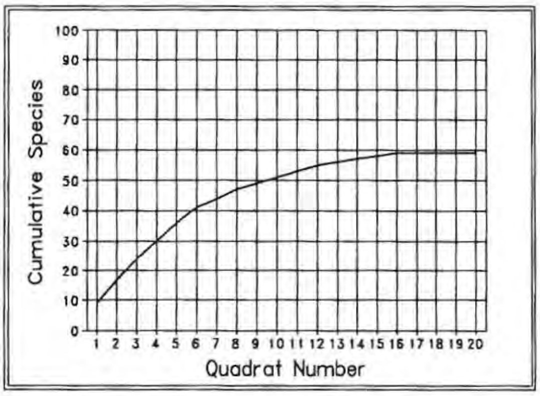
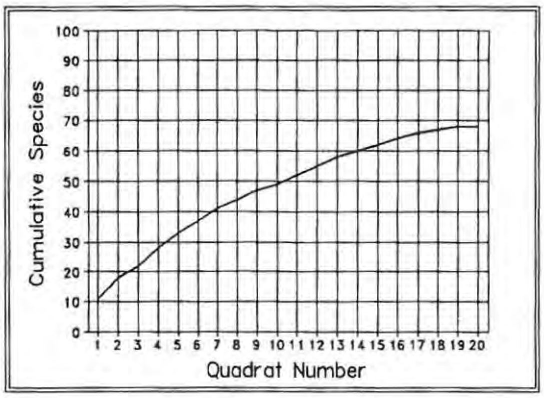
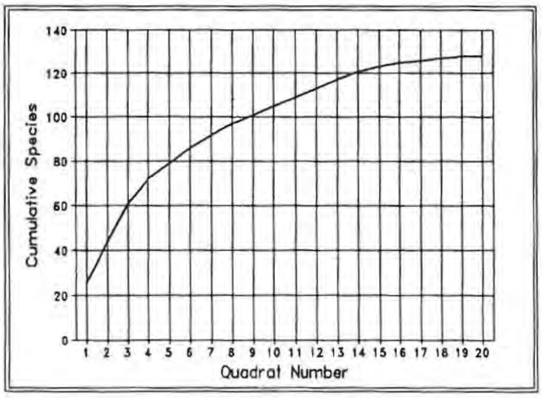


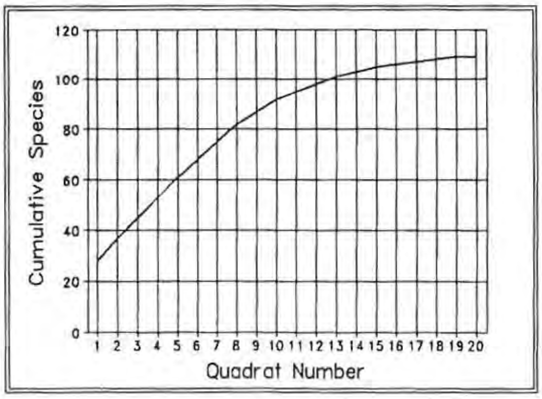
'Mixed' grassland



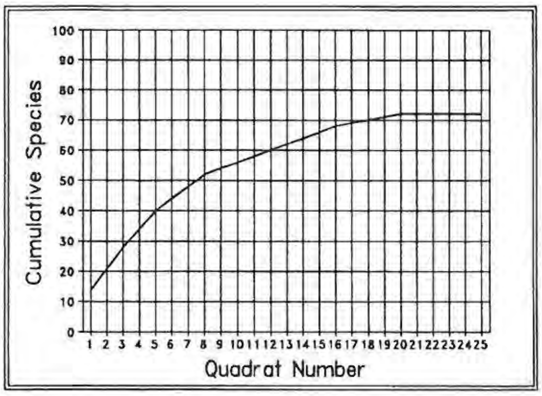
Festuca costata grassland



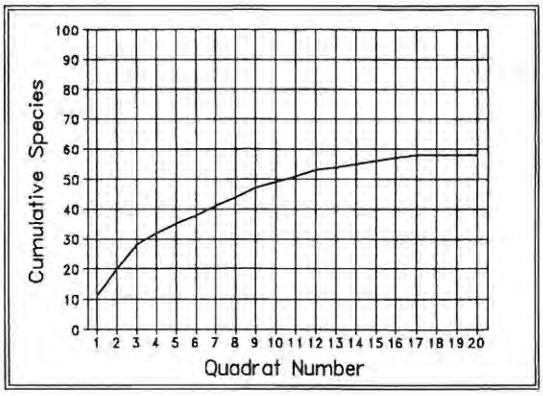
Leucosidea sericea scrubland



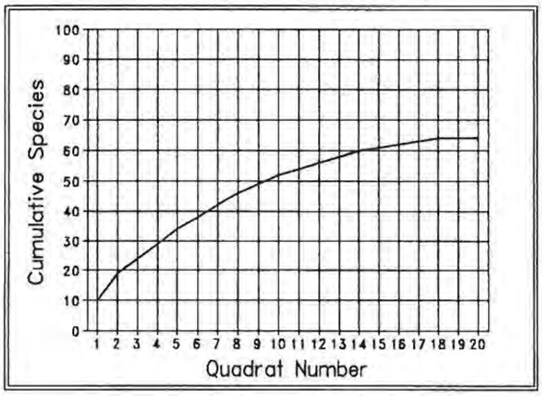
Sub-alpine fynbos



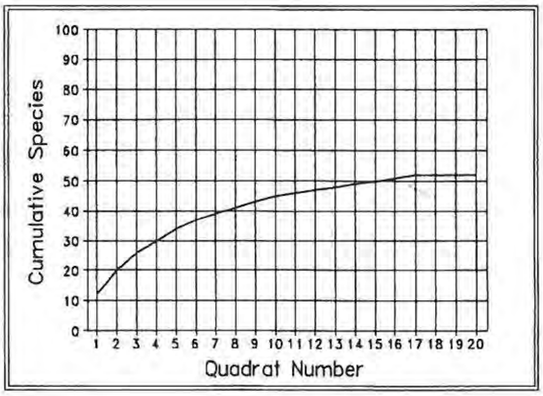
Low altitude vlei



High altitude vlei



Alpine grassland



Erica-Helichrysum heathland

APPENDIX 2

PREPARATION PROCEDURE FOR SURFACE SOIL SAMPLES.

1 Place 5 grams of soil sample into a 50 ml glass centrifuge tube.

2 Add 20 ml 10% NaOH and place in a heated water bath (80-90°C) for 10 minutes stirring occasionally.

3 Strain and wash through a 200 μm mesh sieve, using distilled water. This filtration does not retain or cause material to be discarded rather it acts to 'break-down' the material.

4 Centrifuge and decant the supernatant. All centrifuging is performed at 3 500 rpm for 3 minutes.

5 Wash five times with distilled water or until the supernatant becomes clear.

6 Wash with 20 ml 10% HCl. Centrifuge and decant.

7 Agitate and transfer to 100 ml polypropylene tubes.

8 In a fume cupboard, treat with 20 ml 40% hydrofluoric acid (HF) and place in a water bath for three hours, stir occasionally.

9 Stir, place caps on tubes then centrifuge and decant.

10 Decant sample into 20 ml glass centrifuge tubes using 10 % HCl. Place in heated water bath for 20 minutes.

11 Centrifuge and decant.

12 Wash with distilled water, centrifuge and decant.

13 Add 10 ml glacial acetic acid. Stir, centrifuge and decant.

14 Add acetolysis mixture and place in heated water bath for 5 minutes. Acetolysis mixture consists of 90 ml (9 parts) acetic acid and 10 ml (1 part) concentrated sulphuric acid. The acetloysis process is stopped by placing the samples into cold water.

15 Stir, centrifuge and decant.

16 Add 10 ml glacial acetic acid, centrifuge and decant.

17 Add 9 ml distilled water and 1 ml NaOH, to obtain a neutral pH. Stir, centrifuge and decant.

18 Wash with distilled water three times, adding two drops of aqueous Safranine stain in the last wash.

19 Add 5 ml tertiary butyl alcohol (TBA) to each tube. Stir, centrifuge and decant.

20 Transfer suspension to labelled vials using TBA, centrifuge and decant.

21 Add silicone oil equal in amount to pollen sediment. Store uncapped for 24 hours to allow TBA to evaporate.

For Counting Procedure:-

22 Stir the polliniferous silicone oil, with a magnetic stirrer or clean rod, until the pollen is evenly suspended.

23 Place a drop of silicone oil onto a clean slide.

24 Add drops of the polliniferous oil to the slide with a pasteur pipette. Add coverslip to the slide with a dissecting needle.

25 Relative percentage frequency pollen counts are performed.

APPENDIX 3

PREPARATION PROCEDURE FOR POLLEN TRAP MATERIAL

1 The acetate fibre is removed from the pollen trap and dried at 105°C for 1-3 hours.

2 The sample (acetate fibre, filters and solution of distilled water used to wash-out the pollen trap) is left to soak overnight in acetone, sufficient to cover the whole sample. Mixture is stirred thoroughly.

3 Decant into 50 ml glass centrifuge tubes. All residual material must be washed into the tubes with fresh acetone.

4 Centrifuge and decant. All centrifuging in the procedure is at 3 500 rpm for 3 minutes.

5 Sediment is washed through a 200 μm mesh sieve.

6 Filtrate is washed in acetone, centrifuge and decant.

7 Any excess acetone is evaporated off by placing the tubes in a heated water bath for 20 minutes.

8 Add 25 ml 10% NaOH and place in a heated water bath for 20 minutes. Centrifuge and decant into 100 ml polypropylene tubes.

9 Add 20 ml 40% HF, stir and place in a heated water bath for one hour.

10 Centrifuge (with caps on the tubes) and decant.

11 Decant sample into 20 ml glass centrifuge tubes using 10% HCl. Centrifuge and decant.

12 Wash with 10 ml glacial acetic acid, centrifuge and decant.

13 Acetolysis procedure as with soil samples.

14 Stir and place in a heated water bath for 2-5 minutes. Stop acetolysis process by placing samples into cold water. Centrifuge and decant.

15 Add 10 ml glacial acetic acid, centrifuge and decant.

16 Wash three times with distilled water, adding 1-2 drops of aqueous Safranine stain during last wash.

17 Stir, centrifuge and decant.

18 Add 10 ml TBA, centrifuge and decant.

19 Transfer suspension to small labelled vials using TBA, centrifuge and decant.

20 Add equal amount of silicone oil as sediment. Store uncapped for 24 hours to allow excess alcohol to evaporate.

Counting Procedure:-

21 Stir polliniferous silicone oil until pollen is evenly suspended.

22 Add a known volume of polliniferous oil with a pasteur pipette to a clean slide.

23 Place a coverslip, by means of a dissecting needle, over the suspension.

24 Total number of pollen grains and spores are counted per known volume.

APPENDIX 4

PREPARATION PROCEDURE FOR POLLEN REFERENCE SLIDES

1 Place specimen into a 50 ml glass centrifuge tube.

2 Add 20 ml 10% NaOH to the tube and stir.

3 Heat in a water bath (50-60°C) for five minutes, stirring often.

4 Filter through a clean 200 μm mesh sieve into a 100 ml glass beaker. Lightly crush the material on the screen, and wash through with distilled water.

5 Centrifuge at 3 500 rpm for one minute and decant the supernatant.

6 Transfer contents to a 10 ml centrifuge tube using glacial acetic acid.

7 Stir, centrifuge at 3 500 rpm for three minutes and decant.

8 Add acetolysis mixture. Stir and place in a heated water bath (50-60°C) for five minutes. Place samples in a cold water bath to stop acetolysis. Centrifuge and decant.

10 Add 5 ml glacial acetic acid. Centrifuge and decant.

11 Wash 3-5 times with distilled water, adding 1-3 drops of aqueous Safranine stain into the final wash.

12 Centrifuge and decant.

13 Invert tubes onto blotting paper.

Mounting Slides:-

1 Clean and label slides (replicates of 3 of each specimen).

2 Pick up pollen grains/spores with a small block of glycerine jelly placed on a dissecting needle. Wipe around the sides of the centrifuge tubes to pick up grains still adhering to the tube.

3 Place glycerine jelly on centre of slide and pass slide over a warm surface to melt the jelly. Caution: heating plate must be approximately 40-45°C, if hotter the glycerine jelly will boil and damage the pollen grains.

4 Dip warmed glass rod into paraffin wax. Apply a strip of the wax to slide around the jelly.

5 Lower a cover slip over the jelly, so that it touches both the jelly and the wax, with a dissecting needle. If the slide is inverted the pollen grains will settle near the coverslip surface, thereby facilitating easier light microscope viewing.

6 Reheat under the coverslip, to re-melt the paraffin wax and induce sealing of the slide.

7 Remove any excess wax and ring the coverslip with nail varnish - acts as an extra sealant.

APPENDIX 5

VEGETATION, SOIL AND POLLEN TRAP SPECTRA

Complete vegetation, soil and trap pollen spectra, with "+" denoting values less than 0.5%. List is according to relative percentage dominance within the vegetation communities.

1 MONTANE REGION

Highland Sourveld

Taxa	Vegetation	Soil	Traps
Poaceae	63	79	54
Pteridophyta	8	1	6
Asteraceae	7	5	25
Euphorbiaceae	6	2	1
Anacardiaceae	4	+	+
Cyperaceae	4	2	3
Bare Ground	3	-	-
Santalaceae	2	0.7	+
Campanulaceae	0.5	+	+
Crassulaceae	0.5	1	-
Iridaceae	0.5	1	1
Fabaceae	+	+	0.5
Gentianaceae	+	+	+
Geraniaceae	+	+	0.5
Guttiferae	+	+	+
Hypoxidaceae	+	1	2
Liliaceae	+	0.6	+
Malvaceae	+	+	+
Scrophulariaceae	+	0.6	1
Thymelaeaceae	+	+	0.7
Valerianaceae	+	+	+
Verbenaceae	+	+	+
Ericaceae	-	0.6	0.6
Illecebraceae	-	0.5	0.5
Myricaceae	-	-	+
Polygalaceae	-	-	+
Proteaceae	-	-	+
Rosaceae	-	-	1
Unknowns	-	0.7	+

***Protea* savanna**

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	64	58	35
Proteaceae	46	8	32
Bare ground	5	-	-
Cyperaceae	5	3	3
Pteridophyta	5	7	4
Anacardiaceae	4	2	1
Asteraceae	4	4	11
Myricaceae	4	2	2
Rosaceae	3	3	1
Ebenaceae	1	+	+
Euphorbiaceae	1	2	2
Hypoxidaceae	1	2	0.6
Polygalaceae	1	+	+
Scrophulariaceae	0.5	1	2
Araliaceae	+	+	-
Asclepiadaceae	+	+	+
Campanulaceae	+	+	+
Crassulaceae	+	+	0.7
Gentianceae	+	+	+
Iridaceae	+	+	0.5
Lamiaceae	+	+	+
Liliaceae	+	0.5	+
Linaceae	+	0.6	+
Oxalidaceae	+	+	+
Rubiaceae	+	0.5	+
Santalaceae	+	+	-
Thymelaeaceae	+	+	+
Apiaceae	-	-	+
Begoniaceae	-	+	-
Cornaceae	-	-	+
Dipsacaceae	-	+	-
Ericaceae	-	0.7	0.7
Fabaceae	-	+	+
Geraniaceae	-	-	+
Illecebraceae	-	+	+
Unknowns	-	1	0.7
Valerianaceae	-	-	0.5

***Podocarpus* Forest**

Taxa	**Vegetation**	**Soil**	**Traps**
Podocarpaceae	34	9	12
Pteridophyta	27	18	9
Bare ground	24	-	-
Poaceae	22	33	19
Celastraceae	15	3	0.7
Ulmaceae	15	4	33
Flacourtiaceae	10	4	3
Sapindaceae	8	3	10
Cyperaceae	7	3	1
Aquifoliaceae	6	-	-
Iridaceae	6	1	+
Cornaceae	5	2	+
Rubiaceae	5	1	+
Rutaceae	5	4	0.5
Apocynaceae	5	1	1
Ebenaceae	4	1	0.5
Icacinaceae	4	1	1
Liliaceae	2	1	0.6
Myrsinaceae	2	0.7	+
Rhamnaceae	2	2	2
Balsaminaceae	1	-	-
Scrophulariaceae	1	+	2
Urticaceae	1	+	-
Asclepiadaceae	0.5	-	-
Fabaceae	0.5	+	-
Lamiaceae	0.5	+	+
Ranunculaceae	0.5	+	-
Acanthaceae	+	+	-
Apiaceae	+	+	-
Begoniaceae	+	+	+
Brassicaceae	+	+	-
Campanulaceae	+	-	-
Dioscoreaceae	+	-	-
Euphorbiaceae	+	+	+
Gesneriaceae	+	+	-
Onagraceae	+	-	-
Piperaceae	+	+	-
Solaniaceae	+	-	+
Velloziaceae	+	-	-
Vitaceae	+	-	-
Amaranthaceae	-	-	+
Anacardiaceae	-	+	0.7
Araliaceae	-	-	+
Asteraceae	-	+	1

Crassulaceae	-	+	0.5
Ericaceae	-	+	0.5
Illecebraceae	-	+	-
Myricaceae	-	+	+
Rosaceae	-	-	+
Thymelaeaceae	-	-	+
Unknowns	-	2	+

2 SUB-ALPINE REGION

***Rendlia altera* grassland**

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	55	74	39
Bare ground	21	-	-
Cyperaceae	14	4	5
Asteraceae	6	6	27
Hypoxidaceae	0.7	1	4
Crassulaceae	+	2	0.9
Fabaceae	+	1	1
Geraniaceae	+	+	0.8
Iridaceae	+	0.9	0.8
Liliaceae	+	+	+
Lobeliaceae	+	+	-
Orchidaceae	+	-	-
Oxalidaceae	+	-	+
Polygalaceae	+	+	+
Scrophulariaceae	+	+	1
Acanthaceae	-	+	+
Apiaceae	-	-	+
Apocynaceae	-	+	+
Campanulaceae	-	-	+
Celastraceae	-	+	+
Commelinaceae	-	+	+
Cornaceae	-	+	+
Dipsacaceae	-	-	+
Ericaceae	-	1	0.9
Euphorbiaceae	-	+	+
Flacourtiaceae	-	+	1
Gentianaceae	-	-	+
Icacinaceae	-	-	+
Illecebraceae	-	+	0.6
Lamiaceae	-	-	+
Linaceae	-	-	+
Lobeliaceae	-	-	+

Malvaceae	-	+	+
Myricaceae	-	-	+
Oxalidaceae	-	0.7	-
Podocarpaceae	-	0.7	2
Proteaceae	-	+	5
Pteridophyta	-	0.6	2
Rhamnaceae	-	-	+
Rosaceae	-	0.7	1
Rubiaceae	-	+	+
Sapindaceae	-	+	+
Solanaceae	-	-	+
Thymelaeaceae	-	0.6	+
Ulmaceae	-	0.6	2
Unknowns	-	0.7	0.6

Leucosidea sericea **scrubland**

Taxa	**Vegetation**	**Soil**	**Traps**
Leucosidea sericea	45	9	56
Poaceae	32	41	21
Pteridophyta	30	10	4
Bare ground	7	-	-
Anacardiaceae	5	4	-
Cyperaceae	5	3	2
Ebenaceae	5	1	+
Asteraceae	4	5	6
Ericaceae	4	1	4
Boraginaceae	3	0.8	+
Euphorbiaceae	2	2	+
Rhamnaceae	2	+	+
Geraniaceae	1	+	+
Lamiaceae	1	0.8	+
Liliaceae	1	1	+
Loganiaceae	1	1	+
Myrsinaceae	1	+	+
Rubiaceae	1	+	+
Scrophulariaceae	1	1	0.8
Apiaceae	+	+	-
Asclepiadaceae	+	+	+
Campanulaceae	+	0.7	+
Crassulaceae	+	+	+
Fabaceae	+	0.9	0.6
Gentianaceae	+	+	+
Illecebraceae	+	+	0.5

Iridaceae	+	+	+
Malvaceae	+	-	-
Melianthaceae	+	-	-
Onagraceae	+	-	-
Oxalidaceae	+	-	+
Ranunculaceae	+	1	+
Rosaceae	+	6	0.5
Santalaceae	+	+	-
Solaniaceae	+	-	+
Sterculiaceae	+	+	-
Thymelaeaceae	+	+	+
Anacardiaceae	-	-	+
Commelinaceae	-	0.5	+
Dipsacaceae	-	-	+
Hypoxidaceae	-	+	+
Juncaceae	-	+	-
Myricaceae	-	-	+
Oliniaceae	-	0.8	-
Polygalaceae	-	-	+
Proteaceae	-	+	+
Unknowns	-	0.9	+

Themeda triandra grassland

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	61	62	36
Asteraceae	15	9	43
Anacardiaceae	5	+	+
Ericaceae	5	5	2
Bare ground	2	-	-
Euphorbiaceae	1	2	1
Liliaceae	1	2	+
Pteridophyta	1	3	1
Scrophulariaceae	0.7	2	4
Rubiaceae	0.6	+	+
Asclepiadaceae	0.5	0.5	+
Apiaceae	+	0.8	+
Campanulaceae	+	+	+
Dipsacaceae	+	0.7	+
Fabaceae	+	1	1
Gentianaceae	+	+	0.6
Geraniaceae	+	1	+
Hypoxidaceae	+	1	1
Iridaceae	+	0.5	1

Lamiaceae	+	0.5	1
Linaceae	+	+	+
Onagraceae	+	+	+
Sterculiaceae	+	1	+
Thymelaeaceae	+	+	+
Valerianaceae	+	+	+
Commelinaceae	-	+	+
Crassulaceae	-	-	0.7
Cyperaceae	-	+	2
Illecebraceae	-	1	+
Loganaceae	-	-	0.7
Malvaceae	-	+	+
Myricaceae	-	-	+
Oxalidaceae	-	-	+
Polygalaceae	-	+	+
Proteaceae	-	-	+
Rosaceae	-	+	1
Unknowns	-	2	0.5

'Mixed' grassland

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	62	71	44
Anacardiaceae	16	2	3
Asteraceae	10	8	34
Bare ground	3	-	-
Ericaceae	2	0.6	1
Euphorbiaceae	2	3	1
Liliaceae	2	2	2
Pteridophyta	1	1	1
Geraniaceae	0.5	+	0.7
Apiaceae	+	+	+
Asclepiadaceae	+	+	+
Boraginaceae	+	+	+
Guttiferae	+	+	+
Illecebraceae	+	0.5	0.8
Lamiaceae	+	+	+
Oxalidaceae	+	0.6	+
Rubiaceae	+	0.6	+
Scrophulariaceae	+	0.9	2
Thymelaeaceae	+	+	+
Valerianaceae	+	+	+
Brassicaceae	-	+	+
Campanulaceae	-	+	+

Crassulaceae	-	-	+
Cyperaceae	-	2	2
Gentianaceae	-	-	+
Hypoxidaceae	-	1	0.7
Juncaceae	-	0.7	-
Lamiaceae	-	-	+
Linaceae	-	-	+
Myricaceae	-	+	+
Proteaceae	-	-	+
Ranunculaceae	-	1	-
Rhamnaceae	-	-	+
Rosaceae	-	1	1
Unknowns	-	0.9	+

***Festuca costata* grassland**

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	76	75	49
Asteraceae	9	6	30
Bare ground	8	-	-
Anacardiaceae	2	+	0.7
Ericaceae	1	1	3
Pteridophyta	1	0.7	2
Fabaceae	0.5	1	1
Geraniaceae	0.5	+	-
Liliaceae	0.5	1	1
Aizoaceae	+	+	+
Apiaceae	+	1	+
Dipsacaceae	+	1	+
Euphorbiaceae	+	1	1
Gentianaceae	+	+	+
Illecebraceae	+	+	0.7
Lamiaceae	+	0.5	+
Oxalidaceae	+	+	+
Polygalaceae	+	-	+
Ranunculaceae	+	-	-
Scrophulariaceae	+	2	2
Sterculiaceae	+	0.8	-
Campanulaceae	-	+	+
Commelinaceae	-	+	+
Crassulaceae	-	-	+
Cyperaceae	-	1	3
Geraniaceae	-	-	0.5
Hypoxidaceae	-	+	0.8

Juncaceae	-	+	-
Linaceae	-	-	+
Loganiaceae	-	-	+
Malvaceae	-	-	+
Myricaceae	-	-	+
Proteaceae	-	+	+
Ranunculaceae	-	+	+
Rosaceae	-	1	0.8
Rubiaceae	-	-	+
Santalaceae	-	+	+
Solaniaceae	-	-	+
Sterculiaceae	-	-	+
Thymelaeaceae	-	+	+
Unknowns	-	0.6	0.5

Low altitude vlei

Taxa	**Vegetation**	**Soil**	**Traps**
Cyperaceae	45	17	9
Gunneraceae	15	4	1
Poaceae	12	42	48
Brassicaceae	5	2	+
Pteridophyta	5	10	13
Ranunculaceae	5	3	1
Asteraceae	2	5	15
Dipsacaceae	2	1	0.7
Scrophulariaceae	2	1	1
Bare ground	1	-	-
Boraginaceae	1	1	+
Rosaceae	1	1	1
Liliaceae	0.5	+	+
Papaveraceae	0.5	1	1
Campanulaceae	+	1	+
Fabaceae	+	+	+
Guttiferae	+	1	0.7
Illecebraceae	+	+	+
Iridaceae	+	1	1
Lamiaceae	+	+	+
Linaceae	+	+	+
Oxalidaceae	+	+	+
Rubiaceae	+	+	+
Anacardiaceae	-	-	+
Apiaceae	-	-	+
Commelinaceae	-	0.5	-

Droseraceae	-	+	-
Ericaceae	-	+	1
Geraniaceae	-	+	1
Hypoxidaceae	-	0.9	+
Juncaceae	-	1	-
Leucosidea sericea	-	-	+
Malvaceae	-	-	+
Onagraceae	-	-	+
Polygalaceae	-	-	+
Proteaceae	-	-	+
Thymelaeaceae	-	-	+
Unknowns	-	1	+

Sub-alpine fynbos

Taxa	**Vegetation**	**Soil**	**Traps**
Poaceae	27	39	22
Rosaceae	21	3	4
Thymelaeaceae	20	2	+
Ericaceae	18	13	18
Asteraceae	13	9	15
Bare ground	10	-	-
Gunneraceae	8	+	-
Liliaceae	8	4	+
Cyperaceae	6	2	1
Ebenaceae	6	0.6	0.6
Proteaceae	5	0.9	12
Pteridophyta	5	6	3
Scrophulariaceae	4	2	8
Celastraceae	3	+	+
Euphorbiaceae	3	1	0.9
Myrsinaceae	3	+	+
Rhamnaceae	3	+	0.5
Anacardiaceae	2	+	0.7
Fabaceae	2	2	2
Ranunculaceae	2	2	0.6
Rubiaceae	2	+	+
Lamiaceae	1	1	+
Melianthaceae	1	-	-
Rosaceae	1	-	-
Santalaceae	1	+	-
Campanulaceae	0.6	0.6	+
Boraginaceae	0.5	-	+
Dipsacaceae	0.5	0.6	0.8

Geraniaceae	0.5	+	0.6
Myricaceae	0.5	+	+
Oliniaceae	0.5	-	-
Hypoxidaceae	+	0.5	0.6
Loganaceae	+	0.7	1
Polygalaceae	+	-	+
Primulaceae	+	-	-
Apiaceae	-	+	+
Brassicaceae	-	+	-
Cornaceae	-	+	+
Crassulaceae	-	1	2
Gentianaceae	-	-	+
Illecebraceae	-	+	+
Iridaceae	-	-	+
Lamiaceae	-	-	+
Santalaceae	-	-	+
Solanaceae	-	+	+
Unknowns	-	1	0.9

3 ALPINE REGION

Alpine grassland

Taxa	**Vegetation**	**Soil**
Poaceae	64	70
Cyperaceae	16	7
Asteraceae	11	8
Bare ground	3	-
Ericaceae	2	4
Juncaceae	2	2
Campanulaceae	0.5	+
Aizoaceae	+	+
Boraginaceae	+	+
Brassicaceae	+	+
Crassulaceae	+	1
Fabaceae	+	1
Gentianaceae	+	+
Iridaceae	+	+
Liliaceae	+	0.9
Rosaceae	+	+
Rubiaceae	+	+
Scrophulariaceae	+	0.5
Thymelaeaceae	+	0.5

Apiaceae	-	0.5
Begoniaceae	-	+
Dipsacaceae	-	+
Droseraceae	-	+
Illecebraceae	-	0.5
Proteaceae	-	+
Pteridophyta	-	0.7
Unknowns	+	1

Erica-Helichrysum **heathland**

Taxa	**Vegetation**	**Soil**
Ericaceae	32	55
Asteraceae	30	8
Bare ground	9	-
Poaceae	9	18
Thymelaeaceae	8	5
Cyperaceae	4	3
Rosaceae	2	0.5
Santalaceae	2	-
Crassulaceae	1	3
Scrophulariaceae	1	+
Euphorbiaceae	0.5	+
Polygalaceae	0.5	+
Campanulaceae	+	0.5
Dipsacaceae	+	0.6
Begoniaceae	-	+
Droseraceae	-	0.9
Fabaceae	-	0.5
Geraniaceae	-	+
Hypoxidaceae	-	+
Illecebraceae	-	0.6
Liliaceae	-	+
Malvaceae	-	+
Oxalidaceae	-	+
Pteridophyta	-	0.7
Unknowns	-	1

High altitude vlei

Taxa	**Vegetation**	**Soil**
Cyperaceae	33	13
Poaceae	16	50
Eriocaulaceae	16	7
Bare ground	15	-
Asteraceae	5	7
Juncaceae	3	3
Ericaceae	2	3
Iridaceae	2	1
Scrophulariaceae	2	0.6
Aizoaceae	1	0.7
Fabaceae	1	0.9
Hypoxidaceae	1	1
Aponogetonaceae	0.5	+
Caryophyllaceae	0.5	0.5
Crassulaceae	0.5	2
Gentianaceae	0.5	+
Dipsacaceae	+	0.5
Geraniaceae	+	+
Liliaceae	+	+
Oxalidaceae	+	0.5
Ranunculaceae	+	0.6
Apiaceae	-	3
Droseraceae	-	0.6
Pteridophyta	-	+
Rosaceae	-	0.7
Rubiaceae	-	+
Rutaceae	-	+
Thymelaeaceae	-	+
Unknowns	-	0.9

APPENDIX 6

SPECIES LIST

List of species from the studied vegetation communties. Species are listed according to dominance within the community with mean percentage cover values of the total number of quadrats. "+" denotes a percentage aerial cover of less than 1%.

1 MONTANE REGION

Highland Sourveld

15	Poaceae	*Themeda triandra* Forssk.
10	Poaceae	*Monocymbium ceresiiforme* (Nees) Stapf
10	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze
5	Euphorbiaceae	*Acalypha punctata* Meisn.
5	Poaceae	*Alloteopsis semialata* (R.Br.) Hitchc.
5	Poaceae	*Eragrostis racemosa* (Thunb.) Steud.
5	Poaceae	*Harpochloa falx* (L.f.) Kuntze
5	Poaceae	*Hyparrhenia dregeana* (Nees) Stapf
5	Poaceae	*Hyparrhenia hirta* (L.) Stapf
5	Poaceae	*Tristachya leucothrix* Nees
5	Pteridophyta	*Pteridium aquilinum* (L.) Kuhn
2	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
2	Asteraceae	*Aster pleiocephales* (Harv.) Hutch.
2	Santalaceae	*Thesium pallidum* A.DC.
2	Cyperaceae	*Bulbostylis humilis* (Kunth) C.B.Cl.
2	Cyperaceae	*Kyllinga pauciflora* Ridley
2	Poaceae	*Andropogon appendiculatus* Nees
2	Poaceae	*Phacelurus franksae* (J.M.Wood) Clayton
1	Cyperaceae	*Cyperus semitrifidus* Schrad var. *semitrifidus*
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Athrixia fontana* MacOwan
+	Asteraceae	*Berkheya speciosa* (DC.) O.Hoffm. subsp. *speciosa*
+	Asteraceae	*Conyza podocephala* DC.
+	Asteraceae	*Haplocarpha scaposa* Harv.
+	Asteraceae	*Helichrysum aureonitens* Weim.
+	Asteraceae	*Helichrysum cephaloideum* DC.
+	Asteraceae	*Helichrysum glomeratum* Klatt
+	Asteraceae	*Helichrysum herbaceum* (Andr.) Sweet
+	Asteraceae	*Helichrysum latifolium* DC.
+	Asteraceae	*Helichrysum miconiifolium* DC.
+	Asteraceae	*Helichrysum nudifolium* (L.) Less
+	Asteraceae	*Helichrysum pilosellum* (L.f.) less
+	Asteraceae	*Helichrysum umbraculigerum* Less.
+	Asteraceae	*Metalasia muricata* (L.) D.Don
+	Asteraceae	*Othonna natalensis* Sch. Bip.
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio erubescens* Ait.
+	Asteraceae	*Senecio isatideus* DC.
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.

+	Campanulaceae	*Cyphia corylifolia* Harv.
+	Campanulaceae	*Cyphia elata* Harv.
+	Crassulaceae	*Crassula vaginata* Eckl. & Zeyh.
+	Cyperaceae	*Ficinia cinnamomea* C.B.Cl.
+	Euphorbiaceae	*Acalypha schinzii* Pax
+	Fabaceae	*Dichilus strictus* E.Mey.
+	Fabaceae	*Eriosema salignum* E.Mey.
+	Gentianaceae	*Sebaea natalensis* Schinz
+	Geraniaceae	*Monsonia attenuata* Harv.
+	Guttiferae	*Hypericum aethiopicum* Thunb.
+	Hypoxidaceae	*Hypoxis acuminata* Bak.
+	Illecebraceae	*Silene burchelli* Otth.
+	Iridaceae	*Gladiolus crassifolius* Bak.
+	Iridaceae	*Gladiolus dalenii* Van Geel
+	Iridaceae	*Watsonia meriana* (L.) Mill.
+	Liliaceae	*Drimia neriniformis* Bak.
+	Liliaceae	*Scilla nervosa* (Burch.) Jessop
+	Malvaceae	*Hibiscus trionum* L.
+	Orchidaceae	*Corycium nigrescens* Sond.
+	Orchidaceae	*Disa patula* Sond. var. *patula*
+	Poaceae	*Digitaria monodactyla* (Nees) Stapf
+	Poaceae	*Digitaria setifolia* Stapf
+	Poaceae	*Elionurus muticus* (Spreng.) Kunth
+	Poaceae	*Eulalia villosa* (Thunb.) Nees
+	Poaceae	*Microchloa caffra* Nees
+	Poaceae	*Panicum natalense* Hochst.
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Scrophulariaceae	*Sopubia cana* Harv.
+	Thymelaeaceae	*Gnidia microcephala* Meisn.
+	Valerianaceae	*Valeriana capensis* Thunb. var. *capensis*

Protea savanna

40	Proteaceae	*Protea caffra* Meisn.
15	Poaceae	*Themeda triandra* Forssk.
10	Poaceae	*Digitaria flaccida* Stapf
10	Poaceae	*Eloinurus muticus* (Spreng.) Kunth
5	Poaceae	*Panicum natalense* Hochst.
5	Poaceae	*Tristachya leucothrix* Nees
5	Proteaceae	*Protea roupillae* Meisn.
5	Pteridophyta	*Pteridium aquilinum* (L.) Kuhn
2	Anacardiaceae	*Rhus dentata* Thunb.
2	Cyperaceae	*Bulbostylis schoenoides* (Kunth) C.B.Cl.
2	Cyperaceae	*Tetraria cuspidata* (Rottb.) C.B.Cl.
2	Myricaceae	*Myrica pilulifera* Rendle
2	Poaceae	*Alloteopsis semialata* (R.Br.) Hitchc.
2	Poaceae	*Harpochloa falx* (L.f.) Kuntz
2	Poaceae	*Monocymbium ceresiiforme* (Nees) Stapf
2	Poaceae	*Trachypogon spicatus* (Rottb.) C.B.Cl.
2	Rosaceae	*Cliffortia linearifolia* Eckl. & Zeyh.
1	Anacardiaceae	*Rhus lucida* L.
1	Cyperaceae	*Ficinia cinnamomea* C.B.Cl.
1	Ebenaceae	*Diospyros austro-africana* De Winter

1	Euphorbiaceae	*Acalypha punctata* Meisn.
1	Poaceae	*Andropogon appendiculatus* Nees
1	Poaceae	*Digitaria setifolia* Stapf
1	Poaceae	*Melinus nerviglumis* (Franch.) Zizka
1	Poaceae	*Rendlia altera* (Rendle) Chiov.
1	Rosaceae	*Cliffortia repens* Schltr.
+	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
+	Araliaceae	*Cussonia paniculata* Eckl. & Zehyh. var. *paniculata*
+	Asclepiadaceae	*Asclepias stellifera* Schltr.
+	Asteraceae	*Anthrixia angustissima* DC.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Aster perfoliatus* Oliv.
+	Asteraceae	*Aster pleiocephales* (Harv.) Hutch.
+	Asteraceae	*Euryops pedunculatus* N.E.Br.
+	Asteraceae	*Helichrysum acutatum* DC.
+	Asteraceae	*Helichrysum aureonitens* Weim.
+	Asteraceae	*Helichrysum latifolium* DC.
+	Asteraceae	*Helichrysum pilodellum* (L.f.) Less.
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio bupleuroides* DC.
+	Asteraceae	*Senecio caudatus* DC.
+	Asteraceae	*Senecio ingeliensis* Hilliard
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Asteraceae	*Vernonia natalensis* Sch.Bip.
+	Campanulaceae	*Wahlenbergia undulata* (L.f.) A.DC.
+	Crassulaceae	*Crassula vaginata* Eckl. & Zeyh.
+	Cyperaceae	*Scleria woodii* C.B.Cl.
+	Euphorbiaceae	*Acalypha schinzii* Pax
+	Euphorbiaceae	*Euphorbia ericoides* Lam.
+	Gentianaceae	*Sebaea filiformis* Schinz.
+	Hypoxidaceae	*Hypoxis argentea* Harv. ex Bak. var. *argentea*
+	Hypoxidaceae	*Hypoxis filiformis* Bak.
+	Hypoxidaceae	*Hypoxis rigidula* Bak.
+	Illecebraceae	*Silene undulata* Ait.
+	Iridaceae	*Watsonia meriana* (L.) Mill.
+	Lamiaceae	*Plectranthus grallatus* Briq.
+	Liliaceae	*Scilla nervosa* (Burch.) Jessop
+	Liliaceae	*Scilla sandersonia* (Hook.f.) Jessop
+	Linaceae	*Linum thunbergii* Eckl. & Zeyh.
+	Myricaceae	*Myrica serrata* Lam.
+	Orchidaceae	*Disa stachyoides* Reichb. f.
+	Orchidaceae	*Disa pulchra* Sond.
+	Orchidaceae	*Eulophia filiosa* (Lindl.) H.Bol.
+	Oxalidaceae	*Oxalis obliquiflora* Steud. ex Rich.
+	Poaceae	*Aristea monticola* Henr.
+	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
+	Poaceae	*Diheteropogon filiformis* (Nees) Clayton
+	Poaceae	*Ehrharta longigloma* C.E.Hubb.
+	Poaceae	*Heteropogon contortus* (L.) Roem & Schult.
+	Poaceae	*Koeleria capensis* (Steud.) Nees
+	Polygalaceae	*Polygala virgata* Thunb.
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn
+	Rubiaceae	*Pentansia prunelloides* (Eckl. & Zeyh.) Walp.
+	Santalaceae	*Thesium racemosum* Bernh.
+	Scrophulariaceae	*Halleria lucida* L.
+	Thymelaeaceae	*Gnidia polystachya* Berg var. *polystachya*

Podocarpus **forest**

35	Podocarpaceae	*Podocarpus latifolius* (Thunb.) R.Br. ex Mirb.
15	Ulmaceae	*Celtis africana* Burm.f.
10	Celastraceae	*Pterocelastrus echinatus* N.E.Br.
10	Poaceae	*Festuca africana* (Hack.) Clayton
10	Pteridophyta	*Pteris captoptera* Kunze
5	Apocynaceae	*Carissa bispinosa* (L.) Desf. ex Brenan
5	Aquifoliaceae	*Ilex mitis* (Linn.) Radlk. var. *mitis*
5	Celastraceae	*Maytenus peduncularis* (Sond.) Loes.
5	Cornaceae	*Curtisia dentata* (Burm.f.) C.A.Sm.
5	Cyperaceae	*Schoenoxiphium sparteum* (Wahlenb.) C.B.Cl.
5	Ebenaceae	*Diospyros whyteana* (Hiern.) F.White
5	Flacourtiaceae	*Kiggelaria africana* L.
5	Flacourtiaceae	*Scolopia mundii* (Eckl. & Zeyh.) Warb.
5	Iridaceae	*Dietes iridoides* (L.) Klatt
5	Poaceae	*Oplismenus hirtellus* (L.) Beauv.
5	Poaceae	*Stipa dregeana* Steud. var. *elongata* (Nees) Stapf
5	Pteridophyta	*Polystichum pungens* (Kaulf.) Presl.
5	Rhamnaceae	*Scutia myrtina* (Burm.f.) Kurz
5	Rubiaceae	*Canthium pauciflorum* (Klotzsch) Kuntze
5	Rutaceae	*Clausena anisata* (Willd.) Hook.f. ex Benth.
5	Sapindaceae	*Allophylus melanocarpus* (Sond.) Radlk.
2	Flacourtiaceae	*Trimeria grandifolia* (Hochst.) Warb.
2	Icacinaceae	*Apodytes dimidiata* E. Mey. ex Arn. subsp. *dimidiata*
2	Icacinaceae	*Cassinopsis ilicifolia* (Hochst.) Kuntze
2	Myrsinaceae	*Myrsine africana* L.
2	Myrsinaceae	*Rapanea melanophloeos* (L.) Mez
2	Pteridophyta	*Polystichum luctuosum* (Kuntz) T. Moore
2	Pteridophyta	*Polystichum setiferum* (Forssk.) Moore ex Woynar var. *fuscopaleaceum* (Alston) Schelpe
2	Pteridophyta	*Pteris cretica* L.
2	Pteridophyta	*Pteris dentata* Forssk.
2	Rutaceae	*Calodendrum capense* (L.f.) Thunb.
1	Celastraceae	*Maytenus undata* (Thunb.) Blakelock
1	Cyperaceae	*Carex spicato-paniculata* C.B.Cl.
1	Ebenaceae	*Diospyros austro-africana* De Winter
1	Liliaceae	*Protoasparagus africanus* Lam.
1	Poaceae	*Ehrharta erecta* Lam. var. *natalensis*
1	Poaceae	*Panicum aequinerve* Nees
1	Rubiaceae	*Canthium ciliatum* (Klotzsch) Kuntze
1	Scrophulariaceae	*Diclis reptans* Benth.
+	Acanthaceae	*Hypoestes triflora* (Forssk.) Roem. & Schult.
+	Anacardiaceae	*Rhus dentata* Thunb.
+	Apiaceae	*Conium chaerophylloides* (Thunb.) Eckl. & Zeyh.
+	Apiaceae	*Sanicula elata* Buch. -Ham.
+	Asclepiadaceae	*Tylophora flanagani* Schltr.
+	Balsaminaceae	*Impatiens hochstetteri* Warb. subsp. *hochstetteri*
+	Begoniaceae	*Begonia sutherlandii* Hook.f.
+	Crassulaceae	*Crassula pellucida* L.
+	Cruciferae	*Cardamine africana* L.
+	Dioscoreaceae	*Dioscorea sylvatica* (Kunth) Ecklon
+	Euphorbiaceae	*Adenocline acuta* (Thunb.) Baill.

+	Fabaceae	*Desmodium repandum* (Vahl) DC.
+	Fabaceae	*Dumasia villosa* DC. var. *villosa*
+	Gesneriaceae	*Streptocarpus gardenii* Hook.
+	Gesneriaceae	*Streptocarpus pusillus* C.B.Cl.
+	Lamiaceae	*Plectranthus grallatus* Briq.
+	Lamiaceae	*Stachys caffra* Benth.
+	Lamiaceae	*Stachys grandifolia* E.Mey. ex Benth.
+	Liliaceae	*Chlorophytum krookianum* Zahlbr.
+	Liliaceae	*Myrsiphyllum asparagoides* (L.) Willd.
+	Onagraceae	*Oenothera indecora* Cambess. subsp. *indecora*
+	Orchidaceae	*Disperis fanniniae* Harv.
+	Orchidaceae	*Huttonaea pulchra* Harv.
+	Orchidaceae	*Polystachya ottoniana* Reichb.f.
+	Orchidaceae	*Stenoglottis fimbriata* Lindl.
+	Piperaceae	*Peperomia tetraphylla* (G.Forst.) Hook. & Arn.
+	Podocarpaceae	*Podocarpus henkelii* Stapf ex Dallim. & Jacks.
+	Polygalaceae	*Polygala confusa* MacOwan
+	Pteridophyta	*Adiantum poiretii* Wikstr. var. *poiretii*
+	Pteridophyta	*Aspleium splendens* Kunze var. *drakensbergense*
+	Pteridophyta	*Asplenium erectum* Bory ex Willd. subsp. *erectum*
+	Pteridophyta	*Asplenium monanthes* L.
+	Pteridophyta	*Asplenium theciferum* (H.B.K.) Mett. var. *concimum* (Schrad.) Shelpe
+	Pteridophyta	*Asplenium varians* Wall. ex Hook. & Grev. var. *fimbriatum* (Kunze) Schelpe
+	Pteridophyta	*Blechnum giganteum* (Kaulf.) Schlechtend.
+	Pteridophyta	*Blechnum punctulatum* (Sw.) var. *punctulatum*
+	Pteridophyta	*Cheilanthes viridis* (Forssk.) Swartz var. *viridis*
+	Pteridophyta	*Hymenophyllum tunbridgense* (L.) Sm.
+	Pteridophyta	*Loxogramme lanceolate* (Swartz) Presl
+	Pteridophyta	*Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.
+	Pteridophyta	*Pleopeltis schraderi* (Mett.) Tard.
+	Pteridophyta	*Polypodium polypodioides* (L.) Hitchc. subsp. *ecklonii* (Kunze) Schelpe
+	Pteridophyta	*Polypodium vulgare* L.
+	Pteridophyta	*Trichomanes pyxidiferum* L. var. *melanotrichum* (Schlechtd.) Schelpe
+	Pteridophyta	*Woodsia montevidensis* (Spreng.) Hieron. var. *burgessiana* (Hook. & Bak.) Schelpe
+	Ranunculaceae	*Thalictrum rhynchocarpum* Dill. & Rich.
+	Rubiaceae	*Galopina circaeoides* Thunb.
+	Scrophulariaceae	*Bowkeria verticillata* (Eckl. & Zeyh.) Schinz
+	Scrophulariaceae	*Halleria lucida* L.
+	Scrophulariaceae	*Nemesia melissaefolia* Benth.
+	Solanaceae	*Physalis peruviana* L.
+	Urticaceae	*Laportea peduncularis* (Wedd.) Chew subsp. *peduncularis*
+	Velloziaceae	*Talbotia elegans* Balf.
+	Vitaceae	*Rhoicissus digitata* (L.f.) Gilg & Brandt

2 SUB-ALPINE REGION

Rendlia altera grassland

15	Poaceae	*Rendlia altera* (Rendle) Chiov.
5	Asteraceae	*Aster perfoliatus* Oliv.
5	Cyperaceae	*Cyperus semitrifidus* Schrad. var. *semitrifidus*
5	Poaceae	*Alloteopsis semialata* (R.Br.) Hitchc.
5	Poaceae	*Eragrostis racemosa* (Thunb.) Steud.
5	Poaceae	*Harpochloa falx* (L.f.) Kuntze
5	Poaceae	*Stiburus alopecuroides* (Hack.) Stapf
5	Poaceae	*Themeda triandra* Forssk.
2	Cyperaceae	*Bulbostylis schoenoides* (Kunth) C.B.Cl.
2	Cyperaceae	*Cyperus obtusiflorus* Vahl var. *obtusiflorus*
2	Poaceae	*Andropogon appendiculatus* Nees
2	Poaceae	*Eragrostis capensis* (Thunb.) Trin.
2	Poaceae	*Heteropogon contortis* (L.) Roem. & Schult.
2	Poaceae	*Koeleria capensis* (Steud.) Nees
2	Poaceae	*Tristachya leucothrix* Nees
1	Cyperaceae	*Bulbostylis humilis* (Kunth) C.B.Cl.
1	Cyperaceae	*Cyperus schlechteri* C.B.Cl.
1	Cyperaceae	*Kyllinga pauciflora* Ridley
1	Cyperaceae	*Scirpus falsus* C.B.Cl.
1	Poaceae	*Diheteropogon filifolius* (Nees) Clayton
1	Poaceae	*Elionurus muticus* (Spreng.) Kunth
1	Poaceae	*Panicum ecklonii* Nees
1	Poaceae	*Panicum natalense* Hochst.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Euryops pedunculatus* N.E.Br.
+	Asteraceae	*Gazania krebsiana* Less.
+	Asteraceae	*Helichrysum acutatum* DC.
+	Asteraceae	*Helichrysum aureonitens* Weim.
+	Asteraceae	*Helichrysum auriceps* Hilliard
+	Asteraceae	*Helichrysum miconiifolium* DC.
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio bupleuroides* DC.
+	Asteraceae	*Senecio speciosus* Willd.
+	Campanulaceae	*Cyphia elata* Harv.
+	Crassulaceae	*Crassula vaginata* Eckl. & Zeyh.
+	Cyperaceae	*Tetraria cuspidata* (Rottb.) C.B.Cl.
+	Fabaceae	*Lessertia thodei* L.Bol.
+	Fabaceae	*Lotononis eriantha* Benth.
+	Geraniaceae	*Monsonia attenuata* Harv.
+	Hypoxidaceae	*Hypoxis argentea* Harv. ex Bak. var. *argentea*
+	Hypoxidaceae	*Rhodohypoxis baurii* (Bak.) Nel
+	Iridaceae	*Aristea woodii* N.E.Br.
+	Iridaceae	*Watsonia meriana* (L.) Mill.
+	Liliaceae	*Kniphofia evansii* Bak.
+	Orchidaceae	*Disa stachyoides* Reichb.f.
+	Oxalidaceae	*Oxalis obliquifolia* Steud. ex Rich.
+	Polygalaceae	*Polygala rehmannii* Chod.
+	Scrophulariaceae	*Zaluzianskya pulvinata* Killick

***Leucosidea sericea* scrubland**

45	Rosaceae	*Leucosidea sericea* Eckl. & Zeyh.
30	Pteridophyta	*Pteridium aquilinum* (L.) Kuhn
10	Poaceae	*Themeda triandra* Forssk.
10	Rosaceae	*Rubus ludwigii* Eckl. & Zeyh.
5	Poaceae	*Diheteropogon filifolius* (Nees) Clayton
5	Poaceae	*Tristachya leucothrix* Nees
2	Anacardiaceae	*Rhus dentata* Thunb.
2	Anacardiaceae	*Rhus lucida* L.
2	Boraginaceae	*Lithospermum afromontanum* H.Weim.
2	Cyperaceae	*Schoenoxiphium rufum* Nees
2	Ebenaceae	*Diospyros austro-africana* De Winter
2	Ericaceae	*Erica evansii* (N.E.Br.) E.G.H.Oliver
2	Poaceae	*Digitaria flaccida* Stapf
2	Poaceae	*Miscanthus capensis* (Nees) Anderss. var. *capensis*
2	Poaceae	*Panicum ecklonii* Nees
2	Rhamnaceae	*Rhamnus prinoides* L'Hérit.
1	Ebenaceae	*Euclea crispa* (Thunb.) Guerke var. *crispa*
1	Ericaceae	*Erica woodii* H.Bol.
1	Euphorbiaceae	*Acalypha punctata* Meisn.
1	Loganiaceae	*Buddleja salviifolia* (L.) Lam.
1	Myrsinaceae	*Mysine africana* L.
1	Poaceae	*Alloteropsis semialata* (R.Br.) Hitchc.
1	Poaceae	*Andropogon appendiculatus* Nees
1	Poaceae	*Diheteropogon amplectans* (Nees) Clayton
1	Poaceae	*Festuca costata* Nees
1	Rosaceae	*Clutia natalensis* Bernh. ex Krauss
+	Apiaceae	*Allepidea anatymbica* Eckl. & Zeyh.
+	Asclepiadaceae	*Asclepias stellifera* Schltr.
+	Asclepiadaceae	*Riocreuxia torulosa* Decne.
+	Asteraceae	*Artemisia afra* Jacq.
+	Asteraceae	*Aster pleiocephales* (Harv.) Hutch.
+	Asteraceae	*Berkheya montana* Wood & Evans
+	Asteraceae	*Berkheya rhapontica* (DC.) Hutch. & Burtt Davy
+	Asteraceae	*Helichrysum acutatum* DC.
+	Asteraceae	*Helichrysum aureonitens* Sch.Bip.
+	Asteraceae	*Helichrysum cooperi* Harv.
+	Asteraceae	*Helichrysum herbaceum* (Andr.) Sweet
+	Asteraceae	*Helichrysum glomeratum* Klatt
+	Asteraceae	*Helichrysum miconiifolium* DC.
+	Asteraceae	*Helichrysum pilosellum* (L.f.) Less.
+	Asteraceae	*Helichrysum platypterum* DC.
+	Asteraceae	*Helichrysum umbraculigerum* Less.
+	Asteraceae	*Nidorella auriculata* DC. subsp. *polycephala*
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio bupleuroides* DC.
+	Asteraceae	*Senecio gerrardii* Harv.
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Asteraceae	*Vernonia natalensis* Sch.Bip.
+	Boraginaceae	*Afrotysonia africana* (H.Bol.) Rauschert
+	Boraginaceae	*Cynoglossum hispidum* Thunb.
+	Boraginaceae	*Cyphia corylifolia* Harv.

+	Boraginaceae	*Myosotis sylvatica* Hoffm.
+	Campanulaceae	*Wahlenbergia squamifolia* V.Brehm.
+	Campanulaceae	*Wahlenbergia fasciculata* V.Brehm.
+	Caryophyllaceae	*Silene undulata* Ait.
+	Commelinaceae	*Commelina africana* L.
+	Crassulaceae	*Crassula pellucida* L.
+	Cyperaceae	*Carex spicato-paniculata* C.B.Cl.
+	Cyperaceae	*Carex zuluensis* C.B.Cl.
+	Cyperaceae	*Pycreus macranthus* C.B.Cl.
+	Cyperaceae	*Schoenoxiphium filiforme* Kuekenth.
+	Euphorbiaceae	*Acalypha schinzii* Pax
+	Euphorbiaceae	*Cliffortia spathulata* Weim.
+	Euphorbiaceae	*Euphorbia epicyparissias* E.Mey.
+	Fabaceae	*Buchenroedera lotononoides* Scott Elliot
+	Fabaceae	*Indigofera longebarbata* Engl.
+	Fabaceae	*Lessertia perennans* DC. var. *perennans*
+	Gentianaceae	*Sebaea macrophylla* Gilg
+	Gentianaceae	*Sebaea sedoides* Gilg
+	Geraniaceae	*Geranium ornithopodon* Eckl. & Zeyh.
+	Geraniaceae	*Monsonia attenuata* Harv.
+	Geraniaceae	*Pelargonium zonale* (L.) L'Hérit.
+	Geraniaceae	*Pelargonium luridum* (Andr.) Sweet
+	Iridaceae	*Gladiolus crassifolius* Bak.
+	Lamiaceae	*Ajuga ophrydis* Benth.
+	Lamiaceae	*Becium filamentosum* (Forssk.) Chiov.
+	Lamiaceae	*Leonotis dubia* Benth.
+	Lamiaceae	*Plectranthus grallatus* Briq.
+	Lamiaceae	*Pynostachys reticulata* (E.Mey.) Benth.
+	Lamiaceae	*Rabdosiella calycina* (Benth.) Codd
+	Lamiaceae	*Satureja reptans* Killick
+	Lamiaceae	*Stachys albifolia* N.E.Br.
+	Lamiaceae	*Stachys grandifolia* E.Mey. ex Benth.
+	Liliaceae	*Anthericum longistylum* Bak.
+	Liliaceae	*Eriospermum copperi* Bak.
+	Liliaceae	*Eucomis bicolor* Bak.
+	Liliaceae	*Kniphofia ritualis* Codd
+	Liliaceae	*Ledebouria cooperi* (Hook.f.) Jessop
+	Liliaceae	*Myrsiphyllum asparagoides* (L.) Willd.
+	Liliaceae	*Myrsiphyllum scandens* (Thunb.) Oberm.
+	Liliaceae	*Protoasparagus microrhaphis* (Kunth.) Bak.
+	Liliaceae	*Scilla nervosa* (Burch.) Jessop
+	Malvaceae	*Hibiscus trionum* L.
+	Melianthaceae	*Melianthus villosus* Bol.
+	Onagraceae	*Epilobium capense* Hochst.
+	Onagraceae	*Oenothera rosea* Ait.
+	Orchidaceae	*Pterygodium hastatum* H.Bol.
+	Oxalidaceae	*Oxalis obliquifolia* Steud. ex Rich.
+	Oxalidaceae	*Oxalis smithiana* Eckl. & Zeyh.
+	Poaceae	*Anthoxanthum ecklonii* (Nees ex Trin.) Stapf.
+	Poaceae	*Aristida monticola* Henrard
+	Poaceae	*Heteropogon contortus* (L.) Roem. & Schult.
+	Poaceae	*Helictotrichon turgidulum* (Stapf) Schweick.
+	Poaceae	*Koeleria capensis* (Steud.) Nees
+	Poaceae	*Poa bonata* Nees

+	Poaceae	*Panicum natalense* Hochst.
+	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn
+	Pteridophyta	*Cheilanthes viridus* (Forssk.) Swartz var. *viridus*
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Ranunculaceae	*Anemone fanninii* Harv. ex Mast.
+	Ranunculaceae	*Clematis brachiata* Thunb.
+	Rosaceae	*Agrimania oderata* Mill.
+	Rosaceae	*Cliffortia linearifolia* Eckl & Zeyh.
+	Rubiaceae	*Anthospermum herbaceum* L.f.
+	Rubiaceae	*Galium thunbergianum* Eckl. & Zeyh. var. *thunbergianum*
+	Santalaceae	*Thesium natalense* Sond.
+	Scrophulariaceae	*Diascia stachyoides* Hiern.
+	Scrophulariaceae	*Hebenstretia dentata* L.
+	Scrophulariaceae	*Nemesia denticulata* (Benth.) Fourc.
+	Scrophulariaceae	*Sutera floribunda* (Benth.) Kuntze
+	Scrophulariaceae	*Zaluzianskya maritima* (L.f.) Walp.
+	Solanaceae	*Solanum nigrum* L.
+	Sterculiaceae	*Hermannia oblongifolia* (Harv.) Hochr.
+	Sterculiaceae	*Hermannia woodii* Schinz
+	Thymelaeaceae	*Passerina montana* Thoday

***Themeda triandra* grassland**

30	Poaceae	*Themeda triandra* Forssk.
10	Poaceae	*Elionurus muticus* (Spreng.) Kunth
5	Ericaceae	*Erica woodii* H.Bol.
5	Poaceae	*Alloteopsis semialata* (R.Br.) Hitchc.
5	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
5	Poaceae	*Tristachya leucothrix* Nees
2	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
2	Asteraceae	*Euryops pedunculatus* N.E.Br.
2	Asteraceae	*Stoebe vulgaris* Levyns
2	Poaceae	*Digitaria flaccida* Stapf
2	Poaceae	*Rendlia altera* (Rendle) Chiov.
1	Asteraceae	*Helichrysum drakensbergensis* Killick
1	Asteraceae	*Helichrysum pilosellum* (L.f.) Less
1	Asteraceae	*Helichrysum oreophilum* Klatt
1	Asteraceae	*Senecio speciosus* Willd.
1	Euphorbiaceae	*Acalypha punctata* Meisn.
+	Apiaceae	*Buplureum mundtii* Cham. & Schlechtd.
+	Asclepiadaceae	*Anisotoma pedunculata* N.E.Br.
+	Asclepiadaceae	*Asclepias stellifera* Schltr.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Aster perfoliatus* Oliv.
+	Asteraceae	*Aster pleiocephales* (Harv.) Hutch.
+	Asteraceae	*Berkheya setifera* DC.
+	Asteraceae	*Cineraria geifolia* (L.) L.
+	Asteraceae	*Helichrysum allioides* Less.
+	Asteraceae	*Helichrysum ecklonis* Sond.
+	Asteraceae	*Helichrysum aureonitens* Sch.Bip.

+	Asteraceae	*Helichrysum cephaloideum* DC.
+	Asteraceae	*Helichrysum grandibracteatum* M.D.Henderson
+	Asteraceae	*Helichrysum herbaceum* (Andr.) Sweet
+	Asteraceae	*Helichrysum latifolium* DC.
+	Asteraceae	*Helichrysum umbraculigerum* Less.
+	Asteraceae	*Schistostephium crataegifolium* (DC.) Fenzl ex Harv.
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio erubescens* Ait.
+	Asteraceae	*Senecio ingeliensis* Hilliard
+	Asteraceae	*Vernonia natalensis* Sch.Bip.
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Asteraceae	*Vernonia flanagani* (Phill.) Hilliard
+	Campanulaceae	*Craterocapsa montana* (A.DC.) Hilliard & Burtt
+	Campanulaceae	*Cyphia elata* Harv.
+	Dipsacaceae	*Scabiosa columbaria* L.
+	Fabaceae	*Lessertia thodei* L.Bol.
+	Fabaceae	*Tephrosia macropoda* (E.Mey.) Harv. var. *diffusa* (E.Mey.) B.D. Schrire
+	Gentianaceae	*Sebaea sedoides* Gilg
+	Geraniaceae	*Monsonia attenuata* Harv.
+	Hypoxidaceae	*Rhodohypoxis baurii* (Bak.) Nel
+	Illecebraceae	*Silene burchelli* Otth.
+	Iridaceae	*Gladiolus longicollis* Bak.
+	Lamiaceae	*Stachys albiflora* N.E.Br.
+	Liliaceae	*Albuca spp.*
+	Liliaceae	*Eucomis autmnalis* (Mill.) Chitt.
+	Liliaceae	*Scilla natalensis* Planch.
+	Linaceae	*Linum thunbergii* Eckl. & Zeyh.
+	Onagraceae	*Epilobium capense* Hochst.
+	Onagraceae	*Oenothera rosea* Ait.
+	Poaceae	*Andropogon appendiculatus* Nees
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Rubiaceae	*Kohauta amatymbica* Eckl. & Zeyh.
+	Rubiaceae	*Pentansia prunelloides* (Eckl. & Zeyh.) Walp.
+	Scrophulariaceae	*Hebenstretia dentata* L.
+	Scrophulariaceae	*Selago hyssopifolia* E.Mey.
+	Scrophulariaceae	*Selago monticola* Wood & Evans
+	Scrophulariaceae	*Sopubia cana* Harv.
+	Scrophulariaceae	*Sutera breviflora* N.E.Br.
+	Scrophulariaceae	*Sutera floribunda* (Benth.) Kuntze
+	Scrophulariaceae	*Zaluzianskya maritima* (L.f.) Walp.
+	Sterculiaceae	*Hermannia woodii* Schinz
+	Thymelaeaceae	*Gnidia fastigiata* Rendle
+	Valerianaceae	*Valeriana capensis* Thunb. var. *capensis*

"Mixed" grassland

20	Poaceae	*Elionurus muticus* (Spreng.) Kunth
15	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
15	Poaceae	*Festuca costata* Nees
10	Poaceae	*Themeda triandra* Forssk.
5	Asteraceae	*Helichrysum tenax* M.D.Henderson

5	Poaceae	*Heteropogon contortus* (L.) Roem. & Schult.
5	Poaceae	*Merxmuellera drakensbergensis* (Schweick.) Conert
2	Anacardiaceae	*Rhus dentata* Thunb.
2	Asteraceae	*Helichrysum oreophilum* Klatt
2	Ericaceae	*Erica woodii* H.Bol.
2	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
2	Poaceae	*Tristachya leucothrix* Nees
1	Asteraceae	*Euryops pedunculatus* N.E.Br.
1	Euphorbiaceae	*Acalypha schinzii* Pax
+	Apiaceae	*Alepidea amatymbica* Eckl. & Zeyh.
+	Asclepiadaceae	*Anisotoma pedunculata* N.E.Br.
+	Asteraceae	*Berkheya setifera* DC.
+	Asteraceae	*Cineraria geifolia* (L.) L.
+	Asteraceae	*Haplocarpha scaposa* Harv.
+	Asteraceae	*Helichrysum drakensbergense* Killick
+	Asteraceae	*Helichrysum latifolium* DC.
+	Asteraceae	*Helichrysum nudifolium* (L.) Less.
+	Asteraceae	*Helichrysum pilosellum* (L.f.) Less.
+	Asteraceae	*Nidorella auriculata* DC. subsp. *polycephala*
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio ingeliensis* Hilliard
+	Asteraceae	*Senecio inornatus* DC.
+	Asteraceae	*Senecio speciosus* Willd.
+	Asteraceae	*Vernonia flanagani* (Phill.) Hilliard
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Asteraceae	*Vernonia natalensis* Sch.Bip.
+	Asteraceae	*Schistostephium crataegifolium* (DC.) Fenzl ex Harv.
+	Boraginaceae	*Myosotis sylvatica* Hoffm.
+	Euphorbiaceae	*Acalypha punctata* Meisn.
+	Euphorbiaceae	*Euphorbia ericoides* Lam.
+	Geraniaceae	*Geranium ornithopodon* Eckl. & Zeyh.
+	Geraniaceae	*Monsonia attenuata* Harv.
+	Geraniaceae	*Pelargonium dispar* N.E.Br.
+	Geraniaceae	*Pelargonium luridum* (Andr.) Sweet
+	Guttiferae	*Hypericum aethiopicum* Thunb.
+	Illecebraceae	*Silene undulata* Ait.
+	Lamiaceae	*Stachys albiflora* N.E.Br.
+	Liliaceae	*Kniphofia angustifolia* (Bak.) Codd
+	Liliaceae	*Kniphofia porphyantha* Bak.
+	Liliaceae	*Scilla natalensis* Planch.
+	Liliaceae	*Scilla sandersonia* (Hook.f.) Jessop
+	Oxalidaceae	*Oxalis Obliquifolia* Steud. ex Rich.
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn
+	Rubiaceae	*Galium scabrelloides* Puff
+	Scrophulariaceae	*Nemesia caerulea* Hiern.
+	Scrophulariaceae	*Selago flanagani* Rolfe
+	Scrophulariaceae	*Selago hyssopifolia* E.Mey.
+	Scrophulariaceae	*Selago monticola* Wood & Evans
+	Thymelaeaceae	*Gnidia microcephala* Meisn.
+	Valerianaceae	*Valeriana capensis* Thunb. var. *capensis*

***Festuca costata* grassland**

50	Poaceae	*Festuca costata* Nees
15	Poaceae	*Heteropogon contortus* (L.) Roem. & Schult.
5	Asteraceae	*Helichrysum umbraculigerum* Less.
2	Poaceae	*Andropogon appendiculatus* Nees
2	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
2	Poaceae	*Poa binata* Nees
1	Poaceae	*Anthoxanthum ecklonii* (Nees ex Trin.) Stapf
1	Poaceae	*Aristea monticola* Henr.
1	Poaceae	*Koeleria capensis* (Steud.) Nees
1	Poaceae	*Tristachya leucothrix* Nees
+	Aizoaceae	*Psammotropha myriantha* Sond.
+	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
+	Apiaceae	*Alepidea amatymbica* Eckl. & Zeyl.
+	Apiaceae	*Alepidea capensis* (Berg.) R.A.Dyer var. *capensis*
+	Apiaceae	*Alepidea setifera* N.E.Br.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Aster perfoliatus* Oliv.
+	Asteraceae	*Athrixia angustissima* DC.
+	Asteraceae	*Chrysocoma ciliata* L.
+	Asteraceae	*Cineraria geifolia* (L.) L.
+	Asteraceae	*Helichrysum adenocarpum* DC.
+	Asteraceae	*Helichrysum appendiculatum* (L.f.) Less.
+	Asteraceae	*Helichrysum latifolium* DC.
+	Asteraceae	*Helichrysum pilosellum* (L.f.) Less.
+	Asteraceae	*Helichrysum subglomeratum* Less.
+	Asteraceae	*Osteospermum thodei* Markotter
+	Asteraceae	*Senecio adnatus* DC.
+	Asteraceae	*Senecio ingeliensis* Hilliard
+	Asteraceae	*Ursinia montana* DC. subsp. *apiculata*
+	Asteraceae	*Vernonia capensis* (Houtt.) Druce
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Asteraceae	*Vernonia natalensis* Sch.Bip.
+	Campanulaceae	*Cyphia elata* Harv.
+	Campanulaceae	*Lobelia flaccida* (Presl) A.DC.
+	Campanulaceae	*Monopsis decipiens* (Sond.) Thulin
+	Campanulaceae	*Wahlenbergia lobulata* V.Brehm.
+	Campanulaceae	*Wahlenbergia undulata* (L.f.) A.DC.
+	Caryophyllaceae	*Cerastium arabidis* E.Mey. ex Fenzl
+	Cyperaceae	*Ficinia cinnamomea* C.B.Cl.
+	Dipsacaceae	*Scabiosa columbaria* L.
+	Ericaceae	*Erica oatesii* Rolfe
+	Ericaceae	*Erica woodii* H.Bol.
+	Euphorbiaceae	*Acalypha punctata* Meisn.
+	Euphorbiaceae	*Euphorbia ericoides* Lam.
+	Euphorbiaceae	*Muraltia saxicola* Chodat
+	Fabaceae	*Argyrolobium rupestre* (Eckl. & Zeyh.) Walp.
+	Fabaceae	*Argyrolobium tuberculata* Walp.
+	Fabaceae	*Indigofera hedyantha* Eckl. & Zeyh.
+	Fabaceae	*Lotononis eriantha* Benth.
+	Fabaceae	*Tephrosia macropoda* (E.Mey.) Harv. var. *diffusa* (E.Mey.) B. D. Schrire
+	Geraniaceae	*Geranium ornithopodon* Eckl. & Zeyh.

+	Geraniaceae	*Monsonia attenuata* Harv.
+	Gentianaceae	*Sebaea procumbens* A.W.Hill
+	Illecebraceae	*Silene undulata* Ait.
+	Lamiaceae	*Satureja compacta* Killick
+	Liliaceae	*Agapanthus companulatus* Leighton subsp. *companulatus*
+	Liliaceae	*Eucomis bicolor* Bak.
+	Liliaceae	*Kniphofia caulescens* Bak.
+	Liliaceae	*Scilla natalensis* Planch.
+	Orchidaceae	*Disa stachyoides* Reichb.f.
+	Oxalidaceae	*Oxalis obliquifolia* Steud. ex Rich.
+	Poaceae	*Digitaria monodactyla* (Nees) Stapf
+	Poaceae	*Haplocarpha scaposa* Harv.
+	Poaceae	*Rendlia altera* (Rendle) Chiov.
+	Poaceae	*Themeda triandra* Forssk.
+	Poaceae	*Trachypogon spicatus* (Rottb.) C. B. Cl.
+	Polygalaceae	*Polygala hispida* Burch.
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn.
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Ranunculaceae	*Anemone fanninii* Harv. ex Mast.
+	Scrophulariaceae	*Diascia purpurea* N.E.Br.
+	Scrophulariaceae	*Manulea crassifolia* Benth.
+	Scrophulariaceae	*Zaluzianskya maritima* (L.f.) Walp.
+	Sterculiaceae	*Hermannia woodii* Schinz

Sub-alpine fynbos

20	Rosaceae	*Cliffortia linearifolia* ECkl. & Zeyh.
20	Thymelaeaceae	*Passerina drakensbergensis* Hilliard & Burtt sp. *nova*
10	Ericaceae	*Erica evansii* (N.E.Br.) E.G.H. Oliver
10	Poaceae	*Festuca costata* Nees
5	Cyperaceae	*Carex spicato-paniculata* C.B.Cl.
5	Ebenaceae	*Diospyros austro-africana* De Winter
5	Ericaceae	*Erica ebracteata* H.Bol.
5	Gunneraceae	*Gunnera perpensa* L.
5	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
5	Poaceae	*Themeda triandra* Forssk.
5	Proteaceae	*Protea subvestita* N.E.Br.
2	Anacardiaceae	*Rhus discolor* E.Mey. ex Sond.
2	Asteraceae	*Helichrysum tenax* M.D.Henderson
2	Celastraceae	*Maytenus undata* (Thunb.) Blakelock
2	Liliaceae	*Myrsiphyllum asparagoides* (L.) Willd.
2	Myrsinaceae	*Myrsine africana* L.
2	Pteridophyta	*Pteridium aquilinum* (L.) Kuhn
2	Rhamnaceae	*Rhamnus prinoides* L'Hérit
2	Scrophulariaceae	*Bowkeria verticillata* (Eckl. & Zeyh.) Schinz
1	Asteraceae	*Senecio haygarthi* Hilliard
1	Asteraceae	*Stoebe vulgaris* Levyns
1	Ebenaceae	*Diospyros whyteana* (Hiern.) F. White
1	Fabaceae	*Calpurnia villosa* Harv. var. *intrusa* (R.Br. ex Ait.f.) E.Mey.
1	Liliaceae	*Aloe aristata* Haw
1	Liliaceae	*Protoasparagus africanus* Lam.
1	Melianthaceae	*Melianthus villosus* Bol.

1	Pteridophyta	*Polystichum setiferum* Forssk. var. *fuscopaleaceum*
1	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze
1	Santalaceae	*Thesium angulosum* DC.
1	Scrophulariaceae	*Halleria lucida* L.
1	Thymelaeaceae	*Passerina montana* Thoday
+	Zamiaceae	*Encephalartos ghellinckii* Lem.
+	Anacardiaceae	*Rhus undulata* Jacq.
+	Asteraceae	*Anthospermum aethiopicum* L.
+	Asteraceae	*Artemisia afra* Jacq. ex Willd.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Berkheya draco* Roessl.
+	Asteraceae	*Berkheya macrocephala* J.M.Wood
+	Asteraceae	*Chrysanthemoides monilifera* (L.) T.Norl.
+	Asteraceae	*Euryops acraeus* M.D.Henderson
+	Asteraceae	*Euryops pedunculatus* N.E.Br.
+	Asteraceae	*Euryops tysonii* E.P.Phill.
+	Asteraceae	*Felicia filifolia* (Vent.) Burtt Davy
+	Asteraceae	*Haplocarpha scaposa* Harv.
+	Asteraceae	*Helichrysum cephaloideum* DC.
+	Asteraceae	*Helichrysum ecklonis* Sond.
+	Asteraceae	*Helichrysum setosum* Harv.
+	Asteraceae	*Helichrysum umbraculigerum* Less.
+	Asteraceae	*Inulanthera montana* (Wood) Kallersjo
+	Asteraceae	*Macowania conferta* (Benth.) Phill.
+	Asteraceae	*Macowania corymbosa* M.D.Henderson
+	Asteraceae	*Macowanii glandulosa* N.E.Br.
+	Asteraceae	*Senecio conrathii* N.E.Br.
+	Asteraceae	*Senecio ingeliensis* Hilliard
+	Asteraceae	*Senecio inornatus* DC.
+	Asteraceae	*Vernonia hirsuta* (DC.) Sch.Bip.
+	Boraginaceae	*Myosotis sylvatica* Hoffm.
+	Campanulaceae	*Lobelia erinus* L.
+	Campanulaceae	*Wahlenbergia undulata* (L.f.) A.DC.
+	Celastraceae	*Maytenus acuminata* (L.f.) Loes.
+	Crassulaceae	*Crassula vaginata* Eckl. & Zeyh.
+	Cupressaceae	*Widdringtonia nodiflora* (L.) Powrie
+	Dipsacaceae	*Cephalaria natalensis* Kuntz
+	Dipsacaceae	*Scabiosa columbaria* L.
+	Ericaceae	*Erica drakensbergensis* Guthrie & Bolus
+	Ericaceae	*Erica woodii* H.Bol.
+	Euphorbiaceae	*Clutia natalensis* Bernh. ex Krauss
+	Euphorbiaceae	*Euphorbia ericoides* Lam.
+	Fabaceae	*Argyrolobium rupestre* (Eckl. & Zeyh.) Walp.
+	Fabaceae	*Buchenroedera lotononoides* Scott Elliot
+	Fabaceae	*Indigofera longebarbata* Engl.
+	Fabaceae	*Otholobium caffrum* (Eckl. & Zeyh.) C.H.Stirton
+	Fabaceae	*Rhynchosia caribaea* (Jacq.) DC.
+	Geraniaceae	*Geranium incanum* Burm.f.
+	Geraniaceae	*Geranium pulchrum* N.E.Br.
+	Hypoxidaceae	*Hypoxis argentea* Harv. ex Bak. var. *argentea*
+	Hypoxidaceae	*Hypoxis rigidula* Bak.
+	Lamiaceae	*Rabdosiella calycina* (Benth.) Codd
+	Lamiaceae	*Syncolostemon macranthus* (Guerke) Ashby
+	Liliaceae	*Aloe ecklonis* Salm-Dyck

+	Liliaceae	*Eucomis autumnalis* (Mill.) Chitt.
+	Liliaceae	*Eucomis bicolor* Bak.
+	Liliaceae	*Kniphofia angustifolia* (Bak.) Codd
+	Liliaceae	*Ledebouria revoluta* (L.f.) Jessop
+	Liliaceae	*Myrisphyllum ramoissimus* (Bak.) Oberm.
+	Liliaceae	*Myrsiphyllum scandens* (Thunb.) Oberm.
+	Liliaceae	*Scilla natalensis* Planch.
+	Liliaceae	*Urginea rubella* Bak.
+	Loganiaceae	*Buddleja loricata* Leeuwenberg
+	Myricaceae	*Myrica pilulifera* Rendle
+	Olinaceae	*Olinia emarginata* Burtt Davy
+	Poaceae	*Digitaria monodactyla* (Nees) Stapf
+	Poaceae	*Pentaschistis pilosogluma* McClean
+	Polygalaceae	*Polygala myrtifolia* L.
+	Polygalaceae	*Polygala virgata* Thunb.
+	Primulaceae	*Lysimachia ruhmeriana* Vakte
+	Pteridophyta	*Asplenium monanthes* L.
+	Pteridophyta	*Cheilanthes quadripinnata* (Forssk.) Kuhn
+	Pteridophyta	*Cheilanthes viridis* (Forssk.) Swartz var. *viridis*
+	Pteridophyta	*Gleichenia umbraculifera* (Kunze) T.Moore
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Ranunculaceae	*Anemone fanninii* Harv. ex Mast.
+	Ranunculaceae	*Clematis brachiata* Thunb.
+	Ranunculaceae	*Ranunculus baurii* MacOwan
+	Ranunculaceae	*Ranunculus multifidus* Forssk.
+	Rosaceae	*Alchemilla colura* Hilliard
+	Rosaceae	*Alchemilla natalensis* Engl.
+	Rosaceae	*Cliffortia spathulata* Weim.
+	Rubiaceae	*Galium thunbergianum* Eckl. & Zeyh. var. *thunbergianum*
+	Thymelaeaceae	*Gnidia anthylloides* (L.f.) Gilg

Low altitude vlei

15	Gunneraceae	*Gunnera perpensa* L.
10	Cyperaceae	*Carex cognata* Kunth var. *cognata*
10	Cyperaceae	*Cyperus semitrifidus* Schrad. var. *semitrifidus*
5	Cruciferae	*Heliophila rigidiascula* Sond.
5	Cyperaceae	*Pycreus macranthus* C.B.Cl.
5	Poaceae	*Harpochloa falx* (L.f.) Kuntze
5	Poaceae	*Stiburus alopecuroides* (Hack.) Stapf
5	Pteridophyta	*Pteridium aquilinum* (L.) Kuhn
5	Ranunculaceae	*Ranunculus multifidus* Forssk.
2	Cyperaceae	*Ascolepis capensis* (Kunth) Ridley
2	Cyperaceae	*Bulbostylis schoenoides* (Kunth) C.B.Cl.
2	Cyperaceae	*Carex cognata* Kunth var. *drakensbergensis* (C B.Cl.) Kuekenth
2	Cyperaceae	*Carex zuluensis* C.B.Cl.
2	Cyperaceae	*Cyperus schlechteri* C.B.Cl.
2	Cyperaceae	*Eleocharis palustris* R. Br.
2	Cyperaceae	*Mariscus congestus* (Vahl) C.B.Cl.
2	Cyperaceae	*Schoenoxiphium lehmanni* (Nees) Steud.
1	Boraginaceae	*Myosotis sylvatica* Hoffm.
1	Cyperaceae	*Fuirena pubesans* (Poir.) Kunth

1	Rosaceae	*Rubus ludwigii* Eckl. & Zeyh.
+	Asteraceae	*Denekia capensis* Thunb.
+	Asteraceae	*Helichrysum cooperi* Harv.
+	Asteraceae	*Helichrysum hypoleucum* Harv.
+	Asteraceae	*Helichrysum mundtii* Harv.
+	Asteraceae	*Helichrysum umbraculigerum* Less.
+	Asteraceae	*Lactuca capensis* Thunb.
+	Asteraceae	*Nidorella auriculata* DC. subsp. *polycephala*
+	Asteraceae	*Pseudognaphalium undulatum* (L.) Hilliard & Burtt
+	Asteraceae	*Senecio brevidentatus* M.D.Henderson
+	Asteraceae	*Senecio inornatus* DC.
+	Asteraceae	*Senecio gregatus* Hilliard
+	Boraginaceae	*Afrotysonia africana* (H.Bol.) Rauschert
+	Campanulaceae	*Lobelia flaccida* (Presl) A.DC.
+	Cyperaceae	*Bulbostylis oritrephes* (Ridley) C.B.Cl.
+	Cyperaceae	*Eleocharis dregeana* Steud.
+	Cyperaceae	*Kyllinga pauciflora* Ridley
+	Dipsacaceae	*Scabiosa drakensbergensis* B.L.Burtt
+	Droseraceae	*Drosera natalensis* Diels
+	Fabaceae	*Indigofera cuneifolia* Eckl. & Zeyh.
+	Fabaceae	*Lessertia perennans* DC. var. *perennans*
+	Geraniaceae	*Geranium pulchrum* N.E.Br.
+	Guttiferae	*Hypericum lalandii* Choisy
+	Illecebraceae	*Silene undulata* Ait.
+	Iridaceae	*Aristea angolensis* Bak.
+	Iridaceae	*Hesparantha radiata* (Jacq.) Ker-Gawl.
+	Iridaceae	*Moraea galpinii* (Bak.) N.E.Br.
+	Liliaceae	*Eucomis bicolor* Bak.
+	Liliaceae	*Kniphofia angustifolia* (Bak.) Codd
+	Liliaceae	*Kniphofia latifolia* Codd
+	Liliaceae	*Linum thunbergii* Eckl. & Zeyh.
+	Liliaceae	*Ornithogalum paludosum* Bak.
+	Liliaceae	*Tulbaghia alliacea* L.f.
+	Oxalidaceae	*Oxalis obliquifolia* Steud. ex Rich.
+	Papaveraceae	*Papaver aculeatum* Thunb.
+	Poaceae	*Bromus natalensis* Stapf
+	Poaceae	*Cymbopogon validus* (Stapf) Stapf ex Burtt Davy
+	Poaceae	*Hyparrhenia dregeana* (Nees) Stapf
+	Poaceae	*Merxmuellera macrowanii* (Stapf) Conert
+	Poaceae	*Miscanthus capensis* (Nees) Anderss. var. *capensis*
+	Poaceae	*Panicum ecklonii* Nees
+	Poaceae	*Pennisetum thunbergii* Kunth
+	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze
+	Pteridophyta	*Mohria caffrorum* (L.) Desv. var. *caffrorum*
+	Ranunculaceae	*Anemone fanninii* Harv. ex Mast.
+	Rubiaceae	*Anthospermum aethiopicum* L.
+	Scrophulariaceae	*Diclis reptans* Benth.
+	Scrophulariaceae	*Melasma scabrum* Berg.
+	Scrophulariaceae	*Zaluzianskya maritima* (L.f.) Walp.

3 ALPINE REGION

Alpine grassland

20	Poaceae	*Merxmuellera disticha* (Nees) Conert
15	Poaceae	*Pentaschistis oredoxa* Schweickerdt
10	Poaceae	*Festuca caprina* Nees var. *caprina*
5	Cyperaceae	*Scirpus falsus* C.B.Cl.
5	Cyperaceae	*Scirpus ficinioides* Kunth
5	Poaceae	*Merxmuellera drakensbergensis* (Schweick.) Conert
5	Poaceae	*Koeleria capensis* (Steud.) Nees
5	Poaceae	*Agrostis barbuligera* Stapf var. *barbuligera*
2	Asteraceae	*Berkheya multijuga* (DC.) Roessler
2	Asteraceae	*Helichrysum argentissimum* J.M.Wood
2	Poaceae	*Eragrostis caesia* Stapf
2	Poaceae	*Merxmuellera stereophylla* (J.G.Anders.) Conert
1	Asteraceae	*Helichrysum subglomeratum* Less.
1	Asteraceae	*Helichrysum odoratissimum* (L.) Sweet
1	Cyperaceae	*Isolepis costata* (Boeck.) A.Rich.
1	Cyperaceae	*Schoenoxiphium filiforme* Kuekenth
1	Ericaceae	*Erica thodei* Guthrie & Bolus
1	Poaceae	*Harpochloa falx* (L.f.) Kuntze
1	Poaceae	*Stiburus alopecuroides* (Hack.) Stapf
+	Aizoaceae	*Psammotropha alternifolia* Killick
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Aster erucifolius* (Thell.) Lippert
+	Asteraceae	*Berkheya macrocephala* J.M.Wood
+	Asteraceae	*Felicia rosulata* Yeo
+	Asteraceae	*Helichrysum adenocarpum* DC.
+	Asteraceae	*Helichrysum chionosphaerum* DC.
+	Asteraceae	*Helichrysum retortoides* N.E.Br.
+	Asteraceae	*Helichrysum monticola* Hilliard
+	Asteraceae	*Helichrysum setosum* Harv.
+	Asteraceae	*Helichrysum sessile* DC.
+	Asteraceae	*Helichrysum stoloniferum* (L.f.) Willd.
+	Asteraceae	*Helichrysum sutherlandii* Harv.
+	Asteraceae	*Hirpicium armerioides* (DC.) Roessl.
+	Asteraceae	*Senecio barbatus* DC.
+	Asteraceae	*Senecio gramineus* Harv.
+	Asteraceae	*Senecio tugelensis* Wood & Evans
+	Asteraceae	*Senecio cryptolanthus* Killick
+	Boraginaceae	*Myosotis afro-palustris* C.H.Wr.
+	Brassicaceae	*Heliophila suavissima* Burch. ex DC.
+	Campanulaceae	*Wahlenbergia lobulata* V.Brehm.
+	Campanulaceae	*Craterocapsa tarsodes* Hilliard & Burtt
+	Crassulaceae	*Crassula setulosa* Harv. var. *setulosa*
+	Cyperaceae	*Bulbostylis schoenoides* (Kunth) C.B.Cl.
+	Cyperaceae	*Bulbostylis humilis* (Kunth) C.B.Cl.
+	Cyperaceae	*Tetraria cuspidata* (Rottb.) C.B.Cl.
+	Ericaceae	*Erica dominans* Killick
+	Ericaceae	*Erica frigida* H. Bol.
+	Ericaceae	*Erica reenenis* Zahlbr.
+	Fabaceae	*Lotononis galpinii* Duemmer
+	Fabaceae	*Lessertia thodei* L.Bol.
+	Gentianaceae	*Sebaea procumbens* A.W.Hill
+	Gentianaceae	*Sebaea thodeana* Gilg

+	Iridaceae	*Hesparantha baurii* Bak. subsp. *baurii*
+	Juncaceae	*Luzula africana* Drege ex Steud.
+	Liliaceae	*Kniphofia caulescens* Bak.
+	Orchidaceae	*Habenaria laevigata* Lindl. subsp. *laevigata*
+	Poaceae	*Aira caryophyllea* L.
+	Poaceae	*Anthoxanthum ecklonii* (Nees ex Trin.) Stapf
+	Poaceae	*Brachypodium bolusii* Stapf
+	Poaceae	*Ehrharta longigluma* C.E.Hubb.
+	Rubiaceae	*Anthospermum hispidulum* E.Mey. ex Sond.
+	Rosaceae	*Geum capense* Thunb.
+	Thymelaeaceae	*Gnidia aberrans* C.H.Wr.

***Erica-Helichrysum* Heathland**

20	Asteraceae	*Helichrysum trilineatum* DC.
15	Ericaceae	*Erica spp.*
15	Ericaceae	*Erica thodei* Guthrie & Bolus
5	Thymelaeaceae	*Passerina montana* Thoday
2	Asteraceae	*Eumorpha sericea* Wood & Evans
2	Asteraceae	*Helichrysum miconiifolium* DC.
2	Asteraceae	*Helichrysum sessile* DC.
2	Asteraceae	*Macowania glandulosa* N.E.Br.
2	Cyperaceae	*Isolepis fluitans* (L.) R.Br.
2	Ericaceae	*Erica algida* H.Bol.
2	Poaceae	*Koeleria capensis* (Steud.) Nees
1	Asteraceae	*Helichrysum evansii* Hilliard
1	Cyperaceae	*Scirpus falsus* C.B.Cl.
1	Ericaceae	*Erica ebracteata* H.Bol.
1	Poaceae	*Merxmuellera drakensbergense* (Schweick.) Conert
1	Poaceae	*Merxmuellera stereophylla* (J.G.Anders.) Conert
1	Rosaceae	*Cliffortia spathulata* Weim.
1	Santalaceae	*Thesium imbricatum* Thunb.
+	Asteraceae	*Athrixia fontana* MacOwan
+	Asteraceae	*Berkheya multijuga* (DC.) Roessler
+	Asteraceae	*Chrysocoma ciliata* L.
+	Asteraceae	*Euryops acraeus* M.D.Henderson
+	Asteraceae	*Helichrysum albo-brunneum* S.Moore
+	Asteraceae	*Helichrysum monticola* Hilliard
+	Asteraceae	*Helichrysum odoratissimum* (L.) Sweet
+	Asteraceae	*Helichrysum retortoides* N.E.Br.
+	Asteraceae	*Helichrysum setosum* Harv.
+	Asteraceae	*Ursinia montana* DC. subsp. *montana*
+	Campanulaceae	*Craterocapsa tarsodes* Hilliard & Burtt
+	Campanulaceae	*Monopsis decipiens* (Sond.) Thulin
+	Campanulaceae	*Wahlenbergia lobulata* V.Brehm.
+	Crassulaceae	*Crassula natans* Thunb.
+	Crassulaceae	*Crassula setulosa* Harv. var. *rubra* (N.E.Br.) Rowley
+	Cyperaceae	*Scirpus ficinioides* Kunth
+	Droseraceae	*Drosera natalensis* Diels
+	Dipsacaceae	*Scabiosa columbaria* L.
+	Ericaceae	*Erica dominans* Killick
+	Ericaceae	*Erica frigida* H.Bol.
+	Ericaceae	*Erica straussiana* Gilg
+	Euphorbiaceae	*Clutia nana* Prain
+	Orchidaceae	*Disa fragrans* Schltr

+	Poaceae	*Agrostis barbuligera* Stapf var. *barbuligera*
+	Poaceae	*Pentaschistis oreodoxa* Schweickerdt
+	Poaceae	*Pentaschistis tysonii* Stapf
+	Polygalaceae	*Muraltia saxicola* Chodat
+	Pteridophyta	*Mohria carrrorum* (L.) Desv. var. caffrorum
+	Pteridophyta	*Woodesia montevidensis* (Spreng.) Hieron. var. *burgessiana* (Hook.& Bak.) Schelpe
+	Scrophulariaceae	*Diascia barberae* Hook.f.
+	Scrophulariaceae	*Selago flanagani* Rolfe
+	Thymelaeaceae	*Gnidia polystachya* Berg var. *polystachya*

High altitude vlei

15	Eriocaulaceae	*Eriocaulon dregei* Hochst. var. *dregei*
15	Cyperaceae	*Carex monotropha* Nelmes
10	Cyperaceae	*Carex killickii* Nelmes
10	Cyperaceae	*Isolepis fluitans* (L.) R.Br.
5	Poaceae	*Agrostis barbuligera* Stapf var. *barbuligera*
5	Poaceae	*Merxmuellera drakensbergensis* (Schweick.) Conert
5	Poaceae	*Pentaschistis oreodoxa* Schweickerdt
2	Cyperaceae	*Schoenoxiphium filiforme* Kuekenth
2	Cyperaceae	*Scirpus falsus* C.B.Cl.
2	Cyperaceae	*Scirpus ficinioides* Kunth
2	Iridaceae	*Moraea spathulata* (L.f.) Klatt
2	Juncaceae	*Luzula africana* Drege ex Steud.
1	Asteraceae	*Senecio cryptolanthus* Killick
1	Ericaceae	*Erica frigida* H.Bol.
+	Aizoaceae	*Psammotropha alternifolia* Killick
+	Aizoaceae	*Psammotropha mucronata* (Thunb.) Fenzl
+	Aponogetonaceae	*Aponogeton junceus* Lehm. ex Schlechtd. subsp. *natalensis* (Oliv.) Oberm.
+	Asteraceae	*Aster bakeranus* Burtt Davy ex C.A.Sm.
+	Asteraceae	*Aster erucifolius* (Thell.) Lippert
+	Asteraceae	*Athrixia angustissima* DC.
+	Asteraceae	*Athrixia fontana* MacOwan
+	Asteraceae	*Euryops decumbens* B.Nord.
+	Asteraceae	*Euryops montanus* Schltr.
+	Asteraceae	*Berkheya multijuga* (DC.) Roessler
+	Asteraceae	*Helichrysum argentissimum* J.M.Wood
+	Asteraceae	*Helichrysum chionosphaerum* DC.
+	Asteraceae	*Senecio achilleaefolius* DC.
+	Asteraceae	*Ursinia montana* DC. subsp. *montana*
+	Asteraceae	*Helichrysum retortoides* N.E.Br.
+	Asteraceae	*Helichrysum subglomeratum* Less.
+	Asteraceae	*Hirpicium armerioides* (DC.) Roessl
+	Caryophyllaceae	*Cerastium arabidis* E.Mey. ex Fenzl
+	Crassulaceae	*Crassula setulosa* Harv. var. *rubra* (N.E.Br.) Rowley
+	Crassulaceae	*Crassula setulosa* Harv. var. *setulosa*
+	Cyperaceae	*Carex glomerabilis* Krecz.
+	Dipsacaceae	*Scabiosa columbaria* L.
+	Droseraceae	*Drosera natalensis* Diels
+	Ericaceae	*Erica alopecurus* Harv. var. *alopecurus*
+	Ericaceae	*Erica thodei* Guthrie & Bolus
+	Fabaceae	*Trifolium burchellianum* Ser. var. *burchellianum*
+	Geraniaceae	*Geranium incanum* Burm.f. var. *multifidum* (Sweet) Hilliard & Burtt
+	Gentianaceae	*Sebaea thodeana* Gilg

+	Hypoxidaceae	*Rhodohypoxis rubella* (Bak.) Nel
+	Iridaceae	*Gladiolus longicollis* Bak.
+	Juncaceae	*Juncus exsertus* Buchen.
+	Orchidaceae	*Disa fragrans* Schltr.
+	Oxalidaceae	*Oxalis obliquifolia* Steud. ex Rich.
+	Poaceae	*Eragrostis caesia* Stapf
+	Poaceae	*Koeleria capensis* (Steud.) Nees
+	Poaceae	*Pentaschistis tysonii* Stapf
+	Ranunculaceae	*Ranunculus capensis* Thunb.
+	Scrophulariaceae	*Limosella capensis* Thunb.
+	Scrophulariaceae	*Limosella longiflora* Kuntze

APPENDIX 7

SEASONAL POLLEN TRAP DATA (Grains/cm^2/90 days)

Highland Sourveld

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Asteraceae	24.9	27.6	43.8	14.5	11.9	23.1	15.2	31.6
Campanulaceae	0.2	0.3	0.3	0.1	0.4	0.3	0.0	0.2
Crassulaceae	0.1	1.1	0.0	0.6	0.7	0.2	0.6	0.3
Cyperaceae	0.2	2.9	5.3	2.3	0.4	3.8	2.7	4.1
Ericaceae	1.1	1.1	0.1	0.1	1.5	0.1	0.7	0.1
Euphorbiaceae	2.1	1.3	0.8	2.5	0.6	1.1	1.6	1.5
Fabaceae	0.3	0.9	0.2	0.9	0.6	0.2	0.9	0.5
Gentianaceae	0.1	0.1	0.1	0.4	0.0	0.0	0.2	0.2
Geraniaceae	1.9	0.5	0.3	0.3	0.0	0.2	0.2	0.3
Guttiferae	0.1	0.4	0.1	0.0	0.0	0.0	0.5	0.0
Hypoxidaceae	1.4	3.4	4.3	0.3	1.1	0.9	0.1	2.6
Illecebraceae	0.0	0.0	0.5	1.6	0.0	0.3	0.9	1.0
Iridaceae	1.4	1.7	0.6	0.3	0.2	0.5	0.8	0.5
Liliaceae	0.1	0.1	0.0	0.0	0.0	0.0	0.3	0.0
Malvaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Myricaceae	0.8	0.0	0.0	0.1	0.2	0.0	0.4	0.0
Poaceae	61.5	48.8	35.1	73.5	70.9	41.9	67.2	51.0
Polygalaceae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Proteaceae	0.0	0.0	0.2	0.0	2.2	0.8	0.7	0.1
Pteridophyta	0.3	3.8	6.5	0.9	4.7	20.5	3.8	4.1
Rosaceae	0.5	2.1	0.2	0.1	1.9	1.7	0.7	0.2
Santalaceae	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.0
Scrophulariaceae	1.2	2.8	0.7	0.8	2.1	0.6	0.6	0.7
Thymelaeaceae	0.6	0.3	0.1	0.1	0.2	3.2	0.1	0.1
Unknowns	0.4	0.1	0.3	0.2	0.0	0.3	0.3	0.2
Valerianaceae	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Verbenaceae	0.1	0.1	0.0	0.0	0.0	0.1	0.0	0.0

Protea **savanna**

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	1.7	0.3	0.1	2.0	1.7	0.7	1.0	1.2
Apiaceae	0.0	0.9	0.0	0.1	0.0	0.1	0.3	0.1
Asclepiadaceae	0.1	0.0	0.0	0.1	0.0	0.1	0.2	0.0
Asteraceae	6.0	6.5	3.3	28.5	7.6	6.8	8.1	17.5
Campanulaceae	0.1	0.2	0.1	0.2	0.2	0.3	0.3	0.2
Cornaceae	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0
Crassulaceae	0.6	0.8	0.2	0.9	1.1	0.3	0.5	0.6
Cyperaceae	3.0	2.5	5.2	1.4	1.5	1.8	2.6	3.0
Ebenaceae	0.0	0.0	0.0	0.1	0.2	0.0	0.1	0.0
Ericaceae	1.9	0.7	0.1	0.3	1.1	0.2	1.2	0.2
Euphorbiaceae	0.9	3.6	1.0	2.6	1.2	1.2	1.6	1.9
Fabaceae	0.3	0.1	0.0	0.0	0.0	0.0	0.1	0.0
Gentianaceae	0.1	0.1	0.0	0.2	0.5	0.2	0.3	0.1
Geraniaceae	0.1	0.3	0.0	0.0	0.0	0.1	0.1	0.0
Hypoxidaceae	1.4	0.7	0.4	0.2	0.8	0.6	0.6	0.3
Illecebraceae	0.1	0.1	0.3	0.7	0.3	0.3	0.7	0.5
Iridaceae	0.9	1.3	0.3	0.2	0.3	0.2	0.3	0.3
Lamiaceae	0.3	0.4	0.1	0.2	0.2	0.1	0.2	0.2
Liliaceae	0.0	0.1	0.1	0.0	0.1	0.0	0.2	0.0
Linaceae	0.0	0.1	0.0	0.1	0.5	0.1	0.6	0.1
Myricaceae	15.3	0.0	0.1	0.1	0.4	0.1	0.6	0.1
Oxalidaceae	0.3	0.2	0.1	0.2	0.1	0.1	0.1	0.2
Poaceae	46.2	25.5	27.1	34.6	52.2	19.8	41.6	31.3
Polygalaceae	0.0	0.7	0.0	0.1	0.0	0.0	0.2	0.0
Proteaceae	9.0	37.8	54.1	18.7	19.8	56.1	30.6	34.1
Pteridophyta	1.9	2.6	4.7	1.9	4.5	7.8	3.4	3.1
Rosaceae	2.7	3.0	0.5	0.3	1.8	0.8	1.2	0.4
Rubiaceae	0.0	0.3	0.0	0.2	0.4	0.1	0.2	0.1
Scrophulariaceae	3.7	4.7	0.5	3.8	1.0	0.3	1.3	2.4
Thymelaeaceae	0.2	0.5	0.2	0.1	0.0	0.1	0.1	0.2
Unknowns	0.4	0.6	0.3	0.7	1.0	0.7	1.0	0.5
Valerianaceae	0.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0

***Podocarpus* forest**

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Amaranthaceae	0.1	0.1	0.2	0.5	0.1	0.3	0.3	0.3
Anacardiaceae	0.3	0.8	0.3	0.4	1.1	1.5	0.3	0.3
Apocynaceae	0.1	1.3	1.0	0.7	0.4	2.3	0.8	0.9
Araliaceae	0.0	0.0	0.1	0.1	0.2	0.0	0.0	0.1
Asteraceae	2.8	0.7	0.9	4.0	1.2	0.9	2.0	2.2
Begoniaceae	0.0	0.0	0.1	0.0	0.1	0.2	0.2	0.0
Celastraceae	0.4	0.6	0.7	2.8	0.1	0.5	1.0	1.6
Cornaceae	0.1	0.2	0.4	1.0	0.0	0.0	0.3	0.6
Crassulaceae	0.1	0.4	0.6	1.2	0.7	0.3	0.4	0.9
Cyperaceae	0.4	0.6	1.9	2.2	0.3	2.4	2.0	2.0
Ebenaceae	0.0	0.6	0.3	0.1	0.3	1.5	1.1	0.2
Ericaceae	0.6	0.7	0.3	0.3	0.4	0.4	0.8	0.3
Euphorbiaceae	0.1	0.1	0.2	0.2	0.0	0.0	0.1	0.2
Flacourtiaceae	0.3	9.9	2.9	1.7	1.1	7.8	0.5	2.4
Icacinaceae	0.1	3.1	0.7	0.2	0.5	1.3	0.1	0.5
Iridaceae	0.2	0.0	0.1	0.2	0.0	0.2	0.6	0.1
Lamiaceae	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.1
Liliaceae	1.3	0.2	0.2	0.2	1.1	0.5	0.0	0.2
Myricaceae	0.6	0.2	0.2	0.2	0.5	0.1	0.5	0.2
Myrsinaceae	0.0	0.0	0.0	0.1	0.0	0.2	0.1	0.1
Poaceae	12.0	13.4	22.8	40.6	6.8	23.8	23.3	30.6
Podocarpaceae	9.0	11.1	15.9	19.0	7.5	14.2	13.3	17.2
Pteridophyta	4.5	3.9	9.1	7.3	3.5	23.8	13.1	8.4
Rhamnaceae	2.3	0.5	0.7	2.1	0.7	0.5	2.3	1.3
Rosaceae	0.0	0.0	0.1	0.1	0.0	0.4	0.6	0.1
Rubiaceae	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1
Rutaceae	0.1	0.6	0.8	0.5	0.2	0.8	0.5	0.7
Sapindaceae	0.7	0.6	36.2	10.3	0.5	11.0	18.7	24.9
Scrophulariaceae	0.4	0.7	1.0	1.3	6.7	1.3	1.0	1.1
Solanaceae	0.0	0.1	0.5	0.1	0.1	0.3	0.0	0.3
Thymelaeaceae	0.0	0.1	0.1	0.1	0.1	0.1	0.0	0.1
Ulmaceae	63.1	48.7	0.8	1.8	65.5	1.7	14.6	1.3
Unknowns	0.1	0.3	0.3	0.3	0.1	0.5	0.8	0.3

Rendlia altera grassland

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Acanthaceae	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Apiaceae	0.0	0.1	0.2	0.2	0.0	0.1	0.4	0.2
Apocynaceae	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Asteraceae	26.6	47.1	24.1	17.3	14.3	28.8	18.6	21.6
Campanulaceae	0.2	0.0	0.2	0.2	0.2	0.1	0.4	0.2
Celastraceae	0.0	0.5	0.1	0.3	0.6	0.4	0.4	0.2
Commelinaceae	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.1
Cornaceae	0.0	0.0	0.2	0.2	0.0	0.4	0.5	0.2
Crassulaceae	0.3	0.6	0.3	1.3	2.3	1.0	1.8	0.7
Cyperaceae	3.7	1.9	6.9	3.5	5.1	9.1	6.0	5.7
Dipsacaceae	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.1
Ericaceae	1.5	1.3	0.6	1.2	1.9	0.2	0.9	0.8
Euphorbiaceae	0.0	0.0	0.1	0.9	0.0	0.2	0.1	0.4
Fabaceae	1.4	1.5	0.5	2.7	2.1	1.1	1.1	1.3
Flacourtiaceae	0.6	2.5	1.3	0.0	0.0	0.3	1.7	0.8
Gentianaceae	0.0	0.0	0.0	0.2	0.1	0.2	0.0	0.1
Geraniaceae	0.6	1.2	0.8	2.1	0.0	0.4	0.4	1.2
Hypoxidaceae	1.9	4.4	10.8	1.3	0.3	3.6	0.9	7.3
Icacinaceae	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Illecebraceae	0.7	0.2	0.4	1.4	0.0	0.4	1.4	0.8
Iridaceae	1.2	0.9	0.6	2.3	0.1	0.5	0.1	1.2
Lamiaceae	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.2
Lamiaceae	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1
Liliaceae	0.0	0.2	0.0	0.1	0.3	0.1	0.2	0.0
Linaceae	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Lobeliaceae	0.0	0.0	0.0	0.1	0.0	0.0	0.2	0.0
Malvaceae	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Myricaceae	0.7	0.0	0.1	0.1	0.0	0.0	0.0	0.1
Oxalidaceae	0.1	0.0	0.3	0.3	0.4	0.4	0.3	0.3
Poaceae	42.9	22.9	26.2	56.1	57.0	38.7	49.3	37.1
Podocarpaceae	2.1	3.2	1.1	0.5	3.6	1.3	4.1	0.9
Polygalaceae	0.0	0.4	0.1	0.1	0.0	0.0	0.0	0.1
Proteaceae	0.3	0.5	19.1	1.0	1.2	1.0	2.2	12.5
Pteridophyta	1.3	1.2	3.1	0.5	2.8	7.2	2.2	2.1
Rhamnaceae	0.4	0.0	0.0	0.1	0.2	0.3	0.0	0.1
Rosaceae	1.8	1.2	0.2	0.4	1.5	0.7	0.9	0.3
Rubiaceae	0.8	0.3	0.1	0.3	0.0	0.4	0.0	0.2
Scrophulariaceae	1.3	1.3	0.9	1.3	0.8	0.7	1.7	1.1
Solaniaceae	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Thymelaeaceae	0.0	0.4	0.2	0.0	0.0	0.4	0.2	0.1
Ulmaceae	2.4	5.3	0.0	0.0	3.8	0.2	1.5	0.0
Unknowns	5.3	2.4	0.4	0.7	0.5	0.7	1.0	0.5

Leucosidea sericea scrubland

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	0.0	0.0	0.1	0.8	0.0	0.0	0.3	0.5
Asclepiadaceae	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asteraceae	0.8	2.4	18.6	10.9	1.9	10.8	6.9	14.7
Boraginaceae	0.3	0.1	0.1	0.3	0.0	0.1	0.1	0.2
Campanulaceae	0.0	0.2	0.1	0.1	0.0	0.0	0.0	0.1
Commelinaceae	0.0	0.0	0.1	0.2	0.0	0.1	0.1	0.1
Crassulaceae	0.0	0.0	0.1	0.2	0.0	0.1	0.1	0.2
Cyperaceae	0.2	1.8	6.7	2.9	0.4	4.4	1.2	4.8
Dipsacaceae	0.0	0.0	0.2	0.2	0.1	0.1	0.0	0.2
Ebenaceae	0.0	0.0	0.2	0.1	0.1	0.5	0.7	0.1
Ericaceae	1.5	1.1	1.8	12.8	3.3	1.7	8.3	7.4
Euphorbiaceae	0.1	0.2	0.7	0.8	0.1	0.6	0.3	0.8
Fabaceae	0.2	0.3	0.6	1.1	0.3	0.9	0.9	0.9
Gentianaceae	0.0	0.1	0.1	0.7	0.1	0.4	0.7	0.4
Geraniaceae	0.0	0.1	0.9	0.1	0.0	0.1	0.6	0.5
Hypoxidaceae	0.0	0.2	1.1	0.1	0.1	0.4	0.2	0.6
Illecebraceae	0.0	0.2	0.7	1.8	0.2	0.4	0.5	1.3
Iridaceae	0.0	0.0	0.1	0.2	0.0	0.5	0.3	0.1
Lamiaceae	0.0	0.0	0.1	0.4	0.1	0.2	0.1	0.2
Leucosidea	88.2	74.9	17.2	11.0	82.1	23.1	47.6	14.0
Liliaceae	0.2	0.2	1.1	0.1	0.1	0.2	0.1	0.6
Loganiaceae	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Myricaceae	0.2	0.0	0.0	0.1	0.1	0.1	0.2	0.1
Myrsinaceae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Oxalidaceae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Poaceae	5.6	12.6	36.7	43.3	7.9	40.5	23.5	40.0
Polygalaceae	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Proteaceae	0.0	0.2	0.4	0.2	0.0	0.1	0.4	0.3
Pteridophyta	1.3	2.5	8.8	6.1	1.7	10.2	4.2	7.5
Ranunculaceae	0.1	0.1	0.0	0.1	0.2	0.8	0.6	0.1
Rhamnaceae	0.1	0.1	0.4	0.6	0.2	0.6	0.2	0.5
Rosaceae	0.2	1.2	0.7	0.5	0.3	1.3	0.5	0.6
Rubiaceae	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1
Scrophulariaceae	0.5	0.5	1.2	3.2	0.2	0.5	0.3	2.2
Solanaceae	0.0	0.1	0.2	0.1	0.1	0.1	0.0	0.1
Thymelaeaceae	0.0	0.4	0.3	0.1	0.0	0.3	0.0	0.2
Unknowns	0.1	0.1	0.4	0.5	0.2	0.5	0.6	0.4

Themeda triandra grassland

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	0.0	0.0	0.7	0.2	0.0	0.1	0.7	0.4
Apiaceae	0.0	0.2	0.1	0.1	0.0	0.1	0.2	0.1
Asclepiadaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Asteraceae	35.3	47.5	34.1	74.8	26.8	38.2	40.7	56.4
Campanulaceae	0.1	0.2	0.2	0.3	0.1	0.3	0.5	0.3
Commelinaceae	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Crassulaceae	0.2	0.2	2.3	0.4	0.1	0.8	0.7	1.3
Cyperaceae	0.8	0.9	3.0	0.4	1.3	4.2	1.2	1.6
Dipsacaceae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Ericaceae	2.0	4.8	1.2	0.2	2.8	2.9	1.0	0.6
Euphorbiaceae	1.7	1.0	1.2	0.4	0.9	0.9	0.7	0.8
Fabaceae	0.2	0.8	1.5	1.5	0.8	1.1	2.0	1.5
Gentianaceae	0.0	0.3	1.5	0.3	0.2	0.5	1.2	0.9
Geraniaceae	0.1	0.2	0.5	0.2	0.5	0.2	0.7	0.3
Hypoxidaceae	0.9	2.0	1.4	0.1	0.8	1.9	0.3	0.7
Illecebraceae	0.1	0.1	0.6	0.4	0.5	0.5	0.5	0.5
Iridaceae	0.6	2.3	0.4	0.3	1.2	1.2	0.2	0.3
Lamiaceae	0.8	0.7	2.6	0.8	1.3	1.7	2.8	1.6
Liliaceae	0.0	0.1	0.0	0.0	0.1	0.4	0.0	0.0
Linaceae	0.1	0.0	0.0	0.0	0.0	0.1	0.4	0.0
Loganiaceae	0.0	0.0	2.1	0.2	0.0	0.3	2.4	1.1
Malvaceae	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Myricaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Onagraceae	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxalidaceae	0.2	0.1	0.2	0.0	0.3	0.1	0.1	0.1
Poaceae	51.4	31.7	36.7	14.7	53.7	35.8	34.1	24.6
Polygalaceae	0.0	0.1	0.0	0.0	0.0	0.3	0.0	0.0
Proteaceae	0.1	0.1	0.2	0.0	0.3	0.1	0.1	0.1
Pteridophyta	0.9	0.3	1.1	0.1	0.8	2.3	0.6	0.5
Rosaceae	1.1	0.9	0.4	0.9	2.1	1.3	0.7	0.7
Rubiaceae	0.1	0.2	0.1	0.2	0.4	0.2	0.4	0.2
Scrophulariaceae	2.3	4.9	6.5	2.9	3.2	2.9	5.3	4.6
Sterculiaceae	0.0	0.0	0.2	0.0	0.1	0.1	0.5	0.1
Thymelaeaceae	0.1	0.2	0.1	0.0	0.4	0.2	0.0	0.0
Unknowns	0.6	0.3	0.7	0.3	0.3	0.7	1.1	0.5
Valerianaceae	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0

'Mixed' grassland

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	1.5	1.6	5.8	1.7	0.9	2.1	3.9	3.7
Apiaceae	0.0	0.1	0.1	0.3	0.1	0.0	0.4	0.2
Asclepiadaceae	0.0	0.1	0.0	0.4	0.1	0.1	0.5	0.2
Asteraceae	25.3	41.8	25.0	43.1	37.7	29.5	36.2	34.2
Boraginaceae	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0
Brassicaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Campanulaceae	0.3	0.3	0.3	0.0	0.2	0.2	0.2	0.1
Crassulaceae	0.2	0.1	0.5	0.0	0.0	0.0	0.0	0.3
Cyperaceae	1.3	2.1	5.7	1.0	1.3	5.0	1.2	3.3
Ericaceae	0.9	2.0	0.7	1.3	1.8	1.9	0.4	1.0
Euphorbiaceae	2.4	1.5	1.0	1.4	0.9	1.1	1.3	1.2
Gentianaceae	0.2	0.0	0.0	0.1	0.1	0.2	0.4	0.1
Geraniaceae	1.2	0.3	1.3	0.5	0.4	0.4	0.9	0.9
Guttiferae	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.0
Hypoxidaceae	0.2	0.8	1.5	0.2	0.3	1.5	0.6	0.9
Illecebraceae	0.3	0.9	0.5	1.0	0.5	0.5	1.9	0.8
Lamiaceae	0.0	0.5	0.6	0.2	0.1	0.7	1.0	0.4
Liliaceae	1.9	3.7	1.1	1.0	2.9	3.5	0.8	1.1
Linaceae	0.0	0.0	0.5	0.1	0.1	0.0	0.0	0.3
Myricaceae	0.1	0.0	0.0	0.0	0.2	0.1	0.3	0.0
Oxalidaceae	0.1	0.0	0.2	0.1	0.3	0.2	1.1	0.1
Poaceae	57.0	35.6	47.0	42.0	45.6	44.0	41.1	44.5
Proteaceae	0.1	0.0	0.2	0.1	0.5	0.1	0.0	0.1
Pteridophyta	0.8	0.7	3.0	0.6	0.5	3.9	1.2	1.8
Rhamnaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Rosaceae	3.0	1.6	0.8	0.7	1.6	1.3	0.7	0.7
Rubiaceae	0.6	0.7	0.2	0.1	0.7	0.2	0.4	0.2
Scrophulariaceae	0.8	3.4	2.4	2.7	2.1	2.0	3.1	2.6
Thymelaeaceae	0.0	0.6	0.1	0.1	0.1	0.3	0.1	0.1
Unknowns	1.0	0.2	0.5	0.3	0.1	0.4	0.4	0.4
Valerianaceae	0.1	0.1	0.2	0.0	0.0	0.0	0.3	0.1

***Festuca costata* grassland**

TAXA	June-Aug 1988	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Aizoaceae	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.1
Anacardiaceae	1.0	1.4	1.5	0.1	0.1	0.3	0.9	0.8
Apiaceae	0.0	0.1	0.2	0.0	0.0	0.1	0.4	0.1
Asteraceae	26.6	30.8	21.0	47.4	21.9	22.3	35.8	33.5
Campanulaceae	0.2	0.2	0.1	0.1	0.1	0.2	0.1	0.1
Commelinaceae	0.0	0.0	0.0	0.4	0.0	0.1	0.2	0.2
Crassulaceae	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Cyperaceae	1.4	1.8	7.6	0.7	0.8	5.7	1.8	4.3
Dipsacaceae	0.0	0.0	0.2	0.0	0.0	0.1	0.4	0.1
Ericaceae	8.1	2.3	1.4	1.4	2.3	1.1	1.3	1.4
Euphorbiaceae	2.0	2.3	2.0	1.2	1.0	1.0	1.6	1.6
Fabaceae	0.8	0.7	0.8	4.1	1.5	0.5	1.4	2.4
Gentianaceae	0.1	0.0	0.2	0.1	0.1	0.1	0.0	0.2
Geraniaceae	0.2	0.2	1.1	0.2	0.1	0.2	1.4	0.7
Hypoxidaceae	0.1	2.1	1.9	0.0	0.6	0.9	0.2	1.0
Illecebraceae	0.1	0.5	0.7	0.8	1.3	0.4	1.5	0.7
Lamiaceae	0.1	0.2	0.2	0.3	0.2	0.8	1.2	0.2
Liliaceae	0.5	1.9	1.6	0.5	0.5	2.7	1.2	1.1
Linaceae	0.0	0.0	0.3	0.2	0.1	0.2	0.0	0.2
Loganiaceae	0.0	0.0	0.7	0.1	0.0	0.0	0.3	0.4
Malvaceae	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
Myricaceae	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Oxalidaceae	0.0	0.1	0.5	0.0	0.0	0.2	0.1	0.3
Poaceae	50.5	49.8	49.9	38.9	61.0	51.9	44.4	44.7
Polygalaceae	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.1
Proteaceae	0.0	0.3	0.2	0.2	0.4	0.0	0.3	0.2
Pteridophyta	3.0	0.4	2.4	0.4	2.0	5.4	1.2	1.4
Ranunculaceae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Rosaceae	0.6	1.4	0.4	0.2	0.8	1.5	0.9	0.3
Rubiaceae	0.2	0.0	0.2	0.1	0.1	0.0	0.1	0.2
Santalaceae	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0
Scrophulariaceae	3.1	2.0	3.2	1.4	2.4	2.0	1.7	2.3
Solanaceae	0.0	0.1	0.3	0.2	0.3	0.3	0.0	0.3
Sterculiaceae	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0
Thymelaeaceae	0.3	0.4	0.2	0.0	0.2	0.2	0.0	0.1
Unknowns	0.9	0.2	0.7	0.4	0.1	0.5	0.7	0.6

Low altitude vlei

TAXA	Sept-Nov 1988	Dec-Feb 1989	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990	Dec-May 1989
Anacardiaceae	0.4	0.2	0.0	0.1	0.1	0.0	0.1
Apiaceae	0.0	0.0	0.2	0.0	0.0	0.0	0.1
Asteraceae	13.5	34.6	15.5	5.5	7.5	18.3	23.0
Boraginaceae	0.1	0.0	0.6	0.1	0.0	0.3	0.4
Brassicaceae	0.1	0.0	0.0	0.0	0.2	0.6	0.0
Campanulaceae	0.0	0.1	0.1	0.1	0.6	0.0	0.1
Cyperaceae	7.2	17.2	2.3	4.9	17.9	4.8	8.2
Dipsacaceae	1.1	0.3	0.4	0.0	0.3	2.7	0.4
Ericaceae	0.2	0.2	0.4	3.4	0.4	2.3	0.3
Fabaceae	0.1	0.0	0.8	0.2	0.2	0.2	0.5
Geraniaceae	0.0	0.0	1.0	0.3	0.6	9.0	0.6
Gunneraceae	0.0	2.4	0.0	0.1	5.8	0.2	1.0
Guttiferae	1.6	0.6	0.2	0.4	0.6	0.5	0.4
Hypoxidaceae	1.0	0.4	0.0	0.1	0.6	0.0	0.2
Illecebraceae	0.1	0.4	0.8	0.1	0.2	0.4	0.7
Iridaceae	1.0	2.0	0.2	1.5	1.3	1.6	0.9
Lamiaceae	0.5	0.1	0.3	0.1	0.2	2.1	0.2
Leucosidea	0.6	0.0	0.6	0.1	0.2	0.8	0.3
Liliaceae	0.1	0.7	0.0	0.3	0.7	0.9	0.3
Linaceae	0.1	0.0	0.1	0.1	0.2	0.8	0.1
Malvaceae	0.0	0.1	0.0	0.0	0.0	0.0	0.1
Onagraceae	0.7	0.1	0.0	0.0	0.0	0.0	0.1
Oxalidaceae	0.5	0.3	0.0	0.0	0.2	0.9	0.1
Papaveraceae	2.5	1.8	0.2	0.0	1.4	0.0	0.8
Poaceae	62.8	31.2	28.7	76.5	43.8	39.0	29.7
Polygalaceae	0.1	0.3	0.0	0.0	0.1	0.0	0.1
Proteaceae	0.0	0.2	0.0	0.3	0.2	0.0	0.1
Pteridophyta	1.4	3.5	44.7	2.6	8.6	10.6	28.5
Ranunculaceae	1.9	1.7	0.7	0.1	0.9	0.5	1.1
Rosaceae	0.6	0.5	0.4	1.0	3.6	0.3	0.4
Rubiaceae	0.0	0.2	0.0	0.0	0.4	0.1	0.1
Scrophulariaceae	1.1	0.4	1.3	1.1	1.8	2.0	0.9
Thymelaeaceae	0.4	0.1	0.0	0.0	0.0	0.0	0.1
Unknowns	0.2	0.2	0.3	0.3	0.7	0.7	0.3

Sub-alpine fynbos

TAXA	March-May 1989	June-Aug 1989	Sept-Nov 1989	Dec-May 1990
Anacardiaceae	0.3	0.9	0.6	1.3
Apiaceae	0.2	0.0	0.0	0.1
Asteraceae	26.8	8.8	11.4	14.0
Boraginaceae	0.1	0.0	0.1	0.6
Campanulaceae	0.1	0.2	0.3	0.9
Celastraceae	0.1	0.0	0.1	0.2
Cornaceae	0.0	0.0	0.3	0.0
Crassulaceae	0.8	3.7	1.6	2.7
Cyperaceae	0.5	0.4	2.5	1.4
Dipsacaceae	0.7	0.4	1.8	0.3
Ebenaceae	0.2	0.4	1.4	0.5
Ericaceae	3.7	49.8	8.7	11.3
Euphorbiaceae	0.8	0.5	1.4	0.6
Fabaceae	2.4	1.8	1.9	2.1
Gentianaceae	0.4	0.1	0.0	0.1
Geraniaceae	0.7	0.5	0.9	0.3
Hypoxidaceae	0.1	0.2	0.7	1.9
Illecebraceae	0.5	0.1	0.2	0.5
Iridaceae	0.0	0.1	0.7	0.2
Lamiaceae	0.1	0.4	0.3	1.1
Liliaceae	0.1	0.5	0.4	0.1
Loganiaceae	0.6	0.9	1.2	1.2
Myricaceae	0.1	0.1	0.0	0.2
Myrsinaceae	0.0	0.0	0.1	0.0
Poaceae	20.7	11.7	33.1	23.4
Polygalaceae	0.0	0.0	0.1	0.0
Proteaceae	20.5	5.5	4.8	20.6
Pteridophyta	1.4	0.8	7.8	2.1
Ranunculaceae	0.8	0.5	0.7	0.3
Rhamnaceae	0.1	0.1	1.5	0.2
Rosaceae	3.1	4.1	6.4	2.6
Rubiaceae	0.3	0.5	0.1	0.2
Santalaceae	0.1	0.0	0.0	0.0
Scrophulariaceae	12.9	5.3	7.1	7.3
Solanaceae	0.0	0.3	0.2	0.1
Thymelaeaceae	0.0	0.1	0.3	0.0
Unknowns	0.6	0.7	0.9	1.6

APPENDIX 8

CANONICAL CORRELATION VALUES

Canonical correlation values for an analysis of the pollen trap data between seasons. The letteres are representative of the seasons:- a = June-Aug 1988, b = Sept-Nov 1988, c = Dec-Feb 1989, d = March-May 1989, e = June-Aug 1989, f = Sept-Nov 1989 and g = Dec-May 1990.

Highland Sourveld

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.986	-	-	-	-	-	-
Dec-Feb 1989	0.849	0.917	-	-	-	-	-
March-May 1989	0.972	0.943	0.739	-	-	-	-
June-Aug 1989	0.971	0.934	0.721	0.959	-	-	-
Sept-Nov 1989	0.904	0.932	0.817	0.872	0.881	-	-
Dec-May 1990	0.987	0.951	0.759	0.989	0.965	0.895	-
Dec-May 1989	-	-	-	-	-	-	0.939

***Protea* savanna**

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.645	-	-	-	-	-	-
Dec-Feb 1989	0.550	0.975	-	-	-	-	-
March-May 1989	0.780	0.767	0.667	-	-	-	-
June-Aug 1989	0.932	0.797	0.717	0.861	-	-	-
Sept-Nov 1989	0.449	0.952	0.986	0.632	0.629	-	-
Dec-May 1990	0.850	0.928	0.878	0.869	0.960	0.816	-
Dec-May 1989	-	-	-	-	-	-	0.957

***Podocarpus* forest**

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.973	-	-	-	-	-	-
Dec-Feb 1989	0.258	0.253	-	-	-	-	-
March-May 1989	0.217	0.300	0.742	-	-	-	-
June-Aug 1989	0.902	0.961	0.125	0.268	-	-	-
Sept-Nov 1989	0.226	0.284	0.745	0.823	0.452	-	-
Dec-May 1990	0.527	0.568	0.856	0.833	0.460	0.842	-
Dec-May 1989	-	-	-	-	-	-	0.905

Rendlia altera grassland

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.804	-	-	-	-	-	-
Dec-Feb 1989	0.822	0.781	-	-	-	-	-
March-May 1989	0.960	0.742	0.760	-	-	-	-
June-Aug 1989	0.955	0.720	0.738	0.910	-	-	-
Sept-Nov 1989	0.973	0.847	0.861	0.919	0.905	-	-
Dec-May 1990	0.980	0.701	0.796	0.904	0.914	0.946	-
Dec-May 1989	-	-	-	-	-	-	0.941

Themeda triandra grassland

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.920	-	-	-	-	-	-
Dec-Feb 1989	0.987	0.963	-	-	-	-	-
March-May 1989	0.698	0.915	0.794	-	-	-	-
June-Aug 1989	0.989	0.857	0.949	0.588	-	-	-
Sept-Nov 1989	0.971	0.981	0.991	0.836	0.930	-	-
Dec-May 1990	0.956	0.987	0.989	0.868	0.907	0.981	-
Dec-May 1989	-	-	-	-	-	-	0.956

'Mixed' grassland

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.892	-	-	-	-	-	-
Dec-Feb 1989	0.987	0.916	-	-	-	-	-
March-May 1989	0.922	0.956	0.940	-	-	-	-
June-Aug 1989	0.951	0.982	0.967	0.928	-	-	-
Sept-Nov 1989	0.977	0.955	0.909	0.970	0.981	-	-
Dec-May 1990	0.946	0.985	0.964	0.954	0.957	0.982	-
Dec-May 1989	-	-	-	-	-	-	0.990

Festuca costata grassland

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.983	-	-	-	-	-	-
Dec-Feb 1989	0.980	0.979	-	-	-	-	-
March-May 1989	0.905	0.938	0.864	-	-	-	-
June-Aug 1989	0.927	0.975	0.977	0.847	-	-	-
Sept-Nov 1989	0.929	0.980	0.959	0.868	0.909	-	-
Dec-May 1990	0.970	0.981	0.950	0.956	0.940	0.953	-
Dec-May 1989	-	-	-	-	-	-	0.974

Leucosidea sericea scrubland

Seasons	a	b	c	d	e	f	g
June-Aug 1988	-	-	-	-	-	-	-
Sept-Nov 1988	0.994	-	-	-	-	-	-
Dec-Feb 1989	0.401	0.494	-	-	-	-	-
March-May 1989	0.252	0.349	0.928	-	-	-	-
June-Aug 1989	0.919	0.968	0.432	0.289	-	-	-
Sept-Nov 1989	0.503	0.594	0.972	0.927	0.534	-	-
Dec-May 1990	0.906	0.943	0.722	0.634	0.922	0.802	-
Dec-May 1989	-	-	-	-	-	-	0.689

Low altitude vlei

Seasons	b	c	d	e	f	g
Sept-Nov 1988	-	-	-	-	-	-
Dec-Feb 1989	0.876	-	-	-	-	-
March-May 1989	0.549	0.545	-	-	-	-
June-Aug 1989	0.968	0.677	0.537	-	-	-
Sept-Nov 1989	0.939	0.884	0.624	0.928	-	-
Dec-May 1990	0.927	0.845	0.721	0.895	0.891	-
Dec-May 1989	-	-	-	-	-	0.863

Sub-alpine fynbos

Seasons	d	e	f	g
June-Aug 1989	0.317	-	-	-
Sept-Nov 1989	0.732	0.441	-	-
Dec-May 1990	0.906	0.529	0.829	-
Dec-May 1989	-	-	-	-

Canonical correlation analysis values comparing the annual pollen trap spectra for each of the studied vegetation communities.

Vegetation Communities	June-May 1989/ June-May 1990
Highland Sourveld	0.963
Protea savanna	0.984
Podocarpus forest	0.807
Rendlia altera grassland	0.954
Leucosidea sericea scrubland	0.902
Themeda triandra grassland	0.955
'Mixed' grassland	0.989
Festuca costata grassland	0.922
Sub-alpine fynbos	0.901
Low altitude vlei	0.923