# Determinants of Pattern in Fynbos Vegetation.

## Physical Site Factors, Disturbance Regime, Species Attributes and Temporal Change.

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# CHAPTER 1. General Introduction

## The issues and objectives

*Time and space are not constants in ecological systems. Environments vary, but they do so with varying amplitudes, periodicities, and degrees of stochasticity in time, and the pattern and extent of these variations change in space as well.*

*Wiens (1986)*

Plant ecologists are challenged by the quest to explain observed patterns in species-rich and spatially complex vegetation. An understanding of the determinants of pattern and community boundaries in these vegetation types was for many decades based on the assumption that natural communities can be described by models with stable equilibria (Chesson and Case 1986 for review). Under the classical equilibrium conditions, historical effects, chance factors and environmental disturbances would be unimportant. The existence of bounds to the local abundance of each species would result in the composition and structure of plant assemblages remaining approximately constant over time. However numerous studies over the last few decades have demonstrated that many communities do not have predictable structures (Pickett and White 1985, Hubbell and Foster 1986). Stable equilibrium theories have been questioned on the grounds that the environments of natural systems are continually changing with pronounced effects on populations (Chesson and Case 1986).

Many plant communities are subjected to repeated disturbances that have a selective influence on life history strategies and community structure and functioning (Sousa 1984, Pickett and Whyte 1985). At the population scale, disturbances may influence the spatial range, abundance, reproduction and extinction probabilities of species, while at the community scale, changes may occur in the composition and relative abundance of species because of their different responses to disturbance. Disturbance itself introduces stochastic influences on community composition, which in turn reduce the predictability of the post-disturbance response (White and Pickett 1985). Therefore, a major challenge for determining contemporary community structure lies in unravelling the relative contribution to pattern of physical setting; deterministic processes associated with disturbance; and stochastic processes both extrinsic and intrinsic to the biota.

To develop an understanding of the role of these factors in ecological time requires the study of a system that is exposed to frequent disturbances. The species-rich fynbos shrublands of South Africa provide an excellent opportunity to explore the determinants of vegetation structure in a fire-prone system. Fires are patchy phenomena that contribute significantly to temporal and spatial heterogeneity in shrublands (Christensen 1985, Bond and van Wilgen 1996). The fynbos biome covers an area of 71 337 km$^2$ in the southern and south-western corner of South Africa. These shrublands are characterised by high diversity and endemism, rainfall concentrated in the winter months and a natural fire interval of between 4 and 40 years. Cowling (1992) and Cowling *et al.* (1997) provide recent reviews of fynbos ecology.

A central issue in phytogeographical and ecological studies of the fynbos has been whether the observed species-based patterns can be explained by environmental influences or whether stochastic events have an overriding effect (Bond 1981, Campbell 1983, Cowling 1984, Richards *et al.* 1995, McDonald *et al.* 1996, Cowling *et al.* 1997). It has been suggested that much of the compositional variation in this system can be attributed to stochastic phenomena such as fire and other historical effects (Cowling 1987, Cowling *et al.* 1997). Most studies on vegetation boundaries in fynbos have invoked edaphic explanations as the major determinants of floristic pattern (Kruger 1979, Bond 1981, Cowling 1984, Campbell 1986a, van Wilgen and McDonald 1992). Despite these and many other detailed phytosociological studies in the fynbos biome (see Cowling 1992 for references), few multivariate vegetation-environmental models have been produced (Richards *et al.* 1995, McDonald *et al.* 1996, Simmons 1996). Those that have been developed were effective at explaining the underlying physical determinants of the broad plant communities. However, despite incorporating a variety of site factors, the multivariate models explained less than half of the variation in species composition. Differences within the broad, environmentally circumscribed communities were attributed to additional, finer-scale environmental parameters, deterministic processes associated with disturbance, and stochastic processes. However, none of these studies has quantified the importance of these potential causes of intra-community variation.

As in the majority of shrublands, fire is the major disturbance factor in fynbos ecosystems. Each fire is a unique event that can differentially influence plant populations and communities (Bond and van Wilgen 1996). Much of the variation in effects and response to fire results from variation in fire regime (Christensen 1985, Bond and van Wilgen 1996). In many fynbos communities tall shrubs belonging to the family Proteaceae dominate the overstorey canopy. Numerous studies have explored how components of the fire regime influence populations of the proteoid overstorey in these communities. They have demonstrated that differences in fire frequency (Bond 1980, van Wilgen 1981), season (Bond 1984, Bond *et al.* 1984, and Le Maitre 1988a&b) and intensity (Bond *et al.* 1990) can all impact densities of the proteoid overstorey. Increases in the proteoid overstorey have in turn been shown to affect community composition by increasing $\alpha$-diversity levels of understorey species through suppression of the sprouting guild, as well as affecting $\beta$-diversity or the patchiness of species in a community (Vlok 1996). Studies on post-fire succession have shown that diversity is greatest in the post-fire phase, and that diversity decreases as cover of overstorey shrubs increases (Kruger 1987, Cowling and Pierce 1988). Comparisons of pre- and post-fire species composition have revealed average similarities ranging from 30% for a dry lowland site (Hoffman *et al.* 1987) to 86% in mountain fynbos (Le Maitre 1987). All of these studies have examined the effects of single fire events on species composition and have consequently provided little information on the stability of populations or communities to repeated fire events over a number of decades.

Information regarding the probability of species remaining at a site following a few fires, and the attributes which allow them to persist in vegetation subjected to frequent fire, is necessary for a better understanding of how management practices influence vegetation. Recent research has demonstrated that high proportions of fynbos taxa are rare, being either locally restricted, or occurring at low densities over wider areas (Simmons 1996). An important issue relating to rarity is the stability of these rare populations over time. We have little understanding of how constant fynbos species are over time, how resilient they are to repeated disturbance or what their probabilities of local extinction are over several fire cycles. The stability of populations over time also has implications for spatial dynamics at any one time. A high tendency for extinction within fixed environmental bounds will result in greater temporal turnover and spatial complexity. The contrast between spatial and temporal landscape patchiness is fundamental to understanding the dynamics of landscapes (White and Pickett 1985).

Given these gaps in our understanding of fynbos dynamics, the main objectives of this thesis were:

1. To quantify the relative contribution of the recent (30-year) disturbance regime versus the major physical habitat characteristics in determining vegetation pattern in a fynbos landscape.

2. To explore the stability of fynbos populations over a period of three decades and determine the characteristics of species which are prone to local extinction and those capable of persisting.

3. To explore the way in which communities have responded to various components of the disturbance regime, including fire and alien plants, over the last 30 years.

**Thesis structure**

This study set out to explore the patterns and determinants of contemporary species distribution in a fynbos landscape based on information on 1) physical habitat characteristics, 2) past disturbance regime, 3) intrinsic properties of individual species and 4) temporal change in communities. The body of the thesis is divided into four parts covering each of these aspects individually. Each chapter has been written up as an individual paper and thus includes some repetition as well as cross-referencing. Each chapter includes a detailed rationale for the study in the introduction, as well as methods, results and a discussion of the findings.

Chapter 2 describes the patterns of vegetation units in the Cape of Good Hope Nature Reserve and provides a quantitative assessment of the importance of physical site features as determinants of these units. These results are compared with the vegetation classifications of the area derived in earlier studies by Taylor (1984b) and Cowling *et al.* (1996a).

Chapter 3 is the first study in fynbos to partition the variance in vegetation pattern into that explained by physical site factors and that explained by the recent disturbance regime. The study explores the role of 30 years of fire and alien plant infestations in influencing species distribution at the community and landscape scale.

While a number of studies have explored spatial determinants of diversity and pattern in fynbos, temporal change within communities has been neglected. High levels of species turnover through time, as a result of colonisation and extinction, could be an important component of diversity at the landscape scale. Hence Chapters 4 and 5 both explore aspects of temporal dynamics in fynbos.

The objectives of Chapter 4 are to determine the stability of populations at the landscape scale over a 30-year period and to establish the determinants of local extinction of species. Information on the stability of species over time and the attributes which enable species to persist or go extinct are important for understanding potential impacts of management practices as well as the importance of temporal dynamics in influencing spatial patterns. This is especially appropriate in the context of the results of Chapter 3, which suggest that a high proportion of the variance in species composition is unexplained despite the inclusion of physical factors, and past disturbance regime.

The fifth chapter provides a descriptive account of the change in vegetation composition over a 30-year period. It is recommended that those readers not familiar with the fynbos system read it as it provides an overview of a variety of aspects of fynbos dynamics. Its objective is to show how the various components of the disturbance regime, as well as fluctuations in abundance of overstorey Proteaceae and their resultant competitive effects can influence community composition.

The final chapter is a general discussion that summarises the major findings of the study.

## Study area

The area encompassed by the Cape of Good Hope Nature Reserve (C.G.H.N.R.) was used for this study. The reserve has many attributes that make it conducive to this study: high species diversity and complexity; the existence of permanent monitoring sites; and detailed management records for the period since their establishment. The vegetation of the C.G.H.N.R. has been well documented and a comprehensive species list of 1073 species of vascular plants has been compiled (Taylor 1969, Taylor 1983, Taylor 1984a and 1984b, Fraser and MacMahon 1995, Fraser in press.). The vegetation of the reserve was described by Taylor (1984b) who noted the complexity and variability of vegetation within certain communities and suggested that historical effects relating to disturbance had influenced their contemporary structure. Hugh Taylor (Taylor 1969) established permanently marked vegetation sites in 1965/66 (Fig.1.1). His original species lists for each of these 100 sites provided the baseline dataset against which to compare contemporary vegetation patterns and explore spatial and temporal dynamics. The management records of the reserve provided detailed information on both fire history and alien vegetation management since Taylor's survey. This provided the opportunity to explore the role of the disturbance factors in influencing vegetation change.

### LOCATION

The C.G.H.N.R. (34°15' S; 18°25' E) is situated on the southern tip of the Cape Peninsula. The reserve occupies an area of 7 750 hectares in the extreme south-western corner of the African continent (Fig. 1.2). It is roughly triangular in shape, narrowing from the north, where it has an overland boundary of approximately 13.5 kilometres, to the Cape of Good Hope in the south. Its western coastal boundary extends for 21.5 kilometres from Schuster's bay to the Cape of Good Hope and its eastern coastline 18 kilometres from Smitswinkel to Cape Point. The reserve is just 9 km across at its widest point.

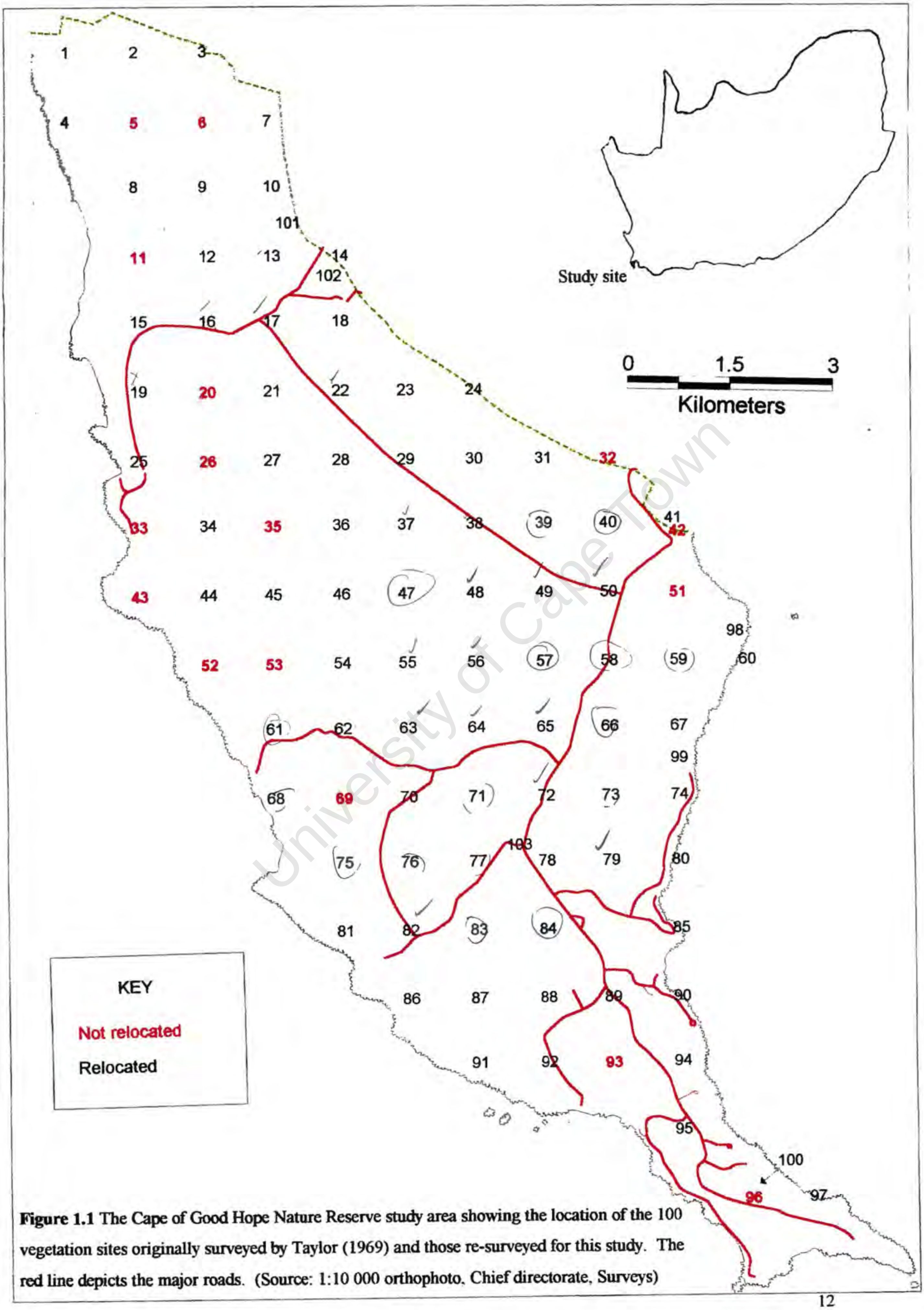

**Figure 1.1** The Cape of Good Hope Nature Reserve study area showing the location of the 100 vegetation sites originally surveyed by Taylor (1969) and those re-surveyed for this study. The red line depicts the major roads. (Source: 1:10 000 orthophoto, Chief directorate, Surveys)

The major topographic features of the reserve is a low plateau rising from 60 m above sea level in the west and reaching peaks as high as 360 m in the east (Fig. 5.2). The highest peaks from north to south are Judas Peak, Paulsberg and Vasco da Gama Peak (Fig. 5.7). These peaks have steep cliffs on their eastern side as a result of undercutting by wave action. The central plateau forms a large level area over much of the reserve. It is characterised by low rock cover and is broken by a series of shallow seepage steps, formed where bands of tilted sandstone intercept the surface. Above these, water is trapped and drainage is very poor, resulting in marsh conditions throughout the year. Many small streams connect these marshy flats. The only perennial rivers of any consequence are the Krom River, Klaasjagers River and Booiskraal River. An unusual feature is Sirkelsvlei, a permanent water body lying on top of a sandstone ridge with no above ground inflow or outflow streams.

The reserve forms part of the Cape Folded Belt, an L-shaped band of erosion-resistant, quartzitic sandstone mountains underlain by softer shales, and mantled at the coastal margins with young siliceous and calcareous sediments (Deacon *et al.* 1992). Sandstones and shales of the Cape Supergroup were deposited on a much older foundation of Malmesbury Shales and intruded by Cape Granite, that is visible only at the base of the Cape Point cliffs. In the reserve, the Graafwater and Peninsula Formations represent the Cape Supergroup. The Graafwater comprises a narrow bed of up to 65m of medium-grained sandstones and mudstones, while the Peninsula Formation comprises a massive bed of up to 1200 m deep of almost pure quartzitic sandstone (Theron *et al.* 1992). The Peninsula Formation forms the dominant surface rock over the entire reserve. These quartzitic sandstones have a pinkish to yellow-brown appearance but are whitish on the surface as a result of weathering (MacVicar 1963). In a few places in the reserve, such as on the southern slopes of Rooihoogte, areas of exposed reddish ferricrete are evident. These consist of pebbles of sandstone, which have been cemented into hard layers by iron oxide leached from the sandstone. Another feature of the reserve is the much younger superficial (aeolian fine to medium grained) deposits of Quaternary sand. Variation in their structure as well as vegetation coverage suggests that they differ widely in age. The youngest dunes are actively forming and have no vegetation cover. Examples of these shifting dunes are to be found along both coastlines. The dune at Olifantsbos Point has demonstrated high mobility in the last 30 years (Fig. 5.1). Older stabilised dunes traverse the reserve between Buffels Bay and Rietveld, as well as from Meadows to near Diaz Monument. These blew across the reserve from False Bay in the direction of the prevailing south-easterly winds. The oldest preserved dunes are now stabilised and cemented and composed almost entirely of shell fragments (MacVicar 1963). The most prominent of these calcrete hills are to be found along the False Bay coastline at the foot of the cliffs between Bordjiesrif and Batsatsa cove.

## SOILS

As is a characteristic of other landscapes of the Cape Folded Belt, the soils of the reserve are nutritionally poor (Deacon *et al.* 1992). The most impoverished soils are those formed from the quartzitic sandstones of the plateaux, summits and upper slopes. These soils are shallow, sandy and well drained; and have a low water-retaining capacity. They are moderately acidic with a pH of approximately 4 to 5 and deficient in all nutrients. Much of the lower lying central plateau is characterised by marshy, humic soils with impeded drainage. These soils are also derived from the sandstone bedrock, but support high levels of organic matter and are highly acidic (pH 3 - 4). Deep calcareous sands of recent (Holocene) origin are common along most of the coastline and make up the longitudinal dunes. The soils associated with the older Quaternary deposits are mainly deep, neutral to moderately acidic and are marginally more fertile than those derived from sandstone. The younger sands along the coastlines are very deep, poorly consolidated and highly alkaline.

## CLIMATE

The C.G.H.N.R. experiences a Mediterranean-type climate with warm, dry summers and cool, wet winters. Less than 10% of the total annual rainfall falls in the months November to January, while more than 70% falls during the winter months between April and September (Fuggle 1981). Winter rainfall is associated with frontal systems budded off from circumpolar westerlies (Deacon *et al.* 1992). They may bring rain and cold conditions for up to a week at a time. Precipitation during the summer months can result from ridging cells of high pressure which bring strong south-easterly winds and some moisture, especially to the high lying peaks. Total rainfall varies considerably over the area of the reserve. Rainfall gradients are very steep and are influenced by altitude, aspect and other topographic features that serve to trap rain-bearing winds. Rainfall is relatively low at Cape Point (402 mm a year) but considerably higher at Klaasjagersberg (565 mm) towards the north. Strong winds can occur throughout the year as is evident by an average yearly speed of 35 km/h at Cape Point (Fraser and McMahon 1995). During the summer months south-easterly winds of 40 km/h (gusting up to 100 km/h) can blow for more than a week at a time. These winds blow in the fire season and can cause fires to spread rapidly over large areas. Winter gales, although of shorter duration, may be even more intense. These winds also play a prominent role in influencing vegetation structure. Coastal vegetations experience severe wind (and salt) 'pruning', and plant growth in general is stunted.

Spatial and temporal variations in temperature are not pronounced on the Cape Peninsula owing to the ameliorating influence of the surrounding ocean. Seasonal variation in temperature at Cape Point itself is low, with mean summer and winter temperatures differing by only about 5°C. Temperatures are generally mild with an average temperature in February of 18.3°C and in July of 13.4°C. Temperatures away from the coast are generally higher and more variable. While summer temperatures may exceed 30°C, temperatures are seldom lower than 10°C and frost has never been recorded.

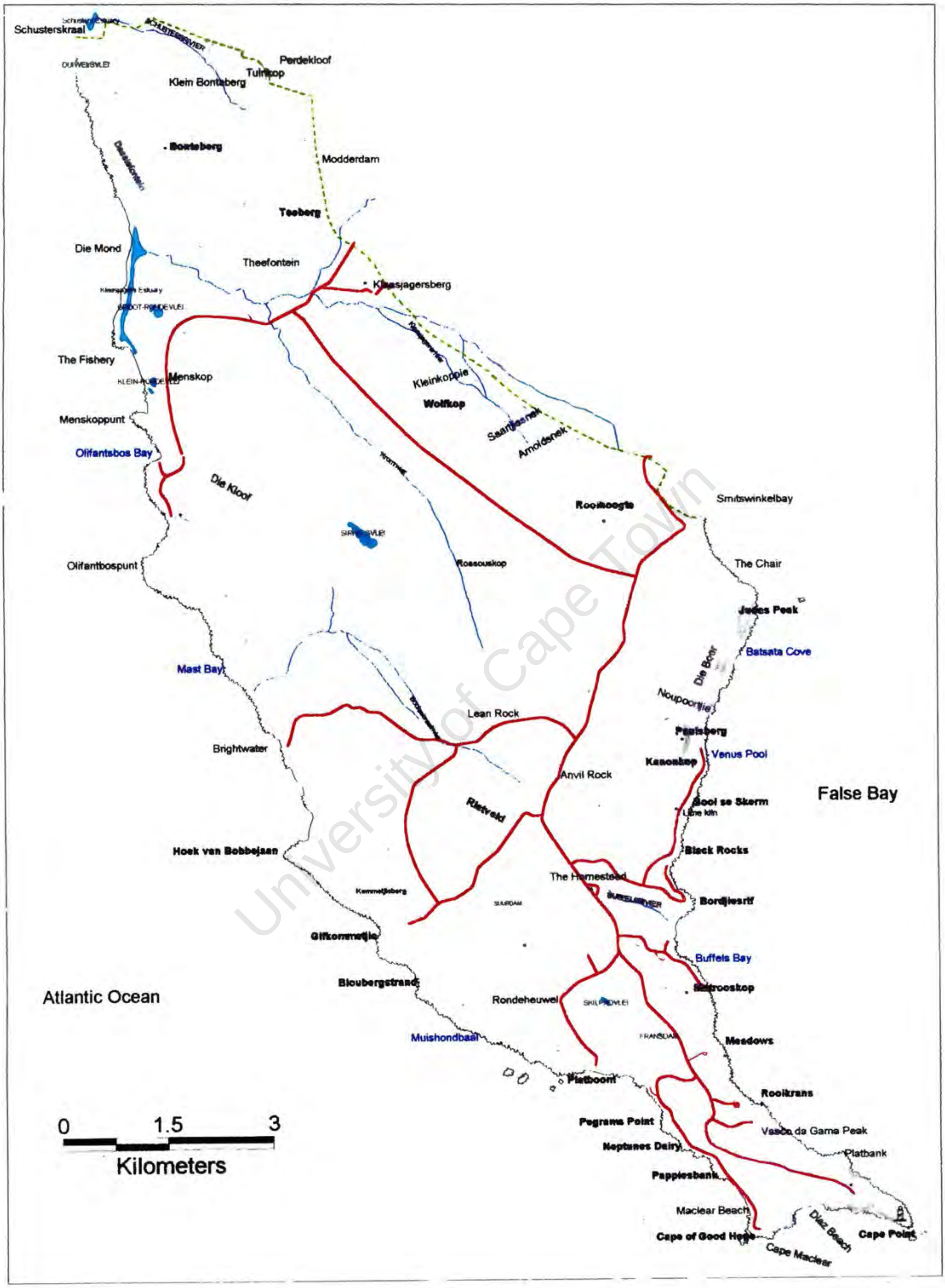

**Figure 1.2** Topographical features, infrastructure and place names in the Cape of Good Hope Nature Reserve.

The CGHNR forms part of the Cape Floristic Region, an area of exceptional diversity and recognised as one of the world's six floral kingdoms (Goldblatt 1978). The Cape Floristic Region has the highest known incidence of local plant endemism in the world (Cowling *et al.* 1992). Taylor (1969, 1983, 1984a, 1984b) comprehensively described the vegetation of the reserve. At least 1073 species of indigenous plants, of which 11 are endemic, occur in the 77 km$^2$ of the reserve. The largest families, in descending order of richness are Asteraceae (116 species), Iridaceae (80), Cyperaceae (72), Orchidaceae (67), Fabaceae (66), Restionaceae (63) and Ericaceae (49) (Fraser and MacMahon 1995). Taylor (1984b) divided the vegetation into two structural formations, fynbos and broad-leaved thicket. Fynbos is a fire-prone, sclerophyllous shrubland uniquely characterised by a relatively high cover (> 5%) of restioids (wiry aphyllous graminoids of the family Restionaceae). The fynbos element was subsequently divided into coast and inland fynbos on the basis of the major soil parent materials of the reserve. Dune fynbos is found on transported coastal sands which are neutral or alkaline and inland fynbos on acidic soils derived from a Table Mountain Group sandstone substratum. The coastal fynbos was then divided into four, and inland fynbos into six, vegetation units on the basis of edaphic and physiographic factors. The thicket element was defined as a simplified, floristically impoverished form of the coastal forests and thickets of the Knysna area of the south coast of South Africa, and divided into two floristically defined vegetation units. The broad-leaved thicket occupies less than 3% of the area of the reserve and is confined to fire protected sites such as coastal screes, dunes and scarps. Taylor (1984b) concluded that fire was the most important biotic factor influencing the vegetation of the reserve and that coastal communities protected from fire would develop into thicket, while the inland communities are characterised by a cyclical, self-perpetuating succession.

More recently Cowling *et al.* (1996a) categorised the vegetation of the Cape Peninsula into 14 units, based on Campbell's (1986b) system derived for mountains of the fynbos biome. This system, using a simple vegetation classification based on visual examination of dominant species and environmental characteristics, has proven very accurate when compared with detailed multivariate classifications (Simmons 1996).

Within the area of the CGHNR, this classification proved very similar to the descriptive community divisions of Taylor (1984b). The vegetation map produced here uses communities characterised on the basis of the Cowling (1996a) classification (Fig. 1.3). For the mapping of the vegetation I used a combination of the maps published by Taylor (1984b) and Cowling *et al.* (1996a), as well as further reconnaissance mapping in the field on 1:10 000 orthophotos. The map was developed using a Geographical Information System (Map info version 4 ).

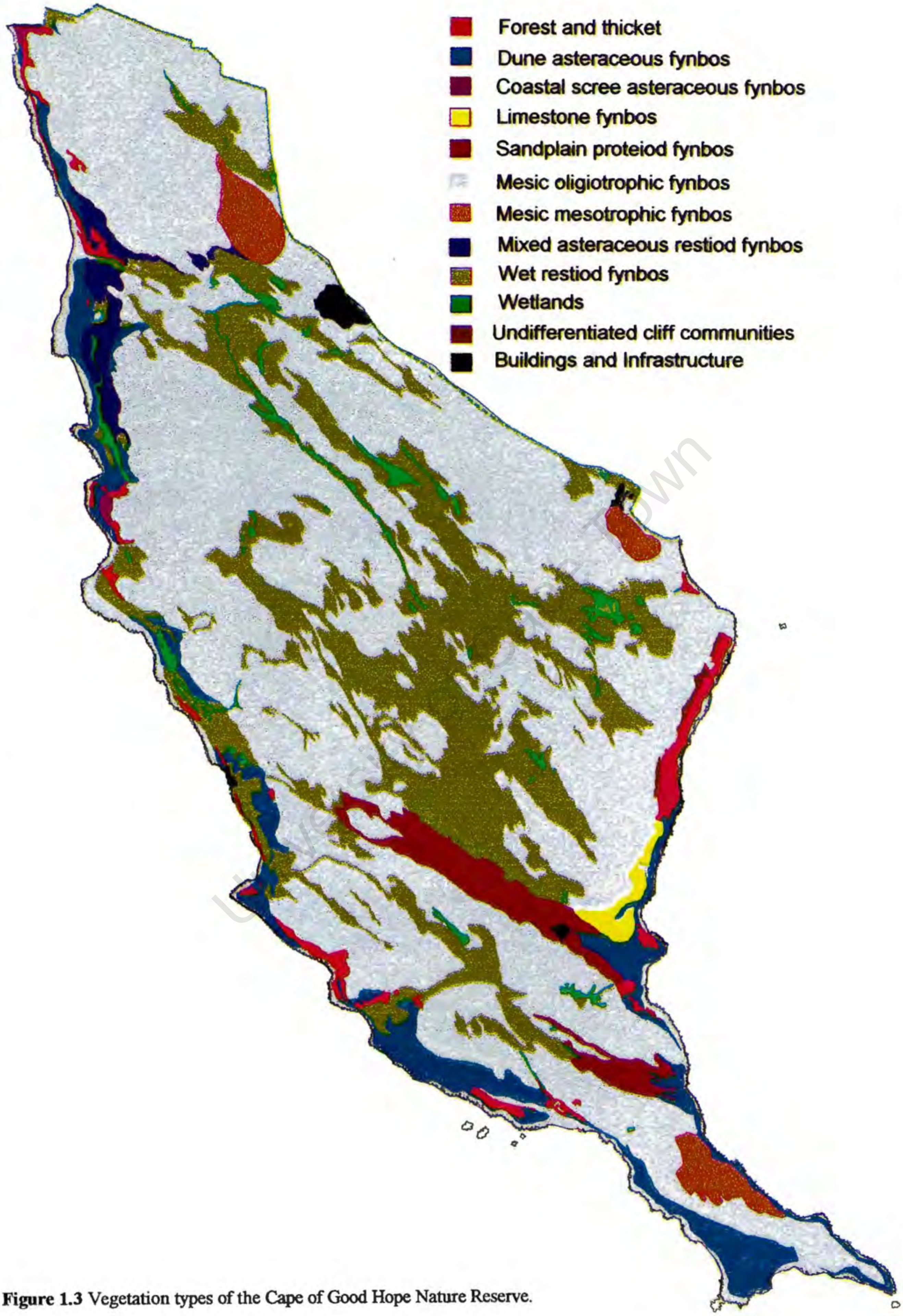

**Figure 1.3** Vegetation types of the Cape of Good Hope Nature Reserve.

## Human settlement and resulting impact on the vegetation

The C.G.H.N.R was not a pristine environment at the time of Hugh Taylor's survey in 1966. Before exploring the last 30 years of human impacts, it is important to have some idea of how earlier human activities influenced the flora. Humans have influenced the natural vegetation of the fynbos region for upwards of half a million years and no part of the fynbos region can be called truly pristine or 'natural' (Deacon 1992). The history of human occupation and impacts in the area, which now comprises the CGHNR, has been well documented (see Opie 1967, Hallinan 1992 for reviews). This brief review covers human activities that may have influenced the flora prior to Taylor's survey (before 1966) as well as between Taylor's and the present surveys (1966 to 1996).

### PREHISTORIC HABITATION

There is a long history of human occupation in the fynbos region and as nearly as long a record of the use of fire (Deacon 1983). This region has been populated by *Homo sapiens* for at least the last half a million years (Deacon 1983, Deacon 1992), while the southern Cape Peninsula has been periodically inhabited by human populations for at least the last 200 000 years (Deacon 1992). Formal hearths at middle stone age sites dating from the beginning of the Late Pleistocene suggest that people could generate fire at will in this region for the last 100 000 years (Deacon 1992). Artifacts reveal that these people were hunter-gatherers who made use of the seashore for much of their food requirements. The food remains excavated from shelters at Smitswinkel Bay (Poggenpoel and Robertshaw 1981) and below Bonteberg (Maggs and Speed 1967) both indicate that shellfish dominated their day-to-day diet and that fish were a supplement to their diet. While no vegetable matter remains at these sites, historical sources yield information that geophytes were a major component of their diets (Maggs and Speed 1967). The impacts of these hunter-gatherers on the vegetation were mainly through the use of fire in hunting and in order to promote the abundance of geophytes.

Evidence from cave sites along the southern Cape coast suggest that nomadic pastoralists, the Khoi-khoi, were established in the Cape some 2 000 years ago (Schweitzer 1979). While large stock numbers were recorded on the fringes of the Peninsula in the early days of Dutch settlement, it is unlikely that significant numbers of stock were kept in the predominantly infertile and mountainous areas of the southern Cape Peninsula (Cowling *et al.* 1996a). However bones of sheep and cattle from the shelter at Smitswinkel Bay indicate that there was some livestock present in the region for perhaps as long as the last 1 400 years (Poggenpoel and Halkett 1990). The Khoi-khoi, therefore, also probably impacted the vegetation through patch burning for improved grazing.

An important aspect that has always influenced natural fire frequencies in the southern Cape Peninsula is that, owing to its peninsular geography, natural fire frequencies would have been longer than in entirely landlocked areas. Thus even prior to the arrival of Europeans, humans are likely to have had a substantive impact on the vegetation by increasing fire frequencies.

## EUROPEAN COLONISATION AND LAND USE

The early colonisation by European settlers of the area that is now the C.G.H.N.R. began in 1738 when a stock farmer, Jurgen Schuster, was granted the area of 'Wildschutsbrand' (Cairns 1976). While his homestead is thought to have been located outside the present reserve (Hallinan 1992), his grazing rights stretched from below Red Hill to the west coast. The presence of Schuster's Kraal in the north of the reserve suggests that his stock farming activities were the first by a European to directly influence the vegetation of the reserve. Early colonisation of the region was slow and by 1786 only three families had grazing rights in the area. These were located at Schuster's Kraal in the north, near the present Olifantsbos Bay on the west coast and at the top of the Buffels River Valley in the area of the farm that later became 'Buffelsfontein' (Hallinan 1992). Following the second British occupation of the Cape in 1806 and the subsequent change of land tenure practices to allow for permanent ownership of land, as well as the decision by the Royal Navy to use

Simon's Town as their only naval base, there was an influx of settlers into the area (Hallinan 1992). Farming practices mostly involved grazing, and some vegetable gardening. Vegetable farming was an important activity of these early settlements, especially along the banks of the Klaasjagers River. The vegetable gardens were confined to the flat lands adjacent to the river, while the surrounding fynbos clad hills were utilised for grazing (Hallinan 1992). Owing to the paucity of fuelwood in the fynbos, both *Leucospermum conocarpodendron* and *Mimetes hirtus* (large proteoid shrubs) were harvested by early settlers. Between 1855 and 1885 the southern portion of the reserve from Cape Point and including the farm Buffelsfontein was used for breeding horses, cattle, pigs and ostriches (Hallinan 1992). These early farming activities by European settlers must have influenced the natural vegetation to some degree. Major vegetation disturbance was probably confined to areas adjacent to homesteads, and richer pockets of alluvial sands with permanent water supplies. Impacts by stock farming were mostly confined to the better grazing in the Schuster's and Krom River valleys and the plateau south of Smith's farm.

The area now occupied by the reserve was also used for military purposes. Prior to the First World War, mobilisation exercises were used to demonstrate the vulnerability of Simon's Town to overland attack (Hallinan 1992). Regular training exercises, including the use of 60-pounder guns, (the shells of which can still be found throughout the reserve) were carried out between the World Wars (Hallinan 1992). The personnel were at first based in temporary camps between Theeberg and the Klaasjagers River, and later in permanent barracks near the present-day administrative offices. During the Second World War the pressures on the area increased as fortress observation posts were established at Cape Point, Da Gama Peak and Olifantsbos, while a radar installation was also established at Cape Point. The impact of these military operations would not have been confined only to the land on which they were built but are likely to have resulted in an increase in the occurrence of fires and subsequent impacts on the vegetation.

The purchasing of the land that now comprises the C.G.H.N.R. occurred between 1939 and 1966. The main objectives laid down by the Cape Divisional Council authorities on 20 July 1939 (when the first land was purchased) was the creation of camping and picnicking areas and establishment of a programme for breeding fauna (Anon 1980). It was also adopted in principal that the area should be preserved as far as possible in its natural state as a fauna and flora reserve. The history of the management of the C.G.H.N.R. can be divided into two eras, pre- and post-1975.

In the period preceding 1975 management adhered to a policy of fire suppression and emphasis was placed on fauna introductions. Fire protection was one of the first management steps employed and several fire belts, traversing the reserve, were established. Appendix 1 provides information on all fires that have influenced the sites since Taylor's initial survey. The reserve was divided into two sections by a game fence along the original farms 'Blaauberg' and 'Buffelsfontein'. The southern portion was managed as a game park, while the northern section was maintained as a botanical reserve, free of introduced game animals. Within the former area, some artificial pastures were created through bush cutting or ploughing and planting exotic grasses (Millar 1970). As early as 1946 Eland and Bontebok were introduced while other species including Springbok, Burchells Zebra, Hartmans Zebra, Fallow Deer, Red Hartebeest, Black Wildebeest and hundreds of tortoises followed over the next two decades.

In May 1974 the fence was removed in accordance with a new policy of keeping game populations within defined limits (Anon 1988). At this time a management plan was produced which incorporated a prescribed burning regime on a ten-year rotation and a plan for the systematic eradication of alien plants (Anon 1974). Although the plan was drawn up in 1974 it was only effectively implemented between 1980 and 1987. In 1987 the policy was revised to a programme of variable frequency burning. The new plan required that blocks be burnt in young (6-10 years), intermediate (12-20 years) and old (>20 years) vegetation between January and April at a ratio of 1:3:1 (Anon 1990). Despite the existence of these various prescribed burning programmes wild fires continued to occur on a regular basis. Since 1992 until present a revised fire management plan based on adaptive interference burning has been in place. This entails only controlling those fires that threaten infrastructure or burn in young vegetation. Old vegetation is only burnt on the basis of advice by recognised fynbos plant ecologists.

## MANAGEMENT OF ALIEN VEGETATION

The CGHNR has a long history of alien plant invasion that has been comprehensively documented in a number of studies (Taylor and Macdonald 1985, Taylor *et al.* 1985, Macdonald *et al.* 1989). The most important alien trees in the reserve are (in order of importance): *Acacia cyclops* (rooikrans), *A. saligna* (port jackson willow), *A. longifolia* (long-leaved wattle) and *Pinus pinaster* (cluster pine). Prior to Taylor's survey in 1966 only small-scale clearing had been undertaken on an *ad hoc* basis and follow-up was sporadic. Invasive species were found in 13% of the 50 $m^2$ quadrats and in 92% of the 10.5 ha sites he surveyed (Taylor and Macdonald 1985). In 1974 a '10-year' plan for the systematic clearance of alien infestations was drawn up and implemented in the late 1970's. A survey between 1976 and 1980 showed that densities of all major species, with the exception of *P. pinaster*, had continued to increase between surveys. In 1986 a large wild fire burnt most of the northern portion of the reserve which contained a number of mature alien thickets. Between 1986 and 1988 all focus was turned to clearing the regrowth following this fire. From a peak in the early 1980's virtually all stands of alien plants had been eliminated by the time of the 1996 field survey. Presently the only remaining dense stands are the *A. cyclops* thickets in the very south of the reserve.

# CHAPTER 2. Plant community classification and vegetation-environment relationships in the Cape of Good Hope Nature Reserve

## Abstract

The vegetation of the Cape of Good Hope Nature Reserve was classified into easily recognisable types using both characteristic species and structurally dominant species. This classification corresponded well with previous accounts of vegetation pattern in the CGHNR and for the Cape Peninsula. The vegetation-environment model suggested that the major vegetation patterns could be explained by physical site factors. Edaphic factors, both chemical and physical, were the most important determinants of broad-scale pattern. Finer-scale patterns relating to within-community membership and species-richness were not well explained by the environmental factors. Despite the comprehensive set of physical environmental factors used in the multivariate study, a large proportion of the variance in species data remained unexplained. This suggested that factors such as fire related phenomena, alien plant invasions and biotic interactions, play an important role in determining pattern in fynbos vegetation.

## Introduction

An important implication of the high diversity in the species-rich Cape fynbos is the difficulty in resolving regional vegetation associations into meaningful, easily identifiable floristic groups (Campbell 1986b). One thousand and seventy three species of indigenous vascular plants have been recorded in the 77 km$^2$ of the Cape of Good Hope Nature Reserve (CGHNR) alone (Fraser in press). The vegetation of the reserve comprises a complex matrix of lowland and upland fynbos and broad-leaved thicket communities separated by a complex array of factors (Taylor 1984b). This high degree of floristic complexity makes it difficult for reserve managers to gain important, in order to enable easy identification in the field, that they be provided with a simplified classification of the major vegetation types, their character species and associated environmental determinants. This information can then be used to develop an understanding of the potential impacts of management operations on individual vegetation units and, ultimately, overall management of the reserve.

Taylor (1969) undertook a very thorough vegetation survey of the C.G.H.N.R flora. An initial reconnaissance survey formed the background for a detailed descriptive account of the vegetation and its physical setting (Taylor 1984b). This was followed by an analytical approach, in the form of association-analysis (Williams and Lambert 1959) and the phytosociological Braun-Blanquet method (Werger 1974), to classify plant communities (Taylor 1984a). While his descriptive account was very thorough, and the Braun Blanquet analysis distinguished consistent floristic relationships, Taylor's quantitative study using association-analysis did not accurately reflect the ecological patterns of the reserve (Taylor 1984a). Furthermore, no attempt was made to quantitatively explore the variation in vegetation in relation to the major environmental variables. Since the work of Taylor, much progress has been made in the field of numerical classification and gradient analysis (Kent and Coker 1992). The availability and ease of use of these techniques has been greatly aided by the development of computer programmes such as TWINSPAN (Hill 1979) and CANOCO (ter Braak 1988a). Using these techniques it is now possible to quickly and efficiently categorise vegetation into communities, define character species and determine underlying environmental gradients.

Cowling *et al.* (1996) categorised the vegetation of the Cape Peninsula into 14 units based on Campbell's (1986a) system of vegetation classification for the mountains of the fynbos biome. This system was developed in order to provide managers with an easy-to-use classification of the flora. They derived communities on the basis of easily identifiable structural features, dominant species and environmental characteristics. This approach was found to be effective (80% similarity) when compared with a more detailed TWINSPAN classification of the communities of the Cape Peninsula (Simmons 1996). In this chapter I attempt to produce a similar user-friendly classification based on the system of Cowling *et al.* (1996a) combined with Taylor's descriptive account and a detailed TWINSPAN classification.

Taylor's descriptive account and a detailed TWINSPAN classification.

In this chapter I also make use of multivariate methods to determine the importance of environmental factors in explaining the complex patterns of species distributions within the reserve. An important issue in fynbos ecological studies is how much of the observed vegetation patterns can be explained by the underlying environmental determinants. The few vegetation-environment models produced for fynbos have shown that there is a predictable structure in the vegetation related to various environmental factors (Richards *et al.* 1995, McDonald *et al.* 1996, Simmons 1996). However, these studies showed that a high proportion of the variation in species patterns could not be explained by the main environmental factors. For example, the multivariate analyses of McDonald *et al.* (1996) explained only about 50% of the compositional variation and was unable to explain the finer-scale community structure.

This chapter forms the background to the rest of the thesis by providing a classification of the reserve's vegetation, determining the major environmental variables associated with these patterns and quantifying their importance.

The aims of this chapter were as follows:

1. To classify the vegetation in the CGHNR into easily recognisable community units using multivariate techniques.

2. To explore whether the results of the classification correspond with that derived by Taylor (1984a & b) and Cowling *et al.* (1996a).

3. To determine to what extent the environmental factors explain the variance in the species data.

## Methods

### STUDY AREA

A detailed account of the study area appears in Chapter 1.

### DATA COLLECTION

One of the major objectives of this survey of the CGHNR was to explore the temporal change in vegetation over the period (ca. 30 years) during which the reserve has been actively managed (see later chapters). Thus, I wished to resample permanent sites established by Taylor (1969 and 1984a) during his earlier (1965) survey (Fig. 1.1). He used rectangular sites of 5 x 10 $m^2$ placed systematically at the intersections of the grids on a 1:18 000 topographical map, at 1 000-yard (914 m) intervals. Three summit samples were added, giving 100 sites in total (Taylor 1984a).

Taylor's sites were relocated by pacing distances from fixed points with the aid of a prismatic compass and altimeter. The location of sites was greatly aided by black-and-white photographs taken of each site at the time of the original survey. The exact positioning of the sites could be ascertained using the permanent marker poles that demarcate the south-western corner of each site. These poles were erected by reserve management during the 1970's to replace the original wooden stakes used by Taylor. Where the marking pole was missing the site positioning was ascertained using the black-and-white photographs and in some cases the original rock cairns which had held the wooden stakes. Each site covered the same area as the original survey with their long border lying from true south to north. Of the original 100 sites, 84 were relocated accurately enough to be used in this study. I added a further three sites in under represented vegetation types (Fig. 1.1). Sampling of the vegetation took place from September 1995 to April 1996.

Species lists were made for each site using the methods of Taylor (1969). The 50 $m^2$ sites were sub-divided into ten sub-plots in order to improve accuracy. Each sub-plot was examined separately and then combined to provide a final species inventory for the site. To avoid sampling error owing to the seasonality of annuals and many geophytes, only perennially identifiable species were recorded. Species identification was carried out in the Guthrie Herbarium, University of Cape Town. The species lists of Taylor (1985) and Fraser (in press) were used to aid with identification. All nomenclature follows Arnold and De Wet (1993).

The number of individuals of each species in a site was counted and later converted to a five-category system that corresponds to a simplified form of Acock's (1975) system of abundance symbols (Table 2.1). This was done in order to be compatible with Taylor's (1969) study that used Acock's (1975) symbols for assessing abundance.

**Table 2.1** Abundance categories used in this study.

| Category used | Condensed Acock's category | Number of individuals on site |
|---|---|---|
| 1 | occasional | 1 to 4 |
| 2 | fairly frequent | 5 to 10 |
| 3 | frequent | 11 to 50 |
| 4 | common | 51 to 100 |
| 5 | abundant | > 100 |

The following environmental variables were recorded at each site: elevation, aspect, slope inclination, solar radiation load, land form, soil depth, soil colour, soil moisture, soil pH and geology. The variables and methods of measurement used are shown in Table 2.2.

Table 2.2 Environmental variables used in analyses.

| Variable | Description and measure |
|---|---|
| Elevation | Height above sea level (m) recorded with an altimeter. |
| Land facet | The land form on which the vegetation was surveyed where 1 = summit, 2 = convex or concave pediment slope, 3 = bottom-lands (flats), 4 = coastal platform, 5 = footslope, 6 = bottom land exposed sheetrock, 7 = bottom land hollow, 8 = terrace on slope, 9 = seepage step, 10 = rocky cliff, 11 = gentle rolling hill. |
| Geology (fertility) | A crude index of increasing fertility where 1 = leached sands derived from sandstone, 2 = poorly drained sandstone-derived soils on the flats, 3 = ferruginised sands (red), 4 = recent dune sands and sandstone-derived colluvium soils, 5 = Plio-Pleistocene dunes and limestone. |
| Aspect | An index of increasing insolation where 0 = south, 1 = sse or ssw, 2 = se or sw, 3 = east or west, 4 = ne or nw, 5 = nne or nnw and 6 = north. |
| Slope | Inclination of the slope measured with clinometer (degrees) and then converted to an index of increasing steepness where 1 = flat (0 to 2°), 2 = gentle (3 to 6°), 3 = moderate (7 to 15°), 4 = steep (16 to 25°) and 5 = very steep (> 25°). |
| South-east cloud | A binomial variable where 0 = no cloud resulting from south-east winds and 1 = cloud cover as a result of south-east winds. |
| Soil moisture | An index of increasing soil moisture where 1 = well drained, 2 = seasonally waterlogged soils, 3 = temporary standing water and 4 = permanent standing water. |
| Rock cover | An index of increasing rock cover where 1 = < 1%, 2 = 1 to 5%, 3 = 6 to 25%, 4 = 26 to 50%, 5 = 51 to 75% and 6 = > 75%. |
| Soil colour | Soil colour coded using taxonomic soil classification system for South Africa (Soil classification working group 1991) and simplified into 8 categories. |
| Soil depth | The depth of the soil (cm) at a site taken as the mean of five measures using a steel rod knocked into the ground. |
| Energy regime | Annual solar energy (Joules.cm$^{-}$1.day$^{-1}$) reaching the ground corrected for latitude, slope and aspect of sample site (Swift 1976). |
| Soil pH | Three soil samples were taken at random locations within each site and the mean pH was measured in 0.01 mol $l^{-1}$ $CaCl_2$ solution. |

DATA ANALYSIS

*Classification*

One of the aims of this chapter was to compare the results of this classification with the communities defined by Taylor (1984a & b). TWINSPAN is at present the most widely used technique for polythetic divisive classification (Kent and Coker 1992) and is frequently used in parallel with ordination techniques. The technique divides complete data sets into distinct groups on the basis of differences in floristics between the various samples or groups of samples. TWINSPAN adapts abundance data to a qualitative equivalent called pseudospecies which are then used in the process of division. Initial vegetation classification was thus undertaken using Two-Way Indicator Analysis (TWA) in the TWINSPAN package (Hill 1979). TWINSPAN produces as output an ordered two-way table that can be displayed as a dendrogram showing the resultant sample hierarchy, and approximates the results of Braun-Blanquet tablework (Hill 1979). Interpretation of the output table is subjective. For example not all groups have to be taken from one level; the decision when to stop divisions is dependent on a subjective understanding of the vegetation boundaries. I used all 88 samples with the default options in the TWINSPAN analysis.

*Ordination*

Detrended correspondence analysis (DCA) was used to group sample sites into communities according to common floristic characteristics. DCA has the advantage that it avoids the problems of interpretation due to the axis compression effect and arch effect phenomena produced by correspondence analysis and reciprocal averaging (Hill and Gauch 1980). According to Gauch (1982), DCA results are usually superior to other ordination techniques and it is computationally very efficient. It is an indirect gradient analysis which ordinates only the vegetation data: environmental gradients are inferred or established by correlation analysis, from the species composition data (Taggart 1994).

Canonical correspondence analysis (CCA) was then used to relate the vegetation gradients to the environmental factors. CCA is a method of direct gradient analysis that produces an integrated ordination of species together with the associated environmental data (ter Braak 1987). The use of DCA and CCA together allows one to judge how much of the variation in species data can be attributed to the environmental variables under investigation (ter Braak 1986). Initially all environmental variables were included in the CCA analysis and a Monte Carlo permutation test was used to test the significance of the eigenvalues of the axes (ter Braak 1988a, 1990). The intra-set correlations between the first two CCA axes and the environmental variables were then used to assess the importance of individual variables (ter Braak 1987, McDonald *et al.* 1996). Intra-set correlations are the inter-set correlations divided by the species-environment correlation of the axis and tend to be a more stable measure than the inter-set correlations alone (ter Braak 1987). The significance of each correlation was calculated using the *t*-statistic with a critical value of 1.96. Forward selection of environmental variables was then used to determine the minimum set of explanatory variables which best explain the variation in the floristic data (ter Braak 1990). Only those variables that proved statistically significant in the forward selection procedure (Monte Carlo; 99 permutations) were included in the CCA biplot (Fig.2.8). All ordination analyses used quantitative data and were done using CANOCO ver. 3.12 (ter Braak 1988, 1990), while Graphpad Prism ver. 1.03 was used for the graphical representation of scatter diagrams and biplots. For the biplots a scaling factor of 0.193 was used to convert sample scores to the same scale as the environmental variables.

## Results

### CLASSIFICATION

The TWINSPAN classification produced seven broad community types which correspond quite well with those of Taylor (1984a & b). The divisive process was stopped at the sixth division as subsequent divisions caused the splitting of communities into apparently meaningless groups. The results of the TWINSPAN analysis are represented as a dendrogram (Fig. 2.1). The communities are described on the basis of the definitions given for the Cape Peninsula by Cowling *et al.* (1996a). The original names used by Taylor (1984b), as well as the floristic and environmental characteristics of each vegetation type, are included in the description below.

While the most useful classification system would be based on true indicator species that occur only in a single vegetation type, the high number of rare and generalist species in fynbos makes this impossible (Simmons 1996). Instead, for each community, I listed character species based on a minimum requirement of occurring in at least 60% of the member sites of a vegetation type, and in less than 10% of the remaining vegetation sites. The only exception to this definition was for the Mesic oligotrophic proteoid fynbos community, where all character species occurred in more than 10% of the non-member sites. In the description below, the character species are ranked according to their abundance across the entire community (the most abundant species is listed first, followed by the second most abundant etc.). Those character species unique to a community are highlighted with an asterisk.

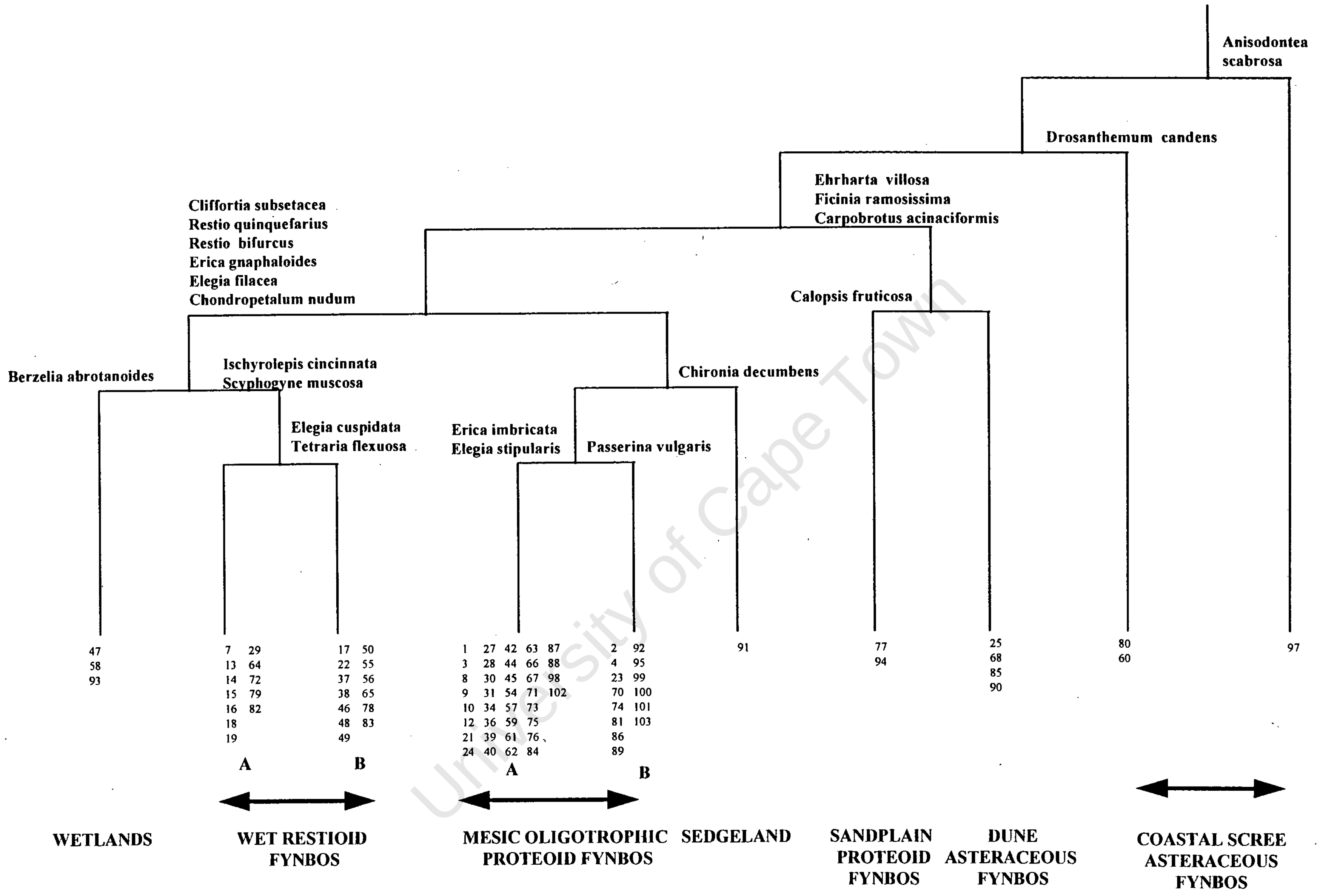

**Figure. 2.1** TWINSPAN dendogram of 89 stands showing the major communities in the Cape of Good Hope Nature Reserve. Species shown are the indicator species as calculated by TWINSPAN and not necessarily the character species used in the text.

## COMMUNITY DESCRIPTION

### *Community 1. Coastal scree asteraceous fynbos. (CSA)*

Taylor's (1984b) community: Coleonema Fynbos on well-drained rocky coasts.

Structural characteristics: Low to mid-dense, open leptophyllous shrublands with low total cover and a high proportion of succulent shrubs.

Character species: *Drosanthemum candens**, *Exomis microphylla**, *Spergularia media**, *Felicia fruticosa* and *Protasparagus capensis*.

**Figure 2.2.** Typical coastal scree asteraceous fynbos at site 60 above the False Bay coastline. Low succulent shrubs of the family Mesembryanthemaceae dominate the vegetation. This photograph was taken at the time of Taylor's initial survey in 1966.

This vegetation type occurs on the rocky cliffs, ledges and scree slopes along the coast and covers approximately 9.3 hectares (0.1%) of the Reserve. All three sites classified as CSA in this study occurred along the eastern coastline of the reserve and are exposed to the strong salt-laden south-easterly winds and sea spray during the dry summer months. Soils are shallow, with bedrock either exposed or close to the surface, well drained and only slightly acidic. This is the False Bay coast variant of Taylor's Coleonema fynbos. On the False Bay coast, the precipitous slopes and ledges are dry and hot. Consequently this variety of CSA differs from that found on the cooler, gentler, south-west facing slopes along the Atlantic coastline. It is characterised by the dominance of low shrubs, many of them with a succulent growth form. The dominant species are *Exomis microphylla*, *Spergularia media* and *Drosanthemum candens*, while other common species include *Anisodontea scabrosa, Mesembryanthemum crystallinum*, *Felicia fruticosa* and *Protasparagus capensis*. Site 97 is separated from sites 60 and 80 in the TWINSPAN dendogram owing to floristic differences caused by the dense invasion of the Australian tree *Acacia cyclops* at this site. The remaining natural vegetation on the site is most closely related to that found in the CSA community. Of the 32 species recorded in this vegetation type, 52% were not found elsewhere in the survey.

*Community 2. Dune asteraceous fynbos. (DAF)*

Taylor's (1984b) community: Eriocephalus Coast-shelf fynbos on well-drained marine sands.

Structural characteristics: Asteraceous fynbos is typically low to mid-dense, open leptophyllous shrublands with low total cover and a high proportion of asteraceous species and non-ericaceous ericoids.

Character species: *Ficinia ramosissima, Euclea racemosa, Ehrharta villosa, Carpobrotus acinaciformis, Helichrysum dasyanthum, Cineraria geifolia, Rhus glauca* and *Rhus laevigata.*

**Figure 2.3.** Dune asteraceous fynbos at site 68 on the west coast of the reserve. Note the stands of dense coastal thicket on the dunes closer to the sea. These form in the absence of fire and are dominated by coastal thicket species such as *Euclea racemosa* and *Sideroxylon inerme.*

Dune asteraceous fynbos is found on the deep, relatively young calcareous coastal soils that are well drained, often mixed with shell fragments and have a high pH. It covers approximately 480 hectares (6%) of the reserve. Four of the coastal samples, two from each coastline, were grouped into this vegetation type. It is characterised by low shrubs, e.g. *Helichrysum dasyanthum*, and graminoids, e.g. *Ficinia ramosissima,* and where unburnt for longer periods can become dominated by woody shrubs such as *Euclea racemosa* and *Rhus* spp. As a result of undersampling of coastal sites in this survey, DAF cannot be classified separately from the coastal thicket communities with which it intergrades. Fifty-two species were recorded in this community of which 38% were not recorded elsewhere in the reserve.

### *Community 3. Sandplain proteoid fynbos. (SPF)*

Taylor's (1984b) community: Dune Mixed Fynbos on well-drained aeolian dunes mainly of marine origin.

Structural characteristics: Open shrubland with > 10% cover of medium-height (1-3m), non-sprouting, proteoid shrubs with a low ericoid and restioid understorey.

Character species: *Leucadendron coniferum, Passerina paleacea, Indigofera brachystachya**, *Ehrharta villosa, Hermannia ternifolia**, *Pelargonium betulinum, Calopsis fruticosa and Carpobrotus acinaciformis*

Sandplain proteoid fynbos occurs on the older (Plio-Pleistocene), inland marine sands which form the longitudinal dunes traversing the reserve. It covers an area of approximately 212 hectares or 2.7% of the reserve. Soils were very similar to those found at the Dune asteraceous fynbos sites, but tend to be finer grained and often enriched by humus, especially in the depressions. The dominant species were *Leucadendron coniferum* and *Passerina paleacea*, while the lower strata were characterised by a high cover of *Indigofera brachystachya, Hermannia ternifolia* and *Pelargonium betulinum*. Only 25% of the 49 species recorded in this type were unique to it.

*Community 4. Plecostachys/Scirpus sedgeland. (PSS)*

Taylor's (1984b) community: Plecostachys-Scirpus Sedgeland on poorly drained coastal flats.

Structural characteristics: Low (<1 m), dense to closed, graminoid shrubland with a high cover of sedges.

Character species: *Scirpus nodosus*, *Helichrysum cymosum**, *Chironia decumbens**, *Plecostachys serpyllifolia*, *Samolus valerandi**, *Pelargonium grossularioides*, *Myrica quercifolia*, *Juncus kraussii*, *Juncus capensis** and *Chondropetalum tectorum.*

This is a very localised vegetation type not described in Cowling *et al.*'s (1996a) broad-scale description of the Cape Peninsula's plant communities and not large enough to be depicted on Fig. 1.3. It is found in the poorly drained, almost permanently wet, depressions of the coastal shelf of the reserve. At these sites a thin layer of marine sands overlie sandstone bedrock causing impeded drainage. PSS is dominated by graminoids, in particular, *Scirpus nodosus*, *Chondropetalum tectorum*, *Juncus capensis* and *J. kraussii.* Other common shrubs include *Helichrysum cymosum* and *Plecostachys serpyllifolia* that form a low ground cover between the graminoids. In this survey only a single sample site fell within this vegetation type, but 50% of the 18 recorded species were unique to it.

*Community 5. Mesic oligotrophic proteoid fynbos. (MOP)*

Taylor's (1984b) community: A combination of Upland Mixed Fynbos on well-drained rocky hill and mountains and *Protea lepidocarpodendron* tall fynbos on well-drained ferricrete slopes.

Structural characteristics: Medium-height (1-3 m) proteoid shrubland (> 10% cover of medium to tall, non-sprouting, proteoid shrubs), with a low (< 1 m) ericoid and restioid understorey.

Character species: *Ischyrolepis cincinnata, Thamnochortus lucens, Elegia stipularis, Salaxis axillaris, Ischyrolepis capensis, Struthiola ciliata, Erica imbricata* and *Metalasia muricata*.

It is important to note that none of these species are true character species as defined in the methods as they all occur in more than 10% of the non-member sites. Only *Struthiola ciliata* and *Salaxis axillaris* occur in less than 20% of the non-member sites.

**Figure 2.4.** Typical mesic oligotrophic proteoid fynbos on the slopes below Bonteberg peak. The trees amongst the rocks are the Proteaceae, *Mimetes fimbriifolius* and *Leucospermum conocarpodendron* (height 2 m).

This is the most extensive and variable vegetation type in the reserve and was recorded at a total of 50 sites in this study. It covers an area of approximately 4984 hectares which is equivalent to 64% of the reserve's surface area. It is the characteristic vegetation of the inland hills and mountain ranges where considerable variability in the physical habitat results in much variation in vegetation composition and structure. In addition to the variability in physical habitat, other factors such as variable fire regimes and the impact of alien plants have caused further variation in the vegetation (see later chapters). The majority of the sites grouped into this community occur on shallow, highly acidic, Table Mountain Sandstone-derived soils. These soils are composed of coarse white sand over bedrock and are well drained. In his descriptive account of the vegetation of the C.G.H.N.R. Taylor (1984b) defined the *Protea lepidocarpodendron* tall fynbos on ferricrete-derived soils as a separate community. Despite obvious edaphic differences, the results of this study suggest that there are insufficient floristic differences to warrant separating these communities. The TWINSPAN analysis did split MOP into two groups at the last (sixth) division. The majority of sites formed a well defined group on the basis of the presence of the character species *Erica imbricata* and *Elegia stipularis.* This group could be defined as the true MOP community and is shown as group A in Fig. 2.1. The second group (B in Fig. 2.1) was an anomalous mixture of sites which included some on deep soils of marine origin (4, 70, 86 and 92) as well as a number of sites with vegetation older than twenty years post-fire (23, 74, 81, 89, 95, 99 and 101). The average age of the sites in sub-group B of MOP (14 sites) was 24.9 years, whereas the sub-group A (36 sites) had a mean age of just 7.9 years post-fire. The environmental variables of these two sub-groups were very similar, suggesting that the division at the sixth level was a result of floristic differences caused by post-fire successional effects rather than underlying environmental gradients. The analysis revealed no true character species in this vegetation type, as most species common to MOP are also found outside of this vegetation type. However certain species are consistently recorded at high abundances and are consequently useful indicator species. The restioids, *Ischyrolepis cincinnata*, *Thamnochortus lucens* and *Elegia stipularis* are amongst the best indicators of MOP, while *Struthiola ciliata* and *Salaxis axillaris* are the two most specific commonly observed species. Despite the lack of true indicator species this vegetation type included a large number of rarer species not found elsewhere in the reserve. Forty percent of the 316 recorded species were specific to this community.

*Community 6. Wet restioid fynbos. (WRF)*

Taylor's (1984b) community: A combination of restionaceous tussock marsh and restionaceous plateau fynbos.

Structural characteristics: Low (< 1 m) to mid-high (1-3 m), medium to closed (> 50%) restiolands with low shrub cover.

Character species: *Restio quinquefarius*, *Restio bifurcus*, *Scyphogyne muscosa*, *Cliffortia subsetacea*, *Chondropetalum nudum* and *Erica gnaphaloides**.

**Figure 2.5.** Wet restioid fynbos at site 83 near Suurdam in the south of the Reserve. Note the dominance of restioids, in particular *Elegia filacea*, at this site. The ridges in the background are covered by mesic oligotrophic fynbos with large bushes of *Leucospermum conocarpodendron*.

This vegetation type covers 1624 hectares (21%) of the reserve and is found predominantly on the level central plateau. Twenty five of the sites in this study were categorised into the WRF community. The physical environment is characterised by highly acidic, deep soils with low rock cover and intermediate to poor drainage. As with MOP, this vegetation type was variable and included both the restionaceous tussock marsh and restionaceous plateau fynbos communities of Taylor (1984b). TWINSPAN divided the WRF type into two sub-groups at the sixth division. Sub-group B was characterised by the presence of *Elegia cuspidata* and *Tetraria flexuosa* and would, according to Taylor's (1984b) classification, be true restionaceous tussock marsh. Sub-group A was a mixture of sites with no character species which occurred on better drained soils and could be categorised as Taylor's restionaceous plateau fynbos. However, while restionaceous tussock marsh was clearly distinguishable by the presence of *E. cuspidata* in the field, the restionaceous plateau fynbos had no character species of its own and was defined rather on the basis of missing species (Taylor 1984b). I therefore prefer a combined restionaceous community characterised by the presence of a dominant restioid component, especially *Restio quinquefarius*, *R. bifurcus* and *Chondropetalum nudum*, and supplemented by low shrubs such as *Cliffortia subsetacea* and the specific *Erica gnaphaloides*. In the field there is a gradual transition from true tussock marsh dominated by *Elegia cuspidata* and *E. filacea* to the Mesic oligotrophic proteoid fynbos with a corresponding decline in restioids and an increase in species diversity. The boundary between MOP and WRF is often vague and as a result there is a high degree of species overlap and low specificity. Only 15% of the 169 species recorded in WRF are specific to the type.

*Community 7. Wetlands. (WET)*

Taylor's (1984b) community: Berzelia-Osmitopsis Seepage Fynbos on permanent seeps.

Structural characteristics: Medium (1-3 m), to tall (> 3 m) ericoid shrubland with an overstorey of ericoid shrubs and an ericoid and restioid understorey.

Character species: *Berzelia abrotanoides*, *Restio dodii*, *Erica hispidula*, *Berzelia lanuginosa* and *Merxmuellera cincta.*

**Figure 2.6.** Wetland vegetation dominated by *Berzelia lanuginosa and B. abrotanoides* along a seepage step near Klaasjagersberg.

The wetland community is found on stream banks as well as on seepage steps formed where the underlying bedrock intersects the surface forming abrupt terraces behind which permanent water collects. It covers an area of approximately 118 hectares (1.5%) of the reserve. The vegetation differs from WRF by having a low cover of restioids and being dominated by the conspicuous *Berzelia abrotanoides*, *B. lanuginosa* and *Osmitopsis asteriscoides*, while *Erica hispidula* and the endemic *Restio dodii* are also typical of these sites. The ground remains permanently damp, litter does not decompose readily and consequently soils are dark in colour and highly acidic. While this vegetation type is easily distinguishable by its dominant species, only 13% of the 45 recorded species were unique to WET.

**Table 2.3** Mean values of environmental variables for the sites associated with each of the communities. Data presented as mean ± standard error. The PSS 'community' was not included as it was represented by only one site.

| | **Coastal scree asteraceous fynbos** | **Dune asteraceous fynbos** | **Mesic oligotrophic proteoid fynbos** | **Sandplain proteoid fynbos** | **Wetlands** | **Wet restioid fynbos** |
|---|---|---|---|---|---|---|
| **No. of sites** | 3 | 4 | 50 | 2 | 3 | 25 |
| **Area (hectares)** | 9.3 | 479.6 | 4983.7 | 212.6 | 117.9 | 1624 |
| **Elevation (m)** | 7.1±2.7 | 9.9±3.8 | 107.5 ±72.4 | 96.0±19.8 | 99.1±20.2 | 79.9±7.7 |
| **Aspect (number of sites)** | | | | | | |
| South-facing | 0 | 0 | 5 | 0 | 0 | 4 |
| SSE or SSW-facing | 0 | 1 | 3 | 1 | 0 | 1 |
| SE or SW-facing | 0 | 0 | 9 | 0 | 0 | 1 |
| E or W-facing | 2 | 1 | 4 | 0 | 0 | 0 |
| NE or NW-facing | 1 | 1 | 4 | 0 | 0 | 0 |
| NNE or NNW-facing | 0 | 0 | 3 | 0 | 0 | 0 |
| North facing or flat | 0 | 1 | 22 | 1 | 3 | 19 |
| **Geology *** | colluvium/ scree | recent calcareous coastal sands | leached sandstone-derived soils | old marine sands | poorly drained sandstone soils | poorly drained sandstone soils |
| **Land facet*** | coastal spray zone | coastal platform | seepage step | rolling hills | seepage step | bottom-land flats |
| **Soil moisture*** | well drained | well drained | well drained | well drained | permanent standing water | temporary standing water |
| **Rock cover (%)** | 50 ± 20.8 | 0 ± 0 | 24.2 ± 4.3 | 0 ± 0 | 0 ± 0 | 1.1 ± 0.5 |
| **Slope (°)** | 25 ± 5.2 | 3 ± 1.5 | 5.7 ± 1.0 | 0.5 ± 0.5 | 0 ± 0 | 0.7 ± 0.4 |
| **Soil colour *** | brown | grey-white | grey | grey | black | brown-black |
| **Soil depth (cm)** | 16 ± 12.5 | > 100 | 27.6 ± 31.1 | 69.0 ± 2.0 | 73.0 ± 13.6 | 75.6 ± 6.9 |
| **Soil pH** | 6.1 ± 0.2 | 7.5 ± 0.1 | 4.4 ± 0.8 | 7.6 ± 0.1 | 3.8 ± 0.5 | 3.7 ± 0.1 |
| **Energy regime ($Joules.cm^{-1}.day^{-1}$)** | 740.7 ± 45.9 | 744.5 ± 12.3 | 734.8 ± 56.8 | 741.5 ± 2.5 | 744.0 ± 0.00 | 738.2 ± 3.4 |

* most common factor used for these variables.

## ORDINATION

### *Detrended correspondence analysis*

The ordination by DCA complemented the TWINSPAN classification. The first two DCA axes were plotted against each other, allowing for a visual assessment of the clustering of samples (Fig. 2.7). The first and second eigenvalues of the DCA were 0.79 and 0.53 respectively, accounting for most of the variance in species data. The first two DCA axes suggested two main compositional gradients in this vegetation. Along axis 1, the sequence was from the WET and WRF communities, through the MOP to the coastal communities. This axis was positively correlated with soil pH ($r$ = 0.65) and geology ($r$ = 0.5). The main compositional gradients along axis 2 was from the driest (CSA and DAF) to the wettest sites (PSS and WET) and corresponded with a gradient of increasing soil moisture ($r$ = 0.44).

### *Canonical correspondence analysis*

The eigenvalues of the CCA axes were lower than for the DCA axes (axis 1 = 0.6 and axis 2 = 0.45) suggesting that not all important site variables were included in the analysis. The complete set of measured environmental variables explained 21% of the inertia in species data (the sum of all constrained eigenvalues, ter Braak 1990), while only 8% of the variance in species data and 38% of the variance in the species environment relation was explained by the first two axes. Despite these low values, an unrestricted Monte Carlo permutation test (99 permutations) showed both the F-ratios for the axis 1 eigenvalue and the trace statistic to be significant ($P < 0.01$).

The highest canonical coefficients were exhibited by soil pH ($r$ = 0.81), geology ($r$ = 0.63) and rock cover ($r$ = 0.23) for axis 1, and soil moisture ($r$ = -0.88) and soil depth ($r$ = 0.56) for axis 2. There was no collinearity between environmental variables and they could therefore all be included in the analysis. The results of the CCA's forward selection procedure produced a minimum set of six environmental variables which best explain the floristic variation. The significant variables in order of decreasing importance were soil pH, soil moisture, SE cloud, soil depth, soil colour and rock cover (Table 2.4). Geology, although being highly correlated with the first axis, was not significant according to the results of a Monte Carlo test at the 5% level, and was therefore excluded from the final "minimum set" (ter Braak 1990).

**Table 2.4.** Eigenvalues and intra-set correlations between CCA axes and the vegetation of the Cape of Good Hope Nature Reserve (CGHNR). The minimum set of variables that explains the species data nearly as well as the full set are shown in italics. The intra-set correlations are shown for all environmental variables under axes 1 and 2. The forward selection rank gives the rank importance of the significant variables calculated from its eigenvalue in a CCA, if the variable was the only one in the analysis. Geology, although being highly correlated with the first axis, was not significant according to the results of a Monte Carlo test at the 5% level.

| | **Axes** | | **Forward Selection** |
|---|---|---|---|
| | **1** | **2** | **Rank** |
| **Eigenvalue** | 0.600 | 0.446 | |
| **Environmental variables:** | | | |
| ***Soil pH*** | 0.806 | -0.334 | 1 |
| ***Soil moisture*** | -0.116 | 0.879 | 2 |
| ***SE cloud*** | 0.023 | -0.08 | 3 |
| ***Soil depth*** | 0.068 | 0.563 | 4 |
| ***Geology*** | 0.632 | -0.041 | NS |
| ***Soil colour*** | -0.138 | 0.244 | 6 |
| ***Rock cover*** | 0.231 | -0.15 | 7 |
| **Land facet** | 0.079 | 0.093 | NS |
| **Altitude** | -0.216 | -0.122 | NS |
| **Aspect** | -0.356 | 0.170 | NS |
| **Slope** | 0.101 | -0.262 | NS |
| **Solar radiation** | -0.067 | 0.044 | NS |

Fig. 2.8 is the biplot of the 89 sites and the six best explanatory variables. Axis 1 again represented a gradient of increasing soil pH, while axis 2 represented a gradient of increasing soil moisture and depth. The other environmental variables all had relatively little value as explanatory variables.

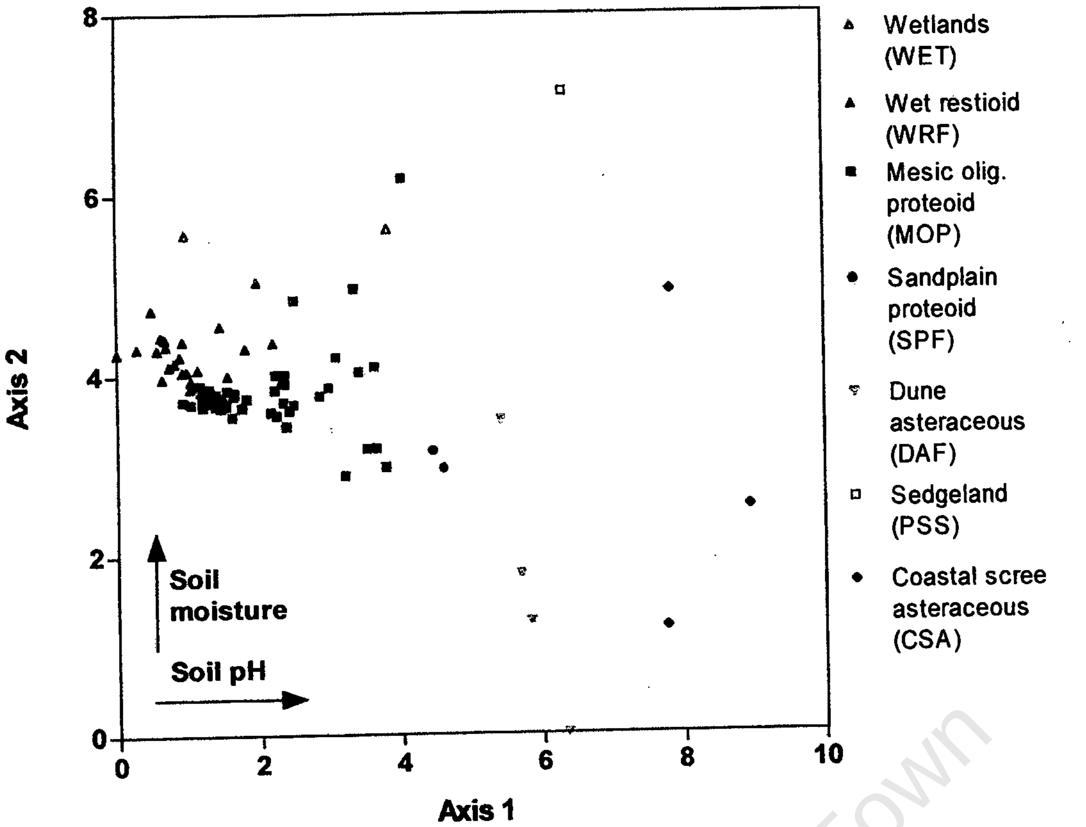

**Figure. 2.7** DCA ordination of the first two axes of the C.G.H.N.R. data-set. Arrows indicate direction of increasing magnitude of primary environmental gradients. The groups of sites associated with each of the major communities (from the TWINSPAN classification) are colour coded and labelled. For details of vegetation characteristics see the community description.

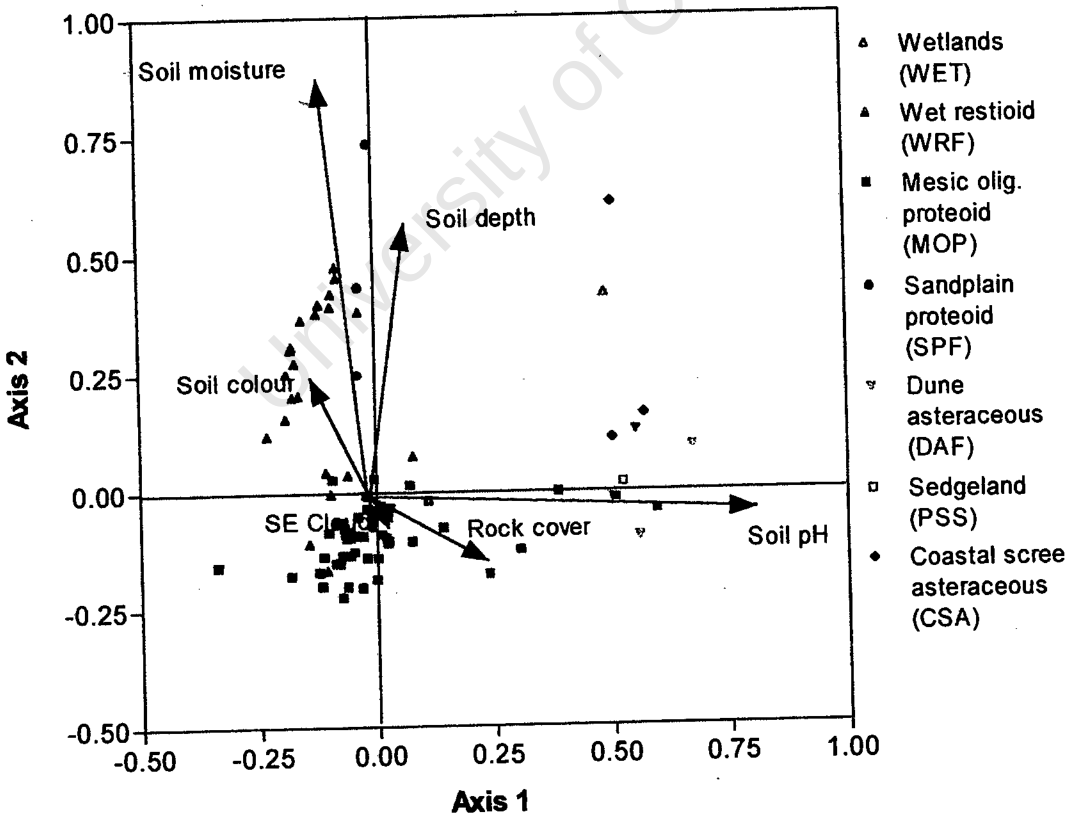

**Figure 2.8** CCA biplot of site scores for 88 sites and the set of six most important environmental factors (determined by forward selection procedure) on the first two CCA axes. The groups of sites associated with each of the major communities (from the TWINSPAN classification) are colour coded and labelled.

## Discussion

### VEGETATION CLASSIFICATION

The TWINSPAN analysis initially divided the vegetation of the reserve into two major groups, the coastal and dune communities (CSA, DAF, SPF and PSS) which are characterised by alkaline soils, and the inland communities (MOP, WRF and WET) which all occur on acid sands. The majority of sites surveyed were then grouped into just two inland communities: Wet restioid fynbos on the poorly drained flats and Mesic oligotrophic proteoid fynbos on the well drained inland hills. The seven vegetation types produced by the TWINSPAN analysis are broadly equivalent to the major communities defined by Taylor (1984b) with a few exceptions.

The present analysis did not distinguish a separate restioid community equivalent to the restionaceous plateau fynbos of Taylor (1984b). Instead member sites of this community were grouped with either the WRF or MOP communities which merge with each other in intermediate habitats.

The *Protea lepidocarpodendron* tall fynbos on ferricrete soils was represented in the data set by three sites, yet did not separate from the MOP sites located on sandstone. In the reserve the major outcrops of ferricrete are easily distinguished by the dominant cover of *P. lepidocarpodendron*. However, this species is often absent on the smaller outcrops. This suggests that on the smaller outcrops the ferricrete specialists may be lacking and as a result there is insufficient floristic differentiation from the surrounding sandstone matrix to justify the classification of a separate community.

Where the MOP vegetation type was divided into two sub-groups by TWINSPAN, it would appear to be rather the result of post-fire age effects than any differences in the physical environment. A central question in phytogeographical studies of this nature is whether the observed floristic patterns can be explained by environmental influences or whether other factors such as fire-related stochastic events, biotic interactions or the endogenous properties of key-stone species have an overriding effect (Campbell 1986a, Cowling 1987, Richards *et al.* 1995, Bond *et al.* 1995, Vlok 1996). The results of the classification showed that while there is predictable broad-scale structure related to obvious environmental constraints, some of the finer scale variation within communities could not be so easily explained. It would appear that the major sub-groups within the well drained, acidic inland community of the reserve are divided on the basis of post-fire age. Succession after fire is marked by changes in the relative abundances of life forms and species as the vegetation ages (Bond 1980). Long fire-free intervals results in the senescence of many species that die, surviving only as propagules in the soil (Bond 1980). The older sites therefore tend to be dominated by the longer-lived species that give them a different floristic character to the younger sites. It is of interest that the majority of sites that fell into the old vegetation sub-group of MOP occur either on summits, or towards the south of the reserve. These localities are likely to have had a longer average fire interval than the rest of the sites in the reserve. The floristic differences might therefore be as a result of longer term differences in fire history rather than the post-fire age alone.

There were certain drawbacks to the grid intersect sampling strategy used in this study. Firstly, this objective sampling method resulted in some of the smaller communities being under sampled or not sampled at all. As a result some of the communities described by Taylor (1984b) did not feature in the final vegetation classification (the Atlantic coast variant of *Coleonema* fynbos, *Protea nitida* woodland and Broad-leaved thicket). Secondly, the grid sampling approach resulted in the positioning of certain sites on ecotones so that transitions between communities were also sampled. This reduced the resolution of the final classification as well as the effectiveness of character species. It might also have resulted in a reduction of the explanatory power of the environmental variables in the ordination analyses.

At a broad scale, the ordination analysis provided an indication of the major environmental determinants of the vegetation. The two main compositional gradients (community changes across the landscape) were strongly correlated with gradients of soil factors, namely pH for the first axis and soil moisture for the second axis. The importance of pH is evidence of the key role of soil chemical characteristics in influencing fynbos community boundaries and corresponds to the findings of earlier studies which have provided evidence that fynbos community boundaries are related to changes in physical and chemical characteristics of the soil (van Wilgen & Kruger 1985, McDonald 1988, McDonald *et al.* 1996, Richards *et al.* 1995). The coastal communities exhibited considerable floristic differences from the inland fynbos sites which could be explained largely by changes in soil pH. Within the inland fynbos, where the majority of sites occurred on acid sands, major floristic differences related to changes in soil moisture availability. Soil moisture availability is a limiting factor for certain growth forms during the dry summer months in Mediterranean-climate regions (Miller *et al.* 1983, Stock *et al.* 1992). Shallow-rooted restioids and ericoid shrubs tend to become stressed, while deeper-rooted species are more tolerant to summer drought (Stock *et al.* 1992). In the reserve the shallow rooted restioids and ericoids dominate the poorly drained central plateau which provides them with moisture throughout the year. Restionaceae have been shown to contain anatomical characteristics that enable them to withstand seasonal waterlogging (Hardcastle and Schutte 1983). The deeper-rooted species, which can withstand drier conditions but are unable to cope with waterlogging, dominate on the drier, well-drained hill slopes.

The other physical variables which influenced the vegetation to a lesser degree were the influence of the clouds during summer south east winds, the soil depth and colour and rock cover. During the summer months the vegetation on the mountain peaks along the eastern coastline of the reserve is often covered in moist clouds resulting from strong south-east winds. These clouds increase the moisture available to the plants that in turn may favour certain species. It is equally likely, however, that this factor is merely a surrogate for the high altitude summit sites that generally contained older vegetation. The floristic variation might rather be as a result of differences in post-fire age or longer fire frequencies than increased moisture availability. The importance of soil depth relates to its link to moisture availability and consequently on nutrient availability (McConaughay & Bazzaz 1991), while soil colour is a composite variable that is a surrogate for drainage, parent material and fertility. Rock cover increased from zero in coastal deep sands and inland dunes through low cover in the damp lowlands to high cover on the well-drained hill slopes.

The above description of vegetation-environment relationships suggests that the existing environmental variables are sufficient to explain the broad-scale community patterns observed in the reserve. However the relatively large difference between the eigenvalues of the first two axes of the DCA and CCA as well as the low percentage variance explained by these axes (8% of the variance in species data, 38% of the variance of species-environment relation) suggests that important explanatory variables were not measured and included in the analysis. The finer scaled differences, especially within the large WRF and MOP communities, cannot be fully explained by the present environmental variables and some additional explanations should be considered.

1) Other environmental factors not considered in this study, especially soil characteristics, could be responsible for some of the variation. The ordination results indicate that soil characteristics were the most important determinants of vegetation boundaries in the reserve. It was decided not to undertake any more detailed, time consuming, soil analyses as the existing soil variables, soil pH and soil moisture, were significantly correlated with the first two eigenvalues of the ordination. Furthermore the inclusion of detailed soil analysis data in similar species-vegetation models in fynbos did not result in a substantial increase in the explained variance (Richards *et al.* 1995). The existing set of physical site variables is otherwise comprehensive and covers the major determinants of vegetation pattern in the reserve.

2) Biotic interactions such as competition and predation could influence species distribution and vegetation boundaries (Cody 1986, Bond *et al.* 1992). The degree to which these processes structure species membership in fynbos communities is poorly understood. However, it has been recently demonstrated that the populations of certain overstorey Proteaceae may oscillate from internal density-dependent causes resulting in huge fluctuations in population sizes (Bond *et al.* 1995). These species in turn play a keystone role in structuring communities by affecting the diversity and composition of understorey species (Cowling and Gxaba 1990, Vlok 1996). Chapter 5 explores temporal dynamics in the reserve including the role of competitive interactions in the form of post-fire succession and the influence of overstorey Proteoid species on understorey diversity.

3) Differential fire regimes influence within-community variation in vegetation composition and structure. Fires are natural phenomena in fynbos where each fire is a unique event which, depending on environmental conditions and fire regime, will influence the vegetation differently. Fires may burn only part of a community favouring certain species and causing local extinction of others. A few years after the fire a phytosociological study may reveal differences within the community that are largely the result of fire and which are less dependent on physical environmental factors. The TWINSPAN classification revealed the importance of post-fire age in influencing floristic differences within a community. Chapter 3 explores the role of the past 30 years fire history in influencing the floristics of the major communities in order to quantify how much of the observed species-based variance might be explained by past fire regimes.

4) The invasion of natural fynbos by stands of alien trees and shrubs results in reductions in species richness (Richardson *et al.* 1989) and changes in community structure (Holmes and Cowling 1997). Alien trees have seriously impacted the natural vegetation of the CGHNR for many years (Taylor and MacDonald 1985, Taylor *et al.* 1985). Holmes and Cowling (1997) demonstrated that reductions in species-richness, cover and frequency increased with increasing period of invasion by *Acacia saligna* in similar vegetation outside of the reserve. A decline in species-richness with an increase in alien plant cover

has also been noted under stands of *Acacia cyclops* in the reserve (Turpey 1986). Alien plants alter the floristic composition of sites by competitive displacement during the invasion process (Richardson *et al.* 1992) and their impact remains even after clearing through their alteration of soil characteristics (Musil and Midgley 1990, Stock and Allsopp 1992). Site 97 is a good example of how invasion by alien trees, in this case *A. cyclops*, can cause changes in floristic composition and ultimately misclassification in studies of this nature. Chapters 5 explores in more detail the impact of alien plants on the reserve's vegetation over the last 30 years, while Chapter 3 examines their importance in influencing the floristic variation within the major communities of the reserve.

## Conclusions

It was possible to discern and explain the broad scale vegetation patterns in the CGHNR using modern multivariate methods and a sample set of environmental factors. This information provides a simple classification of the flora that is useful for management purposes. The results of the classification corresponded well with Taylor's (1984b) descriptive account and Cowling *et al.*'s (1996a) system. The results of this study were consistent with others (e.g. Cowling 1983, Campbell 1985, Richards *et al.* 1995) that have demonstrated predictable broad-scale patterns in fynbos vegetation. However, finer-scale patterns relating to within-community membership and species-richness were not well explained by the environmental factors. Despite the relatively comprehensive set of physical environmental factors used in the multivariate study, a large proportion of the variance in species data remains unexplained. This unexplained variance is possibly due to fire-related stochastic phenomena, as well as other factors such as alien plant invasions and biotic interactions. A further important contributing factor to the complexity of fynbos landscapes is the lack of temporal stability that results from the high probability of colonisation and extinction, especially amongst the many regionally rare species. The remainder of this thesis explores the contribution of some of these factors to complexity of fynbos landscapes.

# CHAPTER 3. Physical site factors and disturbance regime as determinants of floristic variation in the Cape of Good Hope Nature Reserve.

*Perhaps the most noticeable component missing from the data set is that of fire history. Both the nature of last fire and vegetation age would greatly enhance the descriptive power of species-environment models in fynbos.*

*Simmons (1996)*

## Abstract

The relative importance of physical site factors and certain deterministic components of the disturbance regime in influencing vegetation pattern were explored in fire-prone fynbos vegetation. Multivariate methods were utilised to rank variables according to their importance as determinants of pattern, as well as to partition the variance in community patterns according to physical site factors and the disturbance regime. At the landscape scale physical site variables, in particular edaphic characteristics, ranked highest as determinants of species pattern. However, the recent disturbance regime explained nearly as much of the variance in species data as the physical site factors. At the community scale, disturbance factors ranked higher as determinants of pattern, and explained more of the variance, than physical site factors. In all analyses fire frequency proved more important than season in influencing pattern. Post-fire age significantly influenced vegetation composition at the landscape scale in 1966 but not in 1996 as a result of a better distribution of vegetation ages. Despite the inclusion of disturbance regime, the landscape scale species-environment model was unable to explain 60% of the variance in the species data set. Thus much of the pattern observed in fire-prone landscapes could be ascribed to random plant population dynamics, climatic effects on post-fire recruitment and other stochastic processes.

## Introduction

Disturbance plays an important role in influencing pattern in vegetation systems throughout the world (Pickett and White 1985). Early twentieth century theory proposed that disturbance was merely a mechanism which reset the vegetation on its path towards a stable equilibrium (Clements 1916). Under this assumption the species composition of natural communities would be determined solely by constraints imposed on them by the physical environment. Historical effects, chance factors and disturbance would play a small role in influencing vegetation composition (Chesson and Case 1986). However, while long-term stability has been noted for some systems (e.g. the Park Grass Experiment, Rothamsted, England (Silvertown 1987, Dodd *et al.* 1995)), it has been repeatedly demonstrated that history and chance are important contributors to spatial pattern in a variety of the world's vegetation systems (Picket and White 1985, Hubbell and Foster 1986, O'Connor and Roux 1995, Bond and van Wilgen 1996). The challenge of modern community ecology is therefore not merely in determining the patterns of natural assemblages, but also in explaining these patterns in terms of controlling processes (Wiens 1986). This chapter concerns the determinants of vegetation composition in the floristically complex fynbos shrublands of South Africa. This system is suited to a study of this nature as it is characterised by exceptionally high beta and gamma diversity (Cowling *et al.* 1992), high variability in species composition within communities (see Chapter 2, Campbell 1986b) and a regular fire driven disturbance regime (Cowling 1987).

A central question in ecological studies of Cape fynbos vegetation has been how much of the observed vegetation patterns may be explained by underlying environmental determinants, and how much relates to stochastic phenomena and deterministic processes associated with disturbance (Bond 1981, Campbell 1983, 1986a, Cowling and Campbell 1983, Cowling 1984, Taylor 1984b Richards *et al* 1995, Bond *et al.* 1995, McDonald *et al.* 1996, Cowling *et al.* 1997). The few multivariate vegetation-environment models that have explored the role of physical site factors have highlighted the importance of the physical and chemical soil characteristics in determining community boundaries. These models have, however, explained less than 50% of the compositional variation in species data with their environmental data sets (Richards *et al.* 1995, McDonald *et al.* 1996). The high percentage of unexplained floristic variation at both the landscape and community scales could be ascribed to deterministic processes associated with disturbance such as post-fire succession (Kruger 1987), high or low fire frequencies (van Wilgen 1981, Manders *et al.* 1996), seasonal fire effects (Bond 1984), or the impacts of alien plants (Holmes and Cowling 1997). Furthermore, stochastic processes associated with chaotic plant population dynamics (Bond *et al.* 1995) could also play an important role in influencing community composition. The importance of climatic effects on post-fire recruitment should also not be underestimated. Climatic conditions after fire influence recruitment. Patterns of recruitment of certain keystone species, such as overstorey proteas, can in turn influence community composition (Cowling and Gxaba 1990, Vlok 1996). This chapter explores the relative importance of the deterministic component of the disturbance regime in structuring the fynbos vegetation of the Cape of Good Hope Nature Reserve (CGHNR).

A study on the effects of the recent (< 30 years) fire history on the species composition of sandstone (heathland) communities in the Sydney region of Australia suggested that fire frequency may account for as much as 60% of the floristic variation and that both the time since the most recent fire and the length of intervals between fires produce significant effects on the species composition (Morrison *et al.* 1995, Cary and Morrison 1995). No similar study quantifying the importance of fire as a determinant of species composition has been undertaken in the fynbos. There is, however, much evidence to suggest that predictable (deterministic) changes in vegetation result from changes in fire regime and that recent fire history does play an important role in determining floristic patterns. Studies investigating the effect of fire on dominant Proteaceae in fynbos have shown that fire differentially influences species abundance patterns by causing local extinction and population explosions (Bond *et al.* 1984, van Wilgen and Viviers 1985, Cowling 1987). Fires result in different levels of recruitment as determined by a range of interacting density-independent and -dependent factors operating on different demographic parameters. Fire regimes have three interrelated components which can affect plant community composition: fire frequency, season of occurrence and intensity of burn.

Fire frequency is the number of fires experienced by a particular community within a given time period. Frequency studies have shown that fires at short intervals (< 6 years) eliminate longer-lived seed regenerating shrubs and hence reduce plant biomass (van Wilgen 1981). A recent study on the effects of proteoid overstories on species composition indicates that short interval fires not only eradicate the overstorey but also result in an increase in the basal coverage of understorey sprouters (Vlok 1996). This, in turn, results in a reduction in the number of non-sprouting species and an overall reduction in diversity of up to 50% (Vlok 1996). Autecological studies on rare, obligate seed-regenerating fynbos shrubs have indicated that repeated short intervals between fires would eliminate these slow maturing species (Boucher 1981, Moll and Gubb 1981, de Lange and Boucher 1993). Very long intervals (> 30 years) between fires may likewise eliminate the large seed regenerating shrubs due to high mortality and a lack of inter-fire recruitment (Bond 1980, van Wilgen 1981). Intermediate fire frequencies allow for the completion of all species life cycles and the post-fire regeneration of nearly all previously occurring species (van Wilgen 1981). Fire frequencies in fynbos are thought to have varied from anything between one in six, to one in 40 years under natural fire regimes in the past (Kruger 1979). Natural fires on the Cape Peninsula occur predominantly in summer and are fanned by strong SE winds. The study site is situated in the southern tip of the Cape Peninsula and is surrounded by sea except along its northern boundary. Only those fires started in the extreme south would have impacted this area and it is therefore likely that fire frequencies were always longer than the average for inland areas. At times during the last 30 years, fire management programmes aimed at maintaining species-richness have been artificially short (Appendix 1) and have probably resulted in changes in species composition in some parts of the reserve.

Related to fire frequency, and also of importance in determining community composition, is the role of time since the most recent fire. Fires drive succession in fynbos which is notable for a rapid initial recovery characterised by the dominance of fire ephemerals, perennial graminoid herbs and sprouting shrubs (Cowling and Pierce 1988, van Wilgen and Forsyth 1992). This is followed by a sequence of changes in dominance and the gradual loss of species with time. Immigration is not an important process until late in the succession when certain thicket species may be introduced by birds (Manders 1990). The stage in the succession at which a site is surveyed will therefore influence the composition of the vegetation and its position in a classification, or in ordination space.

The occurrence of fire in the fynbos of the winter-rainfall south-western Cape is most common during the dry summer months between November and February (Horne 1981). The flowering and seed set of the majority of species in this region is synchronised according to the probability of fires in this period, thereby ensuring maximum regeneration. Studies on the effects of season of burn on populations of fynbos Proteaceae with canopy-stored seed have shown that regeneration is most successful after autumn and summer fires, while many of the Proteaceae could be eliminated by successive winter or spring burns, owing to the cumulative effect of their decline in population size (Bond 1984, Bond *et al.* 1984, van Wilgen and Viviers 1985, Le Maitre 1987). Season of burn has also been shown to influence the regeneration success of woody sprouting species (Le Maitre *et al.* 1992), and non-sprouting Proteaceae with soil stored seeds (Le Maitre 1988a).

Very little is known about the response of fynbos plants to various fire intensities. However, it has been shown that regeneration of certain myrmecochorous species is strongly, positively related to local fire intensity and that managed fires under cool, moist, windless weather conditions have a detrimental effect on their regeneration (Bond *et al.* 1990). A high percentage of the fires recorded in the reserve's fire history were controlled burns undertaken outside of the natural fire season to reduce the threat of run-away fires. These unseasonal burns would also have been lower intensity fires and may have altered the natural composition of the vegetation in certain areas of the reserve.

Invasive alien trees have also impacted the natural vegetation of the reserve for many decades (Taylor *et al.* 1985, Taylor and Macdonald 1985). In 1966, alien trees were present in the vicinity of 92%, and occurred within 13%, of Taylor's original sample sites (Taylor *et al.* 1985). The density increased further and reached its peak in the late 1970's when an effective eradication programme was finally implemented (Macdonald *et al.* 1989). The major effect of these invasions on the natural flora is a reduction in species-richness by competitive exclusion and the disruption of nutrient cycling processes (Richardson *et al.* 1992, Musil and Midgley 1990, Musil 1993, Holmes and Cowling 1997). Different life forms have varying degrees of resistance to invasion. For example slow maturing, seed regenerating serotinous Proteaceae are particularly susceptible, while many sprouting species are better equipped to survive invasions. Recent research into the regeneration capabilities of fynbos shrublands following invasion by acacias showed that 70% of the flora disappeared following invasion for two or more fire cycles. However, even in these long invaded sites, persistent seed banks enabled many species to re-establish after clearing (Holmes and Cowling 1997). Aspects of this chapter explore the effects of long-term invasion by alien plants by quantifying the role of this disturbance phenomenon in contributing to contemporary vegetation pattern in the reserve.

The very thorough management records pertaining to fires and alien plant disturbance in the CGHNR provided an excellent opportunity for examining the role of recent disturbance effects in influencing the floristic composition of fynbos. In this chapter I use multivariate methods to explore the importance of the last 30-year history of fires and alien plant invasions in shaping the present composition of the vegetation in the reserve. In particular I wished to determine the importance of these disturbance factors as explanatory variables in comparison with the set of physical site factors used in Chapter 2.

The aims of this chapter were as follows:

1. To determine to what extent the disturbance regime (fire frequency, post-fire succession, fire season and alien disturbance), as against physical site factors (see Chapter 2) influence community pattern.

2. To achieve this by partitioning the variance in community patterns according to a) the physical site factors and b) the disturbance regime.

## Methods

### STUDY AREA AND SAMPLING METHODS

A detailed description of the study area, method of sampling and allocation of abundance values to species is given in Chapters 1 and 2. Only the 84 sites of Taylor (1969) which were accurately relocated were utilised in this study (Fig. 1.1).

### SAMPLING DESIGN

This study was based on non-manipulative methods and relied entirely on the grid intersect sampling approach of Taylor (1969) (Fig. 1.1). Sites were not specifically chosen to represent the range of past fire frequencies and seasons, nor the various classes of alien plant impact in the reserve. Better results may have been obtained had sufficient replicate sites been placed within the different classes of past fire and alien plant impact. However, the sampling design did provide a selection of sites with various fire and alien plant histories adequate for quantifying the relative importance of the physical, fire and alien components as determinants of vegetation pattern.

The sampling design assumed that the fire history prior to 1966 was randomised across all sites. Prior to the proclamation of the reserve, fires started by farmers and the earlier indigenous people were probably randomly distributed across the landscape. An active policy of prescribed burning was only implemented in 1975 (Anon. 1974, Macdonald *et al.* 1989).

### EXPLANATORY VARIABLES

An environmental data set including physical site variables, fire history and alien disturbance was compiled for the Cape of Good Hope Nature Reserve.

#### *Physical variables*

Environmental data were collected at each site and are described in full in Chapter 2 (Table 2.1). They covered topographical features (altitude, aspect, land facet, slope, solar load and influence of south east winds), soil characteristics relating to moisture-holding capacity (soil moisture, soil depth and rock cover) and soil characteristics relating to nutrient availability (underlying geology, soil colour and pH). For the sake of clarity in this study, these environmental variables will be defined as the physical site factors.

#### *Fire variables*

The fire history for the CGHNR was obtained from a Map Info (version 4.0) GIS database developed by reserve management and housed at the administrative offices. This database contains a comprehensive record of the date and extent of all fires larger than 5 hectares that have occurred within the reserve since 1975. Taylor's original site record sheets included information on the age of the vegetation in 1966, as well as records of fires which impacted sites during the subsequent five years. Using this information, I was able to reconstruct the fire history for all sites from the time of the fire prior to Taylor's (1969) original survey. This information is recorded in Appendix 1. The fire history for each site was then characterised in terms of frequency and season of burn. To summarise the fire frequency data the following were calculated for each site: time since the most recent fire, the shortest inter-fire interval, the mean inter-fire interval, the longest inter-fire interval and the standard deviation of the inter-fire interval. For analysing the role of season of burn, each fire was categorised into one of four seasons according to the month in which it burnt. The categories used were summer fires (November to February), autumn fires (March to May), winter fires (June to August) and spring fires (September to October). The sequence of seasons in which fire occurred was then documented for each site. The 84 sites could then be divided into eleven different sequences of season of burn (Table 3.1). These were entered into the analysis as nominal environmental variables and transformed to dummy variables for the CCA analysis (ter Braak 1987).

### *Alien vegetation*

During both surveys, a record was made of the density of alien invasive trees occurring at each site. In 1996 a record was also made of the invasion history for the period between surveys. From this information it was possible to construct a simplified history of alien invasion for each site, including both present levels of invasion as well as the impact of past invasions (Table 3.1).

**Table 3.1** Environmental variables used in analyses.

| Variable | Description and measure |
|---|---|
| **Physical variables** | see Table 2.1 |
| **Fire variables** | |
| *Fire frequency:* | |
| Age 66 | years since the most recent fire in 1966 (only used in the 1966 analysis) |
| Age 96 | years since the most recent fire in 1996 |
| Shortest interval | the shortest inter-fire interval since the fire prior to the 1966 survey |
| Mean interval | the mean inter-fire interval since the fire prior to the 1966 survey |
| Longest interval | the longest inter-fire interval since the fire prior to the 1966 survey |
| Std. dev. interval | the standard deviation of the inter-fire interval since the fire prior to the 1966 survey |
| *Fire season* | The sequence of seasons in which fires occurred at an individual site entered as dummy variables in the analysis. The dummy variables were: all fires in summer; all in winter; all in autumn; autumn followed by summer; autumn followed by winter; spring followed by winter; spring followed by autumn; winter followed by summer; autumn followed by winter and then summer; summer followed by autumn; and no fires. |
| **Alien vegetation** | the history of alien invasions at a site grouped into five categories as follows: 1 = never influenced by aliens; 2 = low to moderate densities of aliens on site (< 50% cover); 3 = dense aliens on site (>50 % cover); 4 = dense aliens cleared from site; 5 = low to moderate levels of aliens cleared from site. |

## DATA ANALYSIS

Initial analysis was undertaken on all 84 sites to determine the importance of the various components of the environmental data set at explaining the floristic variation at the landscape scale. The vegetation was then divided into three broad community types, the acidic proteoid group, the acidic restioid group, and the alkaline coastal communities (Table 3.2).

**Table 3.2** The simplified communities of the C.G.H.N.R. separated on the basis of pH and soil moisture (see Chapter 2 for details).

| **Simplified community** | **Member vegetation types (from Chapter 2)** | **Soil characteristics** |
|---|---|---|
| Restioid (28 sites) | Wet restioid fynbos, Wetlands | poorly-drained, sandstone-derived soils with low pH (<4) |
| Proteoid (51 sites) | Mesic oligotrophic proteoid fynbos, sedgeland | well-drained, leached sandstone-derived soils with low pH |
| Coastal (9 sites) | Sandplain proteoid, Dune asteraceous, Coastal scree asteraceous fynbos. | Sands of marine origin with higher pH (>6) |

The results of Chapter 2 indicated that soil pH and soil moisture were the major determinants of vegetation pattern in the C.G.H.N.R. The groupings in Table 3.2 were created to neutralise the importance of theses two variables, and to explore the effects of fire and aliens on vegetation pattern within each major community type. It was not possible to undertake the analysis on the coastal communities owing to its small sample size. The following analyses were therefore undertaken on the complete data set as well as on the restioid and proteoid communities separately.

*Canonical correspondence analysis (CCA)*

CCA was used to select the linear combination of environmental variables that explains most of the variation in the species score on each axis. Initially all the variables in Table 3.1 were included in the CCA analysis. Variables which showed high inflation factors (I.F. > 20) were later removed from the analyses owing to their collinearity with other variables (ter Braak 1988a). A Monte Carlo permutation test was used to test the significance of the eigenvalues of the axes (unrestricted, 99 permutations; ter Braak 1988a, 1990). A significant result indicates that the included environmental variables are sufficient to explain differences in vegetation. I used intra-set correlation to assess the importance of the individual environmental variables (see Chapter 2, ter Braak 1987, McDonald *et al.* 1996). The significance of each correlation was calculated using the *t*-statistic with a critical value of 1.96.

Forward selection of environmental variables was then used to derive the minimum set of variables that explain the species data almost as well as the full set (ter Braak 1990). This method enables one to sequentially select the variable that adds most to the explained variance of the species data. At each step, a Monte Carlo Permutation test was used to determine whether the variable selected was statistically significant in influencing the species data (ter Braak 1990). In this way it was possible to rank the environmental variables according to their importance in determining the species composition. Forward selection was also used to calculate the percentage variance in the species data explained by each significant environmental variable. I used CCA to derive a biplot of the sites and selected species together with the environmental factors. On the biplot, points represent individual species or sites, while arrows represent environmental variables. The length of the arrow is proportional to the magnitude of influence that the environmental variable has on community variation (ter Braak 1987). Only those variables that proved statistically significant in the forward selection procedure (Monte Carlo; 99 permutations) were projected onto the CCA biplot. All ordination analyses was done using CANOCO ver. 3.12 (ter Braak 1988a, 1990), while Graphpad Prism ver.1.03 was used for the graphical representation of biplots. A scaling factor was used to convert the sample scores to the same scale as the environmental variables. These factors differ for each analysis and are given in the individual figure captions.

### *Partial canonical correspondence analysis (PCCA)*

PCCA enables one to display the unimodal relationship between the species composition and the variables-of-interest (fire variables), after the effects of the covariables (physical site variables) are partialled out of the analysis (ter Braak 1988b). I used this method to determine whether the vegetation composition could be fully accounted for by the fire variables alone or whether the variation that remains after fitting the fire data is systematically related to the physical site variables. A Monte Carlo permutation test (99 unrestricted permutations) was used to test the significance of the variables of interest after the covariables had been partialled out. The PCCA was also used to determine what percentage of the total variance in vegetation data could be attributed to the physical site variables and what percentage of the remaining variation could be attributed to fire and alien disturbance.

### *Post-fire succession*

The 1996 species data set was not suitable for exploring the importance of successional effects as it included no sites in vegetation of < 4 years post-fire (Fig. 3.2). Hoffman *et al.*(1987) found no significant difference in terms of species-richness in similar lowland vegetation of 5 to 19 years post-fire age. Taylor's original (1966) species data set included a broader range of post-fire ages (Fig. 3.2). I used his data set to run a CCA, with forward selection, using the physical site variables and vegetation age as environmental variables. I then ran a partial CCA with the physical site variables as partial variables and the age in 1966 as the only variable of interest. A Monte Carlo permutation test (99 unrestricted permutations) was used to test the significance of post-fire age after the physical site variables were partialled out. In this way it was possible to ascertain how much of the variation in fynbos communities of various ages could be ascribed to post-fire successional effects alone.

## Results

### COMPLETE DATA SET OF 1996

### *Canonical correspondence analysis*

The complete data set, incorporating all environmental variables, produced eigenvalues of 0.64 and 0.48 for the first and second CCA axes respectively. The addition of the fire and alien disturbance variables had very little effect on the eigenvalues when compared with the results of the CCA analysis in Chapter 2 (axis 1, 0.6 and axis 2, 0.45). Similarly the percentage variance explained by the first two axes increased only very slightly. However, the total variance explained increased from 20.4 % when only the physical site variables were included to 38.8 % when fire and alien disturbance were included. The Monte Carlo permutation test of the F-ratios of the axis 1 eigenvalue and the trace statistic were both significant ($p < 0.05$) indicating that the complete set of environmental variables adequately explains the variation in species data. The highest coefficients, indicating the main determinants of the CCA axes, were, as in the previous analysis (Chapter 2), soil pH (axis 1, $r = 0.75$) and soil moisture (axis 2, $r = 0.76$). Other strongly correlated physical site variables were geological substrate ($r = 0.60$) on the first axis, and soil colour ($r = 0.34$) and depth ($r = 0.33$) on the second axis. The "minimum set" of environmental variables was dominated by physical site variables (Table 3.3). The only fire related variables of significance (both correlated with the first axis) were the mean interval between fires ($r = 0.59$) and the nominal variable, no fires ($r = 0.57$). The minimum set included the impact of alien disturbance which was significantly correlated with the first axis ($r = 0.49$); however, none of the fire season variables nor post-fire age was significant.

The first two axes of the species-environment biplot of the 84 sites and 10 significant environmental factors are shown in Fig. 3.1. The similarities among the samples are indicated by the spatial relationship of the coloured symbols, each of which represents a different community. The influence of the environmental variables is indicated by the length and direction of the arrows, the longer arrows indicating the more influential variables. The two significant fire frequency variables (no fire in record and the mean fire interval) both had a similar relationship with the floristic composition that was approximately equal in magnitude. They both relate to a gradient of increased fire-free periods and favour a group of species which include typical coastal species such as *Kedrostis nana*, *Cynanchum obtusifolium* and *Passerina paleacea* as well as thicket species such as *Sideroxylon inerme*, *Tarchonanthus camphoratus* and *Rhus glauca* (Fig. 3.1). These species were also correlated with an increased impact of alien plants. The species associated with short mean fire intervals include a number of sprouting graminoids such as *Mastersiella digitata*, *Restio filiformis* and *Willdenowia teres*, as well as short lived species of the genera *Roella*, *Thesium*, *Aspalathus* and *Selago*.

**Table 3.3** Eigenvalues and intra-set correlation's between the CCA axes and the 1996 vegetation data set of the Cape of Good Hope Nature Reserve (C.G.H.N.R.). The fire variables, shortest and longest interval between fire, were removed owing to multicollinearity with other variables. The minimum set of variables that explains the species data nearly as well as the full set are shown in italics. The variables are shown in order of extra fit, which is equivalent to the eigenvalue of a CCA, if the corresponding variable was the only one in a CCA analysis (ter Braak 1990).

| | **Axes** | | **Forward selection procedure rank** | **Percentage of explained variance** |
|---|---|---|---|---|
| | **1** | **2** | | |
| Eigenvalue | 0.64 | 0.48 | | |
| Cumulative percentage variance of: | | | | |
| i) species data | 4.9 | 8.6 | | |
| ii) species-environment relation | 12.6 | 22.1 | | |
| Environmental variables: | | | | |
| *Soil pH* | 0.75 | -0.21 | 1 | 9.2 |
| *Soil moisture* | -0.07 | 0.76 | 2 | 7.9 |
| *No fires* | 0.57 | 0.13 | 3 | 7.1 |
| *Soil depth* | 0.04 | 0.33 | 4 | 4.7 |
| *Alien disturbance* | 0.49 | 0.07 | 5 | 4.5 |
| *Influence of SE cloud* | 0.02 | -0.05 | NS | - |
| *Angle of slope* | 0.14 | -0.07 | 6 | 3.9 |
| *Mean interval between fires* | 0.59 | 0.15 | 7 | 3.7 |
| *Geological substrate* | 0.60 | 0.14 | 8 | 5.1 |
| *Soil colour* | -0.08 | 0.34 | 9 | 4.1 |
| Number of fires | -0.42 | 0.08 | NS | - |
| All fires in autumn | -0.10 | 0.33 | NS | - |
| Rock cover | 0.26 | -0.32 | NS | - |
| Solar radiation | -0.07 | 0.05 | NS | - |
| Summer followed by autumn fires | -0.01 | 0.19 | NS | - |
| Land facet | 0.08 | 0.09 | NS | - |
| Altitude | -0.21 | -0.05 | NS | - |
| Winter followed by summer fires | -0.01 | -0.06 | NS | - |
| Post-fire age | -0.43 | 0.12 | NS | - |
| All fires in summer | 0.04 | -0.26 | NS | - |
| Aspect | -0.38 | 0.13 | NS | - |
| Autumn, summer then winter fires | 0.07 | 0.02 | NS | - |
| Autumn followed by winter fires | -0.09 | 0.15 | NS | - |
| Spring followed by winter fires | -0.06 | -0.06 | NS | - |

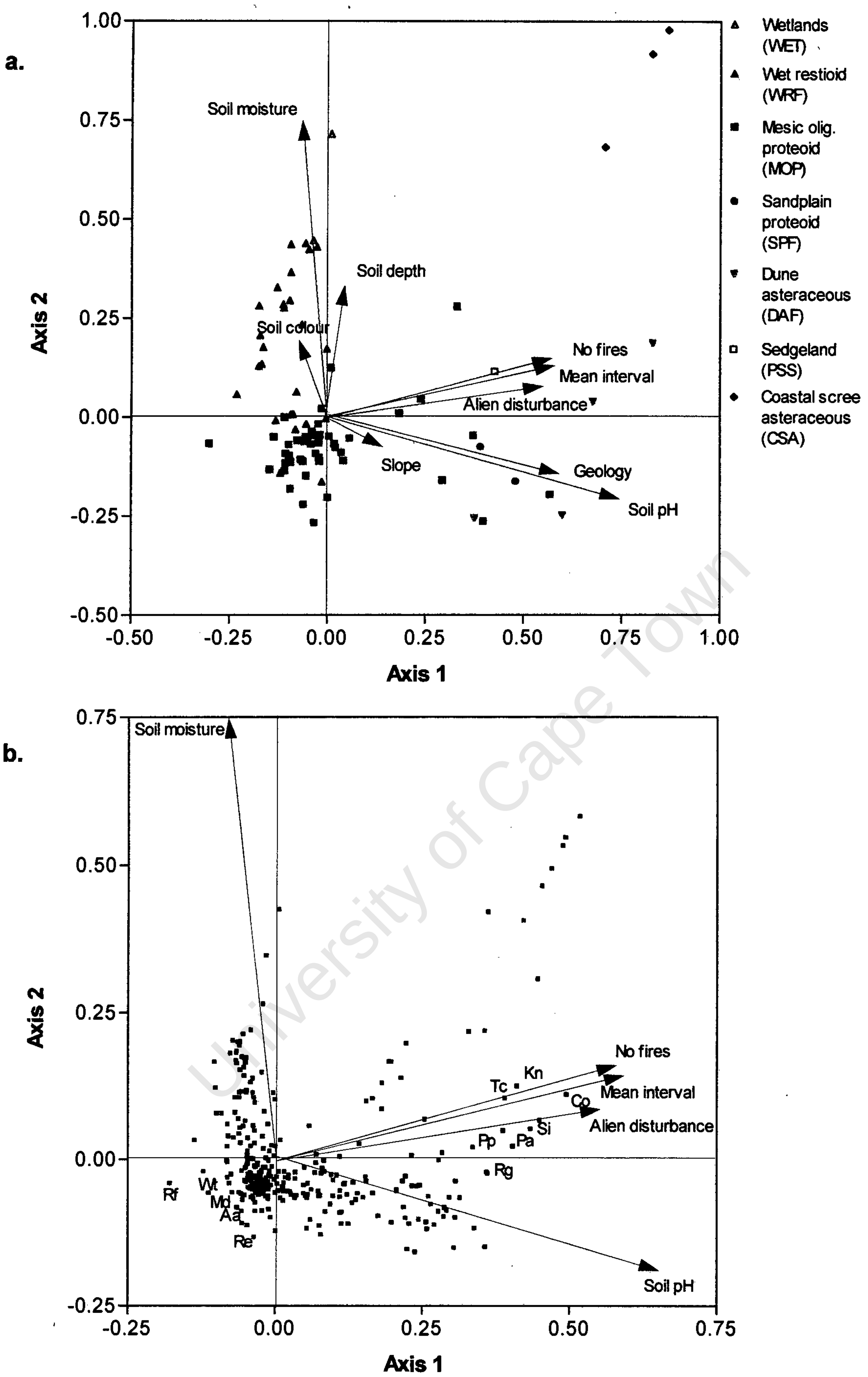

**Figure 3.1** CCA ordination of the first two axes of the complete 1996 data set. Arrows indicate direction and relative magnitude of the significant environmental gradients. Figure 3.1a is the sites - environmental variables biplot which shows the floristic similarities among the sites and their relationship to the significant environmental variables. Figure 3.1b is the species - environmental variable biplot (not all significant variables are displayed). Abbreviated species for reference in the text are as follows; Kn, *Kedrostis nana*; Tc, *Tarchonanthus camphoratus*; Co, *Cynanchum obtusifolium*; Si, *Sideroxylon inerme*; Pa, *Protasparagus aethiopicus*; Rg, *Rhus glauca*; Pp, *Passerina paleacea*; Wt, *Willdenowia teres*; Md, *Mastersiella digitata*; Rf, *Restio filiformis*; Aa, *Aspalathus abietina* and Re *Restio egregius*. A scaling factor of 0.193 was used to convert sample and site scores to the same scale as environmental variables.

*Partial canonical correspondence analysis*

**Table 3.4** Eigenvalues and percentage variance explained by the effects of fire and alien disturbance on the 1996 vegetation dataset of the Cape of Good Hope Nature Reserve (C.G.H.N.R.) after the role of the physical site variables have been partialled out of the analysis.

| | **Axis**<br>**1** | <br>**2** | **% variance in species data** |
|---|---|---|---|
| Eigenvalues when: | | | |
| i) all environmental variables are included | 0.64 | 0.48 | |
| ii) physical site variables are partialled out | 0.36 | 0.28 | |
| Percentage of total inertia explained by: | | | |
| i) all environmental variables | | | 38.8 |
| ii) covariables (physical site variables) | | | 21.0 |
| iii) fire variables | | | 15.9 |
| iv) alien disturbance | | | 1.8 |

The fire variables, shortest and longest interval between fire were removed owing to their collinearity with other variables. The complete set of environmental variables explained 38.8% of the variance in the species composition across the whole reserve. Twenty one percent of this variance could be attributed to the physical site variables, 15.9% to the effects of recent fire and only 1.8% to the impact of alien infestations. Both the Monte Carlo permutation tests (99 unrestricted permutations) on the first eigenvalue and trace statistic were non-significant (P>0.05) indicating that the variation in species composition that remains after fitting the physical site variables is not significantly related to the fire variables and/or alien disturbance.

### POST-FIRE SUCCESSION IN 1966

It is clear from the above results that the post-fire age was not an important factor in influencing the vegetation patterns at the landscape scale in the 1996 data set. This could possibly be attributed to the lack of sites in young vegetation in the 1996 survey (Fig. 3.2). I therefore used the 1966 data set which included a better range of post-fire ages to explore the importance of this factor in influencing fynbos plant communities.

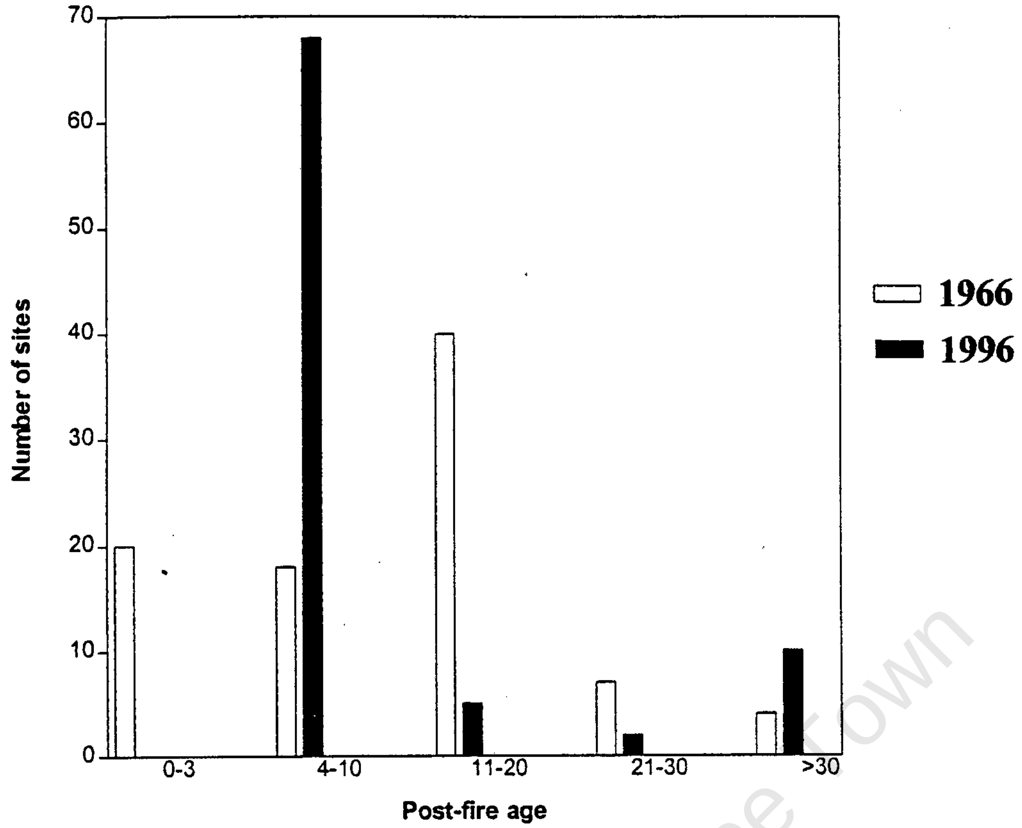

**Figure 3.2** The frequency of sites in the various post-fire age categories in the 1966 and 1996 data set (n=84 sites).

*Canonical correspondence analysis*

The eigenvalues of 0.69 and 0.47 for the first two axes of the CCA on the 1966 data set were higher than for the 1996 data set indicating that the same physical site variables better explained the species data in 1966 than in 1996. A Monte Carlo permutation test of the F-ratios of the axis 1 eigenvalue and the trace statistic showed both to be significant ($P<0.05$). The forward selection analysis of the 1966 data set revealed that post-fire age was the variable that added most to the explained variance of the species data and was most significantly correlated with the primary CCA axis ($r=0.79$) (Table 3.5). In this data set, differences in post-fire ages were a more important variable than either soil pH or soil moisture in influencing species patterns in the vegetation of the reserve. The ranking and correlation coefficients for the physical site variables tended to be quite similar to that observed for the 1996 data set. The group of species associated with long post-fire intervals include a number of thicket species such as *Sideroxylon inerme, Tarchonanthus camphoratus*, *Cassine maritima*, *Olea capensis*, *Rhus laevigata* and *R. glauca*, typical coastal species such as *Passerina paleacea*, *Geranium incanum* and *Eriocephalus africanus* and members of the Mesembryanthemaceae such as *Lampranthus stenus* and *Drosanthemum candens*. The species that show a notable relationship with the early post-fire stages include post-fire ephemerals such as *Selago serrata*, *Syncarpha gnaphaloides, Osteospermum polygaloides, Scabiosa africana* and *Roella recurvata*; relatively short lived shrubs such as *Aspalathus callosa*, *A. chenopoda*, *A. divaricata*, *A. ericifolia*, *A.laricifolia*, *A retroflexa*, *Oedera imbricata*, *Thesium strictum*, *T. carinatum* and *T. acuminatum* and certain sprouting species such as *Erica cerinthoides*, *Cryptadenia grandiflora* and *Knowltonia capensis*.

**Table 3.5** Eigenvalues and intra-set correlation's between the CCA axes and the 1966 vegetation data set of the Cape of Good Hope Nature Reserve (C.G.H.N.R.). All physical site variables as well as the post-fire age at the time of the survey were included as environmental variables. The minimum set of variables that explains the species data nearly as well as the full set are shown in italics. The variables are shown in order of extra fit, which is equivalent to the eigenvalue of a CCA, if the corresponding variable was the only one in a CCA analysis (ter Braak 1990).

| | **Axes** | | **Percentage of explained variance** |
|---|---|---|---|
| | **1** | **2** | |
| Eigenvalue | 0.69 | 0.47 | |
| Cumulative percentage variance of: | | | |
| i) species data | 5.4 | 9.2 | |
| ii) species-environment relation | 21.7 | 36.7 | |
| Environmental variables: | | | |
| *Post-fire age* | 0.79 | 0.38 | 20.9 |
| *Soil moisture* | 0.22 | 0.63 | 10.4 |
| *Soil pH* | 0.45 | -0.36 | 10.1 |
| *Altitude* | -0.26 | -0.05 | 10.1 |
| *Solar radiation* | -0.05 | -0.11 | 8.9 |
| *Influence of SE cloud* | -0.04 | -0.12 | 7.3 |
| *Soil colour* | 0.28 | 0.09 | 6.3 |
| *Soil depth* | 0.20 | -0.01 | 7.0 |
| Angle of slope | -0.03 | -0.07 | - |
| Geological substrate | 0.36 | -0.14 | - |
| Rock cover | 0.03 | -0.07 | - |
| Land facet | 0.18 | 0.13 | - |
| Aspect | -0.14 | 0.23 | - |

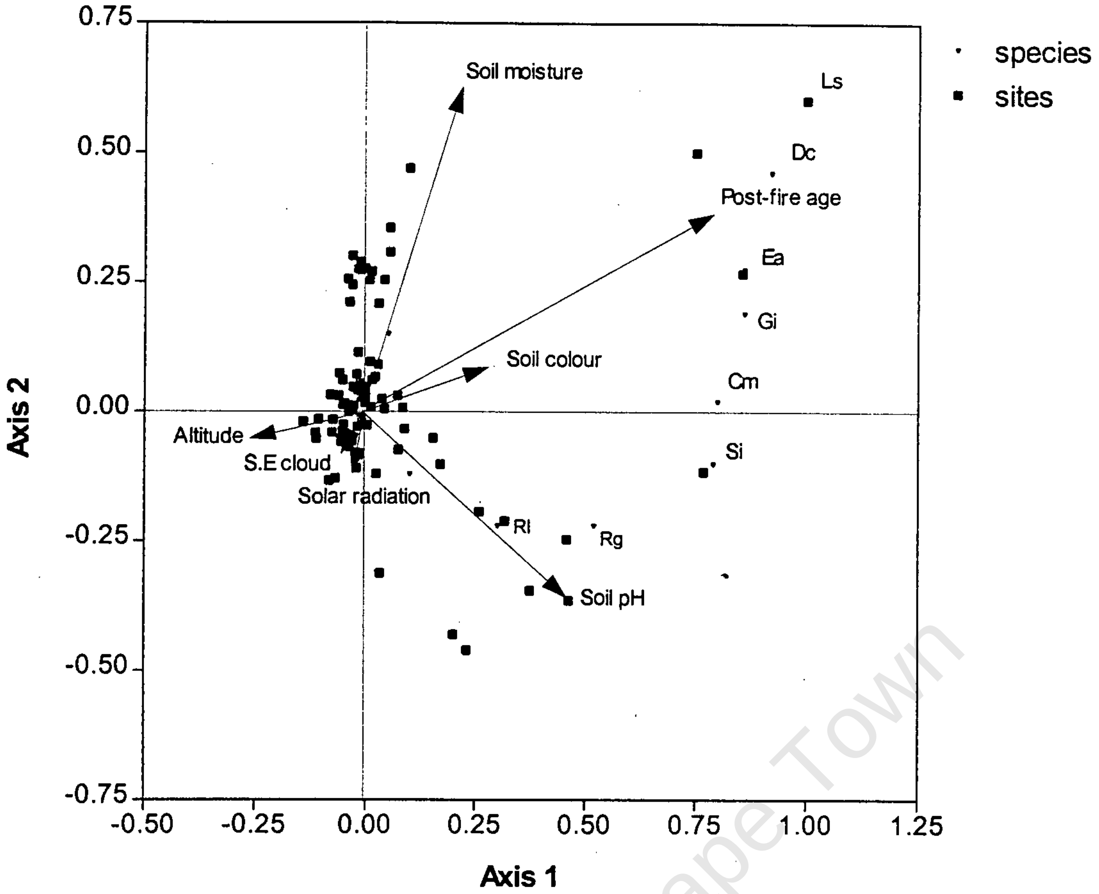

**Figure 3.3** CCA ordination of the first two axes of the complete 1966 data set. Arrows indicate direction and relative magnitude of the significant environmental gradients. Abbreviations for some of the species most common during the late stages of post-fire succession are Rl, *Rhus laevigata*; Rg, *Rhus glauca*; Si, *Sideroxylon inerme*; Cm, *Cassine maritima*; Gi, *Geranium incanum*; Ea, *Eriocephalus africanus*; Dc, *Drosanthemum candens* and Ls, *Lampranthus stenus*. A scaling factor of 0.153 was used to convert the sites to the same scale as the environmental variables.

*Partial canonical correspondence analysis*

**Table 3.6** Eigenvalues and percentage variance explained by the effects of post-fire age on the vegetation of the Cape of Good Hope Nature Reserve (C.G.H.N.R.) in 1966, after the role of physical site variables have been partialled out of the analysis.

| | **Axis** | | **Percentage of** |
|---|---|---|---|
| | **1** | **2** | **explained variance** |
| Eigenvalues when: | | | |
| i) all environmental variables are included | 0.69 | 0.47 | |
| ii) physical site variables are partialled out | 0.37 | 0.61 | |
| Percentage of total inertia explained by: | | | |
| i) all environmental variables | | | 25.0 |
| ii) covariables (physical site variables) | | | 22.1 |
| iii) post-fire age | | | 3.0 |

The post-fire age in 1966 comprised 18% of the explained and 3% of the total variance in the species data. This was considerably higher than its value as an explanatory variable in the 1996 data set where it only explained 4.8% of the explained variance and 1.0% of the total variance. A Monte Carlo permutation test revealed that post-fire age was significant in explaining the variance in the species data (p=0.01).

COMMUNITY ANALYSES OF 1996 DATASET

RESTIOID FYNBOS

*Canonical correspondence analysis*

In the restioid community, the complete set of environmental variables produced eigenvalues of 0.50 and 0.44 for the first two axes of the CCA. The only two significant variables in the forward selection procedure both related to the frequency of fire (Table 3.7). The shortest interval between fires added most to the explained variance of the species data and was the main determinant of the first CCA axes (r=0.64). The second most important variable was the number of fires recorded during the 30 year study period and was negatively correlated with the second axis (r=-0.32). A Monte Carlo test indicated that the complete set of environmental variables were insufficient (p>0.5) to significantly explain the variation in vegetation composition within the restioid community.

The biplot of the restioid data set revealed that the majority of sites are clustered together indicating the expected floristic similarity. The outliers in this community, sites 14, 47, 58 and 93 have all experienced an unusual sequence of recent fires. The vegetation of site 93 experienced a fire-free interval of 45 years before being burnt in an intense summer fire in 1991. Site 14 fell within a fire break tracer that was burnt every three years between 1970 and 1988, while sites 47 and 58 have been burnt twice in prescribed winter burns. The group of species favoured by longer fire intervals included *Calopsis membranacea*, *Ehrharta villosa*, *Leucospermum conocarpodendron* and *Oftia africana*. Species which were favoured in sites exposed to many fires include fast maturing grasses and sedges such as *Ehrharta ramosa, Ficinia indica* and *Tetraria sylvatica;* sprouting shrubs such as *Diosma hirsuta*, *Diospyros glabra*, *Erica cerinthoides*, *Leucadendron salignum* and *Protasparagus rubicundus;* and fast maturing shrublets such as *Osteospermum polygaloides* and *Senecio pubigerus*. The two most important physical site variables were geological substratum and soil colour. However, the additional effects of these variables were not significant on the species data. Although also non-significant, season of burn variables seem to have played a more influential role in structuring the restionaceous fynbos community than was the case for the full 1996 data set.

**Table 3.7** Eigenvalues and intra-set correlations of the first two axes for the restioid fynbos data set (1996). The physical site variables: solar radiation load, angle of slope, altitude and aspect, as well as the fire variables: all fires in summer, post-fire age and longest intervals between fires were excluded from the analysis owing to their collinearity with other variables. The variables are shown in order of extra fit, which is equivalent to the eigenvalue of a CCA, if the corresponding variable was the only one in a CCA analysis (ter Braak 1990). Only the first eight variables are displayed. The statistically significant variables are shown in italics.

| | **Axes** | | **Percentage of** |
|---|---|---|---|
| | **1** | **2** | **explained variance** |
| Eigenvalue | 0.50 | 0.44 | |
| Cumulative percentage variance of: | | | |
| i) species data | 9.4 | 17.7 | |
| ii) species-environment relation | 12.7 | 23.9 | |
| Environmental variables: | | | |
| *Shortest interval between fires* | 0.64 | 0.13 | 8.7 |
| *Number of fires* | -0.02 | -0.32 | 8.9 |
| Geological substratum | 0.21 | -0.17 | 6.4 |
| Soil colour | -0.35 | 0.47 | 5.9 |
| Summer followed by autumn fire | -0.02 | 0.18 | 6.4 |
| Spring followed by autumn fire | -0.07 | -0.06 | 5.9 |
| All autumn fires | -0.02 | 0.13 | 5.6 |
| Soil depth | -0.1 | 0.44 | 5.5 |

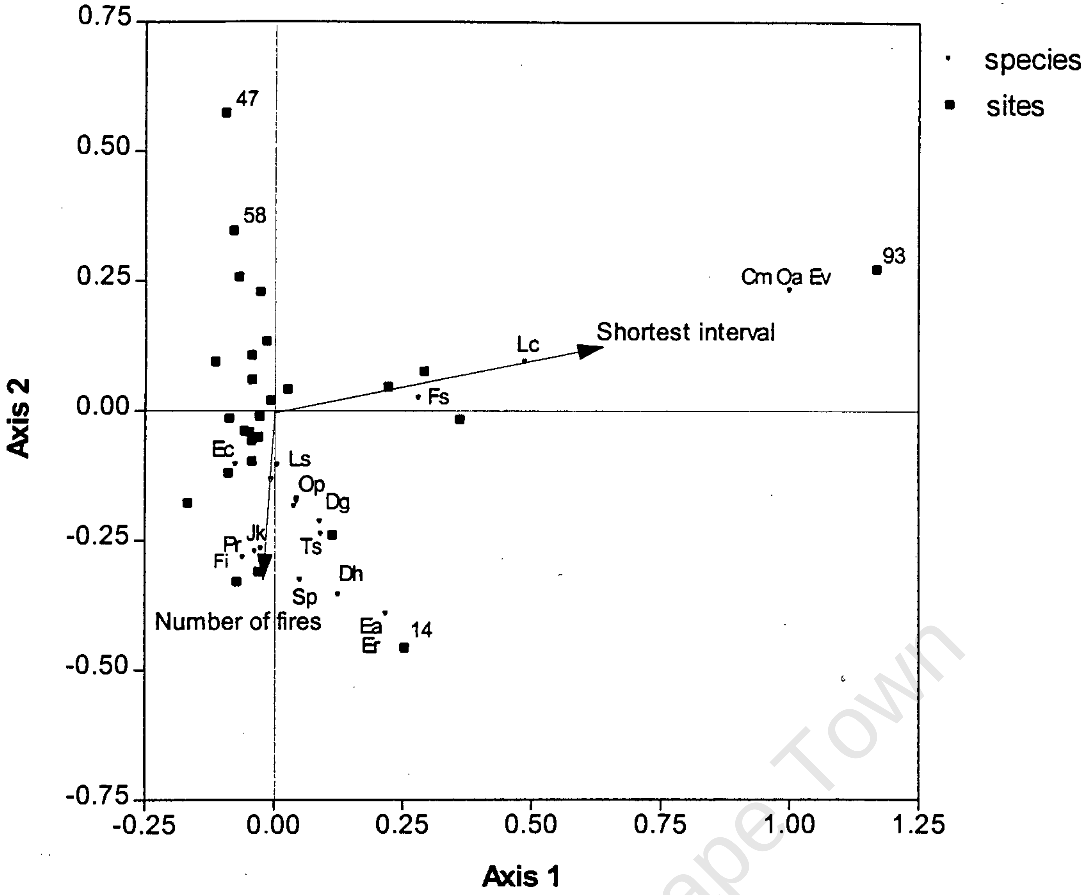

**Figure 3.4** CCA ordination of the first two axes of the restioid fynbos data set (1996). Arrows indicate direction and relative magnitude of the significant environmental gradients. Sites outside of the major cluster are numbered for reference in the text. The species favoured by not having experienced any very short inter-fire intervals are abbreviated for reference in the text as follows; Cm, *Calopsis membranacea*; Oa, *Oftia africana*; Ev, *Ehrharta villosa*; Lc, *Leucospermum conocarpodendron* and Fs, *Ficinia secunda*. Those species favoured by having been exposed to high fire frequencies include; Ec, *Erica cerinthoides*; Ls, *Leucadendron salignum*; Op, *Osteospermum polygaloides*; Dg, *Diospyros glabra*; Jk, *Juncus krausii*; Ts, *Tetraria sylvatica*; Pr, *Protasparagus rubicundus*; Fi, *Ficinia indica*; Sp, *Senecio pubigerus*; Dh, *Diosma hirsuta*; Ea, *Euryops abrotanifolius*; Er, *Ehrharta ramosa*. A scaling factor of 0.165 was used to convert the species and site scores to the same scale as the environmental variables.

*Partial canonical correspondence analysis.*

**Table 3.8** Eigenvalues and percentage variance explained by the effects of fire and alien disturbance on the vegetation of the restioid fynbos data set (1996), after the role of the physical site variables have been partialled out of the analysis. The physical site variables: solar radiation load, angle of the slope, altitude and aspect, as well as the fire variables: all fires in summer, post-fire age and longest intervals between fires were excluded from the analysis owing to their collinearity with other variables.

| | **Axis** | | **Percentage of** |
|---|---|---|---|
| | **1** | **2** | **explained variance** |
| Eigenvalues when: | | | |
| i) all environmental variables are included | 0.50 | 0.44 | |
| ii) physical site variables are partialled out | 0.43 | 0.32 | |
| Percentage of total inertia explained by: | | | |
| i) all environmental variables | | | 74.2 |
| ii) covariables (physical site variables) | | | 31.7 |
| iii) fire variables | | | 37.2 |
| iv) alien disturbance | | | 5.3 |

Within the restioid fynbos data set, the fire variables explain a higher percentage of the total variance in species data than the physical site variables. Together, the fire variables and impact of alien plants explain over 42 % of the variation, while the physical site variables explain only 32 %. The axis 1 eigenvalue and sum of all eigenvalues were however not significant ($p>0.05$) indicating that the fire variables alone are insufficient to statistically explain the variance in species data in the restioid fynbos.

*Canonical correspondence analysis*

The complete set of environmental variables produced eigenvalues of 0.51 and 0.43 for the first and second axes of the CCA. Soil depth was the most important determinant of floristic variation in the proteoid community, while soil pH and soil moisture were of less importance, only being ranked fourth and fifth amongst all environmental variables. The most important fire variable was the occurrence of no fires at a site, while the impact of alien plants was also important in structuring the species composition within this data set. The major determinants of the CCA axis 1 were geological substratum (r=0.60) and soil depth (r=0.59), while soil pH (r=0.47) and the impact of alien disturbance (r=0.45) also had high correlation coefficients. On axis 2, sites were dispersed along a gradient relating to a decrease in the number of recorded fires (r=-0.52), and an increase in the occurrence of sites not burnt since fire records were made (r=0.64). The physical site variables: soil depth (r=0.58), altitude (r=0.57) and rock cover (r=0.51) were also significantly correlated with axis 2. The fire variables, shortest, longest and mean interval between fires as well as the seasonal variable, all fires in summer, were removed owing to their collinearity with other variables. A Monte Carlo test indicated that the trace statistic (sum of all eigenvalues) was significant (P=0.01), but the first eigenvalue was not significant on its own.

The biplot of the proteoid data set consisted of 48 sites, the majority of which were grouped closely together on the central, left-hand side of the ordination space. This group corresponds well with the mesic oligotrophic community described as group A in Chapter 2 (Fig. 2.1). The rest of the sites, which are scattered to the right, across the ordination space, correspond with the anomalous mix of sites defined by the TWINSPAN analysis in Chapter 2 (Fig. 2.1; mesic oligotrophic proteoid group B). This group includes sites 74, 81, 89, 95, 99 and 100, which have not burnt for more than 30 years. All of these sites are situated towards the south of the reserve in areas that are likely to have had a long average fire cycle in the past. The group of species associated with these sites included the thicket species such as *Tarchonanthus camphoratus*, *Cassine peragua*, *Myrsine africana*, *Rhus glauca*, *R. lucida*, *Olea* *capensis* and *Pterocelastrus tricuspidatus.* Other species typical in this group included the shrubs *Polygala myrtifolia*, *Coleonema album*, *Erica coccinea*, *E. tristis*, *Crassula coccinea*, *Berkheya barbata*, *Phylica ericoides*, *Cineraria geifolia*, *Glia prolifera*, *Alciope tabularis*, *Phylica buxifolia* and *Diosma hirsuta* as well as the graminoids *Ficinia nigrescens*, *F. ramosissima*, *Pseudopentameris macrantha*, *Ehrharta calycina* and *Pentaschistis macrocalycina*. The floristic differences between sites 4, 86 and 92 and the main cluster of mesic oligotrophic proteoid sites was mainly the result of physical site determinants relating to their coastal affinity (high soil pH and soil depth) while the past impact of alien plants may also have been important. The last of the anomalous group was site 70 which was situated on an ecotone between acidic sandstone derived soils and calcareous, well drained aeolian dunes. It was therefore grouped into the mesic oligotrophic proteoid community on the basis of a few typical mesic oligotrophic proteoid species despite including a number of species with coastal affinities.

**Table 3.9** Eigenvalues and intra-set correlations of the first two axes for the proteoid fynbos data set (1996). The fire frequency variables: shortest, longest and mean interval between fires as well as the seasonal variable: all fires in summer, were removed owing to their multicollinearity with other variables. Only the minimum set of variables that explains the species data nearly as well as the full set is shown. The variables are shown in order of extra fit, which is equivalent to the eigenvalue of a CCA, if the corresponding variable was the only one in a CCA analysis (ter Braak 1990).

| | **Axes** | | **Percentage of** |
|---|---|---|---|
| | **1** | **2** | **explained variance** |
| Eigenvalue | 0.51 | 0.43 | |
| Cumulative percentage variance of: | | | |
| i) species data | 8.1 | 14.8 | |
| ii) species-environment relation | 12.6 | 23.2 | |
| Environmental variables: | | | |
| Soil depth | 0.59 | -0.58 | 9.2 |
| No fires | 0.37 | 0.64 | 9.0 |
| Alien disturbance | 0.45 | -0.33 | 6.0 |
| Soil pH | 0.47 | -0.18 | 5.2 |
| Soil moisture | 0.04 | -0.16 | 7.5 |
| Influence of SE cloud | 0.16 | 0.57 | 5.5 |
| Number of fires | -0.3 | -0.52 | 4.0 |
| Geological substrate | 0.60 | -0.14 | 4.5 |
| Post-fire age | -0.35 | -0.26 | 4.5 |
| Altitude | -0.09 | 0.57 | 4.0 |
| Rock cover | 0.18 | 0.51 | 3.7 |
| Angle of slope | 0.04 | 0.08 | 3.7 |

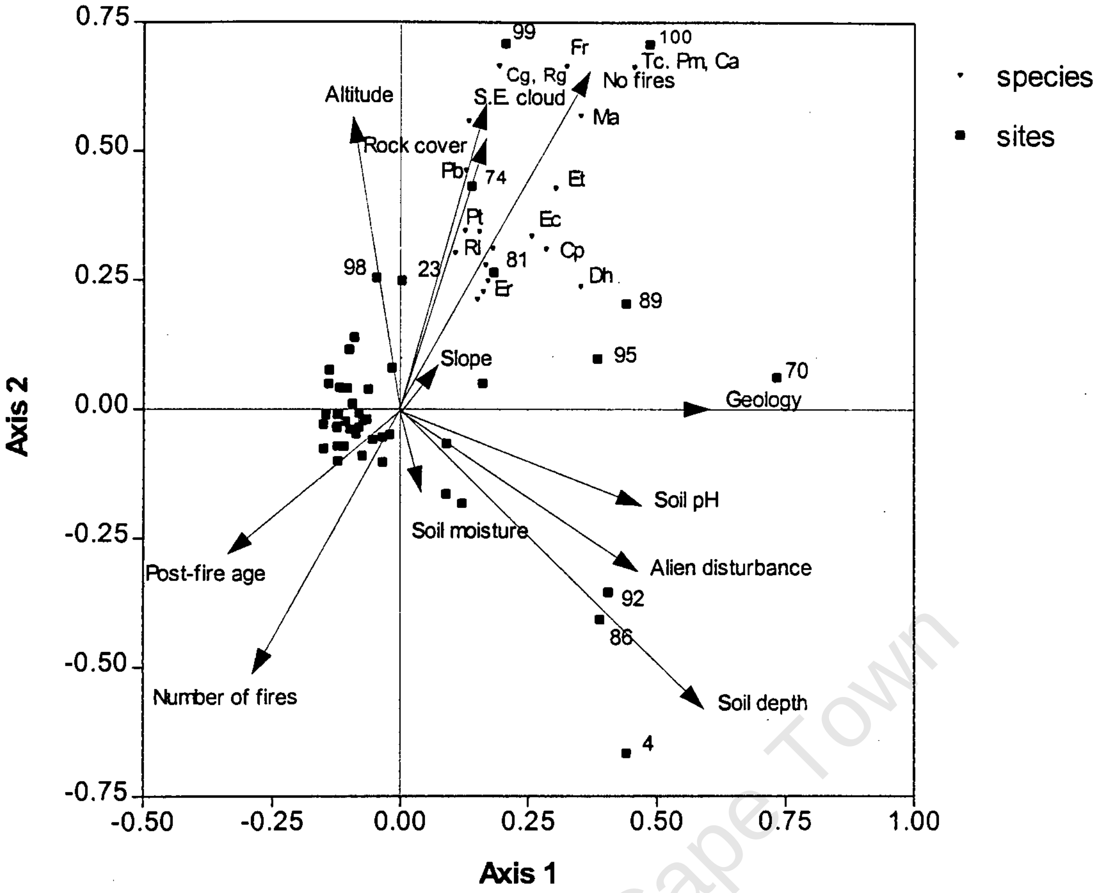

**Figure 3.5** CCA ordination of the first two axes of the proteoid fynbos data set (1996). Arrows indicate direction and relative magnitude of the significant environmental gradients. Sites outside of the major cluster are numbered for reference in the text. Species favoured by the variable no fires are abbreviated for reference in the text as follows; Tc, *Tarchonanthus camphoratus*; Pm, *Polygala myrtifolia*; Ca, *Coleonema album*; Fr, *Ficinia ramosissima*; Rg, *Rhus glauca*; Cg, *Cineraria geifolia*; Ma, *Myrsine africana*; Et, *Erica tristis*; Pb, *Phylica buxifolia*; Pt, *Pterocelastrus tricuspidatus*; Rl, *Rhus lucida*; Er, *Euclea racemosa*; Ec, *Ehrharta calycina*; Cp, *Cassine peragua* and Dh, *Diosma hirsuta*. A scaling factor of 0.181 was used to convert the species and site scores to the same scale as the environmental variables.

*Partial canonical correspondence analysis*

**Table 3.10** Eigenvalues and percentage variance explained by the effects of fire and alien disturbance on proteoid fynbos (1996), after the role of the physical site variables have been partialled out of the analysis. The fire variables, shortest and longest interval and all fires in summer were removed owing to their collinearity with other variables

| | **Axis**<br>**1** | <br>**2** | **Percentage of explained variance** |
|---|---|---|---|
| Eigenvalues when: | | | |
| i) all environmental variables are included | 0.52 | 0.43 | |
| ii) physical site variables are partialled out | 0.31 | 0.27 | |
| Percentage of total inertia explained by: | | | |
| i) all environmental variables | | | 65.5 |
| ii) covariables (physical site variables) | | | 38.4 |
| iii) fire variables | | | 23.4 |
| iv) alien disturbance | | | 3.8 |

The complete set of environmental variables explained 65.5% of the species variation in the proteoid fynbos data set. Of this 38.4% could be attributed to the physical site variables, 23.4% to the effects of recent fire and 3.8% to alien disturbance. While the Monte Carlo permutation test (99 unrestricted permutations) on the first eigenvalue proved non-significant ($P>0.05$), the trace statistic test was significant, suggesting that the variation in species composition that remains after fitting the physical site variables can be related to the fire variables and impact of alien disturbance.

## Discussion

The complex nature of the vegetation of the CGHNR is typical of fynbos landscapes with their high species diversity, and a large proportion of rare and localised species (Simmons 1996, see Chapter 4). The reserve's complexity was noted by Taylor (1984b) who suggested that, in addition to the variable physical environment, other factors such as past fires could be responsible for variation in vegetation structure. Recent multivariate vegetation-environment models in the fynbos have explained less than 50% of the variation in species data using physical site factors alone (Richards *et al.* 1995, McDonald *et al.* 1996). The unexplained variance has been attributed to stochastic processes such as endogenous population dynamics (Bond *et al.* 1995), local extinction (Chapter 4) and more predictable deterministic processes relating to post-fire successional patterns (Kruger 1987), fire season (Bond 1984) and frequency effects (Bond 1980), as well as the impact of past alien plant disturbance. This study provides a first attempt to quantify the importance of these deterministic disturbance related phenomena in explaining floristic variation in fynbos.

The inclusion of the deterministic parameters relating to the last 30 years disturbance regime approximately doubled the explanatory power of the multivariate model. At the landscape scale, the physical site factors accounted for about 55% of the explained floristic variation among all sites. The soil variables, pH and moisture, remained the major determinants of community boundaries despite the addition of the disturbance variables. This supports the findings of previous community-environment studies in fynbos which have invoked edaphic explanations for the major community divisions (Bond 1981, Taylor 1984b, Campbell 1986a, Cowling 1990). However, even at the landscape scale, about 45% of the explained variation in species data can be directly attributed to the effects of the recent (last 30 years) disturbance regime. At the community scale components of the disturbance regime became even more significant and were ranked as more important than most physical site variables. This supports the hypothesis that the recent fire history does affect floristic composition in fynbos vegetation (Cowling 1987). In the context of this thesis these results provide evidence of how species composition can differ considerably within environmentally similar sites and despite being constrained by well-defined physical site gradients.

Components of fire frequency proved more important than fire season as determinants of community structure at both the landscape and community scales in the 1996 dataset. The floristic changes brought about by fire suppression were greater than those caused by any of the other fire variables in the landscape-wide and proteoid community analyses. At the landscape scale much of this floristic differentiation could be attributed to the coastal sites, with their unique physical site characteristics (alkaline, well drained soils), also having lower fire frequencies. It could therefore be argued that the species in the coastal sites are constrained by the physical, in particular edaphic, characteristics of the site and their presence is not linked to fire frequencies. However, the multivariate analysis suggests that the presence of certain 'coastal' species is more a function of fire suppression than physical site constraints. Species generally associated with coastal communities, such as *Kedrostis nana*, *Cynanchum obtusifolium* and *Sideroxylon inerme,* showed a more notable positive relationship with long fire-free intervals than with any physical site variables. Further evidence for the overriding importance of long fire-free periods over physical site constraints came from the proteoid community. There, many of the thicket species associated with coastal communities in fynbos, such as *Euclea racemosa*, *Pterocelastrus tricuspidatus*, *Cassine peragua* and *Rhus* species, were common in fire suppressed sites where they were positively related to long fire-free intervals. For these species to colonise fynbos they require long fire-free intervals which allow for the development of perch sites and adequate time thereafter to reach a fire resistant size (Manders and Richardson 1992, Cowling *et al.* in press). The physical characteristics of a site would appear to be of less importance than the process of fire suppression in the establishment of thicket species in the reserve. It can be predicted from this that the long term absence of fire will result in colonisation of coastal and proteoid fynbos sites by thicket species. However, despite at least a 30 year (in some instances > 50 year) interval since the last fire, none of the sites in the proteoid fynbos community have formed fire resistant forest-nuclei (see Chapter 5 for more details). The colonisation of fynbos by thicket and forest species has a significant impact on species composition. Masson and Moll (1987) found that colonisation by forest and thicket species results in a reduction in fynbos species and may eventually lead to changes in the nature of the community from fynbos into forest. In this study, even the oldest proteoid fynbos sites still include characteristic fynbos species, some of which are not found elsewhere in the study area. Some of these species are able to persist owing to their longevity, such as *Phylica buxifolia, Erica coccinea* and *E. tristis,* while others are not dependent on fire for recruitment and instead recruit in the gaps formed by the mortality of other species between fires (e.g. *Polygala myrtifolia* and *Cineraria geifolia*). From the results of this study it is evident that the process of succession of fynbos into thicket in the reserve requires fire-free intervals in the order of centuries rather than decades. However, long fire-free intervals do result in a reduction in species diversity and the dominance of a different guild of species. Some of these species such as *Erica tristis* and *Tarchonanthus camphoratus* are not merely a function of post-fire age, but are only found in the sites which because of their physical setting at the southern tip of a peninsula have experienced a longer fire-free interval in the past.

A study into the post-fire succession of fynbos at Pella, a lowland site environmentally similar to the lowlands of the CGHNR, demonstrated little change in species composition in vegetation of 5 to 19 years post-fire age (Hoffman *et al.* 1987). They suggested that growth in dry lowland sites is slow and that suppression of understorey species probably only starts after about 30 years. This is supported by the multivariate analysis of the 1996 species data of the reserve in which, with the exception of the very old (> 30 year) sites, post-fire age was not an important cause of floristic variation. None of the sample sites in the 1996 survey had a post-fire age of less than four years. Large fires in 1986 and 1989 burnt the majority of the reserve and as a result most of the vegetation is of a similar age (Fig. 3.2). The 1966 data set provided a better spread of post-fire ages, including a number of young (< 4 years) sites, and demonstrated that succession can explain more variance in species data than any other environmental variables. This has important implications for vegetation-environment models in fynbos as much of the floristic differences within communities could be the result of successional affects. The selection of sites for vegetation surveys of this kind should therefore aim to use sites of equal age as well as uniform physical site conditions.

The proteoid community is characterised by a high number of species and its variability in physical habitat (Taylor 1984b). This community includes many rare and localised species which are habitat specialists (de Lange and Boucher 1993, Moll and Gubb 1981, Taylor

1984b). Despite reducing the importance of soil pH and moisture as environmental determinants, the physical site variables explained more of the variation in species data than recent fire history in the 1996 data set. This community occurs in the mountainous and most environmentally heterogeneous areas of the reserve. Subtle changes in the physical site parameters are responsible for much of the floristic changes. With the exception of the variation resulting from fire suppression, the recent fire history appears to have had little impact on the present composition of this community. This could be because there were no sites burnt on a short rotation and the majority of sites were burnt in summer fires. Consequently both fire season and frequency were not as important as they might have been had their been a better spread of fire histories. Analysis of the 1966 proteoid fynbos data set indicated that much of the variation in this community was a result of floristic differences brought about by stages in the post-fire succession. This result again demonstrates how the importance of individual components of the recent fire history can change with time.

The physical habitat of restioid fynbos is more uniform being characterised by level, poorly drained sites at low to moderate altitudes. This community has been exposed to the majority of prescribed burns in the reserve because of easier control and ease of access. These fires burnt out of the normal fire season, as well as at an abnormally short interval. It is therefore not surprising that 50% of the explained variance in this community could be attributed to the recent fire history. The frequency of fires, as well as the length of the shortest interval between fires, proved important determinants of vegetation pattern in this community. Graminoids, sprouting shrubs and annuals were favoured by frequent fires, while fire sensitive non-sprouters were lost from sites which experienced at least one short interval fire event in the last 30 years. Although not statistically significant, the season of burn also appears to have played more of a role in structuring the composition of some restioid sites. Those combinations of fire seasons which ended with an autumn burn appear to have had the most impact on the vegetation.

These results support the present policy of 'adaptive interference' fire control used in the CGHNR This system uses no formal prescribed burning and relies instead on the occurrence of wild fires to maintain species diversity and a variety of vegetation ages (Erntzen pers. comm.). Fires are only fought if they threaten infrastructure or burn in very young vegetation. Management should be aware of the fact that by its location the reserve's vegetation must be adapted to longer fire frequencies than for inland fynbos areas. The earlier formal fire management programme which was based on a ten year interval and used prescribed autumn or winter burns was undoubtedly detrimental to this vegetation. Every effort should be made to maintain these longer intervals, especially in the southern part of the reserve.

When compared with the role of recent fires, invasive alien trees have played a minor role in influencing vegetation composition in the reserve. Although they have significantly altered species composition both within the proteoid community and at the landscape scale, they have accounted for less than 2% of the variance in the vegetation in 1996. None of the original one hundred sites were located in densely infested areas as the only site situated in an *A. cyclops* thicket was discarded by Taylor at the time of his initial survey (Taylor 1984a). Since that survey a number of sites became infested and most of these were subsequently cleared. It would appear that few, if any, of these sites were densely infested and as a result the indigenous flora was able to recover after clearing. Recent research by Holmes and Cowling (1997) has shown that persistent seedbanks enable many fynbos species to recruit after clearing of Acacia stands. However, they also showed that the ability of fynbos to recover diminishes with the length of invasion time. *Acacia cyclops* does appear to have been associated with larger floristic changes in the coastal community and in the long unburned southern, proteoid sites. Much of the coastal vegetation was densely infested by alien plants in the last 30 years and certain areas have not yet fully recovered following clearing. This study could not quantify the impact of aliens on the coastal community owing to a shortage of samples (but see Chapter 5). In the southern areas of the reserve the sites have never been cleared and as a result some are quite densely invaded by *A. cyclops*. This species has similar life history attributes to indigenous thicket species. It is favoured by long fire-free intervals which allow for the development of perch sites as its seeds are also bird dispersed. Once established, *A. cyclops* is competitively superior to the indigenous species and its recruitment is favoured by fire. It has become a major threat to the unique indigenous flora of the southern reserve. However, with the exception of this southern area which has not yet been cleared, the results of this study indicate that the reserve's flora has not been seriously impacted by alien disturbance. This is a direct consequence of effective clearing operations which have prevented the development of dense stands and minimised lengths of invasion time.

Despite the addition of the disturbance parameters, the multivariate model still explained less than 50% of the compositional variation in species data. Further explanations therefore need to be sought to explain the high percentage of unexplained variance in species pattern in this study.

The 30 year history of disturbance does not explain underlying differences in vegetation composition caused by longer term patterns of disturbance. As an example, there is a pattern of increasing fire-free intervals with increasing latitude in the reserve (see Chapter 5, Fig. 5.8). Over a long period of time this would have resulted in the selection of suites of species favoured by longer intervals in the south and shorter intervals in the north. Similarly, topography influences the movement of fires resulting in certain areas being more fire-prone than others. The last 30 years fire record therefore does not explain the full impact of past fire patterns on vegetation structure.

The high percentage of unexplained variance can also be partly attributed to the sampling design, which was not specifically set up for exploring vegetation-environment relationships (e.g. Richards *et al.* 1995). A number of the sites were situated on ecotones between community types and consequently the physical variables often varied across individual sites. Ideally sites should have been situated in homogenous stands of vegetation with corresponding uniform environmental characteristics. Similarly, problems associated with sampling design were responsible for the low variance accounted for by the fire data. Morrison *et al.* (1995) accounted for 60% of the floristic variation in fire-prone, Australian communities with fire frequency alone, by specifically choosing samples with differing recent fire histories. In this study the variance explained by the recent fire history would have been higher had a reasonable sample of replicate sites been located within each variation of fire history and vegetation type. Instead the sampling design, based on the intersections of a grid across the reserve, resulted in a random assemblage of sites not suited to providing a true indication of the variance explained by physical site and disturbance variables. Nevertheless this study does provide useful information on the relative importance of the physical site and disturbance components in explaining variation in vegetation based on a random sample of sites distributed evenly over a fynbos landscape.

Finally, the low variance explained by the physical site factors and disturbance regime suggest that stochastic factors do play an important role in structuring fynbos communities. Stochastic factors which may contribute to the unexplained variance include the endogenous properties of species which have been shown to cause extreme population oscillations (Bond *et al.* 1995). These oscillations can in turn effect species composition, especially when overstorey Proteaceae are involved (Vlok 1996). Other stochastic events such as climatic conditions following fire or chance introductions by bird or wind dispersal result in local colonisation and extinction and thereby influence community composition.

## Conclusions

This study has demonstrated that at the landscape scale the disturbance regime is nearly as important as physical site factors in determining vegetation pattern in fynbos. Of the explained variance in species composition, nearly half could be attributed to recent disturbance effects, especially the impact of fires. Fire frequency, rather than season, proved the most important component of the fire regime. Long fire-free intervals in proteoid fynbos in the southern part of the reserve are important for the conservation of localised species. The development of thicket and forest from fynbos is a very slow process in this study area and takes longer than has been suggested for inland mountain fynbos. Stages in the post-fire succession play a very important role in determining species composition in fynbos. This study has demonstrated that in cases where vegetation of varying ages is sampled (especially where young vegetation is included), successional effects can play a more important role than any other variable in determining composition. Aspects of the disturbance regime have different influences on the various vegetation types, with short frequencies being most influential in restioid fynbos and long fire-free intervals being most important in proteoid fynbos. Despite having covered large areas of the reserve in the past, alien plants have only played a minor role in influencing vegetation composition.

Despite the inclusion of the disturbance regime into the multivariate model, more than half of the variance in species data at the landscape scale could not be accounted for. This emphasises the complexity of fynbos landscapes. A variety of stochastic phenomena could not be included in the model. These include the immediate post-fire climatic conditions which play an important role in structuring communities, as do biotic interactions and endogenous density dependent phenomena. Furthermore, many fynbos species appear to be unconstrained by physical site determinants. A high proportion of these are widely distributed but occur at low abundances. The next chapter explores the temporal stability of species and the characteristics of species prone to local extinction and colonisation.

# CHAPTER 4. Thirty years of change in the vegetation of the Cape of Good Hope Nature Reserve: a closer look at species resilience and local extinction.

## Abstract

The biological attributes, growth form, regeneration mode, dispersal mode, as well as abundance and geographic range of species, were determined for the flora of the Cape of Good Hope Nature Reserve. The temporal stability of fynbos species was explored by comparing changes in the geographic range and abundance of species surveyed 30 years apart in 1966 and 1996. The attributes of the species were then modelled against the probability of local extinction for each species calculated over the 30 year period using logistic regression analysis. The model tested for the relationship between the independent species attributes and the probability of local extinction as well as interactions between the species attributes. The model was used to determine a numerical estimate of the probability of a species with a specific set of attributes going locally extinct over a 30 year period. No significant change occurred in either the abundance or geographic range of dominant species during this period However, rare and range-restricted species proved prone to local extinction. The probability of extinction by 1996 of species which were rare in 1966 was 1.5 times greater than for those species which were common in 1966. The growth form of the species also significantly influenced its probability of extinction over the thirty-year period. Herbaceous species proved the most prone, while graminoids proved the least prone to extinction. The logistic model provides a first attempt in fynbos to predict the probability of extinction based on a species biological and demographic characteristics.

## Introduction

Fynbos-dominated landscapes in the Cape Floristic Region have exceptionally high plant diversity (Cowling *et al.* 1992). Resource managers are faced with the task of ensuring the maintenance of this high biodiversity. In the Cape of Good Hope Nature Reserve (C.G.H.N.R.) alone, 1073 species of vascular plants have been recorded (Fraser in press). Many of these species are extremely rare, occurring in small localised populations (Moll and Gubb 1981, de Lange and Boucher 1993), or widely dispersed but occurring at low densities (Simmons and Cowling 1996). Other species which are seemingly widely dispersed may be under greater threat than those that are obviously rare, owing to their temporal variability and higher probability of local extinction (Gaston 1994). Species which are common now may not always have been so, while previously common species may have become rarer. We have little understanding of how constant fynbos species are over time, how resilient they are to repeated disturbance, or what their probabilities of local extinction are over relatively short time periods (ca. 30 years).

Fire is the most important natural disturbance factor in fynbos and the major cause of changes in community composition (Bond *et al.* 1984). Each fire is a unique event that can differentially favour suites of species (Cowling 1987). The dynamics of fynbos ecosystems in relation to fire is currently best understood in the case of single fire events on members of dominant overstorey shrubs belonging to the family Proteaceae (Bond 1980, Bond *et al.* 1984). Research has shown that their post-burn densities can differ considerably from the pre-burn population size (Le Maitre 1988a). Fires at an interval shorter than required by a species to reach maturity (ca. 3-5 years) can result in local extinction (van Wilgen 1981), while excessively long fire-free intervals (>40 years) can result in senescence and post-fire population crashes (Bond 1980). Proteaceae populations have also been found to be sensitive to fire season (Bond 1984, Bond *et al.* 1984, Le Maitre 1988a&b). Winter and spring burns result in population declines, while autumn burns can cause substantial population increases (Bond 1984, van Wilgen and Viviers 1985). In addition to these exogenous causes of population oscillations, post-burn seedling densities have been found to be negatively correlated with pre-burn adult densities suggesting some form of endogenous control on post-fire recruitment levels (Le Maitre 1988b, Bond *et al.* 1995).

With the exception of a few autecological studies on high profile, often endangered species (Moll and Gubb 1981, Boucher 1981, Pierce and Cowling 1991, Musil 1991, Killian and Cowling 1992, de Lange and Boucher 1993), very little is known about the dynamics and resilience in relation to fire of non-proteoid fynbos species. Cowling and Gxaba (1990) as well as Vlok (1996) have shown that the composition and density of overstorey proteoid cover affects the understorey composition through the creation of spatially and temporally dynamic habitats which favour different species. Studies on secondary succession in fynbos have generally supported the initial floristic composition model (Egler 1954), with percentage similarity between pre-and post-fire vegetation ranging from 62% in coastal dune fynbos (Cowling and Pierce 1988), to 86% for mountain fynbos (Le Maitre 1987). However, considerably lower values ranging from 29% to 41% led Hoffman *et al.* (1987) and Musil and de Witt (1990) to suggest that a greater degree of sequential species replacement occurs in sandplain lowland fynbos.

While all of these studies have given insight into the temporal dynamics of fynbos following a single fire event, no long-term research has been carried out to explore the stability of communities and resilience to local extinction of species over a time span covering more than one fire. Information on the probability of species remaining at a site following a few fires, and the attributes which allow them to persist in vegetation subjected to frequent fire (e.g. Noble and Slayter 1980), is necessary for a better understanding of how management practices influence vegetation over time. Furthermore, the ability to predict the probability of a particular species becoming locally extinct would have great value to conservation, as it could provide a basis for identifying those species most in need of conservation interventions (Gaston 1994).

The aims of this chapter were as follows:

1. To determine the stability in composition of fynbos at the landscape scale over an interval incorporating a few fires.

2. To determine how constant species remain over time.

3. To determine the characteristics of the species that have a high tendency for local extinction.

I approached these objectives by comparing the species composition in the CGHNR in 1996 with that of 1966. In this way I explored whether 30 years of active management have significantly altered the composition of the reserve's vegetation.

## Methods

### STUDY AREA AND SAMPLING METHODS

A detailed description of the study area, method of sampling and allocation of abundance values to species appears in Chapter 1 and 2.

### COMPARING SPECIES DOMINANCE AT THE TWO SAMPLING TIMES

I tested the null hypothesis that there has been no change in the composition of the dominant species in the CGHNR over the last 30 years of active management. A complete species list for both the 1966 and 1996 surveys was compiled for the eighty-one most accurately relocated sites (see Fig. 1.1; sites 7, 77 and 95 were not used in this chapter). Only perennially identifiable species were used and nomenclature follows Arnold and De Wet (1993). Much attention was paid to ensuring accurate identification and correct nomenclature in both the 1966 and 1996 datasets. I explored changes in both the frequency and abundance of all species at the two sampling times. The frequency of a species was defined as the number of sites it occupied at a particular sampling time, while its abundance was calculated as the sum of the individual abundance values of all sites that the species occupied (for definition of abundance, see Chapter 2).

#### *A. Frequency*

The frequency of all species was ranked for each sampling time. To investigate shifts in dominance the ten most common species at each sampling time were ranked and compared using a Spearman's rank correlation test. To assess for overall stability in species composition, the relationship between species frequency in the 1966 survey, and frequency in the 1996 survey, was determined using correlation analysis (Pearson's coefficient for normally distributed data).

### *B. Abundance*

For each sampling time, I ranked species according to their abundance across all 81 sites. The ten most abundant species at each sampling time were ranked and compared using a Spearman's rank correlation test.

## MODELLING THE BIOLOGICAL ATTRIBUTES OF LOCAL EXTINCTION

There are three potential pathways that a species could have followed in the 30 years between the two surveys. Firstly, a species present within a site in 1966 may have remained there until present; in this case I defined the species as a stayer (1,1). Secondly, the species may have been lost from a site (local extinction); these species I defined as loser (1,0)'s. The third possibility is that a species might have colonised a site in which it was not present in 1966; in this case I defined it as a coloniser (0,1).

From a management perspective the most important pathway is that of local extinction (1,0). I attempted to characterise those species that have shown a high tendency for local extinction in the 30 years between studies. To do this I calculated the probability of local extinction $p(1,0)$ for each species present in 1966 using the equation:

$$p(1,0) = \frac{b_i}{n_{66i}}$$

where $b_i$ is the number of sites in which the species $i$ occurred in 1966 but was no longer observed in 1996, and $n_{66i}$ is the number of sites in which species $i$ occurred in

1966 (Appendix 2).

All the species were characterised according to their growth form, regeneration mode and dispersal mode. The placement of species into biological categories was based on data from Bond and Slingsby (1983), van Wilgen and Forsyth (1992), McDonald *et al.* (1995), Trinder-Smith (1995) and personal observations (Appendix 2). The growth forms, post-fire regeneration strategies and dispersal modes included in the modelling procedure are listed below.

Growth form (G)

1. Low shrub (< 1m)
2. Mid shrub (≥ 1m but < 2m)
3. Tall shrub (≥ 2m)
4. Graminoid
5. Herb (excludes annuals)
6. Geophyte

Regeneration mode (R)

1. non-sprouter
2. sprouter

Dispersal (D)

1. short distance (passive and ant)
2. long distance (wind and bird)

The relationship between abundance, range size and the probability of local extinction was explored. I defined the species according to their abundance as well as their range size using the quartile method of Gaston (1994). This is a discontinuous definition of rarity based on a cut-off of 25% of the recorded species in the 1966 data set.

Mean abundance (A)

Defined as the mean abundance of the species across all occupied sites.

1. Locally rare (25% with the lowest mean abundance)

2. Locally common (75% with the largest mean abundance).

The species defined as locally rare all had a mean abundance of approximately one. (< 5 individuals per 50 $m^2$; n = 103, 24.4% of the species).

Geographic range (GR)

Defined as the number of sites occupied by the species.

1. restricted (occurring only once in the dataset)
2. widespread (occurring more than once in the dataset)

This categorisation does not strictly follow the quartile method as 29% of the species occurred only once in the data set and were therefore defined as the restricted group. (n = 126, 29% of the species).

The list of all species, their biological attributes, abundances, geographic ranges and probability of local extinction is given in Appendix 2.

### *Chi-squared analysis*

I used two-way contingency tables to carry out a preliminary analysis of the relationship between the biological attributes of a species and its probability of local extinction. I divided the species into two groups, those with a probability of local extinction ($p(1,0)$) of greater than 50%, and those with a $p(1,0)$ of less than or equal to 50%. Chi-squared analysis was used to test for significant differences in the frequency of each biological trait within the two categories of local extinction. The statistical package Graphpad Instat was used for the analysis.

### *Generalised Linear Modelling*

Generalised linear modelling (GLIM) (McCullagh & Nelder 1983) was used for a logistic analysis in order to explore the relationship between the biological attributes of a species and its probability of local extinction. The statistical package GENSTAT (Payne 1987) was used for the modelling.

A statistical modelling approach as used in this study is considered superior to other methods such as two-way contingency tables, as it tests for interactions between the biological attributes as well as testing the effect of each attribute independently, in the presence of the others. This enhances the predictive power of the model (Trexler and Travis 1993, McDonald *et al.* 1995)

Model Selection

A hierarchy of models was fitted using a forward selection procedure. Starting with a base model containing only the constant, the biological attributes were added sequentially to the model. Attributes which did not significantly alter the models deviance were omitted (Crawley 1993), until the most parsimonious model was achieved (Trexler and Travis 1993). Initially the significance of the main effects of G, D, R, A and Ra was assessed. The model was then further revised to explore the role of interactions between the significant main effects.

## Results

### COMPARING SPECIES DOMINANCE AT THE TWO SAMPLING TIMES

A comparison of the species composition at the two sampling times revealed that there had been no significant change in the frequency (Table 5.1, $r_s = 0.816$, $P = 0.002$) or the abundance (Table 5.2, $r_s = 0.927$, $P = 0.0003$) of the dominant species over the 30 year interval between surveys. All species present in both surveys have remained relatively constant with regards their geographic range in the reserve (Fig. 5.1, $r = 0.868$, $P < 0.0001$). The dominant species had a high constancy and have tended to remain dominant over the 30 year interval covered by this study. The species which were locally restricted in the 1966 data set have tended to either remain rare, or were completely absent from the 1996 data set. Of the 429 recorded species in 1966, eighty nine (20%) were not recorded again in 1996. However, 59 of these were only found once, and eighty-two occurred in three or less sites in 1966. Sixty-seven (16.4%) of the 408 species recorded in the 1996 survey, were not present at the time of the initial survey. The majority of these were range-restricted species (only 4 were recorded in more than 3 sites).

**Table 5.1.** A ranked comparison of the 10 most frequently observed species in the 1966 and 1996 surveys.

| Rank 1966 | Species | Frequency 1966 | Rank 1996 | Species | Frequency 1996 |
|---|---|---|---|---|---|
| 1 | Ischyrolepis cincinnata | 59 | 1 | Ischyrolepis cincinnata | 55 |
| 1 | Thamnochortus lucens | 59 | 2 | Thamnochortus lucens | 54 |
| 3 | Elegia stipularis | 46 | 3 | Ischyrolepis capensis | 50 |
| 3 | Ischyrolepis capensis | 46 | 4 | Erica corifolia | 47 |
| 3 | Tetraria cuspidata | 46 | 4 | Erica imbricata | 47 |
| 6 | Struthiola ciliata | 43 | 6 | Struthiola ciliata | 44 |
| 7 | Phylica imberbis | 42 | 7 | Elegia stipularis | 43 |
| 8 | Erica imbricata | 40 | 8 | Tetraria cuspidata | 42 |
| 8 | Metalasia muricata | 40 | 9 | Metalasia muricata | 39 |
| 10 | Pentaschistis colorata | 38 | 10 | Leucadendron laureolum | 37 |
| 11 | Tetraria microstachys | 37 | 10 | Phylica imberbis | 37 |

**Table 5.2.** A ranked comparison of the 10 most abundant species in the 1966 and 1996 surveys.

| Species | Rank 1966 | Rank 1996 |
|---|---|---|
| Ischyrolepis cincinnata | 1 | 1 |
| Thamnochortus lucens | 2 | 2 |
| Elegia stipularis | 3 | 3 |
| Erica imbricata | 4 | 4 |
| Struthiola ciliata | 5 | 7 |
| Ischyrolepis capensis | 6 | 5 |
| Tetraria cuspidata | 7 | 9 |
| Salaxis axillaris | 8 | 6 |
| Phylica imberbis | 9 | 23 |
| Aristea africana | 10 | 19 |

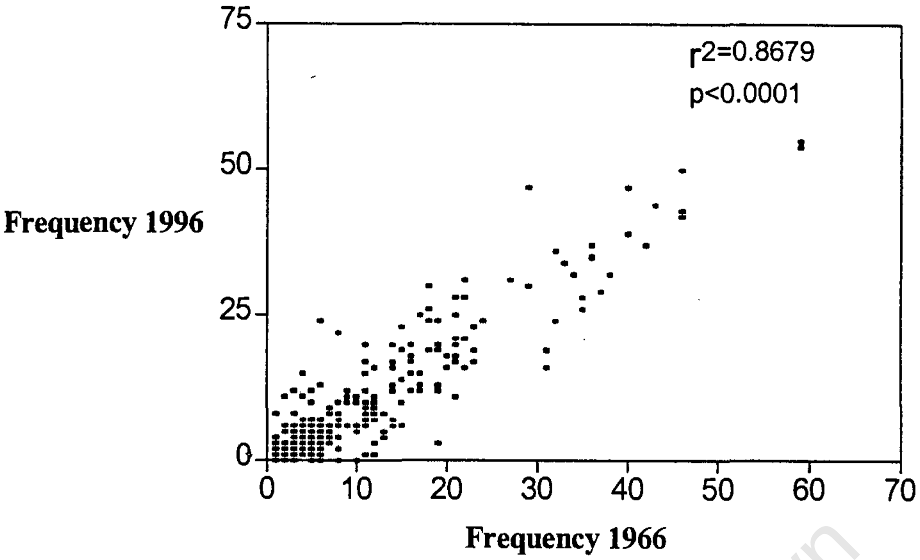

**Figure 5.1** The relationship between the geographic range (frequency) of all species recorded in both surveys.

MODELLING THE BIOLOGICAL ATTRIBUTES OF LOCAL EXTINCTION

*Chi-squared analysis*

The preliminary results obtained from $\chi^2$ analysis suggest that local extinction is a non-random process with respect to the biological attributes of a species (Fig.5.2). Growth form, regeneration mode, mean abundance and geographic range of a species all influence its probability of local extinction. Woody species and graminoids tended to have a low probability of extinction, while the herbaceous guild (herbs, geophytes and low shrubs) showed a higher tendency for extinction. Those species which are able to persist through fire by resprouting had a lower probability of local extinction than those which rely entirely on recruitment from seedlings. Abundant and widespread species also proved less susceptible to local extinction than rare and restricted species.

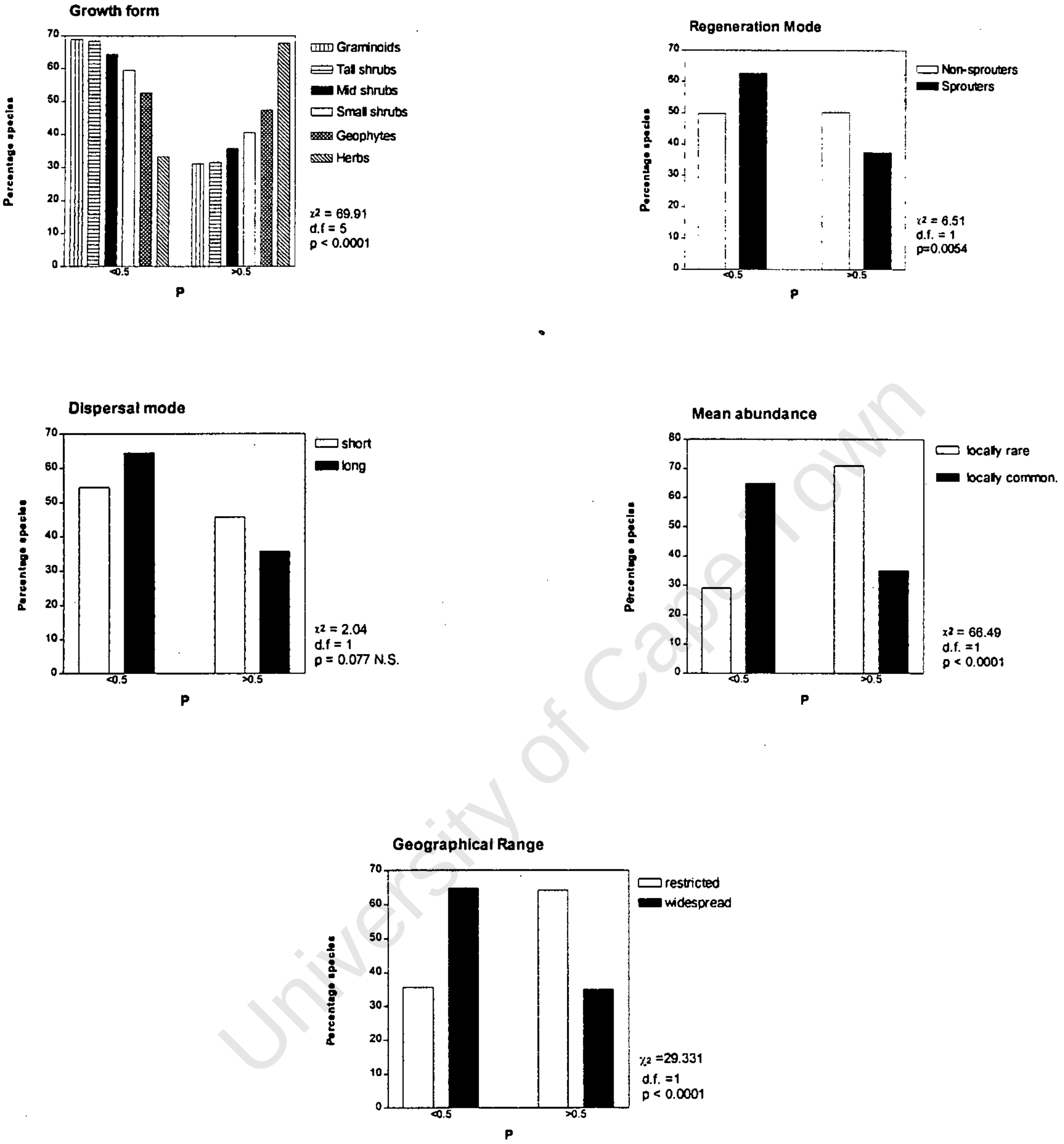

**Figure 5.2** The relationship between the biological attributes of species and their probability of local extinction (P). The percentage species was used for graphical representation, while count data were used for the contingency analysis.

Model selection.

Initially the significance of the main effects of G, R, D, A and Ra on the probability of local extinction $p(1,0)$ were assessed by examining the change in deviance when the main effects were added sequentially.

**Table 5.3** Analysis of deviance table for logistic regression with all the main effects included in the model.

| Models | Constan | Growth form | Regeneration mode | Dispersal mode | Abundance | Range | Deviance |
|---|---|---|---|---|---|---|---|
| 1. | √ | √ | | | | | 151.85* |
| 2. | √ | √ | √ | | | | 3.531 |
| 3. | √ | √ | √ | √ | | | 2.49 |
| 4. | √ | √ | √ | √ | √ | | 49.867* |
| 5. | √ | √ | √ | √ | | √ | 14.022* |

* $\chi^2 < 0.01$

The deviance is the change from the model immediately proceeding it. The deviance therefore represents the effect of the new factor, adjusted for all factors above it in the table. From these results it is evident that neither dispersal nor regeneration mode significantly influence a species probability of local extinction. Furthermore, it was not possible to include mean abundance and geographic range together in the model as this led to numerical instability. Mean abundance proved more significant than geographic range in influencing local extinction. This suggests a model using only growth form and abundance.

The basic assumption of logistic regression is that the distribution of b (where b is the number of sites in which the species occurred) is binomial. This implies that the variance of b for a given pattern = n × $\pi$ × (1-$\pi$), where $\pi$ is the probability of the given pattern. The data exhibited variation that was greater than this so we estimated the variation of b as $\Sigma^2 \times n \times \pi\ (1-\pi)$ which equalled 2.039. By including this parameter in the model most of the over-dispersion was accounted for, but the model still tended to underestimate the probability of extinction for small b and overestimate it for large b. The parameters for the model including growth form and abundance as well as the over-dispersion parameter are given in Table 5.4

**Table 5.4** Parameter estimates for a logistic regression with all growth form parameters and abundance included in the model.

| Model | Estimate | S.E. | t |
|---|---|---|---|
| Constant | -0.483 | 0.079 | -6.09* |
| medium shrubs | -0.169 | 0.194 | -0.87 |
| tall shrubs | -0.492 | 0.264 | -1.86 |
| graminoids | -0.339 | 0.086 | -3.96* |
| herbs | 0.362 | 0.074 | 4.86* |
| geophytes | -0.093 | 0.177 | -0.52 |
| abundance (common) | -0.452 | 0.075 | -6.04* |

t <0.05

There is some evidence for tall shrubs being kept in the model, although not quite attaining statistical significance at the 5% level. The parameter estimates for medium shrubs and geophytes are not significantly different from zero. This implies that the odds on local extinction for these growth forms are not significantly different from the odds on extinction of low shrubs. On removal of these parameters from the model, the deviance of the model only changed by 2.4 for 2 d.f., confirming their non-significance.

I then checked for the presence of interactions between the significant main effects (including tall shrubs), abundance and growth form.

**Table 5.5** Analysis of deviance table for logistic regression with the interactions of the significant main effects. (standard errors are based on a dispersion parameter with value 2.04)

| Model | Change in deviance | F |
|---|---|---|
| Constant +abund.+ tall shrubs + gram.+ herbs | | |
| + abund. x tall shrubs | 3.6 | 1.74 N.S. |
| + abund. x graminoids | 14.43 | 7.67 * |
| + abund. x herbs | 2.216 | 1.09 N.S. |

The only significant interaction term was abundance x graminoids. This interaction was retained in the final model. Tall shrubs, which were not quite significant as a main effect and non-significant as an interaction effect was therefore also removed from the model at this stage.

Final Model.

**Table 5.6** Analysis of deviance table for the final model. (standard errors are based on dispersion parameter with value 2.04).

| Model | Estimate | S.E. | t(*) |
|---|---|---|---|
| Constant | -0.5675 | 0.0787 | -7.21* |
| graminoids | -0.442 | 0.145 | 3.04* |
| herbs | 0.4241 | 0.072 | 5.91* |
| abundance (common) | -0.3978 | 0.077 | -5.17* |
| abundance (common) x graminoids | -0.787 | 0.163 | -4.83* |

* $t < 0.05$

Final model's fit.

The Pearson $\chi^2$ goodness of fit for the final model equalled 413.1 for 417 degrees of freedom, $P = 0.55$, indicating that the model fits the data well.

Below I calculated the probability of a species being absent in 1996 given that it was present in 1966 for all combinations of significant biological attributes. Table 5.7 also provides the odds ratio which is equal to the probability of being absent divided by the probability of being present in rare versus common species from the significant growth forms. Thirdly the table provides the odds on extinction of rare versus common species for the different growth forms.

**Table 5.7** The probabilities of extinction, odds on extinction of each growth form and comparison of odds on extinction of rare and common species in each growth form.

| Biological attributes | | Probability of extinction | Odds ratio | Comparison of odds on rare with common |
|---|---|---|---|---|
| rare | (not herb or graminoid) | 0.362 | 0.567 | 1.5* |
| common | (not herb or graminoid) | 0.276 | 0.381 | |
| rare | herb | 0.464 | 0.866 | 1.5 |
| common | herb | 0.368 | 0.582 | |
| rare | graminoid | 0.267 | 0.364 | 3.3 |
| common | graminoid | 0.100 | 0.111 | |

* indicates that there is a 1.5 times greater chance of a rare species which is not a herb or graminoid becoming extinct when compared with a common species which is neither a herb nor graminoid.

## INFERENCES MADE FROM THE MODEL

1. The seed dispersal distance of a species does not influence its probability of local extinction.

2. The regeneration mode does not significantly influence the probability of local extinction. However, while not statistically significant, sprouters appeared to have a lower probability of local extinction when compared with non-sprouters.

3. The growth forms defined in this study show significantly different probabilities of extinction. The odds on local extinction of herbs was 1.5 times greater than for shrubs and geophytes.

4. The mean abundance of the species on the landscape scale in 1966 influenced the probability of it being present in 1996. The odds on extinction of species from growth forms other than herbs or graminoids which were rare in 1966 was 1.5 times greater than for common species. Similarly, the odds on extinction of rare herbs was 1.5 times that of common herbs. The odds on extinction of rare graminoids was 3.3 times higher than for graminoid species which were common in 1966.

5. Species with large geographic ranges in 1966 had a lower probability of local extinction at the site-level than species which were geographically restricted. The numerical instability created by the inclusion of both abundance and range meant, however, that range was left out of the final model.

## Discussion

There have been no major shifts in the abundance or geographic range of the common species across all the sites enumerated in the Cape of Good Hope Nature Reserve (CGHNR) over the last 30 years. This stability in the rank of the common species indicates that management policies in the reserve have not resulted in any dramatic compositional shifts in the flora during this period. These results are in agreement with other studies which have shown that local assemblages are temporally predictable in species composition and rank abundance (Obeso 1992, Gaston 1994). The only other study of this kind in fynbos, which covered a six year interval, also demonstrated little change in the frequency and mean cover of the dominant species (van Wilgen and Kruger 1981).

While there has been substantial change in many of the individual sites (Chapter 5), the strong correlation between the frequency of species present at both sampling times suggests that the majority of species have remained relatively constant at the landscape scale. However, despite this significant temporal concordance, some species have shown changes: local extinction and colonisation have been common phenomena over the 30 year interval. Twenty percent of the species present in 1966 were not relocated in 1996, while fourteen percent of the species were recorded for the first time in 1996. The majority of these species were rare and had small geographic ranges. A common observation in studies of this type is that the changes in vegetation over time tend to be among the rarer species (Rogers 1983, Gaston 1994). In extremely rich vegetation types such as fynbos, the majority of species are sparse having low population sizes and patchy distributions (Rabinowitz 1981, Grubb 1986, Simmons 1996). It is chiefly within this group that the relatively large number of extinction and colonisation events were recorded. This high degree of temporal heterogeneity is an important factor contributing to the small-scale floristic complexity of fynbos communities (Cowling 1987) and contributes towards the high regional species-richness of the region (Simmons and Cowling 1996).

The process of local extinction shows distinctly non-random patterns with respect to the biological attributes of species. It could be deduced from the model that the abundance of a species in 1966 was the major factor determining its probability of local extinction by 1996. Species which were locally rare in 1966 had a 1.5X greater probability of local extinction by 1996 than species which were common. In the case of graminoid species the odds on local extinction of rare graminoids was three (3.3) times that of common graminoids. This supports the view that rare species tend to have a higher probability of local extinction than do more common ones (Gaston 1994). Great care was taken during the sampling phase of this study to ensure that rare species were not overlooked. This ensured that the observed pattern of greater probability of local extinction in rare plants was not a result of sampling error, but rather a consequence of demographic stochasticity.

The model showed that growth form plays a significant subordinate role in influencing extinction. Herbs have an increased probability and graminoids a lower probability of extinction when compared with shrubs and geophytes. The majority of herbs are relatively short lived and many are fire ephemerals which either regenerate from soil stored or widely dispersed seed after fire. Few species are able to resprout after fire and in order to remain at a site they require that their propagules germinate close to the parent plant, or alternatively be dispersed in from outside the site. Given the nature of the windy climate at the study site, together with the typically small, light and wind dispersed seed of the herbaceous group, it is not surprising that these species show a high tendency for local extinction. Their vulnerability to local extinction can also be explained in part by their position in the post-fire succession in fynbos (Bond *et al.*

1988). Studies in fynbos succession have generally shown that the herbaceous component is at its peak in the youth phase, one to five years post fire (Kruger and Bigalke 1984, Cowling and Pierce 1988, van Wilgen and Forsyth 1992). The number of sites with a post-fire age of less than five years was lower in the second survey than in the first (Chapter 3, Fig.3.2) and consequently a number of herbs had been lost from the regional species pool. This study showed that many herbs are sparsely distributed, short lived and temporally variable, making them a difficult group to monitor for management purposes. This also makes them unreliable as indicator species in vegetation classification studies.

The graminoids proved to be the least prone to local extinction. They are a diverse group which include species that are relatively short lived non-sprouters as well as persistent sprouters. Short interval disturbance, especially fire, has long been regarded as beneficial in promoting the graminoid component in fynbos (Trollope 1973, Cowling 1984). In the CGHNR there has been little change in the overall frequency of graminoids over the last 30 years (frequency 1966 = 1005, 1996 = 966). While graminoids as a whole proved the least prone to extinction, the model shows that the interaction between the graminoid growth form and abundance plays a role in determining the probability of local extinction. Common graminoids, especially the abundant Restionaceae such as *Elegia filacea* and *E. cuspidata*, proved to be highly stable over time, while species which were infrequent on a site were prone to extinction. This again emphasises the importance of abundance in influencing the probability of local extinction in species.

One of the determinants of species extinction is thought to relate to the probability of dispersal failure (Bond 1994, Gaston 1994). The probability of a species such as *Leucadendron laureolum*, which is a non-sprouter and dispersed by wind, remaining at a site is partly dependent on the strength of prevailing winds following fire (Cowling and Gxaba 1990). Strong winds can result in the movement of these species across the landscape and their loss from a particular site over time (see Chapter 5). In this study the dispersal ability of a species did not influence its probability of local extinction. This could be a sampling artefact resulting from two potential sources of error. Firstly, the dispersal mechanism was not well known for all species and some guesswork was required. Secondly, error could have arisen from the subjective splitting of dispersal ability, which is a continuous variable, into long and short dispersed species.

The lack of a clear relationship between regeneration mode and probability of local extinction is surprising. Bond (1989) developed a stochastic model of recruitment in serotinous Proteaceae based on the post-fire seedling to pre-fire parent ratios. He suggested that the probability of population extinction was high unless the mean ratio exceeded four seedlings per parent. Furthermore, the recruitment of non-sprouting shrubs is strongly influenced by fire regime, while sprouters are more resilient to variable fire regimes. Hence the probability of local extinction should be higher for non-sprouting species (Bond *et al.* 1984, Cowling and Lamont 1985). The lack of a clear relationship may have been as a result of the inclusion of facultative sprouters as sprouters, which might have had the same fate as non-sprouters given two or more fires over the last 30 years. Alternatively, if fires were rare over the 30 year period, it is unlikely that either life form would have been adversely affected. The net effect was a lack of a distinct pattern, with sprouters only showing a slightly lower probability of local extinction than non-sprouters.

## Conclusions

While there has been a stasis in the abundance and frequency of common species over the last 30 years, the rare and range-restricted species have proven more prone to local extinction and colonisation. Extinction-prone species proved not to be a random assemblage of plants. Herbaceous species were the most prone to local extinction, while graminoid species proved the least prone to extinction. There was also a significant interaction between the graminoid growth form and abundance, with rare graminoids having a far greater probability of extinction than common ones. In the context of this thesis, these findings demonstrate the temporally variable nature of many fynbos species. Rare and range-restricted species comprise the bulk of fynbos floras, and their high tendency for extinction and colonisation plays a major role in creating the spatially variable patterns which proved so difficult to explain in earlier chapters. Thus much of the turnover in fynbos systems can be explained by fire-induced demographic variation and successional processes amongst the rarer species. The next chapter takes a closer look at the causes of temporal change in species composition in fynbos.

# CHAPTER 5. Thirty years of change in the vegetation of the Cape of Good Hope Nature Reserve: A descriptive account

*"The ecological phenomena that we study often operate on temporal scales longer than our own existence and certainly longer than the time span of a research grant"*

*Wiens et al. (1986)*

## Abstract

This study used permanently marked sites, surveyed at a 30 year interval, to provide a descriptive account of the temporal change in the fynbos vegetation of the Cape of Good Hope Nature Reserve. Management records on fire history and alien plant invasions were used to examine the role of these factors in influencing vegetation change over this period. The study explored the role of post-fire age, fire frequency, intensity and season, as well as biotic interactions (competition from overstorey proteoids and alien plants) in influencing vegetation composition. The mean similarity in species composition between surveys was 62%, indicating an average of nearly 40% turnover in species over the 30 year period. The main causes of this change included sampling during different stages in the post-fire succession as well as the impacts of differential fire regimes (especially frequency effects). Competition from serotinous Proteaceae, which proved highly mobile after fire, as well as invasive Australian Acacias also impacted the composition of the vegetation over time. The study demonstrated that fynbos communities are temporally dynamic and that the changes over time in species composition are caused by a variety of processes. The study also provided evidence for the role of temporal diversity in contributing to the high species diversity in fynbos systems.

## Introduction

A major challenge facing vegetation scientists is to determine the resilience of communities, as well as individual species, to the varying components of the disturbance regime (Cowling 1987). Fire and invasion by alien plants are the major disturbance factors acting on the fynbos vegetation of the southern Cape Peninsula. For practical reasons studies on the effects of these disturbances on fynbos dynamics have always been temporally restricted. Studies on succession following fire have monitored recovery after a single fire event. Similarly, the impact of the various components of the fire regime on recruitment have looked at parent : seedling ratios at the same site following a single fire event (e.g. Bond 1980, Van Wilgen 1981, Hoffman *et al* 1987, Cowling and Gxaba 1990). These studies are limited as they base their results on single fire events. Most studies on the impact of alien plants on indigenous vegetation have compared adjacent invaded versus non-invaded sites (e.g. Richardson *et al.* 1989, Holmes and Cowling 1997, but see Richardson and Van Wilgen 1985 for an exception). There is always the problem with this approach that differences in stands may reflect pre-existing differences in the physical environment and not the effects of fire or alien plants per se.

While many studies on decade-scale vegetation change have been undertaken internationally (e.g. Fojt and Harding 1995, Rose *et al.* 1995, Minnich *et al.* 1995, Dodd *et al.* 1995) and some local research has explored long term changes in the semi-arid Karoo (Hoffman and Cowling 1990, O'Connor and Roux 1995), no work on medium-term temporal dynamics has been carried out in fynbos. Thus, while spatial patterns in the complex and diverse fynbos vegetation have been extensively researched over the last few decades (Taylor 1978, Kruger 1984, Campbell 1985, Cowling and Holmes 1992), no studies have explored the contribution of the temporal component to this complexity. Consequently little is known about the resilience of fynbos to change over time or how repeated disturbances influence patterns in vegetation distribution at the community and landscape scale. Chapter 3 of this thesis demonstrated the importance of the past disturbance regime as a determinant of contemporary vegetation pattern in fynbos. Chapter 4 showed that while common species have remained relatively constant at the landscape scale over the last 30 years, the rarer species have demonstrated a high probability for colonisation and extinction. This chapter explores community-scale resilience of fynbos vegetation in the Cape of Good Hope Nature Reserve (C.G.H.N.R.) to 30 years of variable disturbance, both natural and managed. I use mostly a descriptive approach to explore changes in the composition of permanent vegetation sites established in 1966 and attempt to invoke explanations for the observed change from historical fire and alien plant records.

This chapter provides a broad overview of a variety of aspects of fynbos dynamics by attempting to answer the following questions.

1. How much change has occurred in the vegetation of the reserve between 1966 and 1996?
2. How important is post-fire age as a determinant of species composition and diversity?
3. What effects have long fire-free intervals had on vegetation dynamics in upland and coastal fynbos?
4. What impact have unusually short and long fire frequencies had on vegetation composition?
5. What impact has high intensity fire following long fire-free intervals had on vegetation composition and structure?
6. How important has the seasonal component of the fire regime been in influencing vegetation composition?
7. What has been the dynamics of the common serotinous overstorey species *Leucadendron laureolum,* and what impact has it had on understorey species diversity?
8. How has the abundance and range of invasive alien plants changed over the last 30 years, and what effect have these changes had on the indigenous flora of the reserve?

## Methods

### STUDY AREA AND SAMPLING METHODS

The study area and method of sampling is fully explained in Chapters 1 and 2 of this thesis. Fig. 1.1 shows the location and numbers of all sites used in this chapter. Site numbering corresponds with that used by Taylor (1969 and 1984b). Eighty-one of the original 100 sites were sufficiently accurately relocated to be used in this study (sites 7, 77 and 85 were excluded). The location of these sites corresponds exactly with Taylor's original sites and the quadrats therefore covered the same 50 $m^2$.

All species present in each quadrat were noted with the exception of annuals and seasonally apparent geophytes, both of which were not perennially identifiable. Much effort went into ensuring that species were accurately identified, as this was crucial to achieving the objectives of this study. The nomenclature of all species was corrected according to Arnold and De Wet (1993). The original species lists of Taylor (1969) were used to assist with identification.

### MEASUREMENT OF ASSOCIATION BETWEEN SURVEYS

One of the simplest means of analysing floristic differences in vegetation over time is to look at the levels of similarity between samples. There are a variety of measures that can be used to calculate similarity or dissimilarity between sites. Two of the most widely used similarity indices are the Sorenson coefficient and the Jaccard coefficient. Generally, Sorenson's coefficient is preferred to the Jaccard coefficient because it gives weight to the species that are common to the samples rather than to those that occur in only one of the samples (Kent and Coker 1992).

I calculated the Sorenson coefficient of similarity for each site using the following equation:

$$S_s = \frac{(2 \times c)}{(a+b)} \quad X\ 100$$

where $S_s$ is the Sorenson coefficient as a percentage, *a* is the number of species present at a site in 1966, *b* is the number of species present at the same site in 1996 and *c* is the number of species present at both sampling times. This coefficient was used throughout this chapter to quantify temporal changes in species composition.

### DESCRIPTIVE ACCOUNT OF CHANGES IN VEGETATION

This chapter uses a descriptive approach to explore some of the interesting floristic changes and possible causative effects of change in the reserve over the last 30 years. I used a comparison of the two temporally separated species data sets and matched photographs to test some established hypotheses relating to determinants of vegetation dynamics and temporal change. I do not attempt to provide a detailed analysis of any aspect of fynbos dynamics nor to cover all the paired sites recorded in the reserve. Instead I use specific examples of sites which have undergone changes relating to recorded fire or alien plant impacts to emphasise the role of these factors in structuring the vegetation. At the beginning of each topic I briefly summarise the relevant literature and then compare the predicted changes with those found in this study.

## Results and Discussion

Of the 19 sites not used in this study, three were not resurveyed accurately enough, 12 were not found as a result of lack of permanent markers, two sites now fall outside the boundaries the reserve and two sites had been bulldozed for parking areas. The potential for extreme environmental change was graphically illustrated by site 43 occurring near Olifants Point on the western seaboard of the reserve. This site had to be excluded from the analyses as it has been inundated by mobile dune sands during the last 30 years (Fig. 5.1).

## MEASUREMENT OF ASSOCIATION BETWEEN SURVEYS

The 81 sites used in this study showed considerable variability in their similarity between the two surveys (Appendix 3). The mean similarity for all sites was 61.8±8.9%, while the lowest value was 43.8% and the highest 84.3%. The mean number of perennial species recorded in 1966 was 38.2±17.4 per site, the maximum was 79 and the minimum was six. In 1996 there were on average fewer species per site (35.6 ± 15.5). The maximum number of species in a quadrat was 66 and the minimum was again only six. The lower number of species recorded in 1996 was a result of the data set not including any sites younger than four years post-fire (Fig. 3.2): local diversity in fynbos peaks in the immediate post-fire years (Kruger 1983). In 1966 nearly 25% of the sites were in this age group and included many more early successional species.

## DESCRIPTIVE ACCOUNT OF CHANGES IN VEGETATION

### *Fire effects*

#### Post fire succession.

Post-fire succession in fynbos is noted for a rapid initial recovery resulting from the appearance of fire ephemerals, perennial graminoids, herbs and sprouting shrubs. Species diversity is greatest in the immediate post-fire environment and there is a marked decrease in species diversity as the cover of overstorey shrubs increase (Kruger 1987, Cowling and Pierce 1988, Cowling and Gxaba 1990). The rate of decline in the successional sequence differs between areas with different environmental conditions. Growth in dry lowland fynbos sites is generally slower than in moister mountain fynbos and suppression of understorey species is predicted to start later, probably only after 30 years (Hoffman *et al.* 1987).

**1966**

**1996**

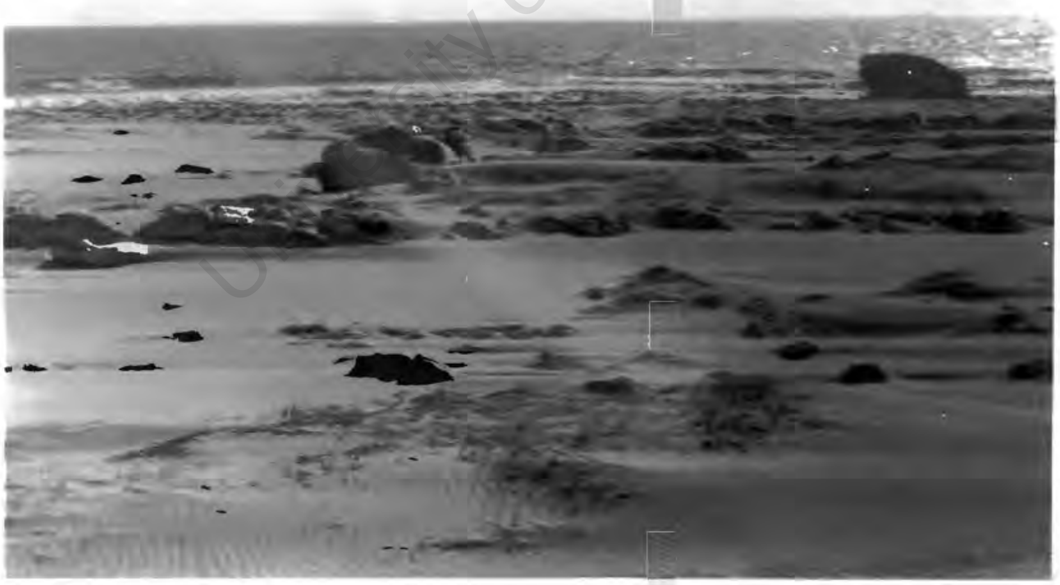

**Figure 5.1** Site 43 on the western seaboard near Olifantsbos Point. This coastal site was covered by asteraceous fynbos in 1966. Over the last 30 years the entire area has been inundated by shifting dune sands resulting in the local extinction of all species with the exception of the pioneer grass *Ehrharta villosa*. The wreck of the Thomas T. Tucker is visible in the background of both photographs.

I explored the rate of post fire succession for the reserve as a whole as well as the role of post-fire age in influencing species diversity and composition. By including the data sets for both surveys it was possible to examine the effect of the full spectrum of vegetation ages on species diversity. Differences in the successional sequence between communities complicates the trend and I therefore only include the fire-prone mesic oligotrophic proteoid community.

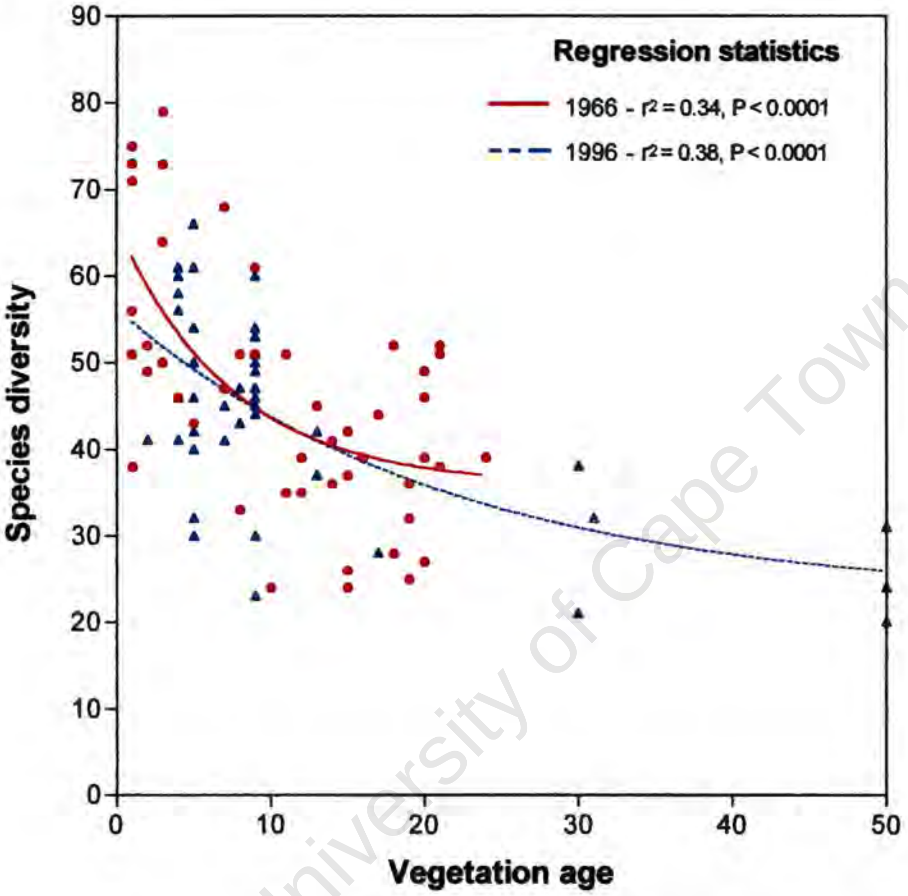

**Figure 5.2** The relationship between vegetation age and species diversity in 50 mesic oligotrophic proteoid sites at the two sampling times. Curves fitted using negative exponential equation.

There was a significant negative relationship between vegetation age and species diversity within this community (Fig. 5.2). The initial peak in species diversity was followed by a gradual decline over time. The significantly steeper negative slope of the 1966 data set (-1.19 ± 0.24 as against -0.54 ± 0.1; F = 5.97, df = 1, $P < 0.02$) resulted from the inclusion of a number of young sites (< 4 years post-fire) which had high species diversity. This suggests that there is a rapid decline from an initial post-fire peak and that the majority of post-fire ephemerals have seeded and died within four years after fire. Thereafter species are lost at a slower rate.

A. Early successional changes.

Fig. 5.2 illustrated the initial decline in species diversity during the first four years following fire. Site 15 provides a good opportunity for exploring the differences in vegetation composition between very young (<4 years) and slightly older vegetation (Fig. 5.3). In 1966 this site was only three years old and included 66 species, while in the nine year old vegetation in 1996 only 27 species were recorded. Despite only six years difference in the post-fire age at the two sampling times, successional effects have resulted in major compositional changes in this site between surveys ($S_s$ = 49.46%). Only four of the 27 species recorded in 1996 were new to this site suggesting that the compositional change which has occurred was as a direct result of losses due to successional effects. A look at the forty-three species lost from this site suggests that this is indeed the major cause of the observed changes. Species only recorded in the young phase in 1966 included a number of fire ephemerals in the genera *Aspalathus* (*A. abietina, A. linguiloba* and *A. retroflexa*), *Roella* (*R. ciliata* and *R. triflora*), *Selago* (*S. spuria*) and *Thesium* (*T. carinatum* and *T. acuminatum*) as well as the predominantly early succesional species such as *Edmondia sesamoides* and *Ursinia crithmifolia* (Asteraceae) and *Acrolophia lamellata* (Orchidaceae).

The stage in the post-fire succession of fynbos vegetation influences the composition and diversity of communities. This has important implications for ecologists developing community-environment models (see Chapters 2 and 3 for examples). Successional effects should, wherever possible, be partialled out by only sampling in similar-aged stands.

1966

1996

**Figure 5.3** Site 15 near Groot Rondevlei. This site has shown a marked decline in species diversity as a result of successional effects. The low, white flowering shrubs in the 1966 photograph (3 year post-fire) are the post-fire ephemeral *Edmondia sesamoides* which were not present in the older vegetation in 1996 (9 years post-fire). The 1966 vegetation is characterised by the visible dominance of the resprouting graminoid guild, whereas in the older 1996 vegetation the non-sprouting shrubs, *Leucadendron laureolum* and *Serruria villosa* are dominant. Note the invasion between surveys of the Witsands dune field (headland in the middle,background of the photograph) by the invasive alien, *Acacia cyclops*.

### B. Successional changes after long fire-free intervals in upland fynbos.

Fynbos is a fire type vegetation whose component species have a variety of fire-regeneration traits. Fire is an important process for the regeneration of many species and in its absence these species senesce and eventually die (Bond 1980, van Wilgen 1981). With long fire-free intervals species diversity declines but at the same time bird-dispersed species are introduced as perch sites develop (Manders and Richardson 1992, Cowling *et al.* in press). The late stages of fynbos succession are characterised by autogenic changes and follow the facilitation model of Connell and Slayter (1977). Seeds of forest and thicket species are dispersed into shrublands, and seedlings sometimes establish in mature fynbos communities, especially in sheltered sites. The slow-growing, colonising thicket species are usually knocked back by fire before thicket patches have developed sufficiently to exclude fires. However, where fire-free intervals exceed approximately fifty years, dense thickets form which eventually coalesce into closed-canopy vegetation that excludes fire (Manders *et al.* 1992, Richardson and van Wilgen 1985). In drier lowland fynbos the rate at which species senesce and thicket develops presumably takes longer than for wet mountain fynbos (Hoffman *et al.* 1987, Chapter 3). Five of the sites enumerated in 1966 had not burnt once at the time of the second survey (sites 74, 81, 95. 99 and 100). These provide an opportunity to determine the rate of senescence and thicket development in the relatively dry fynbos of the southern Cape Peninsula.

The mean of the Sorenson coefficient for these sites was 58.5 ±7%; the lowest value was for site 95 (46%) and the highest was for site 81 (66.7%). The diversity of all sites, with the exception of site 99 which remained constant, declined between surveys. I concentrate on two of these sites which have not burnt for more than fifty years (74, Fig. 5.4 and 81, Fig. 5.5). Both of these sites have similar habitat characteristics, being located on relatively steep slopes at approximately 90 metres above sea level and adjacent to the coast. However site 74 is situated on an east-facing slope above False Bay, while site 81 is located on a west-facing slope above the Atlantic Ocean. Site 74 is therefore exposed to the strong salt laden south-easterly winds during the summer months, while site 81 is more protected from wind but still exposed to strong north westerlies in winter. Both sites are characterised by the predicted late successional senescence and reduction in diversity. However, neither has experienced significant thicket development (Fig. 5.4 and 5.5). Both sites have lost several species, most of which are shorter lived non-sprouters such as *Anthospermum aethiopicum*, *Chironia baccifera*, *Erica mammosa*, *Leucospermum conocarpodendron* (a weak sprouter), *Metalasia muricata*, *Struthiola ciliata* and *Serruria villosa*. However, the species that have been lost from these sites also include some sprouting species such as *Adenandra villosa*, *Corymbium africanum*, *Erica cerinthoides* and *Liparia parva*. Therefore, a variety of species with different regeneration modes had a lifespan long enough to survive the initial twenty years without fire but were unable to survive for fifty years.

Even within the reserve, differences exist in the potential for, and rate of, thicket colonisation. The habitat of site 81 appears to be more suitable for the development of thicket than that of site 74. The thicket species, *Euclea racemosa*, *Myrsine africana*, *Olea capensis*, *Rhus lucida* and *R. laevigata* were already present at this site in 1966, while site 74 supported no thicket species. The better early colonisation of site 81 is probably a result of its taller structure, thereby providing more perch sites, and its peripheral location to the existing thicket at Gifkommetjie. Since the initial survey, neither site has demonstrated a notable increase in thicket species. The bird-dispersed *Rhus lucida* and *Pterocelastrus tricuspidatus* colonised sites 74 and 81 respectively. *Erica tristis*, a tree erica associated with fire-free sites, colonised site 81. The few other species which have colonised the sites are mostly small wind dispersed shrubs and graminoids. There has been a small increase in the number of individuals of thicket species present at site 81, but they have shown virtually no increase in relative dominance over the last 30 years. After 30 years *Olea capensis* is still only present as suppressed seedlings, while seven of the nine *Euclea racemosa* individuals are also seedlings or suppressed saplings.

The physical environment of the southern Cape Peninsula appears unsuitable for the relatively rapid development of thicket or forest. Thicket colonisation in this area is an extremely slow process which under favourable conditions appears to require fire-free intervals in the order of centuries rather than decades. Even under the long natural fire regimes of the past, the vegetation of the mountainous southern reserve comprised an assemblage of longer-lived fynbos plants, rather than a thicket community.

**1966**

**1996**

**Figure 5.4** Site 74, oligotrophic proteoid fynbos on the southern slopes of Paulsberg overlooking False Bay. This site is exposed to strong south east winds during the dry summer months. This vegetation was at least 20 years old in 1966 and has not been burnt between surveys. There has been very little change in species composition or structure over the last 30 years. While there has been some senescence among both the sprouting and non-sprouting species, there has been no colonisation by thicket species despite fifty years without fire.

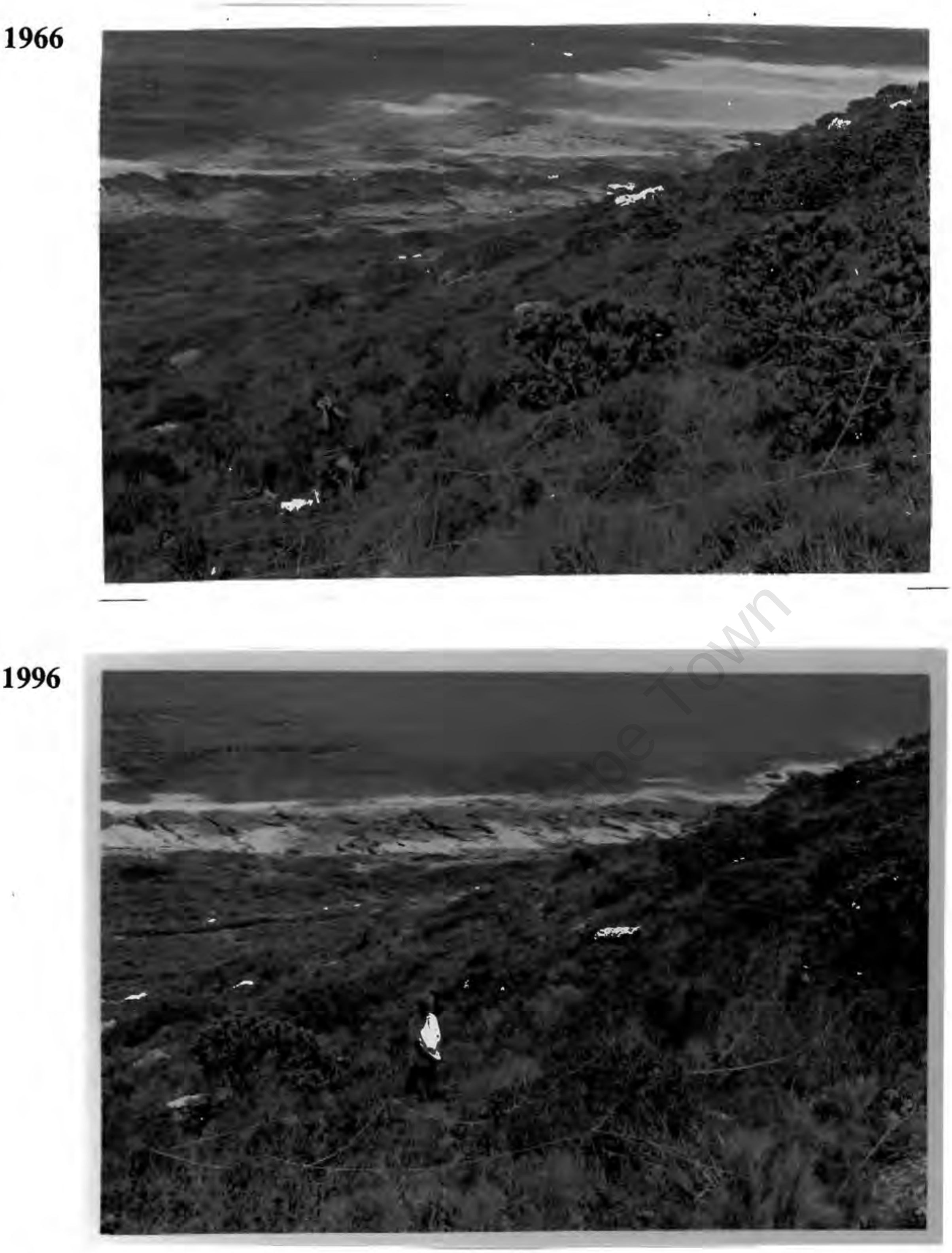

**Figure 5.5** Site 81, oligotrophic proteoid fynbos above the large coastal thicket at Gifkommetjie. This site is situated on the upper slopes of a fire protected amphitheatre above the Atlantic coast. The vegetation was 17 years old in 1966 and has not burnt between surveys. In 1966 the site contained some seedlings of thicket species. These have not developed into adult trees over the last 30 years. The vegetation has remained very stable with only the loss of a few non-sprouting species and the addition of some short lived colonisers between surveys. Despite a fire-free period of approximately 50 years, and it close proximity to a well established thicket this site has not developed into a thicket. Some individuals of *Leucospermum conocarpodendron* are visible in both photographs suggesting that this species has a lifespan in excess of 50 years.

C. Successional changes after long fire-free intervals in lowland fynbos.
Unlike the inland and upland fynbos, coastal asteraceous and coastal thicket communities are less frequently burnt owing to their location adjacent to the sea. It can therefore be hypothesised that species occurring in these communities are not fire adapted, and that they are more stable in the long term absence of fire.

Taylor estimated the ages of sites 80 (Fig. 5.6) and 90 (Fig. 5.7) as very old in 1966 and neither have experienced fire between the two surveys. These two sites are quite different in their floristic composition. Both are situated adjacent to the False Bay coastline. However, site 80 is dwarf scrub on shallow, rocky and damp soils, while site 90 is a typical coastal dune thicket on deep well-drained calcareous sands. The Sorenson coefficients for these sites were 71.1% and 79.0% respectively. They were therefore amongst the most stable in this study. They showed no change in the relative proportion of growth form or regeneration mode between surveys. Numbers of species only decreased slightly between surveys. The most obvious change in site 80 was the large increase in the sedge *Scirpus nudosus* (Fig. 5.6). This could be attributed to the eradication of stands of *Acacia cyclops* above this site, and the subsequent improvement in the hydrological regime. At site 90 there has been virtually no change in species composition and dominance. The coastal thicket species *Sideroxylon inerme*, *Cassine peragua* and *Rhus* species have remained dominant with approximately the same relative cover.

It can be concluded that the vegetation of the coastal communities, especially the dune thicket, is very stable in the absence of fire. These communities tend to be dominated by long-lived, slow-growing species that are able to persist for many decades (or centuries) in the absence of fire.

**1966**

**1996**

**Figure 5.6** Site 80, coastal scree asteraceous fynbos near Black Rocks on the False Bay coast. This site was already very old in 1966 and has not been burnt since. The species composition has remained stable between surveys. There has been an increase in the cover and biomass of *Scirpus nudosus* (graminoid in the middle of the site). This is most probably the result of an improvement in soil moisture since stands of *Acacia cyclops* were removed above the site between surveys. Evidence for the longevity of some shrubs is provided by the persistence of a single individual of the resprouting *Protasparagus capensis* in the bottom left hand corner of both photographs. This individual is well over 30 years old.

**1966**

**1996**

**Figure 5.7** Site 90, coastal dune thicket on the False Bay coast at Buffels Bay. This vegetation type has remained very stable in composition over the last 30 years. It is dominated by the thicket species *Sideroxylon inerme*, *Cassine peragua* and *Rhus* species. All of these species are long-lived and, as a result, the community is stable in the absence of fire. The mountain peaks in the background are from left to right: Paulsberg, Die Boer and Judas Peak. The person in both photographs is Hugh Taylor, who initially established the permanent sites in 1966.

Fire frequency.

Fires in fynbos occur with intervals of between four and 40 years (Le Maitre and Midgley 1992). The natural fire frequency for fynbos in the Cederberg mountain range was estimated at between 11 and 15 years (Brown *et al.* 1991). Owing to its peninsular geography, the vegetation of the southern Cape Peninsula would probably have burnt less frequently than landlocked areas further inland. An analysis of the average fire interval in the reserve over approximately the last fifty years revealed a value of 23.2 years. This was calculated as the average of the frequencies for all sites from the fire prior to Taylor's survey and included prescribed burns. The pre-colonial fire interval was probably even longer. The area was inhabited by the Peninsular Khoi-khoi who had little incentive to start fires as they subsisted on marine resources rather than animal products (Elphick 1977). There was a significant positive relationship between increasing latitude in the reserve and the mean fire interval (Fig. 5.8). Sites in the southern areas of the reserve, where the Cape Peninsula narrows to less than a few kilometers, have had a longer average fire frequency than those in the northern areas.

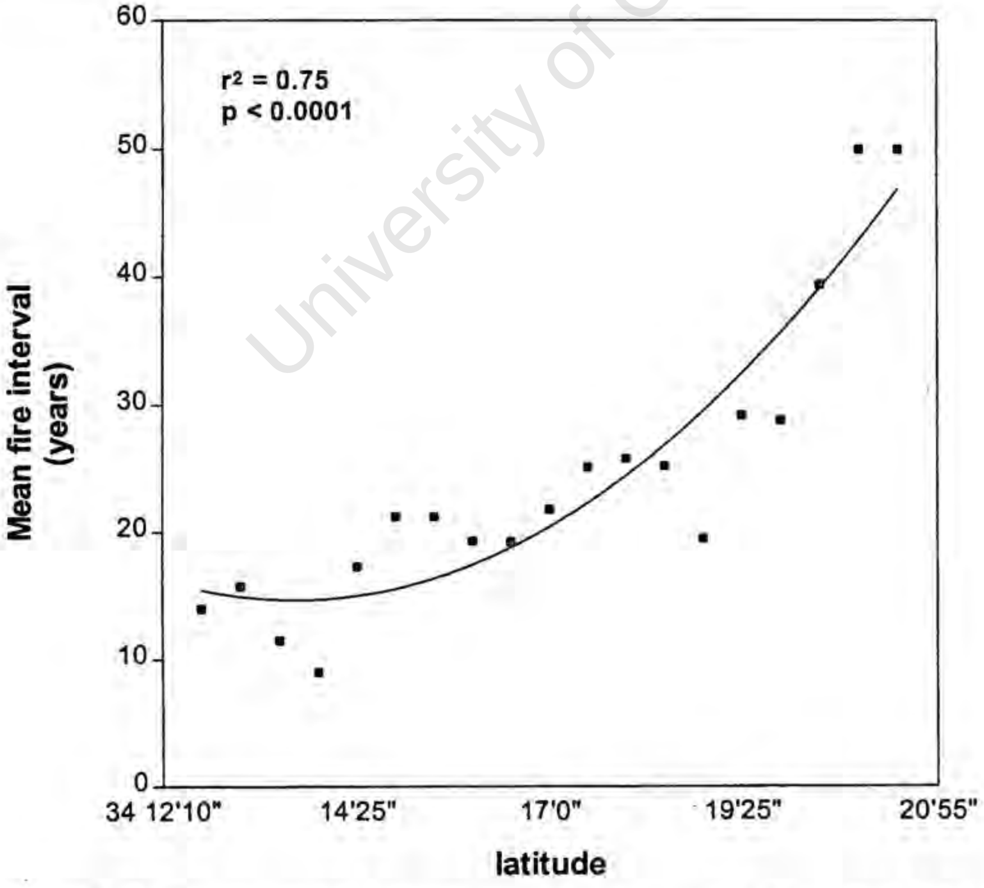

**Figure 5.8** The relationship between mean fire interval and latitude in the Cape of Good Hope Nature Reserve.

Fires at unusually short, or long intervals, can alter the species composition of fynbos (van Wilgen 1981, van Wilgen and Forsyth 1992, Vlok 1996, Schwilk *et al.* 1997). Frequent burning can alter species composition by eliminating the large non-sprouting shrubs, especially Proteaceae, as they do not have sufficient time to reach maturity between fires (van Wilgen and Kruger 1981, van Wilgen 1981). Fast maturing and sprouting species should be favoured by a short fire frequency (Vlok 1996). Increased competition from the sprouters also results in a decline in non-sprouters, and a decline in overall diversity of a site (Vlok 1996).

Where fire is excluded for more than approximately 30 years, senescence occurs in some species and seed stores become depleted. Poor regeneration and even local extinction may follow such long intervals between fires (Bond 1980). A further consequence of long intervals between fires is that fuel loads increase resulting in higher fire intensities. These fires have been shown to increase seedling recruitment of myrmecochorous Proteaceae (Bond *et al.* 1990), as well as to cause higher mortality among certain resprouting species (Le Maitre 1986).

### A. Short intervals between fires.

Only one site in this study was burnt at a very short frequency (site 14) and could be used to infer the impacts of short fire intervals on the vegetation (no photograph available for 1966). Between 1970 and 1988 site 14 on the eastern boundary of the reserve was burnt on a three year rotation as one of three tracer belts making up a boundary fire break. These fires were carried out under cool conditions during late autumn or winter. At the time of Taylor's original survey the vegetation on site 14 was only three years post-fire, while in 1996 it was eight years old.

This site has undergone considerable compositional change over the last 30 years. The Sorenson coefficient of only 55.0% was below average for the entire data set and only 48% of the original species were still present on the site. The changes in species composition were generally as predicted for short fire intervals. Species diversity decreased: there were 12 fewer species in the second survey. This decline was as a result of a combination of the impact of repeated short fire intervals and the later stage in the post-fire succession in the 1996 survey. Some of the locally extinct species are relatively slow maturing, non-sprouters and were probably lost as a direct consequence of the short fire intervals. These include *Erica plukenetii*, *Psoralea imbricata* and *Leucadendron laureolum;* the last mentioned being common in the vegetation adjacent to the old fire break. Other species lost from this site such as *Roella ciliatum*, *R. prostratum* and *Thesium spicatum*, are early successional species which under a normal fire regime are unlikely to be present in vegetation of eight years post-fire age. Interestingly, the changes were not restricted to the non-sprouters as only 54 % of the original sprouting species were present in the second survey. It would appear that the short fire frequencies may have also been detrimental to some of these species. However the relative dominance of sprouting species has increased between the surveys with species such as *Hypodiscus aristatus* and *Chondropetalum nudum* showing considerable increases in cover.

Evidence from this single site supports the findings of Vlok (1996) that short fire frequencies result in an increase in the coverage of sprouting species, and as a result, a decline in non-sprouters and in overall diversity. The most plausible explanation for this change is that short fire frequencies eliminate non-sprouting species (as was the case at this site) thereby reducing competition and favouring sprouters.

### B. Long intervals between fires

Eighteen of the sites have experienced at least one long (>30 year) fire interval since the fire prior to Taylor's survey and have not been invaded by alien vegetation. On average these sites showed a higher similarity in species composition between surveys (65.2%) than the average for the complete data set. I used these sites to examine what effects the long interval between fires had on the numbers of individuals of serotinous and myrmecochorous Proteaceae.

**Table 5.1**. A comparison of the response of serotinous and myrmecochorous Proteaceae to long fire-free intervals (higher intensity fires) in the C.G.H.N.R. Data are from the 18 (5 X $10m^2$) sites sampled in 1966 and 1996 and which experienced a long interval (>30 years) between fires. Data refer to the numbers of sites in which serotinous and myrmecochorous species were observed.

| | **Serotinous Proteaceae** | **Myrmecochorous Proteaceae** |
|---|---|---|
| Absent in both surveys | 6 | 12 |
| Present with similar abundances in both surveys | 7 | 1 |
| Abundance increased in 1996 | 1 | 2 |
| Colonised between surveys | 0 | 4 |
| Abundance declined in 1996 | 4 | 0 |
| Locally extinct between surveys | 4 | 0 |

The response of serotinous and myrmecochorous species to long fire intervals differed in the reserve. Serotinous non-sprouting Proteaceae such as *Leucadendron coniferum*, *L. xanthoconus* and the common *L. laureolum* showed a tendency to decline in sites that have experienced long fire-free intervals (>30 years). This supports the findings of Bond (1980) that fire in senescent fynbos results in smaller daughter populations or even local extinction of serotinous species. As predicted, myrmecochorous species showed an increase in abundance and even colonised some sites after high intensity fires. This supports the hypothesis of Bond *et al.* (1990) that seedling recruitment in these species is strongly and positively related to local fire intensity. Adult mortality is, however, often high after these intense fires. A random survey of individuals of *Leucospermum conocarpodendron* and *Mimetes fimbrifolius* in the vicinity of site 92 (Fig. 5.9) showed that 97% (n = 66) of the adult trees were killed in forty-five year old vegetation during the 1991 summer wildfire. Because of its sea-bound geography, the southern Peninsula experiences unusually long fire intervals. This has favoured species with unusual life histories such as the myrmecochorous tree proteoids, *Leucospermum conocarpodendron* and *Mimetes fimbrifolius* and the tree erica, *Erica tristis*. It would appear that the myrmecochorous tree Proteaceae are adapted to long fire-free intervals which facilitate high seedling regeneration and subsequent maturation after long-interval, intense fires. Although adult survival is much higher in low intensity fires, seedling recruitment is low and the species can be expected to decline following repeated short intervals between fires.

**1966**

**1996**

**Figure 5.9** Site 92, oligotrophic proteoid fynbos near Platboom. At this site the vegetation was 45 years old when it burnt in an intense summer fire in 1996. The species turnover between sampling times was 50%. A large proportion of this change was as a result of the colonisation of post-fire (asteraceous) species in 1996. The intense fire resulted in high mortality of *Leucospermum conocarpodendron* (tall proteoid bush in the middle of the 1966 photograph), but seedling recruitment of this species was high in the area. The thicket of *Acacia cyclops* in the background in 1966 was destroyed by the 1991 fire and the post-fire seedling cohort removed by clearing teams.

There was no significant change in the proportion of sprouting versus non-sprouting species recorded at the two sample times ($\chi^2$=2.8x$10^{-6}$, p=0.99 NS), nor the number of occurrences of sprouting versus non-sprouting species ($\chi^2$=0.37, 1 d.f., p=0.53 NS). This suggests that long fire-free intervals have not differentially favoured either regeneration strategies in the reserve.

It can be concluded that high intensity fire after long (>30 year) intervals have only minor effects on species composition but may result in a decline of serotinous, and an increase in myrmecochorous Proteaceae. The frequency of occurrence and average abundance of *L. conocarpodendron* and *M. fimbrifolius* for all sites in the reserve has remained constant between surveys (frequency; 1966, 11 sites, 1996 10 sites, mean abundance; 1966 1.8, 1996, 1.9).

### Fire Season

Prior to Taylor's initial vegetation survey in 1966 the majority of fires in the study area would have occurred naturally during the summer fire season. In the period 1975 to 1989, 40% of the study sites were burnt in prescribed fires as part of the reserve's vegetation management programme (Appendix 1). These fires were ignited under much milder conditions than would be experienced in the natural, summer fire season. Season of burn in fynbos has been shown to influence post-fire recruitment in serotinous Proteaceae (Bond *et al.* 1984, van Wilgen and Viviers 1985, Le Maitre 1988a&b, Midgley 1989), Proteaceae with soil-stored seed (Le Maitre 1988a&b), and a rare, sprouting member of the Bruniaceae (de Lange and Boucher 1993). These studies have shown that seedling establishment is greatest after autumn fires, followed by those in summer, and is poor after spring and winter burns. Le Maitre (1987) found that seedling densities of some grasses and non-sprouting shrubs were closest to parent plant densities after fires from January to April, and that the smallest changes in species composition occurred after fires from December to April. I used the two species data sets and the interim fire history to test the null hypothesis that season of burn has had no effect on species composition over the last 30 years.

Using Sorenson's coefficient as the measure of similarity between sample times I averaged the values for each season of burn. For information on the definitions of the seasons see the methods section in Chapter 3. Difficulties arose where sites were burnt by more than one fire occurring in different seasons. The averages for summer and autumn were calculated using sites burnt exclusively in these seasons. However, owing to their small sample sizes the spring and winter averages had to be calculated on the criteria that the site had burnt at least once in these seasons. Sites which had been influenced by alien species or had young fynbos at one of the sampling times, thus leading to successional differences, were not included in the analysis.

**Table 5.2.** Mean, minimum and maximum values of the Sorenson coefficient of similarity for 5 X 10m$^2$ sites in the Cape of Good Hope Nature Reserve which have experienced fires in particular seasons over the last 30 years. The sites were sampled in 1966 and 1996.

| | **Mean similarity** | **Maximum similarity** | **Minimum similarity** |
|---|---|---|---|
| All fires in summer | 67.0 (n=23) | 84.3 | 51.6 |
| All fires outside of summer | 62.3 (n=33) | 76.9 | 44.4 |
| All fires in autumn | 62.2 (n=8) | 76.9 | 46.1 |
| At least one fire in spring | 67.0 (n=3) | 73.7 | 60.5 |
| At least one fire in winter | 61.5 (n=17) | 73.7 | 44.4 |

The relative importance of season as a determinant of change is complicated by the influence of the other components of the fire regime. Differences in frequency and intensity override the effects of fire season. Despite this, it would appear that sites burnt during summer showed the least change in species composition (Fig. 5.10), while fires in winter and autumn showed the most change. This supports the findings of Le Maitre (1987) that the lowest changes in composition occur after fires in the summer months. The relatively high value for spring burns could be related to the low sample size in this class.

Dynamics of *Leucadendron laureolum*.

The species data sets collected for this study provide an opportunity to explore the long term (30 year) spatial and temporal dynamics of *Leucadendron laureolum*, a common serotinous species in the reserve. I attempt to invoke exogenous explanations for its population fluctuations in terms of fire regime over the past 30 years. Serotinous Proteaceae are well known for their tendency for density fluctuations after fire. A variety of hypothesis have been proposed to explain these fluctuations (see Midgley 1989 for a review). The 'phenological hypothesis' emphasises the importance of seed availability at the time of fire and predicts that optimum regeneration will occur after fires which take place immediately after seed crops mature (Jordaan 1965). However seed limitation is unlikely to be a major cause of fluctuations in *L. laureolum* as it is serotinous resulting in the availability of seed throughout the year (Le Maitre 1988b). The 'predation hypothesis' predicts that maximum regeneration occurs when fire takes place immediately before the germination period thereby reducing seed predation (Bond 1984). This hypothesis predicts that for *L. laureolum* spring fires which precede the summer dry period would be the most detrimental, while autumn fires would be the most favourable (Le Maitre 1988). The 'competition hypothesis' suggests that density-dependent variation is an important cause of population fluctuations. Several studies have inferred that pre-fire population density is a major determinant of post-fire population size in serotinous Proteaceae (Bond *et al.* 1984, Le Maitre 1988, Bond *et al.* 1995). Finally, the 'dispersal hypothesis' emphasises the importance of post-fire climatic conditions in influencing seed dispersal and the subsequent movements of populations after fire (Bond 1988, Cowling and Gxaba 1990).

*Leucadendron laureolum* is very widely distributed in the reserve and its densities are known to fluctuate over time (Le Maitre 1988b, Cowling and Gxaba 1990). *L. laureolum* is a habitat generalist (Williams 1972) which Taylor (1969) described as a "weedy" species capable of forming dense stands in most of the Inland fynbos communities of the southern Cape Peninsula. A comparison of the distribution and

However, seven sites only experienced summer and/or autumn fires. Therefore nearly 50% of the sites at which *L laureolum* declined were exposed to fires during theoretically favourable seasons. The decline in species at these sites could not be explained by fire regime (predation hypothesis) and was more likely related to dispersal and/or competitive effects. Three of these sites had moderately dense stands (2 000 to 10 000 stems per hectare) of *L. laureolum* present on them in 1966. Population declines at these densities could therefore have resulted from high levels of intraspecific competition. Cowling and Gxaba (1990) suggested that the most plausible explanation for the shifting abundance of *L. laureolum* is the dispersal of its small, winged seeds by persistently strong south-easterly winds in the summer months after fire. Recent research into the desiccation tolerance of newly emerged Proteaceae seedlings demonstrated that *L. laureolum* had only moderate resistance to post-emergence desiccation (Mustart and Cowling unpublished data). It would appear that these stochastic climatic events were the most likely explanation for population declines at least four sites in this study.

B. Causes of increase. (see Fig. 5.12 and 5.13)

All sites that have been colonised or shown an increase in cover have experienced at least one autumn or summer fire (24 sites). Sixty seven percent of these were burnt exclusively in summer fires and only one had a winter fire as its last burn. Season of burn, therefore, appears to be an important determinant of post-fire population increases in *L. laureolum:* both summer and autumn fires favour increases in density. Nine of the eleven sites colonised were burnt exclusively in summer, while the remaining two were last burnt in an autumn fire. Colonisation relies on effective dispersal of seeds into uninhabited sites. The high proportion of sites colonised following summer fires is most likely the result of dispersal of seeds into new sites by the strong SE winds during the summer months. Prescribed burns tend to be undertaken during the relatively windless autumn months resulting in less wind dispersal of seeds. Rapid germination following winter rains also results in the lower mobility of the species following autumn or winter burns.

**1966**

**1996**

**Figure 5.11** Site 62, oligotrophic proteoid fynbos on the sandstone hill above Brightwater. The 1966 photograph shows *Leucadendron laureolum* as a common overstorey species at this site. It was burnt in a natural autumn fire in 1979 and a prescribed winter burn in 1988. The combined effects of these two fires resulted in the local extinction of this species from site 62. It would appear from the photographs that the autumn fires have favoured the survival of the fire-tolerant adult *Leucospermum conocarpodendron*'s (large proteoid bushes in 1996 photograph) at this site.

**1966**

**1996**

**Figure 5.12** Site 29, an unusual form of wet restioid fynbos on the Smitswinkel flats which Taylor (1984b) described as "a distinctive woodland-like variety of seepage scrub with scattered *Psoralea pinnata* above a dense layer of grasses and Restionaceae". This site has undergone considerable changes over the last 30 years (56% similarity). While the composition of the graminoid field layer has remained similar, the scattered overstorey of *P. pinnata* has been replaced by a dense cover of *Leucadendron laureolum*.

**1966**

**1996**

**Figure 5.13** Site 73, oligotrophic proteoid fynbos near Kanonkop. These matched photographs demonstrate the highly mobile nature of the non-sprouting serotinous species, *Leucadendron laureolum*. This species only recruits after fire. In the 1966 survey this species was not recorded in the vicinity of site 73. Between surveys the site burnt twice, the second time in 1983 was during the favourable autumn months. As a result in 1996, the species was common throughout the area. Changes such as this, which result in compositional shifts in understorey species, were common at many sites between surveys

The impact of *L. laureolum* overstorey on understorey species diversity.
The highly mobile nature of this species poses questions as to what effect dense stands have on understorey species composition. The majority of work on the impact of proteoid overstories has shown reductions in local richness of understorey species under dense stands (Campbell and van der Meulen 1980, Esler and Cowling 1990, Cowling and Gxaba 1990). Cowling and Gxaba (1990) found that stands with sparse overstories of *L. laureolum* in the reserve had double the number of understorey species per square metre than dense stands. However recent research by Vlok (1996) showed that high densities (> 3000 plants per hectare) of overstorey proteoids before a fire enriched the local diversity levels of understorey species after a fire. Vlok (1996) noted that the spatial scale at which local diversity was measured affected the results of these studies. I used fixed sites which have undergone changes in the density of their proteoid overstorey to explore the consequence of these changes on understorey community composition.

I explored the relationship between changes in the abundance of *L. laureolum* between surveys and the corresponding changes in species diversity using a linear regression model. Both changes in abundance and in diversity were calculated by subtracting the values for 1996 from those of 1966. As succession can influences diversity, only sites with vegetation age >4 and <20 years at both sampling times were included in the analysis.

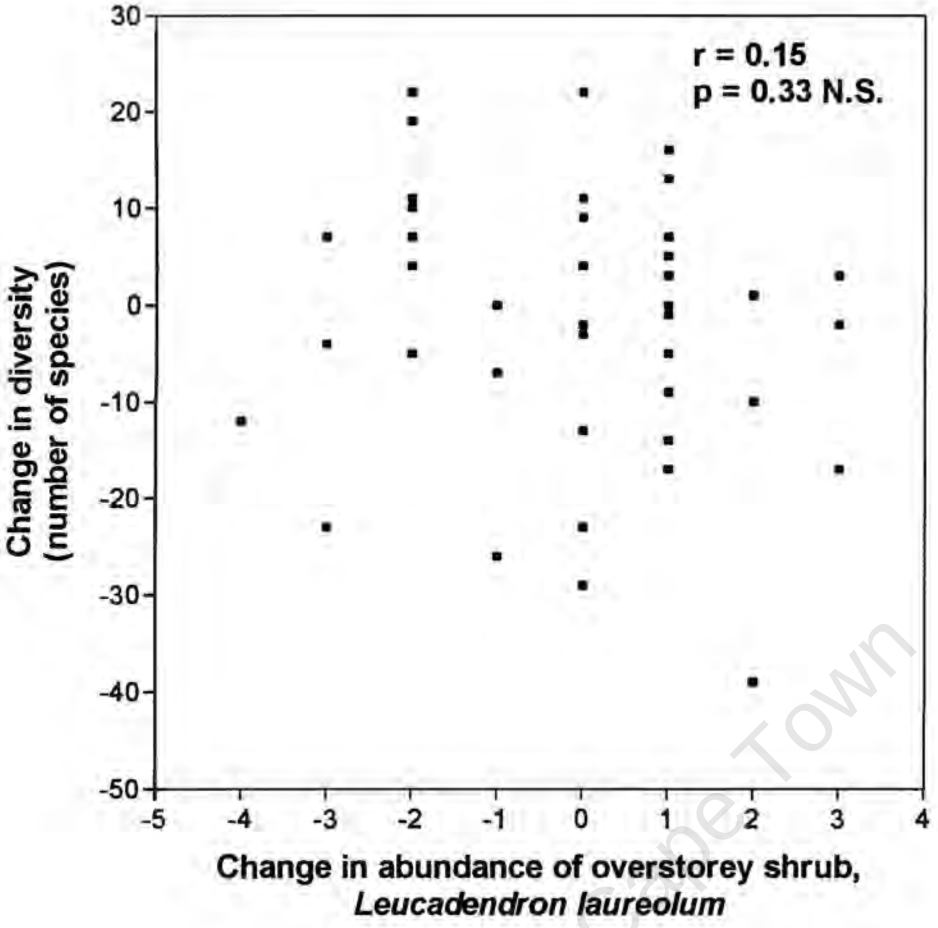

**Figure 5.14** The relationship between fluctuations in the density of *L. laureolum* over the last 30 years, and changes in species diversity. The abundance values can be converted to approximate densities per hectare as follows: 1 = 1-1 000 stems $ha^{-1}$, 2 = 1 000-2 000 stems $ha^{-1}$ and 3 = 2 000-10 000 stems $ha^{-1}$.

There was no significant relationship between changes in overstorey cover and changes in species diversity in this study (Fig. 5.14). The 50% reduction in diversity recorded by Cowling and Gxaba (1990) was in small quadrats of 1 $m^2$. This study utilised much larger quadrats (50 $m^2$ ) thus allowing for greater heterogeneity and patchiness in the overstorey and consequently better survival opportunities for a range of understorey shrubs. The lack of pattern in this study could be the result of their being insufficient sites with high densities of *L. laureolum*. The increase in understorey diversity recorded by Vlok (1996) was under stands with densities of greater than 3000 $stems.ha^{-1}$. It would appear that competition from overstorey proteoids only becomes important at very high densities.(>3000 stems.ha$^{-1}$). Light to moderate densities of proteoid overstorey do not significantly impact species diversity at the community scale.

The timespan of this study provides an indication that over the medium term overstorey proteoid shrubs have little effect on the diversity of understorey species. Populations of overstorey proteoids remain remarkably constant at the landscape scale over time and appear to only influence understorey diversity at high densities.

### *Alien plants*

Much of the fynbos biome has been impacted by dense stands of alien vegetation (Macdonald and Richardson 1986, Richardson *et al.* 1992). The establishment of an overstorey of alien trees and shrubs markedly reduces the richness of fynbos communities (Richardson and Van Wilgen 1985, Richardson *et al.* 1989, Holmes and Cowling 1997). The rate of fynbos recovery following the removal of alien thickets declines with increasing period of invasion as well as with time after clearing (Holmes and Cowling 1997). Some 750 fynbos species are currently at risk of extinction as a consequence of alien plant invasion (Richardson *et al.* 1992). The C.G.H.N.R. has a long history of invasion by alien trees (Taylor and Macdonald 1985, Taylor *et al.* 1985, Macdonald *et al.* 1989). Intensive mechanical control measures, involving initial felling of stands and subsequent follow up on a 2-year rotation have been undertaken in the reserve since 1981. These measures have probably been the most intensive continual clearing operation undertaken anywhere in the world and have cost approximately R 23 million (R. Erntzen pers. comm.). As the density of alien plants on each site was recorded at both sampling times, I was able to determine changes in density of alien plants across the reserve as well as to explore the impacts of invasion on the indigenous vegetation.

A comparison of the alien threat in 1966 and 1996.

**Table 5.4.** Record of alien species in the 50 $m^2$ sites in 1966 and 1996.

| **Sites impacted by woody aliens in 1966.** | | **Sites impacted by woody aliens in 1996.** | |
|---|---|---|---|
| *Site* | *Density and species* | *Site* | *Density and species* |
| 16 | Occasional *Pinus pinaster* seedlings | 3 | Occasional *Acacia saligna* seedlings |
| 18 | Occasional *P. pinaster* seedlings | 18 | Occasional *P. pinaster* seedlings |
| | Moderate *A. saligna* adult and seedlings | 95 | Occasional *A. cyclops* seedlings |
| 24 | Occasional *A. saligna* adults | 97 | Closed *A. cyclops* thicket |
| 68 | Occasional *Acacia cyclops* seedlings | 100 | Occasional *A. cyclops* adults |
| 80 | Occasional *A. cyclops* seedlings | | |
| 89 | Moderate *A. cyclops* adults | | |
| 95 | Occasional *A. cyclops* adults | | |
| 100 | Moderate *A. cyclops* adult and seedlings | | |

The effectiveness of the reserve's alien control programme was evident from the low occurrence and densities of alien plants in all except one site in the second survey (Table 5.4). In 1966 eight of the 81 sites contained alien plants whereas in 1996 only five sites were infested. In addition there were a further four sites (4, 25, 90 and 92) which showed evidence of having been invaded by alien trees after the 1966 survey and have subsequently been cleared prior to the second survey in 1996. *Acacia cyclops* is the only species which still poses a major threat to the indigenous flora of the reserve and is now concentrated on the steep slopes in the extreme south west from Vasco da Gama peak to Cape Point. This area has been included in the eradication programmeme and is at present being cleared. The only site which included a dense cover of alien plants was site 97, which is located in this area of the reserve. Outside of this area, alien plants were only encountered as scattered juveniles. The reserve's eradication programme uses a system of covering the entire reserve every two years to ensure that these seedlings will not mature. *Pinus pinaster* and *Acacia saligna,* which were both abundant at the time of the first survey, have been brought almost completely under control, with only occasional juveniles recorded in 1996.

The alien eradication programme in the C.G.H.N.R. has been effective at considerably reducing the threat of alien plants on the indigenous flora of the reserve.

### Impact of aliens on indigenous vegetation

The multivariate model developed in Chapter 3 demonstrated that the past impact of alien plants accounts for a low percentage of the variance in species data. Here I explore in more detail changes in the vegetation of sites which have been, or are at present, invaded by alien trees.

### A. Sites invaded between surveys and subsequently cleared

The two sites (25 and 95) which were densely invaded by alien trees in the period between surveys and subsequently cleared have regained less than 50% of their original species since clearing (mean Sorenson's coefficient of 45.28±2.1). Sites 4, 18, 90 and 92 were only moderately infested between surveys and have shown better recovery since clearing (mean Sorenson's coefficient of 58.66 ± 13.6). I use site 25 to explore the impacts of dense alien invasion on coastal dune vegetation (Fig. 5.15).

This site is situated near Olifantsbos Bay on coastal dunes within 20 m of the Atlantic coastline. In 1966 the vegetation was a dense coastal dune thicket of at least 30 years post-fire age. It was dominated by the thicket species *Euclea racemosa*, *Rhus laevigata and R. glauca* with a lower abundance of *Pterocelastrus tricuspidatus* and *Cassine peragua*. The ground layer was dominated by the graminoids *Ficinia ramosissima* and *Ischyrolepis eleocharis*. At that time there were no alien plants on the site but moderate densities of *Acacia cyclops* within a 200 m radius (Taylor 1969). The site was invaded by this species during the following twenty years, becoming densely infested before clearing in 1986 (C.G.H.N.R., unpublished records).

Seven of the 14 species present in 1966 still occupied the site in 1996. Of these, only *Helichrysum dasyanthum* was a non-sprouter. The typical coastal non-sprouters present in the initial survey such as *Passerina paleacea*, *Coleonema album* and *Metalasia muricata* had become locally extinct. Clearing of the alien trees has created gaps which have permitted colonisation by a group of weedy, post-disturbance non-sprouting species including *Cineraria geifolia*, *Senecio purpureus* and *Cullumia squarrosa* as well as the sprouting pioneer graminoids *Ehrharta villosa*, *Stenotaphrum secundatum* and *Pentaschistis pallida*. None of these species was present in the 1966 thicket and, consequently, diversity on this site has temporarily increased as a result of clearing tree invaders. The six sprouting species that have persisted on the site included *E. racemosa, R. laevigata* and *R. glauca*. These species were again dominating the site in 1996. The less abundant thicket species have all been lost as a consequence of invasion.

The invasion of this site by dense stands of *A. cyclops* had a major impact on the natural vegetation, especially non-sprouting species. The indigenous species are, however, recovering well since the aliens were eradicated.

**1966**

**1996**

**Figure 5.15** Site 25, coastal dune thicket within 20 m of the Atlantic coastline at Olifantsbos Bay. In 1966 the site was characterised by a well developed thicket. The site was subsequently invaded by *A. cyclops*. These trees were removed in 1986 and the natural vegetation has since started to recover. The sprouting guild is recovering well, while most of the non-sprouting species present in 1966 have been lost and have been replaced by short-lived post-disturbance species.

B. The impact of existing stands of alien plants

Only one of the sites in this study has received no attention from clearing teams since the 1966 survey. Site 97 is situated below steep cliffs on the False Bay coast, close to Cape Point (Fig. 5.16). In 1966 it contained only seven species, being dominated by a few low shrubs and succulent species of the family Mesembryanthemaceae. There were no aliens on site but by 1973, H. Taylor (pers comm.) reported that the site had become densely invaded. In 1996 *A. cyclops* formed an impenetrable thicket over the entire 50m$^2$ quadrat.

While the diversity of the site has remained constant (seven species), the six indigenous taxa now cover less than 5% of its area. The only species to persist between surveys were *Felicia fruticosa* and *Exomis microphylla* which grow on the coastal edge of the site and the tree species *Tarchonanthus camphoratus*. However, most of the original *T. camphoratus* thicket which grew just outside of the site has been eliminated as a direct result of invasion by *A. cyclops* (Fig. 5.16).

Within less than 30 years *A. cyclops* has virtually eliminated the vegetation of this site and much of this geographically restricted community in the south of the reserve. If it were not for the intensive and highly effective alien management programme administered by reserve staff over the last 15 years a far greater proportion of the reserve's vegetation would have been similarly impacted by alien plants.

**1966**

**1996**

**Figure 5.16** Site 97, coastal scree asteraceous fynbos at Platbank on the False Bay coast near Cape Point. In 1966 the alien thicket was outside of the site (dark trees in the top of the photograph). Note the indigenous thicket of *Tarchonanthus camphoratus* in the bottom right hand corner (lighter trees). The site was invaded by 1973, and by 1996 *Acacia cyclops* covered the entire area. The result is that the cover of indigenous species has declined dramatically and most of the species have been eliminated (e.g. the skeletons of *T. camphoratus* are evident in the foreground of the 1996 photograph).

## Conclusions

The vegetation of the CGHNR has undergone considerable change over the last 30 years. On average there has been a temporal turnover in species of 40% across the entire reserve. There was a negative relationship between post-fire vegetation age and species diversity in both the 1966 and 1996 data sets. In proteoid fynbos the early post-fire succession was characterised by a predominance of resprouting graminoids, and ephemeral species which live for less than five years. After five years the vegetation composition stabilises and is generally dominated by an overstorey proteoid layer. While predictions from moister inland localities suggest that fire-free intervals in excess of 30 years should result in the establishment of thicket patches, fynbos communities persisted even after 50 years in the reserve. Thicket and forest development is much slower in the dry and windy southern Cape Peninsula than in the wetter inland mountain ranges. Coastal thicket communities remain constant in composition and relative cover in the absence of fire. Short fire frequencies (< 5 years) favoured fast-maturing and sprouting species, while long fire-free intervals (> 30 years) resulted in high intensity fires which favoured myrmecochorous Proteaceae and negatively impacted serotinous Proteaceae. Fire season was less important than frequency in determining the vegetation composition. However, the least temporal change occurred in those sites only burnt during the summer months. The common non-sprouting serotinous proteoid shrub, *Leucadendron laureolum* showed a high degree of spatial mobility over the sampling period. However, despite its considerable changes in distribution, the abundance and number of sites occupied by this species remained constant at the landscape scale over the last 30 years. Stands of alien plants have impacted large areas of natural vegetation in the reserve. However, evidence from this study suggests that the natural flora is recovering well after clearing of alien stands. The threat posed by alien plants on the natural vegetation has been considerably reduced over the last 30 years.

Thus, while some of this change can be traced to human interference (prescribed burning and alien plants), most is a result of natural colonisation and extinction. Temporal diversity resulting from high levels of colonisation and extinction after patchy fires contributes to the high species diversity in fynbos systems.

# CHAPTER 6. General Conclusions

## Preamble

This thesis set out to explore the determinants of pattern in a species-rich and spatially complex vegetation system which is subject to recurrent disturbance. The causes of pattern explored were deterministic phenomena relating to physical environmental constraints and disturbance parameters (fire regime and alien plant invasions). I also explored the causes of plant extinction and the role of temporal dynamics in influencing contemporary spatial patterns. While numerous studies have examined the physical determinants of pattern in fynbos, this study is the first which attempts to quantify the role of disturbance in influencing spatial pattern. Furthermore, earlier studies on fynbos dynamics following fire have all explored patterns after single fire events. This study covered a longer period incorporating a few fires to explore temporal change. I believe that the approach of this study provides a successful attempt at invoking a broad range of explanations for the complex patterns observed in fynbos landscapes. This chapter examines the major findings as well as limitations of the study and makes suggestions for future research.

The specific aims of the study were to:

- examine the relative contribution of physical site factors and the disturbance regime as determinants of spatial pattern in fynbos
- explore the stability of fynbos species over time and the causes of their local extinction over a 30 year period
- explore the causes of temporal change in vegetation composition and its contribution to spatial pattern

Below I discuss the main findings of my study in the context of each of these major aims.

## Major findings

### RELATIVE CONTRIBUTION OF SITE FACTORS VERSUS DISTURBANCE

The physical site factors, in particular edaphic characteristics, explain much of the broad-scale vegetation patterns in fynbos. Finer scale patterns within vegetation types are not well explained by the physical site variables. Disturbance factors explained nearly as much of the variance in species data as the physical site variables. The recent fire history (30 years) explained nearly 20% of the variation at the landscape scale and even more at the community scale. These findings demonstrated the importance of fire as a determinant of pattern in species-rich, fire-prone environments. However, despite the combined explanatory power of the physical site factors and disturbance regime, approximately 60% of the variance in vegetation pattern remained unexplained. This indicates that other stochastic factors, post-fire climatic fluctuations and random colonisation and extinction play an important role in structuring vegetation pattern in fynbos.

### THE STABILITY OF FYNBOS SPECIES OVER TIME AND CAUSES OF LOCAL EXTINCTION

Species with high abundances and large geographic ranges were relatively stable at the landscape scale over the thirty year interval of this study. However, species with low abundance and/or small geographic ranges proved unstable and were prone to colonisation and extinction during this period. Rare and range-restricted species, which make up the bulk of the flora, have a high probability of local extinction. The process of local extinction showed non-random patterns with respect to the biological attributes of species. Species abundance proved the most important determinant of extinction, while growth form played a less important role. Both dispersal mode and regeneration mode proved non-significant as determinants of extinction. Thus it would appear that the majority of colonisation and extinction events are random occurrences which are common in fynbos owing to the high proportion of locally rare and range restricted species. These random events must contribute to the complexity of fynbos systems and be responsible for much of the unexplained variance in species pattern.

Previous studies on the effects of fire on fynbos communities have demonstrated that species composition changes after fire. I have demonstrated that species composition can alter dramatically over a few fires and even in the absence of fire. At the scale of the $50m^2$ sites there was on average nearly 40% change in species over the 30 year period of this study. The least change in composition over time occurred in upland fynbos sites exposed to regular summer fires (10 to 20 year intervals) and to lowland coastal sites not burnt between surveys. The species composition at individual sites changed considerably depending on the stage in the post-fire succession and the characteristics of the last 30 years of fire history, especially past fire frequencies. The majority of fynbos species only regenerate after fire and as a result, fire resets the succession in fynbos systems. However much of the change observed over time could not be explained by deterministic processes relating to the nature of the disturbance. The dynamics of *Leucadendron laureolum*, a common overstorey proteoid shrub, provided evidence for the importance of the post-fire climatic conditions in influencing the dispersal of species after fire. It would appear that the climatic conditions following fire may be more important than the characteristics of the fire itself in influencing vegetation pattern. It was clear from this study that fynbos communities can change considerably over time and that many more species than are observed can potentially occupy a site.

## A final word

This thesis has again demonstrated that bounds to the local abundance and distribution of many plant species are weak. Consequently the composition and structure of plant assemblages varies over time. Broad-scale community structure in fynbos is largely determined by the physical characteristics of the site. However the composition of communities can vary considerably within the constraints of the physical environment. Fig. 6.1 provides a schematic representation of the results of this study.

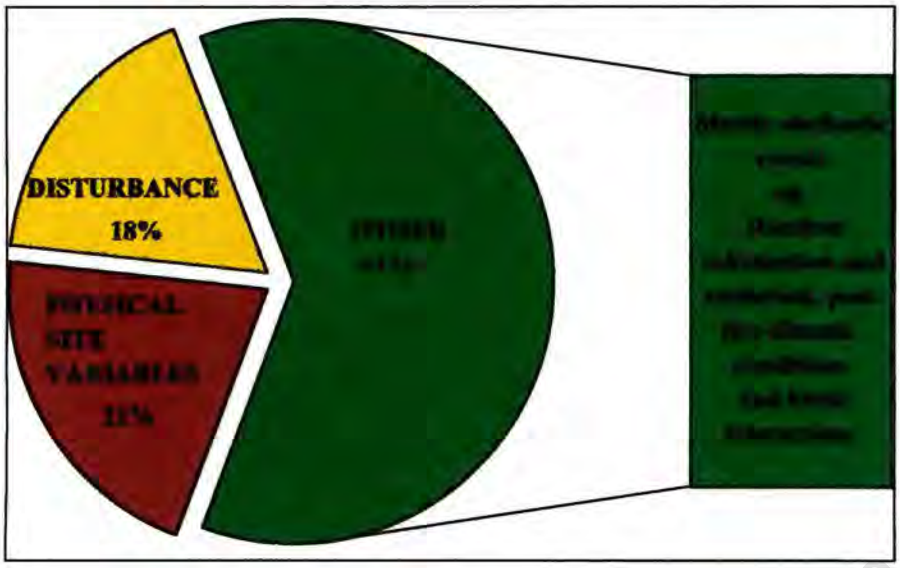

**Figure 6.1 Determinants of vegetation pattern in the Cape of Good Hope Nature Reserve.**

Within the constraints of the physical environment there is generally a very large pool of species which could occupy a given site. Despite further constraints imposed by deterministic processes relating to the influence of past fire regime, there still remains a large number of potential species which could occupy the site after fire. The assemblage of species finally observed is largely dependent on random events such as dispersal into or out of the site after fire, post-fire climatic conditions or biotic interactions both preceding (e.g. density-dependent population oscillations, seed predation and myrmecochory) or following (eg. interspecific competition and predation) fire. These biotic interactions influence species composition throughout the post-fire succession and, as a result, the stage at which the site is examined after fire will influence its observed composition.

### Limitations of study and future research

This study has demonstrated the importance of long-term monitoring of vegetation in order to gain better insight into contemporary vegetation patterns. The effectiveness of my data was limited by only providing two time points over a thirty year continuum. Better insight into the temporal dynamics of fynbos might have been achieved had the permanent sites been resurveyed more regularly. This would provide information on the influence of each fire-event in a sequence of individual fires rather than a single view at the end of the fire sequence. Given the importance of edaphic characteristics in determining fynbos boundaries, I could have included a more detailed soil analysis in the physical environmental dataset. Similarly, a disturbance record going back longer than the 30 years used in this study might have increased the descriptive power of the fire and alien plant component.

More long-term studies using permanent monitoring sites surveyed on a regular basis should be initiated in fire-prone vegetation systems. This study has emphasised the importance of a variety of determinants of pattern (eg. random colonisation and extinction between fires) which can only be recorded using regularly surveyed sites. Future research into the determinants of pattern in fynbos systems should explore the effects of post-fire climatic conditions (rainfall and wind) on the regeneration of species. Finally, investigations into the role of biotic interactions, at all stages of the succession, are also needed if we are to better understand the remarkable variation in species pattern within fynbos landscapes.

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# Appendix 1. The fire histories of all sites used in this study.

Fires are given by the months in which they occured in the table but were converted to four categories relating to the four seasons for the analysis.

| 1996 site number | Taylor's site number | Fire history |
|---|---|---|
| 1 | 1 | 1958, summer 1975, summer 1986 |
| 2 | 2 | 1958, summer 1975, summer 1986 |
| 3 | 3 | 1958, summer 1975, summer 1986 |
| 4 | 4 | 1948, summer 1975, summer 1986 |
| 5 | 7 | 1961, summer 1975, summer 1986 |
| 6 | 8 | 1963, summer 1975, summer 1986 |
| 7 | 9 | 1963, summer 1975, summer 1986 |
| 8 | 10 | 1963, summer 1975, summer 1986 |
| 9 | 12 | 1963, summer 1975, summer 1986 |
| 10 | 13 | 1963, summer 1975, summer 1986 |
| 11 | 14 | 1963, winter 1970, winter 1973, winter 1976, winter 1979, winter 1982, winter 1985, winter 1988. |
| 12 | 15 | 1963, summer 1986 |
| 13 | 16 | 1963, summer 1986 |
| 14 | 17 | 1963, summer 1975, summer 1986 |
| 15 | 18 | 1963, summer 1975, summer 1986 |
| 16 | 19 | 1949, summer 1986 |
| 17 | 21 | 1951, autumn 1977, summer 1986 |
| 18 | 22 | 1945, summer 1975, summer 1986 |
| 19 | 23 | 1951, summer 1975, summer 1986 |
| 20 | 24 | 1962, summer 1975, summer 1986 |
| 21 | 25 | 1935?, summer 1986, summer 1991 |
| 22 | 27 | 1945, summer 1977, summer 1986 |
| 23 | 28 | 1945, summer 1977, summer 1986 |
| 24 | 29 | 1956, summer 1975, summer 1986 |
| 25 | 30 | 1948, summer 1975, summer 1986 |
| 26 | 31 | 1955, summer 1975, summer 1986 |
| 27 | 34 | 1953, summer 1991 |
| 28 | 36 | 1951, summer 1977, summer 1986 |
| 29 | 37 | 1940, summer 1977, summer 1986, winter 1988 |
| 30 | 38 | 1954, autumn 1975, summer 1986 |

| | | |
|---|---|---|
| 31 | 39 | 1945, summer 1975, summer 1986 |
| 32 | 40 | 1955, summer 1975, summer 1986 |
| 33 | 42 | 1965, summer 1975, summer 1986, 1992? |
| 34 | 44 | 1957, summer 1991 |
| 35 | 45 | 1957, summer 1991 |
| 36 | 46 | 1951, autumn 1979, winter 1988 |
| 37 | 47 | 1948, autumn 1977, winter 1988 |
| 38 | 48 | 1956, autumn 1975, autumn 1977, autumn 1989 |
| 39 | 49 | 1948, autumn 1975, autumn 1989 |
| 40 | 50 | 1958, summer 1975, autumn 1989 |
| 41 | 54 | 1952, autumn 1979 |
| 42 | 55 | 1952, autumn 1979, winter 1988 |
| 43 | 56 | 1952, autumn 1977, winter 1988 |
| 44 | 57 | 1947, autumn 1975, autumn 1989 |
| 45 | 58 | 1947, autumn 1975, autumn 1989 |
| 46 | 59 | 1951, autumn 1975, summer 1992 |
| 47 | 60 | No Fires |
| 48 | 61 | 1959, summer 1991 |
| 49 | 62 | 1947, autumn 1979, winter 1988 |
| 50 | 63 | 1947, autumn 1979, winter 1988 |
| 51 | 64 | 1951, autumn 1979, winter 1988 |
| 52 | 65 | 1951, autumn 1983, autumn 1989 |
| 53 | 66 | 1951, autumn 1983 |
| 54 | 67 | 1946, autumn 1983 |
| 55 | 68 | 1963, summer 1991 |
| 56 | 70 | 1964, summer 1991 |
| 57 | 71 | 1954, spring 1968, winter 1981, autumn 1989 |
| 58 | 72 | 1941, spring 1968, autumn 1983 |
| 59 | 73 | 1954, spring 1968, autumn 1983 |
| 60 | 74 | No Fires |
| 61 | 75 | 1965, autumn 1979, summer 1991 |
| 62 | 76 | 1965, winter 1981, summer 1991 |
| 63 | 77 | 1953, autumn 1974, winter 1981, summer 1991 |
| 64 | 78 | 1961, bushcut 1966, autumn 1983, summer 1992 |
| 65 | 79 | 1946, spring 1968, autumn 1983, |
| 66 | 80 | No Fires |
| 67 | 81 | No Fires |
| 68 | 82 | 1965, winter 1981, summer 1991 |

| | | |
|---|---|---|
| 69 | 83 | 1958, winter 1981, summer 1991 |
| 70 | 84 | 1958, winter 1981, summer 1991 |
| 71 | 85 | No Fires |
| 72 | 86 | 1965, winter 1981, summer 1991 |
| 73 | 87 | 1965, winter 1981, summer 1991 |
| 74 | 88 | 1955, winter 1981, summer 1991 |
| 75 | 89 | 1951, winter 1966 (tracer ?) |
| 76 | 90 | No fire |
| 77 | 91 | 1946, winter 1981, summer 1991 |
| 78 | 92 | 1942, summer 1991 |
| 79 | 93 | 1946, summer 1991 |
| 80 | 94 | 1951, autumn 1992 |
| 81 | 95 | No Fire |
| 82 | 97 | No Fire |
| 83 | 98 | 1946, Autumn 1975, summer 1992 |
| 84 | 99 | No Fire |
| 85 | 100 | No Fire |

# Appendix 2. The attributes of the species used in Chapter 4.

The data gives biological attributes, abundances, geographic ranges and probability of local extinction for the period 1966 to 1996. The growth forms are abbreviated as follows: D=Dispersal mode; R=Regeneration mode; and GF=Growth form. Frequency is defined as the number of sites that the species occupied at each sampling time, while cover (divided into 5 categories) is the mean value for all sites occupied.

| FAMILY | SPECIES | | FREQUENCY | | COVER | | NUMBER OF EXTINCTIONS | NUMBER OF COLONISATIONS | NUMBER MAINTAINED | p(10) | p(01) | D | R | GF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1966 | 1996 | 1966 | 1996 | (1,0) | (0,1) | (1,1) | | | | | |
| RUTACEAE | Adenandra | uniflora | 5 | 5 | 3.00 | 2.17 | 2 | 2 | 7 | 0.22 | 0.03 | 1 | 1 | 1 |
| RUTACEAE | Adenandra | villosa | 35 | 26 | 2.83 | 2.59 | 11 | 1 | 26 | 0.30 | 0.02 | 1 | 2 | 1 |
| EUPHORBIACEAE | Adenocline | pauciflora | 2 | 1 | 1.67 | 1.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| SELAGINACEAE | Agathelpis | dubia | 20 | 18 | 2.48 | 2.21 | 11 | 9 | 9 | 0.55 | 0.15 | 1 | 1 | 1 |
| RUTACEAE | Agathosma | bifida | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 1 |
| RUTACEAE | Agathosma | capensis | 0 | 2 | 0.00 | 1.33 | 0 | 2 | 0 | / | 0.02 | 1 | 2 | 1 |
| RUTACEAE | Agathosma | ciliaris | 2 | 11 | 1.67 | 2.42 | 0 | 9 | 2 | 0.00 | 0.11 | 1 | 2 | 1 |
| RUTACEAE | Agathosma | hookeri | 12 | 11 | 2.69 | 2.17 | 4 | 3 | 8 | 0.33 | 0.04 | 1 | 2 | 1 |
| RUTACEAE | Agathosma | imbricata | 21 | 17 | 3.18 | 2.83 | 7 | 3 | 14 | 0.33 | 0.05 | 1 | 2 | 1 |
| RUTACEAE | Agathosma | lanceolata | 2 | 0 | 1.67 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| RUTACEAE | Agathosma | serpyllacea | 2 | 6 | 2.67 | 2.29 | 0 | 4 | 2 | 0.00 | 0.05 | 1 | 1 | 1 |
| AIZOACEAE | Aizoon | paniculatum | 1 | 1 | 1.00 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 5 |
| AIZOACEAE | Aizoon | sarmentosum | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| ASTERACEAE | Alciope | tabularis | 6 | 3 | 1.71 | 1.50 | 5 | 2 | 1 | 0.83 | 0.03 | 2 | 2 | 1 |
| FABACEAE | Amphithalea | ericifolia | 21 | 20 | 2.91 | 2.90 | 5 | 4 | 16 | 0.24 | 0.07 | 1 | 1 | 1 |
| ASTERACEAE | Anaxeton | laeve | 21 | 18 | 2.68 | 2.58 | 8 | 5 | 13 | 0.38 | 0.08 | 2 | 1 | 1 |
| MALVACEAE | Anisodontea | scabrosa | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 2 |
| APIACEAE | Annesorhiza | altiscapa | 0 | 1 | 0.00 | 1.50 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| RESTIONACEAE | Anthochortus | capensis | 1 | 0 | 2.00 | 0.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Anthochortus | laxiflorus | 0 | 1 | 0.00 | 3.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| RUBIACEAE | Anthospermum | aethiopicum | 23 | 19 | 2.83 | 3.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| RUBIACEAE | Anthospermum | bergianum | 11 | 7 | 2.75 | 1.75 | 8 | 4 | 3 | 0.73 | 0.06 | 1 | 1 | 1 |
| RUBIACEAE | Anthospermum | galioides | 31 | 16 | 2.78 | 2.29 | 17 | 2 | 14 | 0.55 | 0.04 | 1 | 1 | 1 |
| APIACEAE | Apium | graveolens | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| ASTERACEAE | Arctotis | acaulis | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 2 | 5 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ASTERACEAE | Arctotis | aspera | 5 | 2 | 1.67 | 1.67 | 4 | 1 | 1 | 0.80 | 0.01 | 2 | 1 | 1 |
| ASTERACEAE | Arctotis | stoechadifolia | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 5 |
| FABACEAE | Argyrolobium | filiforme | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| IRIDACEAE | Aristea | africana | 29 | 30 | 3.70 | 3.32 | 9 | 11 | 19 | 0.32 | 0.21 | 1 | 1 | 6 |
| IRIDACEAE | Aristea | glauca | 2 | 0 | 4.00 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 6 |
| IRIDACEAE | Aristea | major | 1 | 1 | 1.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 6 |
| FABACEAE | Aspalathus | abietina | 6 | 1 | 2.14 | 1.00 | 6 | 1 | 0 | 1.00 | 0.01 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | argyrella | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | callosa | 2 | 3 | 1.67 | 1.50 | 2 | 3 | 0 | 1.00 | 0.04 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | capensis | 4 | 5 | 2.20 | 2.17 | 0 | 1 | 4 | 0.00 | 0.01 | 1 | 1 | 2 |
| FABACEAE | Aspalathus | carnosa | 11 | 20 | 2.58 | 2.71 | 0 | 1 | 4 | 0.00 | 0.01 | 1 | 1 | 1 |
| FABACEAE | Aspalathus | chenopoda | 1 | 1 | 3.00 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 3 | 2 |
| FABACEAE | Aspalathus | divaricata | 4 | 3 | 2.40 | 3.00 | 2 | 1 | 2 | 0.50 | 0.01 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | ericifolia | 2 | 3 | 2.00 | 2.25 | 1 | 2 | 1 | 0.50 | 0.03 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | hispida | 5 | 3 | 2.33 | 2.50 | 2 | 0 | 3 | 0.40 | 0.00 | 1 | 1 | 1 |
| FABACEAE | Aspalathus | laricifolia | 1 | 2 | 1.00 | 1.33 | 1 | 2 | 0 | 1.00 | 0.03 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | linguiloba | 7 | 4 | 2.00 | | 2 | 0 | 5 | 0.29 | 0.00 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | microphylla | 7 | 6 | 2.50 | 1.71 | 6 | 5 | 1 | 0.86 | 0.07 | 1 | 2 | 1 |
| FABACEAE | Aspalathus | retroflexa | 3 | 0 | 1.50 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | sericea | 2 | 0 | 2.00 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| FABACEAE | Aspalathus | serpens | 4 | 2 | 1.60 | 1.33 | 4 | 2 | 0 | 1.00 | 0.03 | 1 | 3 | 1 |
| ASTERACEAE | Berkheya | barbata | 5 | 5 | 2.17 | 2.00 | 0 | 0 | 5 | 0.00 | 0.00 | 2 | 2 | 5 |
| BRUNIACEAE | Berzelia | abrotanoides | 11 | 8 | 3.00 | 3.33 | 3 | 0 | 8 | 0.27 | 0.00 | 1 | 2 | 2 |
| BRUNIACEAE | Berzelia | lanuginosa | 3 | 3 | 1.75 | 2.25 | 0 | 0 | 3 | 0.00 | 0.00 | 1 | 2 | 2 |
| ERICACEAE | Blaeria | ericoides | 4 | 2 | 3.00 | 2.67 | 4 | 0 | 1 | 0.80 | 0.00 | 1 | 1 | 1 |
| IRIDACEAE | Bobartia | gladiata | 20 | 18 | 2.71 | 2.84 | 4 | 2 | 16 | 0.20 | 0.03 | 1 | 1 | 6 |
| IRIDACEAE | Bobartia | indica | 4 | 3 | 2.80 | 1.50 | 3 | 2 | 1 | 0.75 | 0.03 | 1 | 1 | 6 |
| FABACEAE | Bolusafra | bituminosa | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| ASPHODELACEAE | Bulbine | asphodeloides | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 6 |
| ASPHODELACEAE | Caesia | contorta | 1 | 3 | 1.00 | 1.75 | 0 | 2 | 1 | 0.00 | 0.03 | 1 | 2 | 6 |
| RESTIONACEAE | Calopsis | fruiticosa | 1 | 2 | 2.00 | 2.67 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Calopsis | gracilis | 3 | 6 | 2.25 | 2.29 | 1 | 4 | 2 | 0.33 | 0.05 | 1 | 2 | 4 |
| RESTIONACEAE | Calopsis | membranacea | 1 | 1 | 1.50 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Calopsis | viminea | 3 | 2 | 2.00 | 1.33 | 2 | 0 | 2 | 0.50 | 0.00 | 1 | 2 | 4 |
| RUBIACEAE | Carpacoce | spermacocea | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| RUBIACEAE | Carpacoce | vaginellata | 8 | 2 | 2.78 | 1.33 | 7 | 1 | 1 | 0.88 | 0.01 | 1 | 2 | 1 |
| MESEMBRYANTHEMACEAE | Carpobrotus | acinaciformis | 5 | 6 | 1.83 | 2.00 | 2 | 3 | 2 | 0.50 | 0.04 | 1 | 2 | 5 |
| MESEMBRYANTHEMACEAE | Carpobrotus | edulis | 0 | 2 | 0.00 | 1.67 | 0 | 2 | 0 | / | 0.02 | 1 | 1 | 5 |
| CELASTRACEAE | Cassine | maritima | 2 | 0 | 1.67 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 2 |
| CELASTRACEAE | Cassine | peragua | 4 | 4 | 1.80 | 1.60 | 3 | 3 | 1 | 0.75 | 0.04 | 2 | 2 | 3 |
| LAURACEAE | Cassytha | ciliolata | 14 | 13 | 2.93 | 3.14 | 4 | 3 | 3 | 0.57 | 0.04 | 2 | 1 | 1 |
| ASTERACEAE | Castalis | nudicaulis | 12 | 9 | 2.31 | 2.10 | 7 | 4 | 5 | 0.58 | 0.06 | 1 | 1 | 5 |
| APIACEAE | Centella | affinis | 3 | 1 | 2.25 | 2.00 | 3 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 5 |
| APIACEAE | Centella | glabrata | 2 | 1 | 1.67 | 1.50 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 2 | 5 |
| APIACEAE | Centella | macrocarpa | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| APIACEAE | Centella | tridentata | 5 | 1 | 2.83 | 1.00 | 5 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 5 |
| CHENOPODIACEAE | Chenolea | diffusa | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| GENTIANACEAE | Chironia | baccifera | 2 | 0 | 1.67 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| GENTIANACEAE | Chironia | decumbens | 2 | 1 | 2.67 | 3.00 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 1 | 5 |
| GENTIANACEAE | Chironia | linoides | 12 | 3 | 2.23 | 1.50 | 9 | 0 | 3 | 0.75 | 0.00 | 1 | 1 | 5 |
| RESTIONACEAE | Chondropetalum | hookerianum | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 4 |
| RESTIONACEAE | Chondropetalum | microcarpum | 2 | 3 | 2.00 | 3.50 | 0 | 1 | 2 | 0.00 | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Chondropetalum | nudum | 17 | 15 | 3.00 | 3.88 | 6 | 4 | 11 | 0.35 | 0.06 | 1 | 2 | 4 |
| RESTIONACEAE | Chondropetalum | tectorum | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| ASTERACEAE | Chrysanthemoides | monilifera | 1 | 1 | 1.00 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 2 | 1 | 3 |
| ASTERACEAE | Chrysochoma | coma - aurea | 6 | 3 | 2.57 | 1.50 | 3 | 0 | 3 | 0.50 | 0.00 | 2 | 1 | 1 |
| ASTERACEAE | Cineraria | geifolia | 5 | 4 | 2.50 | 1.80 | 2 | 1 | 3 | 0.40 | 0.01 | 2 | 1 | 5 |
| ROSACEAE | Cliffortia | atrata | 7 | 9 | 1.75 | 1.80 | 2 | 4 | 5 | 0.29 | 0.05 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | falcata | 8 | 7 | 2.78 | 2.50 | 2 | 1 | 6 | 0.25 | 0.01 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | ferruginea | 1 | 1 | 1.00 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| ROSACEAE | Cliffortia | filifolia | 2 | 2 | 1.67 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | glauca | 1 | 1 | 1.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | obcordata | 1 | 1 | 2.00 | 2.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | polygonifolia | 3 | 1 | 3.25 | 1.00 | 2 | 0 | 1 | 0.67 | 0.00 | 1 | 1 | 1 |
| ROSACEAE | Cliffortia | ruscifolia | 1 | 1 | 1.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 2 |
| ROSACEAE | Cliffortia | stricta | 3 | 1 | 1.75 | 2.00 | 2 | 0 | 1 | 0.67 | 0.00 | 1 | 1 | 2 |
| ROSACEAE | Cliffortia | subsetacea | 21 | 21 | 3.23 | 3.36 | 6 | 6 | 15 | 0.29 | 0.10 | 1 | 1 | 1 |
| EUPHORBIACEAE | Clutia | alaternoides | 14 | 6 | 2.40 | 2.14 | 5 | 0 | 8 | 0.38 | 0.00 | 1 | 2 | 1 |
| EUPHORBIACEAE | Clutia | ericoides | 2 | 3 | 1.67 | 2.00 | 0 | 1 | 2 | 0.00 | 0.01 | 1 | 2 | 1 |
| EUPHORBIACEAE | Clutia | polygonoides | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| RUTACEAE | Coleonema | album | 4 | 1 | 1.80 | 2.00 | 3 | 0 | 1 | 0.75 | 0.00 | 1 | 1 | 1 |
| ASTERACEAE | Conyza | pinnatifida | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 5 |
| ASTERACEAE | Corymbium | africanum | 19 | 19 | 3.30 | 3.10 | 8 | 8 | 11 | 0.42 | 0.13 | 2 | 2 | 5 |
| ASTERACEAE | Corymbium | glabrum | 32 | 24 | 2.85 | 2.68 | 12 | 4 | 20 | 0.38 | 0.08 | 2 | 2 | 5 |
| CRASSULACEAE | Crassula | capensis | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | coccinea | 1 | 1 | 1.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | cymosa | 4 | 3 | 1.80 | 2.00 | 2 | 1 | 2 | 0.50 | 0.01 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | fascicularis | 11 | 17 | 2.42 | 2.22 | 3 | 13 | 6 | 0.33 | 0.18 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | flava | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 3 |
| CRASSULACEAE | Crassula | muscosa | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | nudicaulis | 8 | 0 | 1.89 | 0.00 | 8 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| CRASSULACEAE | Crassula | subulata | 6 | 1 | 2.00 | 2.00 | 5 | 0 | 1 | 0.83 | 0.00 | 1 | 1 | 5 |
| THYMELAEACEAE | Cryptadenia | grandiflora | 4 | 4 | 2.60 | 2.40 | 4 | 2 | 1 | 0.80 | 0.03 | 1 | 1 | 1 |
| ASTERACEAE | Cullumia | setosa | 16 | 20 | 2.65 | 2.43 | 2 | 6 | 14 | 0.13 | 0.09 | 1 | 1 | 1 |
| ASTERACEAE | Cullumia | squarrosa | 1 | 2 | 2.00 | 2.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 1 | 1 |
| ARALIACEAE | Cussonia | thyrsiflora | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 3 |
| POACEAE | Cymbopogon | marginatus | 5 | 7 | 2.83 | 2.88 | 0 | 2 | 5 | 0.00 | 0.03 | 1 | 2 | 4 |
| ASCLEPIADACEAE | Cynanchum | africanum | 1 | 0 | 2.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| ASCLEPIADACEAE | Cynanchum | obtusifolium | 1 | 1 | 1.00 | 2.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 5 |
| POACEAE | Cynodon | dactylon | 3 | 2 | 1.75 | 1.67 | 1 | 0 | 2 | 0.33 | 0.00 | 1 | 2 | 4 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LOBELIACEAE | Cyphia | bulbosa | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 5 |
| PROTEACEAE | Diastella | divaricata | 18 | 30 | 3.00 | 2.61 | 2 | 16 | 15 | 0.12 | 0.25 | 1 | 1 | 1 |
| HAEMODORACEAE | Dilatris | corymbosa | 15 | 14 | 2.19 | 2.27 | 0 | 2 | 1 | 0.00 | 0.03 | 1 | 2 | 6 |
| RUTACEAE | Diosma | hirsuta | 4 | 7 | 2.20 | 2.63 | 1 | 4 | 3 | 0.25 | 0.05 | 1 | 2 | 1 |
| RUTACEAE | Diosma | oppositifolia | 23 | 23 | 2.63 | 2.50 | 6 | 6 | 17 | 0.26 | 0.10 | 1 | 2 | 1 |
| EBENACEAE | Diospyros | glabra | 1 | 3 | 1.00 | 1.50 | 1 | 3 | 0 | 1.00 | 0.04 | 2 | 2 | 1 |
| SELAGINACEAE | Dischisma | ciliatum | 1 | 2 | 2.00 | 1.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 1 | 1 |
| ASTERACEAE | Disparago | anomala | 1 | 3 | 1.50 | 1.75 | 0 | 2 | 1 | 0.00 | 0.03 | 1 | 1 | 1 |
| ASTERACEAE | Disparago | lasiocarpa | 7 | 8 | 2.38 | 3.00 | 2 | 3 | 5 | 0.29 | 0.04 | 2 | 1 | 1 |
| MESEMBRYANTHEMACEAE | Drosanthemum | candens | 2 | 2 | 2.67 | 2.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 1 | 5 |
| DROSERACEAE | Drosera | aliciae | 1 | 1 | 1.50 | 2.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 5 |
| DROSERACEAE | Drosera | trinervia | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| ASTERACEAE | Edmondia | sesamoides | 16 | 18 | 2.53 | 2.68 | 6 | 8 | 10 | 0.38 | 0.12 | 2 | 1 | 1 |
| POACEAE | Ehrharta | bulbosa | 3 | 0 | 2.00 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| POACEAE | Ehrharta | calycina | 6 | 6 | 2.86 | 2.57 | 3 | 3 | 3 | 0.50 | 0.04 | 1 | 2 | 4 |
| POACEAE | Ehrharta | ramosa | 2 | 1 | 2.33 | 1.00 | 2 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 4 |
| POACEAE | Ehrharta | rehmannii | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 4 |
| POACEAE | Ehrharta | setacea | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| POACEAE | Ehrharta | villosa | 4 | 6 | 2.80 | 3.00 | 1 | 3 | 3 | 0.25 | 0.04 | 1 | 2 | 4 |
| RESTIONACEAE | Elegia | cuspidata | 9 | 12 | 3.40 | 4.31 | 0 | 3 | 9 | 0.00 | 0.04 | 1 | 2 | 4 |
| RESTIONACEAE | Elegia | filacea | 16 | 15 | 4.59 | 4.56 | 3 | 2 | 13 | 0.19 | 0.03 | 1 | 2 | 4 |
| RESTIONACEAE | Elegia | juncea | 10 | 5 | 2.82 | 2.33 | 4 | 0 | 5 | 0.44 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Elegia | neesii | 4 | 1 | 2.20 | 2.50 | 3 | 0 | 1 | 0.75 | 0.00 | 1 | 1 | 4 |
| RESTIONACEAE | Elegia | stipularis | 46 | 43 | 3.36 | 4.09 | 6 | 3 | 40 | 0.13 | 0.09 | 1 | 2 | 4 |
| RESTIONACEAE | Elegia | thyrsifera | 0 | 1 | 0.00 | 2.50 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| RESTIONACEAE | Elegia | vaginulata | 4 | 2 | 2.20 | 2.33 | 2 | 0 | 2 | 0.50 | 0.00 | 1 | 2 | 4 |
| ASTERACEAE | Elytropappus | scaber | 15 | 14 | 2.63 | 2.47 | 7 | 8 | 7 | 0.50 | 0.12 | 2 | 1 | 1 |
| CYPERACEAE | Epischoenus | quadrangularis | 2 | 1 | 1.33 | 2.00 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 2 | 4 |
| MESEMBRYANTHEMACEAE | Erepsia | anceps | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Erepsia | bracteata | 7 | 3 | 2.13 | 2.00 | 5 | 1 | 2 | 0.71 | 0.01 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Erepsia | promontorii | 1 | 2 | 1.00 | 1.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 1 | 5 |
| ERICACEAE | Erica | blancheana | 1 | 1 | 2.00 | 1.50 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | bruniades | 0 | 7 | 0.00 | 3.13 | 0 | 7 | 0 | / | 0.09 | 1 | 1 | 1 |
| ERICACEAE | Erica | capensis | 3 | 4 | 3.25 | 3.20 | 0 | 1 | 3 | 0.00 | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | capillaris | 1 | 1 | 1.00 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| ERICACEAE | Erica | cerinthoides | 15 | 6 | 2.31 | 2.29 | 10 | 1 | 5 | 0.67 | 0.02 | 1 | 2 | 1 |
| ERICACEAE | Erica | clavisepala | 1 | 3 | 2.50 | 3.75 | 0 | 2 | 1 | 0.00 | 0.03 | 1 | 1 | 1 |
| ERICACEAE | Erica | coarctata | 1 | 1 | 2.00 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| ERICACEAE | Erica | coccinea | 8 | 6 | 2.56 | 2.57 | 3 | 1 | 5 | 0.38 | 0.01 | 1 | 2 | 1 |
| ERICACEAE | Erica | coriifolia | 29 | 47 | 3.17 | 3.13 | 2 | 19 | 26 | 0.07 | 0.36 | 1 | 1 | 1 |
| ERICACEAE | Erica | eburnea | 0 | 1 | 0.00 | 3.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | exleeana | 10 | 10 | 2.91 | 3.55 | 2 | 2 | 8 | 0.20 | 0.03 | 1 | 1 | 1 |
| ERICACEAE | Erica | gnaphaloides | 4 | 15 | 2.20 | 3.44 | 0 | 11 | 4 | 0.00 | 0.14 | 1 | 1 | 1 |
| ERICACEAE | Erica | hispidula | 0 | 6 | 0.00 | 3.43 | 0 | 6 | 0 | / | 0.07 | 1 | 1 | 1 |
| ERICACEAE | Erica | imbricata | 40 | 47 | 3.49 | 3.50 | 2 | 9 | 38 | 0.05 | 0.22 | 1 | 1 | 1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ERICACEAE | Erica | laeta | 1 | 4 | 2.50 | 3.80 | 1 | 4 | 0 | 1.00 | 0.05 | 1 | 1 | 1 |
| ERICACEAE | Erica | mammosa | 14 | 13 | 2.33 | 2.50 | 6 | 5 | 8 | 0.43 | 0.07 | 1 | 1 | 1 |
| ERICACEAE | Erica | palliiflora | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | parviflora | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| ERICACEAE | Erica | phylicifolia | 2 | 3 | 2.00 | 2.25 | 1 | 2 | 1 | 0.50 | 0.03 | 1 | 1 | 1 |
| ERICACEAE | Erica | plukenetii | 22 | 21 | 2.61 | 2.59 | 8 | 7 | 14 | 0.36 | 0.12 | 1 | 1 | 1 |
| ERICACEAE | Erica | pulchella | 27 | 31 | 3.18 | 3.69 | 6 | 10 | 21 | 0.22 | 0.19 | 1 | 1 | 1 |
| ERICACEAE | Erica | spumosa | 0 | 1 | 0.00 | 3.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | subdivaricata | 1 | 1 | 1.50 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 1 |
| ERICACEAE | Erica | tristis | 0 | 3 | 0.00 | 1.50 | 0 | 3 | 0 | / | 0.04 | 1 | 1 | 2 |
| ASTERACEAE | Eriocephalus | africanus | 1 | 1 | 1.00 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 1 |
| ASTERACEAE | Eriocephalus | racemosus | 2 | 2 | 2.00 | 1.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 1 | 1 |
| EBENACEAE | Euclea | racemosa | 6 | 5 | 2.57 | 2.67 | 1 | 0 | 5 | 0.17 | 0.00 | 2 | 2 | 3 |
| EUPHORBIACEAE | Euphorbia | caput - medusae | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 5 |
| EUPHORBIACEAE | Euphorbia | erythrina | 2 | 2 | 1.67 | 1.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 2 | 1 |
| EUPHORBIACEAE | Euphorbia | genistoides | 11 | 9 | 2.83 | 2.50 | 5 | 3 | 6 | 0.45 | 0.04 | 1 | 2 | 1 |
| EUPHORBIACEAE | Euphorbia | silenifolia | 6 | 0 | 1.86 | 0.00 | 6 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| EUPHORBIACEAE | Euphorbia | tuberosa | 14 | 20 | 2.60 | 2.81 | 2 | 7 | 13 | 0.13 | 0.11 | 1 | 2 | 5 |
| ASTERACEAE | Euryops | abrotanifolius | 3 | 4 | 2.00 | 2.60 | 1 | 2 | 2 | 0.33 | 0.03 | 2 | 1 | 1 |
| CHENOPODIACEAE | Exomis | microphylla | 3 | 3 | 2.25 | 2.00 | 0 | 0 | 3 | 0.00 | 0.00 | 1 | 1 | 1 |
| CONVOLVULACEAE | Falkia | repens | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| ASTERACEAE | Felicia | fruticosa | 2 | 3 | 2.67 | 1.75 | 0 | 1 | 2 | 0.00 | 0.01 | 2 | 1 | 1 |
| POACEAE | Festuca | scabra | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | acuminata | 0 | 2 | 0.00 | 2.00 | 0 | 2 | 0 | / | 0.02 | 1 | 1 | 4 |
| CYPERACEAE | Ficinia | anceps | 6 | 2 | 2.43 | 2.67 | 4 | 0 | 2 | 0.67 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | brevifolia | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | bulbosa | 24 | 24 | 2.92 | 3.16 | 8 | 8 | 16 | 0.33 | 0.14 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | capitella | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| CYPERACEAE | Ficinia | deusta | 14 | 17 | 2.20 | 2.56 | 7 | 10 | 6 | 0.54 | 0.15 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | dunensis | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| CYPERACEAE | Ficinia | ecklonia | 1 | 1 | 1.00 | 2.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | filiformis | 36 | 35 | 2.89 | 3.22 | 9 | 8 | 27 | 0.25 | 0.18 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | indica | 0 | 1 | 0.00 | 3.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | lateralis | 2 | 0 | 3.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | nigrescens | 2 | 2 | 2.00 | 1.33 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | paradoxa | 5 | 1 | 2.33 | 2.00 | 4 | 0 | 1 | 0.80 | 0.00 | 1 | 1 | 4 |
| CYPERACEAE | Ficinia | pinquior | 14 | 7 | 2.80 | 2.38 | 10 | 3 | 4 | 0.71 | 0.04 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | ramosissima | 5 | 6 | 3.67 | 3.71 | 0 | 1 | 5 | 0.00 | 0.01 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | rigida | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | secunda | 9 | 11 | 3.20 | 4.25 | 1 | 3 | 8 | 0.11 | 0.04 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | stolonifera | 0 | 2 | 0.00 | 2.33 | 0 | 2 | 0 | / | 0.02 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | tenuifolia | 14 | 16 | 2.47 | 3.06 | 6 | 8 | 8 | 0.43 | 0.12 | 1 | 2 | 4 |
| CYPERACEAE | Ficinia | zeyheri | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| FRANKENIACEAE | Frankenia | repens | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| RUBIACEAE | Galium | tomentosum | 2 | 1 | 1.67 | 1.50 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 1 | 5 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ASTERACEAE | Gazania | pectinata | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 5 |
| GERANIACEAE | Geranium | incanum | 2 | 1 | 2.33 | 1.00 | 1 | 0 | 1 | 0.50 | 0.00 | 2 | 1 | 5 |
| ASTERACEAE | Gerbera | crocea | 4 | 1 | 1.80 | 1.00 | 3 | 0 | 1 | 0.75 | 0.00 | 2 | 2 | 5 |
| APIACEAE | Glia | prolifera | 1 | 2 | 1.50 | 1.33 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| THYMELAEACEAE | Gnidia | imbricata | 21 | 11 | 2.55 | 2.50 | 13 | 3 | 8 | 0.62 | 0.05 | 1 | 1 | 1 |
| THYMELAEACEAE | Gnidia | pinifolia | 13 | 5 | 2.21 | 1.83 | 8 | 0 | 5 | 0.62 | 0.00 | 1 | 2 | 1 |
| THYMELAEACEAE | Gnidia | subulata | 23 | 17 | 2.42 | 2.50 | 13 | 7 | 0 | 1.00 | 0.10 | 1 | 2 | 1 |
| ASTERACEAE | Haplocarpha | lanata | 5 | 0 | 1.67 | 0.00 | 5 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 5 |
| SCROPHULARIACEAE | Harveya | tubulosa | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| ASTERACEAE | Helichrysum | crispum | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 1 |
| ASTERACEAE | Helichrysum | cymosum | 1 | 1 | 1.00 | 3.00 | 1 | 1 | 0 | 1.00 | 0.01 | 2 | 1 | 1 |
| ASTERACEAE | Helichrysum | dasyanthum | 3 | 2 | 2.25 | 2.00 | 1 | 0 | 2 | 0.33 | 0.00 | 2 | 1 | 1 |
| ASTERACEAE | Helichrysum | niveum | 1 | 1 | 1.50 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 1 | 1 |
| ASTERACEAE | Helichrysum | patulum | 4 | 1 | 2.00 | 1.00 | 4 | 1 | 0 | 1.00 | 0.01 | 2 | 1 | 1 |
| ASTERACEAE | Helichrysum | tinctum | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 5 |
| BRASSICACEAE | Heliophila | linearis | 1 | 0 | 1.50 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| BRASSICACEAE | Heliophila | scoparia | 3 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| BRASSICACEAE | Heliophila | elongata | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| STERCULIACEAE | Hermannia | multiflora | 2 | 1 | 1.67 | 1.50 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 2 | 1 |
| STERCULIACEAE | Hermannia | ternifolia | 1 | 1 | 2.00 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| APIACEAE | Hermas | villosa | 1 | 1 | 1.00 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 5 |
| ASTERACEAE | Hippia | pilosa | 3 | 3 | 2.75 | 2.00 | 1 | 1 | 2 | 0.33 | 0.01 | 1 | 1 | 5 |
| RESTIONACEAE | Hypodiscus | albo - aristatus | 5 | 1 | 1.67 | 1.00 | 4 | 0 | 1 | 0.80 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Hypodiscus | aristatus | 34 | 32 | 2.94 | 3.21 | 7 | 5 | 27 | 0.21 | 0.11 | 1 | 2 | 4 |
| RESTIONACEAE | Hypodiscus | willdenowia | 14 | 12 | 2.60 | 2.85 | 6 | 4 | 8 | 0.43 | 0.06 | 1 | 2 | 4 |
| ASTERACEAE | Ifloga | ambigua | 6 | 4 | 2.14 | 2.20 | 3 | 1 | 3 | 0.50 | 0.01 | 1 | 1 | 1 |
| FABACEAE | Indigofera | angustifolia | 1 | 1 | 1.00 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| FABACEAE | Indigofera | brachystachya | 1 | 1 | 2.00 | 3.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |
| FABACEAE | Indigofera | glomerata | 5 | 3 | 1.83 | 1.75 | 4 | 2 | 1 | 0.80 | 0.03 | 1 | 1 | 1 |
| FABACEAE | Indigofera | mauritanica | 1 | 2 | 1.00 | 1.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 1 | 1 |
| FABACEAE | Indigofera | sarmentosa | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| RESTIONACEAE | Ischyrolepis | capensis | 46 | 50 | 3.02 | 3.16 | 8 | 12 | 38 | 0.17 | 0.34 | 1 | 2 | 4 |
| RESTIONACEAE | Ischyrolepis | cincinnata | 59 | 55 | 3.68 | 4.54 | 6 | 2 | 53 | 0.10 | 0.09 | 1 | 2 | 4 |
| RESTIONACEAE | Ischyrolepis | eleocharis | 11 | 10 | 3.50 | 3.55 | 2 | 1 | 9 | 0.18 | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Ischyrolepis | paludosa | 1 | 2 | 1.50 | 2.67 | 1 | 2 | 0 | 1.00 | 0.03 | 1 | 2 | 4 |
| CYPERACEAE | Isolepis | marginata | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| APIACEAE | Itasina | filifolia | 6 | 2 | 1.86 | 1.33 | 5 | 1 | 1 | 0.83 | 0.01 | 1 | 2 | 5 |
| JUNCACEAE | Juncus | capensis | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| JUNCACEAE | Juncus | krausii | 2 | 2 | 3.00 | 2.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 1 | 4 |
| CURCUBITACEAE | Kedrostis | nana | 4 | 3 | 1.80 | 2.00 | 1 | 0 | 3 | 0.25 | 0.00 | 1 | 2 | 5 |
| RANUNCULACEAE | Knowltonia | capensis | 2 | 3 | 1.67 | 1.75 | 0 | 1 | 2 | 0.00 | 0.01 | 1 | 2 | 5 |
| THYMELAEACEAE | Lachnaea | densiflora | 11 | 1 | 2.17 | 1.00 | 10 | 0 | 1 | 0.91 | 0.00 | 1 | 1 | 1 |
| MESEMBRYANTHEMACEAE | Lampranthus | austricolus | 8 | 4 | 2.22 | 1.60 | 5 | 1 | 3 | 0.63 | 0.01 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Lampranthus | bicolor | 5 | 10 | 1.67 | 2.27 | 2 | 7 | 3 | 0.40 | 0.09 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Lampranthus | falciformis | 1 | 3 | 1.00 | 1.50 | 0 | 2 | 0 | / | 0.02 | 1 | 1 | 5 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MESEMBRYANTHEMACEAE | Lampranthus | promontorii | 2 | 2 | 1.67 | 1.33 | 2 | 2 | 0 | 1.00 | 0.03 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Lampranthus | stenus | 1 | 2 | 1.50 | 2.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 1 | 5 |
| MESEMBRYANTHEMACEAE | Lampranthus | tenuifolius | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| HALORAGACEAE | Laurembergia | repens | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| FABACEAE | Lebeckia | meyeriana | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| PROTEACEAE | Leucadendron | coniferum | 2 | 3 | 2.67 | 2.75 | 0 | 1 | 2 | 0.00 | 0.01 | 2 | 1 | 3 |
| PROTEACEAE | Leucadendron | laureolum | 36 | 37 | 2.92 | 2.92 | 10 | 11 | 26 | 0.28 | 0.24 | 2 | 1 | 2 |
| PROTEACEAE | Leucadendron | salignum | 12 | 8 | 2.08 | 2.11 | 4 | 0 | 8 | 0.33 | 0.00 | 2 | 2 | 1 |
| PROTEACEAE | Leucadendron | xanthoconus | 5 | 5 | 2.50 | 2.00 | 1 | 1 | 4 | 0.20 | 0.01 | 1 | 1 | 3 |
| PROTEACEAE | Leucospermum | conocarpodendron | 8 | 8 | 1.89 | 2.00 | 4 | 4 | 4 | 0.50 | 0.05 | 1 | 2 | 3 |
| PROTEACEAE | Leucospermum | hypophyllocarpodendron | 2 | 2 | 1.33 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 1 |
| APIACEAE | Lichtensteinia | lacera | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 5 |
| CAMPANULACEAE | Lightfootia | longifolia | 13 | 4 | 2.57 | 2.20 | 10 | 1 | 3 | 0.77 | 0.01 | 1 | 1 | 1 |
| CAMPANULACEAE | Lightfootia | parvifolia | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| CAMPANULACEAE | Lightfootia | tenella | 2 | 1 | 2.33 | 2.00 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 1 | 1 |
| CAMPANULACEAE | Lightfootia | tenuis | 1 | 4 | 1.50 | 2.20 | 0 | 3 | 1 | 0.00 | 0.04 | 1 | 2 | 1 |
| PLUMBAGINACEAE | Limonium | scabrum | 3 | 1 | 2.00 | 1.00 | 3 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 5 |
| LINACEAE | Linum | africanum | 2 | 1 | 1.67 | 1.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| LINACEAE | Linum | thunbergii | 1 | 0 | 2.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| FABACEAE | Liparia | parva | 19 | 13 | 2.50 | 2.14 | 8 | 2 | 11 | 0.42 | 0.03 | 1 | 2 | 1 |
| LOBELIACEAE | Lobelia | anceps | 1 | 1 | 1.50 | 1.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 5 |
| LOBELIACEAE | Lobelia | comosa | 10 | 0 | 2.64 | 0.00 | 10 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| LOBELIACEAE | Lobelia | coronopifolia | 17 | 12 | 2.56 | 1.92 | 9 | 4 | 8 | 0.53 | 0.06 | 1 | 2 | 5 |
| LOBELIACEAE | Lobelia | pinifolia | 14 | 12 | 2.47 | 2.46 | 3 | 1 | 11 | 0.21 | 0.01 | 1 | 1 | 1 |
| LOBELIACEAE | Lobelia | setacea | 17 | 13 | 2.44 | 2.00 | 13 | 9 | 4 | 0.76 | 0.14 | 1 | 1 | 5 |
| BORAGINACEAE | Lobostemon | fruticosus | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| RUTACEAE | Macrostylis | villosa | 19 | 12 | 2.85 | 2.69 | 7 | 0 | 12 | 0.37 | 0.00 | 1 | 2 | 1 |
| SCROPHULARIACEAE | Manulea | tomentosa | 3 | 0 | 2.00 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| CYPERACEAE | Mariscus | thunbergii | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Mastersiella | digitata | 2 | 3 | 2.67 | 2.75 | 0 | 1 | 2 | 0.00 | 0.01 | 1 | 2 | 4 |
| CELASTRACEAE | Maurocenia | frangularia | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 3 |
| CELASTRACEAE | Maytenus | lucida | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 2 | 1 |
| POACEAE | Merxmuellera | cincta | 3 | 3 | 2.25 | 2.00 | 1 | 1 | 2 | 0.33 | 0.01 | 1 | 2 | 4 |
| POACEAE | Merxmuellera | rufa | 19 | 24 | 2.55 | 3.44 | 5 | 9 | 15 | 0.25 | 0.15 | 1 | 2 | 4 |
| POACEAE | Merxmuellera | stricta | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| MESEMBRYANTHEMACEAE | Mesembryanthemum | cristallinum | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| ASTERACEAE | Metalasia | brevifolia | 17 | 25 | 3.28 | 3.08 | 5 | 13 | 12 | 0.29 | 0.20 | 2 | 1 | 1 |
| ASTERACEAE | Metalasia | cephalotes | 22 | 28 | 2.70 | 3.66 | 6 | 12 | 16 | 0.27 | 0.20 | 2 | 1 | 1 |
| ASTERACEAE | Metalasia | muricata | 40 | 39 | 2.73 | 3.15 | 15 | 14 | 25 | 0.38 | 0.34 | 2 | 1 | 2 |
| PROTEACEAE | Mimetes | fimbriifolius | 3 | 2 | 1.50 | 1.33 | 2 | 1 | 1 | 0.67 | 0.01 | 1 | 2 | 3 |
| LOBELIACEAE | Monopsis | lutea | 1 | 1 | 1.50 | 1.50 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| POLYGALACEAE | Muraltia | acipetala | 2 | 1 | 3.67 | 1.00 | 2 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 1 |
| POLYGALACEAE | Muraltia | demissa | 0 | 2 | 0.00 | 2.00 | 0 | 2 | 0 | / | 0.02 | 1 | 2 | 1 |
| POLYGALACEAE | Muraltia | filiformis | 1 | 0 | 2.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| POLYGALACEAE | Muraltia | pageae | 0 | 7 | 0.00 | 2.75 | 0 | 7 | 0 | / | 0.09 | 1 | 1 | 1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| POLYGALACEAE | Muraltia | rosmarinifolia | 2 | 2 | 1.33 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 1 |
| POLYGALACEAE | Muraltia | satureioides | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| POLYGALACEAE | Muraltia | thunbergii | 3 | 3 | 2.75 | 2.00 | 1 | 1 | 2 | 0.33 | 0.01 | 1 | 2 | 1 |
| MYRICACEAE | Myrica | cordifolia | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 2 | 2 |
| MYRICACEAE | Myrica | quercifolia | 2 | 5 | 3.33 | 2.67 | 1 | 4 | 1 | 0.50 | 0.05 | 2 | 2 | 1 |
| MYRSINACEAE | Myrsine | africana | 5 | 3 | 2.33 | 2.25 | 2 | 1 | 3 | 0.40 | 0.01 | 2 | 2 | 1 |
| POLYGALACEAE | Nylandtia | spinosa | 0 | 3 | 0.00 | 1.75 | 0 | 3 | 0 | / | 0.04 | 2 | 2 | 1 |
| ASTERACEAE | Oedera | imbricata | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 1 |
| OLEACEAE | Olea | capensis | 5 | 7 | 2.00 | 2.63 | 0 | 2 | 5 | 0.00 | 0.03 | 2 | 2 | 3 |
| OLEACEAE | Olea | exasperata | 1 | 1 | 2.00 | 3.00 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 2 | 1 |
| ASTERACEAE | Osmitopsis | asteriscoides | 1 | 1 | 2.50 | 2.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 2 |
| ASTERACEAE | Osteospermum | polygaloides | 11 | 15 | 2.83 | 2.69 | 7 | 11 | 4 | 0.64 | 0.16 | 1 | 1 | 1 |
| ASTERACEAE | Othonna | digitata | 1 | 2 | 1.00 | 1.33 | 0 | 2 | 1 | 0.00 | 0.03 | 2 | 2 | 5 |
| THYMELAEACEAE | Passerina | paleacea | 3 | 2 | 3.25 | 2.00 | 1 | 0 | 2 | 0.33 | 0.00 | 1 | 1 | 1 |
| THYMELAEACEAE | Passerina | vulgaris | 15 | 19 | 2.81 | 3.00 | 2 | 6 | 13 | 0.13 | 0.09 | 1 | 1 | 3 |
| GERANIACEAE | Pelargonium | betulinum | 2 | 2 | 2.33 | 3.33 | 0 | 0 | 2 | 0.00 | 0.00 | 2 | 2 | 1 |
| GERANIACEAE | Pelargonium | capitatum | 2 | 1 | 1.33 | 1.50 | 1 | 0 | 1 | 0.50 | 0.00 | 2 | 2 | 5 |
| GERANIACEAE | Pelargonium | cucullatum | 8 | 6 | 2.33 | 1.86 | 6 | 4 | 2 | 0.75 | 0.05 | 2 | 2 | 1 |
| GERANIACEAE | Pelargonium | grossulariodes | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 5 |
| GERANIACEAE | Pelargonium | longifolium | 1 | 8 | 1.00 | 1.78 | 1 | 8 | 0 | 1.00 | 0.10 | 2 | 2 | 5 |
| GERANIACEAE | Pelargonium | myrrhifolium | 1 | 2 | 1.00 | 1.67 | 1 | 2 | 0 | 1.00 | 0.03 | 2 | 2 | 5 |
| GERANIACEAE | Pelargonium | tabulare | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 5 |
| GERANIACEAE | Pelargonium | triste | 2 | 6 | 2.00 | 1.86 | 1 | 5 | 1 | 0.50 | 0.06 | 2 | 2 | 5 |
| PENAEACEAE | Penaea | mucronata | 20 | 16 | 2.86 | 2.82 | 6 | 2 | 14 | 0.30 | 0.03 | 1 | 2 | 1 |
| POACEAE | Pentaschistis | acinosa | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | aurea | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | colorata | 38 | 32 | 3.00 | 2.55 | 10 | 4 | 28 | 0.26 | 0.09 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | curvifolia | 31 | 19 | 3.09 | 3.15 | 14 | 2 | 17 | 0.45 | 0.04 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | macrocalycina | 6 | 7 | 2.86 | 2.50 | 1 | 2 | 5 | 0.17 | 0.03 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | malouinensis | 5 | 3 | 2.00 | 1.50 | 4 | 2 | 1 | 0.80 | 0.03 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | pallida | 9 | 6 | 2.90 | 2.71 | 4 | 1 | 5 | 0.44 | 0.01 | 1 | 2 | 4 |
| POACEAE | Pentaschistis | papillosa | 16 | 12 | 2.41 | 2.23 | 8 | 4 | 8 | 0.50 | 0.06 | 1 | 2 | 4 |
| ASTERACEAE | Petalacte | coronata | 10 | 11 | 2.64 | 2.67 | 3 | 4 | 7 | 0.30 | 0.06 | 2 | 1 | 1 |
| ASTERACEAE | Phaenocoma | prolifera | 4 | 3 | 1.80 | 1.75 | 1 | 0 | 3 | 0.25 | 0.00 | 2 | 3 | 1 |
| AIZOACEAE | Pharnaceum | cordifolium | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| AIZOACEAE | Pharnaceum | lanatum | 6 | 3 | 2.00 | 1.50 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| RHAMNACEAE | Phylica | buxifolia | 3 | 4 | 2.00 | 2.00 | 0 | 1 | 3 | 0.00 | 0.01 | 1 | 1 | 3 |
| RHAMNACEAE | Phylica | ericoides | 0 | 4 | 0.00 | 2.80 | 0 | 4 | 0 | / | 0.05 | 1 | 1 | 1 |
| RHAMNACEAE | Phylica | imberbis | 42 | 37 | 2.88 | 2.68 | 8 | 3 | 34 | 0.19 | 0.08 | 1 | 2 | 1 |
| RHAMNACEAE | Phylica | parviflora | 4 | 5 | 2.60 | 2.83 | 3 | 4 | 1 | 0.75 | 0.05 | 1 | 1 | 1 |
| RHAMNACEAE | Phylica | stipularis | 10 | 10 | 3.00 | 2.91 | 3 | 3 | 7 | 0.30 | 0.04 | 1 | 2 | 1 |
| PLANTAGINACEAE | Plantago | crassifolia | 1 | 1 | 2.00 | 3.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 5 |
| RESTIONACEAE | Platycaulos | compressus | 3 | 2 | 3.00 | 3.33 | 1 | 0 | 2 | 0.33 | 0.00 | 1 | 2 | 4 |
| ASTERACEAE | Plecostachys | serpyllifolia | 4 | 2 | 2.20 | 2.67 | 2 | 0 | 2 | 0.50 | 0.00 | 2 | 1 | 1 |
| AIZOACEAE | Polpoda | capensis | 1 | 1 | 2.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| POLYGALACEAE | Polygala | bracteolata | 6 | 0 | 2.57 | 0.00 | 6 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| POLYGALACEAE | Polygala | garcini | 4 | 1 | 2.00 | 1.50 | 4 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 5 |
| POLYGALACEAE | Polygala | myrtifolia | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 2 |
| POLYGALACEAE | Polygala | recognita | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| POACEAE | Polypogon | strictus | 0 | 1 | 0.00 | 1.50 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| CAMPANULACEAE | Prismatocarpus | sessilis | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| ASPARAGACEAE | Protasparagus | aethiopicus | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 6 |
| ASPARAGACEAE | Protasparagus | capensis | 3 | 4 | 1.50 | 1.60 | 0 | 1 | 3 | 0.00 | 0.01 | 1 | 2 | 6 |
| ASPARAGACEAE | Protasparagus | compactus | 8 | 7 | 1.78 | 1.75 | 1 | 0 | 7 | 0.13 | 0.00 | 1 | 2 | 6 |
| ASPARAGACEAE | Protasparagus | rubicundus | 1 | 2 | 1.00 | 1.33 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 2 | 6 |
| PROTEACEAE | Protea | acaulos | 1 | 1 | 2.00 | 2.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| PROTEACEAE | Protea | cynaroides | 2 | 3 | 1.33 | 1.50 | 1 | 2 | 1 | 0.50 | 0.03 | 1 | 2 | 2 |
| PROTEACEAE | Protea | lepidocarpodendron | 2 | 2 | 1.33 | 2.00 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 2 |
| POACEAE | Pseudopentameris | macrantha | 12 | 10 | 2.69 | 3.27 | 3 | 1 | 9 | 0.25 | 0.01 | 1 | 2 | 4 |
| FABACEAE | Psoralea | asarina | 2 | 0 | 2.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| FABACEAE | Psoralea | imbricata | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| FABACEAE | Psoralea | laxa | 0 | 2 | 0.00 | 1.67 | 0 | 2 | 0 | / | 0.02 | 1 | 2 | 1 |
| FABACEAE | Psoralea | pinnata | 1 | 1 | 2.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 3 |
| FABACEAE | Psoralea | repens | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| DENNSTAEDTIACEAE | Pteridium | aquilinum | 1 | 1 | 2.00 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 2 | 1 |
| CELASTRACEAE | Pterocelastrus | tricuspidatus | 2 | 2 | 2.00 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 2 | 2 | 3 |
| FABACEAE | Rafnia | crassifolia | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 1 |
| RESTIONACEAE | Restio | ambiguus | 1 | 1 | 2.00 | 2.00 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | bifurcus | 15 | 23 | 3.50 | 4.04 | 2 | 10 | 13 | 0.13 | 0.15 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | dodii | 8 | 10 | 2.22 | 3.45 | 1 | 3 | 7 | 0.13 | 0.04 | 1 | 1 | 4 |
| RESTIONACEAE | Restio | egregius | 3 | 1 | 2.25 | 3.00 | 2 | 0 | 1 | 0.67 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | filiformis | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | leptostachyus | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | quinquefarius | 18 | 24 | 3.42 | 3.88 | 0 | 6 | 19 | 0.00 | 0.10 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | sarcocladus | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| RESTIONACEAE | Restio | triticeus | 1 | 1 | 1.50 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 4 |
| ANACARDIACEAE | Rhus | glauca | 4 | 5 | 2.20 | 2.00 | 1 | 2 | 3 | 0.25 | 0.03 | 2 | 2 | 3 |
| ANACARDIACEAE | Rhus | laevigata | 7 | 4 | 2.25 | 2.20 | 3 | 0 | 4 | 0.43 | 0.00 | 2 | 2 | 1 |
| ANACARDIACEAE | Rhus | lucida | 16 | 18 | 2.06 | 2.26 | 2 | 4 | 14 | 0.13 | 0.06 | 2 | 2 | 3 |
| ANACARDIACEAE | Rhus | rosmarinifolia | 2 | 1 | 1.67 | 3.00 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 2 | 1 |
| FABACEAE | Rhynchosia | ferulifolia | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 5 |
| CAMPANULACEAE | Roella | amplexicaulis | 3 | 0 | 1.50 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | ciliata | 19 | 3 | 3.70 | 1.50 | 17 | 1 | 2 | 0.89 | 0.02 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | decurrens | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | prostrata | 3 | 0 | 2.25 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | recurvata | 3 | 8 | 2.25 | 2.67 | 8 | 1 | 1 | 0.89 | 0.01 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | squarrosa | 1 | 1 | 2.00 | 1.50 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 3 | 1 |
| CAMPANULACEAE | Roella | triflora | 6 | 13 | 3.29 | 2.36 | 5 | 12 | 1 | 0.83 | 0.16 | 1 | 3 | 1 |
| POLYGONACEAE | Rumex | saggitatus | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 2 | 5 |
| MESEMBRYANTHEMACEAE | Ruschia | promontorii | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MESEMBRYANTHEMACEAE | Ruschia | sarmentosa | 7 | 5 | 2.50 | 1.83 | 4 | 2 | 3 | 0.57 | 0.03 | 1 | 1 | 5 |
| ERICACEAE | Salaxis | axillaris | 32 | 36 | 3.61 | 3.95 | 7 | 11 | 25 | 0.22 | 0.22 | 1 | 1 | 1 |
| PENAEACEAE | Saltera | sarcocolla | 11 | 8 | 2.58 | 2.22 | 3 | 0 | 1 | 0.75 | 0.00 | 1 | 2 | 1 |
| LAMIACEAE | Salvia | africana - lutea | 1 | 1 | 1.00 | 1.50 | 1 | 1 | 0 | 1.00 | 0.01 | 1 | 1 | 2 |
| PRIMULACEAE | Samolus | valerandi | 1 | 1 | 3.00 | 2.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 1 | 5 |
| DIPSACACEAE | Scabiosa | africana | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| SCHIZAEACEAE | Schizaea | pectinata | 12 | 8 | 2.23 | 1.89 | 6 | 2 | 6 | 0.50 | 0.03 | 2 | 2 | 4 |
| CYPERACEAE | Scirpus | nodosus | 2 | 2 | 2.33 | 3.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 2 | 4 |
| ERICACEAE | Scyphogyne | muscosa | 21 | 25 | 3.91 | 3.62 | 3 | 7 | 18 | 0.14 | 0.12 | 1 | 1 | 1 |
| SELAGINACEAE | Selago | dregei | 1 | 2 | 2.00 | 2.00 | 1 | 2 | 0 | 1.00 | 0.03 | 1 | 3 | 1 |
| SELAGINACEAE | Selago | scabrida | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| SELAGINACEAE | Selago | serrata | 2 | 0 | 2.00 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 5 |
| SELAGINACEAE | Selago | spuria | 12 | 1 | 2.77 | 1.00 | 12 | 1 | 0 | 1.00 | 0.01 | 1 | 3 | 5 |
| ASTERACEAE | Senecio | amiciflorus | 1 | 1 | 1.00 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 1 | 5 |
| ASTERACEAE | Senecio | burchellii | 3 | 0 | 1.50 | 0.00 | 3 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 5 |
| ASTERACEAE | Senecio | pubigerus | 2 | 2 | 2.00 | 2.33 | 0 | 0 | 2 | 0.00 | 0.00 | 2 | 1 | 5 |
| ASTERACEAE | Senecio | purpureus | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 5 |
| ASTERACEAE | Senecio | triqueter | 11 | 6 | 2.33 | 2.14 | 7 | 2 | 4 | 0.64 | 0.03 | 2 | 2 | 1 |
| ASTERACEAE | Senecio | umbellatus | 4 | 1 | 1.60 | 1.00 | 4 | 1 | 0 | 1.00 | 0.01 | 2 | 1 | 5 |
| PROTEACEAE | Serruria | glomerata | 4 | 5 | 2.60 | 2.67 | 1 | 2 | 3 | 0.25 | 0.03 | 1 | 1 | 1 |
| PROTEACEAE | Serruria | villosa | 12 | 16 | 3.23 | 3.18 | 2 | 6 | 10 | 0.17 | 0.09 | 1 | 1 | 1 |
| SAPOTACEAE | Sideroxylon | inerme | 1 | 1 | 1.50 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 2 | 3 |
| ILLECEBRACEAE | Silene | burchellii | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| ERICACEAE | Simocheilus | depressus | 22 | 31 | 3.70 | 3.81 | 2 | 11 | 20 | 0.09 | 0.19 | 1 | 1 | 1 |
| SOLANACEAE | Solanum | guineense | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 1 |
| CARYOPHYLLACEAE | Spergularia | media | 2 | 2 | 1.67 | 1.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 1 | 5 |
| POACEAE | Sporobolus | virginicus | 2 | 2 | 2.00 | 1.67 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 2 | 4 |
| BRUNIACEAE | Staavia | radiata | 3 | 4 | 1.50 | 1.60 | 0 | 1 | 3 | 0.00 | 0.01 | 1 | 2 | 1 |
| RESTIONACEAE | Staberoha | banksii | 10 | 10 | 3.18 | 3.45 | 1 | 1 | 9 | 0.10 | 0.01 | 2 | 2 | 4 |
| RESTIONACEAE | Staberoha | cernua | 35 | 28 | 3.17 | 2.93 | 10 | 5 | 24 | 0.29 | 0.11 | 2 | 2 | 4 |
| RESTIONACEAE | Staberoha | distachyos | 4 | 11 | 2.60 | 2.83 | 1 | 8 | 3 | 0.25 | 0.10 | 2 | 2 | 4 |
| POACEAE | Stenotaphrum | secundatum | 2 | 5 | 2.33 | 2.00 | 0 | 3 | 2 | 0.00 | 0.04 | 1 | 2 | 4 |
| STILBACEAE | Stilbe | ericoides | 4 | 2 | 2.40 | 2.00 | 3 | 1 | 1 | 0.75 | 0.01 | 1 | 2 | 1 |
| STILBACEAE | Stilbe | vestita | 1 | 1 | 1.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| ASTERACEAE | Stoebe | capitata | 3 | 5 | 2.50 | 2.00 | 1 | 3 | 2 | 0.33 | 0.04 | 2 | 1 | 1 |
| ASTERACEAE | Stoebe | fusca | 0 | 1 | 0.00 | 2.50 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 1 |
| ASTERACEAE | Stoebe | incana | 3 | 12 | 1.50 | 2.77 | 2 | 11 | 1 | 0.67 | 0.14 | 2 | 1 | 1 |
| ASTERACEAE | Stoebe | plumosa | 1 | 1 | 1.50 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 1 | 2 |
| ASTERACEAE | Stoebe | rosea | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 2 | 1 | 1 |
| ASTERACEAE | Stoebe | sphaerocephala | 18 | 26 | 2.89 | 3.11 | 3 | 11 | 15 | 0.17 | 0.17 | 2 | 1 | 1 |
| THYMELAEACEAE | Struthiola | ciliata | 43 | 44 | 3.18 | 3.31 | 7 | 8 | 36 | 0.16 | 0.21 | 1 | 2 | 1 |
| THYMELAEACEAE | Struthiola | dodecandra | 1 | 1 | 1.00 | 1.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| THYMELAEACEAE | Struthiola | salteri | 1 | 1 | 2.00 | 3.00 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 1 |
| PENAEACEAE | Stylapterus | fruticulosus | 10 | 6 | 2.18 | 2.00 | 6 | 2 | 4 | 0.60 | 0.03 | 1 | 2 | 1 |
| SCROPHULARIACEAE | Sutera | lychnidea | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ERICACEAE | Sympieza | labialis | 8 | 22 | 3.89 | 4.00 | 0 | 14 | 8 | 0.00 | 0.19 | 1 | 1 | 1 |
| ASTERACEAE | Syncarpha | canescens | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 2 | 3 | 1 |
| ASTERACEAE | Syncarpha | gnaphaloides | 2 | 0 | 1.33 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 2 | 3 | 1 |
| ASTERACEAE | Syncarpha | speciosissima | 6 | 7 | 1.71 | 2.25 | 3 | 4 | 3 | 0.50 | 0.05 | 2 | 3 | 1 |
| ASTERACEAE | Syncarpha | vestita | 6 | 24 | 2.00 | 2.96 | 2 | 20 | 4 | 0.33 | 0.27 | 2 | 3 | 1 |
| ERICACEAE | Syndesmanthus | articulatus | 11 | 12 | 3.17 | 3.38 | 2 | 5 | 8 | 0.20 | 0.07 | 1 | 1 | 1 |
| ASTERACEAE | Tarchonanthus | camphoratus | 2 | 2 | 1.33 | 1.67 | 0 | 0 | 2 | 0.00 | 0.00 | 1 | 2 | 3 |
| AIZOACEAE | Tetragonia | decumbens | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 5 |
| AIZOACEAE | Tetragonia | fruiticosa | 1 | 2 | 1.50 | 1.67 | 0 | 1 | 1 | 0.00 | 0.01 | 2 | 1 | 1 |
| CYPERACEAE | Tetraria | autumnalis | 0 | 2 | 0.00 | 1.33 | 0 | 2 | 0 | / | 0.02 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | brevicaulis | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | bromoides | 1 | 1 | 1.50 | 1.50 | 0 | 0 | 1 | 0.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | compar | 21 | 28 | 2.55 | 2.69 | 4 | 11 | 17 | 0.19 | 0.18 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | crassa | 0 | 2 | 0.00 | 2.67 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | cuspidata | 46 | 42 | 2.89 | 3.35 | 12 | 8 | 35 | 0.26 | 0.24 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | eximia | 33 | 34 | 2.65 | 2.57 | 4 | 5 | 29 | 0.12 | 0.10 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | fasciata | 16 | 17 | 2.76 | 3.06 | 6 | 7 | 10 | 0.38 | 0.11 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | fimbriolata | 0 | 1 | 0.00 | 1.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | flexuosa | 14 | 13 | 3.13 | 3.21 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| CYPERACEAE | Tetraria | microstachys | 37 | 29 | 3.08 | 3.80 | 11 | 3 | 26 | 0.30 | 0.07 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | pygmaea | 1 | 1 | 2.50 | 1.50 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 4 |
| CYPERACEAE | Tetraria | sylvatica | 8 | 10 | 3.00 | 2.82 | 3 | 5 | 5 | 0.38 | 0.07 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | thermalis | 9 | 10 | 2.20 | 2.00 | 0 | 1 | 9 | 0.00 | 0.01 | 1 | 2 | 4 |
| CYPERACEAE | Tetraria | ustulata | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | arenarius | 0 | 1 | 0.00 | 2.00 | 0 | 1 | 0 | / | 0.01 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | erectus | 2 | 1 | 2.67 | 1.50 | 1 | 0 | 1 | 0.50 | 0.00 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | fraternus | 1 | 1 | 2.00 | 2.50 | 0 | 0 | 1 | 0.00 | 0.00 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | fruticosus | 13 | 8 | 2.57 | 2.89 | 5 | 0 | 8 | 0.38 | 0.00 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | gracilis | 0 | 2 | 0.00 | 2.00 | 0 | 2 | 0 | / | 0.02 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | lucens | 59 | 54 | 3.53 | 3.65 | 8 | 3 | 51 | 0.14 | 0.14 | 2 | 2 | 4 |
| RESTIONACEAE | Thamnochortus | obtusus | 0 | 2 | 0.00 | 3.00 | 0 | 2 | 0 | / | 0.02 | 2 | 2 | 4 |
| SANTALACEAE | Thesidium | hirtum | 2 | 2 | 2.00 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 1 |
| SANTALACEAE | Thesium | acuminatum | 15 | 10 | 2.81 | 1.91 | 12 | 5 | 4 | 0.75 | 0.08 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | aggregatum | 2 | 2 | 1.67 | 1.33 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 1 | 1 |
| SANTALACEAE | Thesium | carinatum | 5 | 0 | 3.00 | 0.00 | 5 | 0 | 0 | 1.00 | 0.00 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | ericifolium | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | schumannianum | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | spicatum | 18 | 24 | 2.42 | 2.68 | 3 | 9 | 15 | 0.17 | 0.14 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | strictum | 4 | 5 | 2.20 | 1.67 | 1 | 2 | 3 | 0.25 | 0.03 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | virgatum | 18 | 19 | 2.68 | 2.30 | 12 | 16 | 6 | 0.67 | 0.25 | 1 | 3 | 1 |
| SANTALACEAE | Thesium | viridifolium | 9 | 10 | 3.00 | 2.36 | 5 | 5 | 5 | 0.50 | 0.07 | 1 | 3 | 1 |
| ASPHODELACEAE | Trachyandra | hirsutiflora | 5 | 12 | 2.17 | 2.08 | 2 | 9 | 3 | 0.40 | 0.12 | 1 | 2 | 6 |
| ASPHODELACEAE | Trachyandra | revoluta | 1 | 0 | 1.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 6 |
| ASPHODELACEAE | Trachyandra | tabularis | 8 | 7 | 2.33 | 1.88 | 6 | 5 | 2 | 0.75 | 0.07 | 1 | 2 | 6 |
| POACEAE | Tribolium | hispidum | 1 | 0 | 2.50 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| POACEAE | Tribolium | uniolae | 5 | 2 | 2.33 | 1.33 | 4 | 1 | 1 | 0.80 | 0.01 | 1 | 2 | 4 |
| CRASSULACEAE | Tylecodon | paniculatus | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 1 | 5 |
| ASTERACEAE | Ursinia | paleacea | 22 | 16 | 2.35 | 2.47 | 9 | 4 | 12 | 0.43 | 0.07 | 1 | 1 | 1 |
| ASTERACEAE | Ursinia | tenuifolia | 3 | 5 | 2.00 | 2.33 | 2 | 5 | 1 | 0.67 | 0.06 | 1 | 1 | 5 |
| ASTERACEAE | Vellereophyton | dealbatum | 1 | 2 | 1.00 | 1.67 | 0 | 1 | 1 | 0.00 | 0.01 | 2 | 1 | 5 |
| VISCACEAE | Viscum | capensis | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 2 | 1 | 1 |
| HAEMODORACEAE | Wachendorfia | paniculata | 1 | 2 | 1.00 | 1.67 | 0 | 1 | 1 | 0.00 | 0.01 | 1 | 2 | 6 |
| CAMPANULACEAE | Wahlenbergia | obovata | 1 | 0 | 3.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 5 |
| IRIDACEAE | Watsonia | meriana | 0 | 1 | 0.00 | 2.50 | 0 | 1 | 0 | / | 0.01 | 2 | 2 | 6 |
| IRIDACEAE | Watsonia | tabularis | 12 | 7 | 2.23 | 2.13 | 7 | 2 | 5 | 0.58 | 0.03 | 2 | 2 | 6 |
| RESTIONACEAE | Willdenowia | glomerata | 19 | 20 | 3.20 | 3.90 | 3 | 4 | 16 | 0.16 | 0.06 | 1 | 2 | 4 |
| RESTIONACEAE | Willdenowia | humilis | 1 | 0 | 1.50 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 4 |
| RESTIONACEAE | Willdenowia | incurvata | 3 | 1 | 2.75 | 3.00 | 1 | 0 | 1 | 0.50 | 0.00 | 1 | 1 | 4 |
| RESTIONACEAE | Willdenowia | teres | 2 | 2 | 2.67 | 2.67 | 1 | 1 | 1 | 0.50 | 0.01 | 1 | 2 | 4 |
| ARACEAE | Zantedeschia | aethiopica | 1 | 0 | 1.00 | 0.00 | 1 | 0 | 0 | 1.00 | 0.00 | 1 | 2 | 6 |
| ZYGOPHYLLACEAE | Zygophyllum | flexuosum | 0 | 1 | 0.00 | 1.00 | 0 | 1 | 0 | / | 0.01 | 1 | 2 | 1 |
| ZYGOPHYLLACEAE | Zygophyllum | procumbens | 3 | 0 | 1.50 | 0.00 | 2 | 0 | 0 | 1.00 | 0.00 | 1 | 1 | 1 |
| ZYGOPHYLLACEAE | Zygophyllum | spinosum | 2 | 3 | 1.33 | 1.75 | 1 | 1 | 2 | 0.33 | 0.01 | 1 | 2 | 1 |

# Appendix 3 A comparison of the species composition in each of the 81 sites at the two sampling times.

The vegetation types were described in chapter 2 and are abbreviated as follows; WET - wetlands, WRF - wet restioid fynbos, MOP - mesic oligotrophic proteoid fynbos, SED - sedgeland, SPF - sandplain proteoid fynbos, DAF - dune asteraceous fynbos, CSA - coastal scree asteraceous fynbos.

| Site number | Vegetation type | Number of species in 1966 | Number of species in 1996 | Number of species shared | Sorenson's coefficient X 100 |
|---|---|---|---|---|---|
| 1 | MOP | 51 | 46 | 33 | 68.04 |
| 2 | MOP | 43 | 30 | 24 | 65.75 |
| 3 | MOP | 68 | 45 | 35 | 61.95 |
| 4 | MOP | 28 | 24 | 14 | 53.85 |
| 8 | MOP | 79 | 50 | 41 | 63.57 |
| 9 | MOP | 73 | 50 | 41 | 66.68 |
| 10 | MOP | 50 | 53 | 31 | 60.19 |
| 12 | MOP | 64 | 47 | 32 | 57.66 |
| 13 | WRF | 44 | 34 | 26 | 66.67 |
| 14 | WRF | 44 | 32 | 21 | 55.24 |
| 15 | WRF | 66 | 27 | 23 | 49.46 |
| 16 | WRF | 52 | 29 | 23 | 56.79 |
| 17 | WRF | 30 | 27 | 19 | 66.67 |
| 18 | WRF | 18 | 14 | 8 | 50.00 |
| 19 | WRF | 27 | 28 | 15 | 54.55 |
| 21 | MOP | 37 | 32 | 24 | 69.57 |
| 22 | WRF | 34 | 34 | 25 | 73.53 |
| 23 | MOP | 26 | 23 | 16 | 65.31 |
| 24 | MOP | 46 | 44 | 27 | 60.0 |
| 25 | DAF | 14 | 18 | 7 | 43.75 |
| 27 | MOP | 52 | 53 | 40 | 76.19 |
| 28 | MOP | 38 | 49 | 29 | 66.67 |
| 29 | WRF | 15 | 17 | 9 | 56.25 |
| 30 | MOP | 52 | 60 | 39 | 69.64 |
| 31 | MOP | 51 | 51 | 43 | 84.31 |
| 34 | MOP | 45 | 61 | 41 | 77.36 |
| 36 | MOP | 41 | 46 | 31 | 71.26 |
| 37 | WRF | 34 | 43 | 25 | 64.96 |
| 38 | WRF | 20 | 20 | 13 | 65.00 |
| 39 | MOP | 51 | 54 | 36 | 68.57 |
| 40 | MOP | 35 | 46 | 23 | 56.79 |
| 42 | MOP | 56 | 41 | 26 | 53.61 |
| 44 | MOP | 61 | 60 | 40 | 66.12 |
| 45 | MOP | 51 | 58 | 38 | 69.73 |
| 46 | WRF | 28 | 32 | 20 | 66.67 |

| | | | | | |
|---|---|---|---|---|---|
| **47** | **WET** | 6 | 15 | 5 | 47.62 |
| **48** | **WRF** | 20 | 15 | 9 | 51.43 |
| **49** | **WRF** | 21 | 43 | 19 | 59.375 |
| **50** | **WRF** | 22 | 41 | 14 | 44.44 |
| **54** | **MOP** | 36 | 28 | 15 | 46.88 |
| **55** | **WRF** | 33 | 29 | 19 | 61.30 |
| **56** | **WRF** | 17 | 27 | 10 | 45.46 |
| **57** | **MOP** | 32 | 45 | 27 | 70.13 |
| **58** | **WET** | 18 | 25 | 11 | 51.16 |
| **59** | **MOP** | 42 | 61 | 32 | 62.14 |
| **60** | **CSA** | 15 | 11 | 7 | 53.85 |
| **61** | **MOP** | 47 | 46 | 26 | 55.91 |
| **62** | **MOP** | 25 | 47 | 22 | 61.11 |
| **63** | **MOP** | 36 | 43 | 25 | 63.3 |
| **64** | **WRF** | 36 | 40 | 27 | 71.05 |
| **65** | **WRF** | 12 | 22 | 8 | 47.06 |
| **66** | **MOP** | 39 | 37 | 29 | 76.32 |
| **67** | **MOP** | 49 | 42 | 35 | 76.93 |
| **68** | **DAF** | 25 | 26 | 15 | 58.82 |
| **70** | **MOP** | 49 | 40 | 23 | 51.69 |
| **71** | **MOP** | 35 | 41 | 28 | 73.68 |
| **72** | **WRF** | 36 | 27 | 17 | 53.97 |
| **73** | **MOP** | 39 | 37 | 23 | 60.53 |
| **74** | **MOP** | 39 | 31 | 21 | 60.00 |
| **75** | **MOP** | 75 | 61 | 46 | 67.65 |
| **76** | **MOP** | 71 | 50 | 39 | 64.46 |
| **78** | **WRF** | 24 | 24 | 16 | 66.67 |
| **79** | **WRF** | 58 | 41 | 33 | 66.67 |
| **80** | **CSA** | 25 | 20 | 16 | 71.11 |
| **81** | **MOP** | 44 | 31 | 25 | 66.67 |
| **82** | **WRF** | 74 | 48 | 39 | 63.93 |
| **83** | **WRF** | 14 | 13 | 8 | 59.26 |
| **84** | **MOP** | 33 | 54 | 29 | 66.67 |
| **86** | **MOP** | 51 | 41 | 28 | 60.87 |
| **87** | **MOP** | 73 | 66 | 47 | 67.63 |
| **88** | **MOP** | 24 | 30 | 17 | 62.96 |
| **89** | **MOP** | 24 | 21 | 13 | 57.78 |
| **90** | **DAF** | 20 | 18 | 15 | 78.95 |
| **91** | **SED** | 11 | 16 | 6 | 44.44 |
| **92** | **MOP** | 39 | 42 | 21 | 51.85 |
| **94** | **SPF** | 27 | 36 | 22 | 69.84 |
| **95** | **MOP** | 27 | 20 | 11 | 46.81 |
| **97** | **CSA** | 4 | 6 | 3 | 60.00 |
| **98** | **MOP** | 46 | 56 | 33 | 64.71 |
| **99** | **MOP** | 38 | 38 | 24 | 63.16 |
| **100** | **MOP** | 52 | 32 | 24 | 57.14 |