

# Thirty years of change in the fynbos vegetation of the Cape of Good Hope Nature Reserve, South Africa

S.D.J. PRIVETT \*†, R.M. COWLING\* and H.C. TAYLOR\*\*

**Keywords:** fire effects, fynbos, succession, temporal change, vegetation monitoring

## ABSTRACT

This study used permanently marked 50 m<sup>2</sup> 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, South Africa. Management records were used to examine the role of post-fire age, fire frequency and intensity, as well as biotic interactions (competition from overstorey proteoids and alien plants) in influencing vegetation composition over this time period. The mean similarity in species composition of sites 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 differences resulting from different stages in the post-fire succession as well as the impact 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 on 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.

## CONTENTS

## INTRODUCTION

Introduction .....	99
Study area .....	101
Methods .....	101
Results and discussion .....	102
1. Fire effects .....	102
1.1. Post-fire succession .....	102
1.1.1. Early successional changes .....	103
1.1.2. Successional changes after long fire-free intervals in upland fynbos .....	103
1.1.3. Successional changes after long fire-free intervals in coastal fynbos .....	105
1.2. Fire frequency .....	105
1.2.1. Short intervals between fires .....	106
1.2.2. Long intervals between fires .....	106
2. Dynamics of serotinous Proteaceae .....	107
2.1. Causes of decline of serotinous Proteaceae ..	108
2.2. Causes of increase of serotinous Proteaceae ..	108
2.3. The impact of serotinous Proteaceae on understorey species diversity .....	109
3. Alien plants .....	110
3.1. A comparison of the alien threat in 1966 and 1996 .....	110
3.2. Impact of aliens on indigenous vegetation ..	110
3.2.1. Sites invaded between surveys and subsequently cleared .....	110
3.2.2. The impact of existing stands of alien plants .....	111
Conclusions .....	112
Acknowledgements .....	112
References .....	112
Appendix 1 .....	114
Appendix 2 .....	115

*'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)

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, South Africa. 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 impacts of the various components of the fire regime on recruitment have looked at parent to seedling ratios at the same site following a single fire event (Bond 1980; Van Wilgen 1981; Hoffman *et al.* 1987; Cowling & 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 (Richardson *et al.* 1989; Holmes & Cowling 1997), but see Richardson & 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.

While many studies on decade-scale vegetation change have been undertaken internationally (e.g. Fojt & 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 & Cowling 1990; O'Connor & 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 re-

\* Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, 7700 Rondebosch, Cape Town.

\*\* Late, of the National Botanical Institute, Private Bag X7, 7735 Claremont, Cape Town.

† Present address: Grootbos Nature Reserve, P.O. Box 148, 7220 Gansbaai, South Africa.

MS. received: 2000-02-15.

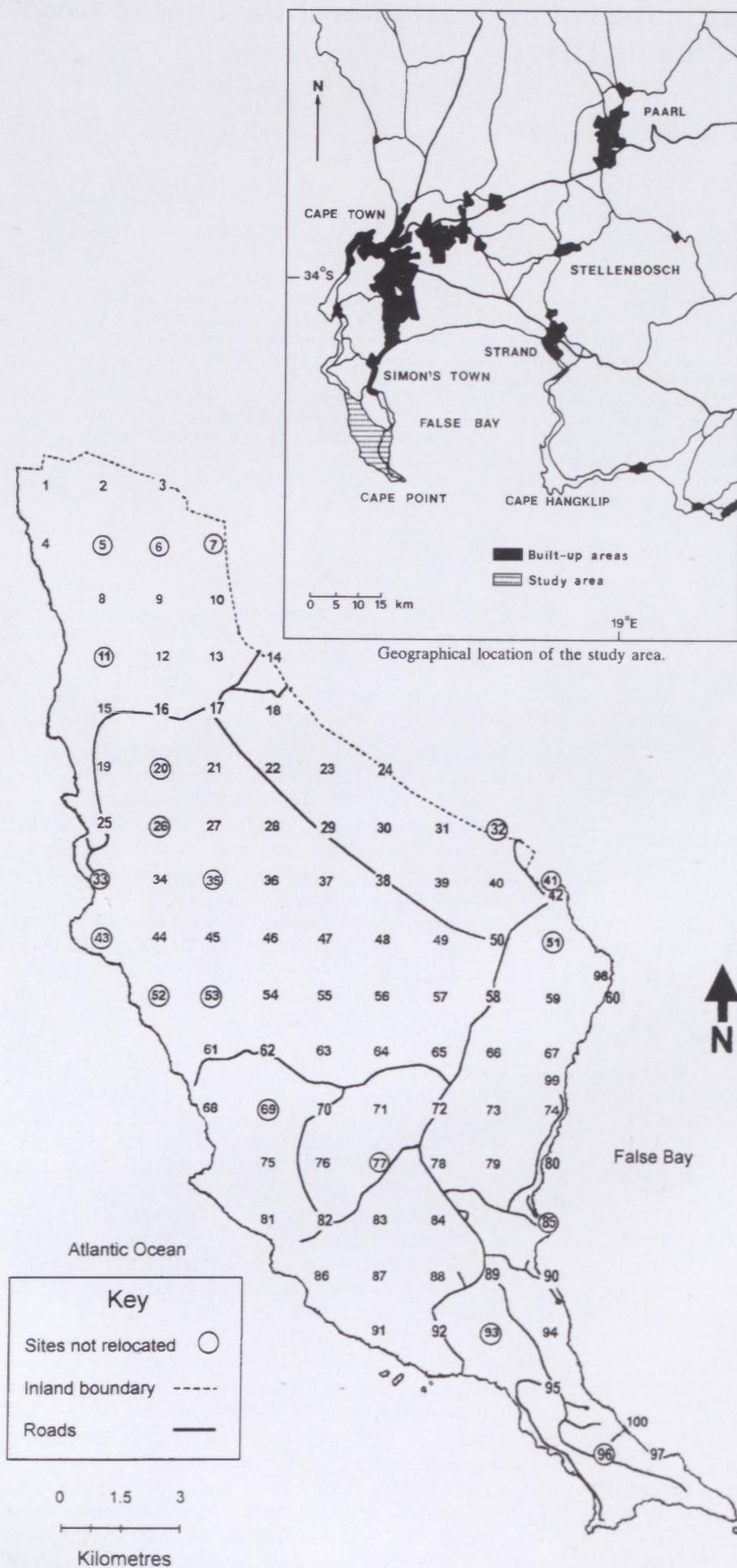


FIGURE 1.—The Cape of Good Hope Nature Reserve study area showing location of 100 original vegetation sites surveyed by Taylor (1969). Sites 5, 6, 7, 11, 20, 26, 32, 33, 35, 41, 43, 51–53, 69, 77, 85, 93 and 96 were not relocated and therefore were excluded from this study. Source: 1:10 000 ortho-photo, Chief Directorate, surveys.

searched over the last few decades (Taylor 1978; Kruger 1984; Campbell 1985; Cowling & 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. This study explored the resilience of fynbos vegetation in the Cape of Good Hope Nature Reserve (CGHNR) to 30 years of variable disturbance, both natural and managed. The study used mostly a descriptive approach to explore changes in the composition of permanent vegetation sites established in 1966. It attempted to invoke explanations for the observed change from historical fire and alien plant records by asking the following questions:

1. How much change has occurred in the vegetation of the CGHNR between 1966 and 1996?
2. How important was 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. What has been the dynamics of the common serotinous overstorey species *Leucadendron lauroleum*, and what impact has it had on understorey species diversity?
7. 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?

#### STUDY AREA

The area encompassed by the Cape of Good Hope Nature Reserve (CGHNR) was used for this study (Figure 1). A detailed description of the physical setting and historical background of the Reserve is documented in Taylor (1984a). The Reserve had certain attributes that made it suitable for this study: high species diversity and complexity; the existence of permanent monitoring sites; and detailed management records including fire histories (Appendix 1) for the period since the establishment of the sites. The vegetation of the CGHNR has been well documented and a comprehensive list of 1 073 species compiled (Taylor 1969, 1983, 1984a, b; Fraser & McMahon 1995; Fraser in press.). The vegetation communities were described by Taylor (1984b) who emphasized the variability within communities and suggested that historical effects relating to disturbance had influenced within-community species heterogeneity.

#### METHODS

Taylor (1969) established 100 permanently marked vegetation quadrats of 50 m<sup>2</sup> (5 × 10 m) during 1965/66 (Figure 1). These provided the baseline species dataset against which a contemporary species list could be compared. The management records of the Reserve provided

detailed information on both fire history and alien vegetation from 1960 to the present. Eighty-one of the 100 quadrats were relocated using Taylor's original site markers that demarcated the southwestern corner of each quadrat (Figure 1). 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 sites were precisely relocated and that species were accurately identified. This was crucial for achieving the objectives of the study. The nomenclature of all species was corrected according to Arnold & De Wet (1993). The original species lists of Taylor (1969) were used to assist with identification.

The number of individuals of each species in a site was counted (estimates were made when distinction between individuals was difficult, e.g. resprouting Restionaceae) and later converted to a five-category system that corresponds to a simplified form of Acock's (1975) system of abundance symbols (Table 1). This was done in order to be compatible with Taylor's (1969) study that used Acock's (1975) symbols for assessing abundance. Hugh Taylor assisted with initial field work and was satisfied that the methodology corresponded with that used in his initial survey.

The changes in floristic composition within sites over the thirty year interval between surveys was explored using the Sørensen's coefficient (Kent & Coker 1992) in the form of the following equation:

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

where  $S_s$  is the Sørensen 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 the study to quantify temporal changes in species composition. These results, together with the two temporally separated species data sets and matched photographs were used to explore established hypotheses relating to determinants of vegetation dynamics and temporal change in fynbos. We do not attempt to provide a detailed analysis of any aspect of fynbos dynamics in this study. We use specific examples of sites which have undergone changes relating to recorded fire or alien plant impacts to emphasize the role of these factors in structuring contemporary vegetation patterns.

TABLE 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



FIGURE 2.—Site 43 on western seaboard near Olifantsbos Point, 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*. Wreck of Thomas T. Tucker is visible in background of both photographs.

## RESULTS AND DISCUSSION

Nineteen of the original 100 sites were not included in this study due to problems with accurate re-location or through loss to infrastructure development. The 81 sites used in this study showed considerable variability in their floristic similarity between the two surveys (Appendix 1). The mean similarity for all sites was  $61.8 \pm 8.9\%$ , while the lowest value was 43.8% and the highest 84.3%. The potential for extreme environmental change to alter the composition of a site 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 mobile dune sands have inundated it during the last 30 years (Figure 2).

### 1. Fire effects

#### 1.1. Post-fire succession

Post-fire succession in fynbos is noted for a rapid initial establishment of all components of the community including those (fire ephemerals) that only appear in the first years after fire. Therefore, 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 increases (Kruger 1987; Cowling &

Pierce 1988; Cowling & 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).

We 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 therefore only the fire-prone mesic oligotrophic proteoid community was included. This community occurs on the well-drained rocky hills and is the dominant vegetation type of the Reserve (Privett 1998).

There was a significant negative relationship between vegetation age and species diversity within this community (Figure 3). The initial peak in species diversity was followed by a gradual decline over time. The significantly steeper negative slope of the 1966 data set ( $-1.19 \pm 0.24$  as against  $-0.54 \pm 0.1$ ;  $F = 5.97$ ,  $df = 1$ ,  $P < 0.02$ ) resulted from the inclusion of a number of young sites ( $< 4$  years post-fire) which had high species diversity. The mean number of perennial species recorded in 1966 was  $38.2 \pm 17.4$  per site, the maximum was 79 and the minimum was six. In 1996 there were on average fewer species per site ( $35.6 \pm 15.5$ ). 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 from the community at a slower rate.

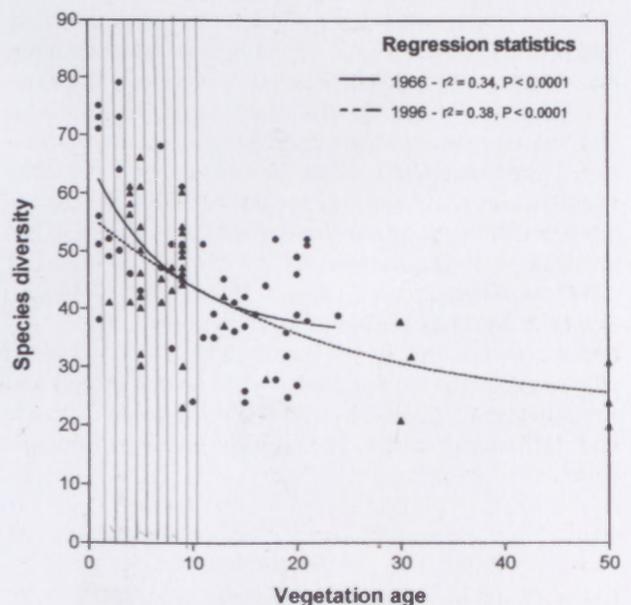


FIGURE 3.—Relationship between vegetation age and species diversity in 50 mesic oligotrophic proteoid sites at the two sampling times. Fitted curves are negative exponential, circles represent 1966 sites and triangles 1996 sites.



FIGURE 4.—Site 15 near Groot Rondévelei, has shown a marked decline in species diversity between surveys as a result of successional effects. The low, white flowering shrub in the 1966 photograph (three years post-fire) is the post-fire ephemeral *Edmondia sesamoides* which was not present in the older vegetation in 1996 (nine years post-fire). The 1966 vegetation is characterized 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 middle, background of photograph) by the invasive alien, *Acacia cyclops*.

#### 1.1.1. Early successional changes

Figure 3 illustrates the initial decline in species diversity during the first four years following fire. One of the relocated sites (15) provided an opportunity for exploring the differences in vegetation composition between very young and slightly older vegetation (Figure 4). The impact of fire season and frequency on the site's vegetation between surveys should be negligible as the site was burnt twice in summer wildfires at intervals of twelve and then eleven years. In 1966 this site was only three years old and included 66 species, whereas 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. The 43 species lost include a number of fire ephemerals such as *Aspalathus abietina*, *A. linguiloba*, *A. retroflexa*, *Roella ciliata*, *R. triflora*, *Selago spuria*, *Thesium cari-*

*natum* and *T. acuminatum* as well as the predominantly early successional species such as *Edmondia sesamoides* and *Ursinia crithmifolia* (Asteraceae).

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 and wherever possible successional effects should be controlled by only sampling in similar-aged stands.

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

Fynbos is a fire-prone 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 & Richardson 1992; Cowling *et al.* 1997). The late stages of fynbos succession are characterized by autogenic changes and follow the facilitation model of Connell & Slayter (1977). Seeds of forest and thicket species are dispersed into shrublands, and seedlings sometimes establish in mature fynbos communities, especially in sheltered sites (Cowling *et al.* 1997). The slow-growing seedlings of thicket species are usually killed 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 & Richardson 1992; Richardson & Van Wilgen 1985, Cowling *et al.* 1997). 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; Privett 1998). Five of the sites enumerated in 1966 had not burnt once at the time of the second survey (74, 81, 95, 99 and 100). These provided 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 Sørensen coefficient for these upland fynbos sites was  $58.5 \pm 7\%$ ; 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. Two of these sites have not burnt for more than fifty years and have similar habitat characteristics (74, Figure 5 and 81, Figure 6). They are located on relatively steep slopes at approximately 90 m above sea level and adjacent to the coast. The one is situated on an east-facing slope above False Bay (74), while site 81 is located on a west-facing slope above the Atlantic Ocean. Site 74 is therefore exposed to the strong salt-laden southeasterly winds during the summer months, whereas site 81 is more protected from wind but still exposed to strong northwesterlies in winter.

Predictably, both sites were relatively species poor. However, neither had experienced significant thicket development (Figures 5, 6). Both sites had lost several

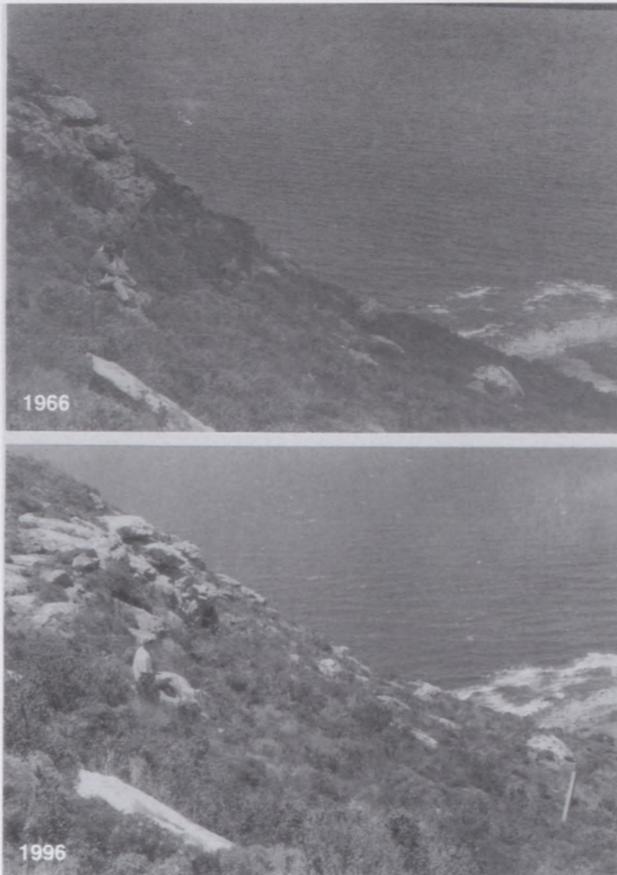


FIGURE 5.—Site 74, oligotrophic proteoid fynbos on the southern slopes of Paulsberg overlooking False Bay, is exposed to strong southeast winds during the dry summer months. This vegetation was at least 20 years old in 1966 and has not been burnt between surveys. There has been very little change in 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 colonization by thicket species despite fifty years without fire.

species, most of which were 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 had been lost from these sites also included 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 colonization. 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, whereas site 74 supported no thicket species. The better early colonization of site 81 is probably a result of its taller structure, thereby providing more perch sites, and its peripheral location to a nearby thicket. Since the initial survey, neither site has demonstrated a notable increase in thicket species. The bird-dispersed *Rhus lucida* and *Pterocelastrus tricuspidatus* colonized sites 74 and 81 respectively. *Erica tristis*, a tree



FIGURE 6.—Site 81, oligotrophic proteoid fynbos above large coastal thicket at Gifkommetjie, is situated on the upper slopes of a fire-protected amphitheatre above the Atlantic coast. The vegetation was at least 20 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 colonizers between surveys. Despite a fire-free period of  $\pm 50$  years, and its 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.

erica associated with fire-free sites, colonized site 81. The few other species, which have colonized 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, whereas 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 rapid development of thicket or forest. Thicket colonization 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 probably comprised an assemblage of longer-lived fynbos plants, rather than a thicket community.

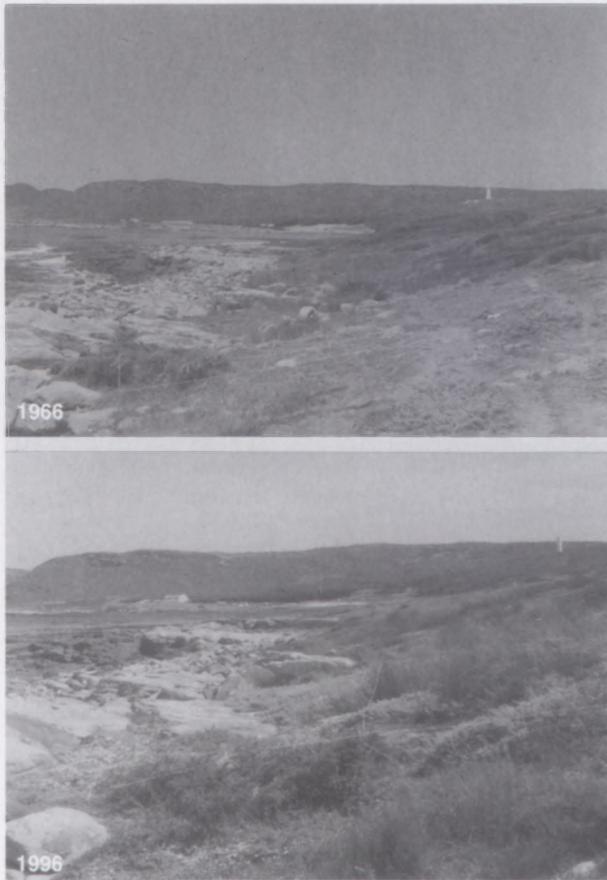


FIGURE 7.—Site 80, coastal scree asteraceous fynbos near Black Rocks on the False Bay coast, was already very old in 1966 and has not been burnt since. The species composition has remained stable between surveys. There has been an increase in the cover and biomass of *Scirpus nudosus* (graminoid in the 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 *Asparagus capensis* in the bottom left hand corner of both photographs. This individual is well over 30 years old.

### 1.1.3. Successional changes after long fire-free intervals in coastal fynbos

Unlike the upland fynbos, coastal asteraceous and coastal thicket communities are less frequently burnt owing to their location adjacent to the sea. It can therefore be hypothesized 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 (Figure 7) and 90 (Figure 8) 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 Sørensen 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

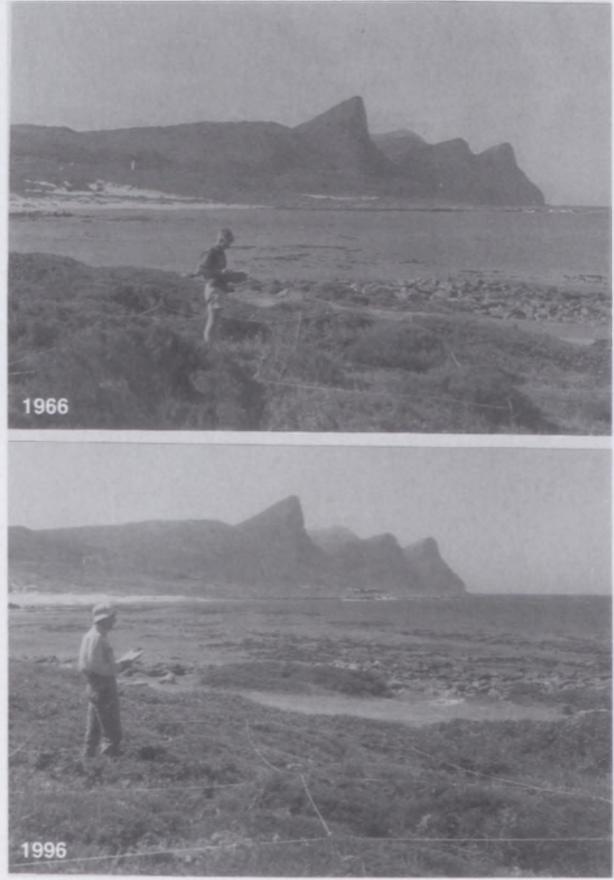


FIGURE 8.—Site 90, coastal dune thicket on the False Bay coast at Buffelsbaai. This vegetation type has remained very stable in composition over the last 30 years. It is dominated by the thicket species *Sideroxylon inerme*, *Cassine peragua* and *Rhus* species. All of these species are long-lived and, 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.

increase in the sedge *Scirpus nudosus* (Figure 7). 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.

### 1.2. Fire frequency

Fires in fynbos occur with intervals of between four and 40 years (Le Maitre & Midgley 1992). The natural fire frequency for fynbos in the Cederberg Mountain Range, some 200 km to the north, 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 fre-

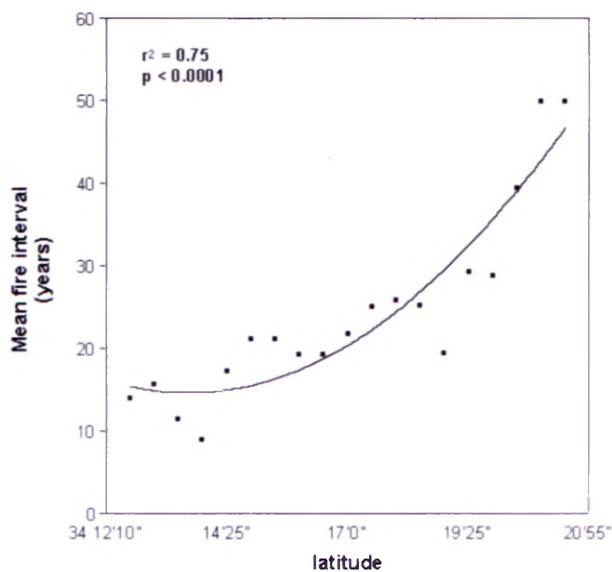


FIGURE 9.—The relationship between mean fire interval and latitude in the Cape of Good Hope Nature Reserve.

quently than landlocked areas further inland. An analysis of the last fifty years' fire records for the Reserve revealed an average fire interval 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 livestock products (Elphick 1977).

There was a significant positive relationship between latitude in the Reserve and the mean fire interval (Figure 9). Sites in the southern areas of the reserve, where the Cape Peninsula narrows to less than a few kilometres, have had a longer average fire frequency than those in the northern areas. Fires at unusually short, or long intervals, can alter the species composition of fynbos (Van Wilgen 1981; Van Wilgen & 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 & 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  $\pm 30$  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).

### 1.2.1. 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, whereas in 1996 it was eight years old.

This site has undergone considerable compositional change over the last 30 years. The Sørensen coefficient of only 55% was below average for the 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. 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 might have also been detrimental to some sprouting 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.

### 1.2.2. 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. These sites were used to examine the effects of long intervals between fires on the numbers of individuals of serotinous and myrmecochorous Proteaceae.

TABLE 2.—Comparison of response of serotinous and myrmecochorous Proteaceae from 18 ( $5 \times 10 \text{ m}^2$ ) sites sampled in 1966 and 1996, which experienced a long interval ( $> 30$  years) between fires in Cape of Good Hope Nature Reserve

	No. sites	
	Serotinous spp.	Myrmecochorous spp.
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 (Table 2). 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 colonized some sites after high intensity fires. This supports the hypothesis that seedling recruitment in these species is strongly and positively related to local fire intensity (Bond *et al.* 1990). Adult mortality is, however, often high after these intense fires. A random survey of individuals of the myrmecochorous species *Leucospermum conocarpodendron* and *Mimetes fimbriifolius* in the vicinity of site 92 (Figure 10) 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 fimbriifolius* 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 (Midgley *et al.* 1998).

There was no significant change in the proportion of sprouting versus non-sprouting species recorded at the two sample times ( $\chi^2 = 2.8 \times 10^{-6}$ ,  $P = 0.99$  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 fires 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. fimbriifolius* 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).

## 2. Dynamics of serotinous Proteaceae

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. We 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 hypotheses have been proposed to explain these fluctuations (see Midgley 1989 for a review).

*Leucadendron laureolum* is very widely distributed in the Reserve and its densities are known to fluctuate over time (Le Maitre 1988; Cowling & Gxaba 1990). This species is a habitat generalist (Williams 1972) which Taylor (1969) described as a 'weedy' species capable of forming dense stands in most of the fynbos communities

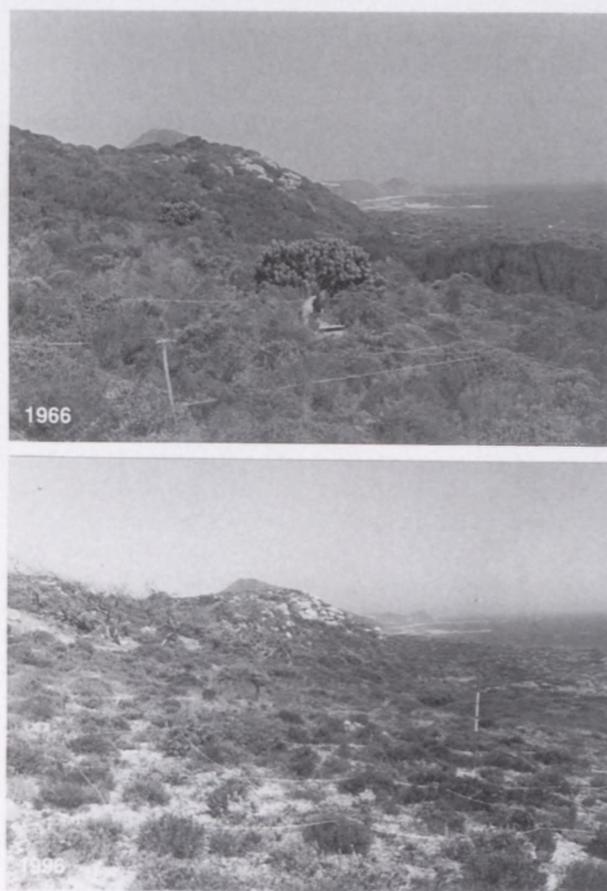


FIGURE 10.—Site 92, oligotrophic proteoid fynbos near Platboom: vegetation was 45 years old when it burnt in an intense summer fire in 1991. The species turnover between sampling times was 50%. A large proportion of this change was as a result of the colonization of post-fire (asteraceous) species in 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.

TABLE 3.—Comparison of range and abundance of serotinous proteoid species, *Leucadendron lauroolum* for 81 (5 × 10 m) sites surveyed in 1966 and 1996 in Cape of Good Hope Nature Reserve. Sites colonized: species absent in 1966 and present in 1996. Sites extinct: species present in 1966 and absent in 1996

	1966	1996
No. sites occupied	36	37
Mean abundance at all sites	2.91	2.92
Sum of abundance at all sites	72	74
No. sites colonized	-	11
No. sites extinct	-	10

on sandstone-derived soils of the southern Cape Peninsula. A comparison of the distribution and density of *L. lauroolum* in 1966 and 1996 showed that at the landscape scale this species has remained remarkably constant over the last 30 years (Table 3).

However, at the scale of the 50 m<sup>2</sup> site most populations have fluctuated considerably over this time. While the number of sites occupied and overall abundance has remained constant, the species has undergone colonization and extinction at many sites (Table 3). *L. lauroolum* has become extinct on nearly 30% of the sites occupied in 1966, whereas it has colonized a similar number of new sites in the same period. Furthermore, its abundance has remained constant at only nine out of the 26 sites in which it was recorded in both surveys.

### 2.1. Causes of decline of serotinous Proteaceae (Figure 11)

Fire season influences the regeneration of serotinous Proteaceae. Autumn fires favour regeneration of serotinous species, while winter and spring fires result in poor regeneration (Le Maitre 1988). Of the 15 sites at which *L. lauroolum* either declined or went extinct, 40% were burnt at least once in winter. The winter fire was the last in the fire sequence at all except one of these sites. Short fire intervals (< 4 years) were probably responsible for local extinction at a further two sites (14 and 48). Senescence after long fire-free intervals may also have contributed to the decline of this species at some sites. However, seven sites only experienced summer and/or autumn fires. Therefore nearly 50% of the sites at which *L. lauroolum* declined were exposed to fires during theoretically favourable seasons. The decline in species at these sites could not be explained by fire regime 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. lauroolum* present on them in 1966. Population declines at these densities could therefore have resulted from high levels of intraspecific competition. Cowling & Gxaba (1990) suggested that the most plausible explanation for the shifting abundance of *L. lauroolum* is the dispersal of its small, winged seeds by persistently strong southeasterly winds in the summer months after fire. Recent research into the desiccation tolerance of newly emerged Proteaceae seedlings demonstrated that *L. lauroolum* had only moderate resistance to post-emergence desiccation (Mustart & Cowling unpublished data). It would appear that for at

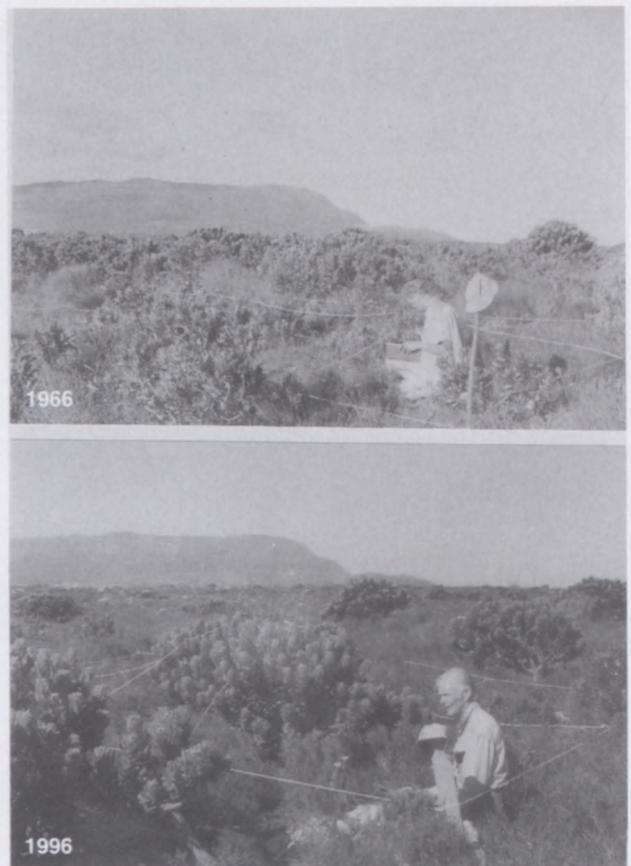


FIGURE 11.—Site 62, oligotrophic proteoid fynbos on the sandstone hill above Brightwater. The 1966 photograph shows *Leucadendron lauroolum* as a common overstorey species at this site. It was burnt in a natural autumn fire in 1979 and a prescribed winter burn in 1988. The combined effects of these two 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.

least four sites in this study, climatic events were the most likely explanation for population declines.

### 2.2. Causes of increase of serotinous Proteaceae (Figures 12, 13)

All sites, which have been colonized 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. lauroolum*: both summer and autumn fires favour increases in density. Nine of the eleven sites colonized were burnt exclusively in summer, while the remaining two were last burnt in an autumn fire. Colonization relies on effective dispersal of seeds into uninhabited sites. The high proportion of sites colonized 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.



FIGURE 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 (only 56% similarity). While the composition of the graminoid field layer has remained similar, a dense cover of *Leucadendron laureolum* has replaced the scattered overstorey of *P. pinnata*.

### 2.3. 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 overstoreys has shown reductions in local richness of understorey species under dense stands (Campbell & Van der Meulen 1980; Esler & Cowling 1990; Cowling & Gxaba 1990). Cowling & Gxaba (1990) found that stands with sparse overstoreys of *L. laureolum* in the reserve had double the number of understorey species per square metre than dense stands. However, 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. We used sites, which have undergone changes in the density of their proteoid overstorey to explore the consequence of these changes on understorey community composition.

A linear regression model was used to explore the relationship between changes in the abundance of *L. laureolum* between surveys and the corresponding changes in

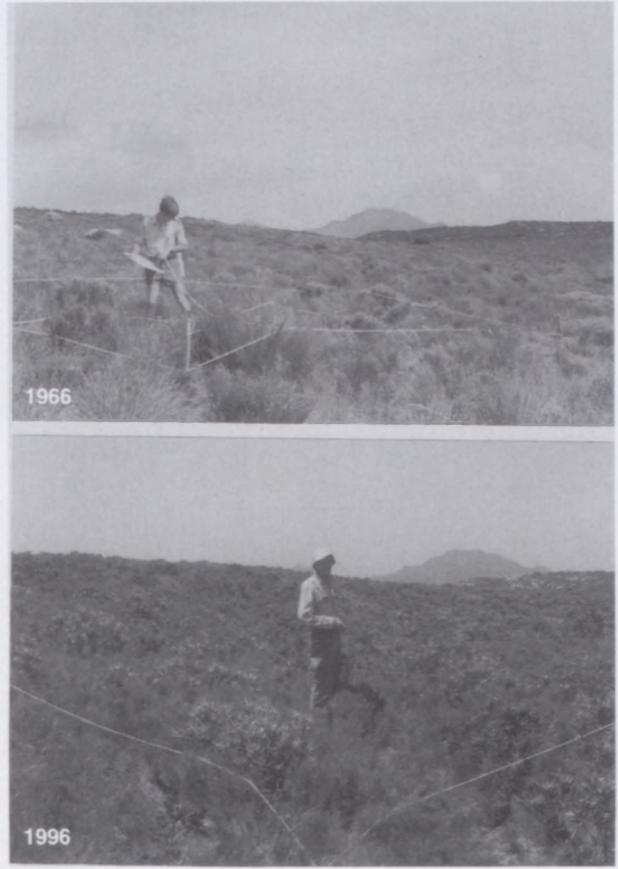


FIGURE 13.—Site 73, oligotrophic proteoid fynbos near Kanonkop. These matched photographs demonstrate the highly mobile nature of the non-sprouting serotinous species, *Leucadendron laureolum*. This species only recruits after fire. In the 1966 survey this species was not recorded in the vicinity of 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.

species diversity. Both changes in abundance and in diversity were calculated by subtracting the values for 1996 from those of 1966. As succession can influence diversity, only sites with vegetation age > 4 and < 20 years at both sampling times were included in the analysis.

There was no significant relationship between changes in overstorey cover and changes in species diversity in this study (Figure 14). The 50% reduction in diversity recorded by Cowling & Gxaba (1990) was in small quadrats of 1 m<sup>2</sup>. This study utilized much larger quadrats (50 m<sup>2</sup>) 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 there 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<sup>-1</sup>. It would appear that competition from overstorey proteoids only becomes important at very high densities (>3000 stems.ha<sup>-1</sup>). 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, low to medium densities of over-

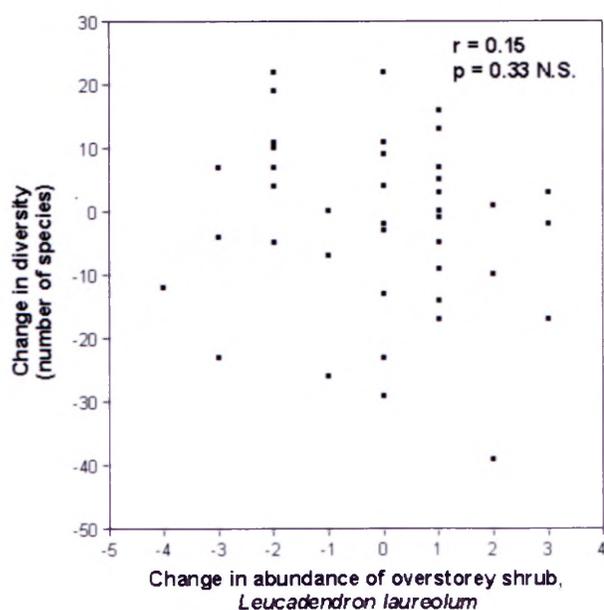


FIGURE 14.—The relationship between fluctuations in the density of *L. laureolum* over the last 30 years, and changes in species diversity. The abundance values can be converted to approximate densities per hectare as follows: 1 = 1–1 000 stems.ha<sup>-1</sup>; 2 = 1 000–2 000 stems.ha<sup>-1</sup>; 3 = 2 000–10 000 stems.ha<sup>-1</sup>.

storey proteoid shrubs have little effect on the diversity of understorey species. Populations of overstorey proteoids demonstrated high mobility at the site level, yet remained remarkably constant at the landscape scale over time and appear to only influence understorey diversity at high densities.

### 3. Alien plants

Much of the fynbos biome has been impacted by dense stands of alien vegetation (Macdonald & Richardson 1986; Richardson *et al.* 1992). The establishment of an overstorey of alien trees and shrubs markedly reduces the richness of fynbos communities (Richardson & Van Wilgen 1985; Richardson *et al.* 1989; Holmes & Cowling 1997). The rate of fynbos recovery following the removal of alien thickets declines with increasing period of invasion (Holmes & Cowling 1997). The CGHNR has a long history of invasion by alien trees (Taylor & 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 under-

taken in the Reserve since 1981. These measures have probably been the most intensive continual clearing operation undertaken anywhere in the world. As the density of alien plants on each site was recorded at both sampling times, we were 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.

#### 3.1. A comparison of the alien threat in 1966 and 1996

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 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 that have subsequently been cleared prior to the second survey in 1996. *Acacia cyclops* is the only species still posing a major threat to the indigenous flora of the Reserve and is now concentrated on the steep slopes in the extreme southwest. This area has been included in future alien eradication planning. The only site that 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 CGHNR 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 CGHNR has been effective at considerably reducing the threat of alien plants on the indigenous flora of the Reserve.

#### 3.2. Impact of aliens on indigenous vegetation

##### 3.2.1. 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 Sørensen's coefficient of  $45.28 \pm 2.1$ ). Sites 4, 18, 90 and 92 were only moderately infested between surveys and have shown

TABLE 4.—Record of alien species in the 50 m<sup>2</sup> 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 <i>Pinus pinaster</i> seedlings	3	Occasional <i>Acacia saligna</i> seedlings
18	Occasional <i>P. pinaster</i> seedlings	18	Occasional <i>Pinus pinaster</i> seedlings
	Moderate <i>Acacia saligna</i> adult and seedlings	95	Occasional <i>Acacia cyclops</i> seedlings
24	Occasional <i>A. saligna</i> adults	97	Closed <i>A. cyclops</i> thicket
68	Occasional <i>A. cyclops</i> seedlings	100	Occasional <i>A. cyclops</i> adults
80	Occasional <i>A. cyclops</i> seedlings		
89	Moderate <i>A. cyclops</i> adults		
95	Occasional <i>A. cyclops</i> adults		
100	Moderate <i>A. cyclops</i> adults and seedlings		



FIGURE 15.—Site 25, coastal dune thicket within 20 m of the Atlantic coastline at Olifantsbos Bay. In 1966 the site was characterized by a well-developed thicket. *A. cyclops* subsequently invaded the site. 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.

better recovery since clearing (mean Sørensen's coefficient of  $58.66 \pm 13.6$ ). Site 25 provided an opportunity to explore the impacts of dense alien invasion on coastal dune vegetation (Figure 15).

This site is situated 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 graminoids *Ficinia ramosissima* and *Ischyrolepis eleocharis* dominated the ground layer. 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 (CGHNR, 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 colonization by a group of weedy, post-disturbance non-sprouting species including



FIGURE 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).

*Cineraria geifolia*, *Senecio purpureus* and *Cullumia squarrosa* as well as the sprouting pioneer graminoids *Ehrharta villosa*, *Stenotaphrum secundatum* and *Pentstemonis pallida*. None of these species were 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.

### 3.2.2. 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 (Figure 16). In 1966 it contained only seven species, being dominated by a few low shrubs and succulent species of the family Aizoaceae. There

were no aliens on site, but by 1973, H. Taylor reported that the site had become densely invaded. In 1996 *A. cyclops* formed an impenetrable thicket over the entire 50 m<sup>2</sup> 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* (Figure 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.

#### 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 characterized by a predominance of resprouting graminoids, and ephemeral species which live for less than five years. After five years the vegetation composition stabilizes 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 mountain ranges. Coastal thicket communities maintain a stable 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. The common non-sprouting serotinous proteoid shrub, *Leucadendron lauroleum* 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 colonization and extinction. Temporal diversity resulting from high levels of colonization and extinction after patchy fires contributes to the high species diversity in fynbos systems.

#### ACKNOWLEDGEMENTS

Our grateful thanks are due to the Western Cape Regional Services Council for permission to undertake research in the Cape of Good Hope Nature Reserve. Thanks also to the management staff of the CGHNR, especially Mr R. Erntzen who provided past management records and useful interpretative discussions. Many thanks to W. Bond, B. Lamont and P. Zedler for comments on an earlier version of this manuscript. This research was financially supported by the Foundation for Research and Development and Pew Charitable Trusts.

#### Footnote

Since the submission of this manuscript, Hugh Taylor has passed away. His co-authors would like to acknowledge Hugh's pioneering research in fynbos, particularly his meticulous research in the Cape of Good Hope Nature Reserve, and his foresight in establishing the permanent plots used in this study.

#### REFERENCES

- ACOCKS, J.P.H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* No. 40.
- ARNOLD, T.H. & DE WET, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* No. 62: 1–825.
- BOND, W.J. 1980. Fire and senescent fynbos in the Swartberg, southern Cape. *South African Forestry Journal* 114: 68–71.
- BOND, W.J., LE ROUX, D. & ERNTZEN, R. 1990. Fire intensity and regeneration of myrmecochorous Proteaceae. *South African Journal of Botany* 56: 326–330.
- BROWN, P.J., MANDERS, P.T., BANDS, D.P., KRUGER, F.J. & ANDRAG, R.H. 1991. Prescribed burning as a conservation management practise: a case history from the Cederberg Mountains, Cape Province, South Africa. *Biological Conservation* 56: 133–150.
- CAMPBELL, B.M. 1985. A classification of the mountain vegetation of the fynbos biome. *Memoirs of the Botanical Survey of South Africa* No. 50: 1–115.
- CAMPBELL, B.M. & VAN DER MEULEN, F. 1980. Patterns of plant species diversity in fynbos. *Vegetatio* 43: 43–47.
- CONNEL, J.H. & SLAYTER, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist* 111: 1119–1144.
- COWLING, R.M. 1987. Fire and its role in coexistence and speciation in Gondwana shrublands. *South African Journal of Science* 83: 106–111.
- COWLING, R.M. & GXABA, T. 1990. Effects of a fynbos overstorey shrub on understorey community structure: implications for the maintenance of community-wide species-richness. *South African Journal of Ecology* 1: 1–7.
- COWLING, R.M. & HOLMES, P.M. 1992. Flora and vegetation. In R.M. Cowling, *The ecology of fynbos. Nutrients, fire and diversity*: 23–61. Oxford University Press, Cape Town.
- COWLING, R.M., KIRKWOOD, D., MIDGLEY, J.J. & PIERCE, S.M. 1997. Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone fynbos. *Journal of Vegetation Science* 8: 475–488.

- COWLING, R.M. & PIERCE, S.M. 1988. Secondary succession in coastal dune fynbos: variation due to site and disturbance. *Vegetatio* 76: 131–139.
- DODD, M., SILVERTOWN, J., MCVONWAY, K., POTTS, J. & CRAWLEY, M. 1995. Community stability: a 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment. *Journal of Ecology* 83: 277–285.
- ELPHICK, R. 1977. *Kraal and castle: Khoikhoi and the founding of white South Africa*. Yale University Press, London.
- ESLER, K.J. & COWLING, R.M. 1990. Effects of density on the reproductive output of *Protea lepidocarpodendron*. *South African Journal of Botany* 56: 29–33.
- FOJT, W. & HARDING, M. 1995. Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *Journal of Applied Ecology* 32: 561–577.
- FRASER, M. (in press). *Bishops and baboons: a guide to the wildlife of the Cape of Good Hope Nature Reserve*.
- FRASER, M. & MCMAHON, L. 1995. *Between two shores. Flora and fauna of the Cape of Good Hope*. David Phillip Publishers, Cape Town.
- HOFFMAN, M.T. & COWLING, R.M. 1990. Vegetation change in the semi-arid Karoo over the last 200 years: an expanding Karoo—fact or fiction? *South African Journal of Science* 86: 286–294.
- HOFFMAN, M.T., MOLL, E.J. & BOUCHER, C. 1987. Post-fire succession at Pella, a South African lowland fynbos site. *South African Journal of Botany* 53: 370–374.
- HOLMES, P.M. & COWLING, R.M. 1997. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology* 34: 317–332.
- KENT, M. & COKER, P. 1992. *Vegetation description and analysis*. Belhaven Press, London.
- KRUGER, F.J. 1984. Patterns of vegetation and climate in the Mediterranean zone of South Africa. *Actualites Botaniques* 131: 213–225.
- KRUGER, F.J. 1987. *Succession after fire in selected fynbos communities of the southwestern Cape*. Ph.D. thesis, University of the Witwatersrand.
- LE MAITRE, D.C. 1986. *Kogelberg season of burn trial IV. Effects of fire season and intensity on post-fire understorey growth*. Unpublished report, Jonkershoek Forestry Research Centre.
- LE MAITRE, D.C. 1988. The effects of parent density and season of burn on the regeneration of *Leucadendron laureolum* (Proteaceae) in the Kogelberg. *South African Journal of Botany* 54: 581–584.
- LE MAITRE, D.C. & MIDGLEY, J.J. 1992. Plant reproductive ecology. In R.M. Cowling, *The ecology of fynbos. Nutrients, fire and diversity*: 135–174. Oxford University Press, Cape Town.
- MACDONALD, I.A.W., CLARK, D.L. & TAYLOR, H.C. 1989. The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941–1987. *South African Journal of Botany* 55: 56, 57.
- MACDONALD, I.A.W. & RICHARDSON, D.M. 1986. Alien species in terrestrial ecosystems of the fynbos biome. In I.A.W. Macdonald, K.J. Kruger & A.A. Ferrar. *The ecology and management of biological invasions in southern Africa*: 77–91. Oxford University Press, Cape Town.
- MANDERS, P.T. & RICHARDSON, D.M. 1992. Colonisation of Cape Fynbos communities by forest species. *Forest Ecology and Management* 48: 277–293.
- MIDGLEY, J.J. 1989. Season of burn of serotinous Proteaceae: a critical review and further data. *South African Journal of Botany* 55: 165–170.
- MIDGLEY, J.J., ENRIGHT, N.J. & COWLING R.M. 1998. Co-existence, demography and distribution patterns of two co-occurring ecologically equivalent fynbos Proteaceae species. *Australian Journal of Botany* 46: 505–510.
- MINNICH, R.A., BARBOUR, M.G., BURK, J.H. & FERNAU, R.F. 1995. Sixty years of change in Californian conifer forests of San Bernardino Mountains. *Conservation Biology* 9: 902–914.
- O'CONNOR, T.G. & ROUX, P.W. 1995. Vegetation changes (1949–71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* 32: 612–626.
- PRIVETT, S.D.J. 1998. *Determinants of pattern in fynbos vegetation. Physical site factors, disturbance regime, species attributes and temporal change*. M.Sc. (Botany) thesis, University of Cape Town.
- RICHARDSON, D.M., MACDONALD, I.A.W. & FORSYTH, G.G. 1989. Reductions in plant species-richness under stands of alien trees and shrubs in the fynbos biome. *South African Forestry Journal* 149: 1–8.
- RICHARDSON, D.M., MACDONALD, I.A.W., HOLMES, P.M. & COWLING, R.M. 1992. Plant and animal invasions. In R.M. Cowling, *The ecology of fynbos. Nutrients, fire and diversity*: 260–308. Oxford University Press, Cape Town.
- RICHARDSON, D.M. & VAN WILGEN, B.W. 1985. Effects of thirty five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *South African Journal of Botany* 52: 309–315.
- ROSE, A.B., PLATT, K.H. & FRAMPTON, C.M. 1995. Vegetation change over 25 years in a New Zealand short tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* 19: 163–174.
- SCHWILK, D.W., KEELEY, J.E. & BOND, W.J. 1997. The intermediate disturbance hypothesis does not explain fire and diversity patterns in fynbos. *Plant Ecology* 132: 77–84.
- TAYLOR, H.C. 1969. *A vegetation survey of the Cape of Good Hope Nature Reserve*. M.Sc. thesis, University of Cape Town.
- TAYLOR, H.C. 1978. Capensis. In M.J.A. Werger, *Biogeography and ecology of southern Africa*: 173–223. Junk, The Hague.
- TAYLOR, H.C. 1983. The vegetation of the Cape of Good Hope Nature Reserve. *Bothalia* 14: 779–784.
- TAYLOR, H.C. 1984a. A vegetation survey of the Cape of Good Hope Nature Reserve. I. The use of association-analysis and Braun-Blanquet methods. *Bothalia* 15: 245–258.
- TAYLOR, H.C. 1984b. A vegetation survey of the Cape of Good Hope Nature Reserve. II. Descriptive account. *Bothalia* 15: 259–291.
- TAYLOR, H.C. & MACDONALD, A. 1985. Invasive alien woody plants in the Cape of Good Hope Nature Reserve. I. Results of a first survey in 1966. *South African Journal of Botany* 51: 14–20.
- TAYLOR, H.C., MACDONALD, A. & MACDONALD, I.A.W. 1985. Invasive alien woody plants in the Cape of Good Hope Nature Reserve. II. Results of a second survey from 1976 to 1980. *South African Journal of Botany* 51: 21–29.
- VAN WILGEN, B.W. 1981. Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. *South African Forestry Journal* 118: 42–55.
- VAN WILGEN, B.W. & FORSYTH, G.G. 1992. Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen, *Fire in South African mountain fynbos*: 1–20. Springer-Verlag, Berlin.
- VAN WILGEN, B.W. & KRUGER, F.J. 1981. Observations on the effects of fire in mountain fynbos at Zachariashoek, Paarl. *Journal of South African Botany* 47: 195–211.
- VLOK, J.H.J. 1996. *The role of overstorey proteoid shrubs in maintaining species-richness in a southern Cape mountain fynbos community*. M.Sc. thesis, University of Natal, Pietermaritzburg.
- WIENS, J.A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. In J. Diamond & T.J. Case, *Community ecology*: 154–172. Harper & Row, New York.
- WILLIAMS, I.J.M. 1972. A revision of the genus *Leucadendron* (Proteaceae). *Contributions to the Bolus Herbarium* 3: 1–402.

APPENDIX 1.—Comparison of species composition in 81 sites in 1966 and 1996. Vegetation types 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 no.	Vegetation type	No. spp. 1966	No. spp. 1996	No. spp. shared	Sorenson's coefficient $\times 100$	Site no.	Vegetation type	No. spp. 1966	No. spp. 1996	No. spp. shared	Sorenson's coefficient $\times 100$
1	MOP	51	46	33	68.04	55	WRF	33	29	19	61.30
2	MOP	43	30	24	65.75	56	WRF	17	27	10	45.46
3	MOP	68	45	35	61.95	57	MOP	32	45	27	70.13
4	MOP	28	24	14	53.85	58	WET	18	25	11	51.16
8	MOP	79	50	41	63.57	59	MOP	42	61	32	62.14
9	MOP	73	50	41	66.68	60	CSA	15	11	7	53.85
10	MOP	50	53	31	60.19	61	MOP	47	46	26	55.91
12	MOP	64	47	32	57.66	62	MOP	25	47	22	61.11
13	WRF	44	34	26	66.67	63	MOP	36	43	25	63.3
14	WRF	44	32	21	55.24	64	WRF	36	40	27	71.05
15	WRF	66	27	23	49.46	65	WRF	12	22	8	47.06
16	WRF	52	29	23	56.79	66	MOP	39	37	29	76.32
17	WRF	30	27	19	66.67	67	MOP	49	42	35	76.93
18	WRF	18	14	8	50.00	68	DAF	25	26	15	58.82
19	WRF	27	28	15	54.55	70	MOP	49	40	23	51.69
21	MOP	37	32	24	69.57	71	MOP	35	41	28	73.68
22	WRF	34	34	25	73.53	72	WRF	36	27	17	53.97
23	MOP	26	23	16	65.31	73	MOP	39	37	23	60.53
24	MOP	46	44	27	60.0	74	MOP	39	31	21	60.00
25	DAF	14	18	7	43.75	75	MOP	75	61	46	67.65
27	MOP	52	53	40	76.19	76	MOP	71	50	39	64.46
28	MOP	38	49	29	66.67	78	WRF	24	24	16	66.67
29	WRF	15	17	9	56.25	79	WRF	58	41	33	66.67
30	MOP	52	60	39	69.64	80	CSA	25	20	16	71.11
31	MOP	51	51	43	84.31	81	MOP	44	31	25	66.67
34	MOP	45	61	41	77.36	82	WRF	74	48	39	63.93
36	MOP	41	46	31	71.26	83	WRF	14	13	8	59.26
37	WRF	34	43	25	64.96	84	MOP	33	54	29	66.67
38	WRF	20	20	13	65.00	86	MOP	51	41	28	60.87
39	MOP	51	54	36	68.57	87	MOP	73	66	47	67.63
40	MOP	35	46	23	56.79	88	MOP	24	30	17	62.96
42	MOP	56	41	26	53.61	89	MOP	24	21	13	57.78
44	MOP	61	60	40	66.12	90	DAF	20	18	15	78.95
45	MOP	51	58	38	69.73	91	SED	11	16	6	44.44
46	WRF	28	32	20	66.67	92	MOP	39	42	21	51.85
47	WET	6	15	5	47.62	94	SPF	27	36	22	69.84
48	WRF	20	15	9	51.43	95	MOP	27	20	11	46.81
49	WRF	21	43	19	59.375	97	CSA	4	6	3	60.00
50	WRF	22	41	14	44.44	98	MOP	46	56	33	64.71
54	MOP	36	28	15	46.88	99	MOP	38	38	24	63.16
						100	MOP	52	32	24	57.14

## APPENDIX 2.—The fire histories of all sites used in this study

1996 site no.	Taylor's site no.	Fire history	1996 site no.	Taylor's site no.	Fire history
1	1	1958, summer 1975, summer 1986	43	56	1952, autumn 1977, winter 1988
2	2	1958, summer 1975, summer 1986	44	57	1947, autumn 1975, autumn 1989
3	3	1958, summer 1975, summer 1986	45	58	1947, autumn 1975, autumn 1989
4	4	1948, summer 1975, summer 1986	46	59	1951, autumn 1975, summer 1992
5	7	1961, summer 1975, summer 1986	47	60	No fires
6	8	1963, summer 1975, summer 1986	48	61	1959, summer 1991
7	9	1963, summer 1975, summer 1986	49	62	1947, autumn 1979, winter 1988
8	10	1963, summer 1975, summer 1986	50	63	1947, autumn 1979, winter 1988
9	12	1963, summer 1975, summer 1986	51	64	1951, autumn 1979, winter 1988
10	13	1963, summer 1975, summer 1986	52	65	1951, autumn 1983, autumn 1989
11	14	1963, winter 1970, winter 1973, winter 1976, winter 1979, winter 1982, winter 1985, winter 1988	53	66	1951, autumn 1983
			54	67	1946, autumn 1983
			55	68	1963, summer 1991
12	15	1963, summer 1986	56	70	~ 1964, summer 1991
13	16	1963, summer 1986	57	71	1954, spring 1968, winter 1981, autumn 1989
14	17	1963, summer 1975, summer 1986	58	72	1941, spring 1968, autumn 1983
15	18	1963, summer 1975, summer 1986	59	73	1954, spring 1968, autumn 1983
16	19	1949, summer 1986	60	74	No fires
17	21	1951, autumn 1977, summer 1986	61	75	~ 1965, autumn 1979, summer 1991
18	22	1945, summer 1975, summer 1986	62	76	~ 1965, winter 1981, summer 1991
19	23	1951, summer 1975, summer 1986	63	77	1953, autumn 1974, winter 1981, summer 1991
20	24	~ 1962, summer 1975, summer 1986	64	78	1961, bushcut 1966, autumn 1983, summer 1992
21	25	1935?, summer 1986, summer 1991	65	79	1946, spring 1968, autumn 1983
22	27	1945, summer 1977, summer 1986	66	80	No fires
23	28	1945, summer 1977, summer 1986	67	81	No fires
24	29	1956, summer 1975, summer 1986	68	82	~ 1965, winter 1981, summer 1991
25	30	1948, summer 1975, summer 1986	69	83	1958, winter 1981, summer 1991
26	31	1955, summer 1975, summer 1986	70	84	1958, winter 1981, summer 1991
27	34	1953, summer 1991	71	85	No fires
28	36	1951, summer 1977, summer 1986	72	86	~ 1965, winter 1981, summer 1991
29	37	1940, summer 1977, summer 1986, winter 1988	73	87	~ 1965, winter 1981, summer 1991
30	38	1954, autumn 1975, summer 1986	74	88	1955, winter 1981, summer 1991
31	39	1945, summer 1975, summer 1986	75	89	1951, winter 1966
32	40	~ 1955, summer 1975, summer 1986	76	90	No fires
33	42	~ 1965, summer 1975, summer 1986, 1992?	77	91	1946, winter 1981, summer 1991
34	44	1957, summer 1991	78	92	1942, summer 1991
35	45	1957, summer 1991	79	93	1946, summer 1991
36	46	1951, autumn 1979, winter 1988	80	94	1951, autumn 1992
37	47	1948, autumn 1977, winter 1988	81	95	No fires
38	48	1956, autumn 1975, autumn 1977, autumn 1989	82	97	No fires
39	49	1948, autumn 1975, autumn 1989	83	98	1946, autumn 1975, summer 1992
40	50	1958, summer 1975, autumn 1989	84	99	No fires
41	54	1952, autumn 1979	85	100	No fires
42	55	1952, autumn 1979, winter 1988			