ASPECTS OF THE STRUCTURE AND PHENOLOGY OF TWO FYNBOS COMMUNITIES

by

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ABSTRACT

Data on the floristics, biomass, pattern, growth forms and regeneration modes of two tall, mid-dense, proteoid shrublands are analysed. The phenology of a number of species in different growth forms is examined in terms of current hypotheses about growth form related timing of shoot growth, and general patterns of periodicity in nutrient-poor mediterranean environments. Taxa typical of the fynbos flora are dominant in both communities, but the drier Cedarberg community has fewer species in these taxa and more annuals than the moister Kogelberg environment. These floristic changes are reflected also in the growth form spectra and the stratification of the communities. The biomass of the Cedarberg community is higher at 1820 g/m2 against 1100 g/m2 for the Kogelberg community. This difference is discussed in terms of the greater effectiveness of the rainfall at the Cedarberg (664 mm/yr), than at the Kogelberg (1016 mm/yr), and the availability of soil nutrients. There are more sprouting plants, excluding annuals, in the flora of the Cedarberg site. This is in line with the prediction that, within limits, the drier the climate, the more reliable the investment in vegetative regrowth after fire. The similarity in community physiognomy is confirmed by the quantitative analyses which show that there are differences and also strong similarities between the communities. The overstorey Proteaceae grow from spring to mid-summer,

as do the Restionaceae, but the other growth forms follow a variety of patterns, including opportunistic summer growth. The sequence of phenological events is partly related to morphological sequences in plant development and partly to resource partitioning. The current hypotheses concerning community structure and phenology in mediterranean environments cannot be refuted, but they do not account for the variations observed within and between growth forms and need to be critically examined.

ACKNOWLEDGEMENTS

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1. PREFACE

During the last 10 years there has been a marked increase in literature dealing specifically with the ecology of the Mediterranean regions of the world (Cody & Mooney, 1978; Di Castri & Mooney, 1973; Di Castri et al., 1981; Kruger, et al., 1983; Miller, 1981; Mooney, 1977; Specht, 1969a, b, 1979, 1981). The focus of these syntheses has been on testing the theory of ecological convergence in these areas as they have similar climatic regimes and vegetation physiognomy. The initial studies concentrated largely on California, Chile and the Mediterranean basin and to a lesser extent Australia. As the amount of information on Mediterranean ecosystems in Australia and South Africa has increased the divergence between them and the other Mediterranean regions has become more obvious. The dissimilarities are not easily explained because they are the product of interactions between many factors. The interpretation of the roles of these factors, in turn, depends on answers to fundamental ecological questions, such as the origin and maintenance of species diversity (Deacon, 1983), to which there are no simple answers.The scope of the syntheses has been limited by a paucity of published data on the South African Mediterranean (Fynbos) biome and its component ecosystems. The analyses that follow are intended to provide useful data on analogous plant communities in different environments. A comprehensive study of community structure and function is not possible because the data were gathered for use in comparing the effects of fire season and the emphasis therefore differs. Miller (M.Sc., in prep.) and Miller *et al.* (1983) have studied the water relations and photosynthesis of a number of species in the Cedarberg community and their studies, therefore, complement those detailed here.

2. DESCRIPTION OF THE STUDY AREAS

2.1 Introduction

The sites were selected for studies of the effects of season of burn on plant communities using "replicated" plots and consequently had to be topographically uniform and have an homogenous plant community. The sites also had to be representative of the montane fynbos of each region but easy access for equipment and for removal of sampled plant material was essential. Both sites are, therefore, located in valleys near a road (Fig. 2) rather than on the higher mountain slopes. The Cedarberg community is not representative of those found on the upper slopes and plateaux but is structurally allied to communities found on both the lower and inland parts of this range and adjacent mountain ranges nearer the coast. The plant communities of the Cedarberg and Kogelberg study sites are similar in structure and, therefore, allow for detailed comparisons of community and species responses to fire season in different environments.

2.2 Location

Both study sites are located in the south-west Cape Province, South Africa (Fig. 1). They fall within the vegetation type

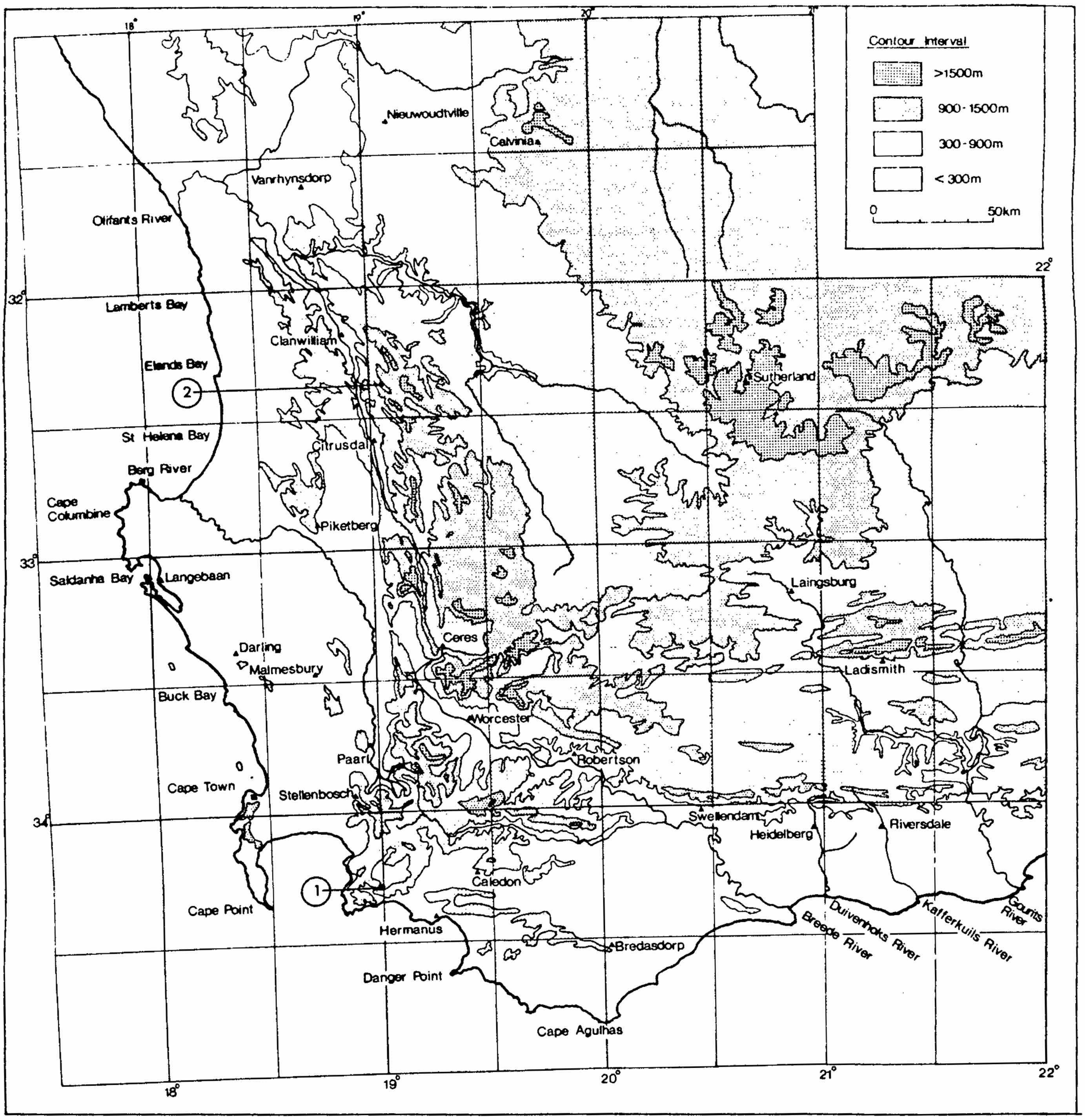


FIGURE 1: A simplified topographical map of the south-western Cape showing the location of the Kogelberg (1) and Cedarberg (2) study sites, the major towns and the major river systems.

Mountain fynbos (Acocks (1953) Veld Type No. 69: Macchia), a vegetation restricted almost entirely to the soils formed from rocks of the Cape System (Taylor, 1978). The Kogelberg site is situated in the Palmiet river valley, near the eastern boundary of the Kogelberg State Forest, at about 34 16'S and 19 00'E. The Cedarberg site is situated in the Rondegat river valley at about 32 20'S and 19 03'E, near the western boundary of the Cedarberg State Forest.

2.3 History

The two major fold axes of the present Cape folded mountains, i.e the Cedarberg (north-south axis) and Worcester (east-west axis) date from the late Paleozoic era (Deacon, 1983) at about 350 - 225 and 200 - 100 million years B.P. respectively (Van Eeden, 1972). The major topographic features of the study areas therefore have a history of approximately that period of time. The mediterranean climatic regime dates back to the Pliocene, around 3 million years B.P., but many of the fynbos taxa probably arose during the upper Cretaceous around 100 million years B.P (Deacon, 1983). There were marked climatic fluctuations during Pliocene and Pleistocene which resulted in changes in the distribution of tree and shrub dominated vegetation (Deacon, 1983; Cowling, 1983). The present climatic regime dates from the end of the last glacial maximum at around 18 000 years B.P. (Deacon, 1979). Fynbos communities have, therefore, developed in geologically and topographically stable environments under a variety of climatic regimes (Deacon, 1983).

Shelters in the Kogelberg area have been occupied by man since at least the Early Stone Age, about 120 to 140 000 years B.P. (Gatehouse, 1955 in Boucher, 1972). The influence of these early hunter-gatherers on the vegetation in the study area is unknown but they used fire in hunting game and to reveal food plants such as geophytes (Kruger, 1979). More consistent use of fire began with the change to a pastoral culture and the use of fire to rejuvenate the vegetation and provide pasture for flocks (Kruger, 1979). The earliest evidence of domestic sheep in South Africa has been found at De Kelders near Gansbaai (about 35km SE of the Kogelberg site) and is dated at 1 500 - 2 000 B.P. (Schweitzer and Scott, 1973 in Boucher and Moll, 1981). No date is available for the appearance of pastoralists in the Olifants river valley, but hunter-gatherer cultures used the valley seasonally in the Late Stone Age (Parkington 1976, 1977) and may also have used the Rondegat river valley which runs into this system.

Regular pasturing of stock in the Kogelberg area probably began after 1747 when the farm "Arieskraal" was granted to the north of the study site (Burman, 1970 in Boucher, 1972). The majority of the area remained State Land because of the rugged terrain and poor soils. The demarcation of the area as State Forest land in 1940 (Reynecke, 1975) put an end to this low intensity pasturing of domestic livestock. The valley was also used for access to the sea and flower pickers frequented the area (Boucher, 1972), but the effects of these activities on the study site community are unknown.

The Kogelberg site was last burnt, as planned (Rycroft, 1953), in 1956 when it formed part of the original system of protective fire breaks in the reserve. It was probably also burnt in the large 1945 wildfire (Reynecke, 1975) and was therefore 11 years old when burnt in 1956.

The first European settlers established themselves along the Olifants river valley during the early 1700s (Andrag, 1977), and presumably some of the farms along the Rondegat river valley also date from around this time. Both the lower slopes and the upper mountain areas were used for extensive pasturing of stock. In 1876 a forest ranger was appointed in the area to control the exploitation of the "cedar" tree Widdringtonia cedarbergensis (Cupressaceae) and to issue and check on the use of permits for grazing. The present forest station, Algeria, was established in 1903. There are signs in parts of the Rondegat river valley and near the study site that injudicious burning has eradicated or thinned out Protea laurifolia and in some areas possibly also Leucadendron pubescens and Paranomus bracteolaris. P. laurifolia is particularly sensitive to manipulation

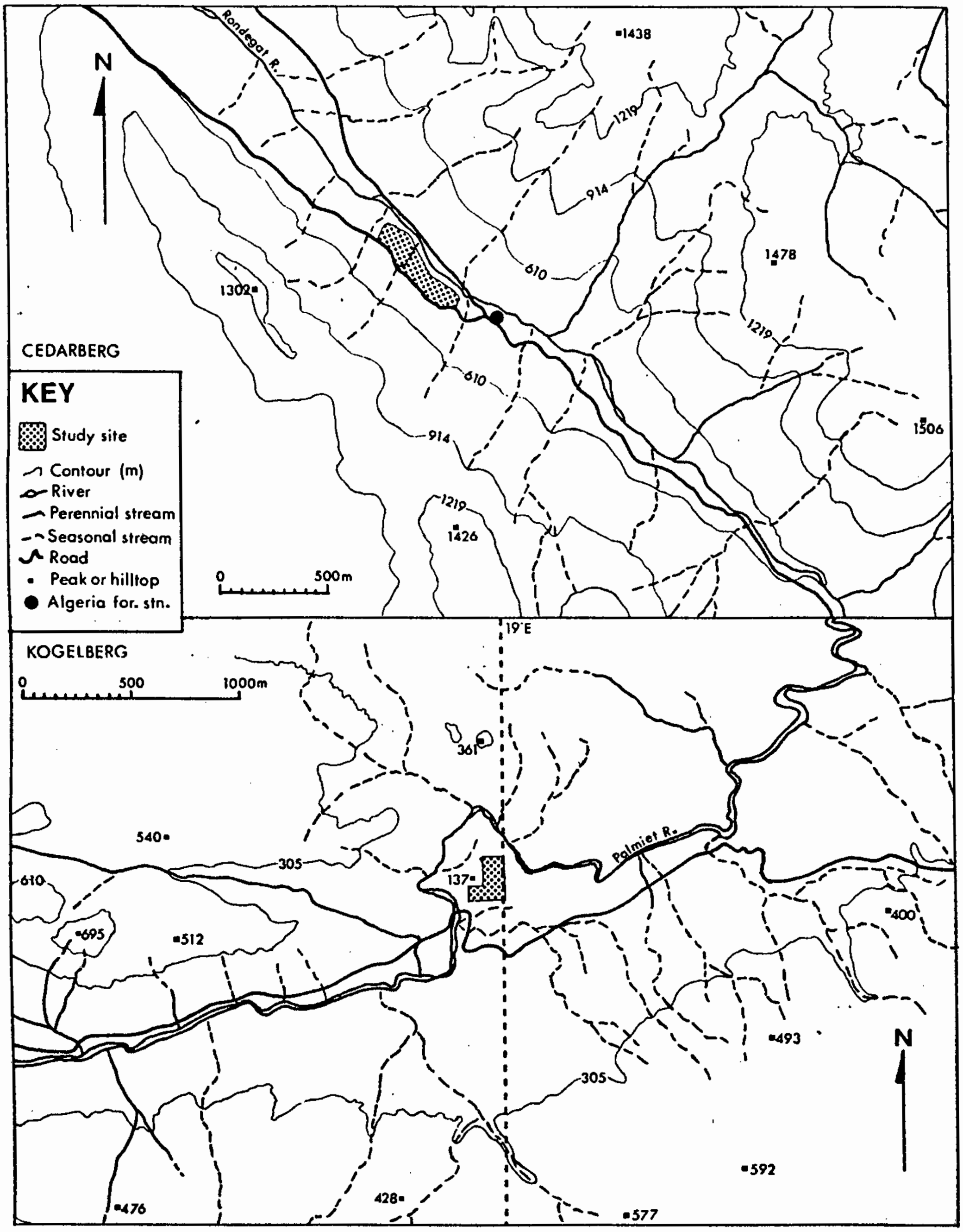


FIGURE 2 : Simplified topographic maps of the two study areas to show the main features of the terrain.

of the fire regime as regeneration is dependent on canopy stored seed. Fires before sufficient seed reserves have been built up in the canopy, or burns in late winter and spring - which can lead to poor seedling recruitment because of seed predation (Bond in press, Van Wilgen, *in prep*.) - can lead to drastic population reductions or even local extinction. The Rondegat valley may, therefore, have had a much greater cover of tall Proteaceae before its occupation by European settlers who also used *Protea* bark for tanning leather and the wood for domestic fires (Andrag, 1977).

The Cedarberg study site forms part of a fire break system which may date back to 1900 but more probably dates from about 1956. It lies across two broad fire breaks which were last burnt during the 1960's. The vegetation is therefore of two ages, about 14 and about 18 years old. These fire breaks seem to have been burnt only once before the protection plan was changed and the study area was excluded from the fire protection system.

2.4 Environment

2.4.1 Geology and Physiography

The geology of the fynbos region is dominated by the Cape System

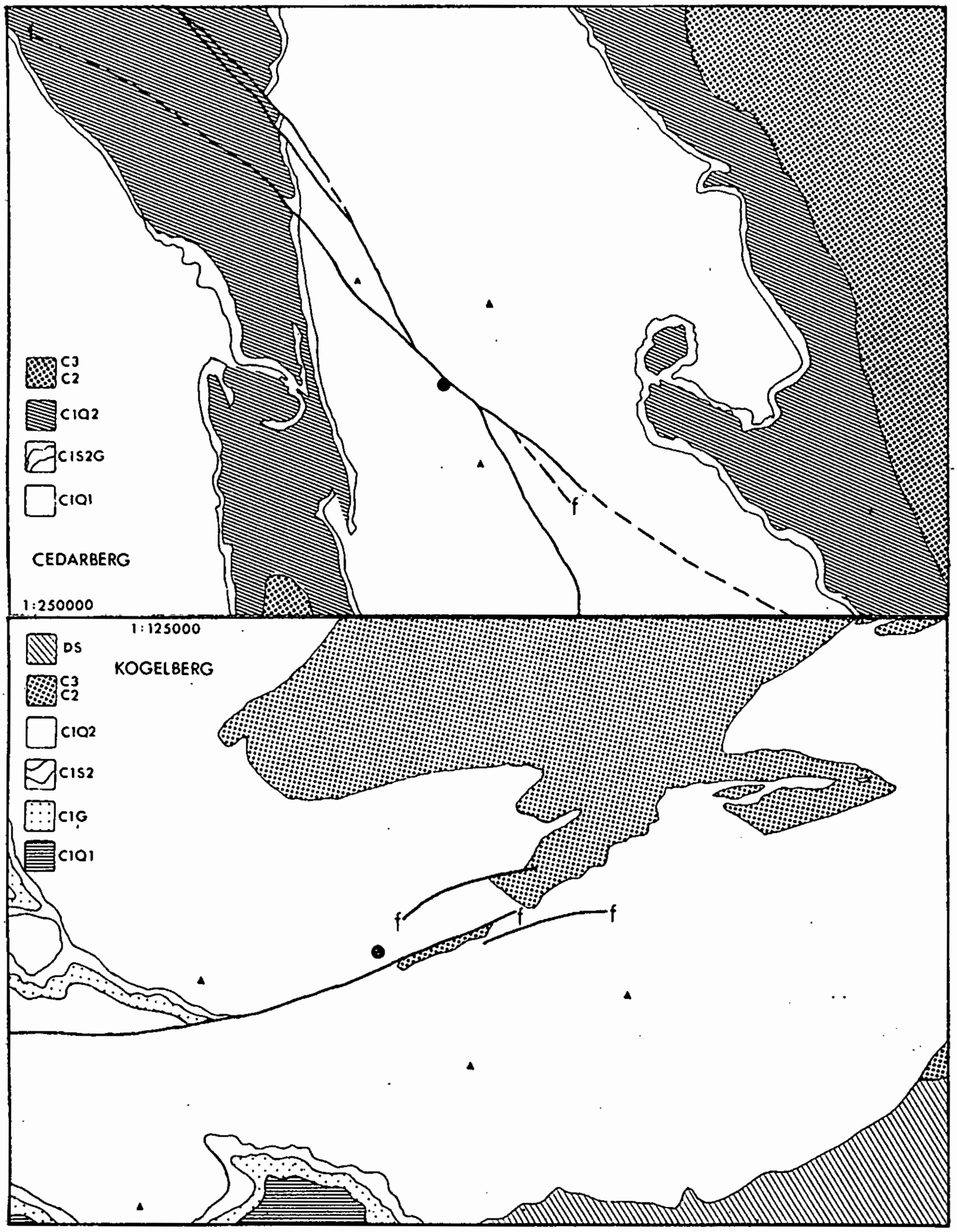


FIGURE 3 : Geological maps of the Cedarberg (upper) and Kogelberg (lower) areas. The abbreviations correspond to those used by the Geological Survey of South African and are explained in the text.

● = study site, ▲= main mountain peaks,

f = fault line

which consists of three series of sedimentary rocks, i.e. the Table Mountain (C1 Fig. 3), the Bokkeveld (C2 Fig.3) and the Witteberg series (C3 Fig.3). The first series forms the base of the system and lies unconformably on the pre-Cape rocks (Du Toit, 1926; Van Eeden, 1972). The Bokkeveld series consists of alternate layers of shales and quartzitic sandstones in which the shales are dominant, but in the other two series the quartzitic sandstones are dominant.

The Table Mountain series is composed of the Peninsula (C1Q1 Fig.3), Pakhuis (C1G Fig.3), Cedarberg (C1S2 Fig.3) and Nardouw (C1Q2 Fig.3) formations. The Pakhuis formation consists of glacial tillite, grit and conglomerate and the Cedarberg formation of shales. These two formations are rarely thicker than 100 metres (Van Eeden, 1972) and the majority of the series is composed of the quartzitic sandstones of the Peninsula and Nardouw formations. In most of the Cedarberg the two middle formations are difficult to map separately and so are grouped as one (C1S2G Fig.3) in the geological map (Geological Survey, 1973). The Table Mountain Series dates from the Silurian and the succeeding Bokkeveld series from the Devonian (Deacon, 1979; Du Toit, 1926; Van Eeden, 1972). Quaternary sands (DS Fig.3) (De Villiers et al., 1964) are found on the coastal plain south of the Kogelberg study site valley. The hard, quartzitic sandstones that make up the majority of the Cape System are highly resistant to erosion and the physiography of the study areas therefore follows the underlying geological structure.

The Kogelberg study area lies in an east-west oriented fault-line valley (Fig. 3) which defines a part of the Palmiet river's course. The site lies across a shallow sandstone ridge running east from Stokoe kop (137m) between 105 and 115 metres above sea level (Fig. 2). It therefore has both a southerly and a northerly aspect. The inclination of the slope varies from horizontal to six degrees. The underlying sandstone of the Nardouw formation is rarely visible on the surface and the loose stones are generally less than 75mm in diameter. The soils of the Kogelberg site are generally grey to very dark grey (Munsell, 1954, 2,5YR 6/1 to 2,5YR 3/1) and vary from a shallow sand A horizon over fractured rock (Mispah form) to a better developed Clovelly form (S.A. Binomial system, Macvicar et al., 1977) with a coarse sandy A horizon and a yellow apedal B horizon over rock. In some areas the "Clovelly form" appears over an impermeable clay (pers. obs.), indicating a duplex soil probably derived from previously overlying or presently neighbouring Bokkeveld shales at some period in the past (Fry pers.comm.). Soil analyses were done for the Mispah and Clovelly soils at Kogelberg (Appendix 1 Durand, 1981).

The Cedarberg study area lies in a north-west south-east oriented, fault-line valley which defines the bed of the Rondegat river (Fig. 2). It is situated on a north-east facing slope with an inclination varying from six to 15 degrees, and between 460 and 480 metres above sea level. The soils are of a predominantly dusky red to red colour (Munsell, 1954, Number 2,5YR 3/2 to 2,5YR 4/8), gravelly, sandy and rarely deeper than 600mm. They are composed of rocky colluvium derived primarily from the quartzitic rocks of the Peninsula formation. The bedrock is frequently exposed and the loose stones are frequently larger than 75mm in diameter. A prominent feature of the soil is the ferruginous concretions (ferricrete, Lamplugh in Du Toit, 1926) which probably represent the remains of an earlier pedogenic cycle (relictual plinthitic surfaces Kruger pers. comm.) by analogy with the description of Quaternary ferricretes in De Villiers et al. (1964). They fall into the Mispah soil form with an orthic A1 horizon over rock or hard plinthite and are well drained.

Campbell (1983) gives mean soil analysis values that typify the soils derived from Table Mountain series quartzites. The samples were taken from a depth "of 20-30cm except where the soils were shallower" (Campbell, 1983). In Table 1 these values are compared with those from the Kogelberg (Durand, 1981). The nutrient content of the Cedarberg soils probably does not exceed those reported by Kruger (1979), Specht and Moll (1983), Day (1983) and Rundel (1979 for N and P), i.e. low levels of exchangeable cations and very low P and N levels.

TABLE 1: Soil values for quartzite soils (mean of 51 samples, Campbell, 1983) and the corresponding values for the Kogelberg soils (Durand, 1981)

Variable	T.M. Quartzites (Campbell, 1983)	Mispah A1 (0-40cm) (Durand, 1981)	Clovelly A (0-120cm) (Durand, 1981)
[1]S value (me/100g soil)	2,0	0,50	0,33
Total N (%)	0,07	0,03	0,04
Available P (ppm)	11,9	1,0	9,0
Onidisable Carbon (%)	3,2	0,35	0,8
pH (KCl)	4,1	4,5	3,7
Coarse sand (%)	13	92	87
Medium sand (%)	36		
Fire sand (%)	36		
Silt (%)	8	2	6
Clay (%)	7	6	7
Stone 2mm (%)	-	10,7	12,1

S value = Sum of exchangeable cations and was calculated for Kogelberg soils using the procedure in Buckman and Brady (1979).

The good drainage suggests that the plants should experience a moisture deficit during the summer period although Miller *et al*. (1983) found almost no moisture deficit at the Cedarberg site and at a site at Jonkershoek - 20km due north of the Kogelberg site. Miller (M.Sc., in prep.) has found varying degrees of moisture stress in plant species at the Cedarberg site. This stress was generally confined to the shallow rooted understorey species, as the tall overstorey shrubs have deep root systems that can access water in fractures in the bedrock (Bond, 1981).

2.4.2 Climate

The study sites are both situated in the true winter rainfall region of the south-western Cape (Fuggle, 1981), and experience the same broad climatic regime. The climate is controlled by the dynamic interaction of two meteorological systems. In the north there is the sub-tropical system consisting of high pressure cells (anti-cyclones) positioned over the southern Atlantic ocean, the southern Indian ocean and the interior plateau of southern Africa. In the south there is the circumpolar westerly system consisting of a succession of eastward moving low pressure cells (depressions or cyclones) which bring cold fronts (Fuggle, 1981).

In the summer the coastward and southward movement of the sub-tropical system displaces the circumpolar westerlies. The weather pattern is dominated by dry conditions with strong southerly winds, except when a depression from the circumpolar westerly system or a small low pressure system (coastal low) brings showers or rain storms (Fuggle, 1981). During the winter the high pressure cells move north and the circumpolar westerly system dominates, bringing a succession of cold fronts. These are preceded by strong north-westerly winds and heavy rain. The winds back from north-westerly to south-westerly as the front passes and air temperatures may also fall rapidly. If the depression is intense enough snow-falls may occur on the higher mountain ranges. The snow generally does not persist for than a month, even on the highest peaks. The area is also subject to "berg" winds which blow coastwards as air subsides from the interior and bring dry, hot conditions (Fuggle, 1981).

Some local data are available for each site. The Kogelberg weather station was established in March 1976 and uses weekly chart recorders to measure rainfall, air and soil temperature, relative humidity, wind speed and direction, and more recently, A-pan evaporation. The Cedarberg has a daily rainfall record extending back to 1908. An automatic weather station measuring hourly values for rainfall, air and soil temperature, relative humidity, wind speed and direction and solar radiation was set up in September 1982.

(a) Rainfall: The rainfall data are summarised in Table 2 and Figure 4. The rainfall regime differs for each site. In the Cedarberg the rainfall is clearly more variable with July being the only month of the year which has always had some rain during the period 1908 - 1982. The values for the coefficient of variation are also higher despite the 75 year record. There are two primary reasons for this. Firstly, the Cedarberg site lies about two degrees further north than the Kogelberg site and receives rain only from the more intense circumpolar westerly cold fronts. Secondly, the Cedarberg site is more affected in summer by the convectional rains, often thunderstorms, of the sub-tropical high-pressure system over the inland areas. This results in a higher proportion of days per month with more than 10 mm of rain, and accounts for the much of the summer rain experienced at the Cedarberg site.

The seasonal distribution (Fig.6) of the rainfall differs, the Kogelberg having a marked peak in June and the Cedarberg having a June maximumum and proportionately more rain in July and August. The Kogelberg has a higher proportion of its rain in summer (12% December-February) and less in winter (46% June-August) than the Cedarberg (7% and 51% respectively). The mean monthly rainfall at the Cedarberg between December and March has a Coefficient of Variation greater than 100% (Table 2). January and February have the highest probability of no rain in the Cedarberg. From October 1979 to April 1980 there was only one day with

TABLE 2: MONTHLY RAINFALL IN MILLIMETRES FOR THE STUDY SITES

Site	Variable	J	F	M	A	M	J	J	A	S	O	N	D	Total
Kogelberg	Mean	49,5	37,0	45,3	63,0	127,0	203,9	161,4	119,8	105,3	58,1	52,6	40,9	[3] 1015,6
	[1] C.V.	88	84	56	66	70	59	45	56	68	83	125	23	
	[2] S.E.M.	16,5	11,7	10,7	15,7	31,5	45,13	27,2	25,5	27,1	17,0	23,2	3,6	20
	Max.	143,4	104,7	75,4	119,0	284,4	420,9	237,8	263,5	244,4	149,5	185,1	50,6	1338,8
	Min.	10,9	18,3	6,6	9,1	26,4	31,7	49,0	62,5	39,1	12,9	3,0	23,1	812,1
Cedarberg	Mean	13,9	15,3	16,9	46,8	89,8	125,2	106,9	106,0	54,9	43,4	27,1	17,7	663,9
	C.V.	124	144	118	87	74	76	61	57	76	72	97	133	29
	S.E.M.	2,0	2,6	2,3	4,7	7,7	11,0	7,5	7,0	4,8	3,6	3,0	2,7	22,2
	Max.	81,0	103,5	98,0	191,5	317,5	394,8	300,5	337,0	165,6	131,5	144,6	155,7	1412,4
	Min.	0,0	0,0	0,0	0,0	0,0	0,0	7,0	0,0	0,0	0,0	0,0	0,0	367,3
Kogelberg	Rain days	5,3	5,8	7,0	6,7	13,0	16,3	14,0	10,3	9,7	8,8	7,3	7,0	111,2
	with > 10mm ppt.	0,5	1,0	0,3	1,3	6,0	6,7	5,0	4,0	2,3	2,0	0,8	1,0	30,9
Cedarberg	[4] Rain days	2,7	2,0	2,0	5,9	5,7	7,9	6,0	7,9	5,9	5,0	4,0	2,7	57,7
	with >10mm	0,9	0,4	0,6	2,3	3,3	5,0	3,3	3,3	2,6	1,9	1,3	1,3	26,2
	Proportion with no rain 1908 - 1982	0,20	0,21	0,15	0,05	0,05	0,03	0,00	0,01	0,05	0,03	0,13	0,08	

[1] Coefficient of Variation (%).

[2] Standard Error of the Mean.

[3] This is not the same as the sum of the averages because of gaps in the record during 1978.

[4] Analysed for the period 1972 - 1982 to make the data more comparable.

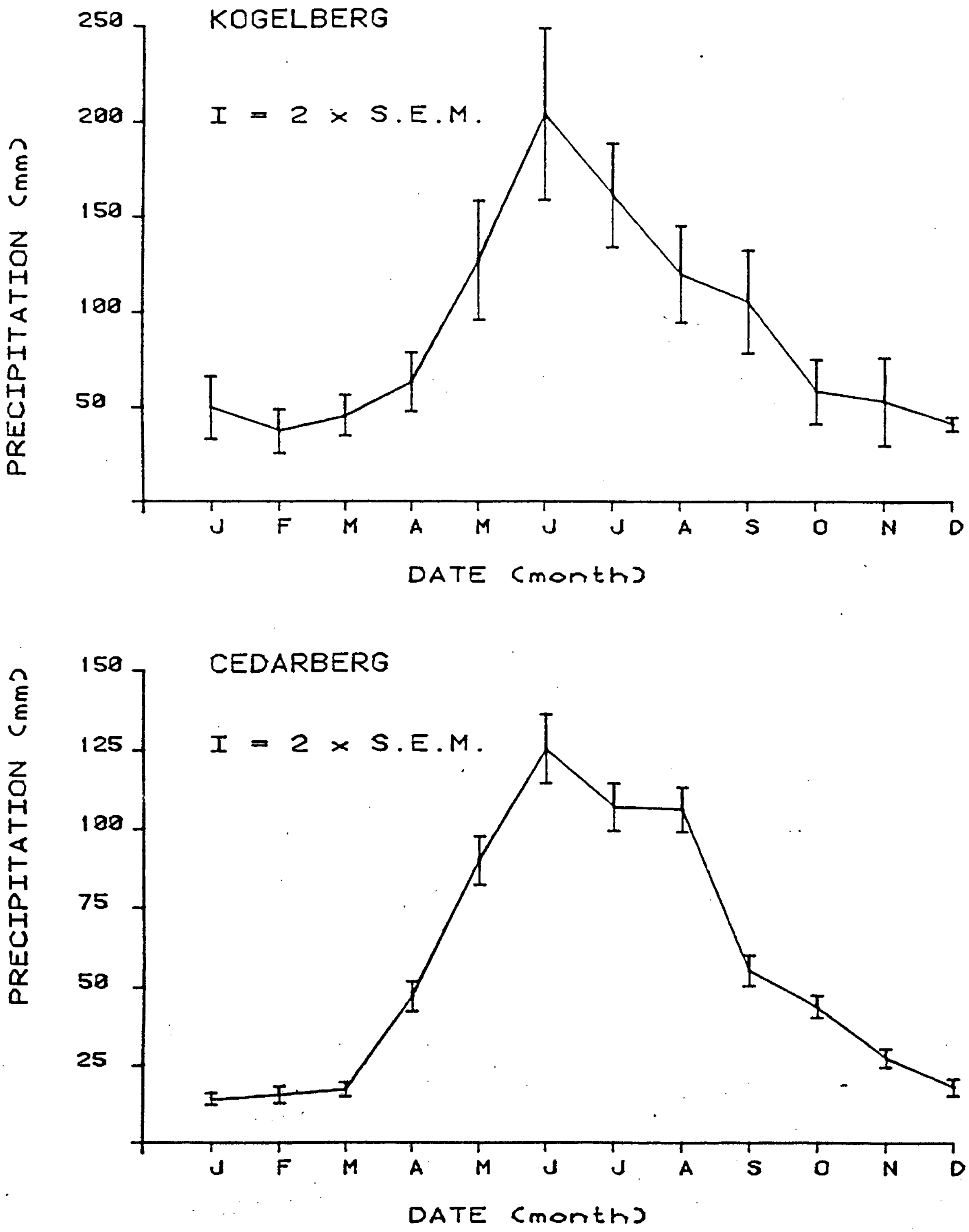


FIGURE 4: Monthly rainfall at the two study sites. The Kogelberg graph is based on data from March 1976 to December 1983, with a break of several months during 1978. The Cedarberg graph is based on data from 1908 to 1983.

more than 10 mm of rainfall in the Cedarberg and the shallow rooted plant species must have experienced high levels of moisture stress.The record for the Kogelberg shows that there have been no completely dry months to date.

The differences between the rainfall regimes are significant because the vegetation is affected more by the soil moisture regime than the rainfall _per_ _se_ (Miller _et_ _al_., 1983; Specht and Moll, 1983). The heavier rains at the Cedarberg will compensate, in part, for the lower frequency as the soil is moistened to a greater depth. This will reduce the stress on the plants and allows for opportunistic summer growth.

(b) Air temperature: The Cedarberg data covers the period from October 1982 to September 1983 (Fig.5). A full months data is available only for February to June, August and October. The Cedarberg climate is warmer (Fig.6) with a mean annual, mean maximum and mean minimimum temperature of about 19, 26 and 12 degrees Centigrade respectively. The corresponding figures for the Kogelberg site are 16, 22 and 11 degrees. The daily temperature range is greater in the Cedarberg and this is reflected in the difference between the mean annual maximum and minumum of 14 degrees as against 11 degrees for the Kogelberg site. This is a consequence of the greater altitude of the Cedarberg site and the strong maritime influence at the Kogelberg site. There are often periods of several days in the Cedarberg in the summer

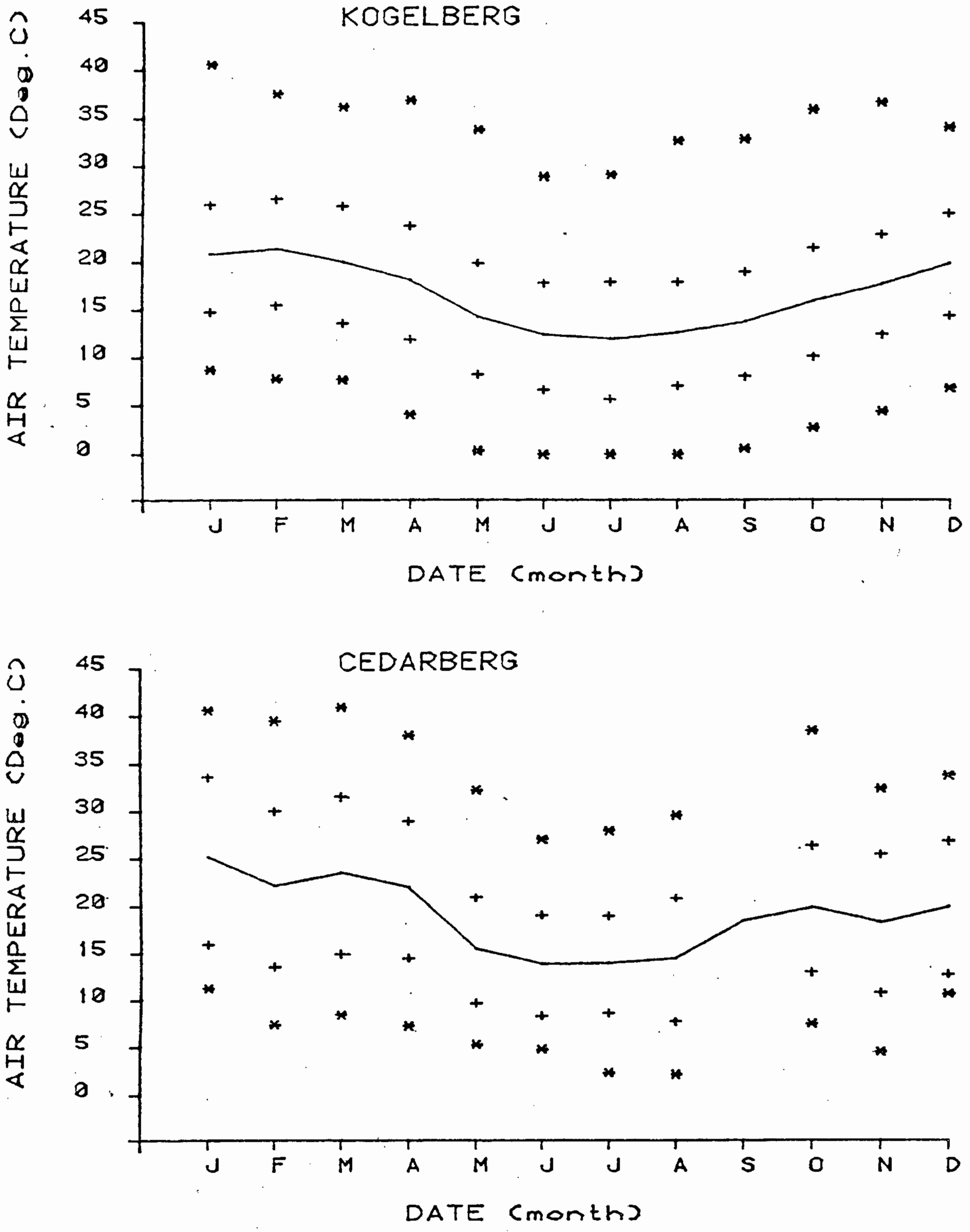


FIGURE 5: Mean monthly air temperatures at the two study sites. —— = mean; + = mean monthly maximum or minimum; ✱ = absolute monthly maximum or minimum. The data for September in the Cedarberg are insufficient to use for calculating more than an (approximate) mean temperature.

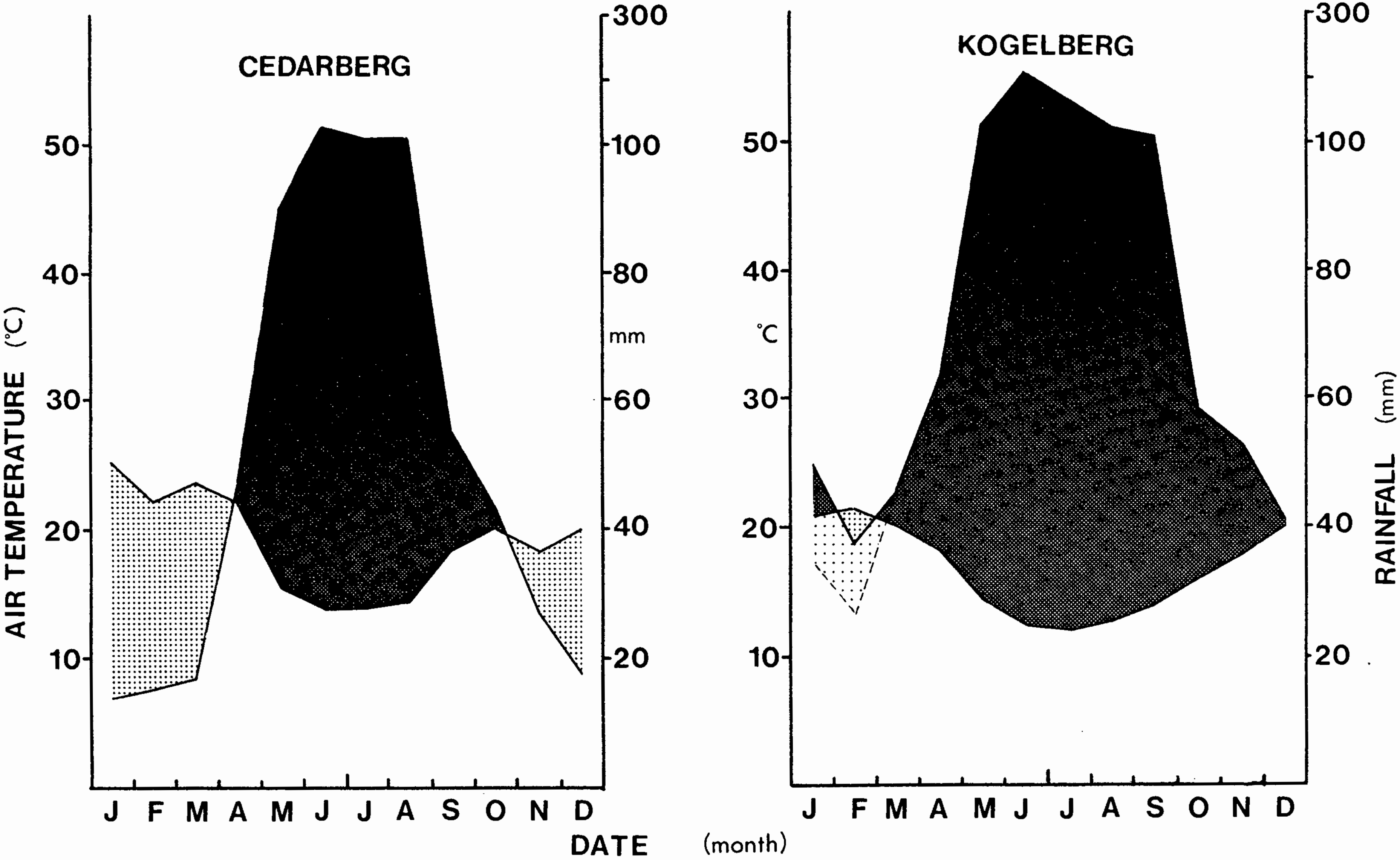


FIGURE 6: Walter climate diagrams for the study sites. The dashed line indicates the mean rainfall excluding the high rainfall in January 1981 (143 mm) and February 1983 (105 mm) at the Kogelberg site.

when the daily maximum temperature is between 30 and 40 degrees and the minimum temperatures do not drop below 20 degrees. These high temperatures, together with the the low moisture levels will place a strain on a plant's physiology, particularly its ability to maintain optimum leaf temperatures by evaporative cooling. This is particularly important for seedlings which do not have root systems that can reach moisture deep in the soil. Seed germination cues should, therefore, ensure that germination is limited to the months with reliable rainfall. These cues should also prevent germination in the spring as this would not give the seedlings enough time to establish sufficiently extensive root systems to survive the ensuing summer drought. This means that the spring germination reported at the Kogelberg (Durand,1981) should not occur in the Cedarberg.

2.4.3 General characteristics of the plant community

Early botanical work on the fynbos vegetation concentrated almost entirely on the taxonomic diversity, and the first concerted ecological studies were those of Marloth in the early 20th century, followed by Adamson, Levyns and Phillips in the period up to the 1960's.

Taylor (1978) reviewed the origins, phytogeography and ecology of the fynbos flora, and based his broad divisions of fynbos largely on the those used by Adamson (1938) and Acocks (1953). The communities of both sites fall within the proteoid zone of the lower slopes of the mountain fynbos, as the broad sclerophyll shrubs of the family Proteaceae are dominant. The Cedarberg site with *Protea laurifolia* and *Leucadendron pubescens* shrubs is also allied to the arid fynbos on the lower inland slopes of the Cedarberg.

Kruger (1979) provided more detail on the structure and patterning of the major fynbos vegetation formations. The communities of both sites are close to his "tall shrubland mountain fynbos of the drier slopes and foothills". The Cedarberg community also has close ties with the drier arid fynbos communities with a tall shrub overstorey and heathy understorey, although Ericaceae are rare in the study site area. The Kogelberg site also has close affinities with his broad sclerophyllous or open scrub. Both sites have the three layered structure of this last formation, with an upper stratum almost exclusively dominated by *Leucadendron laureolum* in the Kogelberg and by *Leucadendron pubescens* and to a lesser extent *Paranomus bracteolaris* in the Cedarberg. The middle stratum contains primarily mid-height shrubs and Restionaceae, and the lower stratum mainly small Cyperaceae, Restionaceae, Geophytes and a few therophytes. In the Kogelberg the smaller plants of this lower stratum, particularly the Restionaceae, can form an almost continuous layer. In the Cedarberg, partly because of the rockier soils and partly because of the drier soil moisture regime (Bond, 1981) this layer is sparse and open. In terms of the structural classification put forward by Cambell _et al_. (1981), the communities are tall, mid-dense, proteoid shrubland formations, the Kogelberg site having a closed, and the Cedarberg an open, low, restioid-ericoid understorey.

Boucher (1978) classified the plant communities of the Cape Hangklip area into a hierarchical floristic units. The Kogelberg community is classified as _Protea_ - _Tetraria_ dry short fynbos, but also has strong affinities with _Berzelia_- _Leucadendron_ tall moist fynbos. Both occur on yellow plinthic soils, the latter community being a moister phase of the first. _Leucadendron laureolum_ is prominent in both phases, but more so in the moister communities.

2.4.4 Animal community

(i) General description

Very little information is available on the ecology of the terrestrial fauna of the Fynbos biome. The ecology and biology of the invertebrates is particularly poorly documented except where they are agricultural or horticultural pests. The recent increase in the cultivation indigenous flowers for export has resulted in some studies of the invertebrate herbivores and frugivores on Proteaceae (Meyburgh and Rust, 1975, 1977). The indigenous invertebrate fauna of the Jonkershoek valley is being studied (Day pers.comm.; Donelly, 1983; Giliomee pers. comm.) but the results are not freely available. Breytenbach (pers. comm.) is compiling a review of the data on the fauna which will incorporate the available information on plant-animal interactions such as herbivory and pollination.

There are unusual paleogenic invertebrate groups in the region such as the Onchyophora (e.g. Peripatopsis), Megaloptera and some groups in the Diptera, Orthoptera and Coleoptera (Jarvis, 1979). These are Gondwanaland relicts (Keast, 1972 in Bigalke, 1979). There are also many fynbos endemics in the Lepidoptera, Coleoptera, Mollusca (Jarvis, 1979) and other invertebrate groups (Endrody-Younga pers. comm.). In general, there is a decrease in endemism through the zoological phyla with the Aves and Mammalia having few endemics and no distinctive element (Jarvis, 1979).

(ii) The communities of the study sites

Durand (1981) provides a general list of vertebrates for the Kogelberg study area and Andrag (1977) and Rautenbach and Nel (1980) provide lists for all vertebrates and mammalia respectively for the Cedarberg Mountain area. Durand's (1981) list and a selection of vertebrate species that probably occur or have been seen in the Cedarberg study area are given in Appendix II.

(a) Invertebrates

There are numerous earthworm (Annelida) casts on the soil surface in sandy areas on the Cedarberg study plots and they probably play an important part in nutrient cycling as they bury the leaf litter in those areas (pers. obs.). Hypodiscus neesii provides moist environment for many organisms in the base of its tufts. These include woodlice (Isopoda), fishmoths (Thysanura), cockroaches (Dictyoptera), a scorpion (Scorpionidae), several small Coleoptera and smaller invertebrates. The effect of this diverse fauna, which also includes a small gecko (Gekkonidae), on the plant is unknown. This moist micro-environment is the result of rainfall collection and is similar to the mist trapping reported for

Thamnochortus punctatus (Moll and Romoff, 1983).

Geometrid larvae (Lepidoptera : Geometridae) are common on Leucadendron pubescens, Paranomus bracteolaris and Protea laurifolia in the wet season, and can consume a large proportion of the plant leaf area (pers. obs.). The presence of a similar herbivore on L. laureolum in the Kogelberg can be inferred from the incidence of leaf damage (Durand, 1981, pers. obs). These herbivores certainly influence the carbon balance of these plants and may also play a role in nutrient cycling. Both areas support termite colonies (Isoptera), the Cedarberg more so than the Kogelberg. The harvester termites remove large amounts of litter and seed to their nests (pers. obs.), but their influence on nutrient cycling and community dynamics is unknown at present.
Durand (1981) noted that the ovules and seed of Erica pulchella were eaten by small beetles (Coleoptera) and that up to 90% were damaged in this way. This was seen in the Cedarberg in the legumes, particularly Podalyria and Rafnia species, where attempts to collect intact seed proved fruitless.

There are a variety of ants (Hymenoptera : Formicidae), in the Cedarberg study area, some of which have been identified and are given in Appendix II. Both Anaplolepis custodiens and Camponotus maculatus have been observed collecting exuded "moisture" on the leaf tip calluses of L. pubescens and from the bracts at the base of the flowers of P. bracteolaris. Lamont (pers. comm.)

considers the leaf tip calluses in Leucadendron to be extra-floral nectaries and this exudate may, therefore, be a source of food for these ants. P. bracteolaris is pollinated by carpenter bees (Xylocopa capensis). An unidentified larva (Coleoptera) has been found in the cones of L. pubescens. It is present in the cone from a early age and inhabits the woody cone axis. From there it bores into the seed and feeds on the embryo. It can destroy the seed in up to 20 percent of the cones, and this must affect seed stores and seedling recruitment. The cones of L. laureolum are also damaged by borers but the organism has not been collected yet.

(b) Vertebrates

No amphibia have been seen on the Cedarberg study plots but Durand (1981) found those given in Appendix II on the Kogelberg study site plots, probably because the latter site is wetter in winter. Both adult and juvenile tortoises (Chersine angulata) have been found in the Cedarberg study area during the spring and summer months.

Sunbirds (Nectarinia famosa) and the sugarbird (Promerops cafer) are occasional visitors when the Protea species in the study area are in flower and provide a source of insects and nectar (Mostert et. al., 1980). The most ubiquitous birds are those that feed on insects on plant foliage (Winterbottom 1966 in Bigalke 1979) such as Prinia maculosa, Bradypterus victorinii, Cisticola fulvicapilla and C. subruficapilla. Another bird common on the sites is the Cape Francolin, Francolinus capensis. This bird is an important consumer of bulbs in the Kogelberg study area, but not in the Cedarberg study area, perhaps because the bulbs are generally deeper and the rocky soil makes it more difficult to dig them out.

Rodents were trapped for two nights on the Cedarberg plots. Four species were captured: Rhabdomys pumilio, Aethomys namaquensis, Acomys subspinosus and Otomys sp. L. pubescens seed is dispersed during the breeding season of small mammals (Botha, pers. comm.) and, judging by the numbers of gnawed seed observed, is a major source of food. Shrews, Aethomys namaquensis and Rhabdomys pumilio were trapped at the Kogelberg site (Durand, field notes).

Raphicerus melanotis (Grysbuck) is present in both areas and browses on various plants, including Nivenia stokoei (Iridaceae) a shrubby "geophyte" on the Kogelberg study site. Troops of Papio ursinus (Chacma baboon) visit the study areas and dig up corms of Watsonia zeyheri (Iridaceae, Cedarberg) and Pillansia tempelmannii (Iridaceae, Kogelberg). In the Cedarberg they frequently break off branches and cones of Leucadendron pubescens and also Protea laurifolia. The seed is then removed and eaten. In the former species the seed is large (about 0,1 - 0,2 g with shell) and the kernel has a pleasant mild flavour. Parkington and Poggenpoel (1971) found seeds of Leucadendron species, probably

L.pubescens, amongst others in excavations at De Hangen. The seed was collected by the hunter-gatherers who inhabited the cave was presumably used for food. Baboons do not remove cones of *L. laureolum*, probably because the seed is smaller and more difficult to extract.

3. PLANT COMMUNITY STRUCTURE

3.1 Introduction

Advances in technology have allowed ecologists to do intensive analytical studies of communities. These have revealed a complex network of interactions within the community, between its structure and its processes, and between the community and the environment it has evolved in and inhabits. This increase in understanding has led to a critical examination of ecological tenets and hypothese about the functioning of ecosystems and the adaptations of organisms to their environment (Lewin, 1983). The definition of what constitutes a functional attribute of community is so ambiguous that Webb et al. (1970) and Bond (1981) could not find a practical distinction between structural and functional plant or community features and combined them under the heading structural- physiognomic. In this study structure is taken to be the spatial and physiognomic features and function to be the processes, i.e. periodicity, in the community (Mueller-Dombois & Ellenburg, 1974). This division is based on an arbitrary time scale of a year, as all the aspects of the structure of the community are in fact dynamic when viewed over a longer period such as the fire-cycle and succession (Gill and Groves, 1981; Kruger, 1983, Westman, 1983).

Warming (1909) defined plant growth forms as the fundamental unit of ecological botany. The growth form is seen as a plant's response to its environment, so that its external structure (morphology) and internal structure (anatomy) are in harmony with the environmental constraints on its physiology (Warming, 1909). The external characteristics of a plant are, therefore, a means of measuring the less easily quantifiable environmental constraints on it. Various ecologists and biogeographers have devised growth-form systems, from Clements (1916) and Raunkiaer (1934) through to Mueller-Dombois and Ellenburg (1974) and Orshan (1982), for use in quantifying the relationships between plants and their environment and identifying their adaptive strategies.

The hypothesis of ecological convergence can be seen as an extension of growth form concept to include whole communities and similarities in structure should, therefore, be a consequence of similar patterns in community function (Cody and Mooney, 1978). Comparative studies of ecosystems in analogous environments can, therefore, assess the extent to which the relationship between environment and community structure and function holds, and also the degree to which knowledge of one ecosystem can be used in understanding analogous ecosystems elsewhere (Di Castri and Mooney, 1973). Miller (1981) stated the concept as "To the extent that the form and function of vegetation relate to resource use, evolution should produce a vegetation with specific physiognomy and physiology under given environmental conditions, which is only limited by the evolutionary potential of the organisms concerned".

The relationships between vegetation form and resource utilization are, however, complex and may well be limited by the constraints placed on resource use efficiency by the need to survive the prevailing disturbance regimes (Mayr, 1983; Miller, 1981).

A vegetation type where regeneration is largely confined to gaps created by fire, should exhibit patterns of plant characteristics that reflect the prevailing fire regime and the history of the plant community. The nature of the pre-historic fire regime, e.g. frequency and season, is unknown although it can be estimated from probabilities of natural ignition and climate data, assuming no change in climate. In areas with drier soil moisture regimes plant fuel mass will accumulate more slowly and fires should therefore occur less frequently. However, in drier areas the soils are less leached (Bond, 1981, Lambrechts, 1979) and nutrients are probably more freely available to the plants enabling them to grow more rapidly. The drier inland ranges also have more frequent thunderstorms and therefore a higher probability of fire ignition (see Horne, 1981) as they border on the inland plateaux high pressure system with its convectional rainfall regime. Within limits, the drier the climate, the more reliable the investment in vegetative regrowth and established root systems, even at the expense of seed production (Carpenter & Recher, 1979; Miller, 1981). A relatively low fire frequency favours sprouting plants as they are generally longer lived (Kruger, 1983) and also long-lived seed regenerating plants such as trees (Keeley, 1977, 1978). A low fire frequency may also favour seeding plants because the high fuel mass results in intense fires which kill many sprouting plants. This would favour long-lived seed regenerating plants (Keeley, 1978),but most seed regenerating species in fynbos are relatively short-lived (Kruger, 1977a, 1983). The lack of firm data on the past fire regime makes it difficult to estimate its role in influencing the proportions of the regeneration types and other community features on the study sites, but the Cedarberg site should have a higher proportion of sprouting species than the Kogelberg site because of the drier environment.

Specht and Morgan (1981) have put forward the hypothesis that the proportion of overstorey foliage cover in a community is determined by the water regime, and decreases with increasing aridity. The understorey foliage cover is in an equilibrium with that of the overstorey and with the environment. During the post-fire succession the understorey cover increases to an environmentally controlled maximum and then declines, as the overstorey strata attain maturity, until a balance is struck. Disturbance of the overstorey opens up the canopy and allows the understorey to increase. The Cedarberg site should, therefore, have a lower average overstorey foliage cover and the undergrowth cover should be lower and decline more rapidly with increasing overstorey cover levels. Vegetation in low nutrient environments will have inherently low photosynthetic rates (Mooney *et al*., 1983, Miller, 1983) and the overstorey-undestorey equilibrium should be less affected by low light levels than by soil moisture stress under overstorey species with high water loss rates (Miller _et al_., 1983; Westman, 1983). In many ways this scheme is similar to that put forward by Bond (1981, after Walter, 1979) in which fynbos is seen as being analogous to a savannah in that it has a deep-rooted overstorey competing with a shallow rooted understorey. The understorey in turn is composed of competing graminoid growth forms, with short ranging dense root systems, and shrubs, with shallow, spreading root systems.

3.2 Methods

Both areas have been divided into sub-plots to facilitate burning in different seasons. The methods used were designed to provide the data needed to interpret the seasonal response and the fuel parameters to assess the intensity of the fires.

(i) Floristics

Floristic sampling for the Kogelberg study was done by listing species in sample quadrats. Ocular cover estimates and a modified Braun-Blanquet scale (Durand, 1981) were used in order to obtain importance values for each species. In the Cedarberg study presence and absence data were used for the species area curves, with ocular estimates of cover values for assessment of changes in species composition on the permanent sampled areas. Durand (1981) found that for optimum sampling of species composition a set of 20 quadrats each of 2x2m should be used, but this was not used as a standard throughout as sample sizes were reduced on some of the smaller plots (30 x 45m as against 50 x 50m) to give a constant sample density. A pattern analysis (Greig-Smith, 1964) was done on two transects 1m wide and 50m long in the Kogelberg and the data was also used for a species-area analysis. In the Cedarberg five nested quadrat sets (1, 2, 4, 8, 16, 32, 64 and 128m^2) and two transects one 1m wide and 32m long and one 3m wide and 20m long have been surveyed.

(ii) Biomass

Biomass sampling has been done for the undergrowth using clipped plots in which all aerial plant material is clipped, subdivided into categories and massed. The categories used are essentially those used by Kruger (1977) and are as follows:

(a) Shrub and Sub-shrubs - micro and nanophanerophytes belonging mainly to the Compositae, Leguminosae, Rutaceae and Ericaceae.

(b) Restionaceae - Leafless hemicryptophytes belonging to the family Restionaceae.

(c) Graminoids - Hemicryptophytes belonging mainly to the Cyperaceae and Gramineae.

(d) Herbs and Geophytes - Geophytes and all otherwise unclassified plants.

At the Kogelberg site 2x2m quadrats were used in most cases. Durand (1981) found that 1x1m quadrats were unsatisfactory and switched to 2x2m quadrats as the species-area relationship indicated this to be a suitable size. Kruger (1977b) estimated fynbos biomass at a number of fynbos sites (Table 6). The variation in mass between samples in the same community resulted in unreliable estimates. Two stage sampling, in which plants with a large individual mass were measured for allometric relationships and only the remainder clipped, was suggested as a solution to this problem (Kruger, 1977). This approach was used at the Kogelberg on some plots but the samples cannot be pooled to estimate the variance of the total mass because of unequal sample sizes and differing techniques (Van Laar, pers. comm.). In the Cedarberg a pilot study was done to determine the relationships between biomass and numbers of sample units of different sizes. An area of 20 x 5m was chosen and the aerial plant material on each 1m^2 sub-plot was separately clipped and weighed. The larger sub-dominant shrubs were kept separate from the remainder of the shrubs. The dominant shrubs Leucadendron pubescens and Paranomus bracteolaris had been separately sampled for allometric biomass regressions. The stem diameter below the first branch, height canopy diameter, and canopy depth was recorded for estimates of the mass of these shrubs and its distribution on the clipped area.

Twenty-five P. bracteolaris and 25 of each sex of the two Leucadendron species were sampled. Five Protea laurifolia shrubs have also been sampled because there is a dense stand of them on one of the sub-plots in the Cedarberg. In all cases a range of shrub sizes was sampled so as to get reasonable regressions for the range of sizes found in the field. In the Kogelberg some Restionaceae, Sympieza articularis and Phaenocoma prolifera were sampled separately for allometric regressions. In the Cedarberg Hypodiscus neesii and Cannomois acuminata were also sampled for allometric regressions. Stem diameter (for shrubs), tuft base diameter (for Restionaceae), plant height and canopy diameter and depth were recorded.

For the allometric sampling the power relationship (Y = AXb) was used as this gives the best results in plant sampling (Westman and Rogers, 1977; Whittaker and Woodwell, 1968). The relationships between parameters were first examined using a Nonlinear regression programme (NONLIN, Commonwealth Institute of Forestry, Oxford, England) that uses a least-squares method to derive coefficients for various equations and then an iterative method (Gaussian-Newtonian) to obtain the minimum sum of squares of deviations by modifying the values of the coefficients. This method although it gave a better overall fit, tended to overvalue outlying values and give an uneven distribution of residuals. A least squares method was therefore used to fit natural logarithms of the values for stem diameter (X) and mass component (Y) to the linearised form of the power equation ($\ln Y = \ln A + B\ln X$) (Snedecor and Cochran, 1980). Rutherford (1978) used the following regression for estimating of *Protea laurifolia* biomass: $\ln(\text{dry mass}) = -2{,}47 + 0{,}93\,[\ln(\text{stem diameter})\hat{}2\text{x}(\text{height})]$. This form was tested on *L. pubescens* but gave less accurate results than stem diameter alone and was therefore not used in this study.

The Cedarberg shrubs were subdivided into the following categories in order to estimate fuel parameters (Countryman and Philpot, 1962):

- twigs < 6mm diameter
  - leaves
    - live
    - dead (for *P. laurifolia* only)
  - woody shoot
    - live
    - dead
- branches > 6mm diameter and < 25mm diameter
  - leaves
    - live
    - dead
  - branches
    - live
    - dead
- branches > 25mm diameter (including stem) - live
- inflorescences
  - old (previous seasons crops)
  - new (most recent)

The Kogelberg shrubs were divided into:

- leafy branches - leaves
  - shoot
- leafless branches
- stem below first branching
- old inflorescences
- new inflorescences

(iii) Pattern

The two dimensional horizontal dispersion of plant species is termed pattern and the vertical distribution of plant species stratification (Greig-Smith, 1964). Stratification was analysed using foliage height profiles (see Bond et al., 1980), the inverse of the horizontal distance needed to cover half a 200mm segment of a 2m board held vertically in the vegetation. This gives an estimate of the vegetation density at different heights and a set of 16 such profiles was obtained at each site. This measure is closely related to biomass (Bond, 1981) and has value also as a predictor of small-mammal communities (Bond et al., 1980; Breytenbach, 1983; Fox, 1983), and bird communities (Cody, 1975, 1983). Durand (1981) used a modification of Trabaud's (1973) method of counting vegetation contacts on a vertical rod to analyse the stratification in the Kogelberg community up to a height of one metre.

A hoist was used to raise a camera 7,5m into the air to take colour transparencies of the plant canopies from above. These transparencies were projected onto a glass topped table and the outlines of the plant canopies traced onto paper. This gives a good idea of the relative cover, distribution and overlap of the understorey and overstorey. In the Cedarberg two photographs of the area were taken one before and one after the overstorey was removed. In the Kogelberg the understorey plants outlines have been drawn in where possible, as only one photograph including the overstorey cover was taken.

Durand (1981) did a pattern analysis (Greig-Smith, 1964) for an area of the Kogelberg community, but without more detail about the causes of the pattern these analyses do not reveal much, and have been left out of this study.

(iv) Growth forms

Observations and notes on the plant species listed in Appendix IV were used to group them into growth forms. Numerous classifications have been used to characterise plant communities. Orshan's (1982) technique requires an initial analysis using an extensive list of plant characteristics and then reducing these by inspection those which show a meaningful variation between the communities being studied. However, the detailed data base the initial analyses require was beyond the scope of this study. The system adopted is essentially that used by Cowling and Campbell (1983) which is similar to that used by Bond (1981) (Table 3a). This system also avoids contentious growth form types such as chamaephytes (see Orshan, 1982). The distinction between shrubs and herbs is ambiguous and lignification of the aerial shoots (Orshan, 1982) is difficult to assess in the field. For this reason I used a grouping based on whether the young shoots are obviously woody or not i.e. woody plants are equivalent to holoxyles (Orshan, 1982). Shrubs were separated into low, medium and tall at one and two metres respectively as this approximates a natural division in the communities (see Kruger, 1979).

The growth forms were also grouped according to their means of reproduction following fire. The problem here is to decide in which way these groupings must be done, and Gill's (1981) scheme has been selected (Table 3b). It is difficult to choose an exact criterion for the division between sprouting and seeding for two main reasons. The first is that a plant species ability to sprout is dependent on fire intensity, in most cases, as a high intensity fire will kill the regenerative buds. The second is that there are few plant species that reproduce purely vegetatively. Gill's (1981) criterion of 100% leaf scorch is probably the best for rating the ability to sprout. The second problem can be dealt with by also subdividing the sprouters to include the seed regeneration types. Gill (1981) suggests that a plant's ability to sprout should be assessed during its reproductive phase, but this was difficult to apply and has been left out.

TABLE 3A: Growth forms classification used in the analysis of the communities, after Cowling Campbell (1983)

Growth form			Seasonality
Woody plants	Tall shrubs	2 m	Evergreen or Drought-deciduous
	Low shrubs	0,25 - 1 m	
	Medium shrubs	1 - 2 m	
	Sub-shrubs	0,25 m	
Herbaceous plants	Graminoids - Seasonal		Evergreen or Drought-deciduous
	Non-seasonal		
	Geophytes		
	Non-geophytic Forbs - Perennial		
	Annual		
	Climbers - Perennial		
	- Annual		

TABLE 3B: Fire regeneration classification of the plants of the two communities, after Gill (1981). The woody-herbaceous division is the same as that used above.

Group		Code
Woody	1. Plants die following 100% leaf scorch	WD
	(a) Seed store on the plant	WDP
	(b) Seed store in the soil	WDS
	2. Plants recover following 100% leaf scorch	WR
	(a) subterranean buds	WRS
	(b) aerial buds	WRA
Herbaceous	1. Annual	HA
	2. Perennial	HP
	(a) Plants die following 100% leaf scorch	HPD
	(b) Plants recover after 100% leaf scorch	HPR

Three more of his subdivisions have also been left out because they do not apply or are difficult to determine. These are the absence of a seed store in the area, the continued growth of pre-fire active aerial buds - which may be the case with *Tetraria thermalis* - and the class "fire ephemerals", as these are by definition absent from pre-fire vegetation.

3.3 Results and discussion

3.3.1 Floristics

(i) Notes on the dominant shrubs

The dominant proteoid shrub species at both sites belong to the dioecious genus *Leucadendron*. The following descriptions are taken largely from Williams (1972). *L. pubescens* R.Br. has a wide distribution from the west-coast forelands to the Bokkeveld mountains in the north west corner of the biome, and along the southern inland mountain ranges north of the Berg and Breede rivers to the Witteberge near Ladismith. Populations are found at all altitudes, from 60 metres a.s.l. at Aurora on the coastal plain up to about 1750 metres near Tafelberg in the Cedarberg.

The rainfall in these areas is generally low but in the upper Cedarberg the rainfall is probably much higher. Leaf size and pubescence varies but there are always intermediates, which is unusual for an insect pollinated, poorly dispersed species (Williams, 1972). It occurs mainly on soils derived from the sandstones of the Table Mountain group. It is a robust shrub, up to 2,6m tall, with greyish green foliage. The leaves are oblanceolate and are smaller in the male which also has more shoots. The bracts of the cone (infructescence) are densely pubescent and are the source of this species' name (Williams, 1972). The smaller leaf size in the male is conspicuous in the study area and the sexes could, at a glance, be considered separate species. The seed is mature three to four months after flowering and is dispersed shortly before the cone itself is shed. Bond (pers. comm.) considers this species to be myrmecochorous, but I have found no evidence of this and the accumulation of a soil seed store must rely on chance escapes. The seed coat is thick enough to prevent fire damage, and the seed must be scarified before it will germinate in the autumn (pers.obs.). Seedlings can be found in mature vegetation and some of these do survive and develop to maturity (pers.obs.).

L. laureolum (Lamarck) Fourcade is not as widespread and occurs in scattered but dense populations from the Cape Peninsula westwards to the Potberg, generally south of the Berg and Breede rivers. Its range in altitude extends from near sea level close to Cape Agulhas to about 920 metres a.s.l. on the northern slopes of Jonaskop near Worcester. The rainfall in these areas is generally higher than that for L. pubescens. It occurs on a wide range of soils from limestone to sandstone. The sexes differ in the form of their canopies, the male having a spreading rounded canopy and the female a vertically elongated canopy. The foliage is dark green, the leaves of the female being somewhat larger than those of the male and oblong in shape. The species is insect pollinated (Williams, 1972) and the seed is retained in the cone for three to five years in older shrubs (Durand, 1981). Seedling recruitment and establishment can occur between fires (Durand, 1981, pers. obs.), but mass regeneration takes place only after fires. The seed is winged and so limited dispersal is possible. Insect predation of the seed in the cones has not been examined although damaged cones are found on *L. laureolum* (pers. obs.).

The strong sexual dimorphism in *L. pubescens* may be related to wind pollination, although the stigma is not typical of a wind pollinated plant (Williams, 1972). The wind pollinated *L. rubrum* (Williams, 1972) which also occurs in the area shows the same dimorphism, with small male leaves and inflorescences and more male shoots. This is not a consistent pattern in *Leucadendron* and more information is needed before a definite conclusion can be reached (see also section 4.3.2). The dimorphism in canopy form in *L. laureolum* is probably a consequence of the structural requirements (McMahon and Kronauer, 1976) of supporting the heavy cones.

(ii) Species composition

An analysis of the flora of the study sites is presented in Table 4. Families and genera typical of the Cape flora (Goldblatt, 1978) are strongly represented, although the Cedarberg site clearly has a smaller variety of species in each of the taxa. The families absent in the Cedarberg are those typical of moist, marshy habitats e.g. Bruniaceae, which are absent in the study area. The proportion of monocotyledons is lower in the Cedarberg, primarily because of the reduced number of species in the Restionaceae and Cyperaceae, especially the small species which form a continuous ground layer in parts of the Kogelberg study area. The number of species in the Liliaceae is higher in the Cedarberg. In the Dicotyledons the Ericaceae decline from 20 species in 7 genera including 13 _Erica_ species in the Kogelberg study area to just one minor genus and one species _Simocheilus multiflorus_ in the Cedarberg study area. The Leguminosae and Compositae both increase their representation in the Cedarberg, as do the Selaginaceae which are all annuals. The presence of plant species with succulent leaves, _Crassula_ sp., and stems, _Euphorbia_ sp., on rocky outcrops in the Cedarberg study area, confirms the dryer moisture regime of the site.

The data from species-area relationships is summarised in Table 5 and Figure 7. Also included are data from Bond (1983a) for comparable sites. The species area curves for the one metre

TABLE 4: Analysis of taxa in the communities at the two study sites. Families and genera selected from lists in Goldblatt (1978).

SITE	KOGELBERG				CEDARBERG			
Taxon	Genera		Species		Genera		Species	
	Number	% of flora	Number	% of flora	Number	% of flora	Number	% of flora
<u>Angiospermae - Monocotyledones</u>	35	35,4	80	41,5	35	30,4	44	26,8
Cyperaceae	3	3,0	16	8,3	2	1,7	5	3,0
Restionaceae	9	9,1	33	17,1	4	3,5	4	2,4
Iridaceae	12	12,1	16	6,3	9	7,8	10	6,1
Liliaceae	5	5,1	6	3,1	8	7,0	13	7,9
<u>Angiospermae Dicotyledones</u>	63	64,6	113	58,1	80	69,6	120	73,2
Proteaceae	5	5,1	10	5,2	3	2,6	9	5,5
Aizoaceae	0	0	0	0	2	1,7	2	1,2
Mesembryanthemaceae	0	0	0	0	1	0,9	1	0,6
Bruniaceae	1	1,0	1	0,5	0	0	0	0
Leguminosae	4	4,0	11	5,7	5	4,3	17	10,4
Penaeaceae	2	2,0	3	1,6	0	0	0	0
Rutaceae	4	4,0	7	3,6	4	3,5	5	3,0
Anacardiaceae	0	0	0	0	1	0,9	4	2,4
Rhamnaceae	1	1,0	2	1,0	1	0,9	5	3,0
Ericaceae	7	7,1	20	10,4	1	0,9	1	0,6
Stilbaceae	1	1,0	1	0,5	0	0	0	0
Selaginaceae	2	2,0	2	1,0	5	4,3	5	3,0
Compositae	14	14,1	26	13,5	23	20,0	30	18,3
Total	99	100	193	100	115	100	164	100
Spp/genus Monocot	2,3				1,3			
Dicot	1,8				1,5			
Total	1,9				1,4			

TABLE 5: Species-area curves using the power function (S = CA^b) in its linearised form (logarithms base e) as in many studies (Gould 1979) and the logarithmic function S = C + B log A (logarithms base 10) as used by Bond (1983a after Gleason 1925). Some data for comparable sites has also been included (Bond, 1983). The linear least squares regression technique was used on the transformed values (Snedecor & Cochran, 1980).

Sample type	Site	C	B	Correlation coefficient (r)	Mean species in 1 m^2	Min. species in 1 m^2	Max. species in 1 m^2
POWER FUNCTION							
1 m wide transect 32 m long	Cedarberg	16,198	0,305	0,982	7,7+/-3,2*	2	14
Two 1 m wide transects 50 m long regressed together	Kogelberg	15,122	0,329	0,962	13,3+/-2,9*	7	22
Five sets of nested quadrats 1 m^2 doubling to 128 m^2 regressed together	Cedarberg	9,870	0,326	0,940	8,6	6	11
LOGARITMIC FUNCTION							
32 m in transect	Cedarberg	13,242	20,871	0,989	7,7	2	14
50 m in transects	Kogelberg	8,996	25,421	0,946	13,3	7	22
Nested quadrats Bond (	Cedarberg	7,983	15,985	0,969	8,6	6	11
Bond (1983)							
Tall open proteoid shrubland - heath	Swartberg S2	23,2	17,5	-	18,6	-	-
understory South aspect	Swartberg S2	19,7	10,4	-	16,8	-	-
Tall open proteoid shrubland - restioid	Swartberg S6	10,3	9,1	-	10,2	-	-
heath	Swartberg S7	13,3	12,2	-	12,4	-	-
W. Cape Fynbos (from Naveh and Whittaker, 1980)		17,3	19,0	-	16,7	-	-

*standard deviation

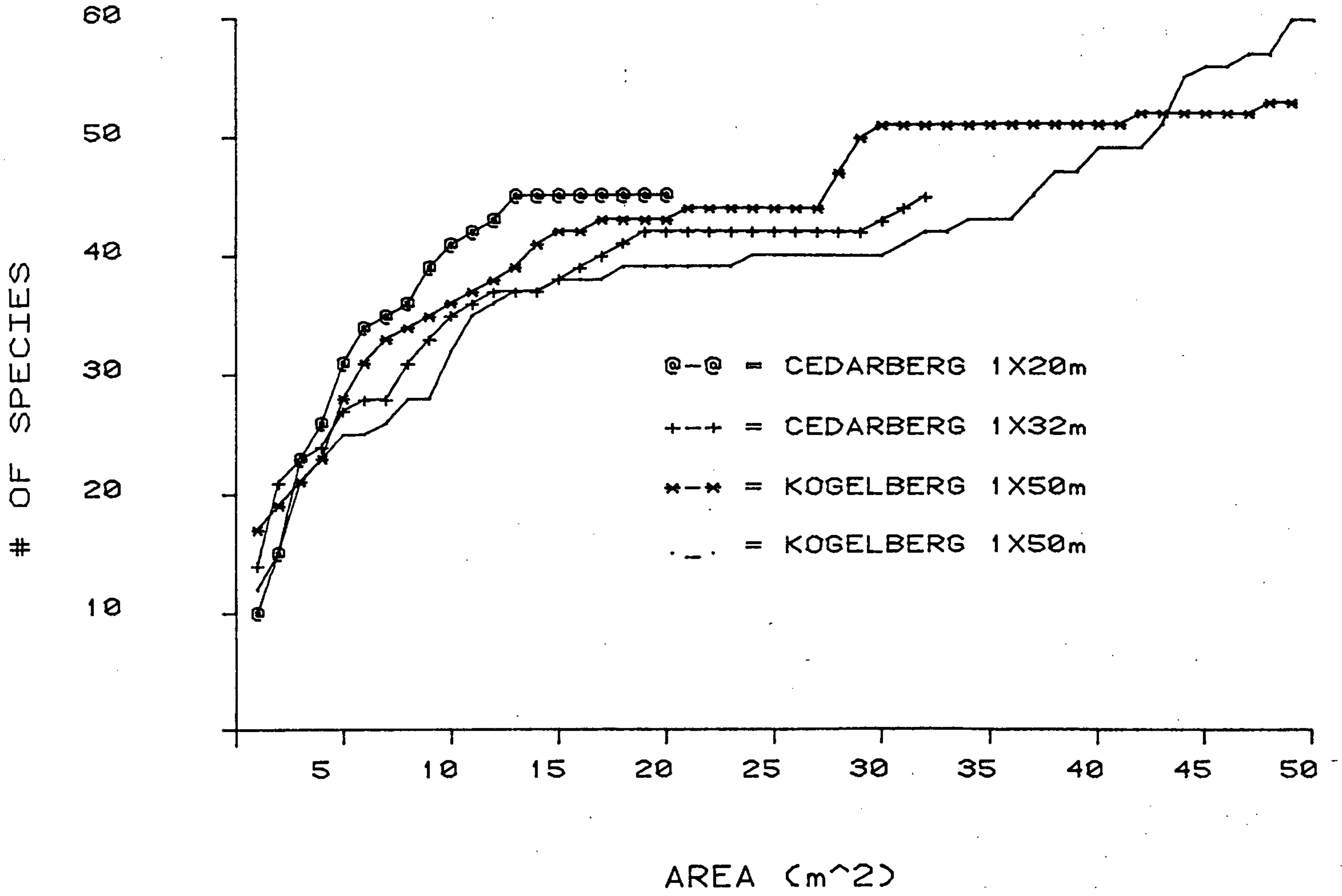


FIGURE 7 : Species area curves from one metre wide transects at the two study sites. Geophytes and annuals dormant in summer are included.

wide transects at the Kogelberg and Cedarberg are remarkably similar (Fig.7) and also show the steps in the rate of species addition as the boundaries of what could be termed micro-communities (Whittaker and Levin, 1977) are crossed. The small scale patchiness at both sites is evident in the wide range in the number of species per square metre and the low value of 2 species in a square metre found at the Cedarberg. Biological or ecological interpretation of the coefficients and exponents of species area curves is difficult, and Connor and McCoy (1979) consider them to be just fitted constants. Bond (1983a), however, found a close relationship between the number of species per square metre and the intercept for the logarithmic function. The rate of increase in species is a measure of the intra-community diversity Whittaker (1977). The intercepts and mean number of species per square metre for both study sites are closer to those for Bond's (1983a) north aspect Swartberg sites (S6 and S7 Table 5), especially as the Cedarberg curves include the seasonal geophytes and annuals which Bond (1983a) did not include. The high slopes for the study transects are largely due to the stepped nature of the addition of species over micro-community transitions in these long strips (Fig.7) as the nested quadrat slopes are much closer to those given by Bond (1983a).

3.3.2 Biomass

Table 6 : Selected data on aerial plant biomass in fynbos plant communities

Site	Community	Climate		Site factors			Age	Biomass (kg/ha)						
		Precip.	Mean. Temp.	Altitude	Geology	Aspect	(yrs)	Shrubs	Sub-shrubs	Restioid	Graminoid	Herbs & Geo.	Total	Litter
Jonkershoek[1]	Shrubland	1700mm	16,9°C	425m	Quartzite	North	21	32275	209	632	488	1818	35422	14259
	Shrubland			425m	Cape Granite	S-West	37	21581	1	258	155	357	22639	52990
Jakkalsrivier[2]	Heathland	849mm	13,6°C	785m		East	16	3253	±0	1819	6946	347	12365	2230
Silvermine[3]	Shrubland	1281mm	-	±600m	Quartzite	North	10	3093	-[5]	1234		545	4871	8000
	Shrubland		-		Quartzite	North	20	13117	-	4146		512	17775	25440
Jonaskop[4]	Restioid	1200mm	-	1520m	Quartzite	North	±14	347	-	13949		14	14311	199[6]
	Shrubland	800mm	-	910m	Quartzite	North	±14	7594	-	3470		5	11064	358[6]

[1] Van Wilgen (1980) [2] Kruger (1977) [3] Kathan (1979) [4] Rutherford (1978) [5] Sub-shrub mass grouped with herbaceous species. [6] "Mass dead individuals" (Rutherford, 1978).

Some data on biomass in fynbos communities are given in Table 6 and values for various samples in the two study areas are given in Table 7. The same general patterns holds for all sites with a high proportion of the mass being in the shrub and restioid growth forms (Kruger, 1977b; Van Wilgen, 1982). The Kogelberg total live mass is low for a 20 year old sclerophyllous shrubland (Kruger, 1977b). The total live mass for the 14 to 18 year old Cedarberg community is nearly 500 g/m^2 more than the maximum for the Kogelberg site, largely due to the considerable restioid mass of nearly 600 g/m^2. About three quarters of this is Hypodiscus neesii, a single tuft of which can be as much as 2400 grammes or 45200 g/m^2 basal area, but less than half of this is live shoots (pers. obs.). The large contribution a single restioid species can make is also evident from the high mass of Restio egregius in the one Kogelberg sample. The high graminoid mass in the one Kogelberg sample is due to the presence of Tetraria thermalis which forms dense clumps. It has large sclerophyllous leaves that, when dead, form a dry sheath around the aerial shoot (morphologically a rhizome). This dry sheath may protect the dormant buds from fire as is the case in some Aloe sp. (Bond, 1983b) and in Xanthorrhea sp. (see Gill and Ingwersen, 1976). The litter mass is also higher at the Cedarberg site, probably a result of slower decomposition and the higher live biomass. The relationship between sample size and sample variability is presented in Table 8. The data show a clear decrease in sample variability with increased sample size even with a decrease

Table 7 : Aerial plant biomass (g/m^2) at the Kogelberg and Cedarberg study sites as estimated from clipped plots and separate species samples. The Kogelberg data are from different sub-plots within the community and the Cedarberg data are from a single 5 x 20m area with randomly drawn sub-samples.

Site	Kogelberg				Cedarberg					
Quadrate size	1m^2	4m^2	4m^2	4m^2	1m^2	1m^2	2m^2	4m^2	5m^2	*10m^2
No. of quadrats	61	53	20	20	100	20	20	20	20	10
<u>Component</u>										
Shrubs and sub-shrubs	309,79	339,55	327,87	366,63	232,00	244,82	240,45	221,93	264,37	232,00
Restionaceae	243,50	297,96	143,24	131,14	530,81	583,89	561,52	548,01	490,32	530,81
Graminoids	3,01	102,60	37,00	56,72	9,20	9,71	9,71	9,08	9,90	9,20
Herbs and Geophytes	2,05	12,07	4,47	8,56	13,39	12,35	12,93	13,63	13,40	13,39
Total Live	558,33	752,43	512,58	563,06	785,43	850,80	824,61	792,65	778,00	785,43
Standard Error of the Mean	62,75	42,98	28,57	38,57	69,57	136,43	115,02	88,62	60,82	101,49
Coefficient of Variation (%)	87,77	41,59	24,93	30,64	88,58	71,71	62,38	50,00	34,96	40,86
<u>Separate Samples</u>										
<u>Species</u>										
<u>Restio egregius</u> (mean)	-	-	190,36	206,63	-	-	-	-	-	-
<u>Phaenocoma prolifera</u> (mean)	-	-	56,57	130,80	-	-	-	-	-	-
<u>Hypodiscus argenteus</u> (mean)	-	-	-	42,36	-	-	-	-	-	-
<u>Hypodiscus aristatus</u> (mean)	-	-	-	19,50	-	-	-	-	-	-
Litter	336,87	466,79	378,64	496,05	756,21	754,30	812,60	841,16	711,61	756,21
Total	895,20	1219,22	1138,15	1458,40	1541,64	1605,10	1637,21	1633,81	1489,61	1541,64
<u>Overstory Shrubs</u>										
<u>Leucadendron</u> spp. male	76,94	224,35	325,31	199,59	380,08	-	-	-	-	-
female	58,44	100,12	192,30	211,82	430,74	-	-	-	-	-
<u>Paranomus bracteolaris</u>	-	-	-	-	224,01	-	-	-	-	-
Total hive	694,41	1076,90	1084,82	1373,78	1820,26					

*Data from all the 5 x 2m areas within the 5 x 20m sample area.

Table 8 : Frequency distribution and statistics of the total live undergrowth biomass (g/m^2) for the study sites.

Site	Cedarberg						Kogelberg	
Clip-plot Area	1 x 1m	1 x 2m	1 x 3m*	1 x 4m*	1 x 5m	2 x 5m*	1 x 1m	2 x 2m
Number	100	50	33	25	20	19	61	53
Frequency in Class 1	69	15	11	4	4	2	35	26
2	25	18	11	9	4	2	20	19
3	4	11	9	8	6	9	3	6
4	0	4	0	2	5	5	1	1
5	2	2	2	2	1	1	2	1
Mean	785,43	785,43	791,27	785,43	785,43	780,12	558,32	752,43
Median Value	624,92	702,19	768,45	755,65	798,12	801,43	442,9	685,20
Class width	876,2	385,0	372,2	279	266,8	215,4	512,6	342,2
Max	4422,95	2055,31	2074,30	1599,44	1549,24	1315,84	2575,10	2041,25
Min	42,34	131,15	214,86	205,58	216,93	293,10	13,01	330,73
Median***	676,93	729,89	708,45	747,50	798,12	765,89	459,69	681,71
Mode***	459,92	661,2	734,5	671,64	944,74	844,04	262,42	540,26

*All possible 5 x 2m areas within the 5 x 20m sample areas

**Zar (1980)

in the number of samples. The larger the quadrat area, the more normally distributed the range of biomass values becomes, and the closer the median moves to the mean. This is analogous to a problem in point cover sampling where the spacing of the sample points must be greater than the size of individual plants or the sample becomes biased (Goodall, 1952; Tidmarsh and Havenga, 1955). The closer the sample size to the gap size or alternatively, patch size of large individuals in a community, the greater the probability of such an individual filling the entire quadrat. A larger quadrat size greatly decreases this probability and results in a greater probability of an "average" sample and also therefore results in a more normal sample mass distribution. The very high maximum value of 4423 g/m^2 in the Cedarberg is the result of sampling an area with two Hypodiscus neesii individuals.

The full set of allometric regressions for the different biomass components of the Proteaceae is given in Appendix 4. Some regressions for these and other species (Van Wilgen, 1982) are given in Table 9. The regression relationships are generally similar, the low coefficient for P. laurifolia probably being the result of the small sample size and the absence of small plants from the sample. The high coefficient for P. neriifolia cannot be explained at present, although Van Wilgen (1982) did find that the curves for P. repens and P. neriifolia did not differ in a Furnivals test, a test which compares the linearised form

Table 9 : Allometric regression equations fitted using the least squares regression technique on the linearised power equation, $M = AX^b$ in the form $\log_e Y = \log_e A + B \log_e X$. The X-variable is stem diameter below the first branch (Durand, 1981) and the Y variable total shrub mass excluding inflorescences. Also included in the table are the allometric relationships given by Van Wilgen (1980, 1982) for his aerial plant mass (recalculated to give grammes not kilogrammes).

Species	Coefficient	Exponent (B)	Correlation Coefficient (r)	n	Mass estimate St. di 10 cm
Leucadendron pubescens female	67,03	2,325	0,983	25	14167
L. pubescens male	66,75	2,348	0,983	25	14875
L. laureolum female	64,67	2,155	0,961	25	9241
L. laureolum male	78,49	2,119	0,973	25	10323
Paranomus bracteolaris	64,76	2,169	0,975	25	9557
Protea laurifolia	24,02	2,712	0,988	5	12376
*P. repens (Van Wilgen, 1980)	66,90	2,460	0,916	24	19249
*P. neriifolia (Van Wilgen, 1980)	107,10	2,259	0,954	22	19444

*Sub-sampling used in the analysis to estimate dry mass of the whole shrub.

of the data, regression slope and intercept (Furnival, 1961). A separate regression analysis for L. laureolum that included the inflorescence mass in the total mass, using the Furnival test, showed that the regression slopes differed significantly. This reinforces the suggestion that the amount of wood required support to this cone mass (McMahon and Kronauer, 1976), is minimised by having a taller narrower canopy in the female.

The total mass estimated for a stem diameter of 10cm (Table 9) reveal distinct differences between the species. Protea repens and P. neriifolia have the highest mass, but P. laurifolia attains a lower mass than L. pubescens. When allowance is made for the moister climate and the better developed soils at Jonkershoek, where Van Wilgen's (1982) sampling was done, the differences between the Protea species are probably a result of differences in environment rather than resource-use efficiency. The difference between L. pubescens and P. laurifolia is more apparent than real as very few L. pubescens achieve this stem diameter, which is less than the mean of about 14,5cm for P. laurifolia. The mass estimated for P. laurifolia for this mean stem diameter is 33900 grammes, more than double that for L. pubescens. The study being done at present by Miller (in prep) may help to clarify some of these differences.

In Table 10 the distribution of biomass within sampled shrubs is given. Unfortunately the division of the L. laureolum shrubs

Table 10: Comparison of the component biomass for the different species in the study, using actual shrubs with a stem diameter close to the mean of a sampled population.

Component	Species	L. pubescens female	L. pubescens male	L. laureolum female	L. laureolum male	Paranomus bracteolaris	Protea laurifolia
	Stem dia.	5,50cm	5,73cm	4,19cm	4,65cm	7,29cm	13,02cm
Leaves (%)		25,0	31,2	36,3	32,2	28,1	20,0
Twigs* (%)		25,9	27,3	5,9	6,3	25,8	2,8
Branches* (%)		50,1	41,5	57,8	61,5	46,1	77,2
Total (g)		3529	4023	1417	2038	4812	25313
New Inflorescences (%)**		2,3	-	0,8	-	2,4	2,3
Old Inflorescences (%)**		1,4	-	4,5	-	-	5,8
Leaf/Wood g/g		0,33	0,45	0,57	0,48	0,39	0,25

*Divided by fuel class into smaller or larger than 6mm (Countryman & Philpot, 1962) for the Cedarberg species and into shoots with or without leaves for the Kogelberg species.

**Mass not included in the total for the percentage calculations.

into leafy shoots and non-leafy branches does not give the same proportional distribution of the twig and branch mass. Protea laurifolia clearly supports the largest amount of wood per gramme of leaf, which is to be expected in a species that can attain a height of 5 metres and apparently has a long life-span and therefore should have a ratio closer to that of trees (see for example Westman and Rodgers, 1977). In all the samples to date the mean male Leucadendron shrub stem diameter and therefore mass is higher, probably because the absence of seed production makes more resources available for vegetative growth (Hoffman, 1981). The small proportion of old inflorescence mass in the female L. pubescens is a result of the retention of cones because the abscission layer has not developed. In all such cases investigated to date the cause has been the seed eating larva, mentioned earlier, which also bores into the end of the shoot and so disrupts the development of the abscission layer.

P. bracteolaris has a low leaf to wood mass ratio. The leaves of this species have a dissected, dichotomously branched form with acicular segments. The acicular form gives a higher leaf surface area to volume ratio than a flat form and may also allow the plant to maintain an optimum leaf temperature in full sunlight more easily (Miller, 1981). The low leaf : wood mass ratio suggests that the plant is maximising on its returns per gramme of leaf produced by this means, and must also have a higher rate of photosynthesis per gramme of leaf.

Table 11: Allometric regressions for undergrowth ericoid shrub species and medium to large Restionaceae. The regressions were derived using NONLIN (Commonwealth Forestry Research Institute, Oxford) with canopy or base diameter (m) for shrubs and restios respectively as the independant (x) variable and total mass (g) as the dependant (Y) value as this gave the best relationships.

Site		Kogelberg						Cedarberg	
Morphology		Shrub	Shrub	Restioid	Restioid	Restioid	Restioid	Restioid	Restioid
Species		Phaenocoma prolifera	Sympieza articulata	Restio egregius	Leptocarpus byalines	Hypodiscus aristatus	Hypodiscus argenteus	Hypodiscus nesii	Cannomois acuminata
Model	n	20	15	20	15	10	10	25	10
Linear	A	-61,11	-4,02	-176,97	-19,07	-395,90	-139,45	-921,26	-681,13
$Y = A + BX$	B	578,54	47,90	1733,4	209,17	2122,7	753,97	9014,7	5885,3
	r^2	0,79	0,67	0,42	0,71	0,88	0,80	0,60	0,64
Power	A	556,23	52,33	1589,2	709,69	1932,0	935,98	17812,0	611390
$Y = AX^b$	B	1,33	1,39	1,21	2,35	1,79	1,98	1,8965	4,79
	r^2	0,77	0,67	0,42	0,80	0,91	0,81	0,60	0,82
Logistic	A	0,0033	0,038	-0,00015	-0,022	-0,00018	0,0017	0,00050	-0,0017
$Y = 1/(A + B \exp(-CX))$	B	0,20	2,14	3542,7	0,18	0,01	0,079	0,14	0,024
	C	11,56	11,59	1,64	4,26	2,81	6,97	26,33	8,215
	r^2	0,85	0,70	0,42	0,84	0,92	0,81	0,635	0,87

The allometric relationships for the undergrowth species (Table 11) reflect the morphology of the plant species. Phaenocoma prolifera, for example, a tall, slender shrub, up to 1,5 metres tall, has a much higher coefficient than Sympieza articulata, a lower shrub with a spreading canopy. In the Kogelberg study the mean grammes per square metre value and an estimate of the percentage cover of the species was used to estimate the biomass. This method of estimating the mass is reasonable because the data when plotted show an essentially linear relationship.

In Figures 8 and 9 the relationships between the overstorey mass and understorey mass and between the understorey exponents for the Kogelberg sub-plots are presented. The general pattern suggests that the overstorey and understorey do not compete within the range of overstorey mass found at that site. However, the overstorey cover, from calculations, ranges from eight to forty percent and is rarely continuous (Durand, 1981, pers. obs.). These values may be too low for Specht and Morgan's (1981) hypothesis to be tested. There are also, however, differences in habitat between the plots, as Reciprocal Averaging of the floristic data suggests that the plots at the low and high ends of the overstorey mass differ floristically. Personal observations substantiate this and suggest the following interpretation of Bonds (1981) hypothesis. In areas with a low overstorey biomass

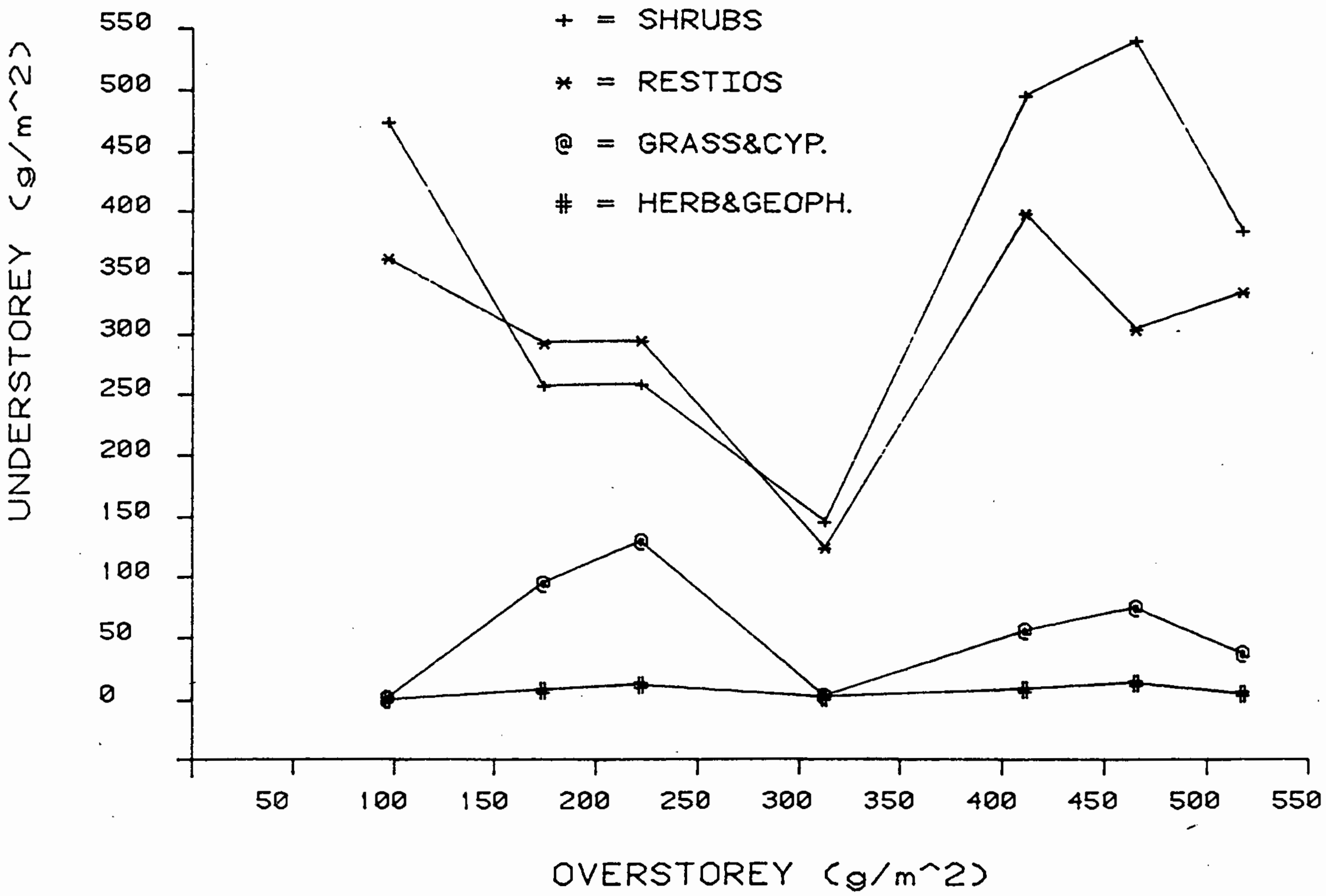


FIGURE 8 : Overstory mass and understory mass as measured in the different sub-plots at Kogelberg.

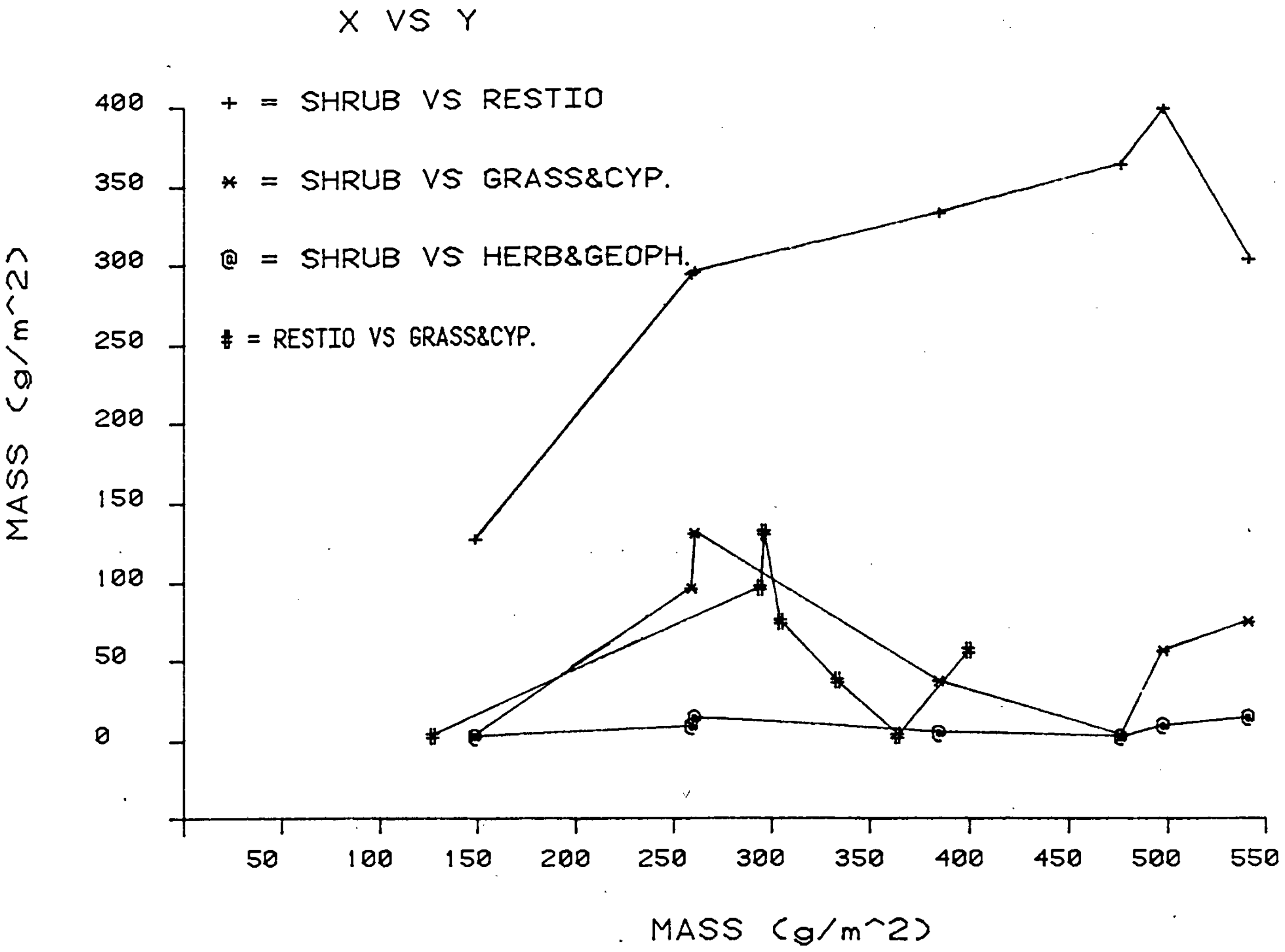


FIGURE 9 : Relationships between the understory components as measured in the different sub-plots at Kogelberg.

the soils are shallow and the underlying bedrock does not store enough water to allow the overstorey to develop. The decrease in understorey mass in with an increase in overstorey mass is the result of a very shallow soil which reduces the understorey and a bedrock fractured enough to support the denser overstorey. The subsequent increase in both understorey and overstorey mass is the result of a deeper soil which supports both components. The relationships between the understorey components are more difficult to explain. In Figure 8 the shrub and restioid mass both increase (linear regression: Restio mass (g/m^2)= -37,1791+ 1,3344(Shrub mass), r=0,78, P<0,025) suggesting that both growth forms are able to benefit from the variation in soil depth, the shrubs more so than the restioids. This differential rate of increase may be a result of the fact that the site is not seasonally waterlogged and the restioids do not therefore displace the shrubs (Bond, 1981). The restioid or shrub to graminoid relationship indicates that the graminoids can, under certain conditions, co-exist with the dominant understorey components. However, the sub-plot in question has a high percentage cover of Tetraria thermalis, a plant which has a high biomass. This relationship may therefore reflect a habitat requirement of this species, and not graminoids in general, and Bonds (1981) ideas on the rooting patterns and water relations of graminoids and restioids cannot be tested. This pattern is only in evident in the averages as the individual samples vary too much to predict any general pattern to for fynbos communities.

3.3.3. Pattern

The stratification of the vegetation is summarised by means of the foliage profiles in Figure 10 and in the stylized horizontal views in Figures 12 and 13 . Figure 11 summarises the results of the survey using the modified Trabaud method (Durand, 1981) and gives a more detailed picture of the contribution of different growth forms to the 0 to 1 m layer. The horizontal distribution of the plants in an area of each community is presented in Figures 12 and 13 which show the outlines of the plant canopies. The outlines only indicate the major gaps in the canopies and even within the outlines the cover is not complete. The outlines of under- and overstorey plants in the Cedarberg (Fig. 12) were drawn from the separate photographs. In the Kogelberg (Fig. 13) the outlines of plants under the canopy were drawn in as accurately as possible, but some of the plants under the overstorey shrubs may have been missed.

The foliage profiles for the two sites clearly illustrate the differences in the composition of the strata. The dense layer of small restioid and graminoid plants in the first 0,2 m at the Kogelberg is obvious. The Cedarberg community has a much denser middle layer, 0,4 to 1,4 m, which is a result of the dense, tall Restionaceae, the presence of dense shrubs such as Stoebe in this layer and the fact that Leucadendron pubescens has a more rounded canopy and therefore has more leaves at a

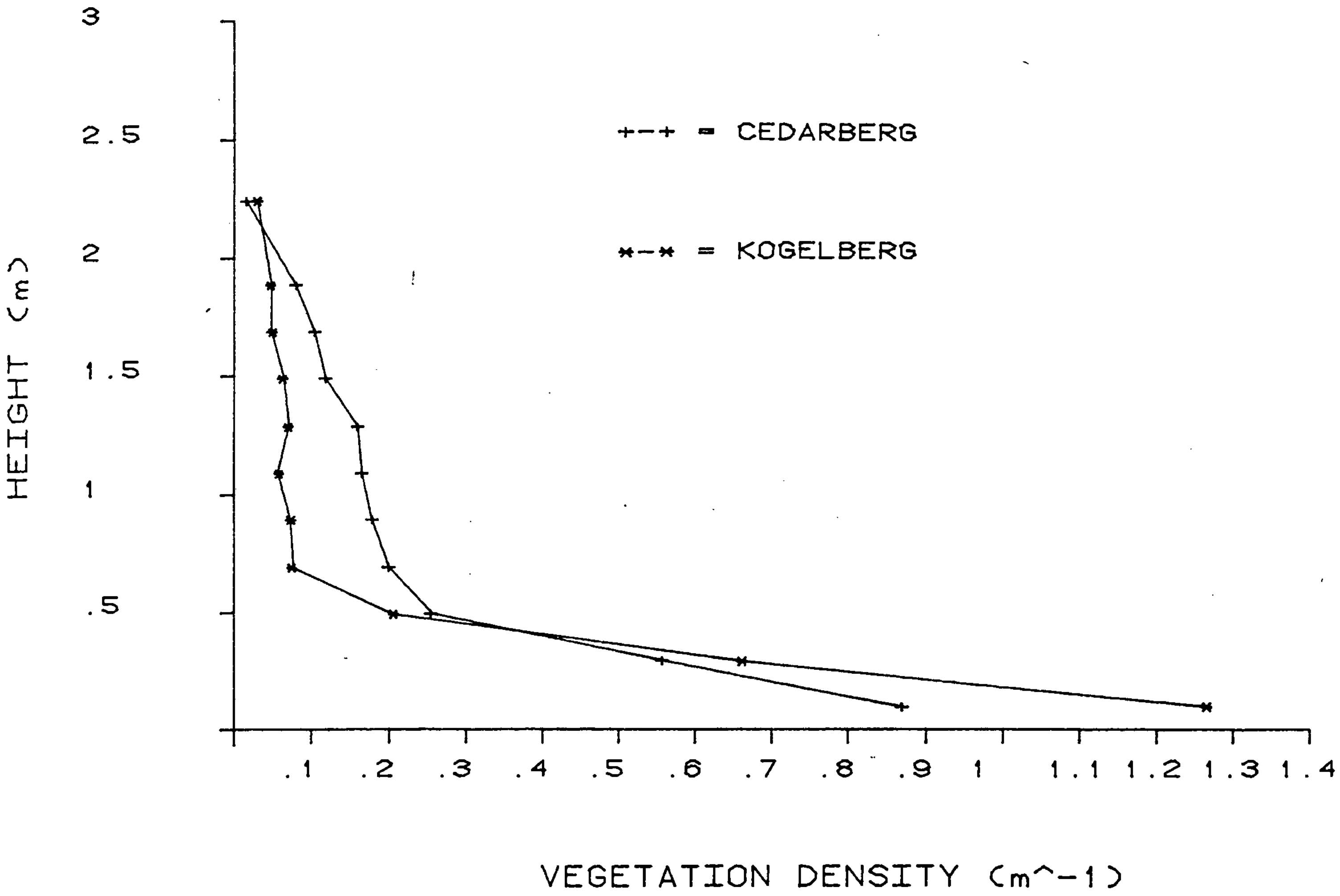
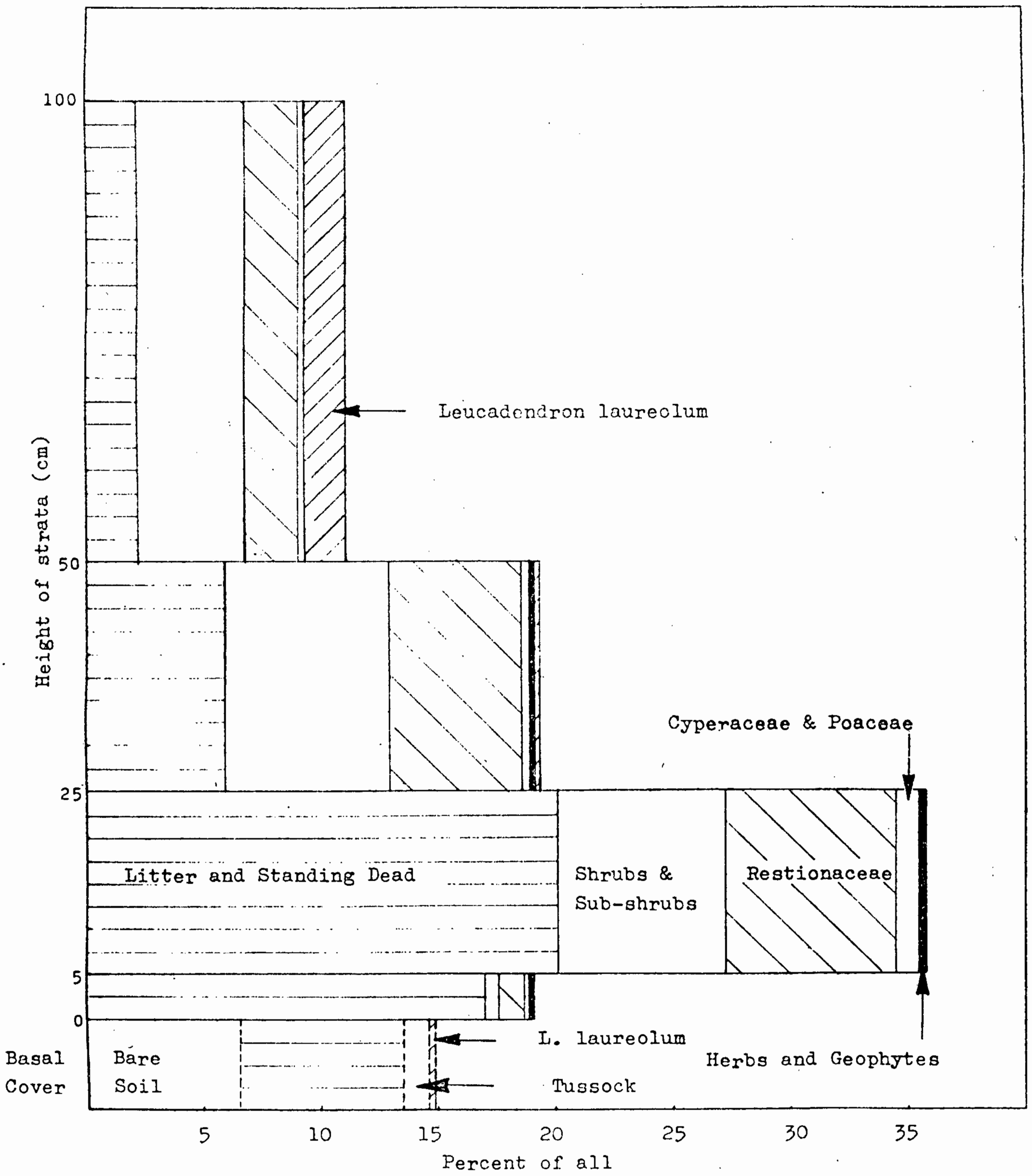


FIGURE 10 : A foliage profile showing the horizontal density of the vegetation at the study sites. The densities are graphed against the mean height of each layer.

Figure 11: The composition of each stratum, with each stratum represented as a proportion of the total number of toutches recorded for all 7 plots (700 points). Sampled at the Kogelberg using a modified Trabaud method (Durand, 1981).



lower height than Leucadendron laureolum. Figure 11 emphasises the large proportion of standing dead material, an important component in determining the behaviour of a fire. Just over a third of all aerial contacts are in the lowest 0,25 m, a fact which confirms the pattern seen in Figure 10. The major reduction in density with height is in the dead material and in the Restionaceae, where the proportion in the 0,5 - 1 m layer is almost entirely Restio egregius which reaches about 1,2 m in height.

The birds-eye view of the canopies of the overstorey shrubs (Figures 12 and 13) clearly shows the patchy nature of the canopy. This emphasises the low light interception of these canopies, and the coarseness of the branching of the Proteaceae which results in a fragmented canopy in older shrubs, particularly in the female Leucadendron pubescens. The only tall shrub which maintains a relatively closed canopy is Protea laurifolia. A dense stand of Paranomus bracteolaris and the Protea laurifolia stand are the only areas where the understorey is notably reduced. This may be a result of low light levels, as well as moisture stress although the dense litter fall may also play a role as the understory plants can be covered by falling leaves. In these cases Specht and Morgan's (1981) hypothesis appears to hold, but identification of the actual controlling factors will only come from carefully designed experiments.

The understorey species in the Cedarberg show no particular

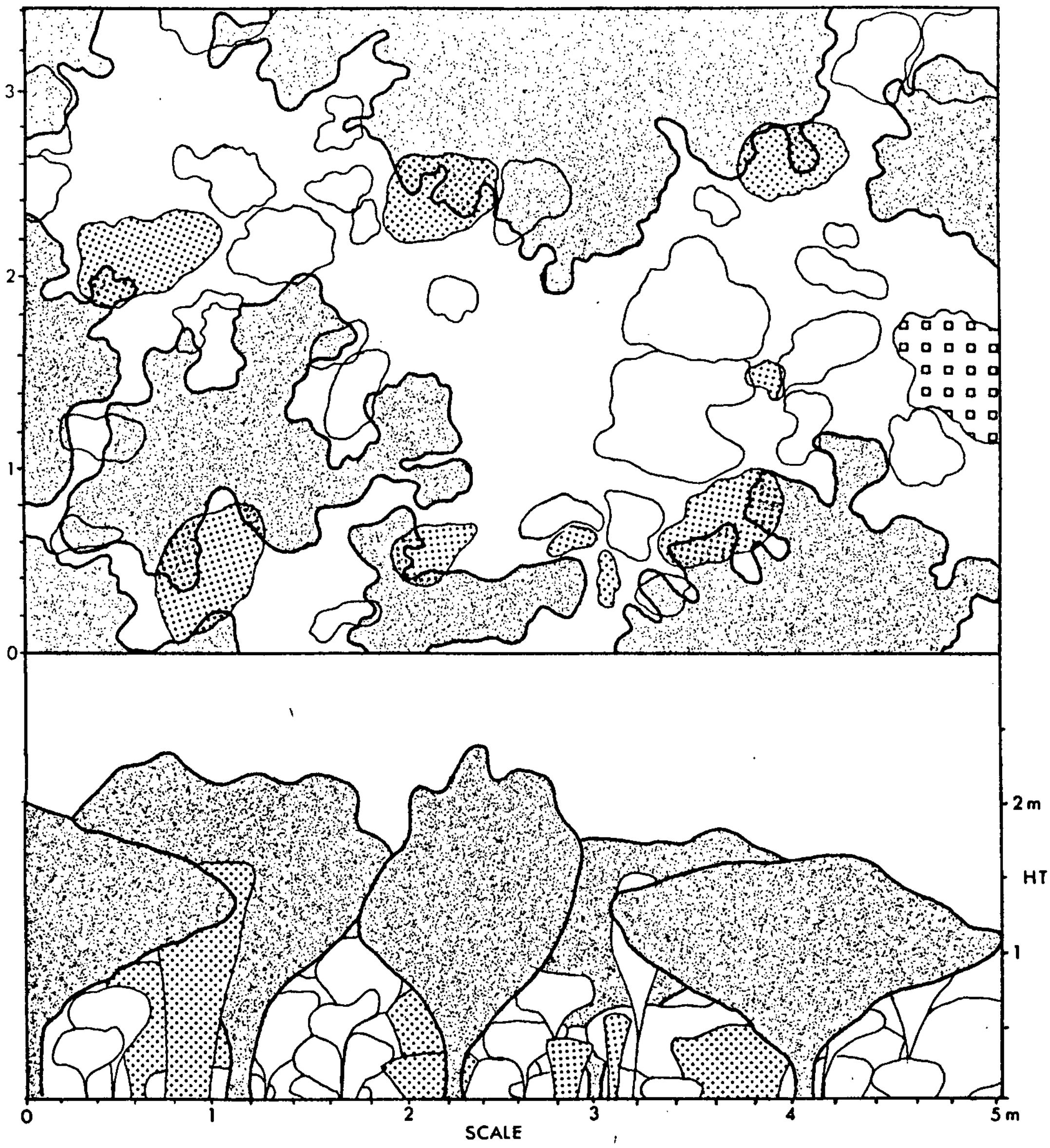


FIGURE 12 : Overstorey and understorey plant canopy outlines for an area at the Kogelberg study site. The upper diagramme is traced from a transparency taken looking vertically downwards from a height of 7,5 m. The lower diagramme gives a stylized horizontal view of the same portion of the vegetation. The height scale in the side view is not the same as the horizontal scale. = overstorey, = understorey graminoids, = understorey shrubs, = exposed soil.

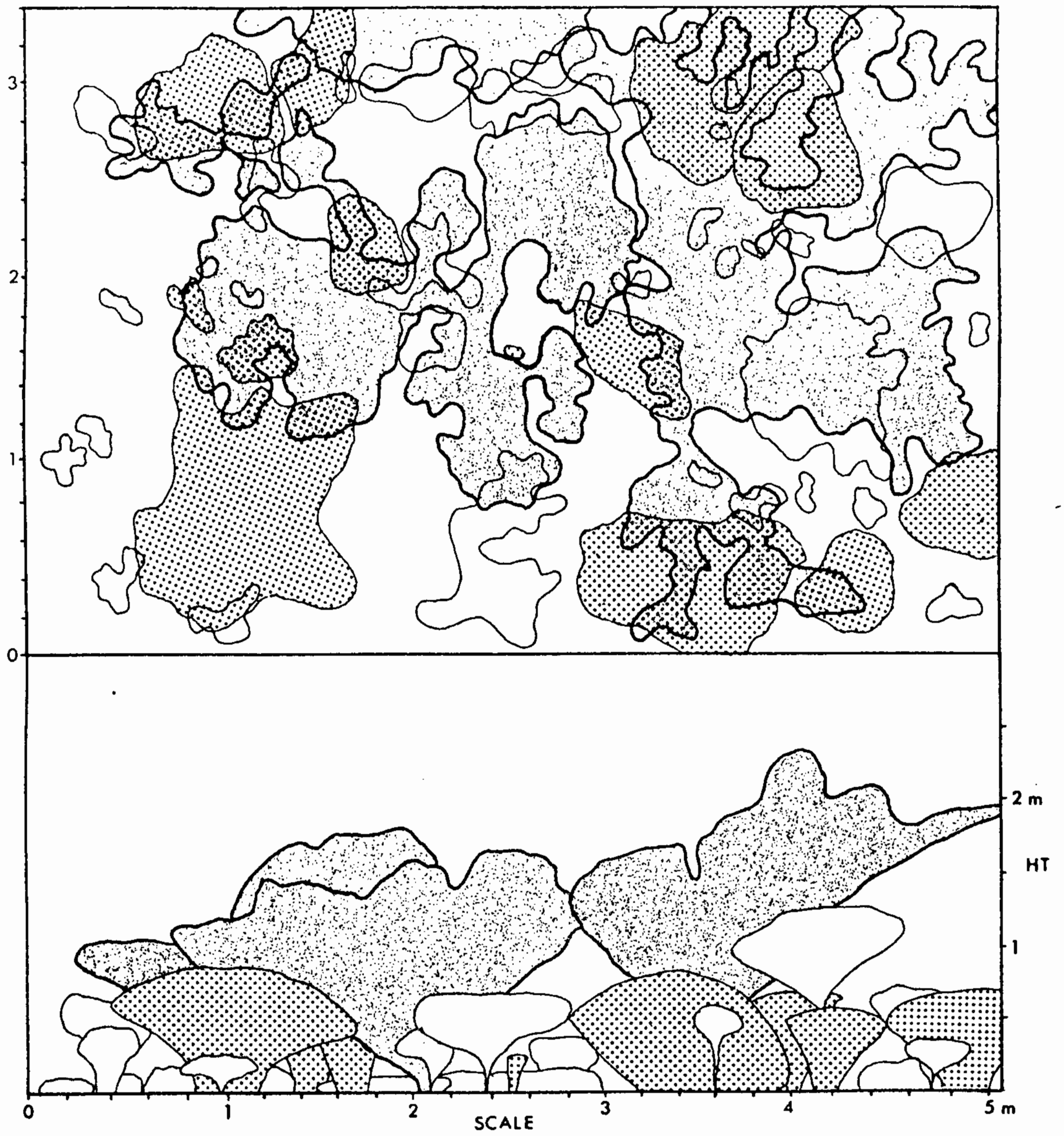


FIGURE 13 : Overstorey and understorey plant canopy outlines for an area at the Cedarberg study site. The upper diagramme is traced from a transparency taken looking vertically downwards from a height of 7,5 m. The lower diagramme gives a stylized horizontal view of the same portion of the vegetation. The height scale in the side view is not the same as the horizontal scale. = overstorey, = understorey graminoids, = understorey shrubs.

tendency to occur between the overstorey shrub canopies. In the Cedarberg most of the area between the understorey species is bare soil, but only a small area of bare soil was visible at the Kogelberg, most of the soil being covered by dead material from restioids and plants too small to indentify clearly on the transparency. These views emphasize the patterning in the associations of species at the sites and the pattern of distribution of the individual growth forms. Westman (1983) examined the various factors that account for plant distributions at both the "supra-organismal" (species association) and "organismal" (species distribution) levels in Mediterranean communities. As Miller (1983) also suggests, moisture requirements are probably more important than light interception to plants where photosynthetic pathways become saturated at low light intensities. Such plants would actually benefit from sparse shade as this would reduce the need to lose water in cooling their leaves even though competition for root zone resources (Westman, 1983) would be increased.

The actual pattern of a species may depend entirely upon its requirements for regeneration (Grubb, 1977) and the factors that have determined the distribution of seeds or dormant buds in the soil. Therefore, the effects of substrate cannot be excluded from the patterning of the plants particularly in the rocky Cedarberg soils. The large Restionaceae in the Cedarberg are myrmecochorous and the pattern of for example, Hypodiscus neesii, is determined by the positioning of ant nests and middens.

Small plants and those with sparse canopies e.g. Ehrharta sp., could not be seen on the transparencies, but the floristic data do not suggest that they are only found in the gaps between overstorey shrubs. Specht and Morgan's (1981) hypothesis that moisture availability controls the overall percentage overstorey cover, may, therefore, hold as a general trend, as for example in Specht and Moll (1983, figure 7). However, many factors, such as fire history (Van Wilgen, 1982), make it difficult to confirm or refute this hypothesis at an intra-community scale and more detailed studies are necessary.

3.3.4 Growth forms

It is relatively easy to find a system by which to classify plants but it is not easy to find one which provides ecologically meaningful associations of characters. As Orshan (1983) observes "mediterranean-type plant growth forms and vegetation are thought to result from convergent evolution, the nature of which regretfully does not reveal much about the morphogenetic processes which resulted in these growth forms, the related physiological properties which are important as adaptations to mediterranean environments, or the nature of processes involved by natural selection in these environments". Parsons (1976) after a detailed analysis of some chaparral and matorral communities concluded that in some cases species in the analogous communities in the regions were more similar to each other than to taxonomically closely related species. This emphasises the genetic plasticity of species, the variety of solutions that plants can find and, at the same time, the similarities in the limiting factors in different mediterranean environments (Miller, 1983).

The analysis of the study site plant communities, using the species given in Appendix III, is presented in Tables 12 and 13. The proportion of graminoid species is higher at the Kogelberg (46%) than at the Cedarberg (16%). There are also fewer non-seasonal graminoids at the Cedarberg, although in terms of mass they are still important. The geophytes increase from 35 to 47% of the flora, again a trend that indicates the greater aridity of the Cedarberg environment. A full analysis of Dafni _et al_.'s (1981) ideas on the distribution of types of geophytes was not possible in this study, but their idea that hysteranthous flowering should increase with increasing aridity holds. There are no hysteranthous species at the Kogelberg whereas there are at least six species at the Cedarberg including one _Pelargonium_ species. Annuals increase from 6% to 22%, an indication that the more open understorey provides regeneration niches for these species which in moister habitats are occupied by shallow rooted perennial species.

There are more tall shrub species in the Cedarberg community. Three of these, _Maytenus oleoides_, _Olea europaea_ subsp _africana_ and _Dodonea viscosa_ are actually trees and can reach large sizes

TABLE 12: The growth form classification of the plant species at the two study sites, using the system outlined in Table 3A

A) KOGELBERG

Herbaceous

Grouping	Evergreen	Deciduous	Annual	
Seasonal graminoid	20	0	0	20
Non-seasonal graminoid	33	0	0	33
Non-geophytic forb	13	0	7	20
Geophytes	15	25	0	40
Climbers	1	0	0	1
	82	25	7	114

Woody

	Evergreen	Deciduous	
Tall shrub	2	0	2
Medium shrub	17	0	17
Low shrub	41	0	41
Sub-shrub	19	0	19
	79	0	79

Geophytes

	Evergreen	Deciduous	
Monocotyledons	9	18	27
Dicotyledons	6	7	13
	15	25	40

B) CEDARBERG

Herbaceous

Grouping	Evergreen	Deciduous	Annual	
Seasonal graminoid	11	0	0	11
Non-seasonal graminoid	4	0	0	4
Non-geophytic forb	10	0	20	30
Geophytes	6	37	0	43
Climbers	3	0	0	3
	34	37	20	91

Woody

	Evergreen	Deciduous	
Tall shrub	9	0	9
Medium shrub	16	0	16
Low shrub	33	1	34
Sub-shrub	20	0	20
	78	1	79

	Evergreen	Deciduous	
Monocotyledons	5	25	30
Dicotyledons	1	10	11
	6	35	41

TABLE 13: Fire regeneration classification of the flora of the two study sites, with the growth forms from Table A) and the regeneration types from Table B).

A) KOGELBERG

Herbaceous	HA	HPD	HPR	
Seasonal graminoid	0	1	19	20
Non-seasonal graminoid	0	13	20	33
Non-geophytic forb	7	10	3	20
Geophyte	0	0	40	40
Climber	0	1	0	1
	7	25	82	114

Woody	WDP	WDS	WRS	WRA	
Tall Shrub	2	0	0	0	2
Medium Shrub	0	14	3	0	17
Low Shrub	0	29	12	0	41
Sub-shrub	0	17	2	0	19
	2	60	17	0	79

Total Flora	D	R	
Herbaceous	32	82	114
Woody	62	17	79
	94	99	193

B) CEDARBERG

Herbaceous	HA	HPD	HPR	
Seasonal graminoid	0	2	9	11
Non-seasonal graminoid	0	1	3	4
Non-geophytic forb	20	6	4	30
Geophyte	0	0	43	43
Climber	0	3	0	3
	20	12	59	91

Woody	WDP	WDS	WRS	WRA	
Tall Shrub	2	4	0	3	9
Medium Shrub	0	13	3	0	16
Low Shrub	0	21	13	0	34
Sub-shrub	0	16	4	0	20
	2	54	20	3	79

Total Flora	D	R	
Herbaceous	32	59	91
Woody	56	23	79
	88	82	170

under suitable conditions (Boucher and Moll, 1981). The first two species are represented by single individuals and the third occurs mainly near stream lines and along the road verge although some do occur in the study area. The remaing six species are all important in terms of cover which is, at least in part, a reflection of the fact that soil water reserves for deep rooted species must be sufficient to support large plants. There are also fewer low shrubs in this community, more a result of the decline in Ericaceae, than a change in the representation of a growth form as such. This is in line with Cowling and Campbell's (1983) hypothesis that there is relatively little change in the representation of the shrub growth form along a moisture gradient in nutrient poor soils. Only one drought deciduous shrub, Rhus dissecta, is found at the Cedarberg study site, and even this shrub only sheds its leaves for a relatively short period. Young resprouts of R. dissecta remain evergreen suggesting that because the leaf area is low, transpiration is reduced and water stress is therefore also less (Rasedovich and Conrad, 1980). Its low importance lends support to the idea that drought deciduousness only occurs in mediterranean communities where the costs of maintaining leaves exceeding those of producing new leaves (Miller, 1981). In a nutrient-poor environment the nutrient costs of leaf construction will compel the plants to maintain at least enough leaves to maintain carbon balance (Specht and Moll, 1983) even under relatively severe drought (Miller, 1983). Rhus rosmarinifolia at Jonkershoek is also deciduous in the summer (Kruger, pers. comm.) and the drought deciduousness of these plants therefore requires more investigation.

There are fewer evergreen dicotyledonous geophytes and more monocotyledonous geophytes in the Cedarberg community. There are also less rhizomatous, evergreen geophytes and more bulbous and tuberous, deciduous geophytes. Both these trends can be related back to the greater aridity of the Cedarberg site. The decrease in dicotyledonous geophytes is primarily the result of a reduction in the rhizomatous, evergreen Corymbium species (Compositae). Drosera is absent from the Cedarberg study site because the seasonally wet habitat it requires is not found in the area.

The high proportion of persistent herbaceous growth forms is typical of fynbos (Cowling, 1982; Cowling & Campbell, 1983; Kruger, 1977b, 1979) and differs only slightly between the sites, a situation which confirms the shallowness of the soil as far as shallow rooted shrubs are concerned (Bond, 1981). At the same time the water reserves accessible to these shrubs are sufficient even in dry years to support a vegetation which is predominantly evergreen. Although the proportion of evergreen species decreases from 83% to 66% with the increase in aridity, the change in terms of community physiognomy is small.

In the Kogelberg 53% and in the Cedarberg 55% of the species (excluding annuals) are capable of sprouting (WR and HPR Table 13). Eighty-three percent of the Cedarberg herbaceous plants can sprout as against 77% of the Kogelberg species, but only 29% and 21%, respectively, of the woody plants. The decrease in herbaceous seeding species at the Cedarberg is largely due to the decline in Restionaceae. This may be a result of the decreasing diversity of Restionaceae in areas away from the foci of speciation in this family (ultimate cause) or the low number of species of this family that can cope with the dryer environment (proximal cause) or both factors acting together. The number of obligate-seeding shrubs with canopy stored seed (WDP) is the same for both areas and all of them belong to the Proteaceae. There are no tall sprouting shrubs in the Kogelberg study area, although _Protea nitida_ and _P. cynaroides_ do occur in the vicinity, and this difference may, therefore, be a consequence of historical factors rather than site factors such as soil moisture regime. In general, the proportion of sprouting shrubs is lower at the Kogelberg, largely as a result of the number of fire sensitive Ericaceae, which are virtually absent in the Cedarberg. As in the case of the Restionaceae, this may be a result of both the speciation in this family (Baker and Oliver, 1967) and the dry soil moisture regime.

3.4 Conclusions

The visual similarity of these two plant communities is consistent with the results of the quantitative analyses of their structure. There are fewer species at both the community and small scale (1m^2) level in the Cedarberg study area. These differences are primarily the result of the reduction in species in the Ericaceae and Restionaceae. There is still much controversy surrounding the relative importance of:

a) the origins of the present flora;

b) the physiography; and

c) past climatic variation in determining the species distribution and speciation patterns observed today (Axelrod and Raven, 1978; Dahlgren, 1963; Deacon, 1983; Goldblatt, 1978; Kruger and Taylor, 1979; Levyns, 1964; Nordenstam, 1969; Taylor, 1978, 1980; Weimarck, 1941). This makes it difficult to separate, or estimate the relative importance of, the role of ultimate (e.g. speciation patterns) and proximal (e.g. present climatic regime) factors in producing the lower species richness in these genera in the Cedarberg study area. In communities in the moister parts of the Cedarberg there are many more species in these genera and this suggests that the present climatic regime is the primary factor cntrolling the number of species in the study area. The differences in growth form spectra and pattern can also be related to these floristic differences. There are more sprouting species in the Cedarberg than in the Kogelberg community if annuals are excluded. This is consistent with the idea that, within limits, a drier climate and unreliable precipitation should favour sprouting species with their established root systems over seeding species. The high proportion of seeding species needs to be investigated more thoroughly (Keeley, 1978), and over a wider range of communities before definite conclusions can be drawn.

The biomass of the community in the Cedarberg study area is higher, which suggests that there must be factors which compensate for the lower annual precipitation. The higher intensity rainstorms at the Cedarberg will replenish the soil water stores and will partially compensate for the lower rainfall and greater potential evaporation.

In the discussion thus far the emphasis has been on explaining the differences between the communities in terms of water relations and speciation patterns. Miller et al. (1983) and Miller (M.Sc., in prep.) have found that moisture deficits may not be as severe as was previously supposed. This lends emphasis to the importance of nutrient availability in fynbos. Although the accuracy of the techniques used for soil nutrient analysis has been questioned (in terms of actual availability to plants; Mitchell, Manders, pers.comms.), the Kogelberg soils, particularly the Mispah form, do have lower values than the average for sandstone soils given by Campbell (1983). Low nutrient availability may, therefore, be the primary reason for the low plant biomass at the Kogelberg site. The Cedarberg site's soils probably have more plant accessible nutrients as they are less leached and may also be derived from more nutrient rich rocks. This would enable the plants to grow more rapidly and may also, in part, account for the greater diversity of annual plants found in Cedarberg community (see Specht and Moll, 1983).

The species richness and endemism of the Cape Floristic region has been described and documented by many authors (Goldblatt, 1978; Kruger, 1977a, 1979; Oliver, 1977; Taylor, 1978). The flora of the Cape Floristic region is marked by a high degree of speciation within taxa in certain families. The Ericaceae, Restionaceae, Leguminosae and Rutaceae, to name a few, all have genera with large numbers of species, the largest genus being Erica with 635 species (Goldblatt, 1978). Deacon (1983) and Goldblatt (1978) both review possible reasons for this richness in species, and consider the long development period of the flora, the diverse topography and the climatic fluctuations in the Pleistocene to be extremely important. Deacon (1983) and Bond (1983a) both note that the flora of mediterranean Western Australia is also species rich and Deacon (1983) considers this to be a result of long evolutionary development on similarly nutrient poor substrates.

These ideas are supported by the views of Whittaker (1972,1977) and Whittaker and Levin (1977), who see an increase in species diversity with time as being an inevitable consequence of Gause's niche exclusion principle (Gause, 1934 in Whittaker, 1972). This principle impels "species toward niche and habitat differentiation, so that every relationship to patchiness in time (and space) that is different from the relationships of other species is a target of opportunity for species evolution" (Whittaker and Levin, 1977). This implies that the high intercepts and fairly steep slopes of the species-area curves (Bond, 1983a) are the result of high levels of resource and niche partitioning, and plant specialization. It is difficult to picture sufficient niche and habitat axes to account for the numbers of ecologically similar plant species found in small areas in fynbos communities.

Disturbances or perturbations are a phenomenon in virtually all communities (Huston, 1979). Disturbance regimes which prevent the establishment of an equilibrium in which competition could eliminate species will maintain species diversity (Connell, 1979; Huston, 1979; Kruger, 1983). Huston's (1979) hypothesis is that natural disturbance rates in most communities are such that populations of organisms never reach a competitive equilibrium. Species populations may be reduced to critical levels but the species will not be eliminated. Competition is, therefore, only one of a number of factors contributing towards the maintenance of community diversity. Fynbos plant communities fit the requirements of this hypothesis in a number of ways:

(i) Population growth rates i.e. the per capita rate of increase in numbers or mass between disturbances, must be low. The majority of fynbos plant populations attain maximum densities after fires and decline between fires (Kruger,1983) and fynbos communities have relatively low growth rates (Kruger, 1977; Van Wilgen, 1982).

(ii) Low nutrient availability should be correlated with high diversity because it results in low growth rates in organisms and extends the period required to reach an equilibrium.

(iii) Speciation may only require reproductive isolation (allopatric or sympatric) because extensive niche and resource partitioning is unnecessary. This would appear to apply particularly well to fynbos with large numbers of species in many communities belonging to a single taxon and where geographic speciation appears to have been important in many genera (Dahlgren, 1963; Deacon, 1983; Goldblatt, 1978). Patterns of resource use (Miller, 1981; Tilman, 1983) and dynamic processes within communities (Whittaker and Levin, 1977; Wiens, 1977), such as plant-animal interactions, also add to the opportunities for species diversification in terms of this hypothesis.

Most of the present theory used for predicting community structure and species diversity patterns is derived from work on animals, and is fairly well established, particularly for birds (Cody, 1983; Siegfried, 1983; Siegfried and Crowe, 1983) and small mammals (Breytenbach, 1983; Fox, 1983; Newsome and Catling, 1983). Plants, however, do not respond so directly to the biotic and abiotic environment at a community scale (Westman, 1983), or to such easily measured parameters as foliage profiles (Bond, 1983). This is partly because it is it is extremely difficult to measure the root environment, and partly because very little is known about the factors in this environment to which plants as species and individuals respond. Seed germination and seedling establishment are affected by small scale variations in their environment(Grubb, 1977). Subsequent community structure may also be radically modified by fire season or frequency influences on regeneration patterns (Bond, 1980, in press; Kruger, 1983; Van Wilgen, in prep.). The unravelling of these regeneration patterns requires a more detailed knowledge of the demography of these plants which entails studies of both the dynamics of plant populations (genets) and the plant parts (ramets,shoots) (Harper, 1980). Animal ecologists have achieved much success with the guild concept (Root,1967) but a similar approach to plant guilds has yet to be clearly set out (Bond, 1983a), primarily because their critical resource use patterns are not as easy to quantify as, for example, cover from predators and trophic levels. The identification of demographic strategies that can be related to post-fire regeneration patterns in plant communities will probably be the first step in this direction.

Large scale changes can be predicted as gradient analyses have shown (Bond, 1981; Campbell, 1983; Cowling, 1983) and their predictions have been borne out in this study. Small scale diversity is poorly understood as yet and will remain so until the complex interactions between individual plants, plant populations and the environment they inhabit are studied intensively.

4. PLANT COMMUNITY PHENOLOGY

4.1 Introduction

In mediterranean climates, especially those with no precipitation during the summer months, soil moisture is the controlling factor determining the seasonality of the plants (Kummerow, 1983; Miller, 1981; Mooney et al., 1974). The regular summer drought provides opportunities for deep-rooted shrubs, shallow rooted shrubs and shallow rooted persistent herbaceous plants to develop different phenological patterns directly related to the accessibility of soil moisture. The phenology of the Australian and South African mediterranean communities is more diverse and the patterns do not appear to be so directly related to plant-water relations. Specht and Rayson (1957) and Specht et al. (1981) have suggested that in Australian heathlands the different evolutionary origins of the overstorey (tropical) and understorey (temperate) flora account for the "anomalous" summer growth of overstorey shrubs in a summer dry climate. The Australian heathland Proteaceae apparently require high air temperatures for the initiation of shoot growth (16 - 25 C) and this is thought to be a relict of their tropical origin (Specht et al., 1981). This is in agreement with taxonomists who have worked on the family and consider the ancestral Proteaceae to have been tropical taxa (for example Johnson and Briggs, 1975; Levyns, 1970; Rourke, 1980; Williams, 1972).

Phenological patterns within plant communities are generally seen as a means of partitioning resources temporally and thereby increasing niche differentiation and reducing competition for pollinators, seed dispersers and other resources (Bond, 1980; Kruger, 1981; Kummerow, 1983). Plant periodicity is also an important aspect of plant-animal interactions because of the influence of temporal resource patchiness on the pollinators, herbivores, frugivores and other biota (Whittaker and Levin, 1977; Wiens, 1976). There are also some indications that seasonality may influence the regrowth of resprouting plants after fire (Le Maitre, ms. in prep.). As this is primarily a consequence of the status of the plants reserves, a good knowledge of at least the aerial shoot phenology is required to estimate the status of below ground reserves. Plants with soil stored seed reserves do not appear to exhibit such a marked response to fire season as do serotinous species, except where the seasonal variation in potential fire intensity determines extent of the exposure of mineral soil. The exposure of mineral soil with a blackened surface of ash and the resultant change in soil temperature regime appears to be essential to stimulate germination of at least the large seeded species. Post-fire recruitment of plants with short-lived, soil stored seed may vary seasonally in relation to the timing of seed store replenishment.

Dioecious plants may also be able to time phases of their growth differently because of differing constraints on resource allocation in the male and female plants. Hoffman (1981) found marked differences between the sexes in *Peumus boldus* (Monimiaceae) and was able to relate these, and differences in plant size, to the differences between the amount of resources the male and female needed to allocate to reproduction. Fynbos has a high incidence of dioecy as both the Restionaceae and the genus *Leucadendron* are dioecious and both are important floristically and in cover or biomass in many communities.

4.2 *Methods*

The following species were selected for the phenology study at the Kogelberg site (Durand, 1981):

Leucadendron laureolum	-	tall shrub, Proteaceae
Phaenocoma prolifera	-	medium shrub, Compositae
Sympieza articulata	-	low shrub, Ericaceae
Erica pulchella	-	low shrub, Ericaceae
Dilatris viscosa	-	evergreen geophyte, Haemodoraceae
Restio egregius	-	tall non-seasonal graminoid, Restionaceae

Ten individuals of each of these species were tagged and shoot and/or leaf growth, bud, flower and fruit development were recorded for the whole plant. Durand (1981) notes that the timing of the phases presented in his graphs (reproduced in Figures 14.1-14.7:Kogelberg) is not exact as observations were too widely and unevenly spaced. A study of the shoot and stem diameter growth and litter fall was also done for *L. laureolum* in the same area, but these results are not available for analysis here.

The following species were selected in the Cedarberg study area:

Leucadendron pubescens - tall shrub, Proteaceae

Paranomus bracteolaris - tall shrub, Proteaceae

Phylica villosa var *pedicellata* - medium shrub, Rhamnaceae

Rhus dissecta - low, rarely medium height shrub, Anacardiaceae, drought deciduous

Cliffortia teretifolia - medium shrub, Rosaceae

Rafnia amplexicaulis - low shrub, Leguminosae

Salvia africana-coerulea - forb, Labiatae

Helichrysum tomentosulum - forb, Compositae

Hypodiscus neesii - large, tufted non-seasonal graminoid, Restionaceae

Restio gaudichaudianus - small, straggling non-seasonal graminoid, Restionaceae

Tetraria compar - seasonal graminoid, Cyperaceae

Ehrharta ramosa - seasonal graminoid, Gramineae

Babiana humilis - geophyte, Iridaceae

Urginea sp - geophyte, Liliaceae

Oxalis sp - geophyte, Oxalidaceae

Ten individuals of each species, 20 of the Proteaceae, were tagged and shoot and/or leaf growth, bud set, bud, flower and fruit development, seed dispersal and leaf death was recorded. Six tagged shoots were followed on each of the tall shrub species and the phenology of the shrubs is based on observations on these shoots.

The phenophases recorded are defined as follows:

Shoot and/or leaf growth - active vegetative growth as evident from elongation of shoots, addition of new leaves or new shoots with young bark.

Bud set - initiation of the inflorescence or flower bud. Not presented in Figures 14.1-14.7

Bud development - active expansion or elongation of the inflorescence or flower bud.

Flower development - flower open, stigma receptive and/or pollen being shed.

Fruit development - from flower closed, pollen shed, stigma shrivelled and brown to seed being dispersed. This may include dormant periods as the beginning and end of this phase were difficult to assess in the field.

Seed dispersal - seed on the soil, loose in the flower or inflorescence or bracts enclosing the fruit open and empty.

Leaf fall - old leaves dead and loosely attatched to the shoot and/or leaves scattered on the soil.

4.3 Results and Discussion

4.3.1 General patterns

The results of the general observations are presented in Figures 14.1 to 14.7. The graphs emphasize the diversity of activities in the vegetation at any one time. The overall pattern of flowering in the communities appears to be a spring maximum, mid-summer minimum and a rapid increase during autumn, at both sites (pers. obs.; see Kruger, 1981). The timing of the separate phases does show a certain amount of partitioning of resources into differing activities at different times. The phenological sequences also reflect the morphologically determined growth patterns of the plants. For example in the Restionaceae bud set appears to take place very close to the initiation of shoot elongation in reproductive shoots. Further development of the buds, which are terminal, is then delayed until the end of shoot growth. Flowering is rapid and is followed by a long seed maturation period. This may include some pre-dispersal dormancy in order to delay dispersal until the optimum summer period. This pattern is quite widespread in the Restionaceae (Bond, 1980; Olivier,

FIGURES 14.1 - 14.7: Phenology summary graphs for all the species measured at both sites. The Kogelberg graphs are copied directly from Durand's (1981) originals in the data files at Jonkershoek. The species have been grouped into the categories used in the growth form analysis. For the Cedarberg Proteaceae the values are the mean of 60 shoots on 10 plants for each species or sex. For the other species the values are based on the percentage of the 10 plants sampled and are therefore whole plant observations.

The abbreviations used are as follows:

VE - vegetative growty

BS - bud development

FL - flowering

FR - fruit development

SD - seed dispersal

LF - leaf fall

For definitions of these categories see the section on methods (4.2).

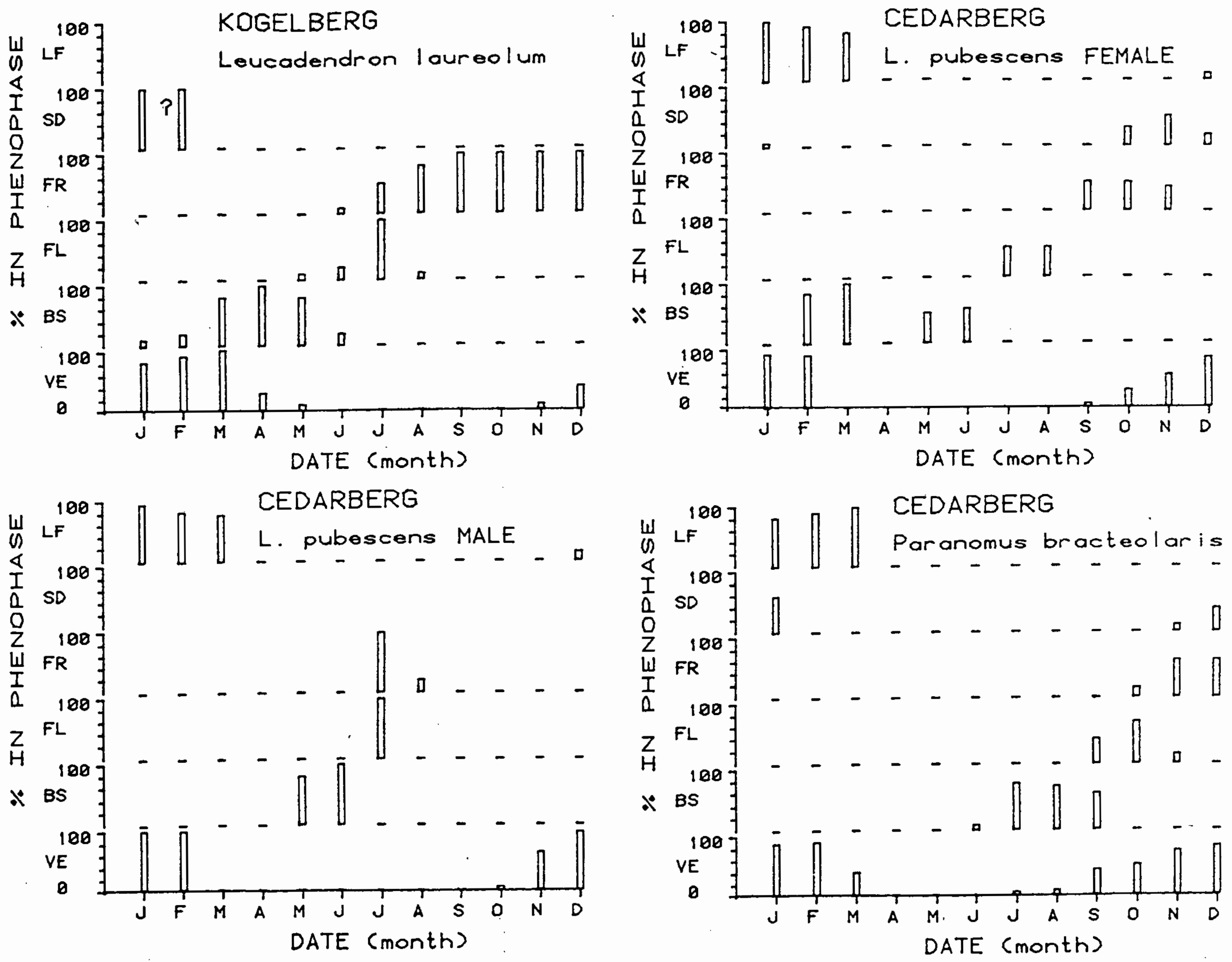


FIGURE 14.1 : Phenology of the overstory shrubs. ? = no values given, just a note on Durand's (1981) original graph.

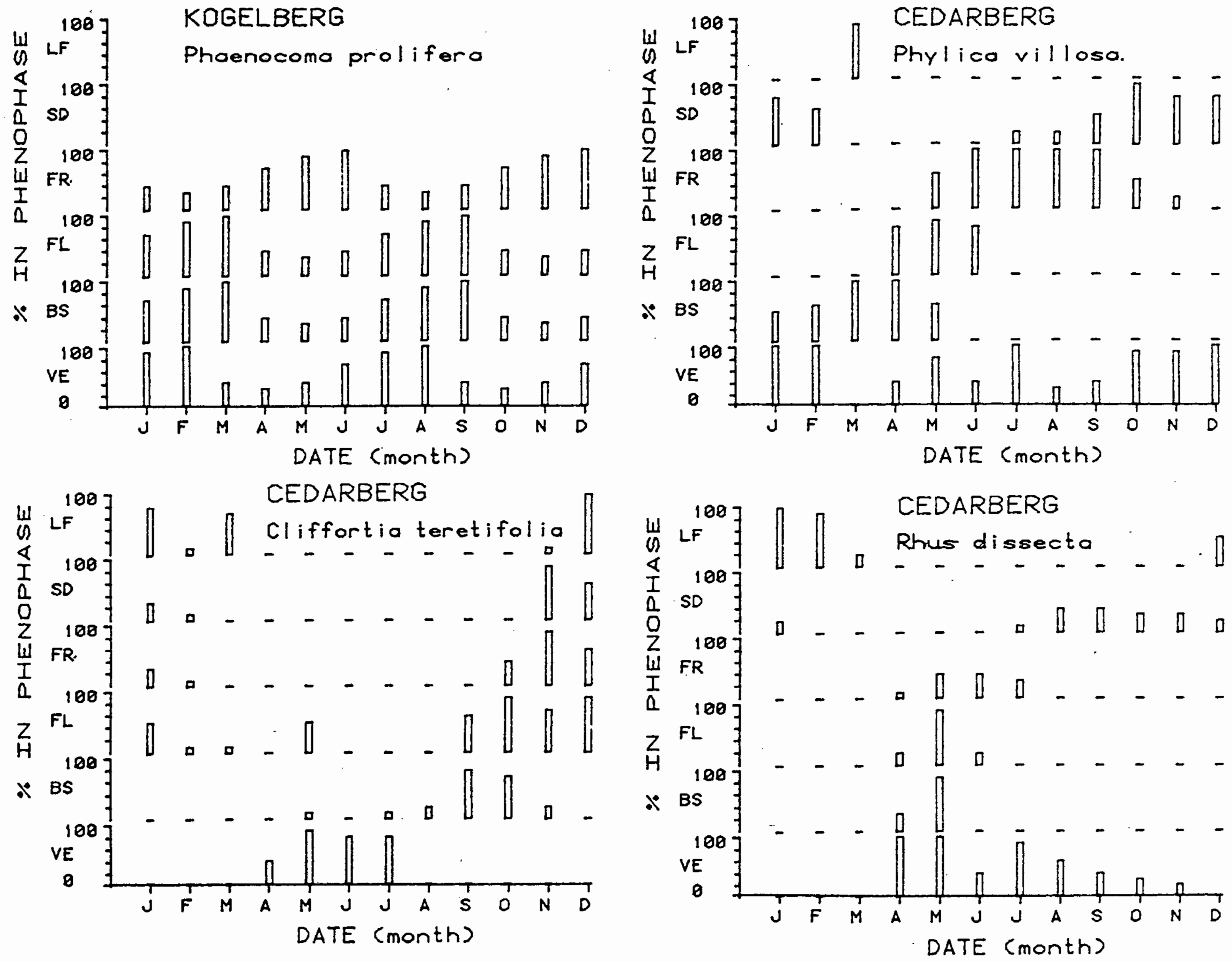
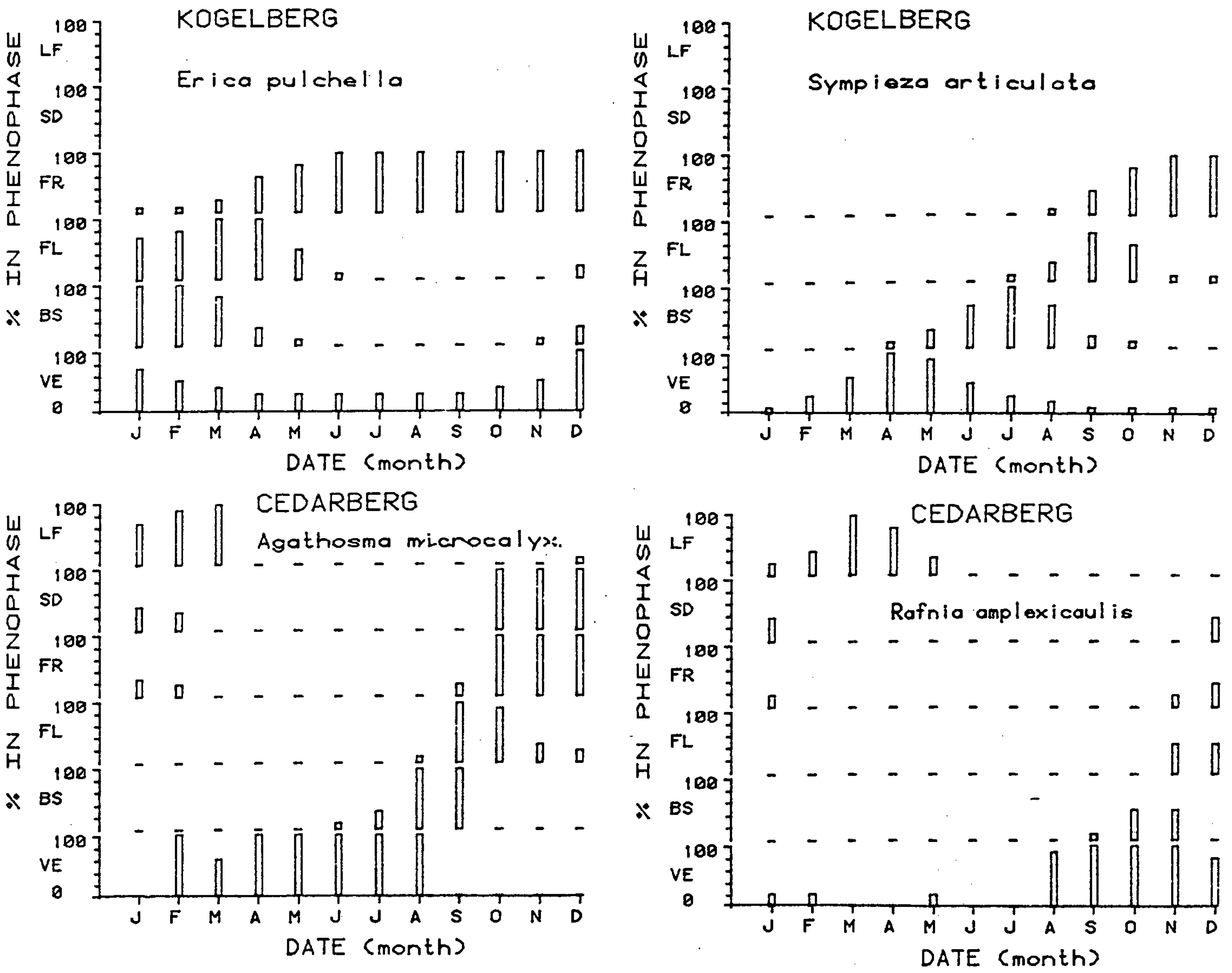


FIGURE 14.2 : Phenology of the middle layer shrubs.



KOGELBERG *Erica pulchella*

KOGELBERG *Sympieza articulata*

CEDARBERG *Agathosma microcalyx.*

CEDARBERG *Rafnia amplexicaulis*

FIGURE 14.3 : Phenology of the low shrubs.

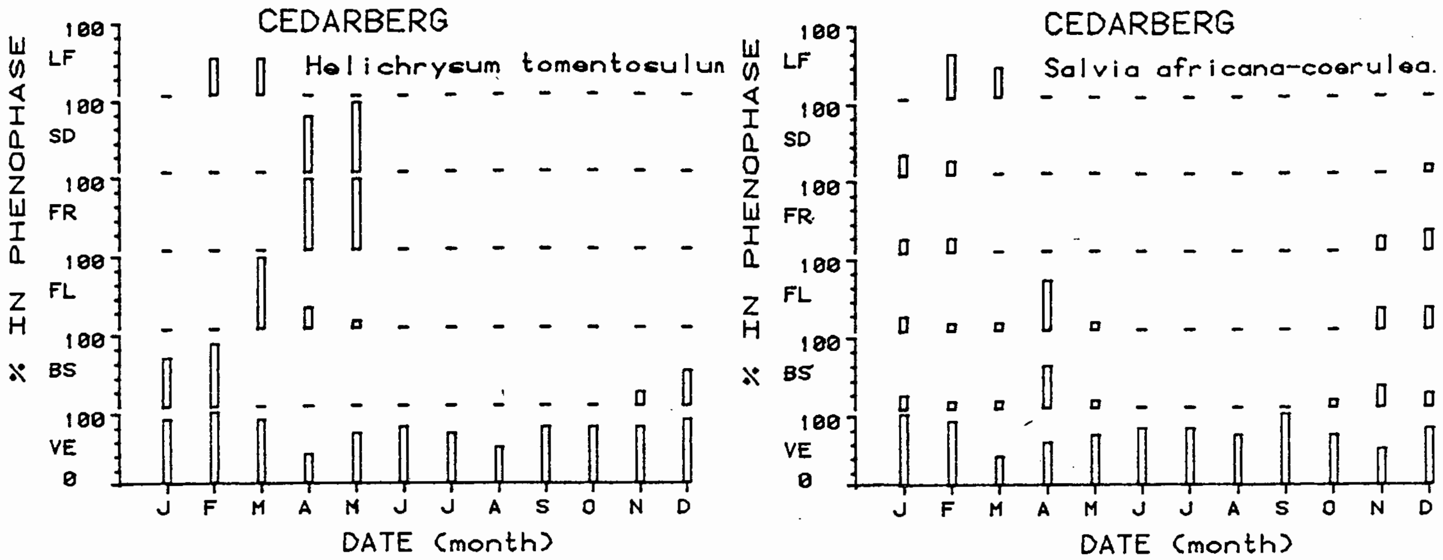


FIGURE 14.4 : Phenology of two forbs.

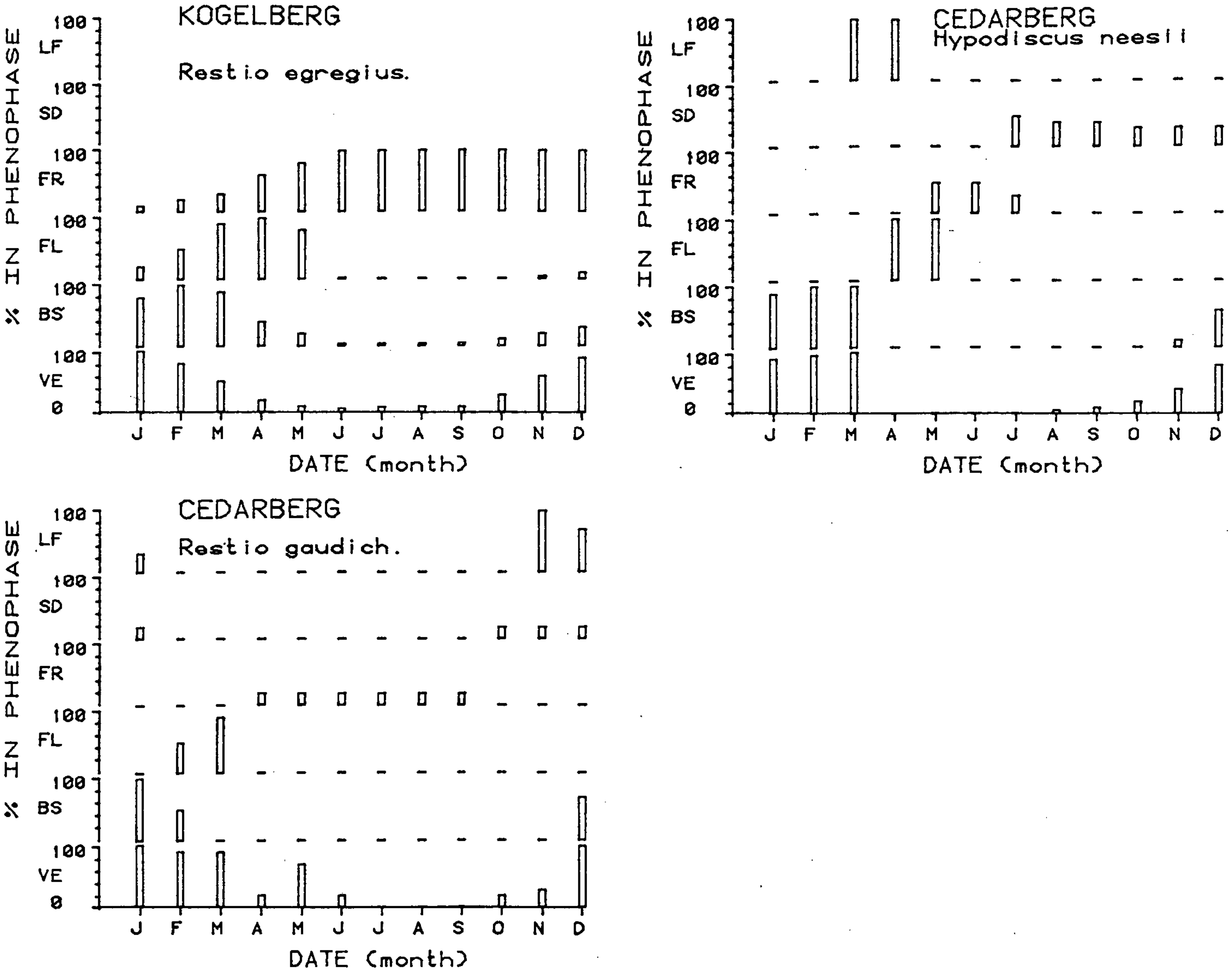
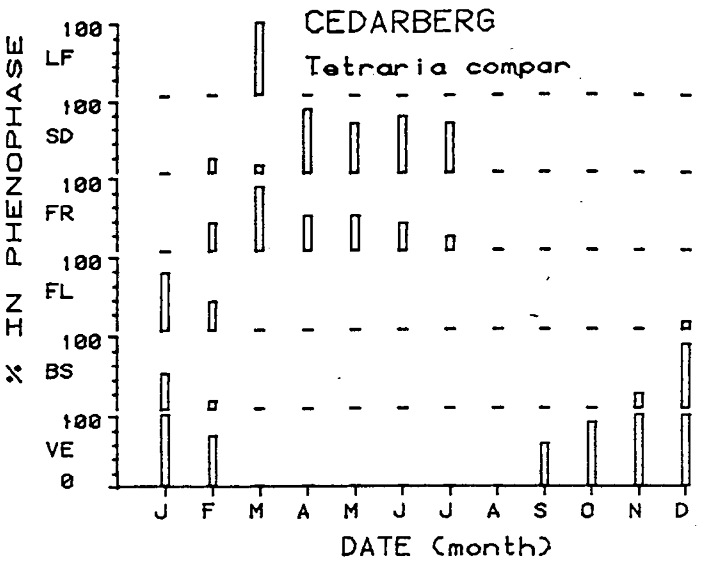


FIGURE 14.5 Phenology of the Restionaceae (non-seasonal graminoids).



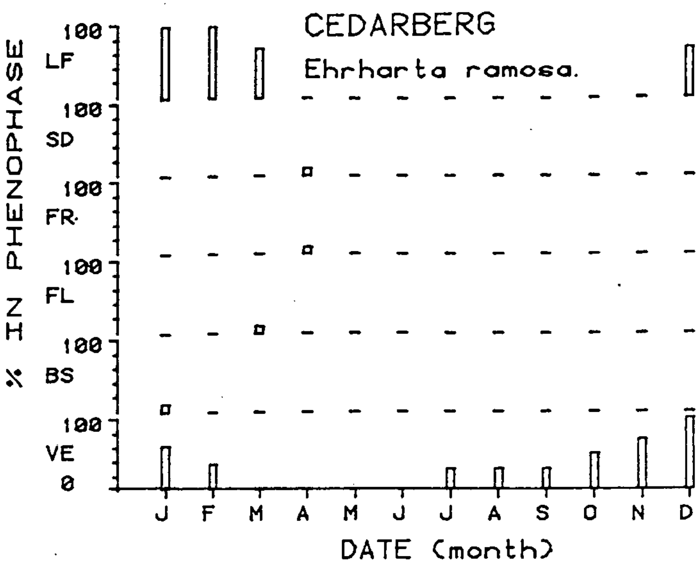


FIGURE 14.6 : Phenology of the seasonal graminoids.

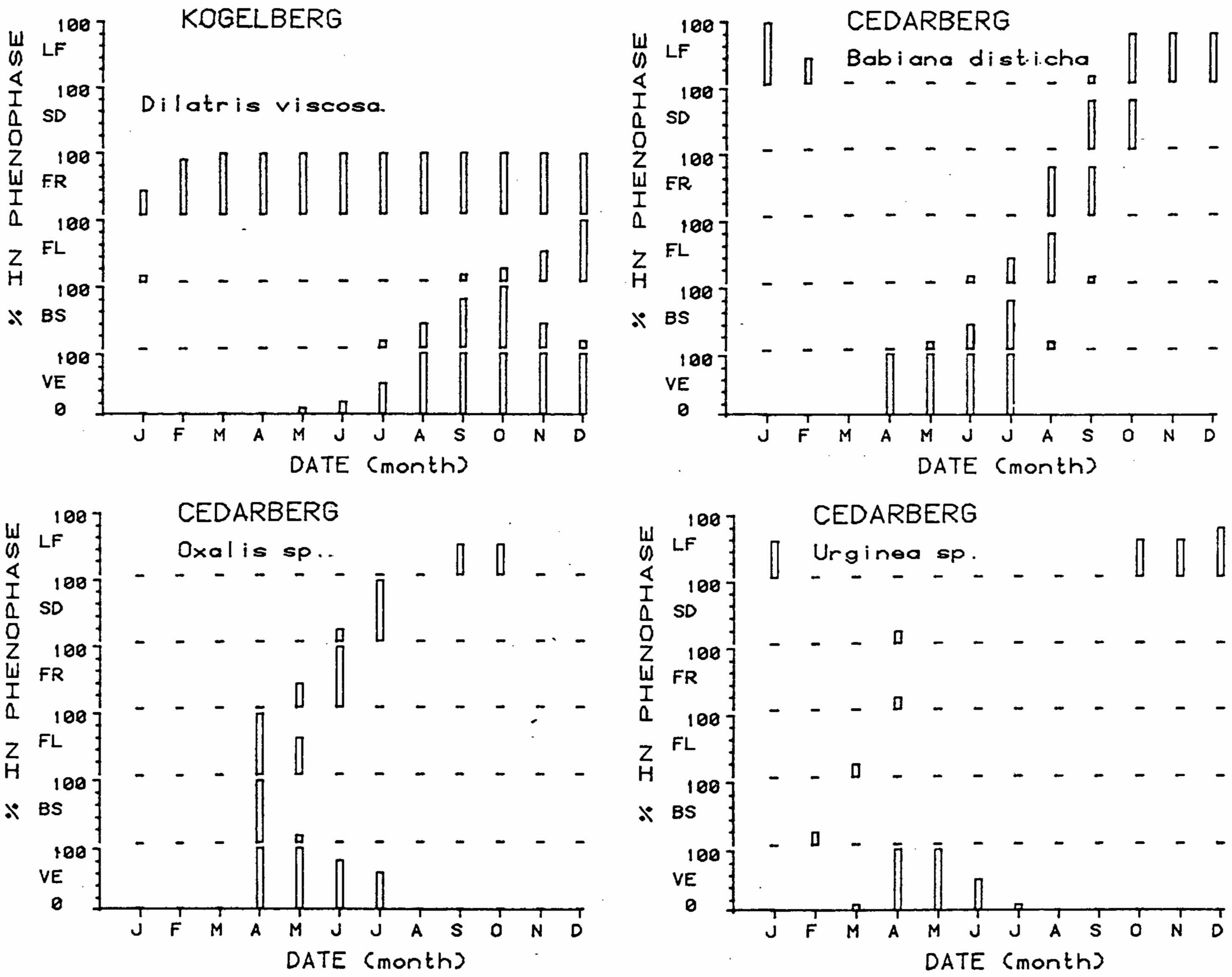


FIGURE 14.7 : Phenology of the geophytes.

1966; Sommerville, pers. comm.) with growth being initiated in the winter and with flowering in autumn, although Elegia parviflora (Bond, 1980) in the Outeniquas and Staberoha disticha at Pella (Sommerville, pers. comm.) follow rather different patterns. These patterns deserve detailed investigation especially as the physiology of the Restionaceae is very poorly understood. The development of Dilatris, Oxalis and Babiana is typical of synanthous geophyte (Dafni et al., 1981; Markotter, 1936) with leaf growth preceding further phases, whose development is based on storage reserve utilization (Dafni et al., 1981). Urginea however has temporally separated its flowering from its leaf growth, its flowering being based on the previous seasons reserves and following a hysteranthous pattern (Dafni et al., 1981; Markotter, 1936).

The two seasonal graminoids are very similar in their phenological pattern. Both grow new leaves and culms during spring and summer flowering, although flowering and subsequent phases are more extended in Tetraria (Cyperaceae). The actual shoot development of this Tetraria has not been examined, but analysis of the growth of a Tetraria species at Jonkershoek showed the same pattern as is found in Tundra grasses (P.C. Miller pers. comm.). This pattern is rhizome growth followed by growth of some leaves in the first year, more leaves and a flowering culm in the second year and shoot senescence after seed dispersal. This may be a fundamental growth pattern in graminoids and deserves more examination in terms of its resource use benefits and the plant's flower and seed requirements. Ehrharta, an essentially leafless graminoid with spreading subterranean rhizomes, follows a pattern that suggests that it employs rhizome reserves to flower, set seed and disperse it rapidly, a pattern that could benefit a plant that is selectively browsed by antelope and probably also Otomys species.

The woody shrubs and forbs show a variety of patterns in the timing of their phenophases, much more so than the graminoids and geophytes in these two areas. Sympieza articularis and Erica pulchella both have a single annual cycle for each pheno phase but they are 3 - 4 months out of phase with each other. In both growth precedes flowering, with flowers on the new growth. This is a simple pattern when compared to the phenology of Erica bauera which has an extended period of long-shoot growth during which it produces short-shoots or flowers alternately on successive long-shoot segments (Taylor, 1981). This means that it has at least two flowering cycles in the course of a year (Taylor, 1981), and can make optimal use of opportunistic growth during favourable conditions (Bond, 1980; Mooney & Morrow in Bond, 1980). Erica pulchella's shoot elogation takes place during the summer, possibly because the relatively reliable summer rains in the region enable this shallow rooted species to obtain the moisture required.

The phenology of the Ericaceae in the two communities cannot be compared because Simocheilus multiflorus, an autumn-winter flowering species, did not occur in the Cedarberg phenology study plot. All of the low woody shrubs and forbs have adopted the opportunistic growth strategy. Most growth occurs between June and November, May for Agathosma, but some growth continues right through the summer drought. Miller (pers. comm. see also Miller et al., 1983) also found that there was some shoot elongation in Agathosma in mid-summer even though its midday xylem water potential was -4MPa. Salvia has a long flowering season with two peaks. Its flowers are terminal and the shoot dies back after seed dispersal so that flowering is a consequence of its ability to produce new shoots twice in a year. Helichrysum produces leafy and flowering shoots (with some new leaves at the base) separately, with the majority of the actual leaf growth being in the spring. The Rafnia like the Agathosma grows opportunistically but has a much shorter flowering season that coincides with the greatest flying insect activity in early summer (pers. obs.). Rhus dissecta has an extended growing season but most growth is between March and June. Leaf fall is in mid-summer but the plants are only deciduous for a short period before new leaves develop in March and April. Cliffortia teretifolia has an extended flowering period with a few flowers to be found on most individuals throughout the year and a spring to summer peak. Most of the flowers seen outside the peak season were male. Phylica villosa also has an extended growing season, but only shoots without flowers grow during the period from April to September. Flowering takes place in autumn and pollination is by bees (Apis sp.?). The inflorescence is a spike and closely resembles that of Paranomus, and is frequently visited by the large carpenter bees that pollinate the Paranomus in the spring. Phaenocoma prolifera has a unique 6 month phenological cycle which suggests that it developed under a bi-seasonal rainfall regime and has been maintained by the reliable summer rains in the western Cape.

The shoot growth of the Cedarberg Proteaceae will be examined in more detail in the next section. L. pubescens has a short flowering period and this is followed by rapid development of the seed and seed dispersal. In L. laureolum shoot growth is also in summer, flowering is also a short phase, but as the seed is retained in the cones seed maturation will take longer than in L. pubescens (Williams, 1972). Paranomus bracteolaris has a more extended flowering period, partly because the flowers develop acropetally and the terminal flowers are still in the bud when the basal flowers have set seed. Seed development is also staggered but seed dispersal is more rapid and is closely synchronised with L. pubescens. One further point is that seed dispersal in all the myrmecochorous species, Paranomus, Phylica, Cliffortia and Rhus (?) but not Hypodiscus, (all in the Cedarberg) is during summer, the peak activity period of ants (De Kock, pers. comm.). The graph for Hypodiscus seed dispersal may however, not be correct as more recent observations suggest that seed dispersal begins in February - March and most seed is dispersed by the end of May.

Bond (1980), Kruger (1981) and Kummerow (1983), amongst others, have noted that leaf senescence and fall is the least variable of all phases, in mediterranean environments, occuring mainly in late summer and autumn. This is primarily the result of moisture deficits and a need to reduce transpiration losses, but may also be a consequence of internal nutrient cycling and translocation to the new vegetative growth and seeds (Specht *et al*., 1983).

4.3.2 Shoot elongation the Cedarberg Proteaceae

The results of the study are summarised in Figures 15 to 17. The growth curves are typically sigmoid with slow initial growth, rapid elongation and a slowing down to the final length. The measurements included the leaves surrounding the bud (Kruger, 1981) as they were too delicate, especially in the male *Leucadendron*, to part to find the length to the terminal bud. In both species, and sexes, examined growth begins in spring and continues through to summer (*L. pubescens* male) and autumn (*L. pubescens* female and *Paranomus*). *Paranomus* showed a very interesting pattern, with two growth cycles separated by a rest phase which co-incides with the final stages of seed maturation

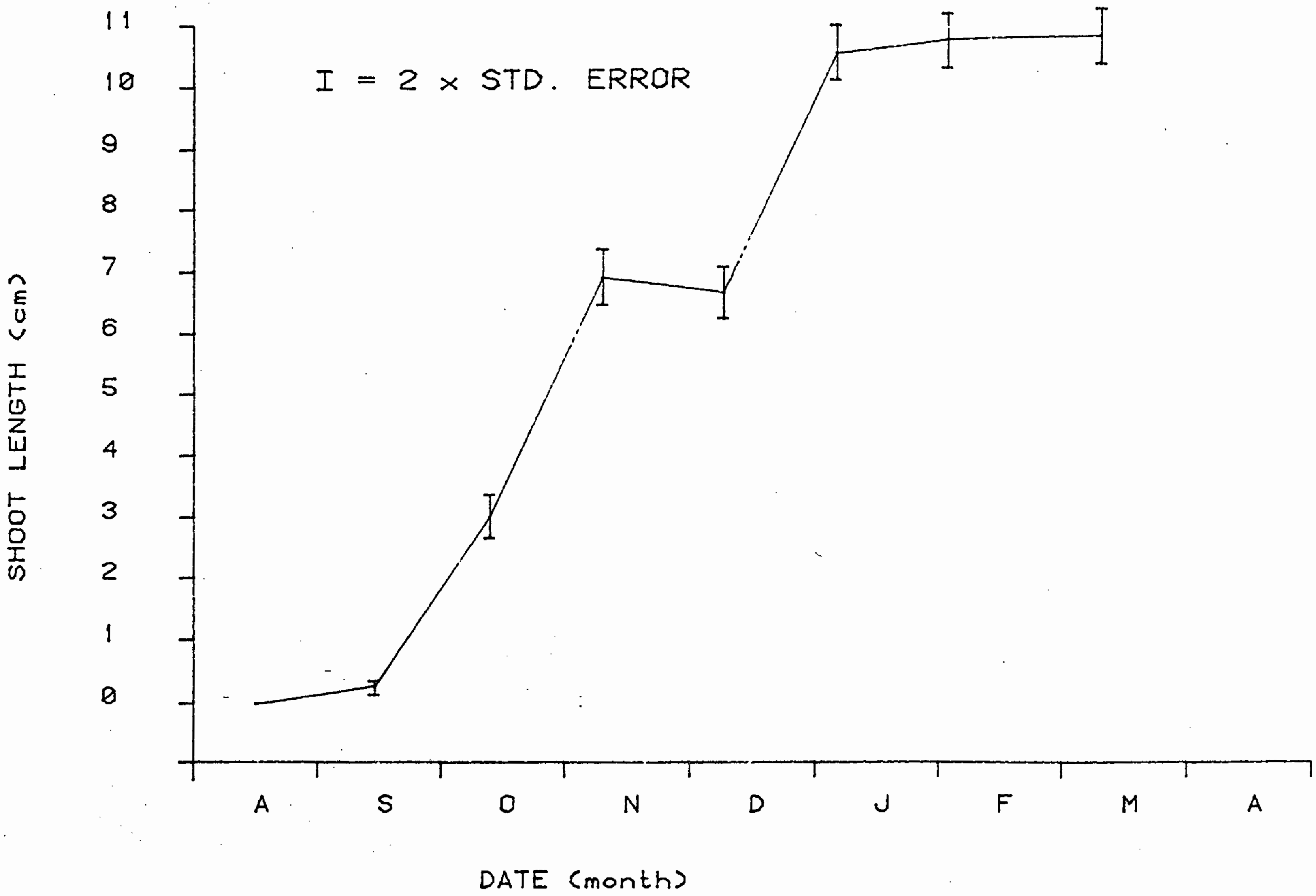


FIGURE 15 : Shoot growth in <u>Paranomus bracteolaris</u>. Measurements were of total length. The negative growth during the rest is at result of the increased lateral spread of the leaves during this period and not shoot shrinkage

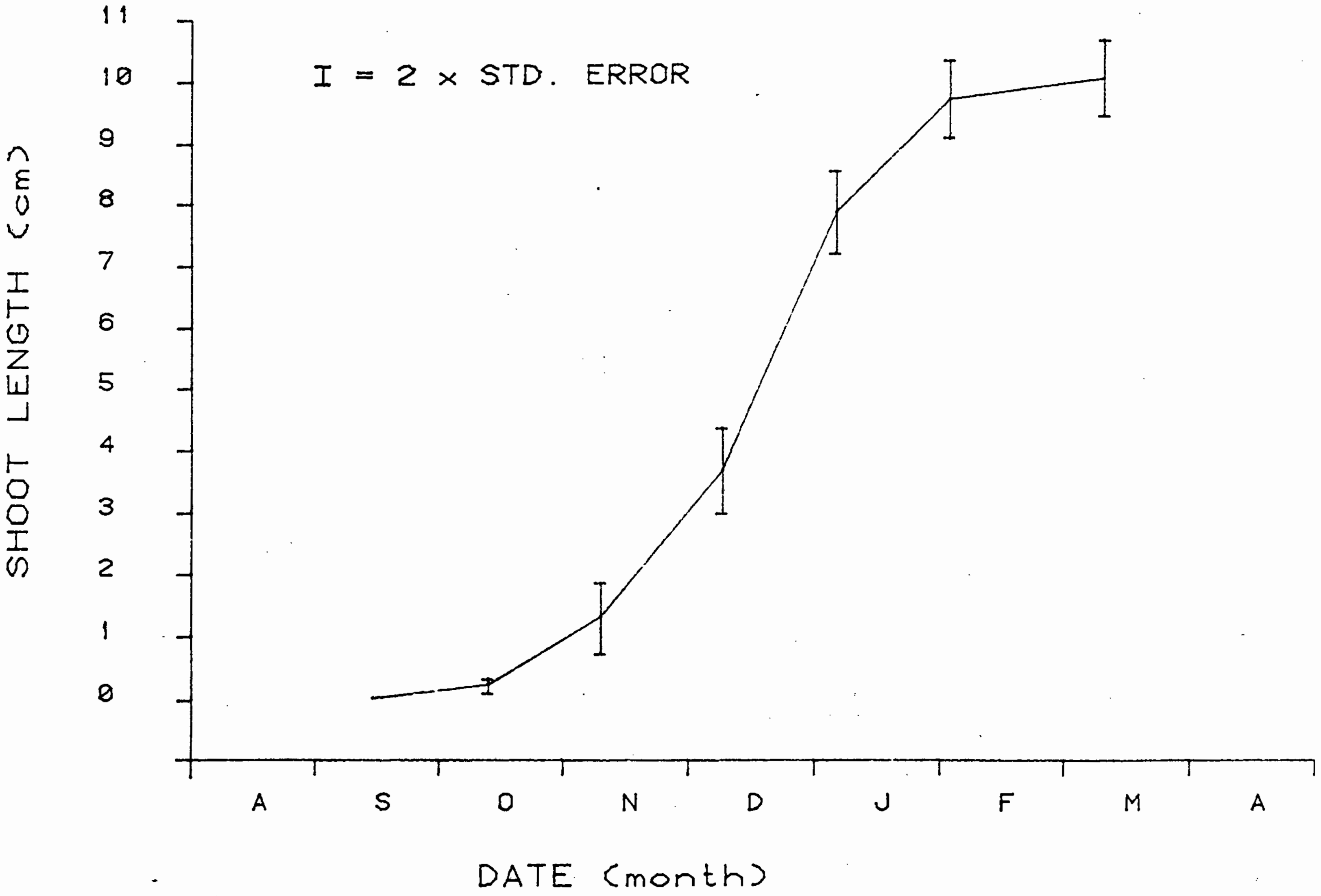


FIGURE 16 : Shoot growth in the female *Leucadendron pubescens*.

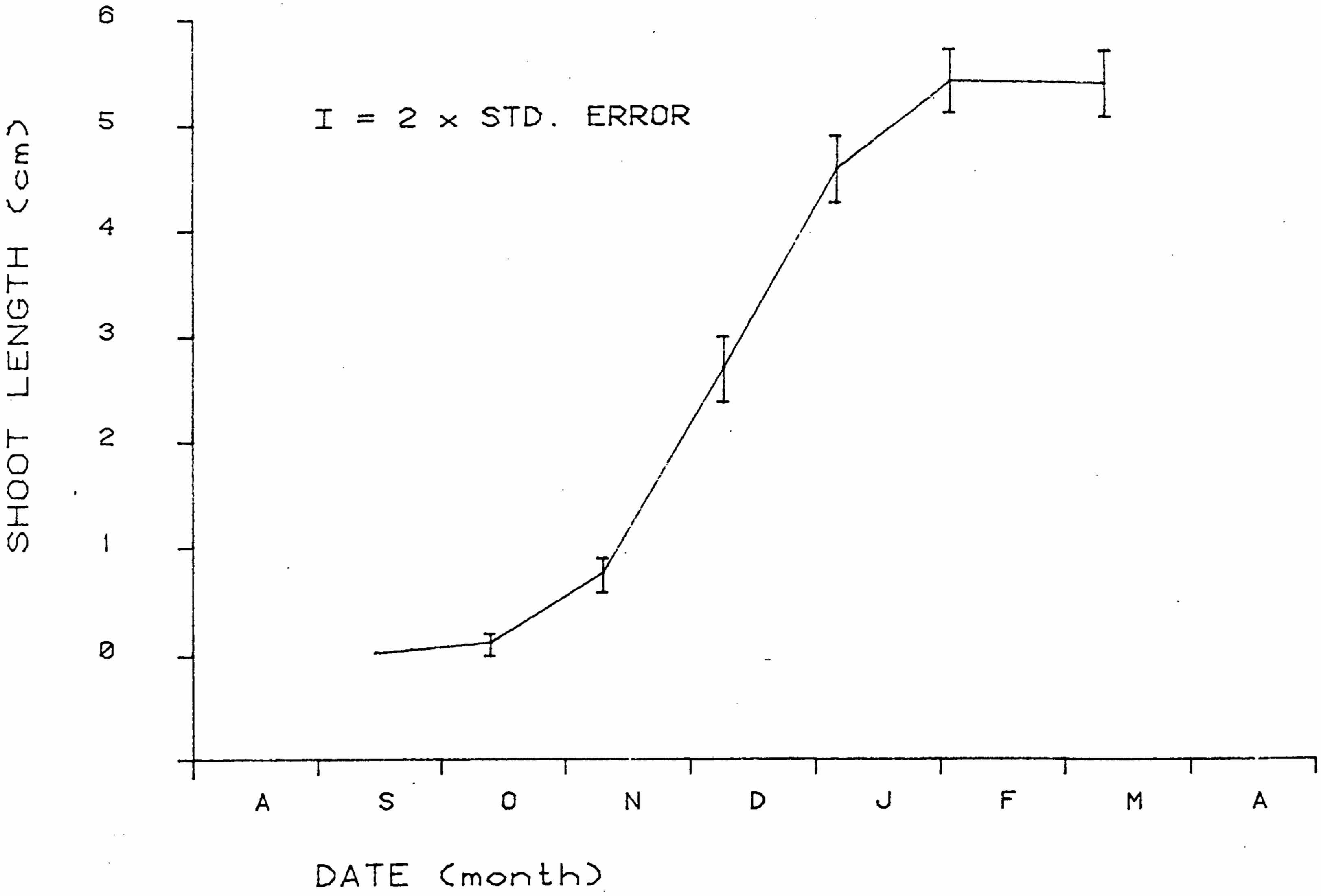


FIGURE 17 : Shoot growth in the male *Leucadendron pubescens*.

and seed dispersal. Subsequent observations show that this is the normal pattern for this species and that it involves all the unsuppressed shoots. It is analogous to the second growth flush reported by Kruger (1981) and Bond (1980) for Proteaceae, but the flushes follow each other closely and growth is complete by March. The data for *Protea repens* in Swartboschkloof show that bimodal shoot growth is not a consistent pattern in this species and that it varies within and between the individuals studied (L.Klaussner, pers. comm). This bimodal growth in the Proteaceae has not yet been clarified, but more detailed analyses and physiological studies may reveal that it is controlled by patterns of resource allocation (see Specht *et al*., 1983), or constraints on nutrient supplies, or moisture availability (P.C.Miller, pers.comm.).

Growth in the *Leucadendron* species is most rapid between November and January, slightly earlier than that observed by Bond (1980) in *L. uliginosum* or reported by Williams (1972) for *Leucadendron* in general. In *Paranomus* shoots that were not supporting flowers began growth as early as August, four to six weeks earlier than shoots with flowers, suggesting that there are limitations on the availability or resources within shoot systems in this species. South African Proteaceae, like the Australian Proteaceae (Kuo *et al*., 1982) seem to have seed rich in nutrients, particularly phosphorus (Jongens-Roberts, pers. comm., Jordaan, 1972) and seed maturation should, therefore, conflict with shoot growth.

This does not appear to be the case in Paranomus, but in L. pubescens (female) growth only starts after most seed development is completed in October - November. The male L. pubescens should, therefore, be able to commence growth earlier as it need allocate no resources to seed (see Hoffmann, 1981), and can benefit from the freely available moisture in the spring. It does not do this, however, as it grows at the same time as the female.

A number of the Paranomus shoots divided to produce two shoots during the second growth flush. The original terminal bud appears to abort and lateral buds, usually only two, grow out in the second flush. In the female L. pubescens the same thing may occur but there are no checks in the growth of these shoots. In the male L. pubescens there is a different pattern. During shoot elongation the dominance of the apical bud is weakened and the axillary buds grow out. In this way a single shoot may develop as many as 25 axillary shoots in a single growth flush. The terminal buds on all these shoots and the lateral buds around the terminal bud may also develop inflorescences and a single shoot may therefore in one year of new growth bear as many as 35 inflorescences. These shoot growth patterns are restricted to the leading shoots on branch systems and represent an interesting departure from the strong apical dominance and sympodial branching characteristic of the Proteaceae. For the male L. pubescens this may be a means of maximising pollen production as most of these axillary shoots do not develop further and adjusted their shoot growth patterns to the "norm" of winter growth. They have, therefore, retained their "anomalous" summer growth because it has other advantages, for example in the ability to utilise nutrients leached during summer rains and in internal cycling of nutrients (Specht _et al._, 1983). Leaf fall in the Proteaceae in this study occured at the end and not during shoot growth as predicted (Specht _et al._, 1983), again a situation which underscores the need for more detailed work on phenological rhythms and their causes. The understorey plants also show a greater diversity in the timing of phenophases, in both relatively arid and moist environments, than is generally suggested. The timing of phenophases within plants or shoot systems indicates both resource partitioning and morphologically determined phenological sequences, but there are many anomalies which cannot be explained at present. There are, however, dangers both in seeing all features of a plants phenology and structure as being "adaptive" (Gould and Lewontin, 1979; Harper, 1980; Mayr, 1980), and in not seeing the common factors behind the multitude of phenological patterns because of that same diversity (Whittaker and Levin, 1977), i.e not seeing the wood for the trees, and both must be avoided.

The studies discussed in this section suffered from three complaints common to much fynbos research, observer inexperience, infrequent observations, and too short a period of observation and recording of the data. Studies under way at present or being planned will be far more valuable if they are (re-)designed to allow for at least three years of observations on the whole plant, its parts and its environment. Phenology studies are just beginning to examine some of the factors involved in the timing of phases in the plants annual cycle. The means observed for areas and species may indicate general patterns, but studies comprehensive enough to elucidate the variation that is found within species and growth forms are urgently required. More studies such as Markotters's (1936) detailed work on the geophytes of the Stellenbosch flats over a number of years, are required if demographic models are to become a practical means of understanding the responses of communities to fire and the dynamic interactions and processes that produce the community being studied. Statistical descriptions are useful as an initial stage and produce results that provide a great deal of insight. A true understanding of the complexity and fragility of ecosystems can only come from diligent and usually laborious field-work and careful interpretation of the variation that is found, as well as close co-operation and communication between scientists working in the various overlapping disciplines.

REFERENCES

ACOCKS, J.P.H., 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa No. 28.

ADAMSON, R.S., 1938. The vegetation of South Africa. British Empire Vegetation Committee, London.

ANDRAG, R.H., 1977. Studies in die Sederberge oor (i) die status van die Clanwilliam seder (Widdringtonia cedarbergensis Marsh), (ii) buitelug ontspanning. M.Sc. Thesis, Universiteit van Stellenbosch, Stellenbosch.

AXELROD, D.I., RAVEN, P.H., 1978. Late Cretaceous and Tertiary vegetation history of Africa. In Biogeography and ecology of Southern Africa, Werger, M.J.A. (ed.), Dr. W. Junk, The Hague pp. 77-130.

BAKER, H.A., OLIVER, E.G.H., 1967. Ericas in Southern Africa. Purnell, Cape Town.

BIGALKE, R.C., 1979. Aspects of vertebrate life in fynbos, South Africa. In Heathlands and related ecosystems. Descriptive studies. Specht, R.L. (ed.). Ecosystems of the world 9A, Elsevier, Amsterdam, pp. 81-95.

BOND, W.J., 1980. Periodicity in fynbos of the non-seasonal rainfall belt. Journal of South African Botany 46: 343-354.

BOND, W.J., 1981. Vegetation gradients in southern Cape mountains. Unpublishd M.Sc. Thesis, University of Cape Town, Cape Town.

BOND, W.J., 1983a. On alpha diversity and the richness of the Cape Flora: a study in southern Cape Fynbos. In Mediterranean-type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 337-356.

BOND, W.J., 1983b. Dead leaves and fire survival in southern Africa tree aloes. Oecologia (Berlin) 58: 110-114.

BOND, W.J., FERGUSON, M. and FORSYTH, G., 1980. Small mammals and habitat gradients in southern Cape mountains. South African Journal of Zoology 15: 34-43.

BOUCHER, C., 1972. The vegetation of the Cape Hangklip area. M.Sc. Thesis, University of Cape Town, Cape Town.

BOUCHER, C., 1978. Cape Hangklip area. II. The vegetation Bothalia 12: 455-497.

BOUCHER, C. and MOLL, E.J., 1981. South African mediterranean shrublands. In Mediterranean-type shrublands. Di Casti, F., Goodall, D.W., Specht, R.L. (eds.), Ecosystems of the world 11, Elsevier, Amsterdam, pp. 1-52.

BREYTENBACH, G.J., 1983. Small mammal responses to environmental gradients in the Groot Swartberg of the southern Cape. M.Sc. Thesis, University of Pretoria, Pretoria.

BUCKMAN, H.O.; BRADY, N.C., 1969. The Nature and property of soils. The Macmillan Co. Toronto. of Mines, Geological Survey, Pretoria.

CAMPBELL, B.M., 1983. Montane plant environments in the fynbos biome. Bothalia 14: 283-298.

CAMPBELL, B.M., COWLING, R.M., BOND, W.J., KRUGER, F.J., 1981. Structural characterization of vegetation in the Fynbos Biome. South African National Scientific Programmes Report No.52.

CLEMENTS, F.E., 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute, Washington.

CODY, M.L., 1975. Towards a theory of continental diversities: bird distributions over mediterranean habitat gradients. In Ecology and evolution of communities, Cody, M.L., Diamond, J.M. (eds.). Harvard University Press, Cambridge, pp. 214-257.

CODY, M.L., MOONEY, H.A., 1978. Convergence versus nonconvergence in mediterranean climate ecosystems. Annual Review of Ecology and Systematics 9: 215 - 321.

CODY, M.L., 1983. Continental diversity patterns and convergent evolution in bird communities. In Mediterranean-type ecosystems: the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin pp. 357-402.

CONNEL, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1309.

CONNEL, J.H., SLATYER, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. American Naturalist 111: 1119-1144.

CONNER, E.F., McCOY, E.D., 1979. The statistics and biology of the species-area relationship. The American Naturalist 113: 791-833.

COUNTRYMAN, C.M., PHILPOT, C.W., 1962. Physical characteristics of chamise as a wildland fuel. U.S.D.A. Forest Service Research Paper P.S.W.-66.

COWLING, R.M., 1983. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Ph.D. Thesis, University of Cape Town, Cape Town.

COWLING, R.M., CAMPBELL, B.M., 1983. A comparison of fynbos and non-fynbos coenoclines in the lower Gamtoos river valley, southeastern Cape, South Africa. Vegetatio 53: 161-178.

DAFNI, A., COHEN, D. NOY-MEIR, I., 1981. Life cycle variation in geophytes. Annals of the Missouri Botanical Garden 68: 653-660.

DAHLGREN, R., 1963. Studies on Aspalathus: phyteographical aspects. Botanisker Notiser 116: 431-472.

DAY, J., 1983. Preface to Mineral nutrients in mediterranean ecosystems. Day, J. (ed.) S. Afr. Nat. Scientific Programmes Report No. 71, C.S.I.R., Pretoria.

DEACON, H.J., 1979. Paleoecology. In Fynbos : a preliminary synthesis, Day, J.; Siegfried, W.R.; Louw, G.N.; Jarman, M.L. (eds.). S. Afr. Nat. Scientific Programmes Report No. 40, C.S.I.R., Pretoria.

DEACON, H.J., 1983. The comparative evolution of Mediterranean-type ecosystems. In Mediterranean-type ecosystems : the role of nutrients Kruger, F.J. Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 3 - 40.

DE VILLIERS, J. JANSEN, H. MULDER, M.P., 1964. Die geologie van die gebied tussen Worcester en Hermanus. Geological Survey, Pretoria.

DI CASTRI, F., MOONEY, H.A. (Eds.), 1973. Mediterranean-type ecosystems, origin and structure. Ecological Studies 7 Springer-Verlag Berlin.

DONNELLY, D., 1983. Comparison of community structure of the epigaeic invertebrate fauna, with particular reference to ants and beetles, between fynbos sites under different management practices. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

DURAND, B.J., 1981. A study of the short-term responses of fynbos to fire in the Kogelberg State Forest, South Africa. Unpublished M.Sc. Thesis, University of Cape Town.

DU TOIT, J.J.N., 1979. Geology of South Africa. Oliver and Boyd, Edinburgh.

FOX, B.J., 1983. Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. In Mediterranean-type ecosystems: the role of nutrients, Kruger, F.J., Mitchell, D.T., and Jarvis, J.U.M. (eds.). Ecological studies 43, Springer-Verlag, Berlin,pp. 473-489.

FUGGLE, R.F., 1981. Macro-climatic patterns within the fynbos biome, Final report December 1981, Fynbos Biome Project, Nat. Progr. for Env. Sci., CSIR, Pretoria.

FURNIVAL, G.M., 1961. An index for comparing equations used in constructing volume tables. Forest Science 7: 337-341.

GEOLOGICAL SURVEY, 1973. 3218 Clanwilliam, 1:250 000 geological map series, Geological Survey, Pretoria.

GILL, A.M., 1981. Coping with fire. In The Biology of Australian plants, Pate J.S., McComb A.J. (eds.), University of Western Australia Press, Nedlands W.A.

GILL, A.M. and GROVES, R.H., 1981. Fire regimes in heathlands and their plant-ecological effects. In Heathlands and related shrublands. Analytical studies Specht, R.L. (ed.), Ecosystems of the world 9B, Elsevier, Amsterdam.

GILL, A.M., INGWERSEN, F., 1976. Growth of Xanthorhoea australis R.Br. in relationship to fire. Journal of Applied Ecology 13: 195-203.

GOLDBLATT, P., 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Garden 65: 369-436.

GOODALL, D.W., 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Australian Journal of Scientific Research Series B, 5: 1-41.

GOULD, S.J., 1979. An allometric interpretation of the species-area curves: the meaning of the coefficient. The American Naturalist 114: 335-343.

GOULD, S.J., LEWONTIN, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proceedings of the Royal Society, London, B 205: 581-598.

GREIG-SMITH, P. 1964. Quantitative plant ecology. 2nd ed., Butterworth, London.

HARPER, J.L., 1980. Plant demography and ecological theory. Oikos 35: 244-253.

HOFFMANN, A.J., 1981. Seasonal growth in Peumus boldus, a dioecious tree of the Chilean mediterranean vegetation. Acta Oecologia, Oecologia Plantarum 2(16): 31-39.

HORNE, I.P., 1981. The frequency of veld fires in the Groot Swartberg mountain catchment area, Cape Province. South African Journal of Forestry 118: 56-60.

HUSTON, M., 1979. A general hypothesis of species diversity. American Naturalist 113: 81-101.

JARVIS, J.U.M., 1979. Zoogeography. In Fynbos ecology : a preliminary synthesis. Day, J., Siegfried, W.R., Louw, G.N., Jarman, M.L. (eds.) S. Afr. Nat. Sci. Prog. Report No. 40, C.S.I.R., Pretoria.

JOHNSON, A.W., 1973. Historical view of the concept of ecosystem convergence. In Mediterranean-type ecosystems. Origin and structure. Di Castri, F.; Mooney, H.A. (eds.). Ecological studies 7, Springer-Verlag, Berlin, pp. 1-7.

JOHNSON, L.A.S., BRIGGS, B.G., 1975. On the Proteaceae - the evolution of a southern family. Botanical Journal of the Linnean Society 70: 83-182.

JORDAAN, P.G., 1972. Die generatiewe voortplanting van die Proteaceae. Journal of the Botanical Society of South Africa 57: 24-29.

KEELEY, J.E., 1977. Fire-dependent reproductive strategies in Arctostaphylos and Ceanothus. In Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems. Mooney, H.A. and Conrad, C.E. (co-ordinators). U.S.D.A. Forest Service General Technical Report WO-3, pp. 391-396.

KEELEY, J.E., 1978. Reproductive cycles and fire regimes. In Proceedings of the conference on fire regimes and ecosystem properties. Mooney, H.A. et al. (technical co-ordinators). U.S.D.A. Forest Service General Technical Report WO-26, pp. 231-277.

KRUGER, F.J., 1977a. Ecology of Cape fynbos in relation to fire. In Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems. Mooney, H.A. and Conrad, C.E. (co-ordinators). U.S.D.A. Forest Service General Technical Report WO-3, pp. 230-244.

KRUGER, F.J., 1977b. A preliminary account of aerial plant biomass in fynbos communities of the mediterranean type climate zone of the Cape Province. Bothalia 12: 301-307.

KRUGER, F.J., 1979. South African heathlands. In Heathlands and related shrublands. Descriptive studies R.L. Specht (Ed.) Ecosystems of the World 9A. Elsevier Amsterdam, pp. 29 - 80.

KRUGER, F.J., 1981. Seasonal growth and flowering rhythms : South African heathlands. In Heathlands and related shrublands of the world. Specht, R.L. (ed.). Ecosystems of the World 9B, Elsevier, Amsterdam. pp. 1-4.

KRUGER, F.J., 1983. Plant community diversity and dynamics in relation to fire. In Mediterranean-type ecosystems : the role of nutrients, Kruger, F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.) Ecological Studies 43, Springer-Verlag, pp. 446-472.

KRUGER, F.J., TAYLOR, H.C., 1979. Plant species diversity in the Cape fynbos: gamma and delta diversity. Vegetatio 41: 85-93.

KRUGER, F.J., MITCHELL, D.T., JARVIS, J.U.M. (Eds.).1983 Mediterranean type ecosystems: the role of nutrients. Ecological Studies 43, Springer-Verlag, Berlin.

KUO, J., HOCKING, P.J., PATE, J.S., 1982. Nutrient reserves in seeds of selected proteaceous species from South-western Australia. Australian Journal of Botany 30: 231-249.

KUMMEROW, J., 1983. Comparative phenology of mediterranean-type plant communities. In Mediterranean-type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 300-317.

LAMPRECHTS, J.J.N., 1979. Geology, morphology and soils. In Fynbos ecology : a preliminary synthesis, Day, J.; Siegfried, W.R.; Louw, G.N.; Jarman, M.L. (eds.). South African National Scientific Programmes Report No. 40, C.S.I.R., Pretoria.

LEVYNS, M.R., 1964. Migrations and origin of the Cape Flora.

Transactions of the Royal Society of South Africa 37: 85-107.

LEVYNS, M.R., 1970. A revision of the genus Paranomus (Proteaceae). Contributions from the Bolus herbarium 5: 79-104.

LEWIN, R., 1983. Predators and hurricanes change ecology. Science 211: 737-740.

MACVICAR, C.N.; DE VILLIERS, J.M.; LOXTON, R.F.; VERSTER, E.; LAMBRECHTS, J.J.N.; MERRYWEATHER, F.R.; LE ROUX, J.; VAN ROOYEN, T.H. AND VON M. HARMSE, H.J., 1977. Soil classification. A binomial system for South Africa. Science Bulletin 390. Soil and Irrigation Research Institute, Department of Agricultural Technical Services, Pretoria.

MARKOTTER, E.D., 1936. Die lewensgeskiedenis van sekere geslagte van die Amaryllidaceae. Annals of the University of Stellenbosch 14, Series A(2).

MAYR, E., 1983. How to carry out the adaptationist program? The American Naturalist 120: 324-334.

McMAHON, T.A., KRONAUER, R.E., 1976. Tree structures : deducing the principle of mechanical design. Journal of Theoretical Biology 59: 443-466.

MILLER, P.C. (Ed), 1981. Resource use by chaparral and matorral: a comparison of vegetation function in two mediterranean type ecosystems. Ecological Studies 39. Springer-Verlag, Berlin.

MILLER, P.C., MILLER, J.M. MILLER, P.M., 1983 Seasonal progression of plant water relations in fynbos in the western Cape Province, South Africa. Oecologia (Berlin) 56: 392 - 396.

MOLL, E.J., ROMOFF, N., 1983. Evidence of mist trapping by Thamnochortus punctatus Pillans at Pella in the southwestern Cape Province. South African Journal of Science 79: 432.

MOONEY, H.A. (Ed.), 1977. Convergent evolution in Chile and California mediterranean climate ecosystems. Dowden, Hutchinson and Ross, Stroudsberg Pennysylvania.

MOONEY, H.A., 1983. Carbonn gaining capacity and allocation patterns of mediterranean-climate plants. In Mediterranean-type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 103-119.

MOONEY, H.A., FIELD, C., GULMON, S.L., RUNDEL, P., KRUGER, F.J. Photosynthetic characteristics of South African sclerophylls. Oecologia (Berlin) 58: 398-401.

MOONEY, H.A., PARSONS, D.T., KUMMEROW, J., 1974. Plant development in Mediterranean climates. In Phenology and seasonality modelling, Lieth, H. (ed.). Ecological studies 8, Springer-verlag, Berlin.

MOSTERT, D.P., SIEGFRIED, W.R. and LOUW, G.N., 1980. Protea nectar and satellite fauna in relation to food requirements and pollinating role of the Cape sugarbird. South African Journal of Science 76: 409-413.

MUELLER-DOMBOIS, D. and ELLENBURG, H., 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

MUNSELL, 1954. Munsell Soil Color Charts, Munsell Color Co. Inc. Maryland U.S.A. 1954 edition.

MYBURGH, A.C., RUST, D.J., 1975. A survey of pests of the Proteaceae in the western and southern Cape Province. Journal of the Entomological Society of Southern Africa 38: 55-60.

MYBURGH, A.C., RUST, D., 1977. Borers of economic importance in proteas (Proteaceae). Proceedings of the first congress of the Entomological Society of Southern Africa, Ent. Soc. Sthn. A., Pretoria.

NAVEH, Z. and WHITTAKER, R.H., 1980. Structural and floristic diversity of shrublands and woodlands in Northern Israel, and other mediterranean areas. Vegetatio 41: 171-190.

NEWSOME, A.E. and CATLING, P.C., 1983. Animal demography in relation to fire and shortage of food: some indicative models. In Mediterranean type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 491-505 .

NORDENSTAM, B., 1969. Phyteogeography of the genus Euryops (Compositae). Opera Botanika 23: 1-77.

OLIVER, E.G.H., 1977. An analysis of the Cape flora. In Proceedings of the Second National Weeds Conference of South Africa. Annecke, D.P. (ed.), Balkema, Cape Town, pp. 1-18.

OLIVIÉR, M.C., 1961. Die plantegroei en flora van die Worcesterse veldreservaat. D.Sc. thesis, University Stellenbosch, Stellenbosch.

ORSHAN, G., 1982. Monocharacter growth form types as a tool is an analytic-synthetic study of growth forms in mediterranean type ecosystems. A proposal for an inter-regional program. Ecologia Mediterranea - T.VIII-1982. Fasc. 1/2, pp. 159-171.

PARKINGTON, J., 1976. Coastal settlement between the months of the Berg and Olifants rivers, Cape Province. South African Archeological Bulletin 31: 127-140.

PARKINGTON, J., 1977. Soaquoa : Hunter-fisher-gatherers of the Olifants river valley, Western Cape. South African Archeological Bulletin 32: 150-157.

PARKINGTON, J., POGGENPOEL, C., 1972. Excavations at De Hangen, 1968. South African Archeological Bulletin 26: 3-36.

PARSONS, D.J., 1976. Vegetation structure in the mediterranean scrub communities of California and Chile. Journal of Ecology 64: 435-447.

RAUNKIAER, C., 1934. The life forms of plants and statistical plant geography. Oxford translation, Oxford, University Press, Oxford.

RAUTENBACH, I.L., NEL. J.A.J., 1980. Mammal diversity and ecology in the Cedarberg Wilderness Area, Cape Province. Annals of the Transvaal Museum 32: 101-124.

REYNECKE, P.G., 1975. Kogelberg - Bestuursplan. Unpublished Management Plan, Directorate of Forestry, Cape Town.

ROOT, R.B., 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecological Monographs 37: 317-350.

ROURKE, J.P., 1982. The Proteas of Southern Africa. Purnell, Cape Town.

RUNDEL, P.W., 1979. Ecological inpact of fires on mineral and sediment pools and fluxes. In Fire and fuel management in Mediterranean-climate ecosystems : research priorities and programmes, J.K. Agee (ed) MAB Technical Note 11, UNESCO, Paris, pp. 17 - 21.

RUTHERFORD, M.L., 1978. Karoo-fynbos biomass along an elevation gradient in the western Cape. Bothalia 12: 555-560.

RYCROFT, H.B., 1953. Report on the proposed special protection of the Kogelberg Forest Reserve, No. 1. Internal Report, Directorate of Forestry, Pretoria.

SIEGFRIED, W.R., 1983, Trophic structure of some communities of fynbos birds. Journal of South African Botany 49: 1-43.

SIEGFRIED, W.R. and CROWE, T.M., 1983. Distribution and species diversity of birds and plants in fynbos vegetation of mediterranean-climate zone, South Africa. In Mediterranean-type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin pp. 403-416.

SNEDECOR,G.W. and COCHRAN, W.G., 1980. Statistical methods. The Iowa State University Press, Iowa, U.S.A. 7th ed.

SPECHT, R.L., 1969A. A comparison of sclerophyllous vegetation characteristic of mediterranean-type climates in France, California and Southern Australia. I. Structure, morphology and succession. Australian Jnl. of Botany 17: 277 - 292.

SPECHT, R.L., 1969b. A comparison of sclerophyllous vegetation characteristic of mediterranean-type climates in France, California and Southern Australia. II. Dry matter, energy and nutrient accumulation. Australian Jnl. of Botany 17: 293 - 308.

SPECHT, R.L. (Ed.), 1979. Heathlands and related shrublands. Descriptive studies. Ecosystems of the World 9A, Elsevier, Amsterdam.

SPECHT, R.L. (Ed.), 1981. Heathlands and related shrublands. Analytical studies. Ecosystems of the World 9B, Elsevier, Amsterdam.

SPECHT, R.L.; MOLL, E.J., 1983. Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In Mediterranean-type ecosystems : the role of nutrients in Kruger, F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 41-65.

SPECHT, R.L., MORGAN, D.G., 1981. The balance between the foliage projective covers of overstory and understory strata in Australian vegetation. Australian Journal of Ecology 6: 193-202.

SPECHT, R.L., RAYSON, P., 1957. Dark Island heath (Ninety-mile plain, South Australia) I. Definition of the ecosystem. Australian Journal of Botany 5: 103-114.

SPECHT, R.L., RODGERS, R.W., HOPKINS, A.J.M., 1981. Seasonal growth and flowering rhythms : Australian heathlands. In Heathlands and related shrublands of the world Specht R.L. (ed.). Ecosystems of the world 9B : analytical studies, Elsevier, Amsterdam, pp. 5-13.

SPECHT, R.L., MOLL, E.J., PRESSINGER, F., SOMMERVILLE, J., 1983. Moisture regime and nutrient control of seasonal growth. In Mediterranean type ecosystems : the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin, pp. 120-132.

TAYLOR, H.C., 1978. Capensis in Biogeography and ecology of Southern Africa, Werger M.J.A. (ed.) Dr. W. Junk, The Hague pp. 171 - 229.

TAYLOR, H.C., 1980. Phytogeography of fynbos. Bothalia 13: 231-235.

TAYLOR, M.A., 1981. Life-cycles of selected fynbos species as related to the mediterranean climate Honours Project, Botany Department, University of Stellenbosch, Stellenbosch.

TIDMARSH, C.E.M., HAVENGA, C.M., 1955. The wheel-point method of survey and measurement of semi-open grasslands and karoo vegetation in South Africa. Memoirs of the Botanical Survey of South Africa 29.

TILMAN, D., 1983. some thoughts on resource competition and diversity in plant communities. In Mediterranean type ecosystems: the role of nutrients, Kruger F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.). Ecological Studies 43, Springer-Verlag, Berlin pp. 322-336.

TRABAUD, L., 1973. Experimental studies on the effects of prescribed burning on a Quercus coccifera garrigue: early results. In Proceedings of the Annual Tall Timbers fire ecology conference 13: 97-129.

VAN EEDEN, O.R., 1972. The geology of the Republic of South Africa. An explanation of the 1 : 1000 000 map, 1970 edition. Special Publication No. 18 Department of Mines, Geological Survey, Pretoria.

VAN WILGEN, B.W., 1980. Some effects of fire frequency on fynbos at Jonkershoek, Stellenbosch, South Africa. M.Sc Thesis, University of Cae Town, Cape Town.

VAN WILGEN, B.W., 1982. Some effects of post-fire age on the above-ground plant biomass of fynbos (Mecchia) vegetation in South Africa. Journal of Ecology 70: 217-225.

WARMING, E., 1909. Oecology of Plants (English trns.). Oxford.

WEIMARCK, H., 1941. Phytogeographical groups, centres and intervals within the Cape flora. Lunds Universiteits Arsskrift 2 (37,no.5) 1-143.

WIENS, J.A., 1976. Population responses to patching environments. Annual Review of Ecology and Systematics 7: 81-120.

WESTMAN, W.E., 1983. Plant community structure - spatial partitioning of resources. In Mediterranean-type ecosystems : the role of nutrients, Kruger, F.J., Mitchell, D.T., Jarvis, J.U.M. (eds.) Ecological studies 43, Springer, Verlag, pp. 417-445.

WESTMAN, W.E. and ROGERS, R.W., 1977. Biomass and structure of a subtropical Eucalypt forest, North Stradbroke Island. Australian Journal of Botany 25: 171-191.

WILLIAMS, I.J.M., 1972. A revision of the genus Leucadendron. Contributions of the Bolus Herbarium, No. 3.

WHITTAKER, R.H., 1972. Evolution and measurement of species diversity in land comunities. Taxon 21: 213-251.

WHITTAKER, R.H., 1977. Evolution of species diversity in land communities. Evolutionary Biology 10: 1-67.

WHITTAKER, R.H., LEVIN, S.A., 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12: 117-139.

WHITTAKER, R.H. and WOODWELL, G.M., 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Journal of Ecology 56: 1-25.

ZAR, J.H., 1974. Biostatistical analysis. Prentis - Hall, Inc. New Jersey.

APPENDIX 1

SOILS OF THE KOGELBERG STUDY SITE FROM DURAND 1981

The soils of the site have been classified according to the South African Binomial System for soil classification (Macvicar et. al., 1977). Two soil pits were dug near experimental plots one and two in the study area. The chemical and physical properties of the horizons identified were analysed by the South African

Co-operative Citrus exchange leaf analysis service. The methods employed by the Citrus exchange are:

A. Physical - the mechanical analysis was done by means of the hydrometer method.

B. Chemical

1. Soil pH determined in a 1:2,5 (soil to water and 1N KCl) suspension with a glass electrode after an equilibrium period of one hour.).

2. Soil resistance determined from a saturated soil paste.

3. The cations Ca, Mg, Na and K are leached with 0,1 N NH4Ac (Ammonium acetate) and determined by means f atomic absorption and flame spectrophotometry.

4. Soil P determined in a Bray No. 2 extracting solution using the vanado molybdate yellow method.

5. Organic carbon according to the Walkley-Black method.

6. Total nitrogen by means of micro Kjeldahl.

7. Exchangeable aluminium index according to the method used

by Reeve and Sumner (Soil Sci. Soc. Amer. Proc. 34 : 263-267).

To determine bulk density soil corer rings that are 3,00 cm high and had a diameter of 5,38 cm were used. The soil cores were dried in a force-draught oven at 105 C for 24 hours. A three decimal accurate top-pan scale was used to determine the masses of the oven dried soil cores. Soil water content was determined gravimetrically.

In a preliminary survey of the research site two soil types were observed. Soil pit samples were taken for every indentifiable horizon. Table 1 summarizes the results of the soil analyses.

Values of the C.E.C. (cation exchange capacity) were calculated from the table omitting the hydrogen exchange capacity and are, therefore, only approximations. The validity of the low C.E.C. values are supported by low clay contents in the analyses. Soil humus content can be calculated from the percentage carbon content, since a definite ratio (about 1: 1,7) exists between the organic carbon and soil humus contents (Buckman & Brady, 1969). The soil humus contents for the upper soil layers of the Mispah and Clovelly soils are 0,6% and 1,4% respectively. According to Buckman & Brady (1969) the Carbon-Nitrogen ratio for humid temperate region soils usually stabilizes in the neighbourhood of 10:1 or 12:1. The Mispah soil form falls into that category.

In contrast the Clovelly soil has a higher ratio in the A horizon (probably due to a buried organic layer in that horizon) and a lower ratio in the B2 horizon.

Bulk density was determined for the surface soil layer of the Mispah soil series (Table II). Sandy soils usually have high bulk densities because they tend to have low organic contents and soil particles lie in close contact. The range of bulk density values for sand and sandy loam is from 1,2 to 1,8 and there is a distinct tendency for the values to rise with depth (Buckman & Brady, 1969). Bulk density is a quantitative measure that may be used to monitor the development of the surface soil layer in the long term under different management practices.

TABLE 1 Description and analysis of soil types on the Kogelberg experimental burning site

Site: Top slope of what may have been an alluvial terrace.

Parent material: Colluvial-alluvial sand.

Drainage class: Some what excessively drained

MISPAH SOIL FORM

Horizon	Depth	Description
A1	0 - 400 mm	Dark grey (2,5 YR 3/1), coarse sand, loose, single grain, gradual transition.
A2	400 mm+	Dark grey (7,5 YR 5/2), coarse sand, loose, single grain, gradual transition.
C		Not sampled, too stony.

CLOVELLY SOIL FORM (MOSSIDALE SERIES)

Horizon	Depth	Description
A	0 - 120 mm	Very dark grey (5Y 3/1), coarse sand, loose, single grain, clear transition.
B1	120 - 400 mm	Dark yellow-brown (10 Y R4/4), loamy sand, weak clod structure, apedal, firm clear transition

		gravelly.
B2	400 - 600 mm	Brownish-yellow (10Y R6/6), sandy loam, medium diffuse reddish brown nodules, apedal, firm, slightly flecked with red-brown, clear transition, stony.
C	600 mm	Yellow (2,5 Y 7/6), coarse sand, medium diffuse reddish-brown nodules, apedal, loose hard, stony.

Table 1 (cont.)

* Soil colours were judged according to the colour of a smear of wet soil on white paper (Munsel soil colour chart, 1951).

Form	Mispah		Clovelly (Mossdale series)			
Soil Horizon		A1	A2	A	B1	B2
Soil Depth (mm)	0-400	400+	0-120	120-400	400-600	
% stone >2 mm	10,66	53,25	12,1	31,8	24,1	
Standard analysis						
Phosphorus (ppm)	1	1	9	5	1	
Potassium (ppm)	14	10	14	18	10	
Calcium (ppm)	60	35	6	6	5	
Magnesium (ppm)	26	24	20	20	20	
Sodium (ppm)	11	8	23	36	26	
pH Water	5,9	5,8	4,8	5,1	5,0	
pH KCL	4,5	4,4	3,7	4,4	4,2	
Resistance 15 C (ohms)	8200	16500	2600	3800	8600	
% soluble salt	0,05	0,05	0,05	0,05	0,05	
% clay	6	6	7	11	13	
% silt	2	6	6	4	8	
% sand	92	88	87	85	79	
Textural class	Sand	Sand	Sand	Loamy sand	Sandy loam	
Organic material (%C)	0,35	0,11	0,8	0,68	0,09	
Total nitrogen (%)	0,03	0,01	0,04	0,06	0,01	

Form	Mispah		Clovelly (Mossdale series)		
Soil Horizon	A1	A2	A	B1	B2
Soil Depth (mm)	0-400	400+	0-120	120-400	400-600
AL index (%me)	0,01	0,06	0,04	0,05	0,03
C E C	0,41	0,49	0,37	0,45	0,36
C:N	11,70	11,00	20,00	11,33	9,00

Table II. Bulk density of a Mispah soil profile.

Depth	Mean bulk density	SD
0 - 100 mm	1,333	0,00645
250 - 350 mm	1,546	0,0446
400 - 500 mm	1,635	0,0864

APPENDIX II

FAUNA OF THE STUDY AREAS

A. A list of vertebrate fauna found in and around the research site in the Kogelberg State Forest after Durand (1981)

(a) Amphibia listed alphabetically.

Breviceps montanus	Rain toad
Rana fasciata-montana	Long toed rana
Rana fasigula	Common rana

(b) Reptilia

1. Bitis arietans	Puff adder
2. Pseudaspis cana (young)	Mole snake

(c) Avifauna

Arranged according to Roberts Birds of South Africa (McLachlan & Liversidge, 1971).

Platalea alba	Spoonbill

Alopochen aegyptiacus	Egyptia goose
Anas sparsa	Black duck
Falco tinnunculus	Rock kestrel
Aquila verreauxi	Black eagle
Buteo rufofuscus	Jackal buzzard
Francolinus capensis	Grey-wing francolin
F. levaillantii	Red-wing francolin
Coturnix coturnix	African quail
Burhinus capensis	Cape dikkop
Larus dominicanus	Southern black-backed gull
L. hartlaubii	Hartlaub's gull
Columba guinea	Rock pigeon
Streptopelia capicola	Turtle dove
Stigmatopelia senegalensis	Laughing dove
Megaceryl maxima	Giant kingfisher
Chaetops fraternus	Rock jumper

Monticola rupestris	Cape rock-thrush
Saxicola torquata	Stone chat
Cossypha caffra	Cape robin
Sphenoeacus afer	Grass bird
Motacilla capensis	Cape wagtail
Macronyx capensis	Orange throated long claw

Lanius collaris	Fiscal shrike
Telophorus zeylonus	Bokmakierie
Onychognathus morio	Redwinged starling
Promerops cafer	Cape sugarbird
Nectarinia famosa	Malachite sunbird
Anthobaphes violacea	Orange-breasted sunbird
Ploceus capensis	Cape weaver
Coliuspasser capensis	Cape widow bird
Estrilda astrild	Common waxbill
Serinus canicollis	Cape canary
Fringillaria capensis	Cape bunting

(d) Mammalia

Aethomys namaquensis	Namaqua rock rat
Rhabdomys pumilio	Striped mouse
Hystrix africaeaustralis	Porcupine
Oreotragus oreotragus	Klipspringer
Pelea capreolus	Grey-rhebuck
Raphicerus melanotis	Grysbuck
Sylvicapra grimmia	Common duiker
Papio ursinus	Chacma baboon

B. List of fauna seen or probably occuring in or passing through the Cedarberg study area.

INVERTEBRATES

Arthropoda

(a) Insecta

Camponotus maculatus

Acantholepis cf. capensis

Monomorium delagoensis

Monomorium sp.

Anoplolepis custodiens

Anaplolepis nuptialis

VERTEBRATES

(a) Amphibians

Bufo rangeri	Raucous Toad
Pyxicephalus delalandei	Pyxie

(b) Reptiles

Typhlops delalandii	Pink Earth Snake
Leptotyphlops gracilior	Slender Thread-Snake
Lycodonomorphus rufulus	Olive-brown Water-Snake

Boaedon guttatus	Spotted House-Snake
Prosymna sundevallii	Southern Shovel-snout
Pseudaspis cana	Mole-snake
Dasypeltis scabra	African Egg-eating Snake
Crotaphopeltis hotamboeia	Herald Snake
Psammophylax rhombeatus	Rhombic Skaapsteker
Hemachatus haemachatus	Rinkals
Naja nivea	Cape Cobra
Naja nigricollis	Western Black Spitting Cobra
Bitis cornuta	Many Horned Adder
Bitis arietans	African Puff-Adder
Phyllodactylus porphyreus porphyreus	Marbled Gecko
Phyllodactylus lineatus lineatus	Striped or Lineated Gecko
Phyllodactylus lineatus rupicolus	Striped or Lineated Gecko
Pachydactylus capensis capensis	Common Cape Gecko
Agama atra	Rock Agama or Bloukop
Microsaura pumila pumila	Cape Dwarf Chameleon
Scelotes bipes sexlineatus	Silvery Sand Skink
Mabuya capensis	Cape Three-Striped Skink
Mabuya damarana	Damara Variegated Skink
Acontias meleagris meleagris	Golden Sand Skink
Acontias lineatus lineatus	Legless Skink
Cordylosaurus trivittatus australis	Black Plated Lizard
Tetradactylus tetradactylus	Whip Lizard
Tropidosaura montana montana	Green-striped Mountain

	Lizard
Nucras tessellata	Banded Sand Lizard
Eremias lineo-ocellata pulchella	Ocellated Sand Lizard
Eremias burchelli	Burchell's Sand Lizard
Scaptira knoxii	Knox's Ocellated Sand Lizard
Cordylus capensis robertsi	Roberts' Girdled Lizard
Chersine angulata	Ploegskaarskilpad, rooipens
Homopus areolatus	Padlopertjie
Homopus signatus	Klipskilpadjie

(c) Birds

Aquila verreauxi	Black eagle
Elanus caeruleus	Black shouldered kite
Buteo buteo	Steppe buzzard
Buteo rufofuscus	Jackal buzzard
Falco tinnunculus	Rock kestrel
Francolinus africanus	Grey-wing francolin
Francolinus capensis	Cape francolin
Streptopelia semitorquata	Red-eyed turtle dove
Streptopelia capicola	Cape turtle dove
Streptopelia senegalensis	Langhing
Cuculus solitarius	Red chested cuckoo
Chrysococcyx klaas	Klaas cuckoo
Merops apiaster	European bee-eater

Bubo africanus	Spotted eagle owl
Apus barbatus	Black swift
Apus melba	Black swift
Apus caffer	White rumped swift
Chaetops frenatus	Rock jumper
Turdus olivaceus	Cape thrush
Oenanthe monticola	Mountain chat
Cercomela familiaris	Familiar chat
Cossypha caffra	Cape Robin
Bradypterus victorini	Victorin's scrub warbler
Sphenoeacus afer	Grass bird
Cisticola fulvicapilla	Neddicky
Cisticola subruficapilla	Grey-backed cisticola
Hirundo rustica	European swallow
Hirundo albigularis	White-breasted swallow
Hirundo dimidiata	Pearl-breasted swallow
Hirundo fuligula	Cliff swallow
Lanius collaris	Fiscal shrike
Laniarius ferrugineus	Boubon shrike
Maloconotus zeylonus	Bokmakierie
Corvus albus	Pied crow
Corvus capensis	Black crow
Corvus albicollis	Cape Roven
Onychognatus morio	Red-winged starling
Spreo bicolor	Piled starling
Nectarinia famosa	Malachite sunbird

Nectarinia violacea	Orange breasted sunbird
Promerops cafer	Protea sugarbird
Serinus canicollis	Cape canary
Serinus leucopterus	Protea seed-eater
Fringillaria capensis	Cape bunting

(d) Mammals (bats excluded)

Elephantulus edwardi	Elephant shrew
Myosorex varius	Shrew
Crocidura flavescens	Shrew
Rhabdomys pumilio	Striped mouse
Otomys laminatus	Laminate vlei rat
Acomys subspinosus	Cape spiny mouse
Aethomys namaquensis	Namaqua rock mouse
Hystrix africaeaustralis	Porcupine
Orycteropus afer	Aardvark (rare)
Pronolagus rupestris	Smith's red rock hare
Lepus saxatilis	Scrub hare
Papio ursinus	Chacma baboon
Panthera pardus	Leopard
Felis pardus	Wild cat
Felis caracal	Lynx
Vulpes chama	Cape fox
Genetta tigrina	Large spotted genet
Herpestes pulverulentus	Cape grey mongoose

Atilax paludinosus	
Proteles cristatus	Aardwolf
Sylvicapra grimmia	Duiker
Raphicerus melanotis	Cape grysbok
Oreotragus oreotragus	Klipspringer

APPENDIX III

FLORA OF THE STUDY AREAS

(A) A list of the flora of the Kogelberg study site

Pteridophyta

SCHIZAEACEAE

Shizaea pectinata (L.) Smith

Angiospermae - Monocotyledones

GRAMINAE

Ehrharta bulbosa Sm.

E. ottonis Kunth.

Merxmuellera rufa (Nees) Conert.

Pentaschistis steudelii (Nees) McClean

CYPERACEAE

Ficinia albicans Nees

F. deusta (Berg.) Levyns

F. dunensis Levyns

F. filiformis (Lam.) Pheiffer

F. lateralis (Vahl.) Kunth

F. levynsae Arnold MS.

F. minutiflora C.B. Cl.

F. zeyheri Buek.

Scirpus ecklonii Steud.

Tetraria compar (L.) Lestib.

T. cuspidata (Rottb.) C.B. Cl.

T. exilis Levyns

T. fasciata (Rottb.) C.B. Cl.

T. flexuosa (Rottb.) C.B. Cl.

T. microstachys (Vahl.) Pheiffer

T. thermalis (L.) C.B. Cl.

RESTIONACEAE

Restio bifarius Mast.

R. bifidus Mast.

R. curviramis Kunth.

R. cuspidatus Thunb.

R. egregius Hochst.

R. filiformis Poir.

R. fraternus Kunth.

R. pedicellatus Mast.

R. purpurascens Nees ex Mast.

R. triticeus Rottb.

Chondropetalum hookeranum Pillans

Elegia juncea L.

E. parviflora Kunth

E. parviflora Kunth var. filacea (Mast.) Pillans

E. persistens Mast.

E. racemosa Pers.

E. spathacea Mast.

E. stipularis Mast.

E. thyrsifera Pers.

E. vaginulata Mast.

Leptocarpus distichus Pillans

L. hyalinus Pillans.

L. membranaceus Pillans

Thamnochortus dichotomus R. Br.

T. pulcher Pillans

Staberoha cernua Dur. & Schinz.

Hypolaena digitata Pillans

H. filiformis Mast.

Hypodiscus albo-aristatus Mast.

H. aristatus Nees

H. argenteus Mast.

Willdenowia humilis Mast.

W. lucaeana Kunth.

LILIACEAE

Bulbinella triquetra (L.F.) Kunth.

Bulbine favosa (Thunb.) Roem. & Schult.

Eriospermum cernuum Bak.

E. pumilum Jacq.

Albuca cooperi Bak.

Urginea filifolia (Jacq.) Steinh.

HAEMODORACEAE

Dilatris Berg.

D. pillansii Barker

D. viscosa L.

Wachendorfia paniculata Burm.

AMARYLLIDACEAE

Lanaria lanata (L.) Dur. & Schinz

HYPOXIDACEAE

Spiloxene circuligoides (N. Bol.) Garside.

IRIDACEAE

Aristea racemosa Ker-Gawl.

Bobartia gladiata. (L.F.) Ker-Gawl.

B. indica L.

Geissorhiza humilis Ker-Gawl.

G. juncea

G. ovata (Burm. F.) Aschers & Graebn.

Gladiolus bullatus Thunb. ex Lewis

G. brevifolius Jacq.

Homeria sp.

Ixia mictandra Bak.

Lapeyrousia micrantha (Meyer ex. Klatt) Bak.

Moraea angusta (L.F.) Ker-Gawl.

Nivenia stokoei N.E. Br.

Pillansia tempelmanii (Bak.) L. Bol.

Romulea gracillima Bak.

Watsonia pyramidata (Andr.) Stapf.

Angiospermae - Dicotyledones

PROTEACEAE

Serruria inconspicua R.Br.

S. elongata Guthrie and Salter

Mimetes cucullatus (L.) R.Br.

Protea scabra R.Br.

Leucospermum truncatulum (Salisb. ex Knight) Rourke

L. cordifolium (Salisb. ex Knight) Rourke

Leucadendron gandogeri Schinz ex Gandoger

L. laureolum (Lam.) Fourcade

L. salignum Berg.

L. xanthoconus (O. Kuntze) K. Schum.

LAURACEAE

Cassytha ciliolata Nees

DROSERACEAE

Drosera trinervia Spreng.

BRUNIACEAE

Nebelia paleaceae (Berg.) Sweet

LEGUMINOSAE

PAPILIONOIDEAE

Aspalatathus abietina Thunb.

A. ciliaris

A. linearis (Burn. f.) Dahlgr.

A. microphylla DC.

A. retroflexa

A. stenophylla Eckl. & Zeyh.

A. tridentata L.

Argyrolobium filiforme Eckl. & Zeyh.

Indigofera digitata Thunb.

Psoralea pinnata L.

P. rotundifolia L.f.

GERANIACEAE

Pelargonium angulosum (Mill.) Ait.

OXALIDACEAE

Oxalis luteola Jacq.

Oxalis purpurea L.

Oxalis truncatula Jacq.

PENAEACEAE

Penaea cneorum Meerb. subsp. lanceolata R. Dahlgr.

P. mucronata

Saltera sarcocolla (L.) Bullock

ZYGOPHYLLACEAE

Zygophyllum fulvum L.

Z. flexuosum Eckl. & Zeyh.

Z. sessilifolium L.

RUTACEAE

Agathosma bifida Bartb. & Wendl.

A. imbricata Wild.

Coleonema juniperum Sond.

Diosma hirsuta L.

D. oppositifolia L.

Euchaetis elata Eckl. & Zeyh.

E. linearis Sond.

POLYGALACEAE

Polygala garcinii DC.

EUPHORBIACEAE

Euphorbia tuberosa L.

E. silenifolia (Haw.) Sweet

E. sp.

RHAMNACEAE

Phylica imberbis Berg.

P. lasiocarpa Sond.

THYMELEACEAE

Gnidia galpinii C.H. Wr.

G. juniperifolia Lam.

G. oppositifolia L.

G. pinifolia L.

G. viridis Berg.

Struthiola ciliata (L.) Lam.

UMBELLIFERAE

Centella glabrata L.

C. virgata

Thunbergiella filiformis (Lam.) Wolff.

ERICACEAE

Erica articularis L.

E. campanularis Salisb.

E. cerinthoides L.

E. corifolia L.

E. cristata Dulfer

E. gysbertii Guthrie & Bolus

E. hispidula L.

E. virgiata L.

E. pectinata

E. perspicua Wendl.

E. plukenetii L.

E. pulchella Houtt.

E. squarrosa Salisb.

Blaeria ericoides L.

B. dumosa Wendl.

Acrostemon stokoei (L.) Guthrie

Anomalathus scoparius Klotsch.

Sympieza articulata (Thunb.) N.E. Br.

Scyphogyne divaricata Benth.

Nagelocarpus serratus (Thunb.) Bullock

GENTIANACEAE

Chironia tetragonia L.f.

C. jasminoides L.

STILBACEAE

Camplyostachys cernua (L.f.) Kunth.

LABIATAE

Stachys reticulata Codd.

SELAGINACEAE

Selago spuria L.

Agathelpis dubia (L.) Hutch.

RUBIACEAE

Anthospermum lichtensteinii Cruse

CAMPANULACEAE

Roella ciliata L.

R. incurva DC.

R. triflora (Good) Adamson

LOBELIACEAE

Cyphia volubilis (Thunb.) Willd.

Lobelia coronopifolia L.

L. linearis

L. tomentosa L.f.

COMPOSITAE

Corymbium africanum L.

C. cymosum E. May. ex DC.

C. glabrum L. sensu Levyns, Adams & Salter

C. scabridum L.f. forma filiforme (L.f.) Thunb.

Euryops abrotanifolius (L.) DC.

Othonna bulbosa L.

O. heterophylla L.f.

Ursinia crithmoides (Berg.) Poir.

U. quinqepartita (DC.) N.E. Br.

Phaenocoma prolifera (L.) D. Don.

Helipterum canescens (L.) DC.

Helichrysum metalasoides

H. sesamoides

H. vestitum

Stoebe cinerea Thunb.

Disparago ericoides Gaertn.

Berkheya barbata (L.f.) Hatch.

B. herbaceae (L.f.) Druce.

Metalasia sp. cf. tennifolia DC.

Lachnospermum umbellatum (D. Don.) Phillips

Senecio arenarius Thunb.

S. pinifolius (L.) Lam.

S. triqueter Less.

S. umbellatus L.

(B) A list of the flora of the Cedarberg study site

Angiospermae-Monocotyledones

GRAMINAE

Ehrharta longifolia Schrad.

E. ramosa Thunb.

Merxmullera rufa (Nees) Conert

Pentaschistis steudelii (Nees) McClean

Eragrostis curvula (Schrad.) Nees

Lasiochloa longifolia (Schrad.) Kunth

CYPERACEAE

Ficinia filiformis (Lam.) Schrad.

F. indica (Lam.) Pfeiffer

F. nigrescens (Schrad.) Raynal

F. rudica (Lam.) Pheiffer

Tetraria compar (L.) Lestib

RESTIONACEAE

Restio gaudichaudianus Kunth

Hypodiscus neesii Mast.

Cannomois acuminata Pillans

Willdenowia affinis Pillans

LILIACEAE

Bulbinella floribunda (Ait.) Dur. & Schinz

Bulbine favosa (Thunb.) Roem. & Schult.

Trachyandra cf. muricata

Chlorophytum undulatum (Jacq.) Oberm.

Albuca cooperi Baker

Ornithogalum fimbrimarginatum Leighton

O. maculatum Jacq.

O. sp. cf. polyphyllum Jacq.

O. subcoriaceum L. Bol.

O. thermophyllum Leighton

Lachenalia sp.

Urginea sp.

HAEMODORACEAE

Dilatris ixioides Lam.

Wachendorfia paniculata Burm.

AMARYLLIDACEAE

Haemanthus cf. rotundifolius

Brunsvigia cf. minor

Gethyllis cf. afra

TECOPHILEACEAE

Cyanella hyacinthoides L.

IRIDACEAE

Romulea atandra Lewis

Homeria collina (Thunb.) Vent.

Bobartia sp. cf. gladiata (L.f.) Ker-Gawl.

Aristea dichotoma (Thunb.) Ker-Gawl.

A. monticola Goldbl.

Engysiphon brevitubus Lewis (Geisshorhiza)

Babiana disticha Ker-Gawl.

Tritoniopis nervosa (Bak.) Lewis

Lapeirousia micrantha (Meyer ex Klatt) Bak.

Watsonia zeyheri L.Bol.

Angiospermae - Dicotyledones

PROTEACEAE

Paranomus bracteolaris Salisb. ex Knight

Serruria aitonii R. Br.

S. cygnea R. Br.

P. acaulos (L.) Reich.

P. nitida Mill.

P. laurifolia Thunb.

Leucadendron pubescens R. Br.

L. rubrum Burm. f.

L. salignum Berg.

SANTALACEAE

Thesium carinatum A.DC.

AIZOACEAE

Adenogramma molluga Reichb.

Pharnaceum elongatum (D.C.) Adam.

MESEMBRYANTHEMACEAE

Erepsia sp.

Aridaria cf. brevicarpa

LAURACEAE

Cassytha ciliolata Nees

CRUCIFERAE

Heliophila cedarbergensis Marais

H. scoparia Burch. ex DC. var. scoparia

Brachycarpaea juncea (Berg.) Marais

ROSACEAE

Cliffortia ruschifolia L.

C. teretifolia L.f.

LEGUMINOSAE

PAPILIONOIDEAE

Podalyria cuneifolia ?

P. sp. cf. pearsonii (Phillips)

Rafnia amplexicaulis Thunb.

R. capensis (L.) Druce

R. fastigiata Eckl. et Zeyh.

Lebeckia simsiana Eckl. & Zeyh.

Aspalathus acuminata (Thunb.) R.Dahlg.

A. altissima Dahlg.

A. bracteata Thunb.

A. comptonii Dahlg.

A. divaricata Thunb. var brevicarpa Dahlg.

A. galeata E.Mey.

A. hispida Thunb.

A. lanata E.Mey.

A. linearis (Burm.f) R.Dahlg. subsp. linearis

A. quinquefolia L.

Indigofera nitida Salter

GERANIACEAE

Pelargonium elongatum (Cav.) Willd.

P. sp.

P. sp

OXALIDACEAE

Oxalis sp.

Oxalis sp.

Oxalis sp.

LINACEAE

Linum africanum L.

ZYGOPHYLLACEAE

Seetzenia lanata (Willd.) Bullock

Zygophyllum fulvum L.

RUTACEAE

Agathosma longicornu Pillans

A. microcalyx Dummer = A. gifbergense?

Acmadenia flaccida Eckl. & Zeyh.

Euchaetis glomerata Bartl. E. Wendl.

E. cf. longicornu

Macrostylis cf tenuis

POLYGALACEAE

Polygala brachyphylla Chod.

Muraltia alopecuroides (L.) DC.

Nylandtia spinosa (L.) Dumort.

EUPHORBIACEAE

Euphorbia sp.

Clutia cf. alaternoides

ANACARDIACEAE

Rhus angustifolia L.

R. dissecta Thunb.

R. incisa L.f.

R. undulata Jacq.

CELASTRACEAE

Maytenus oleoides (Lam.) Loes.

SAPINDACEAE

Dodonea viscosa Jacq. var. angustifolia Benth

RHAMNACEAE

Phylica aemula Schltr.

P. oleaefolia Vent

P. rigidifolia Sond.

P. stipularis L.

P. villosa (Thunb.) DC. var pedicellata Sond.

STERCULIACEAE

Hermannia cuneifolia Jacq.

THYMELEACEAE

Gnidia geminiflora E. Mey. ex Meisn.

Struthiola ciliata (L.) Lam.

UMBELLIFERAE

Centella affinis (Eckl. et Zeyh.) Adamson

Arctopus echinatus L.

ERICACEAE

Simocheilus multiflorus Klotsch

EBENACEAE

Euclea tomentosa E. Mey. ex. DC.

Diospyros glabra (L.) de Wint.

OLEACEAE

Olea africana Mill.

GENTIANACEAE

Sebaea exacoides Eckl. ex Cham.

ASCLEPEDIACEAE

Microloma sagittatum (L.) R.Br.

Asclepias cancellata Burm. f.

CONVOLVULACEAE

Cuscuta nitida E. Mey. ex Choisy

BORAGINACEAE

Lobostemon laevigatus Buek

LABIATAE

Salvia africana-coerulea L.

SCROPHULARIACEAE

Nemesia bodkinii Bol.

Oftia africana (L.) Bocq.

SELAGINACEAE

Hebenstreitia crassifolia Choisy

Dischisma ciliatum Choisy

Selago spuria L.

Gosela eckloniana Choisy

Agathelpis dubia (L.) hutch.

RUBIACEAE

Anthospermum aethiopicum L.

CAMPANULACEAE

Prismatocarpus diffusus (L.f.) DC.

LOBELIACEAE

Cyphia bulbosa (L.) Berg.]

C. digitata (Thunb.) Willd.

Galium capense Thunb.

COMPOSITAE

Corymbium africanum L.

Pteronia camphorata L.

Felicia filifolia (Vent.) Burtt-Davy

Chrysocoma tenuifolia Berg.

Helipterum canescens (L.) DC.

Helichrysum tomentosulum (Klatt) Meisn.

Stoebe aethiopica L.

S. plumosa (L.) Thunb.

Elytropappus gnaphaloides (L.) Levyns

Metalasia cephalotes Less.

M. muricata (L.) R. Br.

Lachnospermum fasciculatum (Thunb.) Baill.

Relhania squarrosa L'Herit.

Eriocephalus africanus L.

Cotula turbinata L.

Hippia pilosa Druce

Pentzia grandiflora Hutch.

Senecio erosus L.f.

S. paniculatus Berg.

S. sp cf S. paarlensis DC.

Euryops abrotanifolius (L.) DC.

E. speciosissimus DC.

Othonna amplexicaulis Thunb.

Osteospermum polygaloides L.

Ursinia anthemoides (L.) Poir. subsp. versicolor (DC.) Prassl.

U. pinnata (Thunb.) Prassl.

U. sericea (Thunb.) N.E. Br.

Arctotis bellidifolia Berg.

Gazania krebsiana Less. subsp. krebsiana

Gerbera sp

Appendix 4 : Parameters of the allometric regression for the components of the tall Proteaceae on the study site using the relationship $\log_e$ (mass) = $\log_e A + B \log_e$ (stem diameter) and the least squares regression technique.

Species		L. pubescens female			L. pubescens male			L. laureolum female			L. laureolum male			Paranomus bracteolaris			Protea laurifolia		
Wood dia. class (mm)	Component	A	B	r	A	B	r	A	B	r	A	B	r	A	B	r	A	B	r
6	Leaf-live	38,164	1,694	0,95	39,115	1,944	0,96	30,329	1,871	0,90	37,210	1,785	0,90	40,645	1,625	0,97	4,593	2,398	0,83
	Leaf-dead	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,003	3,761	0,88
	Twig-live	17,872	2,118	0,96	17,756	2,271	0,97	4,112	1,996	0,88	5,550	1,966	0,86	11,383	2,196	0,97	3,951	2,010	0,74
	Twig-dead	0,158	3,397	0,78	0,057	4,195	0,91	-	-	-	-	-	-	0,168	2,832	0,85	0,506	1,934	0,65
6 & 25	Leaf-live	0,372	1,356	0,45	0,112	2,121	0,66	-	-	-	-	-	-	-	-	-	7,456	2,367	0,94
	Leaf-dead	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,001	3,617	0,48
	Branch-live	2,591	3,609	0,97	6,161	2,971	0,96	23,021	2,389	0,95	26,036	2,438	0,96	1,368	3,181	0,87	3,286	3,016	0,98
	Branch-dead	0,127	2,935	0,73	0,093	0,869	0,22	-	-	-	-	-	-	0,031	2,503	0,51	1×10^{-5}	7,298	0,60
25	Wood-live	1,593	2,515	0,94	0,895	3,561	0,93	16,349	1,659	0,91	18,532	1,547	0,94	0,834	3,524	0,93	12,074	2,650	0,98
	Wood-dead	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	Total	67,028	2,325	0,98	66,749	2,348	0,98	64,665	2,155	0,96	78,490	2,119	0,97	64,763	2,169	0,98	24,017	2,712	0,99
-	New Infl.	1,256	2,295	0,87	-	-	-	0,005	5,400	0,55	-	-	-	3,193	1,814	0,41	0,187	3,127	0,90
-	Old Infl.	0,492	2,543	0,66	-	-	-	1,866	2,461	0,40	-	-	-	-	-	-	1×10^{-5}	8,226	0,90

24 MAY 1984