



A STUDY OF THE SHORT-TERM RESPONSES
OF FYNBOS TO FIRE IN THE KOGELBERG
STATE FOREST, SOUTH AFRICA

BY

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An experimental fire in the Kogelberg State Forest.

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ABSTRACT

The physical environment of a fynbos community was measured from before the experiments began and the work is continuing. Prior to burning 0,25 ha, and slightly smaller plots, were laid out in an approximately 20 year old proteoid-ericoid-restioid community. The community's physiognomy and structure were described with methods that are compatible with the vegetation.

All vegetation and environmental parameters that were measured confirm the classification of the fynbos that it is an evergreen broad to narrow leaved sclerophyllous shrubland with restioid, ericoid and proteoid elements (Taylor, 1978).

Experimental burns in all the seasons, except winter, indicated that the timing of burning for catchment management is very important. Summer and spring burns, in that sequence, have the least short-term effect on fynbos species composition and the rate of vegetative recovery. Autumn fires suppress both the recovery of the vegetation and species survival.

The phenology of species in the fynbos is changed for at least one season after a fire. Geophytes are stimulated to flower in abundance after a summer burn but much less so by a spring burn. The spring burn prevented at least one geophyte species from flowering the following spring which is the flowering time for the species. Records for the autumn burn are from too short a time after a burn for conclusions, but the regrowth of Restio egregius was slower than for any of the other treatments.

Flowering maturity is concomitantly retarded.

Fire intensities varied between the seasons, but the greatest factor determining intensity was rather the amount of fuel available per unit area than the season of the burn. Species composition also determines the heat value of the fuel.

PREFACE

Until very recently the fynbos ecosystem has been exploited for the benefit of Man without much thought being given to the eventual result. Burning veld for grazing and the collection of fire-wood was the earliest form of veld utilization (Boucher, 1972). This was followed by the harvesting of natural products such as wood and flowers (Porter, 1967).

Sadly the introduction of aggressive invasive weeds and commercial plants went unchecked until their destructive force became noticeable (Taylor, 1977). At present the Directorate of Forestry and Environmental Conservation is engaged in a formidable task of rehabilitation on the one hand, and preserving the least affected areas on the other hand, from these alien pests (Kruger, et. al. 1977; Kruger pers. comm.).

Research has been initiated to gain an understanding of the very basic forces and factors involved in the maintenance of climax, natural subclimax and ecotonal communities. Once the dominant controlling factors are identified and the extent of their influence understood, effective management of fynbos can become a reality.

The rugged topography of the catchment areas means that fire is the only practical management tool for maintaining a constant yield of clean water. For urban areas fire management is necessary to control the build-up of fuel that will eventually lead to a conflagration hazardous to life and limb. It is not possible to attain all these aims without knowledge of the natural regulatory mechanisms operating in the system.

In studying natural communities and their responses to being manipulated, the Directorate of Forestry and Environmental Conservation hopes to find ways of combatting invasive alien species and of promoting the well-being of the endemic species.

3. INTRODUCTION

"Fynbos" is the vernacular name for much of the vegetation in the south-western Cape region of South Africa. The name was aptly coined by Bews (1916) to describe the characteristic vegetation of the cape Floral Kingdom. Plant geographers assigned the status of Kingdom to the Cape flora because of the high degree of endemism found there (Takhtajan, 1969; Good, 1974). Another unique biogeographic feature is the pronounced disjunct distributions of many species (Kruger et. al., 1977). Many endemic species have extremely limited ranges, for example a single population being restricted to an isolated mountain peak (Dahlgren, 1963, 1967; Williams, 1972).

Good (1974) listed 43 selected areas of which the Cape Peninsula has the second highest species density of 5,6 species per square kilometer (in Taylor, 1977). The number of species occurring in the Cape was estimated at about 6000 by Marloth (1908), but according to Taylor (1977) this is most probably an underestimation.

Seven plant families are entirely confined to the south-western Cape (six according to Goldblatt, 1978) and specifically to fynbos communities (Taylor, 1977). These are the Bruniaceae, Geissolomataceae (Monotypic), Grubiaceae, Penaeaceae, Retziaceae, Roridulaceae and Stilbaceae (Taylor, 1977). In a detailed study of endemism and disjunctions Weimark (1941) found that of 282 genera had their centre of origin in the south-western Cape fynbos, and of these 212 are confined to that region.

Fynbos dominates the landscape from Van Rynsdorp in the north along a 80 - 100 km mountainous belt parallel to the coast, to Port Elizabeth in the east. Inland, to the north and east, fynbos abruptly disappears where the Cape geological system is overlain by younger rock formations (Goldblatt, 1978). Outliers of the Cape flora, represented by a limited number of species, are only found where the Table Mountain Sandstone soils occur (Goldblatt, 1978). These outliers are indicative of a much wider distribution of fynbos vegetation in the past (Wild, 1968; Oliver, 1977).

Fynbos is characterized by aphyllous restioid species, small shrubs with ericoid leaves, and broad leaved sclerophyll shrubs (Taylor, 1978). All the component life-forms and species contribute to the distinctive physiognomy of fynbos vegetation (Kruger et. al. 1977; Taylor, 1978). Plant families such as the Restionaceae, Ericaceae and Proteaceae invariably dominate the fynbos to a greater or lesser extent (Oliver, 1977). Other typical constituents of the Cape Flora are species of the Iridaceae, Rutaceae, Thymeleaceae, Compositae and Leguminosae (only Papilionoideae). Single species dominance is virtually absent which is a feature usually associated with old floras (Levyns, 1963). The whole floristic component of the fynbos biome differs sharply from the other biomes of southern and tropical Africa (Goldblatt, 1978).

The south-western folded belt has been subjected to denudation for such a long time that essentially the central core of the anticlines remain (Cole, 1949). The major ranges are composed of Table Mountain Sandstone whereas lesser ones comprise smaller sandstone

folds of the Witteberg quartzites in the Cape System. Cape Granites generally form the foothills and lower slopes in the western area. The substrate in the intervening valleys of the Cape folded belt are Bokkeveld shales with sandstones of the Cape System and Malmesbury shales of the Archaean Complex forming the underlying rock bed. Coastal lowlands consist of sands, conglomerates and limestones of Tertiary to recent origin (Taylor, 1978).

Deep soils occur in the valleys and are derived from Bokkeveld shales. The soils are clayey, more fertile and of good texture especially where it is mixed with sands from the mountain slopes (Wellington, 1955). Granite derivatives are mostly sandy loam soils (Taylor, 1978) and are generally of higher nutrient status than those derived from Table Mountain Sandstone (Taylor, 1978).

A profound influence is exerted on the climate of the Cape by the cold north-flowing Benguela Current off the west coast (Rumney, 1968; van Zinderen Bakker, 1975; Tankard & Rogers, 1978). The current wells up near Cape Town and the presence of this cold water off-shore has a drying effect along the whole west coast. In summer this results in a high pressure belt developing over the south Atlantic and west coast that inhibits the flow of moist tropical air moving westward (Goldblatt, 1978). South-east mist clouds relieve much of the summer drought stress of the vegetation at higher altitudes (Bews, 1925).

A second weather system prevails in winter which brings moist air to the west coast and to the southern coast south of approximately 28°S . The south Atlantic anticyclone moves about 4° toward the equator

and north-westerly winds provide cyclonic and orographic rain in the south-western Cape (Kruger, 1974; Goldblatt, 1978). Snow on the higher peaks of the mountain ranges is produced by cyclonic cold fronts in winter.

Climatically the south-west and south coast with summer drought and cyclonic winter rainfall can be classified as typically mediterranean (Goldblatt, 1978). Definitions for a mediterranean-type climate coincide well with the definition for a fire-type climate (Sweeney, 1977). Fynbos, however, occurs in climate types other than mediterranean (Kruger, 1979) but still exhibits flammability characteristics qualifying it as a "fire-type" vegetation (see Philpot, 1977). In the Kogelberg State Forest the combination of a fire-type climate and a fire-type vegetation is present.

The hypothesis that a vegetation that has developed in a fire-type environment and adapted to fire has inherent characteristics that make it flammable (Mutch, 1970) is applicable to fynbos. Kruger (1977) elaborates on the build-up of a fine, porous but reasonably compact fuelbed as a post-fire fynbos community develops. Such a fuelbed and standing dead material can amount up to a quarter of the total biomass of the community (Kruger, 1977). Numerous references to adaptive traits of fynbos species for the survival of fires can be found in the literature (Michell, 1922; Levyns, 1927, 1929a; Jordaan, 1949b; Levyns, 1956; Bean, 1962; Jordaan, 1965; Levyns, 1966; Martin, 1966; van der Merwe, 1966; van der Merwe & van der Merwe, 1968; van der Merwe, 1969; Rourke, 1972; Trollope, 1974; Rourke, 1977b, 1978). Fynbos is considered to be

adapted to its fire-type environment. Life-form composition of the vegetation and adaptive strategies such as bradyspory and serotiny have been used as evidence to support this view point (Wicht, 1945; van der Merwe, 1966; Taylor, 1969; Kruger et. al., 1977).

Man has had a dramatic influence on the distribution, structure and perhaps evolution of fynbos communities. South African and in this case south-western Cape vegetation has been drastically altered by man in the last 100 000 to 700 000 years (Klein, 1974, 1977), and more especially in the last century. These changes have been made with the increasing use of fire, by cultivation, and the introduction of domestic livestock.

Fynbos grazing is low in crude protein, calcium, phosphorus and magnesium throughout the seasons (Louw, 1969). In the eastern Cape shrubby fynbos species invade overgrazed grasslands but can be controlled effectively by fire (Trollope, 1970). Fire has been used to provide green grazing since before the colonization of South Africa by Europeans (Schweitzer & Scott, 1973). Most natural fynbos veldtypes are burnt relatively frequently and veld older than forty years is almost unknown (Kruger, 1979).

An increasing population with concomitant expanding farming activities and a greater demand for recreational areas are endangering the continued existence of natural fynbos. It has therefore become increasingly urgent to devise management policies and prescriptions for preserving the remainder of this unique floral

Kingdom. Only 39% of the area originally covered by fynbos has survived the activities of man (Hall and Boucher, 1977). Much of the remaining "natural" Fynbos is restricted to mountainous terrain and mountain catchment areas. The Directorate of Forestry and Environmental Conservation owns approximately 267 000 hectares of unforested mountain land in the south-western Cape (Kruger, 1974). It is the largest single controller of catchment areas, and also manages private catchments in terms of the Mountain Catchment Areas Act no. 63, Government Gazette, 7 October 1970, no 2858, Government Printer, Pretoria.

To determine those ecological factors necessary for the proper conservation of fynbos the Directorate of Forestry and Environmental Conservation has initiated a number of long-term research projects. Studies such as the optimum interval between burns and the best season to burn form the basis of these research objectives. A "best" season and interval between burns relate to the objectives of a specific treatment. In catchment areas the objective is to maintain a vigorous natural plant cover with maximum species diversity, while maintaining a maximum sustained yield of clean water. The decision to maintain a vigorous vegetation in catchment areas followed on research results of Departmental workers (Wicht & Banks, 1963; Le Roux, 1966; Malherbe, 1968; van der Zel & Kruger, 1975). The Directorate of Forestry and Environmental Conservation adopted a policy of controlled burning in 1972 (Garnett, 1973).

One of the Directorate's major research priorities is to determine

the season in which fynbos is burnt so that regenerative response is most favourable. Regardless of the season of burn fynbos will regain its former structure and composition if burnt at an interval long enough to include the maximum youth period of the most retarded and the senescence of the most precocious fire therophyte (Taylor, 1979). It can be expected, however, that continued burning in a specific season may deflect the climatic-edaphic climax of the vegetation. This is because a fire in a specific season may retard the post-fire flowering of specific species and slowly reduce the seed supply with every subsequent burn in the same season. The shorter the burning cycle the more acute will the reduction in the seed supply be. Burning in specific seasons also influences the rate of soil erosion, either by water or wind. Erosion is of prime importance in the consideration of burning regimes for management.

3.1 AIMS OF THE STUDY

The immediate aims of this study are as follows:-

- a. To describe and analyse the structure of a fynbos community,
- b. To describe and analyse the edaphic and climatic environment of the same fynbos community,
- c. To determine the relative effectiveness of different regeneration strategies after fire in different seasons,
- d. To relate the phenology of some of the dominant species and their responses to burns in different seasons, and
- e. To indicate the over-all, short-term effect of burning treatments in different seasons.

Initially a procedure was established for recording the existing structural edaphic and environmental features of the mature fynbos community. The aim was to establish a reference point to which any possible changes in the vegetation after treatment could be related. Parameters such as pattern, stratification and biomass were analysed to describe the fynbos stands and determine the differences between experimental plots. Evaluation of the results by comparing them with the results of other workers also served to confirm or reject the validity of the methods used to acquire each reference data set. Observations and some measurements were made to determine the effectiveness of the regeneration strategies of a few selected species. The objective was to ascertain whether burning in different seasons significantly influenced either vegetative or seed regeneration.

Some of the dominant plant species were monitored regularly to determine their phenology. After a burning treatment monitoring continued and the goal was to relate the results to the phenological phase of the species at the time of burning. Lastly an overall assessment of the effect of a burning treatment of fynbos was envisaged. The aim of this final assessment was to determine to what degree the treatment achieves the purpose for which it was applied.

3.2 HISTORICAL BACKGROUND

Very little is known about the detailed pre-history of the Kogel-

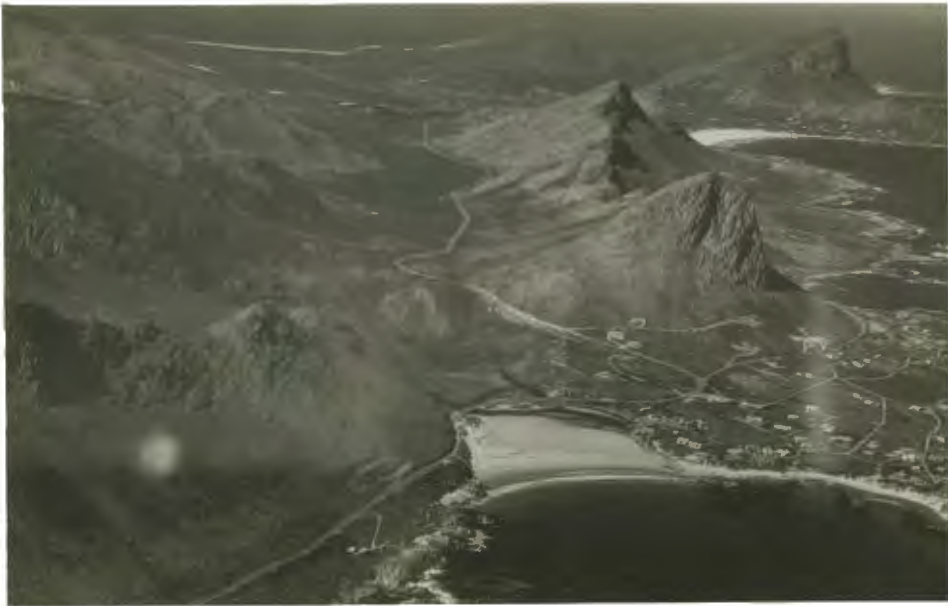


Fig. 1. Cape Hangklip in the back-ground and the mouth of the Rooi-els river in the fore-ground.

berg area. Boucher (1972) summarises the known Quarternary history of Cape Hangklip, which is situated in the immediate vicinity of the Kogelberg State Forest. According to current knowledge the Hangklip site (Fig. 1) was mostly inhabited toward the end of the early paleolithic (Mabbutt, 1955). Evidence suggests that Man has occupied the Hangklip site without a break throughout the period of cultural development (Gatehouse, 1955).

People associated with "Kitchen middens" in the late Paleolithic lived along the whole coast. Cave deposits exhibit abrupt layers rich in shell-lime and shells, and "frequent evidence of fire can be seen" (Goodwin, 1952).

Vasco da Gama tried unsuccessfully to trade horned cattle from the indigenous people on 17 November, 1497. In 1503 he bought one cow and two sheep (Hall, 1934). A period of overland exploration followed after van Riebeeck had settled at the Cape in 1652. The explorers main objectives were to search for cattle, milk and butter for the garrison at Cape Town. Of the eastward routes only one passed in the vicinity of the present day Kogelberg State Forest. The research site in the Kogelberg State Forest lies on the Palmiet river so called after the Dutch name for Prionium serratum (L.f.) Drege that overgrows the riverbed.

Because it was difficult to travel in the rugged mountains, the Kogelberg State Forest and the coastal area from Gordons Bay to Botriver were excluded from rapid settlement and development. W. Paterson toured the coast in 1777 and found a new Erica, E. patersonia Andr.. Buffalo and Eland were abundant, but he declared that the grazing would be poor for cattle (Heap, 1970



in Boucher, 1972).

Many holiday makers from the Caledon district travelled along either the Botriver or Palmietriver to reach the coast. "Miss Cathleen Murray recalls travelling down from Grabouw by wagon following the river, in 1915, in order to camp at Palmiet mouth" (Burman, 1970).

In the 18th century the Louws converted great tracts of land in the Hangklip area to family estate. The name Wynand Louws Bos dates from that time. Later in the 20th century, this estate and others were acquired by Hangklip Beach Estate company (1936 - 1958). A road was constructed by the Hangklip Beach Estate company to link the market garden at Oudenbosch in the present Kogelberg State Forest with the coastal settlements (Departmental files).

Flower picking was a major industry in the Kogelberg, Hangklip and adjacent regions. Helichrysum vestitum (L.) Shrank, an everlasting flower was collected for pillow and mattress fillings as well as funeral tributes and other uses (Porter, 1967). A great variety of other wild flowers were also collected extensively.

At present the Kogelberg State Forest includes the mountainous areas between Kogelberg, almost to Kleinmond where it borders on Highlands State Forest, and to the Elgin Basin. (Fig 2) Steenbras dam forms the other border. Kogelberg Forest Reserve was declared a nature reserve in the Government gazette of 28th October 1962.

Since 1876 the Directorate of Forestry and Environmental Conservation or its predecessors, advocated the complete protection of fynbos ecosystems against fire. Burning was not prohibited until the mountain catchments came under the control of the fire protection committees in terms of the Soil conservation act (No. 45 of 1946) in 1949, but it was strongly discouraged. The impracticability of the policy was accentuated when practically the whole of the Kogelberg reserve (10 200 hectare) burnt in January - February 1945. Relatively small areas burned again in February - March 1950 and in February 1952 (Rycroft, 1969). It was only in 1970 that prescribed burning was formally adopted as a catchment management tool (see Garnett, 1973).

From the above it can be seen that the land surrounding the Palmiet river has not been free from disturbance in the distant or even immediate past. Animals, primitive man, fire and modern man have influenced the ecosystem for much longer than the 300 years of European occupation of the south-western Cape.

3.3 REVIEW OF PREVIOUS RESEARCH

Since Jan van Riebeeck occupied the Cape of Good Hope in 1652 a number of botanists and amateur botanists have contributed to our knowledge of the Cape Flora. Collecting and describing new species were the main objectives of these early botanists. William Burchell and others wrote down their many observations made during overland journeys and

some of these contain valuable ecological information. In 1908 Marloth (in Grobler, 1964) described the vegetation of the Hottentots Holland Mountains and mentions a few families that are distinctive and characteristic of the vegetation. Notable amongst avid plant collectors was T.P. Stokoe after whom a number of species in the Kogelberg have been named. Some of the rare species carrying Stokoe's name are found only in the Kogelberg and adjacent mountains. The work of early plant collectors paved the way towards the descriptive and experimental research in later years.

Today a little more information is available on the Kogelberg State Forest and surrounding areas of the Hottentots Holland mountain range than a few years ago. Since the last great fire of 1945, a number of research projects have been completed in the area.

The first official report on the floristic and conservation status of the Kogelberg State Forest was prepared by Rycroft in 1953. From his preliminary surveys Rycroft assembled a provisional species list which included the conservation status of a few rare and endangered species. He stressed the need for a study of the Kogelberg flora to ensure effective protection of the unique fynbos vegetation.

A phytosociological description of part of the Oudebos farm was completed in 1964, three years after it became the property of the Department of Forestry (Grobler, 1964). Grobler surveyed seventy three hectare of a mountain side on the farm Oudebos. One objective of his study was to prepare a basis for a survey

of the whole Kogelberg State Forest. In an unpublished paper he listed the vertebrates (mammals) observed in the Kogelberg by Mr. J. le Roux and R. Mayer (Grobler, 1969). The phytosociological survey of almost the whole Kogelberg was completed in 1972 by Boucher as advocated by Grobler (1964). Since then the Directorate of Forestry and Environmental conservation established a number of monitoring plots in the rare plant communities of Kogelberg State Forest. It also initiated the current experimental research project on the effect of fire on fynbos in the Kogelberg.

Research of an agricultural kind was performed by Dr. M. Vogts at Oudebos farm under the auspices of the Department of Agricultural technical services. This was before Oudebos became part of the Kogelberg State Forest. Her research concentrated on the cultivation of various Protea species of importance to the flower growing industry. Particular attention was paid to variations occurring in P. cynaroides L. A foreman managed the Kogelberg reserve from Oudebos when it became part of the State Forest. Management control is effected from the adjacent Highland Forest Station.

4. PHYSICAL DESCRIPTION OF STUDY SITE

4.1 LOCATION

The Quarter Degree Grid Reference for the research area is 34 18 BD (Simons Town) or more precisely $34^{\circ}16'$ S latitude and $19^{\circ}00''$ E longitude. Jonkershoek Forest Research Station, which served as the base of research

Outline of Africa to indicate the location of the research area.

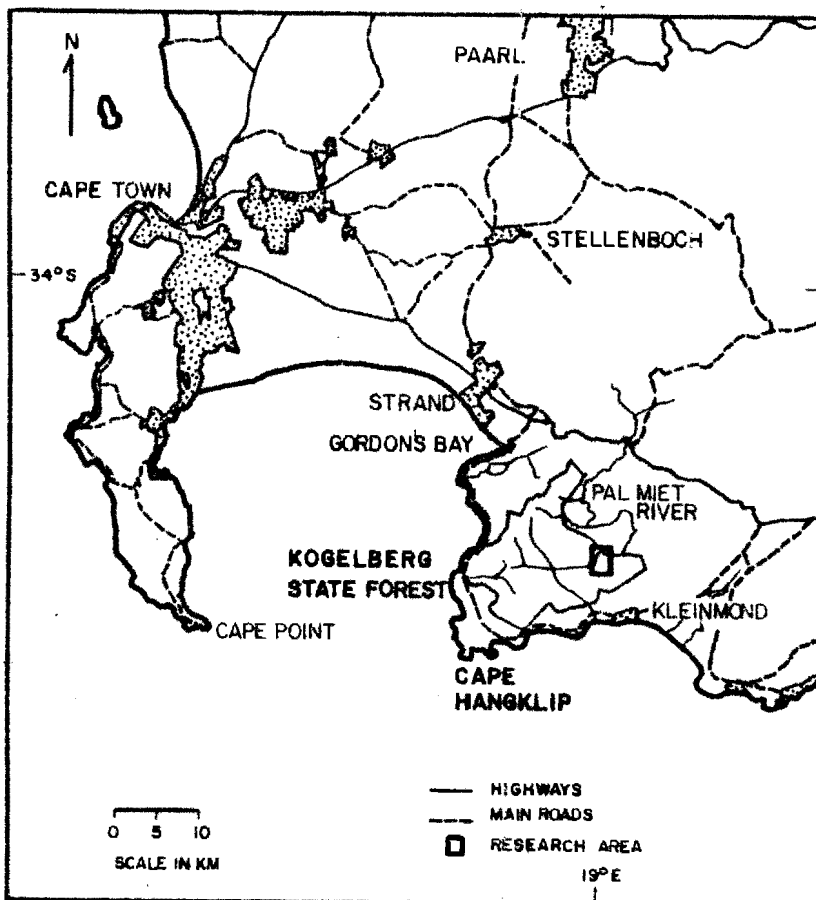
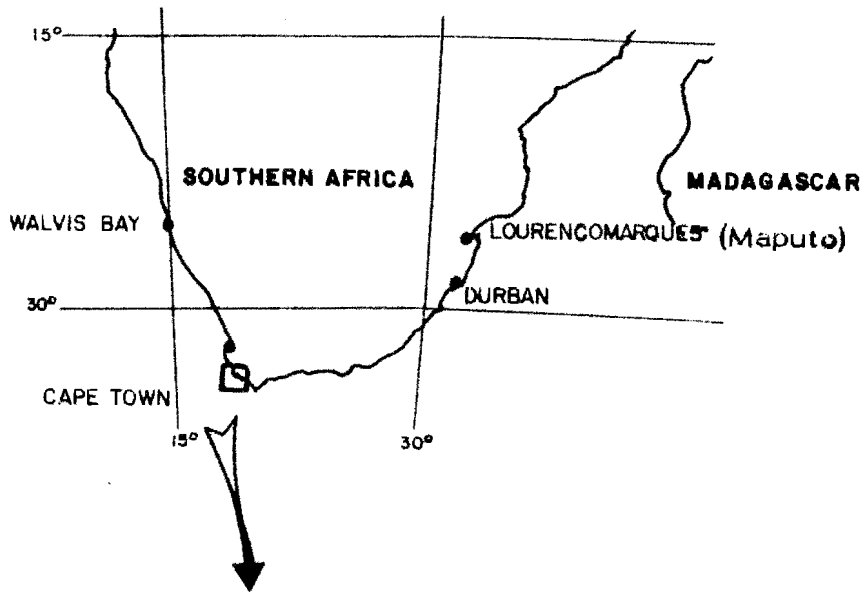


Fig. 3. Location of the Kogelberg State Forest and research site

operations, is situated about 60 km by road to the north-west of Kogelberg reserve.

Kogelberg State Forest has a total area of 16 537 hectare of which most is rugged mountainous terrain. The research area lies in Bot river lot B which has always been state owned (Fig. 2). It is about 7,25 km north of the Palmiet River mouth as the crow flies, and abutts on to the river itself. Although situated so close to the sea the research area is screened from it by the Hottentots Holland range and the Paardeberg mountains. The effect of this climatic divide is ameliorated by the Palmiet River valley being open to the sea. Fig. 3 shows the location of the research site relative to major landmarks and the continent of Africa.

4.2 TOPOGRAPHY

The South-western Cape coastal belt is characterised by mountain ranges of high relief lying parallel to the coastline behind one another separated by long valleys (King, 1967) (Fig. 4). These orogenic mountains can be separated into two folded zones: a western folded zone with a general north-south trend arching towards the east in the south, and an eastern folded zone with a general east-west axis (Boucher, 1972). The Hottentots Holland range is the southern most range of the western folded belt which ends abruptly at Hangklip Mountain (Wellington, 1955). Kogelberg Peak (1 268 m) is the highest in the Reserve, towering above the high ranges with deeply incised gorges and narrow valleys.



Fig. 4. The coastline of Falsebay giving an idea of the topography of the region.

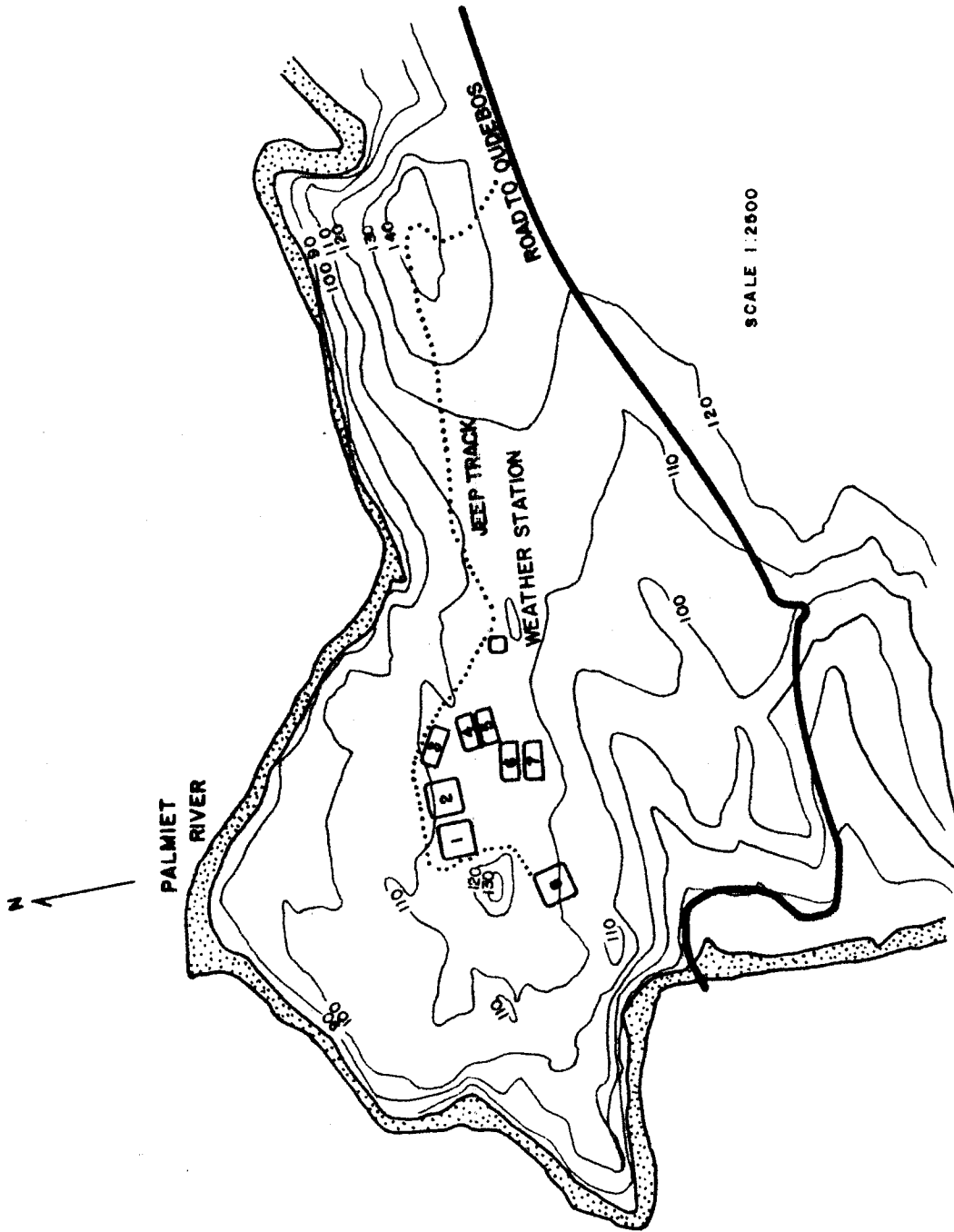


Fig. 5. A topographical map of the research site and the lay-out of the eight experimental plots.

Slowly weathering Table Mountain Sandstone, gives an impression of formidable ruggedness to the mountains.

The Palmiet River valley is relatively broad in the research area, but becomes narrower with steeper sides closer to the mouth. In the area where the experimental plots are laid out, the valley floor undulates gently with a few scattered rocky outcrops. The mean slope of the experimental plots is $0,9^{\circ}$ or (2%) and they have a mean elevation of 113 m. Mean slope was calculated using Hortons formula (mean slope = ae/A where a = area between pairs of contour lines, e = mean elevation of a and A = total area) Kruger (1974). A rocky outcrop with an elevation of about 136 m dominates the area in which the experimental plots occur. There are two definite drainage lines discernable in the "horseshoe bend" of the river and two prominent winter seepage areas, but these do not affect the plots. Fig. 5 is a topographical map of the research site and indicates the positions of the experimental plots, and the weatherstation.

4.3 GEOLOGY:

The south-western Cape mountains are true mountains consisting of the much folded strata of the Cape System which have been subsequently faulted in complex manner (du Toit, 1954 in Goldblatt, 1978). The term Cape System refers to a considerable thickness of sandstones shales and quartzites of Paleozoic age (du Toit, 1926).

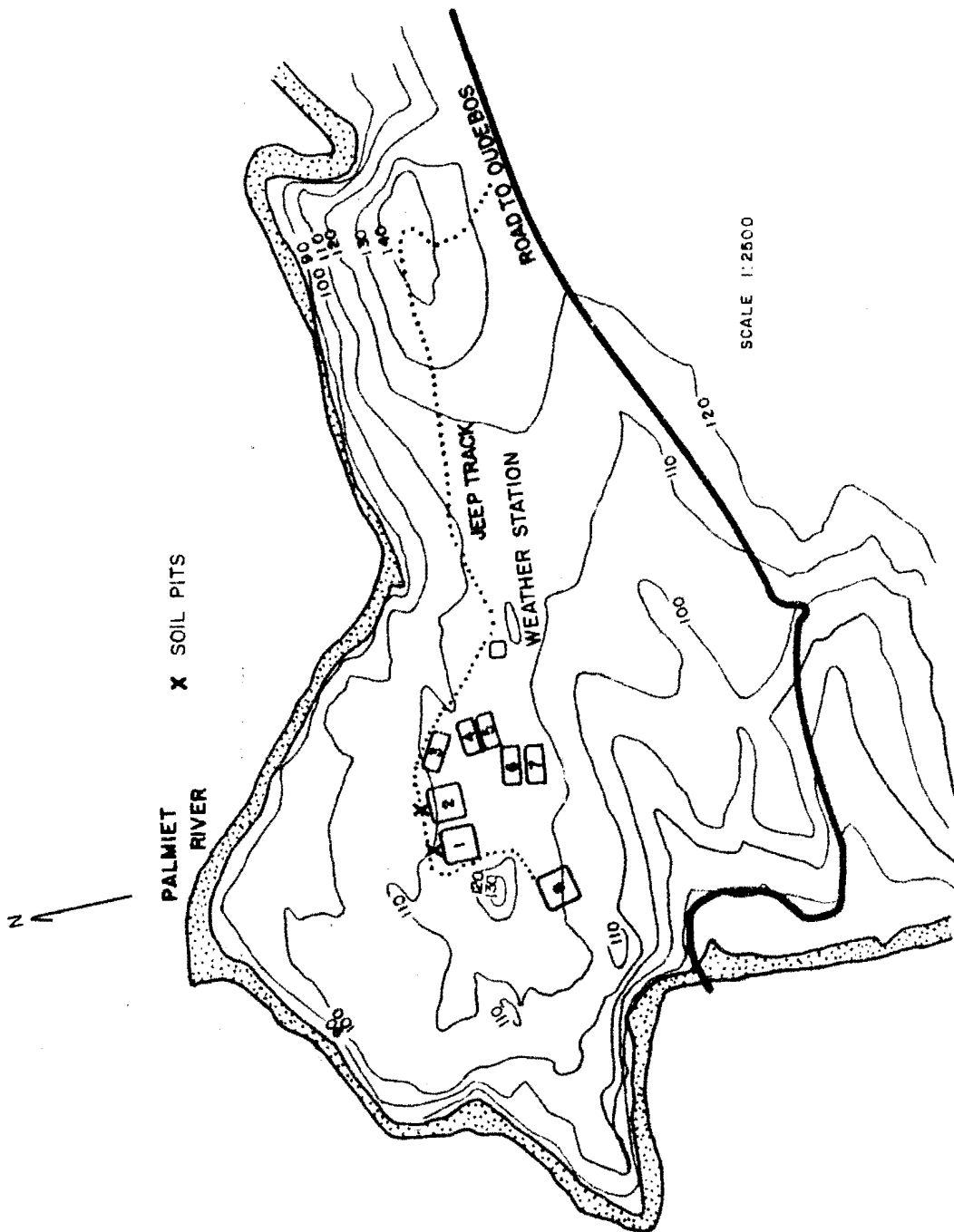
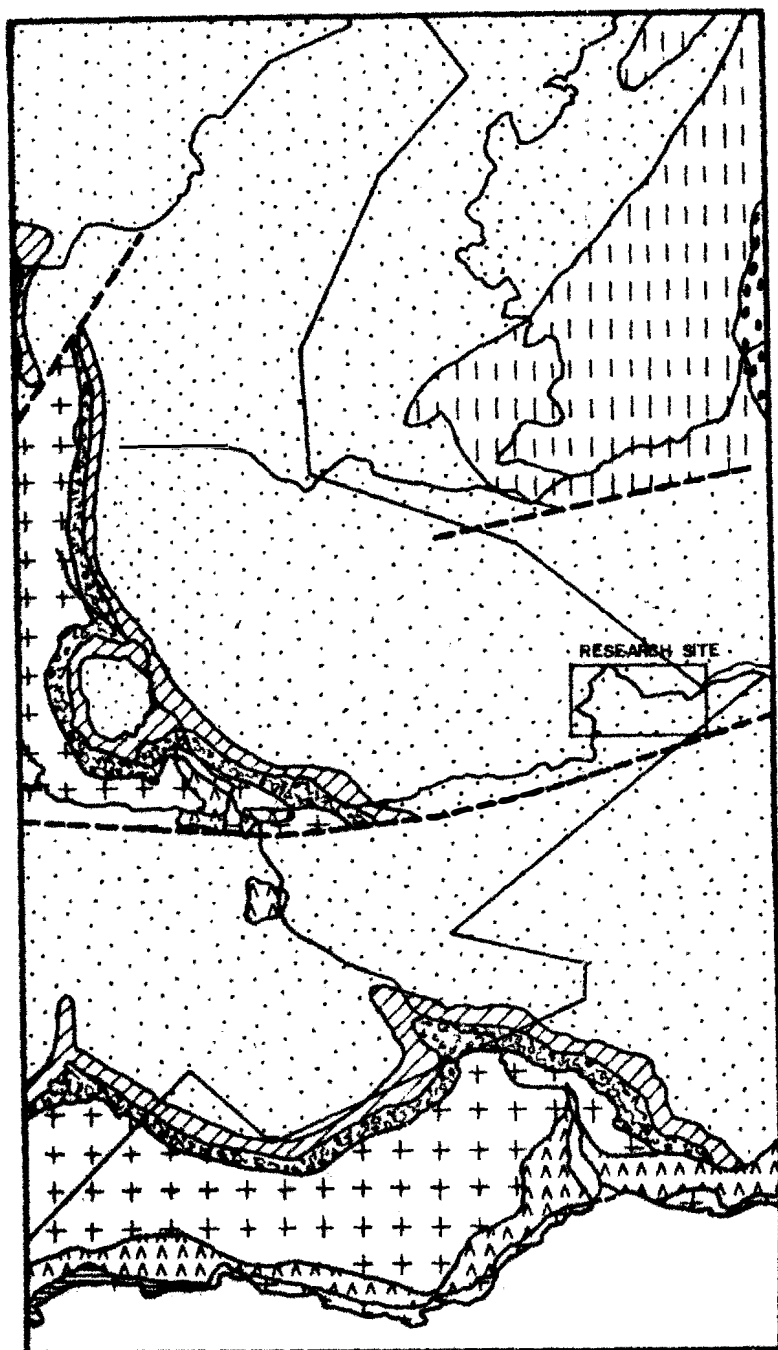
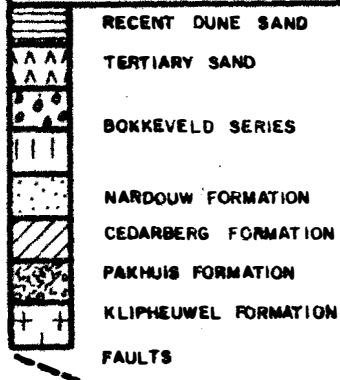


Fig. 7 Topographical map of the research site indicating the location of the soil pits.



Scale 1: 120000



Based on map by J. de Villiers,
1955 (unpublished).

Fig. 6. Part of the geological map of the Kogelberg State Forest to indicate the geology of the research site

It consists of the following series:

3. The Witteberg Series - Carboniferous
2. The Bokkeveld Series - Devonian
1. The Table Mountain Series - thick unfossiliferous grits and sandstones with scattered pebbles (du Toit, 1926)

The research site is situated on the Nardouw formation which forms part of the Table Mountain Series. A fault passes close by the research site but does not influence any of the experimental plots. A map of the present day geology of the research site is depicted in Fig. 6. Orogenic movements of the crust diverted the course of the Palmiet- and related rivers. Certain rivers or stretches of some rivers had nearly reached base level when the movements took place. Present day rivers are actively incising their valleys (Cole, 1949) and some are still very young as can be seen by the very steep sides of eroding valleys. The mean annual flow of the Palmiet river is estimated at approximately 160 million m³ (Dept. of Water affairs, notes of the meeting on 29th May, 1979).

4.4 SOILS

The soils of the site have been classified according to the new South African Binomial System for soil classification (Macvicar et. al., 1977). Two soil pits were dug below experimental plots one and two (Fig. 6). 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 NH_4Ac (Ammonium acetate) and determined by means of 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, and
7. Exchangeable aluminium index according to the method of 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.

The soils derived from Table Mountain Sandstone (T.M.S.) are infertile, acid and coarse grained. The presence of characteristic species of the Cape flora is closely associated with a Table Mountain Sandstone (T.M.S.) substrate (Goldblatt, 1978).

At the research site the soils are quite variable but all are derivatives of T.M.S. and show a marked degree of podzolisation i.e. sometimes these T.M.S. soils become grey to bluish-green with depth due to the deposition of ferrous compounds (van der Merwe, 1941). Owing to the mountainous nature of the Kogelberg State forest the soils are young and poorly developed. Deep soils are only found in local depressions and areas with less intense relief (Cole, 1949). A fair amount of organic matter may be present in the surface layers (van der Merwe, 1941). Charcoal particles, remnants of previous fires, occur in the surface layers of the soil.

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

"These soils are extremely poor in all the elements of plant-food" (van der Merwe, 1941) is a statement well supported by Table I. 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 ration (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 0,5% and 1,4% respectively. According to Buckman & Brady (1969) the Carbon-Nitrogen ration for humid temperate region soils usually stabilizes in the neighbourhood of 10:1 or 12:1. The Mispah soil form falls into that category.

Table I. 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 I (continued)

* 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 (Mosssdale 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
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

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.

4.5 PLANT SOIL RELATIONS

Information on the interactions between fynbos species and the nutrient poor soils are slowly becoming available (Dahlgren, 1968; Rourke, 1972; Williams, 1972; Goldblatt, 1976). In this study comments on interactions are based on the literature and on personal observations.

A great concentration of plant roots are found in the upper

20 cm of the soil. The proteoid and other shrubs exhibit well developed "feeding roots" (a term used by Scheepers, 1966) in the upper layers of the soil. Proteaceae and Restionaceae are unique in having specialized roots, which are dense clusters of short lateral rootlets found in the upper root strata. According to Malajczuk & Bowen (1974) the proteoid roots of the proteaceae are micorbiially induced and enhance the uptake of phosphorus. The proteoid root component greatly increases in pockets of humus rich soil (Lamont, 1973). Because all the growth-forms of the vegetation have a maximum root density in the upper horizon of the soil profile, it is inevitable that fierce competition for water and available nutrients prevail. In the tall shrub species (Mainly Proteaceae) "sinkers" (a term used by Scheepers, 1966) or anchoring roots are evident. Such roots are responsible for anchoring the taller growing plants and probably providing water and perhaps even some nutrients from a deep reservoir to the relatively large transpiring area in the dry season.

Richards (1952) noted that the majority of tropical rain forest tree roots are in the upper layers of the soil. Forest trees in the Knysna region of South Africa are remarkably shallow rooted for their size (Phillips, 1933). This agrees with the concept that species in low nutrient conditions are adapted to utilize the turnover of the litter nutrient pool and use surface condensation as supplementary water supply. Specht and Moll (1980) associate heath with nutrient poor and leached sandy soils in Australia. The same can be said for fynbos. True fynbos and heaths are always associated with nutrient poor, podzolised soils (Birke-land, 1974). Fynbos vegetation depends largely on the recycling of available nutrients. However, due to the hot dry

summers and cool wet winters organic decomposition is slow. Because of the slow recycling the fynbos reaches its climax fairly soon. According to Kruger (1977) and Taylor (1979) in approximately 30 years, and becomes moribund soon after.

"Humic acids" are leached and colour the river waters with a characteristic brown tint. Fires mineralize the litter almost instantly, and much of the ash is lost through leaching by rain (van Wyk, 1975). Erosion of the soil mantle is critical since the parent rock weathers slowly and yields nutrient poor soils.

To summarise, it is appropriate to note that the distribution of fynbos is correlated with the presence of a T.M.S. substrate and to a lesser degree a Mediterranean-type climate. Limited nutrient resources are partitioned by species that grow and reproduce at different times of the year. The species are adapted to survive adverse climatic and edaphic conditions. Limiting factors to a broad spectrum of species seem to favour the presence of a specially evolved species. The influence of fire on succession and development of postfire vegetation has been studied by a number of authors but very little is said about the effect of fire on the soil. Fire influences the soil conditions since erosion is accelerated after a fire where litter is effectively removed. Fire also changes the micro fauna and micro flora not affected by the fire per se, by increasing surface pH and nutrient content (from ash).

There are a host of unknown factors that influence the effect of a burning treatment, especially when applied to sensitive veld types, species and soils.

4.6 CLIMATE - INSTRUMENTS AND DATA PROCESSING

Meteorological data were gathered according to the specifications of the South African weather bureau. The following instruments were used to monitor the climatic variables at the research site:

Instruments	Variable measured
1 Casella recording raingauge (128,5 mm orifice, mounted 1,2 m above ground).	Continuous weekly records of depth, intensity and duration of rain.
1 Snowdon raingauge, with a Nipher shield. (127 mm orifice, elevated 1,2 m above the ground).	Weekly rainfall totals.
In a Stevenson screen:	
3 Mercury (in glass) thermometers	Daily maximum air temperature, wet and dry bulb temperatures.
1 Alcohol (in glass) thermometer	Daily minimum air temperature.
1 Thermohygrograph (Bimetallic thermometer and hair hygrometer).	Continuous weekly records of temperature and relative humidity.
Other:	
1 Thermograph (mercury in steel).	Continuous weekly temperature of soil temperatures at 5 and 20 cm depths.
1 Lambrechts type anemometer	Continuous monthly records of wind direction and windrun.

Data from the weather station were processed according to standard methods. Precipitation weekly totals for the Casella raingauge were checked with the amount measured in the Snowdon gauge. Depth, intensity and duration of rain "storms" were extracted from the chart records and summarised. Maximum and minimum daily temperature

and humidity data were similarly extracted from the thermohygrograph charts. Mean daily and monthly temperatures and humidities were calculated and summarised. The same procedure was followed with the soil thermograph charts.

The windrun records consist of waxed charts where both wind direction and windrun are recorded. Data for analysis were extracted from the charts by converting the analogue records to digital wind data on Hollerith punch-cards by means of a D-Mac encoder.

Co-ordinates for the wind records were the points where the trace line crossed the 0800h lines, and at the end of each 10 km run (Kruger, 1974). A univac series 1100 digital computer was employed to process the data. Summaries of the wind data were obtained with the "wind 2 programme 109" of Jonkershoek Forest research station. A routine for rotation of the chart axes (Meyburgh et. al., 1970) was incorporated in this programme, as well as routines for correction of measured wind-run according to calibration, determination of total wind-run, wind speeds and wind frequencies for different periods from eight compass bearings (Kruger, 1974).

Formulae for computing parameters of recognized descriptive wind characteristics were obtained from WB. 26 (1960) and Conrad and Pollock (1962, in Kruger, 1974). By means of Lambert's formulae the resultant wind vectors were calculated for eight compass directions. The average wind-directions (clockwise from north) is obtained from the angle between west (270°) and the direction of dominant wind-run as explained below.

$$/35 \tan D^C$$

$\tan D^C = CN/CW$ where $CN = N - S + (NW + NE - SW - SE) \cos 45^\circ$ is the total run from north to south and:

$CW = W - E + (NW + SW - NE - SE) \cos 45^\circ$ is the total wind-run from west to east. Symbols as for example N and S, represent total wind-run from the north and south etcetera. The resultant direction in degrees is deduced from D^C as follows (W.B. 26, 1960)

CN	CW	D
+	=	$90^\circ - D^C$
=	+	$90^\circ + D^C$
+	+	$270^\circ - D^C$
		$270^\circ + D^C$

Average wind speed for the total number of hours was calculated from:

$$R = \frac{CN^2 + CW^2}{n}$$

where n is the total number of hours and the expression above the line denotes the resultant total wind-run.

Wind steadiness is expressed as a percentage of the proportion between resultant run and total run for a given period.

Editing errors of a systematic kind are inherent in analyses where only eight wind directions are recognised. The frequency of calms was probably over estimated by 50 - 100 % due to editing errors (Kruger, 1974). A measure of bias was observed in the calculations tending towards higher mean wind-speeds. This discrepancy is due to the difference between the raw data and the data that were coded and digitized by editors. In the raw data, intervals between events i.e. 10 km wind-runs, are recorded by the instrument while the calculations are based on hourly intervals.

In the microclimate study temperature profiles were monitored in summer, autumn and spring. In each season temperatures were measured on two successive days at hourly intervals from approximately 10h00 in the morning until about 17h00 in the afternoon. In spring and summer the days are longer and temperatures could be read for longer periods than in autumn. The apparatus was a simple electronic temperature gauge with connections for six thermister probes that could be monitored one at a time. Each thermister button was taped to a main stem at 5cm, 25cm, 50cm, 1m and 2m heights. The thermistor buttons were taped on to the south side of a main stem and double checked to ensure that the sun did not shine on them. One probe monitored surface soil temperature and it was buried under a thin layer of soil in the shade under the same shrub where the other probes were located. A set of values were measured by taking readings, after a stabilizing period of one minute for each probe, in succession and repeating the process three times. Processing of the data consisted of calculating the mean temperature for each probe and each time.

4.6.1 REGIONAL

The climate of any place on earth is controlled by a multitude of complex factors, a few of which are:

1. It's latitude, which determines the amount of solar radiation received at the top of the atmosphere in a specified interval of time (year, season, day, etc.);
2. The position relative to the distribution of land and sea;
3. Height above sea level;
4. Ocean currents and general circulation of the atmosphere;

5. Vegetation cover or the general nature of the underlying surface (soil type, water, etc.) and the orientation relative to hills or mountains (Schultz, 1965).

Cape Hanglip area which includes the Kogelberg State forest, lies within latitudes which are markedly affected by atmospheric circulation patterns.

A sub-tropical high pressure belt centred on the 28° S latitude straddles the region in summer, but moves three to four degrees to the north in winter. At the same time the region is influenced by the mid-latitude westerlies (Goldblatt, 1978; Kruger, 1974). The considerable sea-temperature anomaly brought about by the warm Mocambique and Agulhas currents on the east and south coast, and the cold Benguela current on the west coast, has a vast influence on the climate. Kogelberg State forest receives 71% of its rainfall from about April to September. During the hot dry summer from December to February rainfall amounts to 10% of total precipitation. Rain occurs mainly during the passage of cyclonic frontal depressions moving over the land from the north-west. Rainfall is profoundly influenced by the very pronounced orographical features resulting in high precipitation on mountains (3 000 mm in some kloofs) while areas in the rainshadow receive much less (less than 250 mm in the Breede river valley). Thunderstorms occur occasionally. Snow occurs on the mountain tops in winter and early spring but never persists throughout the winter. On the coastal flats frost is rare, but in the higher mountain valleys frost is quite common in winter. The average daily maximum temperature is about 28°C in midsummer and 17°C in midwinter. The average

daily minimum temperature is about 15°C in January and 6°C in July. The difference in air and sea-surface temperatures is in the region of $0,5$ to 1°C in summer and roughly 2°C in winter (Schultz, 1965).

"Prolonged spring and autumn seasons and the fact that the so-called summer and winter phenomena are not entirely confined to these seasons, gives rise to a very equable climate" (Boucher, 1972). In summer south and south-easterly winds prevail for about 60% of the time, and are a prerequisite for the orographic "tablecloth" cloud over Table Mountain. These winds are usually associated with fair-weather, though the south-easters may sometimes be notoriously strong and gusty. Occasionally a "black south-easter" may bring some rain to the south-western and southern coast (Jackson and Tyson, 1971). In winter, north-westerly winds are frequent and are almost always accompanied by rain. Winds are frequently strong and may reach gale force strength, uprooting trees and shrubs (Schultz, 1965).

Solar radiation is at a maximum in summer, particularly when clear skies prevail. In winter solar radiation is at a minimum and is reduced even more by cloudy and rainy weather, characteristic of the mediterranean climate. ... "Sunshine duration varies from about 60% of the possible duration in July to over 70% in January" (Schultze, 1965). Average total solar radiation is about $450 - 500 \text{ cal cm}^{-2} \text{ day}^{-1}$. The December rate of radiation at the top of the atmosphere is approximately $700 - 750 \text{ cal cm}^{-2} \text{ day}^{-1}$ while in June it is round about $200 - 250 \text{ cal cm}^{-2} \text{ day}^{-1}$ (Kruger, 1974)

Relative humidity has a seasonal variation of about 40 – 60% in January, to 60 – 80% in July, with an annual mean of approximately 60 – 70%. Seasonal vapour pressure values are in the region of 14 – 18 mb in January and 10 – 12 in July, while the annual mean vapour pressure is around 14 – 16 mb. All these measurements were taken at 14h00. Measurements of the average annual evaporation from a Symons tank is approximately 1250 – 1500 mm and that measured in a class A pan varies from 1750 – 2250 mm (Kruger, 1974).

4.6.2 LOCAL

The local climate corresponds exactly with the regional conditions. In addition a few remarks on specific observations at the research site are mentioned below.

Kogelberg peak, the highest on the State Forest, did not have a snow covering that lasted more than two days during the research period. Summer temperatures at the research site oscillate around 20°C but rose to over 35°C in bergwind conditions. The relative humidity was generally high, falling below 50% only when bergwind conditions prevailed. Dew occurred frequently, especially in summer, and persisted until approximately 10h00. Frost was not observed at the research site at all. Wind is a phenomenon that is always expected in the afternoon and gale-force winds were not uncommon. In the following sections the different climatic factors are described in more detail.



Fig. 8. The meteorological station adjacent to the experimental plots.

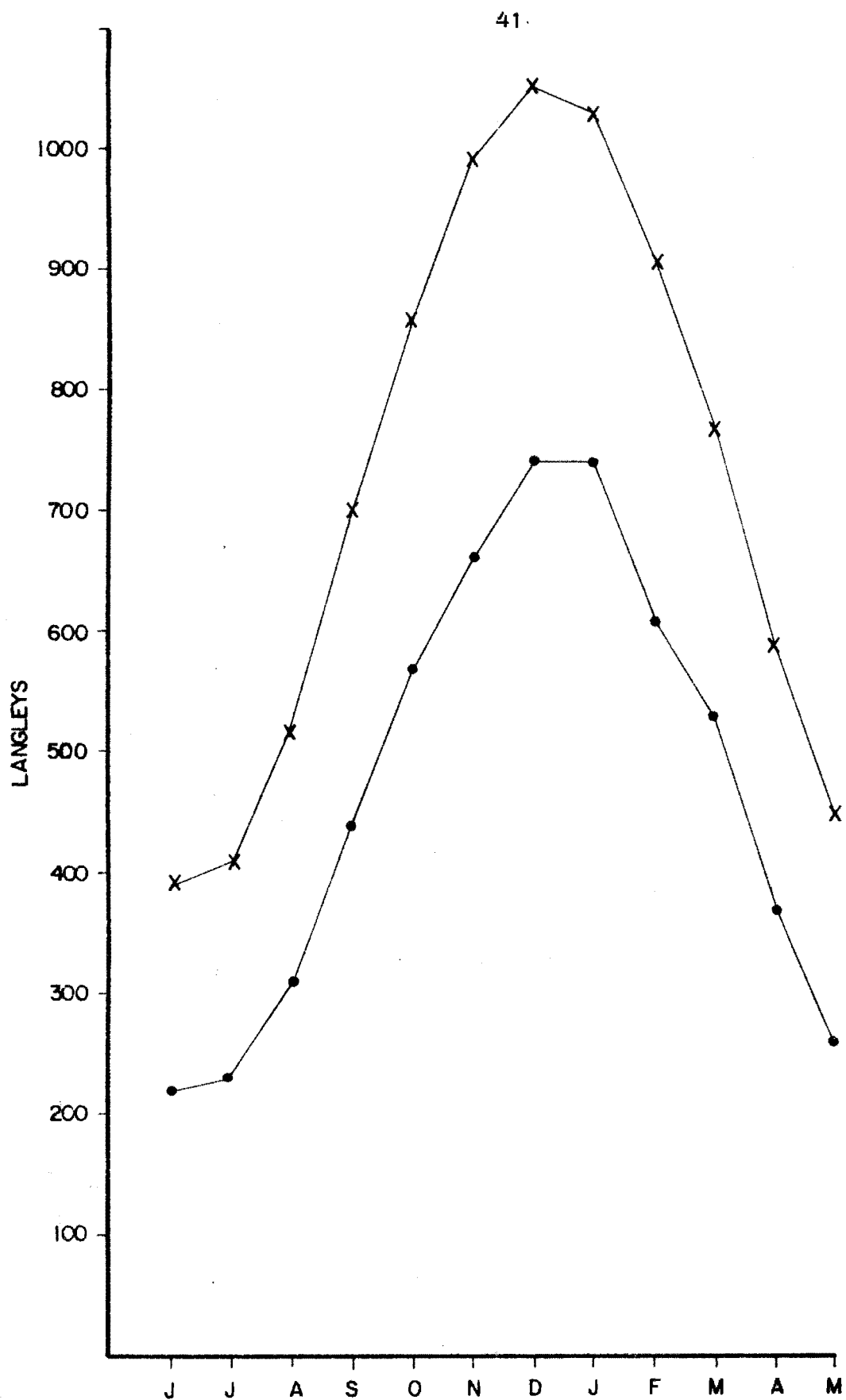


Fig. 9. Graphical presentation of the radiation environment at the research site. x = radiation at the top of the atmosphere. • = projected actual radiation.

4.6.2.1 SOLAR RADIATION

A weather station (Fig. 8) was erected at the research site but unfortunately solar radiation could not be monitored during the research period. Fig. 9 is a graphical presentation of the calculated solar energy in Langley's outside the atmosphere at Kogelberg research site (Program written by Furnival, Wyler, Reifsneider and Siccima (1969) and supplied by N.J.C. Meyburgh). In addition the percentages of total solar radiation over solar radiation at the top of the atmosphere for Cape Town were applied to the Kogelberg data. This gives a very rough idea of the actual distribution of solar radiation received at the research site. In summer total solar radiation is approximately 70% of the amount received at the top of the atmosphere but drops to approximately 58% in winter as can be expected for the rainy season.

4.6.2.2 PRECIPITATION

Precipitation in the South-western Cape is mostly in the form of rainfall. Other types of precipitation include hail, snow, dew and hoarfrost. The deposition of water from clouds or fog was not measured, though it is of common occurrence, and plays a major role in the vegetation water balance during the dry summer months. Snow on the high mountain peaks in winter usually does not persist longer than 48 hours (Kruger, 1974). Whenever there is snow on the mountain peaks, hoarfrost may occur along the drainage lines from the cold air descending off the mountains.

Table III Depth and duration of a one-year record of rainfall at the research site.

DURATION IN HOURS

DEPTH

mm	0-1	1-3	3-6	6-12	12-18	18-24	24-30	30-36	36-42	42-48	48-54	54-60	60-66	66-72	
0- 5	13	12	9	6	3										43
5- 10			2	2	4	1									9
10- 15				3			1								4
15- 20			1	3	2	1									7
20- 25				1	2	1	1			1					6
25- 30				1			1					1			3
30- 35								1							1
35- 40							1								1
40- 45						1					1				2
45- 50						1			1						2
50- 55					1	1									2
55- 60						1									1
60- 65															
65- 70								1							1
70- 75											1				1
75- 80															
80- 85					1										1
85- 90															
90- 95											1				1
95-100															
100-105															
105-110															
110-115															
115-120															
120-125															
125-130															
130-135											1				1
135-140															
140-145															
145-150															
	13	12	12	16	13	7	4	2	1	1	4	1			86

Table IV. Duration of different rainfall intensities over a one-year period at the research site (return period of 15 minutes)

DURATION (HOURS)

MAX I_{15}

mm/hr	0-6	6-12	12-18	18-24	24-30	30-36	36-42	42-48	48-54	54-60	
0-3, 9	36	10	5	2				1			54
4, 0-7, 9	2	2	3	2	2	1				1	13
8, 0-11, 9		2	4		2				2		10
12, 0-15, 9		1	1						1		3
16, 0-19, 9				2		2			1		5
20, 0-23, 9				1							1
24, 0-27, 9											
	38	15	13	7	4	3		1	4	1	86

Table V. Different amounts of rain for different storm intensities calculated for 15 minute intervals.

		DEPTH. mm																			
MAX I ₁₅		0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	130-
mm/hr																					
0- 3,9	43	7	1	2	1																54
4- 7,9	2	1	4	2	3	1				2											15
8-11,9				4	2	1		1	1									1		1	11
12-15,9						1						1								1	3
16-19,9								1		1			1		1	1					5
20-23,9												1									1
24-27,9																					
	45	8	5	8	6	3	1	1	2	2	2	1		1	1		1		1	1	89

The weather station at the Kogelberg State Forest came into operation in March 1976. Data for the rainfall record of one year (June - May 1977) is summarised in tables III, IV and V. Since the record is very short the statistics serve as a broad description of the rainfall regime at the research site. Total rainfall for one year measured with a Cassella type recording rainmeter was 1392,3 mm. A control non-recording rainmeter fitted with a Nipher shield was maintained in conjunction with the recording rainmeter, and registered 1328,3 mm. The discrepancy between the figures may partly be due to the Nipher shield and partly to error in reading the recorder charts.

The rainfall recorded at the research site is considerably higher than the average rainfall figures for stations in the immediate vicinity, as quoted by the weather bureau (W.B. 29). Highlands forestry station (366 mm altitude) lies on a mountain mass east of the research site and has an average rainfall of 955,9 mm. Streenbrass dam is situated north-west of the research site and lies on the climatic divide created by the Hottentots Holland mountain range. The highest recorded average rainfall in the region of the dam (1 309,8 mm), was measured at an altitude of 533 m. Approximately 10% of the annual rain falls in summer while 31% and 33% respectively fall in autumn and winter. The bulk of the rainfall occurred from May to September, which according to Schultz (1965) is the general pattern for the region. Rainfall is therefore largely restricted to winter and is consequently comparable with the rainfall regime of other mediterranean type climates.

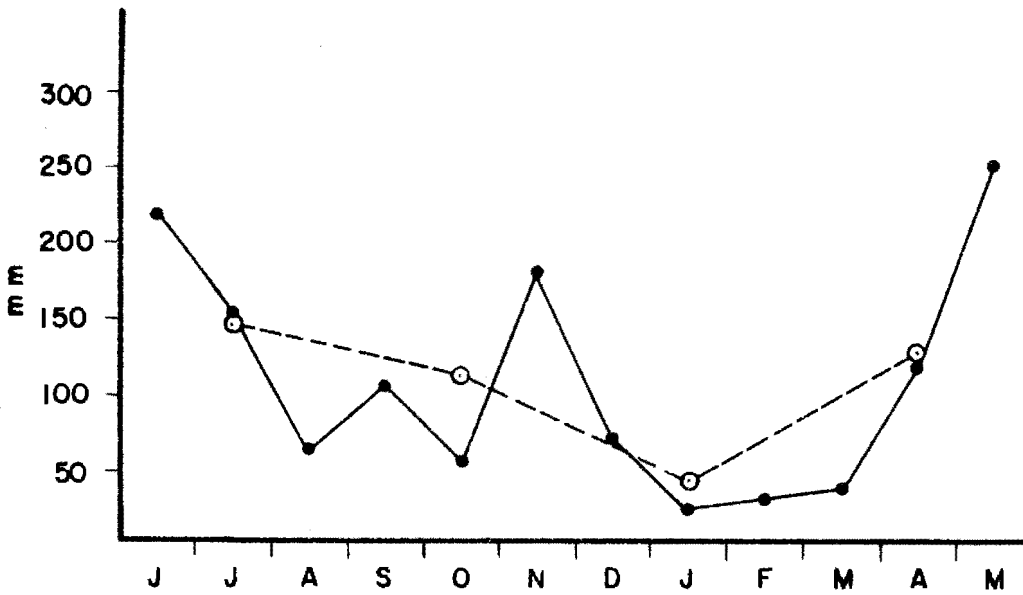


Fig. 10. Distribution of rainfall throughout the year at the research site. ● = monthly, and ○ = three monthly averages

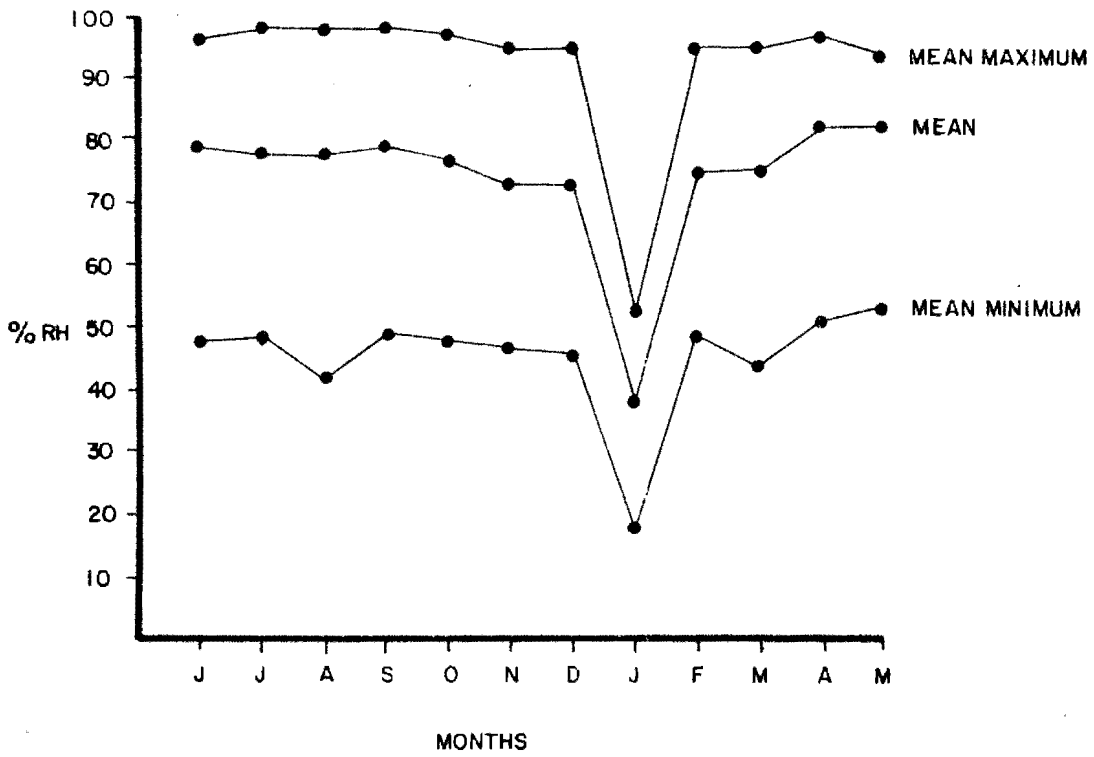


Fig. 11. Mean monthly relative humidities at the research site.

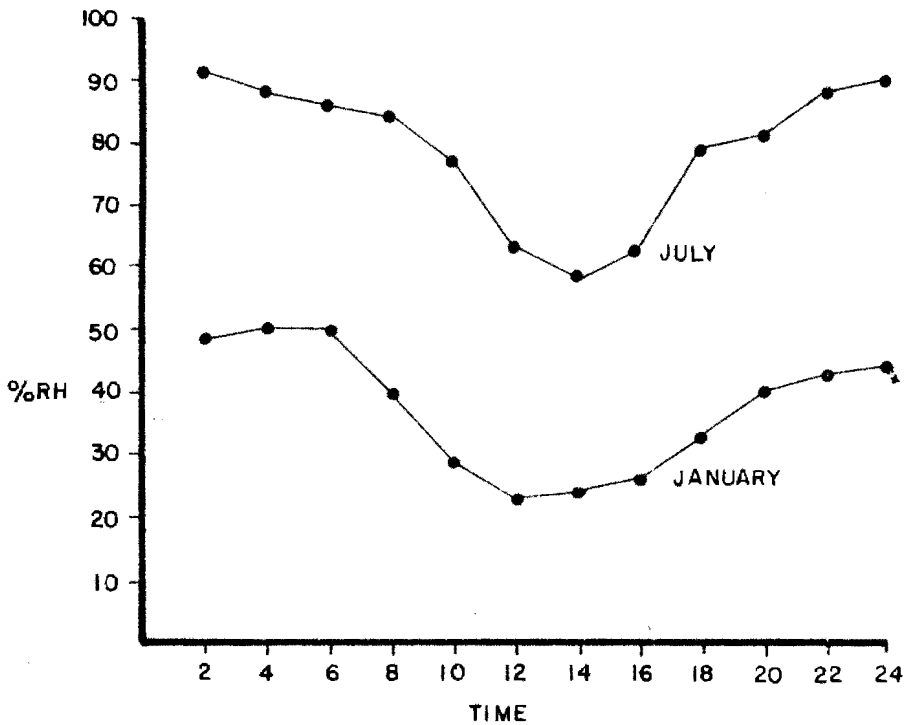


Fig. 12. Mean daily relative humidities for January (summer) and July (winter) at the research site.

Maximum intensity for each rain event in the one year record was determined with a digitizer coupled to a Hewlett-Pachard desk calculator. Duration and total amount of rain intercepted for every rain were recorded. Rainfall intensities at Kogelberg State Forest seem to be low in a frequency analysis of the rainfall. As the records are so short any inferences are avoided except on a broad scale.

In summer anti-cyclonic conditions are responsible for orographic clouds that cover the mountain tops. Orographic rain and deposition of water from the clouds on vegetation and rock occur under these conditions. Kruger (1974) reports that 70 - 75% of the time such conditions occurred in summer at Jakkals river ($\pm$ 20 km due North of Kogelberg State Forest) and it can be expected to be the same in the Palmiet River valley. Much relief of summer drought stress is effected by the deposition of orographic cloud moisture.

Fig. 10 is a graph illustrating the march of annual precipitation in the Kogelberg State Forest.

Relative humidity is included under rainfall since it is a measure of the general moisture content of the atmosphere. Fig. 11 is a graph of the mean maximum, mean and mean minimum relative humidities (RH) at the research site. It is obvious that except when bergwinds blow, as indicated by the sharp drop in January, the general RH is relatively high. This is to be expected so close to the sea. The comparison between the mean diurnal RH for July and January stress the differences between the wet winter and arid summer climate of the research site (Fig. 12). Since bergwinds can occur in seasons other than summer, severe short-term stress conditions manifest

Table VI Summary of the temperature régimes at different sites in the South-western Cape

	J	J	A	S	O	N	D	J	F	M	A	M
Kogelberg 110 m	13,34	11,99	12,12	14,46	16,68	15,99	19,43	20,29	22,17	20,61	18,55	14,05
Steenbras 338 m	11,8	10,6	11,1	12,0	13,9	16,1	17,8	19,2	19,3	17,9	15,8	13,2
Elgin 259 m	10,2	9,6	10,2	11,7	13,9	16,4	17,8	19,2	19,3	17,6	15,1	11,9
Welgevallen	13,6	12,1	12,5	13,7	15,6	17,5	19,8	20,9	21,0	20,1	17,3	14,5

themselves periodically throughout the year. The degree of severity is dependant on temperature and the duration of bergwind conditions.

4.6.2.3 AMBIENT TEMPERATURE

A Cassella type Thermohygrograph was employed to obtain a continuous temperature record for the Palmiet River valley in the Kogelberg State Forest. The temperature charts were analysed manually because a suitable programme for digitizing the analogue graphs was unavailable at the time. Daily maximum and minimum temperatures were extracted and verified with weekly records from conventional thermometers in the same Stevenson screen.

Data for the twelve month period from June 1976 to May 1977 are summarised in Table VI. The weather station was installed six months prior to the commencement of the experimental burns. Subsequent interruptions in the data record restricted the processing to a period covering the experimental burns. The record for May 1977 is incomplete but it is never-the-less included to present data for a full year. Effective temperature (ET) and the number of days (Td) in a year in which temperatures are warmer than ET is included to approximate the active growth period in the Kogelberg State Forest. ET and Td are derived from Bailey's Formulae (Stuckenberg, 1969).

$$ET = (8T + 14AR) / (AR + 8)$$

where T = mean annual temperature

and AR = mean annual range of temperature

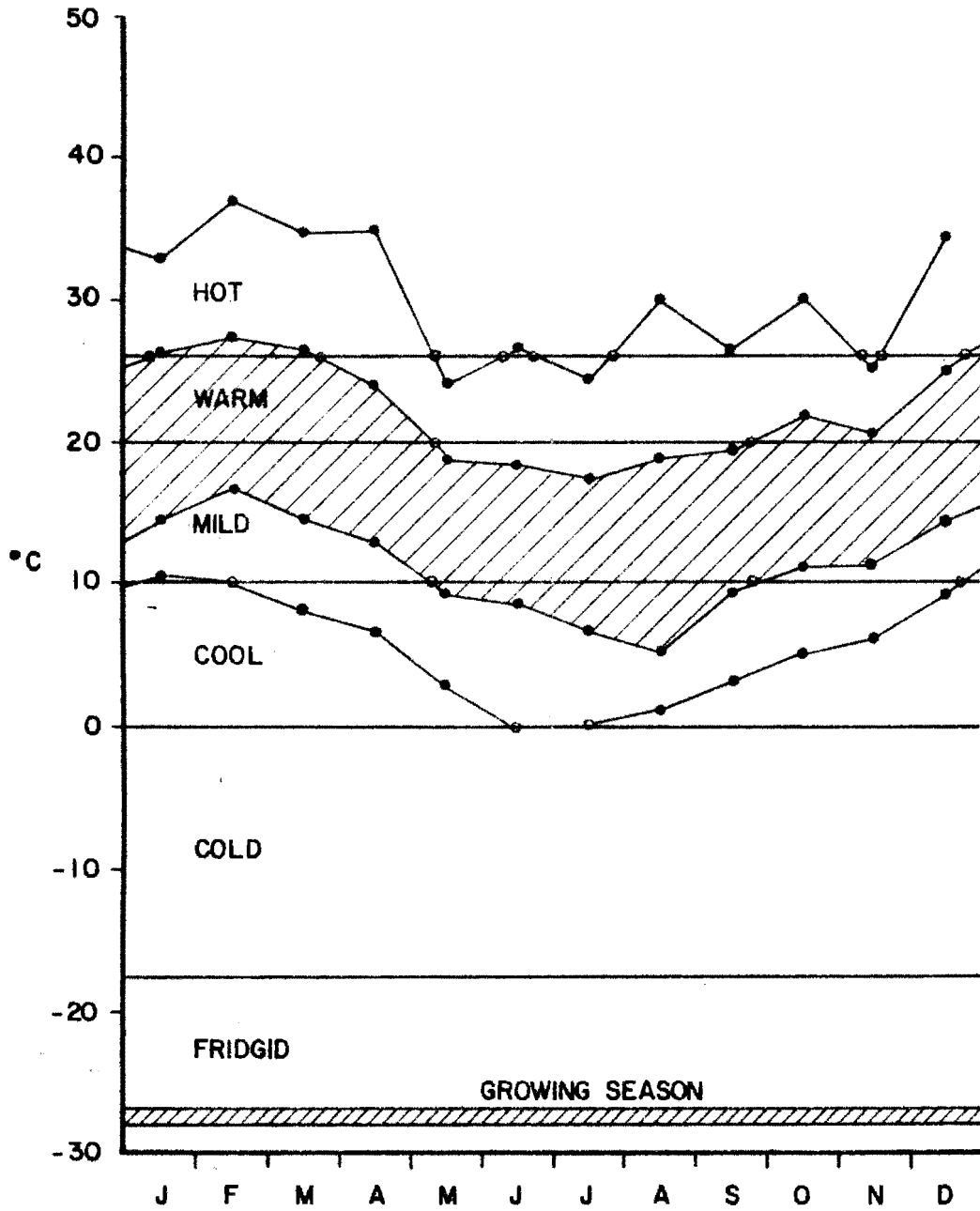


Fig. 13. Deasy diagram of the temperature régime at the research site.

$$T_d = 182,6 + 2,032 \times$$

$$\text{where } \sin x = (ET - 14)/4$$

Effective temperature has been studied more for its effect on animal distributions than that of plant species. Correlations have, however, been found between ET and the distribution of palms in Southern Africa (Stuckenberg, 1969). Though the South-western Cape is biologically the most distinctive part of Sub-Saharan Africa, ET apparently has no significant role in the fynbos biome. According to Stuckenberg (1969) the South-western Cape "does not deserve to be distinguished as a "temperate region".

Another similar term, namely temperature efficiency, attempts to measure the effectiveness of warmth in promoting plant growth. It is determined from the number of days with a mean temperature above 40°F (4,4°C) and the amount of rise above that limit. From Fig. 13 it is immediately clear that plant growth is rarely interrupted in Kogelberg and the South-western districts, and then only for very short periods.

Duration of the thermal summer (Schultze, 1965) is for the period when mean temperature exceeds the temperature halfway between that of the coldest period, and that of the warmest. According to the definition above, the Palmiet River valley has a five to six month long thermal summer period.

A Deasy diagram was drawn although the records are too limited for it to be an accurate representation of the temperature régime of the Palmiet River valley (Deasy, 1941). It is however an easy way of

summarising all the relevant data in one figure.

Table VII. Summary of Temperature data for the Kogelberg and other weather stations in the South-western Cape.

Station	Kogelberg Welgevallen Elgin Steenbras			
location	3418BD			
Attitude (m)	210	119	259	338
Years of record	1	25	23	24
Mean temperature	16,65	16,6	14,41	14,89
Mean warmest period	21,02	20,67	18,77	18,8
Mean coolest period	12,55	12,73	10,00	11,17
Mean maximum	22,1	23,0	21,2	19,1
Mean maximum warmest period	26,1	27,9	25,5	23,4
Mean maximum coolest period	15,1	18,3	16,8	14,9
Mean minimum	11,2	10,1	7,7	10,7
Mean minimum warmest period	18,2	13,4	12,0	14,1,
Mean minimum coolest period	6,9	7,0	3,2	7,4
ET	15,28	15,30	14,20	14,45
Td (days)	220,5	221,1	188,4	195,7
Length of Thermal summer	151	163	181	190
	(days)			

Kogelberg Forest Reserve has a temperature régime that is very similar to that of Welgevallen agricultural experimental farm near Stellenbosch. Steenbras dam and Elgin experimental farms are generally cooler in their long term means than the single year record for Kogelberg. There is also a difference in height above sea level.

Tropical days (Maxima equal to or exceeding 30°C) occurred about 26 times in the 365 day period. Summer days (maxima equal to or exceeding 25°C) occurred approximately 103 times in the 365 day period. By definition there were no cold days (maxima equal to or less than 10°C) in the period from June 1976 to May 1977. The lowest maximum temperature recorded was $10,2^{\circ}\text{C}$. One frost day (Minimum at or below 0°C) occurred during the record period according to the records - no frost was actually observed.

The temperature records are too short for any detailed analysis and serve only as an indication of the prevailing temperature regime at the time of the experiments.

4.6.2.3.1 SOIL TEMPERATURE

Temperatures were measured at two depths with a Cassella type soil thermograph. The probes were buried at 5cm and 20 cm depths under the characteristic restioid-ericoid undergrowth. Probes consisted of hollow tubes and cables filled with mercury, and temperatures were recorded via a lever driven pen on a revolving drum.

The soil temperature data cannot be considered representative since only one sample point was measured at two different depths (see Scharringa, 1976). Horizontal variations in soil temperature are caused, for the greater part, by differences in soil properties (Scharringa, 1976). Even in a homogenous soil the temperature variation can be high and therefore the data presented here only serves to describe a broad soil temperature regime.

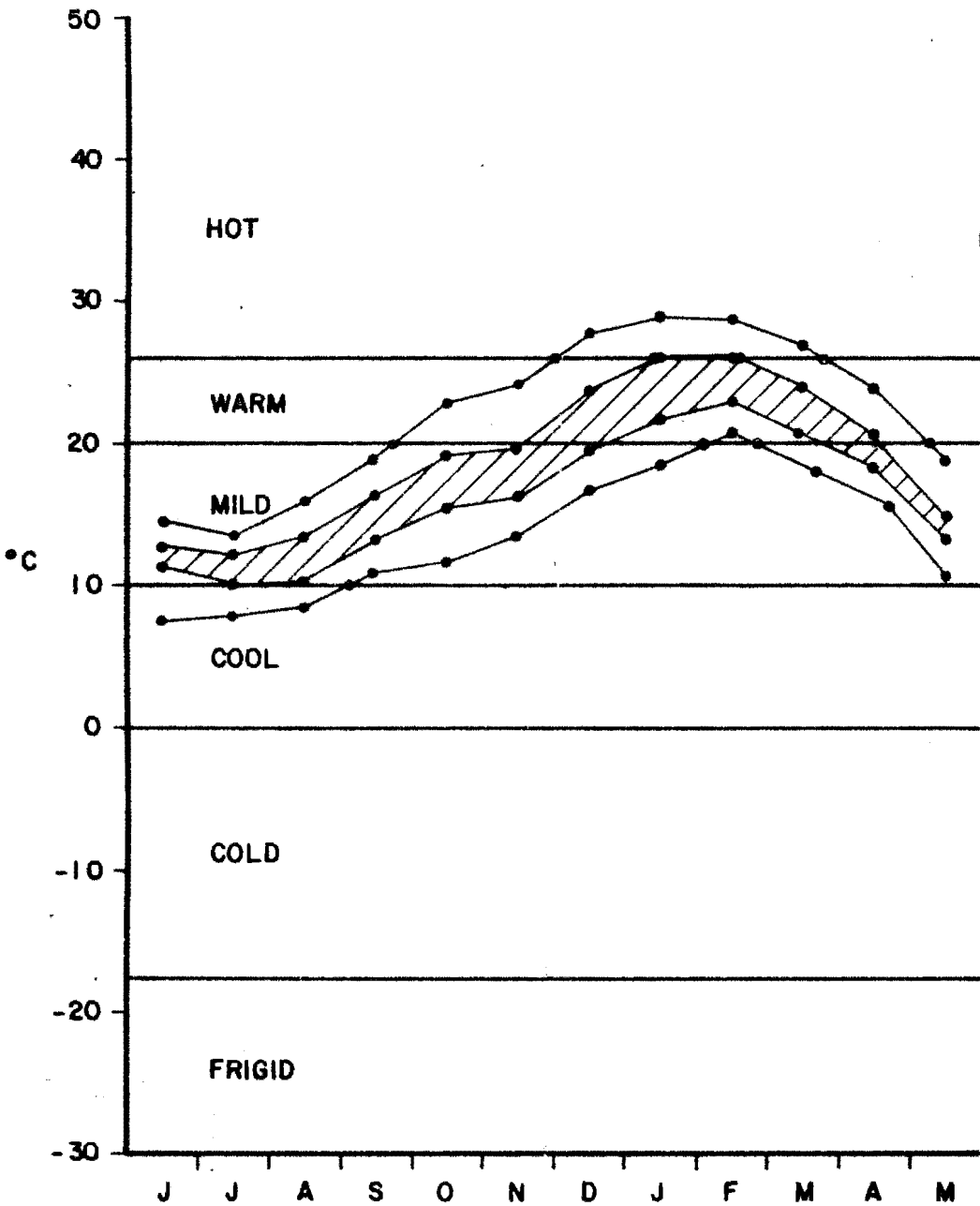


Fig. 14. Deasy diagram of mean soil temperatures at the research site.

Table VIII Soil temperatures at the research site and at Robertson (33°50'S 19°54'E H156m period 5 years)

		J	J	A	S	O	N	D	J	F	M	A	M
Kogelberg	5 cm	12,96	12,12	13,09	16,03	18,75	19,35	23,33	25,54	26,05	23,75	20,46	14,72
Kogelberg	20 cm	12,23	11,21	11,97	14,78	17,40	18,10	21,83	24,01	24,61	22,45	19,55	14,11
Robertson	20 cm	12,05	12,55	13,55	17,45	20,25	24,10	26,70	26,25	26,80	24,95	19,40	17,20

A modified Deasy diagram was drawn for the mean soil temperature and adequately summarise the soil temperature characteristics for the Palmiet River valley (Fig. 14).

A table is included for Robertson which is the nearest weather station to the Kogelberg where soil temperatures were recorded (Schultze, 1965) (Table VIII). Robertson lies north and east of the Kogelberg Forest Reserve fairly deep inland and slightly higher than the weather station on the Palmiet River. It is interesting to note that the soil temperature régime is much hotter at Robertson. This is most probably due to red soils derived from shale at Robertson in contrast to white leached sandy soils of Table Mountain Sandstone at Kogelberg.

According to Schultze (1965) diurnal variation in soil temperature ceases at a depth of 60cm. However, the greatest mass of roots for all the plants occur in the first 20 cm of soil and the temperature régime of that layer is, therefore, considered to be biologically the most significant.

4.6.2.4 SURFACE WIND

Measurement and analysis of surface wind-run was carried out in accordance with prescriptions of the South African weather bureau. Direct comparison of the data obtained with that of the weather bureau is therefore possible.

Because of the short record it may be assumed that the wind record is only a rough estimation of the actual wind régime

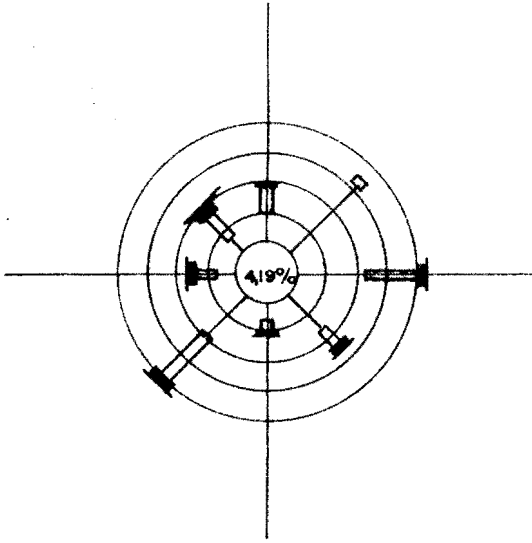
Table IX Summary of seasonal and yearly wind-run

	Calm	N	NE	E	SE	S	SW	W	NW	
Percentage	1, 34	9, 0	10, 96	19, 63	7, 94	5, 84	23, 01	9, 92	12, 37	
Summer	378, 54	2537, 06	3091, 45	5536, 03	2238, 08	1645, 54	6487, 75	2797, 53	3488, 17	
Percentage	1, 45	4, 62	10, 77	14, 30	4, 14	16, 64	26, 67	11, 38	10, 04	
Spring	462, 66	1473, 85	3435, 87	4564, 79	1321, 05	5310, 35	8509, 95	3631, 95	3202, 95	
Percentage	2, 57	7, 02	17, 53	14, 92	4, 26	11, 84	16, 94	11, 61	13, 30	56
Autumn	613, 55	1675, 18	4180, 37	3557, 90	1015, 71	2823, 05	4040, 35	2769, 39	3171, 73	
Percentage	2, 10	14, 01	28, 83	3, 89	3, 78	0, 00	17, 67	8, 39	21, 33	
Winter	521, 63	3484, 57	7168, 54	967, 22	940, 50	0, 00	4392, 75	2086, 43	5304, 53	
Percentage	1, 79	8, 50	16, 28	13, 49	5, 16	8, 80	21, 73	10, 31	13, 94	
Year total	1981, 92	9403, 74	18007, 81	14926, 42	5706, 09	9734, 57	24030, 89	11402, 77	15418, 40	

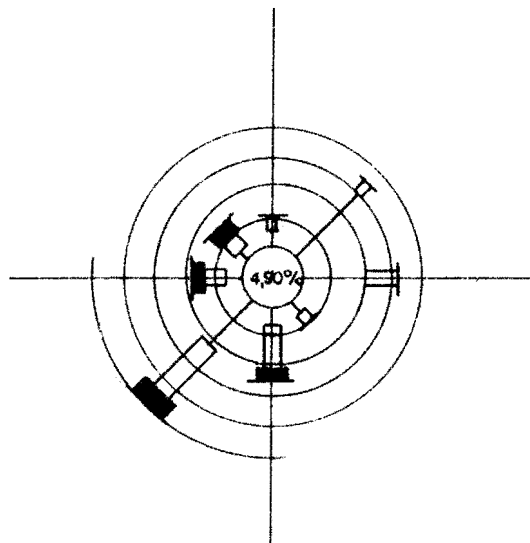
Table X. Percentage time distribution of the total windrun (T) and the mean velocity (S) for the different seasons

	C	N	NE	E	SE	S	SW	W	NW
S T	4,19	9,11	17,85	20,46	6,87	5,03	20,34	7,50	8,65
S	4,38	13,49	8,39	13,11	15,79	15,85	15,45	18,07	19,53
S T	4,90	5,41	17,76	17,12	3,99	13,09	22,44	8,20	7,11
S	4,37	12,62	8,96	12,35	15,33	18,79	17,56	20,50	20,87
A T	7,80	6,63	24,07	17,47	3,41	9,43	14,83	8,17	8,19
S	4,20	13,49	9,28	10,88	15,93	15,99	14,55	18,12	20,70
T	5,42	10,00	44,74	3,39	3,72	0,00	15,92	5,38	11,42
W S	4,41	15,96	7,34	13,08	11,56	0,00	12,63	17,75	21,26
T	5,36	7,90	26,29	14,39	4,60	6,65	18,66	7,24	8,91
Y S	4,40	14,18	8,16	12,36	14,78	17,43	15,34	18,75	20,62

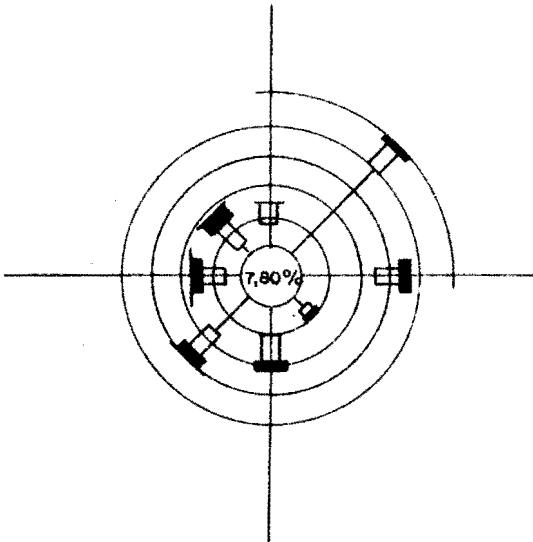
SPRING



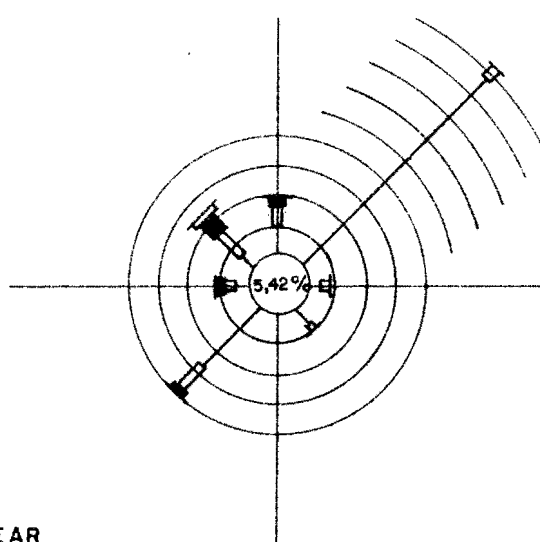
SUMMER



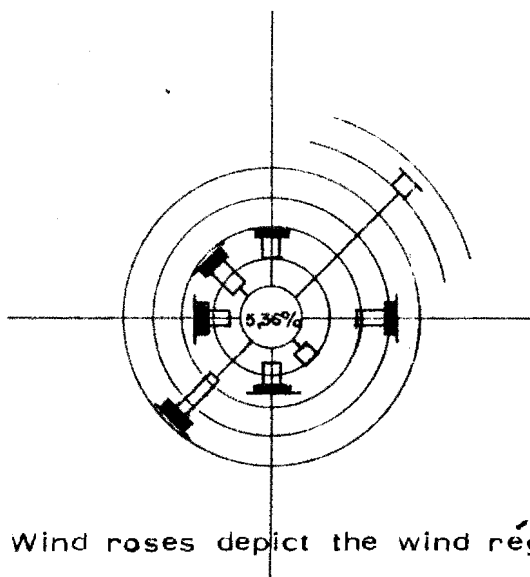
AUTUMN



WINTER



FULL YEAR



WIND ROSES

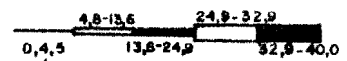


Fig. 15. Wind roses depict the wind régime at the research site.

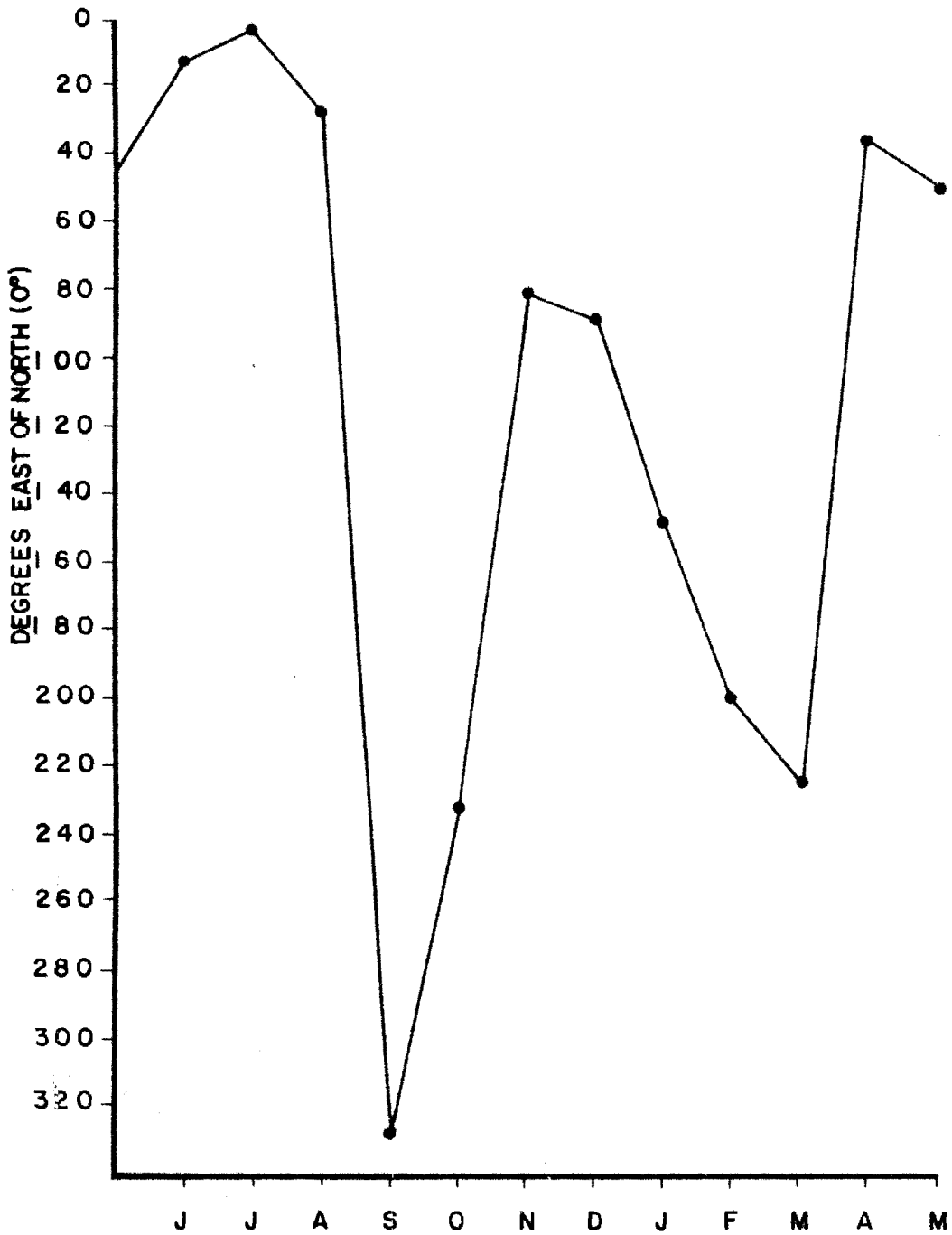


Fig. 16. Graph indicating the frequencies of the different wind directions at the research site.

in the Kogelberg State Forest. Interpretation of the data is therefore mainly based on observed trends.

Data summarized in tables IX and X are deemed sufficiently accurate for a description of the wind regime in the Kogelberg. Fig 15 depicts wind roses and diagrams for the different seasons of the year and a full calendar year.

Critical evaluation of the wind data confirm general observations that wind is a major and dominant environmental factor in the Kogelberg State Forest. According to the Fruit and Fruit Technology Institute at Stellenbosch, Worcester Veld reserve weather station at Worcester (the average wind-run is 270 km per day (Anon, 1972) has the highest wind-run record out of 25 stations that are maintained by the Institute. In contrast Kruger (1974) reports an average of 318 km per day at Jakkalsrivier. Kogelberg State Forest which is south-west of Jakkalsrivier and much closer to the coast has an average wind-run of 316 km per day. Whereas Jakkalsrivier exhibits little variation in average daily wind-run throughout the year (Kruger, 1974), Kogelberg displays a definite summer peak (Fig. 16).

Such a clear seasonal cycle with a definite summer peak is contrary to the findings of Kruger (1974). He found that well defined seasonal cycles occurred west of the Hottentots Holland divide and slightly fluctuating cycles east of the divide.

The dominant wind-run seems to favour an east-north-east to a south-westerly direction. Since the weather station is situated in a valley with a roughly E.N.E. - W.S.W. orientation this is not surprising. In summer the bulk of the wind is from the south-west, north-west and north-east to east. Information published by the

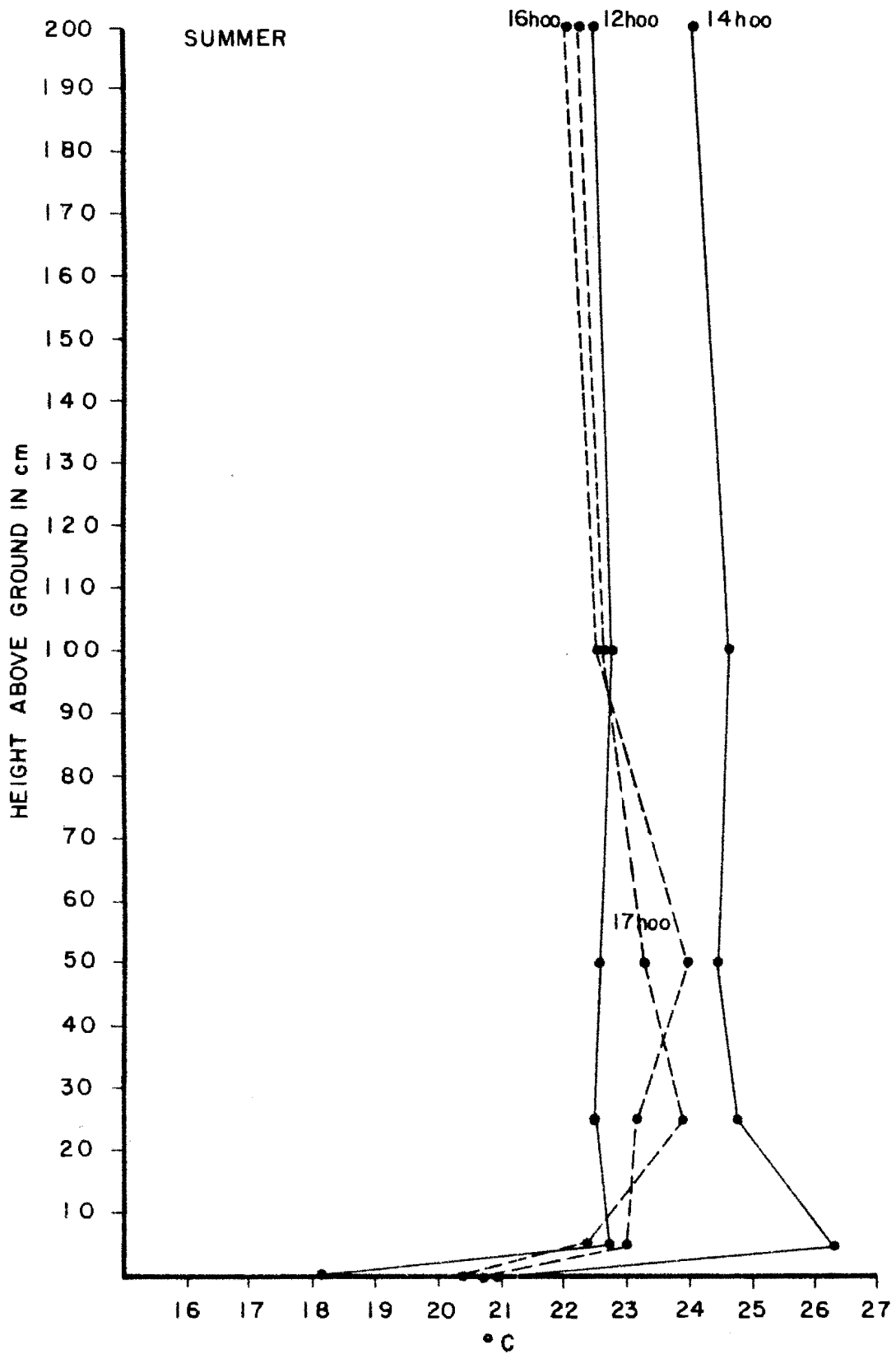


Fig. 17. Graphical presentation of the vertical temperature gradient change throughout a day in summer in a mature fynbos community.

weather bureau indicates that the south-easterly winds are the most significant for the region. From table X it is clear that the north-western winds are the strongest winds and are slightly stronger in winter. South-westerly and north-easterly winds are, however, the most frequent strong winds that occur throughout the year. Wind speeds in general do not vary a great deal through the year except perhaps the southerly wind which drops to zero in winter.

4.6.2.5 MICROCLIMATE

For the purpose of comparing the seasonal microclimate regimes in a fynbos community it was decided to use temperature because it is an easily measurable parameter. Temperature profiles were measured in different seasons. Fig. 17, 18 & 19 depicts the mean daily temperature profiles for the probable wild-fire seasons. It is clear that there are considerable differences in the temperature profiles. The differences can be summarised as follows:

- (i) In Autumn and winter soil temperatures are almost identical, but the summer soil temperature is considerably higher.
- (ii) In Autumn and summer air temperatures are very similar.
- (iii) Both the spring and summer profiles suggest that there is a difference between air temperature and soil temperature during these seasons only.

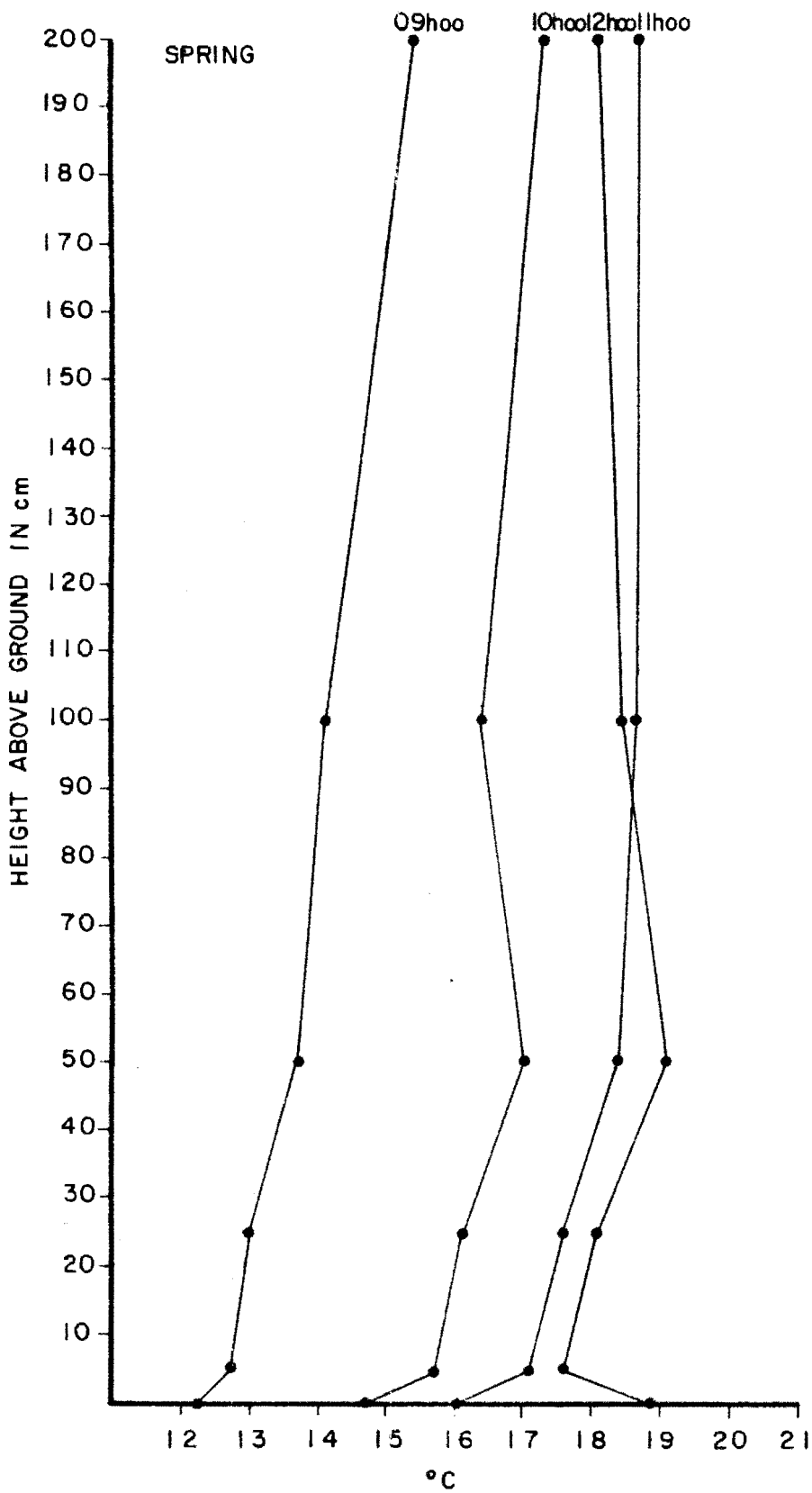


Fig. 18. Graphical presentation of the changing vertical temperature gradient in a mature fynbos community in spring.

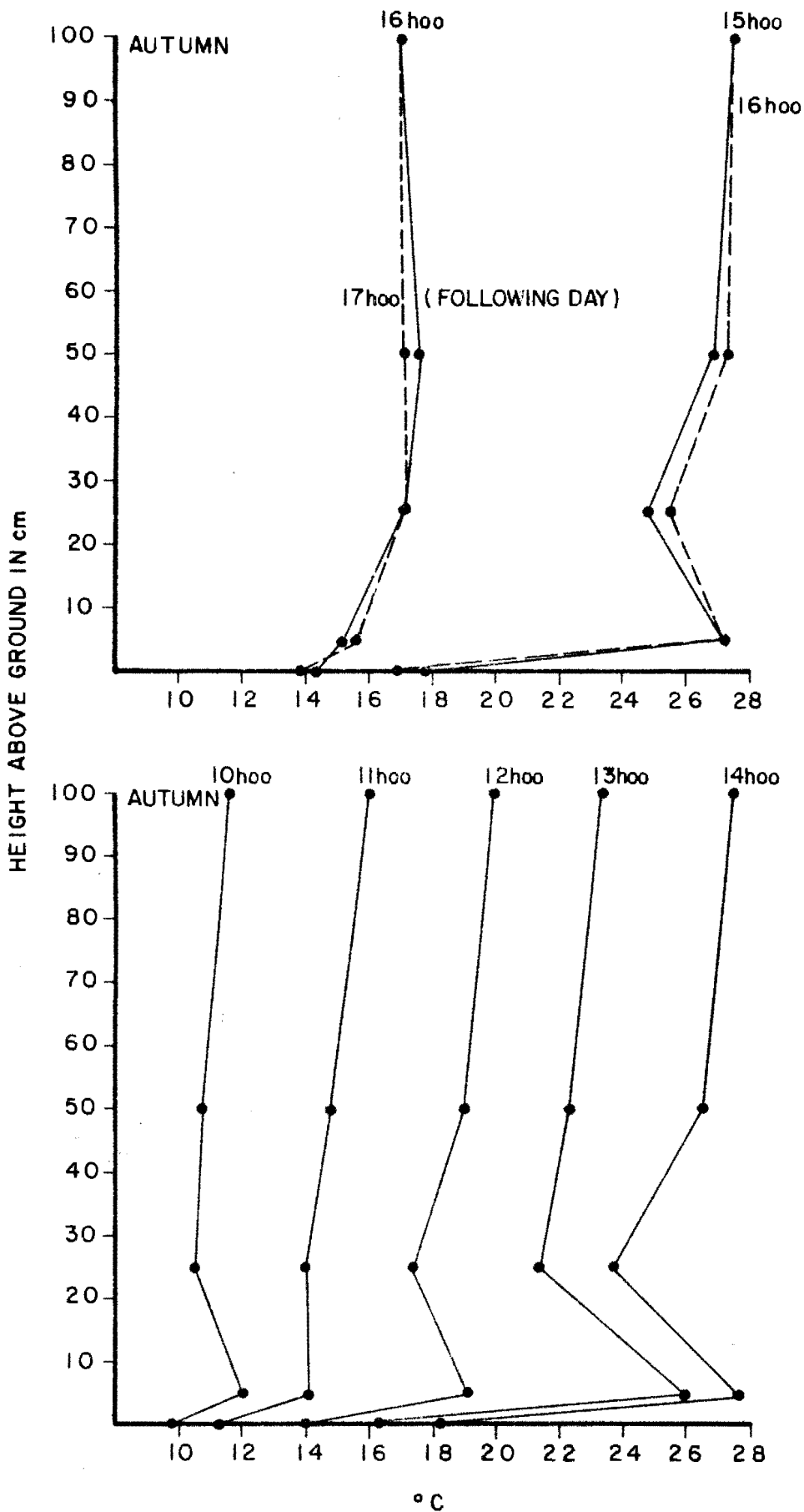


Fig. 19. Vertical temperature gradients for a day in winter in a fynbos community.

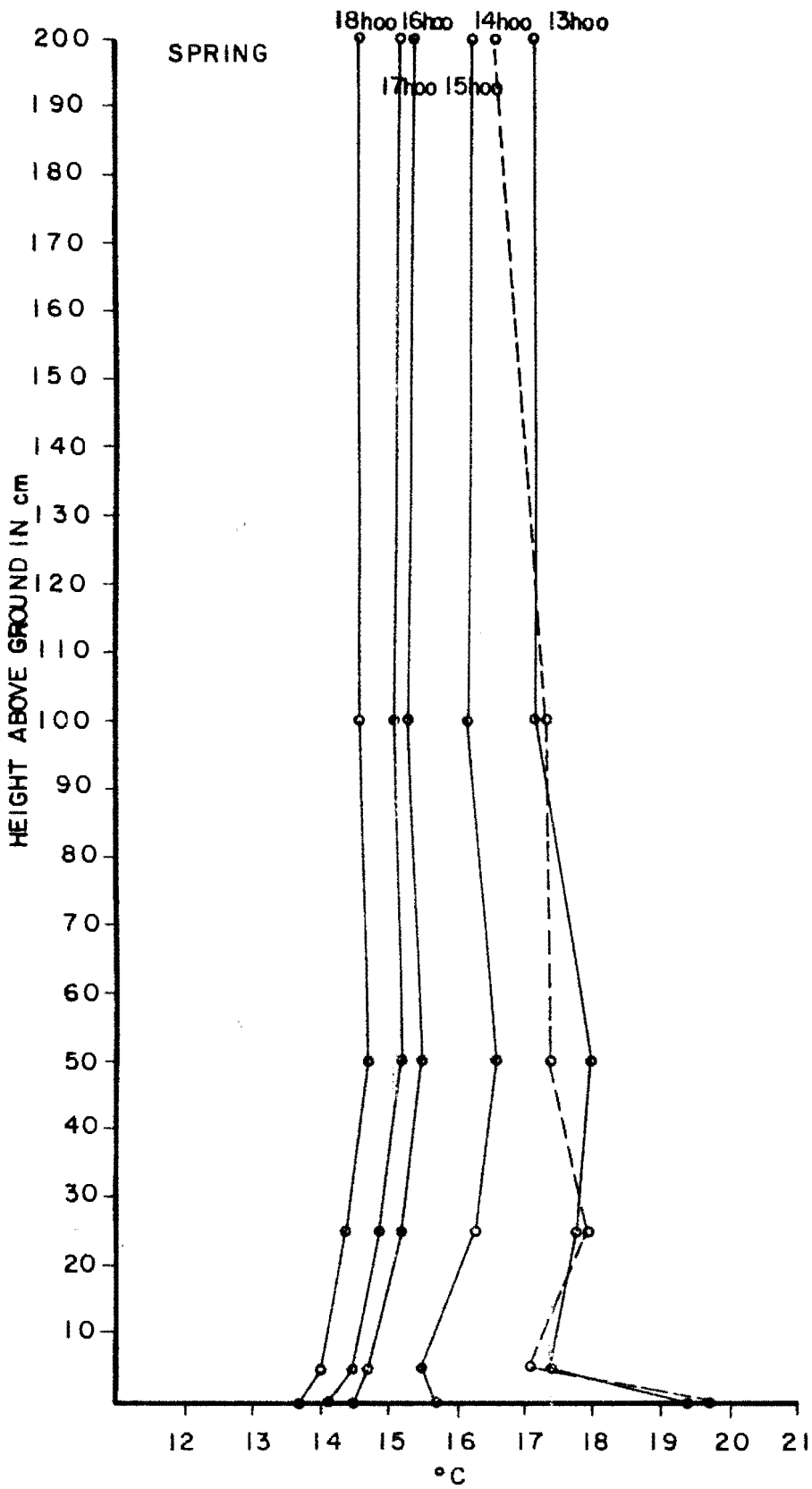


Fig. 20 Vertical temperature profile of a mature fynbos community for a day in spring.

However, in both cases the days on which the measurements were made were cloudy and windy while in autumn it was a sunshine day with windstill conditions in the morning. There is almost always some wind in the afternoons especially in spring and summer.

Air temperature near the ground would not seem to differ much from ambient air temperature. Seeds germinate better at higher soil temperatures (Tevis, 1958a) but the survival of the seedlings is influenced greatly by fluctuating soil temperatures (Rösch, 1977). However, the survival of individuals of a species is depended on the amount of soil water (Beatley, 1967).

Since very little data are available on the temperature profiles of the fynbos community in different seasons no definite conclusions can be drawn. However, it is possible to deduce a few general trends. Firstly, when there is little wind and the sun is shining definite temperature stratification occurs within the undergrowth layers (Fig. 17). Wind tends to produce a homogeneously heated mass of air in and above the undergrowth. Surface soil temperature fluctuates much in sympathy with prevailing weather conditions though usually it is out of phase with ambient air temperatures (Figs. 18 & 19). Air temperature is approximately one hour in advance of soil temperature. In springtime the soil temperature rises to temperatures that can promote general seed germination (Tevis, 1958) (Fig. 20). Summer soil temperatures are even higher and seed germination would be enhanced (Fig. 17). In general seed germinates faster at higher temperatures and the seedlings are larger than those that germinated under colder conditions (Tevis, 1958).

Table XI. Temperatures of different soils and with artificial colouring ($^{\circ}\text{C}$)

Soil	Natural	White	Black
Dark grey garden soil	7,3	5,8	10,5
Loam	6,9	5,7	9,7
Yellow clay	6,7	5,8	9,8
Light grey quarts sand	6,9	6,2	10,6

Table XII. Temperature changes in different materials with the addition of one calorie heat energy

	Specific heat	Increase in temperature on absorption of 1 calorie in $^{\circ}\text{C}$
Water	1,0	1
Quarts sand	0,2	5
Kaolinite clay	0,23	4,3
Humus	0,45	2,2

Finally it is clear that microclimate of which only one parameter was investigated, must have a profound influence on seed germination and seedling establishment. A temperature profile could not be measured above bare ground. When considering the physical properties of bare ground it is clear that conditions would be harsher under equal conditions than in a mature plant community.

Lockwood (1974) gives a table where in the albedo of differently coloured soils and heather are compared. An extract of the table is listed below.

Surface	Albedo (% of incoming shortwave radiation that is reflected).
Black dry soil	14
Black moist soil	8
Sand bright and fine	37
Plowed field-moist	14
Heather	10

In 1830 Schubler compared the temperatures of comparable blocks of soil artificially coloured by dusting the surfaces with magnesium carbonate and soot to give white and black surfaces, the temperatures of which he compared with untreated soils (Comber, 1960) (Table XI).

In the event of a wild-fire the initially bare black soil will represent harsh conditions for seedlings that will be subjected to extreme temperature fluctuations. The temperature differences for each soil are due to differences in the efficiency of heat absorption. Since the specific heat of different types of soils vary, it is important to determine the

effect of a given quantity of heat on the temperature of different soil types. A table presented by Comber (1960) compares the increase of temperature with the application of one calorie heat energy (Table XII).

Evidently a quartzitic sand, such as which is characteristic for the upper soil layers of the research site, is subject to much greater temperature fluctuations than most other soils. When the soil is covered with black soot and carbon remains of plants after a fire, the range of temperatures experienced by seedlings is even greater.

4.6.2.6 CLIMATIC INDICES AND CLASSIFICATION

Thornthwaite (1948) evolved a rational classification of climate based on the important concept of potential evapotranspiration. The classification system comprises four main elements (Schultz, 1947).

1. Moisture index.
2. Seasonal variation of effective moisture.
3. Thermal efficiency.
4. Summer concentration of thermal efficiency.

With decreasing latitude, as the climate changes from frost type to megathermal type, the summer total of potential evaporation falls from 100% to 25%. Evaporation is most significant in summer and the concept is summarised in the term summer concentration. A fixed relationship was found between potential evaporation and its summer concentration of evaporation. This is expressed in a Formula $S = 157,76 - 66,44 \log E$, where S is summer concentration

(%) and E is potential evapotranspiration (inches). The extent is which the local summer concentration falls short of the ideal is a measure of the continentality or oceanity of the region. According to the maps based on water surplus and deficit, Kogelberg State Forest has the following climatic index.

1. Moisture index

Moisture region	Moisture index
	Im
Moist Subhumid	C2 0 to 20

2. Seasonal variation of effective moisture.

Moist climates (A, B4 to B1, G2)	Ia
S. Moderate summer deficit	16,7 - 33,3
or S2 Large summer deficit	733,3

3. Thermal efficiency.

Thermal efficiency	Thermal type.
Index	
ms cm	
28,1 71,2	B ₂ ¹ Mesothermal.

4. Summer concentration of thermal efficiency.

Thermal efficiency (ins)	Thermal efficiency Type	Summer concentr.	Summer concentr. Type
28,1	B ₂ ¹	61,6	b ₂ ¹

Thus Kogelberg State Forest has a climatic type:

	C2sB ₂ ¹ 6 ₂ ¹	C2B ₂ ¹ s2b ₂ ¹
or	C2s2B ₂ ¹ b ₂ ¹	C2B ₂ ¹ sb ₂ ¹

The water deficit is 8 inch = 20,31 cm

Actual evapotranspiration is 20 inch = 50,8 cm

Potential evapotranspiration is 30 inch = 76,2 cm

Another classification system is that of Köppen which is based primarily on twenty year averages. The symbols of the classification system are defined as;

- C = Warm temperature rainy climates; at least one month with mean temperature below 16°C and at least eight months with mean temperature above 1°C ; Coldest month above -3°C .
- f = Sufficient rain in all months, with precipitation of driest month exceeding one third of wettest month.
- a = Mean temperature of warmest month over 22°C .
- b = Mean temperature of warmest month below 22°C .
- s = Dry season in summer. (Swart, 1956 in Boucher, 1972).

According to the Köppen classification the climate in the Kogelberg region is of the Csb type at the lower altitudes. It may be expected that a number of places in the mountainous areas of the southwestern Cape could be found which would be classified as Cfsa or Cfsb (Schultze, 1947).



Fig. 21. Photograph of L. laureolum and lower vegetation with a 2m scale. Subdivisions of the scale are in 20 cm intervals.

5. BIOTIC DESCRIPTION OF THE STUDY SITE

5.1 FLORA

Acocks (1953) described fynbos (Veldtypes 69 and 70) as a complex vegetation, and emphasised that the lack of species dominance is a characteristic feature of fynbos.

The fynbos on the experimental site is a climax community according to the criteria of Adamson (1938). At the research site the community has three layers of which the uppermost consists almost entirely of Leucadendron laurifolium (Lam.) Fourcade. It is a large bushy shrub (Fig. 21) approximately 2 m high with hard, flat and dull leaves of moderate size. A few Aulax kneorifolia Knight and Protea nerifolia R. Br contribute to the physiognomic homogeneousness of the experimental area. The uppermost stratum is rarely continuous and where it is continuous it only occurs in small areas. "Below is a dense layer of small shrubs with thin and more flexible stems and typically small heathlike leaves" (Adamson, (1938). This stratum consists of a large variety of species such as Erica pulchella Houtt. and Sympieza articulata (Thunb.) N.E. Br. which are prominent in the middle stratum. A single species may sometimes assume dominance locally. Shrubby members of Compositae, Ericaceae, Rutaceae and a few others are



Fig. 22. A macro fungus growing on Phaenocoma prolifera.

abundant and may seasonally dominate the aspect of the vegetation. "Below and between these bushes are smaller woody plants, herbs and geophytes in considerable numbers" (Adamson, 1938). At the research site Restionaceae are abundant in the lower and even the middel stratum. Restio egregius Hochst and R. bifarius Mast are important components of the sub-shrub stratum. In the ground layer geophytes, prostrate shrubs and herbs, mosses lichens and macrofungi feature largely (Fig 22). Very few annuals were encountered. Plants of the ground layer contribute little toward total cover, except perhaps seasonally in the case of mosses, lichens and macro-fungi.

Seedlings of most component species can be found in the mature fynbos communities. Where seedlings occur in open patches growth is vigorous in contrast to seedlings that occur between mature plants. Competition for niche space is severe in a mature fynbos community.

Species flower throughout the year with a slight peak in spring time. Some species flower almost continuously as for example Phaenocoma prolifera (L.) D. Don. Fruit ripening and seed release follow soon after the flowering phase except in the case of L. laureolum where the fruits are kept in a bradysporous cone. The samaras of L. laureolum are released 3 to 5 years after maturation of the cone or with the death of the mother plant. Seeds of the different species vary from very small to relatively large. Adaptation for wind dispersal occur in all the lifeforms.

Table XIII. Cape Province ^{fauna}vertebrate taxa represented in the Cape fynbos with emphasis on the number of endemic and near endemic species and sub-species in each taxon.

Taxon	No. of Endemic spp. + sub spp.	No. of spp. occurring elsewhere also,	Total no. of spp. + sub spp.
Class Amphibia	9	15	24
Class Reptilia			
Order Chelonia	1	5	6
Suborder Serpentes	2	31	33
Suborder Sauria	16	35	51
Class Mammalia			
Order Insectivora	4	6	10
Order Chiroptera	5	5	10
Order Primates	1	1	2
Order Carnivora	1	11	12
Order Tubilidentata	0	1	1
Order Proboscidea	0	1	1
Order Hyracoidea	0	1	1
Order Perissodactyla *	0	1	3
Order Artiodactyla +	2	7	9
Order Lagomorpha	5	0	5
Order Rodentia	6	18	24

* 2 extinct.

+ 2 extinct and one does not occur in Cape fynbos areas any more.

In Appendix I a list of plant species found on the research site is arranged according to the classification of R. Wettstein (1935).

5.2 FAUNA

With a rich and relatively old vegetation such as the fynbos it is to be expected that a diverse fauna will be found in the South-western Cape. It is generally stated however that the fynbos lacks a distinctive mammalian fauna (Jarvis, 1979).

In contrast fynbos supports a large avifaunal community which exhibit a surprisingly high diversity (Broekhuysen, 1964).

Characteristic birds for the fynbos are the Cape sugarbird, Rock Jumper, Protea seed-eater and the Orange breasted Sunbird. In Appendix II a list of the avifauna is given, and all species mentioned are characteristic species of the Kogelberg State Forest. Lloyd (1977) compiled a list of mammals occurring in the Cape province and abstracts of this list are presented in Table XIII. Appendix III gives the list of mammalian species identified in the Kogelberg. A number of co-workers supplied additional information and their names are mentioned in the acknowledgements.

Included in Table XIII are data on the Amphibia and Reptilia that occur mainly in fynbos. Greig (pers. comm.) states that there is a marked degree of endemism in the amphibians of the South-western Cape. These endemics are closely associated with three of Acocks's (1953) veld types namely: Coastal Rhenosterbosveld, Coastal Macchia and Macchia or fynbos. A few



Fig. 23. One of the snakes encountered on the research site
(Pseudaspis cana)

amphibians were either collected or identified by their calls. In Appendix IV a list of amphibians found on the research site is given. Data on reptiles are not up-to-date enough to make any statements about the status of the Class Reptilia in fynbos (Jarvis, 1979). Two snakes were found on the research site (Fig. 23 and Appendix V). Of the fynbos fauna the invertebrates have the greatest number of endemic species (Jarvis, 1979). Evidence of a great impact on the fynbos vegetation by insects is readily apparent, however, their effect on the fynbos and their function is largely unknown. Many signs of spiders were observed but little else can be said other than there are a multitude of species and each seems to occupy a different niche.

5.3 BIOTIC COMMUNITIES

The fynbos ecosystem is composed of a large variety of individual species remarkably endemic and specialised. In 5.2 the four characteristic bird species for the fynbos were mentioned. The Cape Sugar bird is confined to vegetation where proteas are in bloom. Although they utilize the nectar of the protea-flowers their main diet seem to be insects.

The Orange breasted Sunbird apparently occupies the same niche. Occurring only in the West and South-west Cape as far east as Cape Hangklip, the Protea Seed-eater lives off the seed of proteas, ericas and a few other plants. Niche differentiation favours both the animals and the vegetation.

Protea flowers may be pollinated by the nectar loving birds while the seed eater balances seed production. A biotic community of interacting plant and animal species may cover a vast area while the function of both members remain unchanged.

There is some evidence of the same degree of interaction between certain mammals and the fynbos vegetation. A number of rodent species have been found to pollinate certain ground proteas (Rourke, 1978).

Little is known of interactions between reptiles or amphibians and fynbos vegetation.

The best studied biotic communities where definite interactions have been proved are those that involve insects and plant species. According to Feeney (1975) invertebrates appear to select their food largely on the chemical nature of the species. As mentioned elsewhere the plant species partition available resources by growing and flowering at different times of the year. Animals, specifically insects, have evolved to fill all available niches and in doing so many have become very specialised.

Sufficient to say that in the fynbos with its high species diversity, topographic and climatic variation, there are a multitude of biotic communities that are largely unknown.

6. METHODS

The following methods were employed to obtain data on the structure

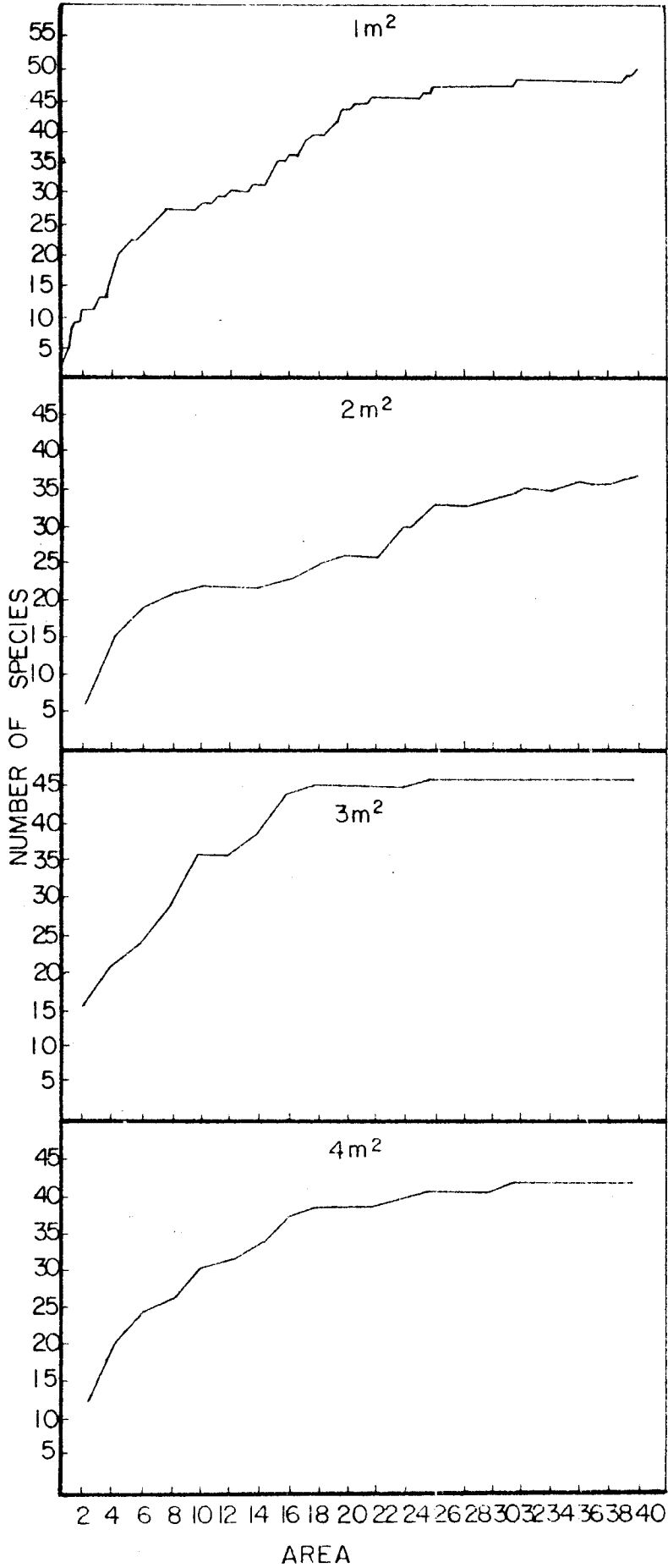


FIG. 24. SPECIES AREA CURVES FOR DIFFERENT QUADRAT SIZES

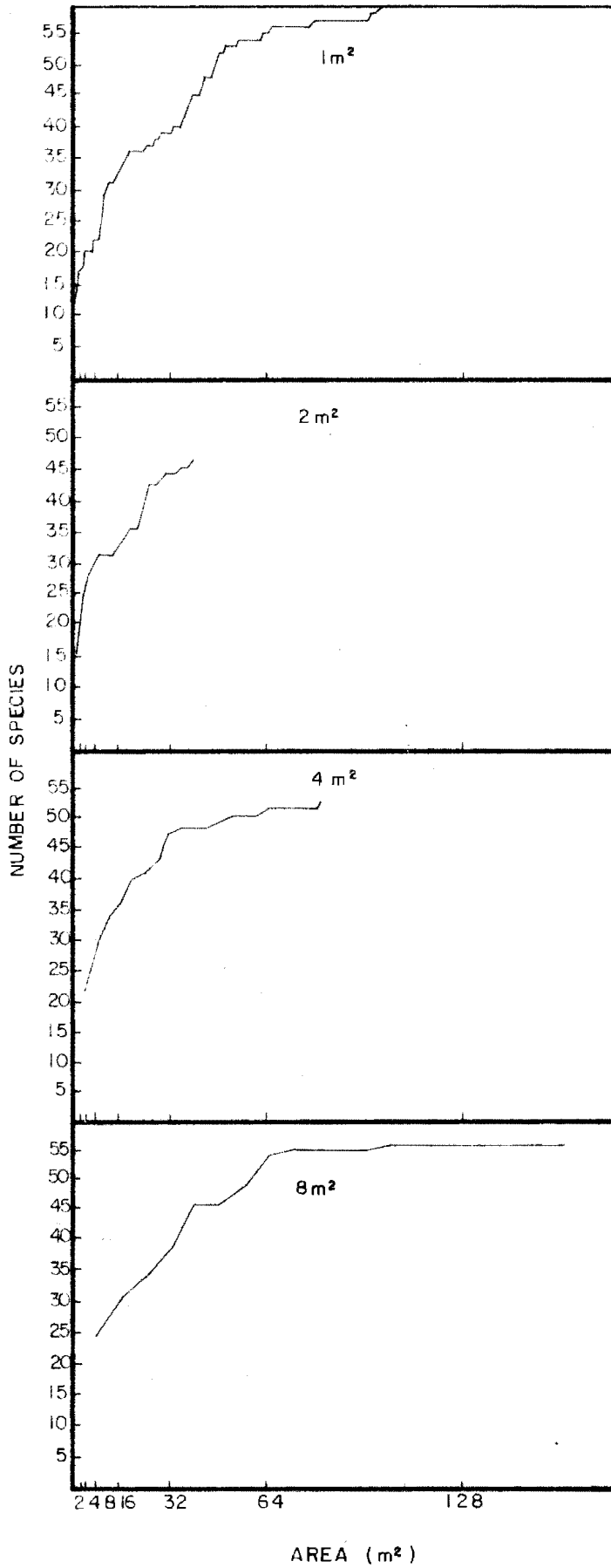


FIG 24 SPECIES AREA CURVES FOR DIFFERENT QUADRAT SIZES

of the vegetation.

Structure	Methods	Analyses
Component		
Species diversity	Braun-Blanquet (B.B.) surveys of randomly placed 4m^2 sub plots.	Mean no. of spp /plot, Simpsons and Shannon-Wiener indices.
Pattern	Sub-plots ranging in size set out as transects and at random.	Species Mean square plot size. Ordinations and species relations.
Stratification	Line transect measurements and surveys according to the "Trabaud" method.	Profile diagram and species present in height classes.
Biomass	Randomly placed 1m^2 and 4m^2 clip-plots.	Oven dry mass of growth forms/ha.

Species diversity determinations are quite straight-forward and do not need any further elaboration. Pattern was analysed in two ways. Firstly a range of quadrat sizes (1m^2 , 4m^2 and 8m^2) were set out randomly and surveyed by the Braun-Blanquet (B.B.) method. A species area curve was drawn up for each quadrat size to determine the most appropriate quadrat size to be used in all subsequent surveys (Fig. 24.).

Two 50 m transects at right angles were layed out on the second experimental plot. The sub-plots (quadrats) were 1m^2 an by lumping quadrats and additional species a simple pattern analysis was performed on the data according to the method described by Kershaw (1957, 1974). The same data were processed with the Reciprocal averaging (RA) package programme developed by the Cornell University (Gaugh et. al., 1972). RA is an ordination method by which definite trends can be detected. All B.B. survey data were subjected to a R.A. analysis in the experimental plots to check for any pronounced pattern. Finally a procedure described by Agnew (1961) was used to test for interspecific associations for the twenty-two most dominant species on plot 3. The method used was adapted by Agnew (1961) from one proposed by Goodall (1953).

Two approaches to the description of stratification were incorporated to obtain a very detailed analysis of the vertical distribution of the fynbos species. The tall shrub stratum was surveyed by measuring the distance of each individual from a baseline (border of the plot) and then recording height, crown diameter and height to the first branch, see Tansley (1939) (Chapman, 1976). All these measurements were done in situ and non destructively along a transect, 4m wide and 50m long. The result is portrayed according to a technique pioneered in the tropics by Davies and Richards (1933, in Shimwell, 1971). Since fine detail in the profile diagram was impossible at the scale employed, graphic symbols were used as described by Dansereau (1958).



Fig. 25. Photograph of the plots (to the right and beyond the car) before the first experimental burn. The general physiognomy of fynbos is depicted with Leucadendron laureolum dominating the late winter aspect, as it comes into full flower.

The small shrub and herbaceous stratum was subdivided into four empirically determined layers to facilitate the description of this stratum. A technique described by Trabaud (1973) was adapted to survey the characteristics of the strata of lower vegetation. Trabaud (1973) subdivided the low vegetation into the following layers; 0 - 5cm, 6 - 25cm, 26 - 50cm, 51 - 100 cm. A steel rod with a diameter of 6 mm was painted with red and white bands alternately corresponding to the different layers.

The method, as it was adapted, does not give a representative sample of all species, but as physiognomy is determined by the dominant species only (Fig. 25) this is not considered a handicap.

Two 50 m lines were set out at random across each of the experimental plots. Table XX summarises the results of three surveys. Each experimental plot was investigated separately, but since the survey method under-samples species it was decided to combine the data and analyse the result as a whole. Combination of the data provided a more representative sample of the vertical structure present in the fynbos vegetation. Three hundred points in all were surveyed before compiling the table, which gives an indication of the percentage participation of each species in every layer.

Since the experimental plots were to be described, analysed and then burnt, biomass determinations had to be carried out with a minimum disturbance of the vegetation. The undergrowth was sampled with 1m^2 and 4m^2 clip-plots and estimates for the dominant shrub biomass were obtained from a regression equation for biomass on stem diameter.

The clip-plots were covered with dead plant material for the experimental burns. One meter square clip-plots were used on the first sampled plot. Analysis of cover data indicated that a 4m^2 clip-plot would ensure less biased results. All the 1m^2 and subsequent 4m^2 clip-plots were layed out randomly. Clipped material was subdivided into the same categories as used by Kruger (1977). However, in this case the shrub category was represented by the dominant proteaceous layer only and was sampled allometrically. Members of the Ericaceae and Leguminosae were included in the sub-shrub category according to their growth-forms. The definition of each category is as follows:

- (i) Shrubs: Microphanerophytes composed entirely of the family Proteaceae and almost exclusively of the species L. lauroolum (Lam.) Fourcade.
- (ii) Sub-shrubs: ligneous and sub-ligneous nanophanerophytes and chamaephytes which include the Ericaceae, Leguminosae and genera such as Stoebe and Metalasia (Asteraceae or Compositae).
- (iii) Graminoid: hemicryptophytes typically of the Poaceae and Cyperaceae.
- (iv) Restioid: leafless hemicryptophytes of the family Restionaceae. Adamson (1931) described restioid vegetation as assimilating stem type hemicryptophytes.
- (v) Herbs (Forbs): non-ligneous elements not included in above categories, and including ferns.

Table XIV. Relative distribution of biomass between functional units of male and female L. laureolum shrub.

Sex	Leafy twigs	Bare wood	Cones (fruit)
% distri-	30,83	69,17	-
bution	27,44	26,15	46,14

Table XV. r values for several regression lines of aerial biomass on diameters for three positions on the stems of L. laureolum.

Regression.	Basal diameter.	Diameter 5cm off the ground.	Diameter under first branch.
Linear	0,09512*	0,9503	0,9451
Exponential	0,9219	0,9388	0,9529*
Power	0,9730	0,9896	0,9803
Cubic	0,9771	0,9823	0,9903
Parabolic	0,9770	0,9816	0,9893*

* Indicates the best correlation between the three diameter readings.

The clipped vegetation was sorted into the different categories in the field. All the collected materials were transported to the laboratory and dried. Because the undergrowth is characterised by finely divided stems and leaves, drying was executed without sub-sampling at 80°C for 48 hours. Previous experiments had indicated that fynbos plant material dried to a constant weight within that time.

On the basis of empirical findings with tree biomass (Madgwick 1970, Baskerville, 1972) it was decided that an allometric equation would be the appropriate model for estimating shrub biomass. A modified dimension analysis (Whittaker and Woodwell, 1968, 1971) was performed on L. laureolum to determine the appropriate measures for an unbiased regression equation. The stem diameters of twenty selected shrubs were measured at three specific heights. Basal diameter was measured on the ground, another measurement was taken 5cm off the ground and the final measurement was taken below the first branch. All the shrubs were cut off as close as possible to the ground and weighed in toto. Four shrubs were sub-divided into leafy twigs, secondary and all leafless branches, and the main stem to determine the mass distribution between these functional units (Table XIV).

Sub samples of each "functional unit" were taken to determine the moisture content. Correlation coefficients for dry mass on the three diameter readings were calculated for a variety of regression equations (Table XV). It was clear from the results that the diameter under the first branch gave consistently better correlations and this measure was then adopted for detailed analysis. This decision is supported by Mc Mahon (1975) who found that the diameter under the first branch

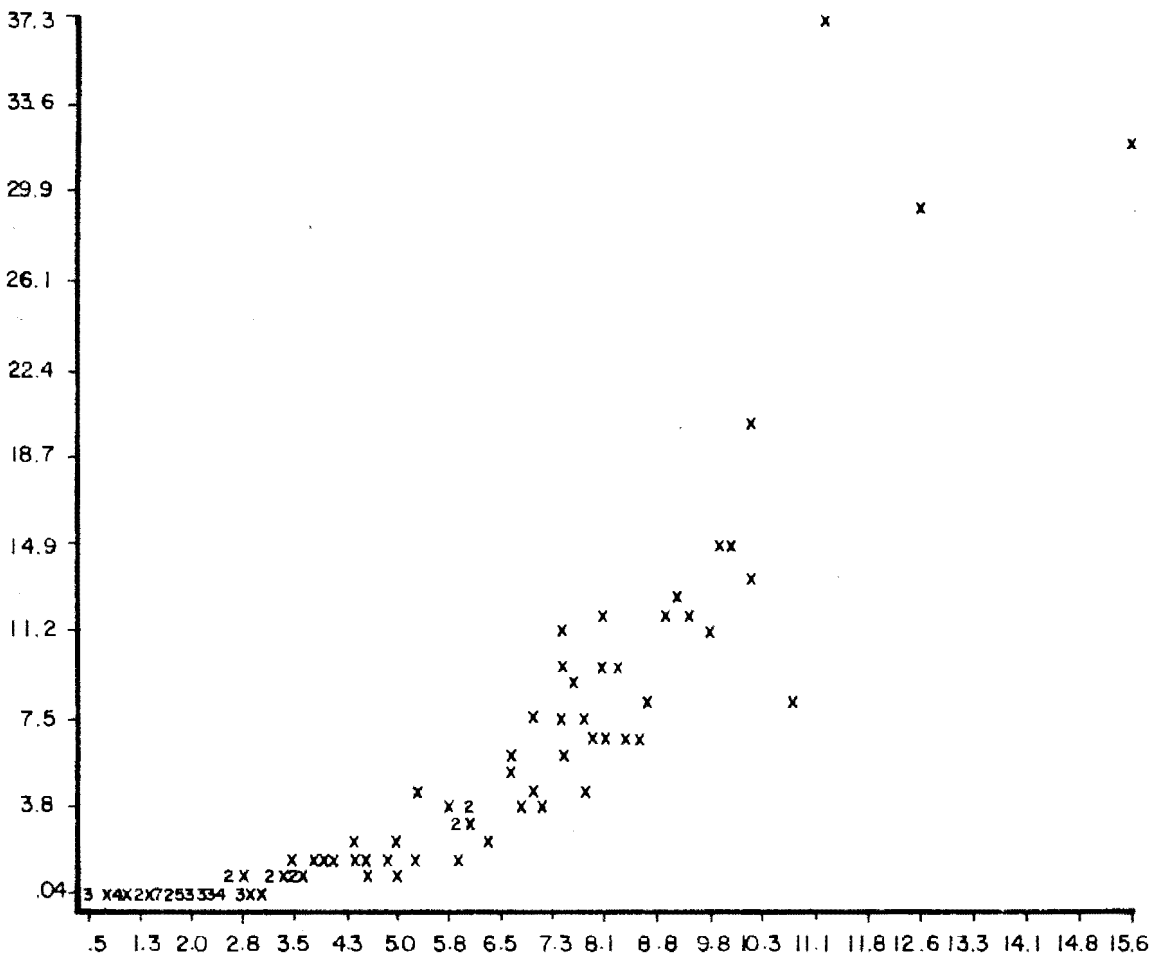


Fig. 26. Scattergram of the O.D.W. of *L. laureolum* over the stem diameter (copy of computer print-out).

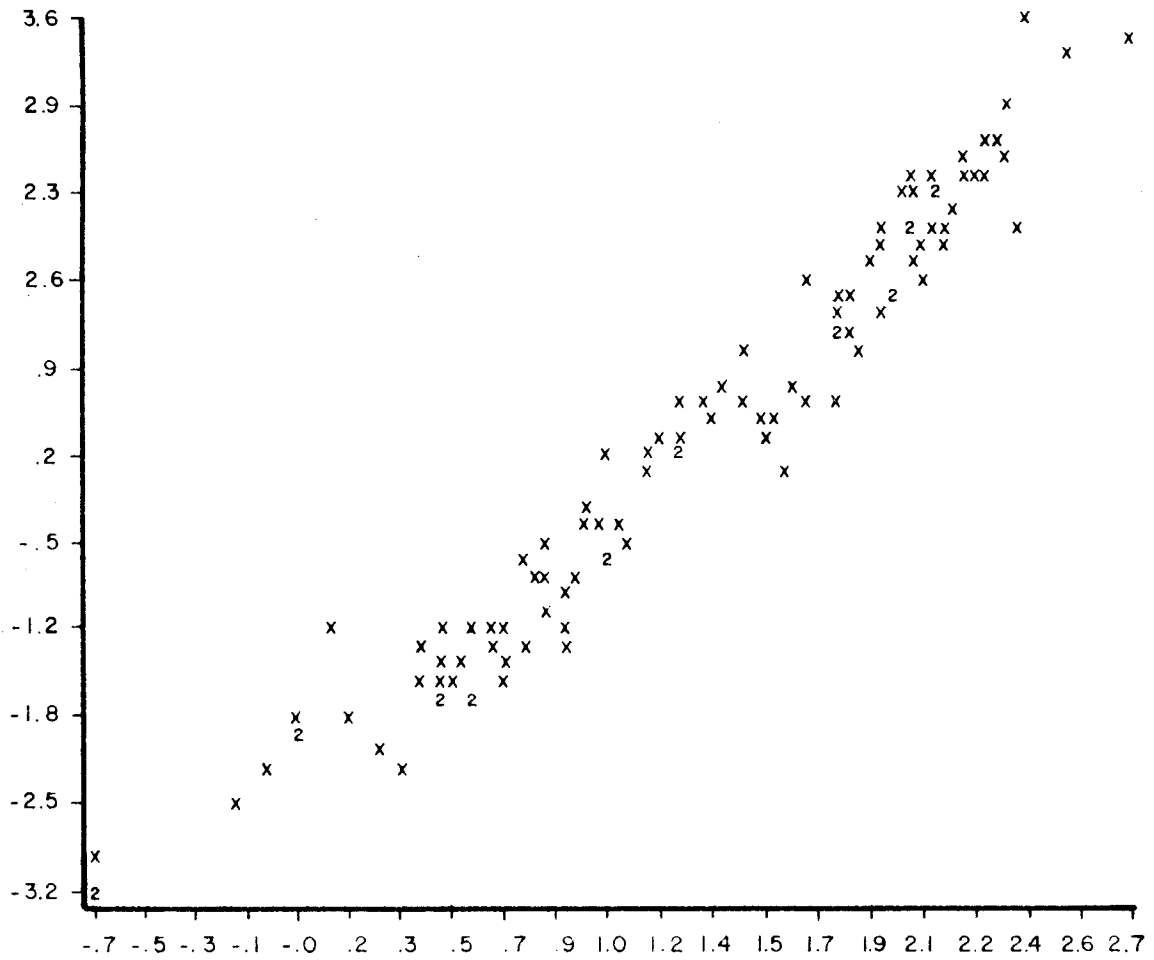


Fig. 27. Linear regression of $\ln$ biomass on $\ln$ stem diameter under the first branch for L. launeolum.

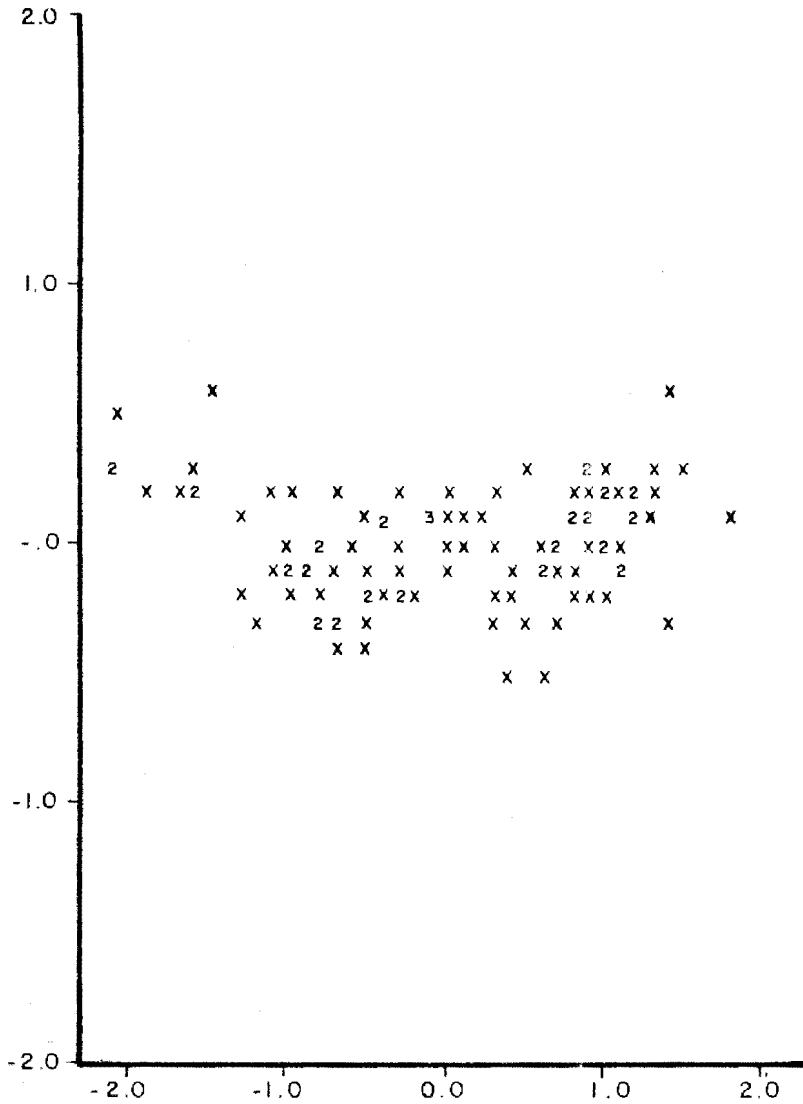


Fig. 28. Residuals for a hundred and seven data points indicating the near normality of the data.

correlates best with aerial biomass of trees.

All L. laureolum shrubs that had to be cleared from tracer belts that were made in preparation for the experimental burns were used for calculating the final regression equation.

Several regression lines were tested for goodness of fit. Transformations of the raw data (Fig. 26) to linearise the regression line were performed and tested for goodness of fit. A log-log transformation of the data fitted best and is generally the most appropriate transformation for biomass/diameter regressions (van Laar, pers. comm.). (Fig. 27).

A Durbin-Watson test for normality was performed and the results indicated that the data were near-normal (Fig. 28).

The regression equation adopted for calculating the biomass of L. laureolum from diameter measurements is: $\ln y = -2,29671 + 2,06495 \ln x$. Natural logarithms were used to be compatible with the Hewlett-Packard 9810 desk calculator available at Jonkershoek forest research station. An analysis of variance for the regression suggest that the linearity of the regression line is highly significant.

Analysis of variance.	D.F.	Sum of squares.	Mean square.	F. ratio.
Regression	1	281,56918	281,56918	2057,33951
residual	105	14,38039	0,13686	

The wandering quarter method (Catana, 1963) was employed to estimate the density of L. laureolum shrubs on the experimental plots. Diameter under the first branch was measured for every shrub encountered in the density survey. A mean biomass per



Fig. 29. Marked sprouting species on plot 2, the summer burn.

shrub was obtained and with the density figures a biomass per unit area calculated for L. laureolum on each experimental plot.

The initial surveys of the experimental plots indicated which species were relatively more important in the community. From the preliminary list ten species were selected and their vegetative, flowering and fruiting stages monitored. To facilitate the estimation of the peak periods in each phase, ten individuals of each species were marked and the percentage occurrence of each phenological stage monitored for the group.

Species survival was measured in two ways:

- (i) The ability of species to regenerate from dormant or protected buds was measured by marking species that are known to sprout and species known to be killed by fire (Fig. 29). Certain species were included in both categories of which the response to fire was only guessed. After the experimental burns the marked species were occasionally visited and finally assessed six months after the last winter rain for the season. Data consisted of lists of species that were either dead or had sprouted and were processed to yield percentage survival for each marked species.

Survival of species by seed was monitored by sampling the soil stored seed reserve before and after each experimental burn. Samples of surface soil were drawn at random on a randomly placed 50m line. Twenty samples were taken, mixed together, sieved through a 2mm² size sieve and "sown" one centimeter deep in ten commercial seed trays on a sterile sand medium. Each sample consisted of a 20cm x 20cm area excavated to a depth of 2cm. The soil was sieved to remove

large litter particles and seed. However no large seeds were recovered.

The seed trays were put on an open air shelf with micro-jet irrigation and a 30 % shade-cloth covering. Irrigation was regular, depending on the season, and a commercial hydroponic fertilizer was applied once a week. Data was subjected to an analysis of variance to test for significant differences in the response of the vegetation to fire in different seasons. L. laureolum regeneration was monitored by counting the number of seedlings in the three experimental plots after the fire on two occasions. The first count took place after the experimental burns, but before the first winter rains. The second count took place seven months after the winter rains commenced.

After the first experimental fire the growth rate of a number of species that sprouted shortly after the fire was measured. All the geophytes however developed drooping leaves that were kept at a constant length by the wind sweeping them over the sand. Subsequently the growth rate of only Restio egregius Hochst was measured. Measurements were taken during visits to the research site and not at specific regular intervals.

A Scholander bomb was obtained from the Fruit and Fruit Technology Research Institute (F.F.T.R.I.) in Stellenbosch to determine some water potential values for fynbos species. Unfortunately the bomb could not be borrowed in the summer season as F.F.T.R.I. used it extensively during that time of the year. Since the leaves of L. laureolum do not have petioles the water potentials of leafy twigs were determined for this study. The bark of the twigs were removed so that phloem exudate could not mask the xylem exudate (Poole and Miller, 1975). The daily course of water potentials were measured

in winter, mid spring and toward the end of spring. Measurement of water potentials were carried out after the early morning dew, that is prevalent during that time of year, had dried off. The water potential measurements were taken at hourly intervals from 10h00 to 16h00 in winter and until 17h00 in spring.

Fire intensity was measured according to a method described by Mc Arthur and Cheney (1965), but modified to suit the circumstances.

The formula:

$$I = Hwr$$

where I = fire intensity (watt/m)

H = heat yield (KJ/Kg)

w = weight of available fuel (Kg/m²)

r = rate of spread (m/s)

was employed to calculate fire intensity for the experimental burns.

Heat yield was determined with the aid of an adiabatic bomb calorimeter. A representative sample of the leaves and twigs of the most common species was milled and sub divided into 5 samples of 2g, 1,5g and 1g for the heat yield determinations. Initially the powdered plant material was compressed into a pill, but the pill would not remain intact and afterwards loose powder was used. Oxygen was let in slowly, to prevent the gas-flow dislodging plant material from the crucible, until a pressure of 30,4 bar was attained. Platinum wire and cotton thread served to ignite the plant material and 1cm³ water was put in the bomb to absorb acid vapours. The bomb was suspended in a water bath with a constant temperature of 22°C. After temperatures stabilized the plant material was ignited and a temperature reading taken as soon as the temperature

stabilized again. A table supplied the correction factors before converting the temperature difference into energy units (J/g).

Available fuel weight was taken from the biomass and litter-mass determinations. After the burns five clip-plot samples were taken from each plot to estimate the quantity of unburnt plant material. Visual estimates were made of the percentage of L. lauroolum shrubs that did not burn. A total weight of unburnt material was calculated and subtracted from the biomass data. The resultant figures were used for the weight of fuel in the fire intensity formula.

A different method than that proposed by Mc Arthur and Cheney (1965) was employed to determine the rate of spread of the fire. Maps were drawn of the experimental plots and a grid of pegs located in the plots. Twelve pegs were connected to weighted wires with pieces of nylon thread. As the fire advanced the nylon thread was burnt off and the time for each weight to fall was noted. Isolines of the fire front were then drawn and a mean rate of advance calculated for each fire. With all these parameters it was possible to calculate the intensity of each experimental burn.

6.1 OBJECTIVES AND HYPOTHESES

The main objective of this study was to determine the extent of the short-term response of fynbos towards fire in different seasons. It is necessary to define "the extent of the short-term response of fynbos towards fire." Short-term response



Fig. 30. Seedling on plot 3, the spring burn.

refers to the regenerative capacity of fynbos after a fire. That is, the rate at which sprouting species regenerate after a fire, and whether fire therophyte species can germinate and establish successfully from the soil stored seed reserve. The extent of regeneration may be defined as the rate at which the bare veld regains the structure and function of a mature fynbos community.

Secondary to the main objective was to describe the mature fynbos community as accurately as possible. This was done so that a direct comparison of the regenerating vegetation of the same area could be made on the newly evolving community. Such a detailed description of the fynbos also served as a basis for comparison of different fynbos types and other mediterranean type vegetations.

The hypotheses that were investigated are the following:

- (i) That seed regenerating species depend on a soil stored reserve of viable seed. (Wind blown seed and seed carried in by other means can only be considered as complimentary to soil stored seed, though it may play a definite role in the propagation of invading or migrating species.)
- (ii) That the return of sufficient vegetation cover to prevent excessive erosion is rapid enough to prevent habitat degradation.
- (iii) All species present in the mature fynbos succeed in regenerating successfully and that species diversity is even improved by a burning treatment.
- (iv) Regeneration proceeds rapidly through successive stages to reach the fynbos climax and sub-climax stage of development.



Fig. 31. An experimental burn in the Kogelberg State Forest.

6.2 LITERATURE

Fire recurs in fynbos communities at varying intervals under natural conditions (Pillans, 1924; Kruger et. al. 1977; Kruger, 1980). Under human influence fires occur frequently and fairly regularly (Marloth, 1924; Phillips, 1965). The seasons in which fires occur naturally are as a rule the hot and dry summers and autumns (Pillans, 1924; Kruger, 1979). Prevailing weather and accumulated fuel conditions are, however, the determining factors and fire may occur at any time of the year (Kruger et. al. 1977; Taylor, 1977; Kruger, 1980).

There are indications that because of a diverse phenology fynbos species have different responses to a fire in a given season. Research into the response aspect of fynbos to a burn, and to repetitive burns, have until very recently, been chiefly confined to observation.

Development of fynbos and allied plant communities after fire have been described by Michell (1922), Levyns (1923, 1929, 1935) Adamson (1935), Wicht (1945, 1948), Taylor (1969) and Martin (1966). Van der Merwe (1966) analysed fynbos communities after a late summer burn and reported in detail on modes of regeneration. Quantitative analyses of post-fire development of vegetation cover has been conducted by Kruger (1972) and the work is continuing.

6.2.1 SPECIES SURVIVAL

The concensus of opinion among the authors is that most fynbos species survive a fire as individuals through vegetative regeneration (Wicht, 1945; van der Merwe, 1966; Taylor, 1969). Sixty-seven percent of species



Fig. 32. Above: Nivenia stokoei
sprouting from
its rootstock.
Left: Geophyte regene-
rated from a
bulb.

in Swartboschkloof fynbos communities, for example, had the potential to regenerate vegetatively (van der Merwe, 1966). Quantitative studies on relative survival rates of sprouting species are not recorded in the literature. Van der Merwe (1966) claimed that all sprouting species regenerated after a February burn in fifteen-year-old fynbos in Swartboschkloof.

Wicht (1945) listed four ways in which fynbos species survive fire. These adaptive traits are also excellent ways to survive the arid summer and autumn conditions in a Mediterranean-type climate.

- (i) Geophytes; plants that sprout from underground organs (Fig. 32).
- (ii) Plants with the potential to regenerate from rootstocks.
- (iii) Species that survive the catastrophe of a fire in the form of seed.
- (iv) Well insulated plants (thick corky bark etc.) that regrow from dormant buds.

In the fynbos, a great number of species avoid fires and adverse climatic conditions by regenerating from seed only. Seeds are variously pre-adapted to survive in the seasonally arid climate and such adaptive strategies are well suited for survival in a fire-type vegetation.

- (i) Bradyspory or serotiny:

Seed is retained on the plant in a protective organ for at least one season after maturation. This is typical of many species in the Proteaceae and Bruniaceae. The strategy is best developed in the genus Leucadendron (Proteaceae) where the seeds are retained in hard, woody "cones" that may remain

on the plant for up to eight seasons.

When adult plants are killed by fire the serotinous organs open as the tissues dry out and seeds are released in a bare environment. There is, however, no evidence that heat is required for seed release as in Banksia species (Coaldrake, 1951).

(ii) Protected seed:

Certain Proteaceae such as Leucospermum species have seeds with hard impervious seed coats with various levels of inherent dormancy (Brown et. al., 1971). The seeds are released annually on ripening and can apparently survive fire on or in the soil. After a fire the seeds germinate readily.

Many Leguminosae, especially Aspalathus (Leguminosae) species, exhibit the same adaptive strategies. Agathosma species (Rutaceae) appear to be similar in this respect (Blommaert, 1977).

(iii) Abundant seed:

Species of the Ericaceae and Compositae have low shrubby growth-forms and typically shed copious amounts of seed annually. Their seeds are not protected in any special way although some seeds show symptoms of dormancy. Levyns (1956) found that a sufficient proportion of the abundant seed supply of Elytropappus glandulosus (DC.) Levyns, survived

a fire to re-establish the population. Martin (1966) contends that Erica chamissonis Kl. ex Benth. regenerates from windborne seed from sources outside the burnt area.

6.2.2 REGENERATION AND ESTABLISHMENT.

Plants that regenerate vegetatively after a fire begin to sprout within about fourteen days after a fire (Adamson, 1935; Wicht, 1948). The timing of a fire in relation to the phenology of the component species determines the rapidity and magnitude of the regeneration response.

The succession of life-forms and species after a fire was described by Adamson (1935). His findings may be summarised as follows:

- (i) After a fire there was an increase in geophytes and a small increase in annuals. Chamaephytes increased progressively with time.
- (ii) Species numbers also increased progressively and was larger than the original number six years after a burn.
- (iii) The immediate effect of a fire is the increase in the ratio of nanophyllous to leptophyllous nanophanerophytes. The former sprout freely while the latter regenerate only from seed.
- (iv) Graminoid-like hemicryptophytes increased while relatively broadleaved hemicryptophytes decreased after burning, giving a more xerophytic aspect to the vegetation.

Adamson (1938) found that a large number of annuals and small plants became temporarily prominent in the Kamiesberg, a zone of arid fynbos. Prominent species varied with the season of the fire and rainfall distribution patterns following it. There was no large increase in geophytes and regeneration of bushes commenced at once from either dormant buds or from seed.

Wicht (1948) analysed the early post-fire response of a fynbos community in detail. Effects of burns in January to April (summer and autumn) were tested in a statistically designed experiment. He reported on results for data gathered in the succeeding winter and spring. Sprouting of grasses commenced within a week after the burns, and shrubs sprouted within three weeks, in spite of hot dry conditions. According to Wicht (1948) sprouting accelerated after the first rains in April, germination began and geophytes began to develop foliage. "The experiment provided no evidence at this stage that germination of seeds and development of geophytes were either promoted or retarded by fire" (Wicht, 1948).

In Wicht's experiment at Jonkershoek (Wicht, 1948) sprouting shrubs had not flowered at the time of the last enumeration in spring, except for quadrats burnt in January (summer burn). Wicht (1948) came to the conclusion that "burning in the late summer or autumn might cause sprouting species to miss the flowering season in spring, or at least delay flowering considerably." Unfortunately Wicht did not publish any further results on his experiment.



Fig. 33. An example of an immature cone of L. laureolum desiccated after a fire.



Fig. 34. Mature cones of L. laureolum are consumed by fire in a great number of cases. These cones are mostly seedless.

6.2.3 DEVELOPMENT OF THE COMMUNITY.

A much later description of post-fire development of a fynbos community by Taylor (1969) was based on general observations. In general it can be said that in the early stages after a fire community stratification is simplest and becomes more complex with advancing age. "Floristically, the community is richest two to five years after fire when annuals, geophytes, sprouting perennials and seed-regenerating shrubs all occur together. In subsequent stages the last-named predominate while the other three classes become moribund and eventually die out ". According to Taylor (1969) all the layers become moribund after twenty years of protection from fire. Qualifying the last statement Taylor (1969) notes that "on more level, less rocky ground (at Cape point), fynbos may be self-perpetuating by regeneration of the early stages in openings caused by the death of shrubs in the mature community."

This account is largely supported by those of Adamson (1935), Wicht (1945), Hall (1959) and Kruger (1972).

Kruger (1972) studied the response of fynbos communities quantitatively. He found that rapid regrowth followed on burns. Both canopy and basal cover reached 70 to 90 percent of original levels within 25 to 30 months after fire. Sprouting graminoid and restioid species contributed most of the cover at this stage. In a later publication Kruger (1977) reported on the early post-fire growth response of

fynbos communities. Phreatic communities grew at a rate of about 4 000 kg per hectare per annum in the first five years, whereas low shrub communities on relatively dry sites had rates of increment as low as 1 000 kg per hectare per annum over the same period. Young stands are dominated by hemicryptophytes which comprise 2 000 to 6 000 kg per hectare or approximately 60 to 75 percent of the biomass in stands four years of age. The hemicryptophyte element persists and is still significant at an age of sixteen years, although it declines relative to shrub biomass.

6.2.4 EFFECTS OF FIRE RÉGIME

Fire régime can be considered under the following headings:

- (i) Fire intensity.
 - (ii) Frequency of fire.
 - (iii) Season of fire occurrence.
- (i) The effects of fires of different intensities have not been studied in the fynbos. An attempt to measure the temperatures of fire in the Cape fynbos failed because the equipment used did not perform up to expectation (Taylor and Kruger, 1978).
 - (ii) Reports on the effects of fires in the fynbos have been on single fires over a vast region. There has up till now never been a comprehensive study of the effects of successive fires at different intervals and in the different seasons. Much has been written on the purported degradation of the Cape fynbos



Fig. 35. An experimental burn in the Kogelberg State Forest.

vegetation by several generations of veld burning practices by herdsman and farmers (Botha, 1924; Marloth, 1924; Pillans, 1924; Compton, 1926, 1934; Jordaan, 1949; D'ewes, 1960; Jordaan, 1965; Joubert, 1977; Taylor, 1977).

- (iii) A number of articles appear in the literature concerning the consequences of fires in specific seasons in the Cape fynbos vegetation (Rycroft, 1947; Wicht, 1948; Jordaan, 1965; Phillips, 1965; Taylor, 1978).

6.2.5 STRUCTURE OF FYNBOS COMMUNITIES

The structure of vegetation is a complementary concept to function (Mueller-Dombois & Ellenberg, 1974), and is essentially the three-dimensional arrangement to individual species in space and the forth dimension, time (Gimingham, 1972). The two major components of structure in vegetation are pattern and stratification. Pattern is the horizontal dispersion of species and species populations while stratification is the vertical distribution of species and species populations (Gimingham, 1972).

Very little quantitative data on fynbos community structure is available. The unusually high species diversity of fynbos communities is often mentioned in the literature (Wicht, 1945; Acocks, 1953; Boucher, 1972; Werger et. al., 1972). Pattern in fynbos vegetation is very complex and is made even more complex by large numbers of endemic

species that occur on single or multiple isolated spots. Quantitative data on the life-form composition of medium and tall shrub communities are presented by Adamson (1938), Rycroft (1953) and van der Merwe (1966).

Adamson (1931) described a fynbos community approaching the climax for fynbos on Table Mountain (Cape Town). He listed the life-forms with percentage species and percentage aerial cover in each life-form as follows:

Life-form	% of species	% aerial cover
Microphanerophyta microphylla	1	14, 175
Nanophanerophyta nanophylla	7	0, 437
Nanophanerophyta leptophylla	15	9, 0
Nanophanerophyta with compound leaves	2	0, 375
Chamaephyta microphylla	1	-
Chamaephyta nanophylla	6	0, 187
Chamaephyta leptophylla	12	0, 5
Chamaephyta with compound leaves	1	-
Hemicryptophyta with assimilating stems	9	6, 875
Hemicryptophyta with "grass habit"	10	0, 93
Others	35	2, 5

Rycroft (1953) found that hemicryptophytes had the highest mean species density and were closely followed by geophytes. The following order of mean species densities are reflected by his data:

Growth-form	Species density
Hemicryptophytes	2,845
Geophytes	2,270
Nanophanerophytes	1,600
Chamaephytes	1,260
Therophytes	0,240

Other life-forms were poorly represented and therefore not included. Van der Merwe (1966) analysed life-forms in Swartboschkloof (Stellenbosch) and his findings are summarized in Table XVI.

Table XVI. Comparison of life-form spectra of Swartboschkloof with the normal spectrum drawn up by Raunklaer.

	S	E	MM	M	N	CH	M	G	HH	Th
Normal spec-										
trum %	1	3	6	17	20	9	27	3	1	13
Swartbosch-										
kloof	0	0,7	0	6,0	27,0	30,8	15,8	15,2	0,2	3,6

S = Succulents

E = Epiphytes

MM = Macrophanerophytes

M = Microphanerophytes

N = Nanophanerophytes

Ch = Chamaephytes

H = Hemicryptophytes

G = Geophytes

HH = Helo- and Hydrophytes

Th = Therophytes



Fig. 38. Plot 8 on the research site with a tracer belt in the fore-ground. A general view of the fynbos vegetation.

It is clear from the table that the fynbos community at Swartboschkloof has a high percentage of geophytes and chamaephytes. This is not considered to be an unusual life-form distribution and can safely be assumed to be fairly characteristic for fynbos vegetation in general.

6.2.6 SEASONALITY

Periodic occurrences such as flowering of species in the fynbos is usually accompanied by a specific seasonal aspect for the vegetation. In California it was found that shrubs and herbs flower abundantly in spring and early summer, though representatives of the community flower throughout the entire year (Mooney et. al., 1973). "Some species flower prior to their growth phase, whereas others flower either during or subsequent to their growth phase (Mooney et. al., 1973).

The same general trend can be identified in fynbos vegetation and its communities. Flowering of certain species are regular for a particular season only, while a large percentage of the species flower throughout the year. Percentages of species flowering in different months of the year have been given by Rycroft (1953) and van der Merwe (1966). Table XVII summarises the phenology data available for the fynbos in Jonkershoek valley near Stellenbosch and it is compared with data for California (Mooney et. al., 1973).

Total species were 298, 448 and 519 respectively for Biesievlei, Swartboschkloof (both in Jonkershoek near Stellenbosch) and California. Swartboschkloof shows peak flowering in September and Biesievlei in November. This difference

Table XVII. Percentage of species flowering in different months:

	Biesie vlei <i>Coelocarpus</i> (Rycroft)	Swartboschkloof (van der Merwe)	California (Mooney)
J	12,4	17	5,0
F	7,7	17	11,2
M	6,7	15	33,9
A	12,8	9	57,6
M	11,1	16	74,0
J	14,1	24	67,1
J	20,1	27	47,3
A	30,5	33	32,6
S	33,6	36	22,3
O	34,9	31	12,6
N	39,9	24	4,5
D	27,5	20	2,7

is attributable to a difference in aspect. Swartboschkloof has a general aspect facing north-east whereas Biesievlei is the direct opposite, facing south-west.

6.2.7 FIRE AND NUTRIENT POOR SOILS

Very little is known of habitat factors and the physiological response of the fynbos vegetation to these. The fynbos environment is very low in nutrients which is like Australia, but not like California, Europe and Chile. In Australia Specht et. al., (1957) investigated adaptation of vegetation to low nutrients. He indicates that where the substrate is very infertile, nutrients steadily accumulate in the underground organs of plants, often at the expense of aerial organs. The translocation of many nutrients (N, P, K, Ca, Cu, Zn and Mn)

to aerial organs may be greatly reduced, that of some elements almost to zero. This must contribute greatly to the decreasing growth rate of the above ground organs of the plants as they grow older. Species with greater nutrient requirements will succumb earlier in the pyric succession than those in which the concentration of nutrient elements are relatively low. Schutte (1960) made some observations on trace element deficiencies in the fynbos vegetation at the present time. He theorised that the impoverished effect observed for the soil is caused by frequent burning of fynbos.

6.3 COMMUNITY STRUCTURE

Vegetation can be described in a number of ways according to different methods, some of which are: physiognomy, biomass structure, life-form structure, floristic structure and stand structure (Mueller-Dombois and Ellenberg, 1974). Physiognomy refers to the sum total of vegetation structure and function. The physiognomy of fynbos is not easily paralleled in other plant formations of the world (Taylor, 1977) though it is broadly similar to that of other mediterranean type vegetations. A formal physiognomic description of fynbos according to the tentative Physiognomic-ecological Classification of Plant formations of the Earth (Mueller-Dombois and Ellenberg, 1974), reads as follows:

Formation class: Scrub. (Shrublands or thickets). Mainly composed of caespitose woody phanerophytes 0,5 - 5 m tall.

Shrubland: most of the individual shrubs not touching each other, often with a grass stratum. (For fynbos grass must be substituted with restioid (author)).

Thicket: individual shrubs interlocked.

(Both of the above divisions are applicable).

Formation subclass: Mainly evergreen shrub.

Formation group: Evergreen broad-leaved shrubland (or thicket).

Formation: Evergreen broad-leaved sclerophyllous shrubland (or thicket). Dominated by broad-leaved sclerophyllous shrubs and immature trees (i.e., chaparral or macchia). May often merge with parkland, grassland or heath.

In a footnote it is stated that additional units may be distinguished. Since the fynbos vegetation is unique the following sub division will serve to distinguish it from similar vegetation types in the physiognomic description.

Subformation: with a restioid-ericoid substratum.

(This classification was chosen because it is the consensus of a number of notable ecologists that it holds promise for becoming a standardized system of physiognomic classification).

Both Kershaw (1964) and Shimwell (1971) distinguish three constituents of vegetation structure namely:

- (a) Quantitative structure (abundance)
- (b) horizontal structure (pattern) and
- (c) vertical structure or stratification into layers.

Mueller-Dombois and Ellenberg (1974) consider the first two components as part of floristic structure since they are described with reference to species rather than growth-form. They consider stratification as part of biomass structure because it relates specifically to the height and spacing of plants in the composite and complex vegetation matrix.

For the purpose of this study the two approaches were married to a degree and vegetation structure is described under the following headings:

- 6.3.1 Species diversity
- 6.3.2 Pattern
- 6.3.3 Stratification
- 6.3.4 Quantitative structure

Stand structure is described according to each of the above mentioned categories for every experimental plot.

Shimwell (1971) includes a further dimension when referring to "structure in time," but in this work consideration is given to spatial structure only.

6.3.1 PATTERN

Greig-Smith (1957, 1964) states that a study of the causal factors determining the distribution of plants and vegetation is a prime objective of ecology. Three types of factors determine the distribution patterns of species and vegetation, and may be grouped under two headings.

1. Environmental Factors: Differences in light, soil depth, nutrient availability, pH and drainage along with micro relief are obviously responsible for some pattern in species and vegetation distribution.
2. Intrinsic Factors:
 - a. Sociological influences; such as shading or parasitic dependence can be readily identified in the veld, and includes all species interrelations.
 - b. Morphological adaptations: the reproductive ability of species and populations, both sexual by spores and seeds or vegetative by rhizomes, are responsible for local distribution patterns.

"It is commonly stated that the rarer species in a community, unless propagated vegetatively, are randomly distributed" (Greig-Smith, 1964).

Some factors remain constant at any specific time in a given area of any size, ^while others will vary from point to point at the same time. The number of constant factors becomes greater as the given area is reduced in size. A small change in some factors may influence plants drastically, depending on the level of such a factor in the tolerance range of the species or community. Performance or survival of species and communities are determined by factors having a disproportionately large effect on the plants. The distribution of species within the community and the community distribution, may then be governed by the particular factor or factors. "We may thus put forward the hypothesis that departure from randomness of distribution of a species indicates that one or few factors are determining the performance or survival of the species" (Greig-Smith, 1964).

No two species have exactly the same ecological and sociological

amplitude. Analysis of vegetation samples through tabular comparisons or mathematical correlations show that some species are so similar in their distribution and ecological requirements that they can be combined into groups. Obtaining such a grouping of species is the first step to an orderly arrangement of plant communities in the context of species composition. A third method for determining species groups is by studying the environmental response of the species. "This method, however, requires a considerable knowledge of the environmental relations of all plant species" (Mueller-Dombois and Ellenberg, 1974). It is therefore not applicable in the initial stages of the research of vegetation in a given area. As ecological knowledge of an area progresses, this method gains importance because it supports the search for the causes of plant distribution and pattern.

An important implication of the concept is that the species of an ecological group must also be closely similar in their life-forms. The scales of pattern of a number of fynbos species were investigated and the results are outlined in table XVIII.

Table XVIII. Positions of variance peaks for percentage cover estimates of different species.

Species	Block size (m ²)	1	4	8	16	32	64
Leucadendron lauratum		x			x	x	
Restio egregius			x		x		
Erica pulchella		x			x		x
Leptocarpus hyalinus		x			x		x

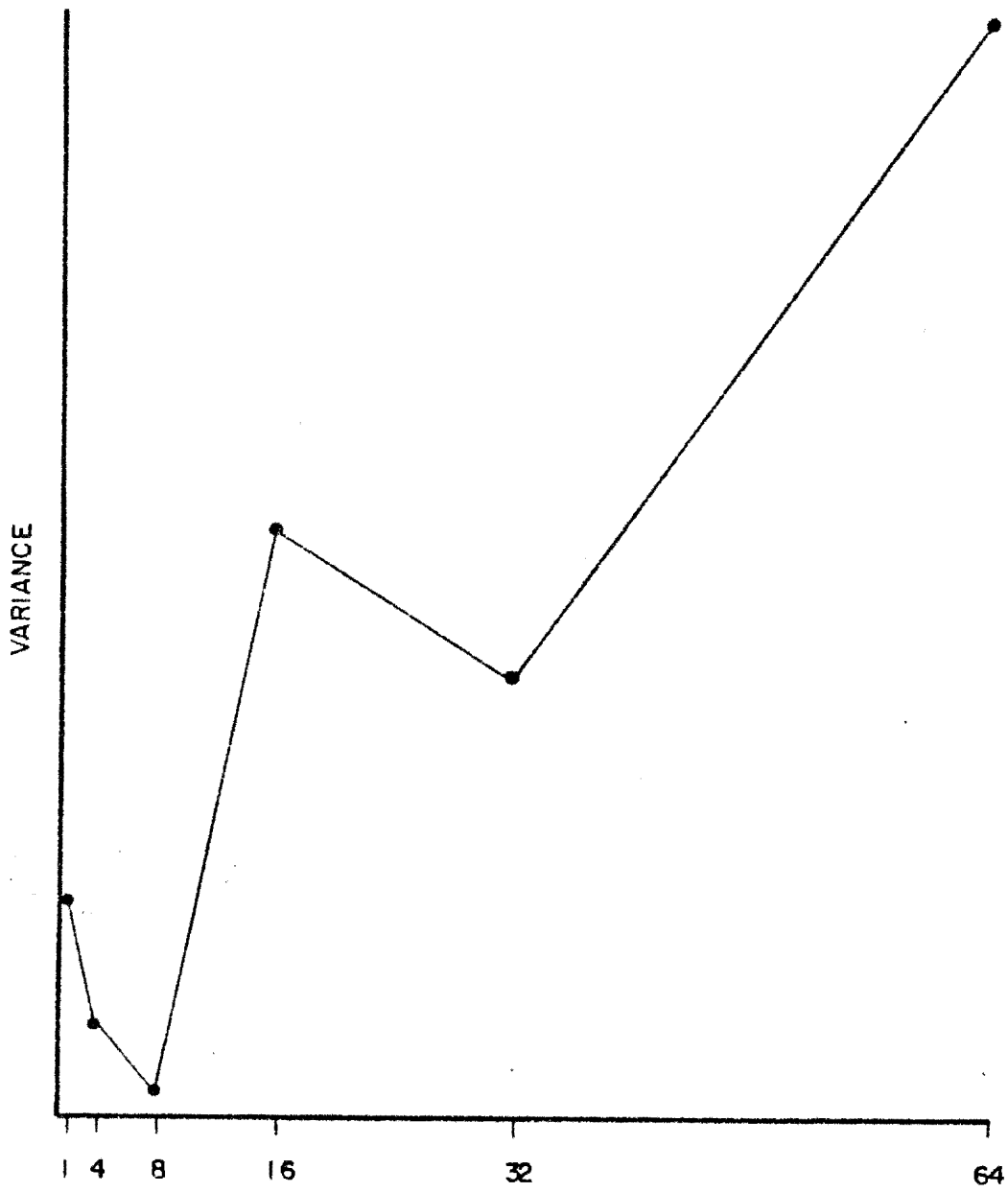


Fig. 37. Mean square (variance) over block size of the quadrats for *L. laureolum*

According to Kershaw (1963) Primary peaks are equivalent to the size of a morphological unit. L. laureolum is generally larger than 1m^2 but smaller than 4m^2 . E. pulchella and L. hyalinus are generally smaller than a square meter but clumps and contagious tussocks (respectively) of the two species may easily exceed one square meter and can be considered as "morphological" units. R. egregius does not form single tussocks of 4m^2 but contagious tussocks can cover to more than three quarters of the area. Secondary peaks at 8, 16 and perhaps 32m^2 is thought by Kershaw (1963) to be the result of competition between species and is present in most associations between species. Sociological pattern is the result of interspecific competition. Mean square peaks in block sizes of 32, 64 and 128 are considered to be tertiary peaks and reflects the size of the clone or clump of the species. Alternatively tertiary peaks can be ascribed to more obscure ecological and historical factors.

Greig-Smith (1964) came to the conclusion that the higher the peak the greater the intensity of pattern. In random samples it will correspond to a measure of non randomness. It is clear from table XVIII and figure 37 that non randomness is only apparent in block sizes exceeding at least 32m^2 for undergrowth and perhaps 64m^2 for the tall shrub stratum of L. laureolum. The table is only accurate for L. laureolum data since it is the only species with a mean cover percentage of more than 10%. According to Greig-Smith (1964) cover values of less than 10% are only reliable when the units are small enough to give maximum sensitivity.

Results for four treatments of the vegetation data, Reciprocal averaging (RA), complemented coefficient of community, Percentage difference and Euclidian distance, are in agreement, in that no

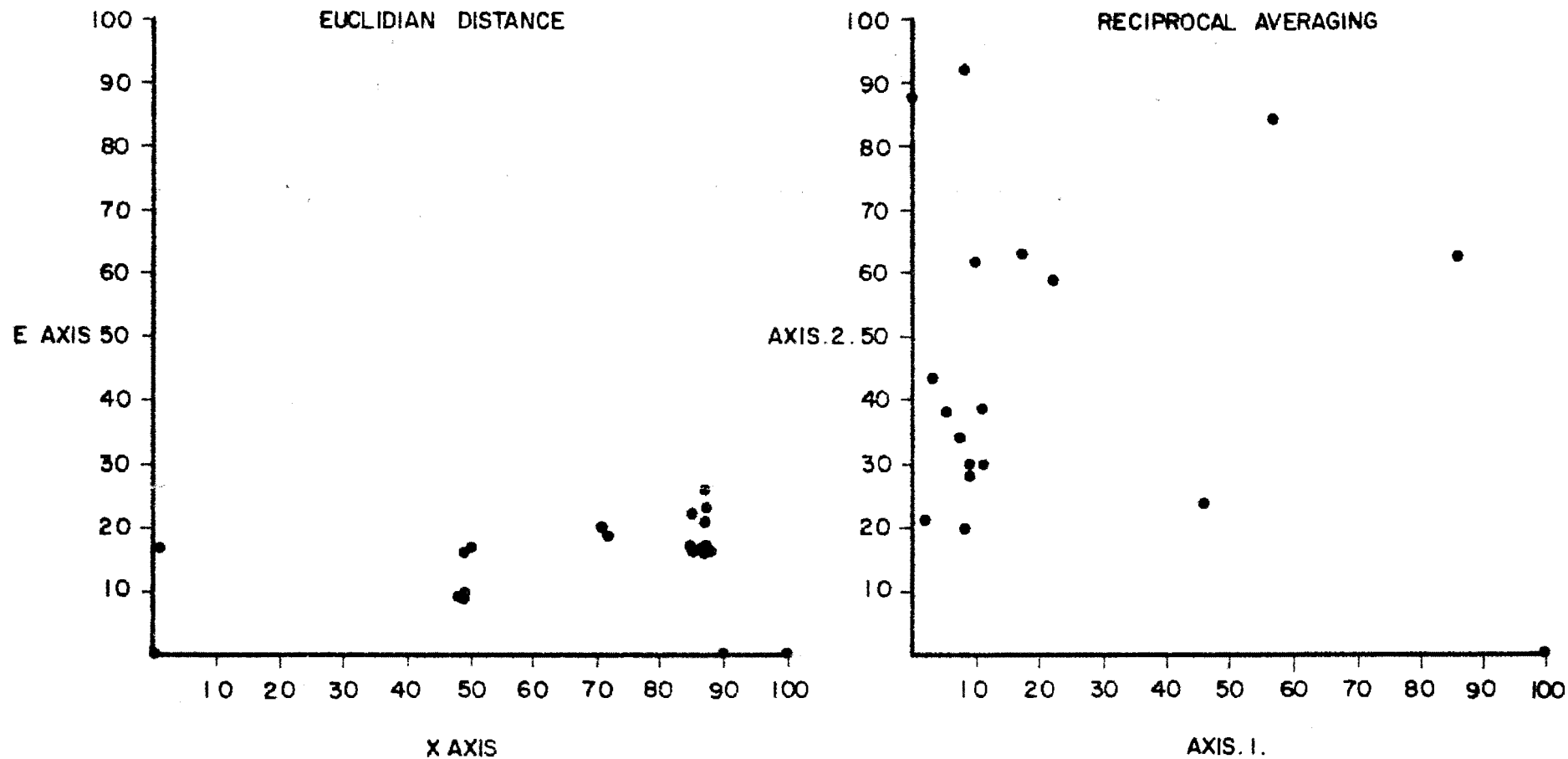


Fig. 38. Results of different ordinations for B.B. surveys on plot 3 (left) and plot 4.

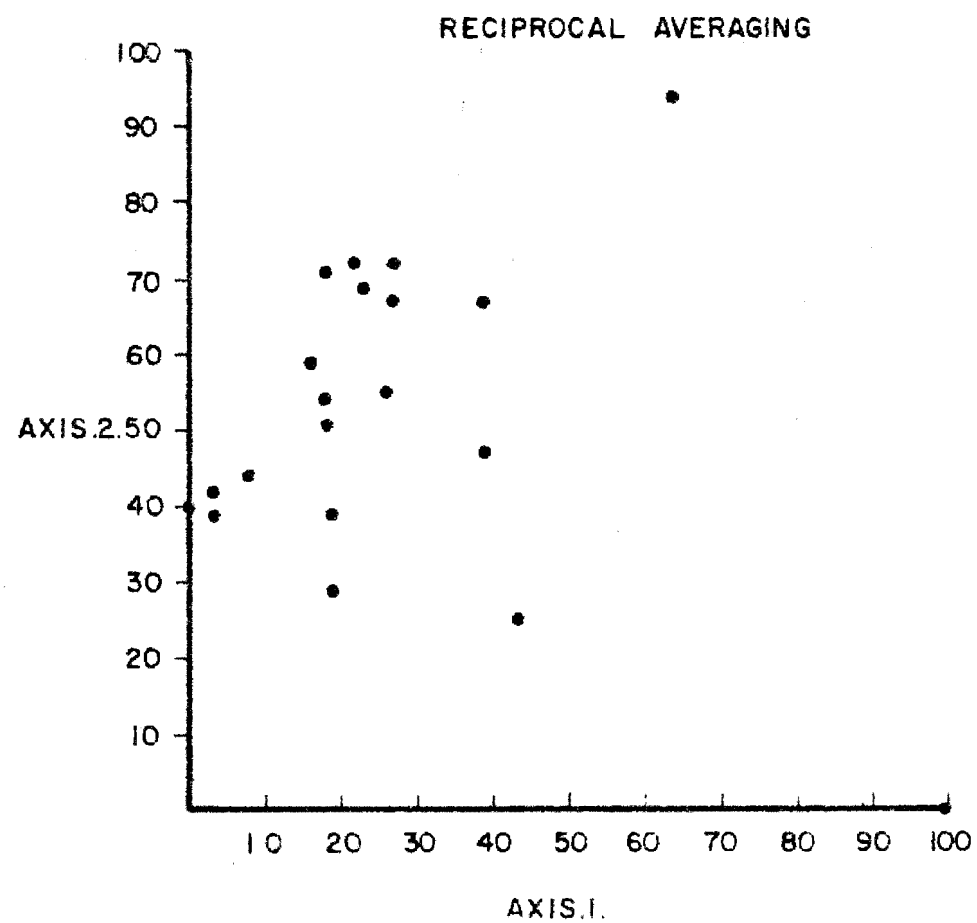
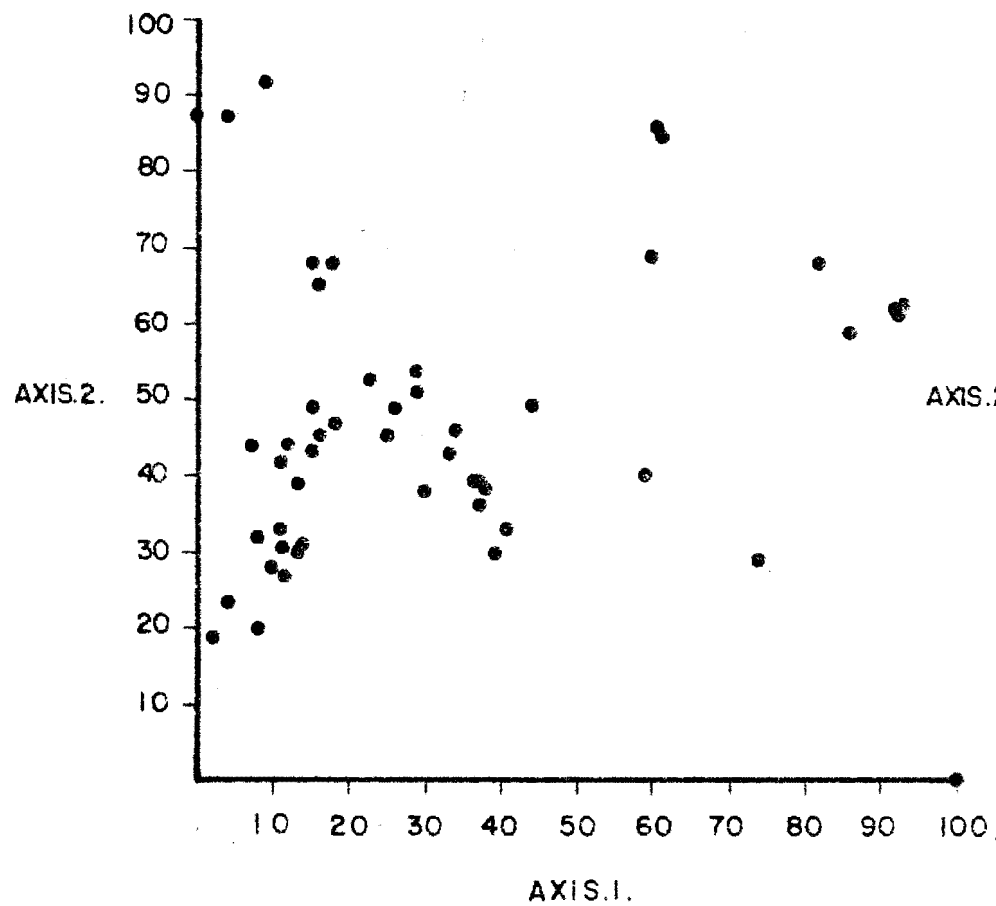
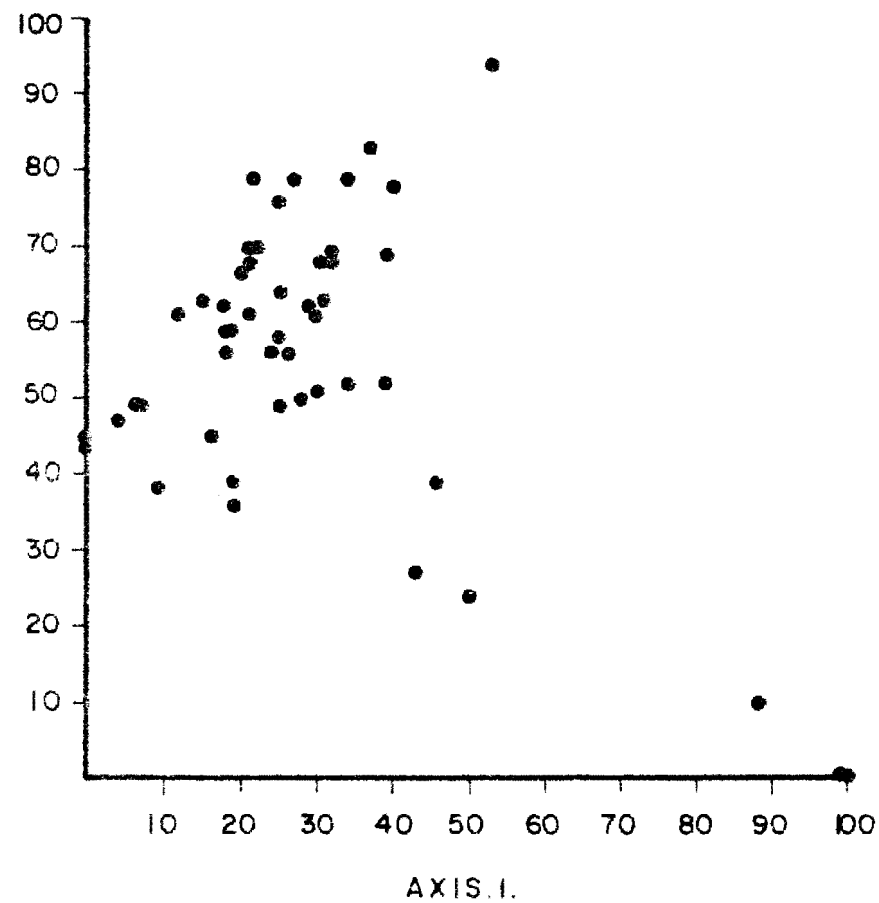


Fig. 39. Ordination results for plot 2 quadrats



PLOT4 SPECIES



PLOT2 SPECIES

RECIPROCAL AVERAGING

4m PLOTS

Fig. 40. Ordination results for the species of the different plots.

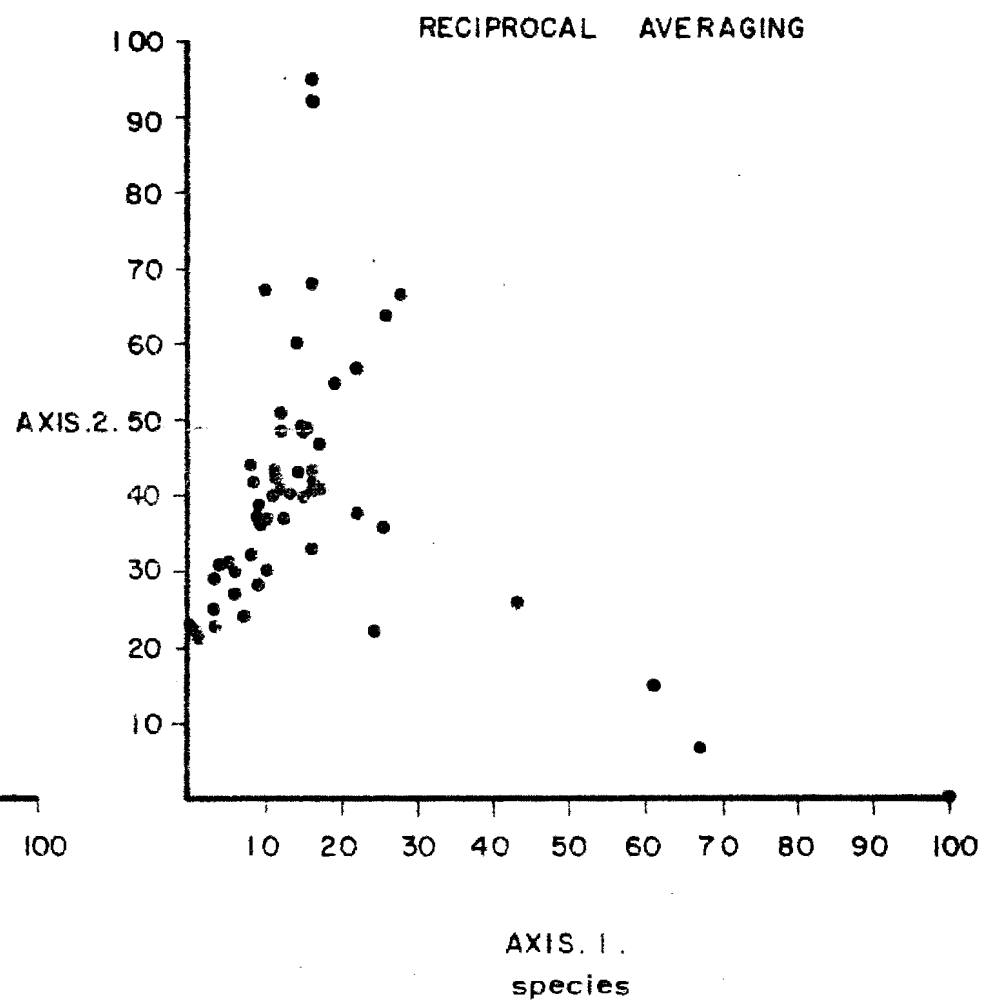
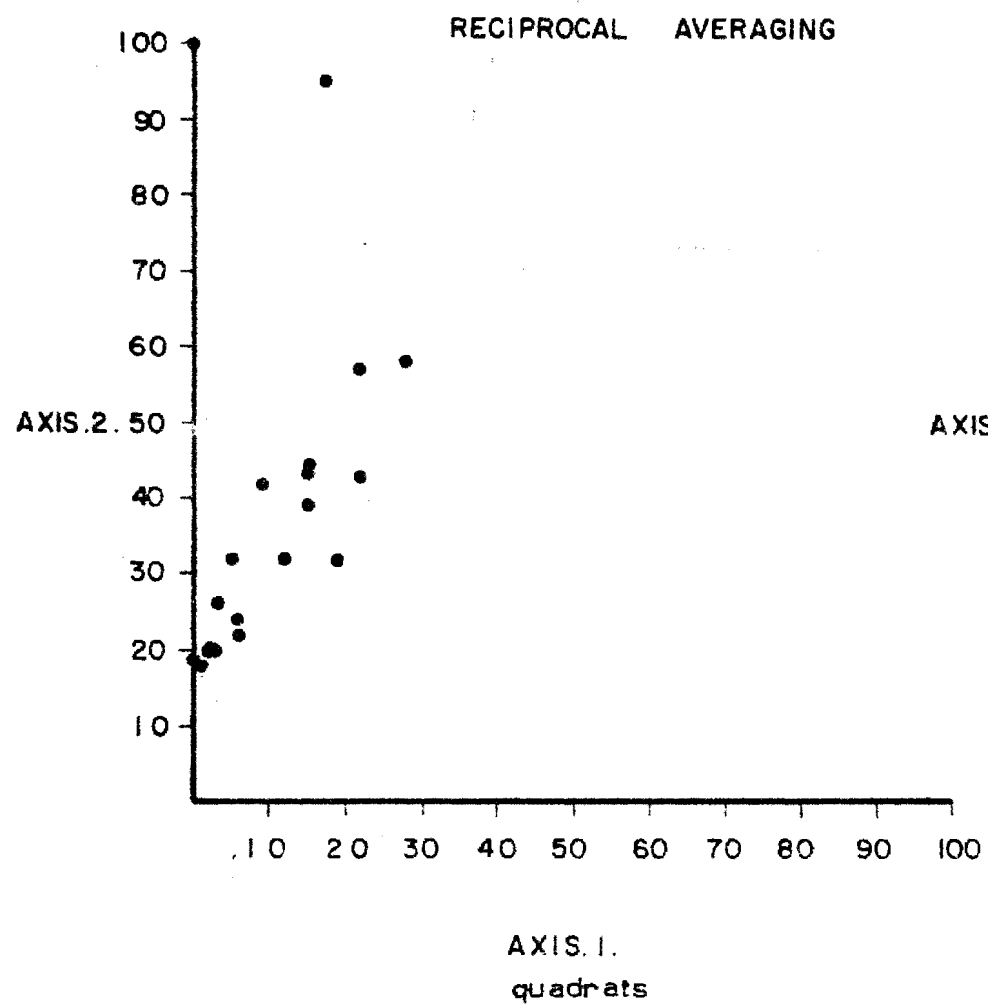


Fig. 41. Ordination of species and quadrats on plot 3.

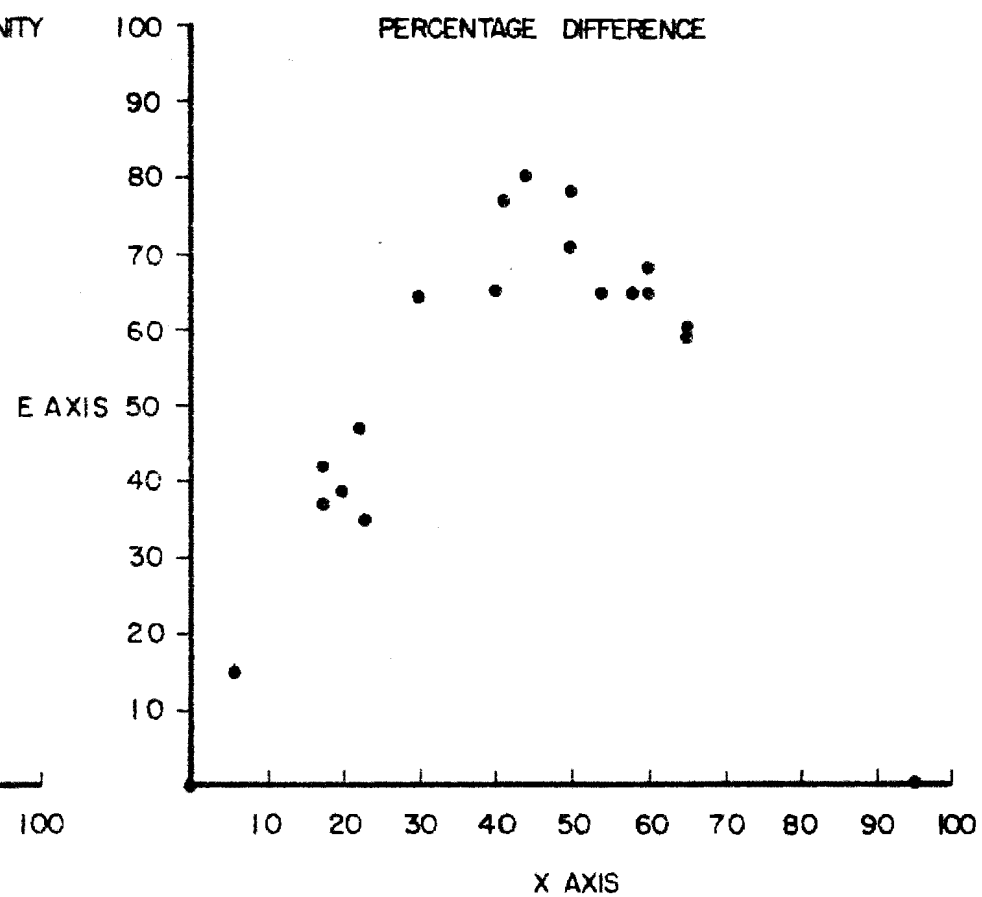
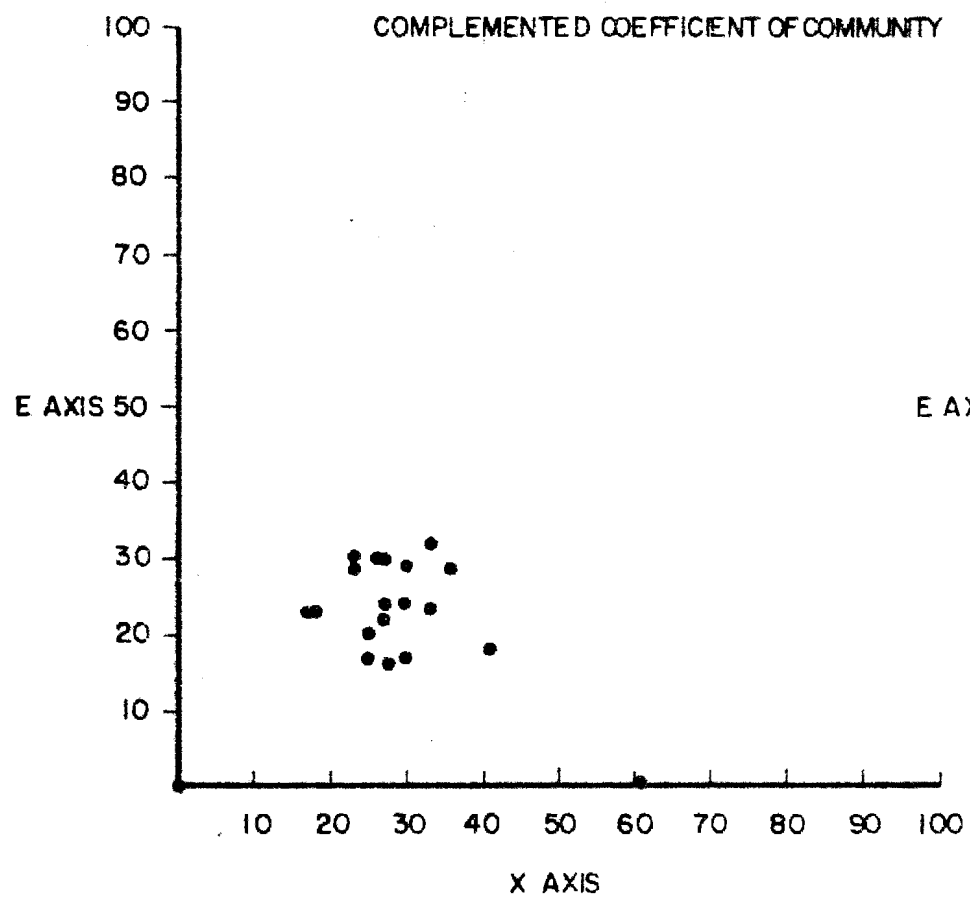


Fig. 42. Ordination results for plot 3.

definite trend exist in the vegetation of the plots. (Figs. 38 - 42). There is, however, a very weak trend that correlates well with shallow soils and dryness on plots. When inspecting the data matrix as arranged by the Cornell CEP 20c programme it is again only possible to discern a very weak trend that may be correlated with dryness and more mesic conditions. (Fig. 42 - percentage difference).

An attempt was made to detect interspecific associations according to the method described by Agnew (1961). Very few deductions can be drawn from table XIX because the number of quadrats (20) sampled is too small for any valid inferences. The relatively large quadrat size ($4m^2$) may also be responsible for the great number of correlated species-pairs (Kershaw, 1964). Table XIX is therefore an absolute relection of the species correlations in $4m^2$ plots. According to Greig-Smith (1964) five percent of the species correlations may be attributed to chance. It is however apparent that the following species are consistently well correlated with all the other species;

Erica pulchella

Restio egregius

Erica corifolia

Phaenocoma prolifera

Restio curviramis

Elegia vaginulata

Leptocarpus hyalinus

Erica imbricata

Sympieza articulata

Willdenowia lucaeana

Such a high degree of species correlations can only be possible with very constant species that are randomly distributed or occur in great

numbers. Field observations confirm that all the species occur in great numbers except Willdenowia lucaeana that may be randomly distributed.

An analysis of larger numbers of quadrats may yield more significant results. Since fynbos is not characterised by single species dominance but more life-form dominance, it is suspected that life-form correlations may yield much more significant results. Time prohibited the exploration of that possibility.

The experimental plots may then be considered comparable in physiognomy, pattern and species association.

6.3.2 STRATIFICATION

Life-form, periodicity and stratification are usefull parameters for describing the physiognomy of vegetation (Chapman, 1976). Stratification is an important structural measure, characterising the vertical distribution of growth forms and species in a community. On a local scale the structural approach can be used to simplify and describe the organization of complex vegetation types. Layers are described in terms of height, and floristic information may be used to supplement this preliminary description.

Because the study was done intensively, the vegetation strata were divided into two distinctive entities namely: a tall shrub stratum consisting mainly of Proteaceae, and a small shrub and herbaceous layer with a mixed composition.

- ◇ MALE L. LAUREOLUM
- ◇ FEMALE L. LAUREOLUM
- ♀ PHAENOCOMA PROLIFERA
- ♀ L. LAUREOLUM SEEDLINGS AND SMALL SHRUBS

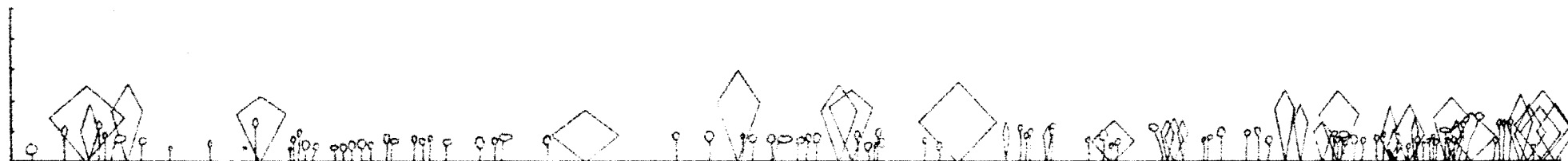


FIG. 44. SCHEMATIC DIAGRAM OF THE STRATIFICATION OF SHRUB AND SUB SHRUB SPECIES IN THE KOGELBERG STATE FOREST

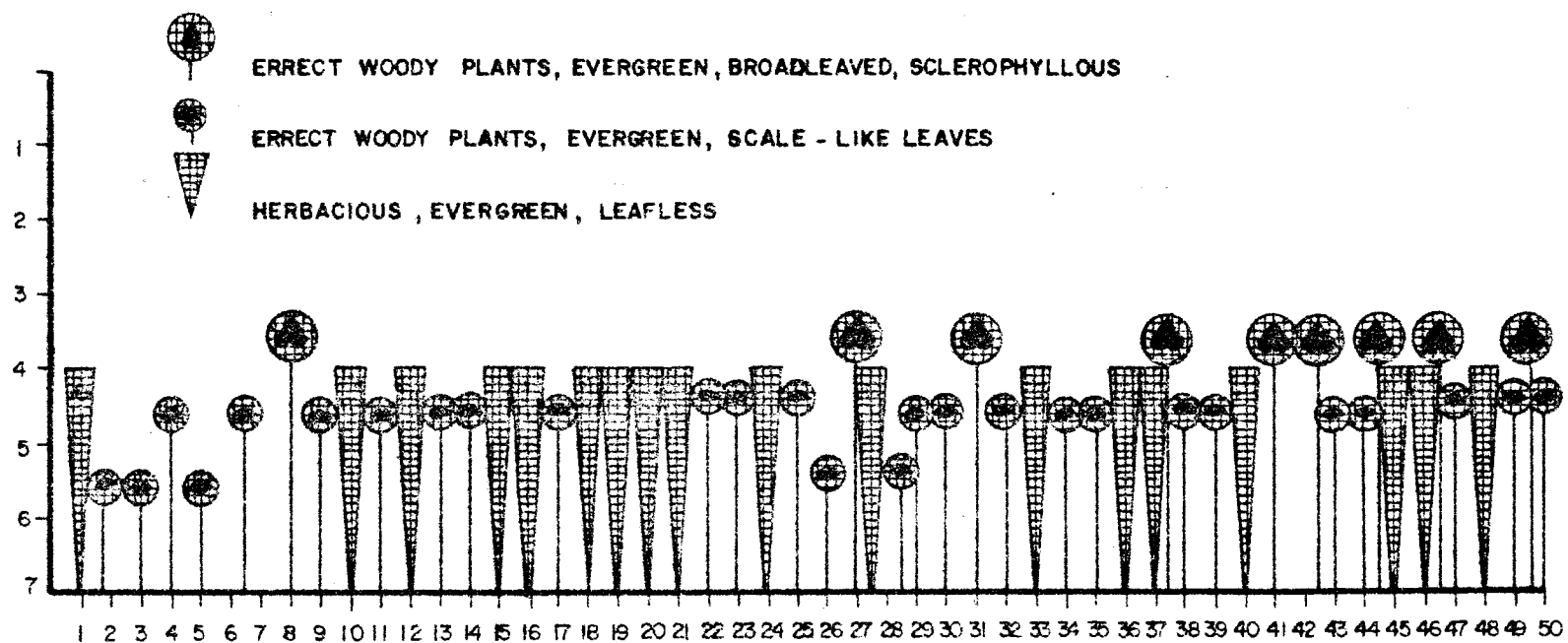


Fig. 45. Schematic presentation of stratification in fynbos according to a technique developed by Danseneau, 1958.

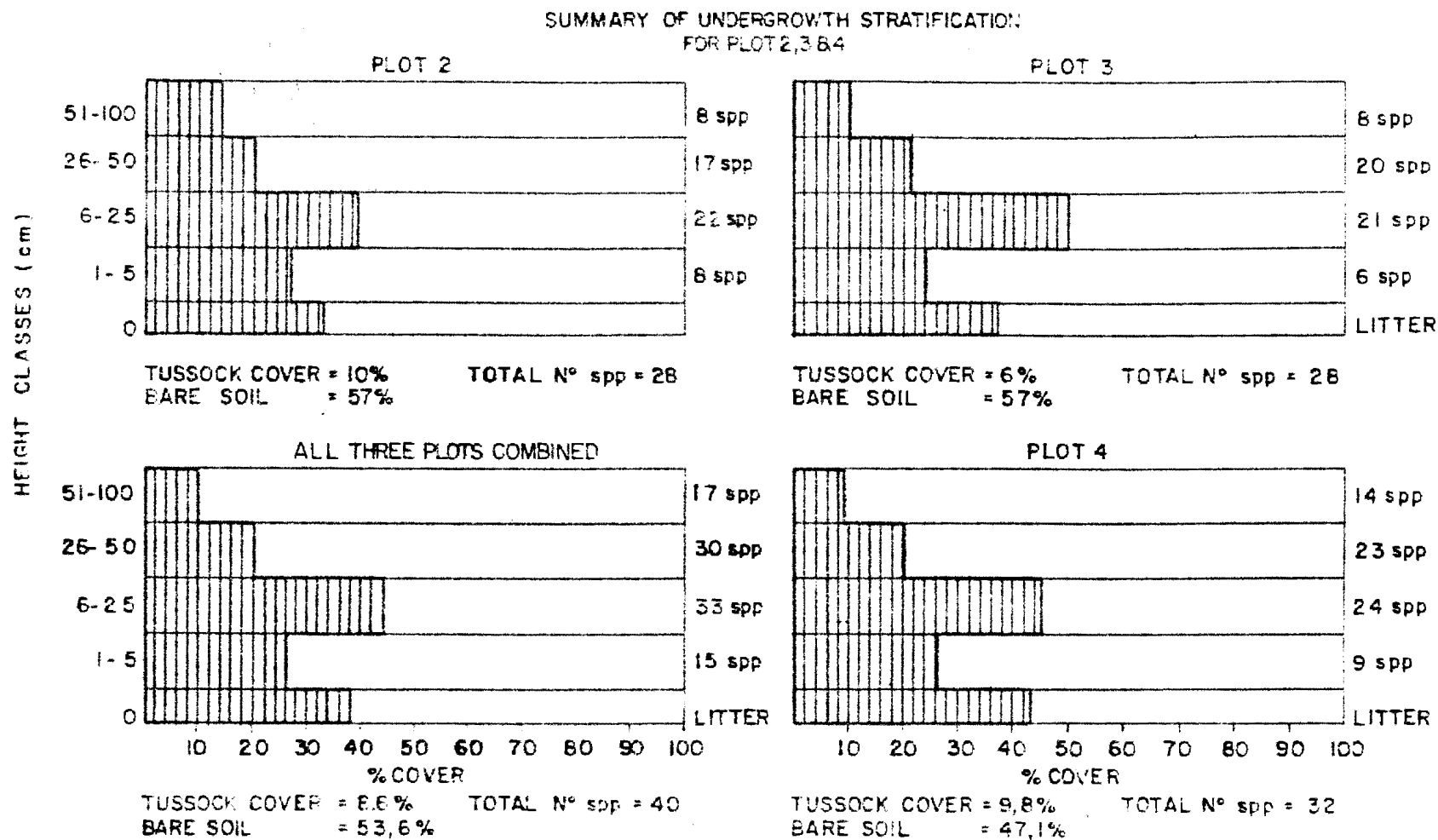


FIG. 46. SCHEMATIC SUMMARY OF STRATIFICATION OF THE UNDERGROWTH IN HEIGHT CLASSES

Fig. 44 is a transect of plot 2 that is 50m long and 4m wide. Definite clumps of L. laureolum can be identified. There is very little separation between the different strata but only the undergrowth is near-continuous and occasionally form a closed canopy layer. Fig. 45 is a profile diagram of the same transect according to the graphic representation as suggested by Dansereau (1958). Since the study is aimed at understanding the reaction of fynbos to fire treatments, the presence of dead material or fuel, was recorded in all the sub-strata. The vertical distribution of dead material is not uniform, but greatly concentrated in the lower 25cm of the herbaceous stratum (Table XX). Included in the next table are records of the ground cover, be it bare soil, litter or tussock (Table XXI). Less than ten per cent of the ground cover consists of restioid or grass tussock, and it is an indication of a relatively low basal cover in fynbos. Fig. 46 is a layer diagram of the fynbos understory showing the number of species responsible for the corresponding biovolume concentration in each layer. The 0 - 5 cm is designated as the "moss layer" after Mueller-Dombois and Ellenberg (1976), although mosses were not encountered in the survey.

L. laureolum is the dominant tall shrub in this fynbos community, in the context of stratification by height and growth form. L. laureolum does not, however, exclude vegetation under its canopy. The understory vegetation consists of restioid hemicryptophytes, ericaceous small shrub and few herbaceous species. Biovolume concentration is highest in the 6 - 25 cm layer and most species occupy part of that vertical space. It coincides with the maximum concentration of aerial

Table XX Stratification of species and fuel in a fynbos community.

Three hundred points were surveyed.

Spp/fuel	Layers	0-5 cm	-25 cm	-50 cm	-100 cm
		%	%	%	%
Litter		92,77	50,41	23,30	13,14
<u>Tall shrubs</u>					
Leucadendron laurifolium				1,15	21,14
<u>Sub-Shrubs</u>					
Erica corifolia		0,70	6,71	5,90	1,71
Erica pulchella		0,47	4,66	20,94	24,00
Blaeria dumosa		0,23	2,61	2,06	
Serruria inconspicua			0,27		
Phyllaea lasiocarpa			0,55	2,06	
Erica gysbertii			0,27	0,29	
Metastasia sp.			0,14	0,29	
Sympiezia articulata			3,15	5,90	4,57
Nagelocarpus serratus			0,82	1,77	0,57
Erica imbricata				0,59	
Nebelia paleacea				0,88	0,57
Phaenocoma prolifera				0,29	9,13
Polygala garsini					1,14
Salvia sarcocolla					0,57

Table XX (continued)

Spp/fuel	Layers	0-5 cm	-25 cm	-50 cm	-100 cm
		%	%	%	%
<u>Restioid</u>					
<i>Restio curviramis</i>		1,63	6,31	1,18	
<i>Willdenowia lucaeana</i>		0,93	1,23	4,42	
<i>Elegia parviflora</i>		0,23	1,64	4,42	
<i>Elegia vaginulata</i>		0,23	1,64	0,88	
<i>Elegia racemosa</i>		0,23	1,51	1,47	
<i>Thamnochortus dichotomus</i>		0,70	3,56	0,88	0,57
<i>Leptocarpus hyalinus</i>		0,47	5,58	3,72	0,57
<i>Restio egregius</i>			1,64	5,01	16,57
<i>Hypolaena digitata</i>			1,10	3,24	0,57
<i>Restio cuspidatus</i>			0,41	2,06	1,14
<i>Hypodiscus aristatus</i>			0,27	1,77	3,43
<i>Staberoha cernua</i>			1,10	0,59	
<i>Restio triticeus</i>			0,27	1,47	
<i>Hypodiscus argenteus</i>			0,14	0,29	
<u>Cyperaceae and Poaceae</u>					
<i>Ficinia filiformis</i>			0,27	0,29	0,57
<i>Tetraria thermalis</i>		0,47	0,55	1,47	
<i>Ficinia levynsae</i>		0,47	0,68		
<i>Tetraria flexuosa</i>			0,14		



Fig. 47. Phaenocoma prolifera. has a large biovolume at the top of the undergrowth stratum.



Fig. 48. A photograph showing the growth habit of Restio egregius (Just right of the centre of the photograph).

Table XX (continued)

Spp/fuel	Layers 0-5 cm	-25 cm	-50 cm	-100 cm
<u>Geophytes and herbs</u>				
<i>Aristea oligocephala</i>	0, 23	0, 14	0, 29	
<i>Oxalis luteola</i> & <i>O. purpurea</i>	0, 23			
<i>Pillansia tempelmannii</i>		0, 55		
<i>Corymbium cymosum</i>		0, 27		
<i>Dilatra viscosa</i>		0, 27		
<i>Aristea racemosa</i>		0, 14		

dead material, which constitutes the most flammable litter because of the fuel packing, particle and twig size. Only three species contribute much to the upper layer of the vegetation. Phaenocoma prolifera has a biovolume concentration in the upper layer because of its growth habit (Fig. 47). Restio egregius, exhibits the same feature, for the reason that the upright aphyllous stems branch nearly dichotomously, with a resultant biovolume concentration nearer the top of its height-growth (Fig. 48). The fact that L. laureolum dominates the upper layer confirms its shrub status.

6.3.3 BIOMASS

Some information on fynbos production is available in the literature: In a recent article Kruger (1977) reported on the standing biomass in fynbos communities of different ages. Rutherford (1978) summarised all the most recent data on fynbos biomass and production rates. Analogous plant communities in mediterranean type climates have been studied in more detail

Table XXI Features of the soil surface encountered in the stratification surveys, expressed as a percentage of the number of occurrences. Included are the number of species per survey and a summary for the combined data.

Plot no.	bare soil	litter	tussock	no. of species
2	57	33	10	28
3	57	37	6	28
4	48	44	10	32
Combined	53,33	38,00	8,66	40

Relative percentage of species present in each layer

0 - 5 cm	6 - 25 cm	26 - 50 cm	51 - 100 cm
37,5	82,5	75,0	42,5

Actual number of species	Total
15	40

(Specht, 1969a, 1969b) and mean annual increments were estimated and measured. "The over-all growth (dryweight/time) curve for aerial organs of the heath is essentially exponential"(Specht et. al., 1958). Kruger (1977) found that biomass data for fynbos are similar to those of analogous communities in other areas with mediterranean-type climates. It can be assumed that fynbos also exhibits an exponential growth curve, and it is supported by observations of the growth habits of the component species. For the purpose of this study the standing biomass of a twenty year old fynbos community was determined.

PLOT OF STANDARDIZED RESIDUAL

-2,0 -1,0 0,0 1,0 2,0



Fig. 49. Plot of standard residuals for the L. laureolum in biomass over in stem diameter data.

The objective was to relate the community to other fynbos communities and analogous communities elsewhere. Confidence limits for the vegetation biomass exceed the generally accepted 10% limit only marginally and the estimates are deemed sufficiently accurate for descriptive and other purposes. The shrubs were not collected completely randomly and though a 107 shrubs were analysed the data were still not wholly normally distributed (Fig 49). Table XX11 summarises the biomass estimates for L. laureolum on three experimental plots.

Table XX11. Estimates of the mean oven dry biomass of L. laureolum shrubs on three experimental plots.

	Plot 2	Plot 3	Plot 4
Mean (kg)	4,18	1,74	3,89
S.D. (kg)	3,68	1,97	3,32
S.E.M. (kg)	0,51	0,20	0,44
S.E.M. /Mean (%)	12,09	11,25	10,96
Density LI/ha *	530 $\pm$ 22	2140 $\pm$ 59	674 $\pm$ 23
Mean biomass kg/LI.	4,18	1,74	3,89
Mean diameter (cm)	5,52	3,51	5,43

* LI = L. laureolum

Plot 3 was sampled for undergrowth biomass with 1m² clipplots that represented 1,55% of the total plot area. The S.E.M. was 8,8% of the mean. Experimental plots 2 and 4 were sampled with 4m² clipplots representing 3,2% and 3,6% of the total plot areas. The S.E.M. were 8,3% and 13,6% respectively. Because the number of

clip-plots was reduced in plot 4 to keep the sampled area under 4% of the total area, the variance in the data is greater and accuracy is reduced. Some statistics on the biomass data of the plots are summarised in Table XXIII

Table XXIII

Plot	sample size	quadrat size (m ²)	Mean (kg)	SS	Var.	SD	SEM	CV
2	20	4	2,64	18,25	0,96	0,98	0,22	37,16
3	31	1	0,66	16,34	0,11	0,33	0,06	48,94
4	18	4	2,81	44,71	2,63	1,62	0,38	57,71

In comparing the total standing biomass of a twenty year old fynbos community in the Kogelberg State Forest (Table XXIV) with other fynbos and analogous communities the following facts became apparent:

- (i) If compared with Jakkalsrivier data (Kruger, 1977) it is evident that the research site in the Kogelberg State Forest has a very low annual production. Jakkalsrivier sites with biomass production of 11 000 kg per ha at 16 years of age has a 23% greater production than the Kogelberg vegetation of an age of 20 years. Kruger (1977) considers standing biomass of up to 15 000 kg per ha as being low for a 16 year old community. The very low production in the Kogelberg suggests that conditions for fynbos growth is much less than optimal at the research site.
- (ii) Data for Montpellier suggests that the fynbos produces approximately 20% less biomass than a garrigue stand of slightly younger age (Long et. al., 1967 in Specht, 1969b). Australian sand heath at Tidal River produces 24% more biomass in 10% less time than the fynbos at the research site in the

Table XXIV. Total standing biomass of a twenty year old fynbos community in the Kogelberg State Forest.

	Plot 2	Plot 3	Plot 4	Percentage mass distribution between the growth-forms over all the plots.
	t/ha	t/ha	t/ha	
Shrubs	2,218	3,734	2,614	32,0%
Sub-shrubs	2,591	1,484	2,608	26,0%
Restionaceae	2,944	1,269	2,964	29,5%
Cyperaceae + Poaceae	0,968	,039	1,312	11,4%
Geophytes & herbs	0,090	,029	0,138	1,2%
* Litter	2,493	3,745	3,868	
Total	11,304	10,430	13,804	
Total Live biomass	8,811	8,324	9,636	100%

	M.A.I**	at 20 year
	kg per ha	approximately
Montpellier	4200	84t
Sand Dimas	1200	24t
Dark Island S. Australia	640	13t
Southern Victoria	1500	30t

** Mean annual increment

Kogelberg State Forest (Jones et. al., 1969 in Kruger, 1977). Fynbos in the Kogelberg evidently has a much lower growth rate than garrique but is very similar to the Dark Island heath of Southern Australia. The Kogelberg vegetation exhibits the lowest growth rate of all the Mediterranean type vegetations.

The most important structural differences between fynbos and all the analogous vegetations is the significance of a persistent hemicryptophyte element (Kruger, 1977). Australian heath communities do have this feature but the hemicryptophytes are not as prominent as in fynbos (Kruger, 1977). Relative prominence of growth forms change as vegetation matures. The herbaceous strata of vegetation types similar to fynbos disappear almost completely as in chaparral (Sweeney, 1956; Vogl and Schorr, 1972; Mooney and Parsons, 1973; Biswell, 1974) or persist but never attain significance such as in garrique and maqui (Naveh, 1974; Kruger 1977). In contrast the herbaceous layer of fynbos dominates the structure of the post-fire vegetation until the shrub stratum emerges and persists into the sub-climax and climax vegetation. In a mature fynbos community the hemicryptophyte portion of the vegetation is approximately 30% of the total biomass of a twenty year old community (Table XXIV).

From the above it can be concluded that the fynbos community in The Kogelberg State Forest is below average in relation to other fynbos biomass structures. It compares poorly with equivalent vegetation types in other parts of the world. Although the growth rate appears to be lower than some equivalent vegetation types,

fynbos is unique in having a persistent hemicryptophyte fraction which contributes significantly to the structure and function of the ecosystem.

6.4 PHENOLOGY

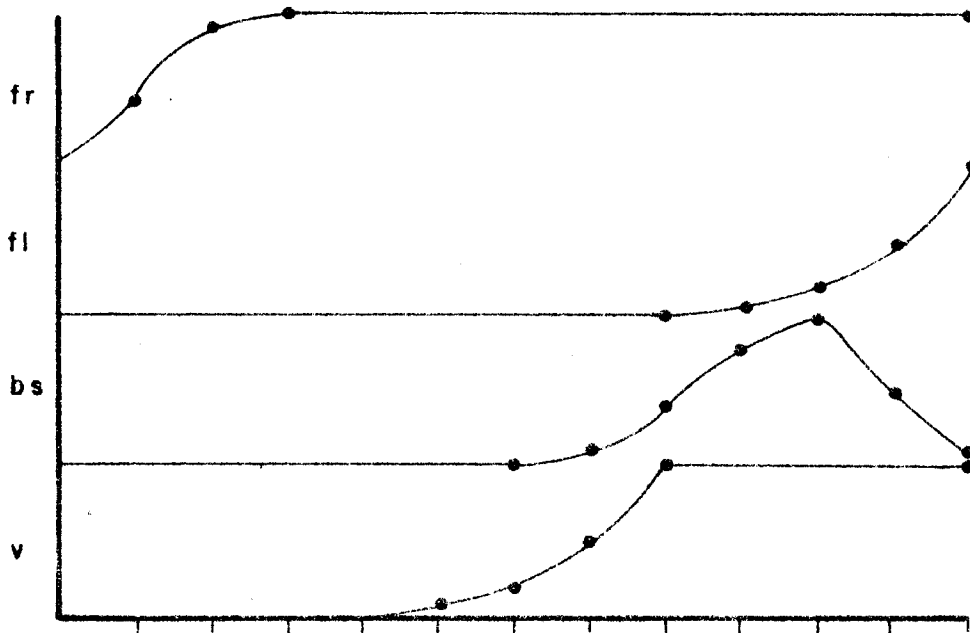
The concepts of phenology was defined by Lieth (1970) as the art of observing life cycle phases, or activities of plants and animals in their temporal occurrence throughout the year. The term "phenology," however was first used by Charles Morren (1859 - 60) a botanist from Jüttich (Abbe, 1950). Two different approaches in phenological research can be identified: the descriptive cum observational, and the analytical approach. The quantitative study of phenological phenomenon is called phenometry and is essentially the same as growth analysis. In South-Africa phenological studies in fynbos vegetation have been mainly observational and descriptive (Levyns, 1929; Wicht, 1948; Jordaan, 1949; Levyns, 1956; Van der Merwe, 1966).

Numerous authors have commented on observations made in the field but only a few conducted experiments in the fynbos (Levyns, 1929; Adamson, 1931, 1935; Levyns, 1935a, 1935b; Wicht, 1948; Jordaan, 1949, 1965; Martin, 1965, 1966; Van der Merwe, 1966; Lombaard, 1971). Most of these studies were primarily concerned with post-fire development of the vegetation and species survival after fire. Phenological observations of selected species were related to the impact on succession and species composition of communities (Michell, 1922; Levyns, 1924, 1927, 1929a, 1929b, 1935a; Wicht, 1945; Jordaan, 1949; Hall, 1959; Jordaan, 1965; Levyns, 1966; Martin, 1966; Van der Merwe, 1966; Jackson, 1976).



Fig. 50. The Restio Fruit (nut) with addressed inner perianth of the flower.

DILATRIS VISCOSA



PHAENOCOMA PROLIFERA

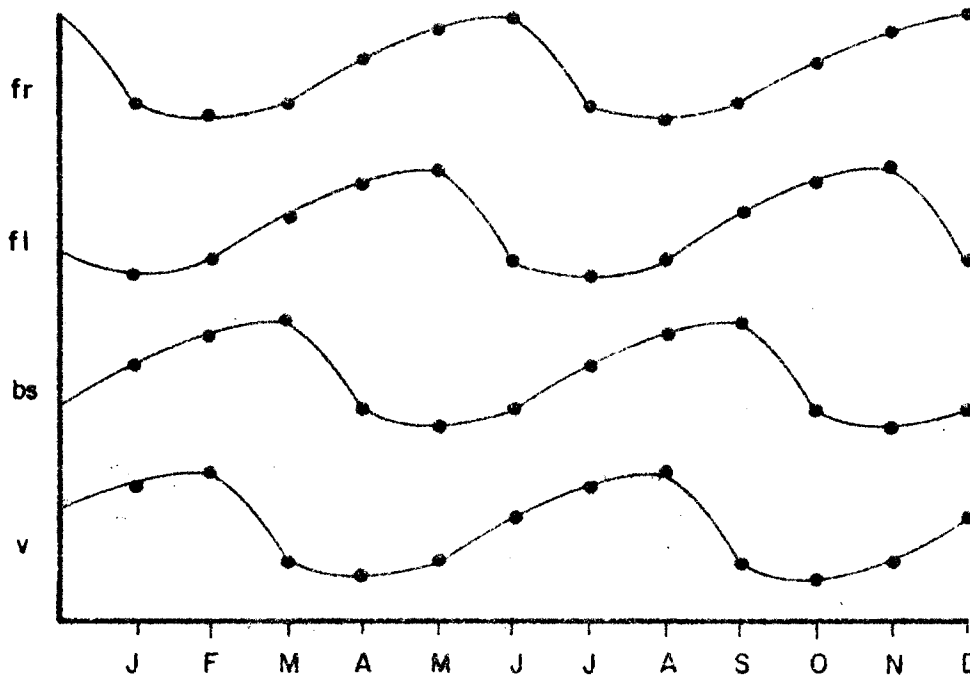


Fig. 51. Phenograms for *D. viscosa* and *P. prolifera* fr = fruiting; fl = flowering; bs = budset; v = vegetative.

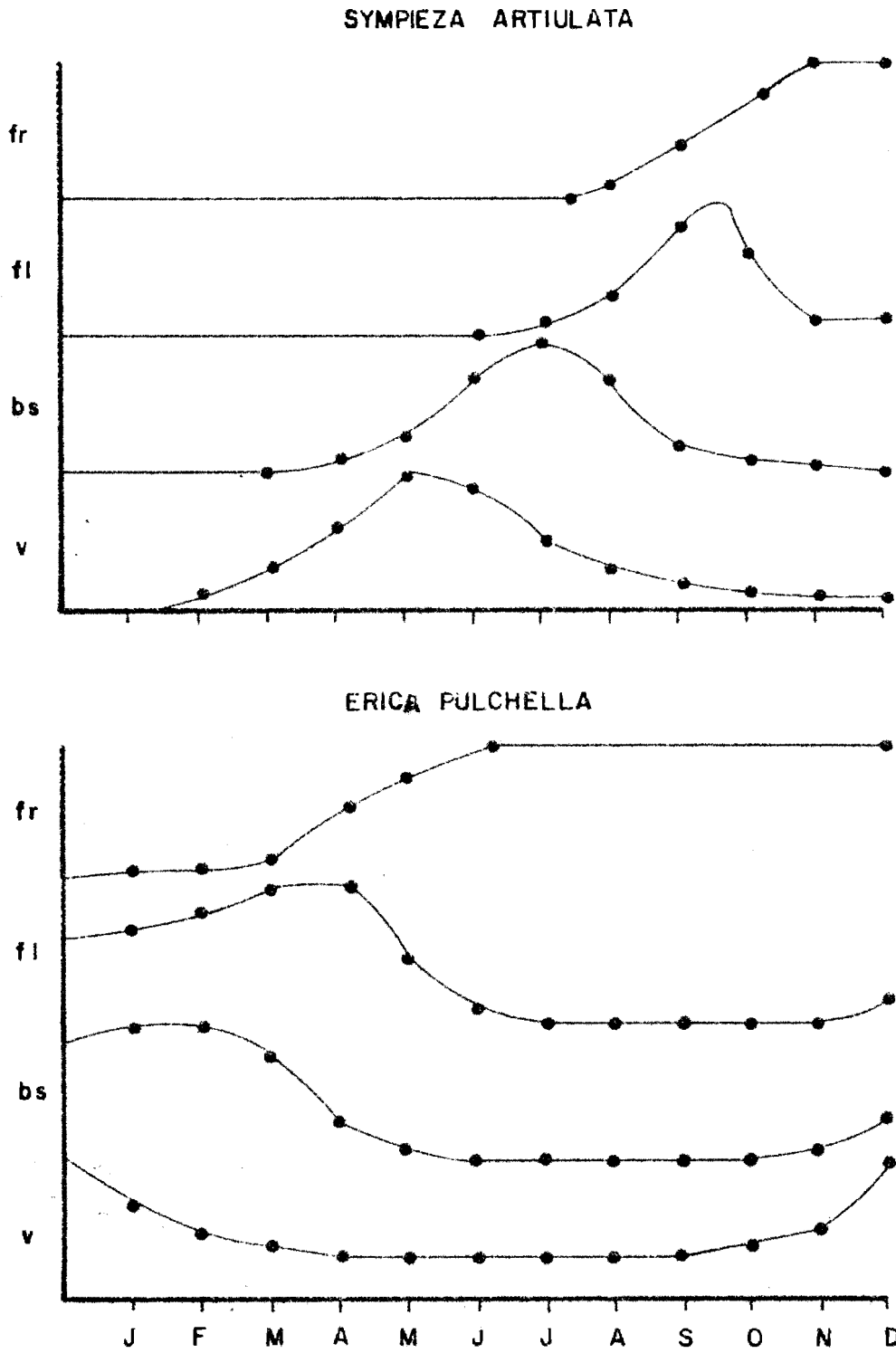
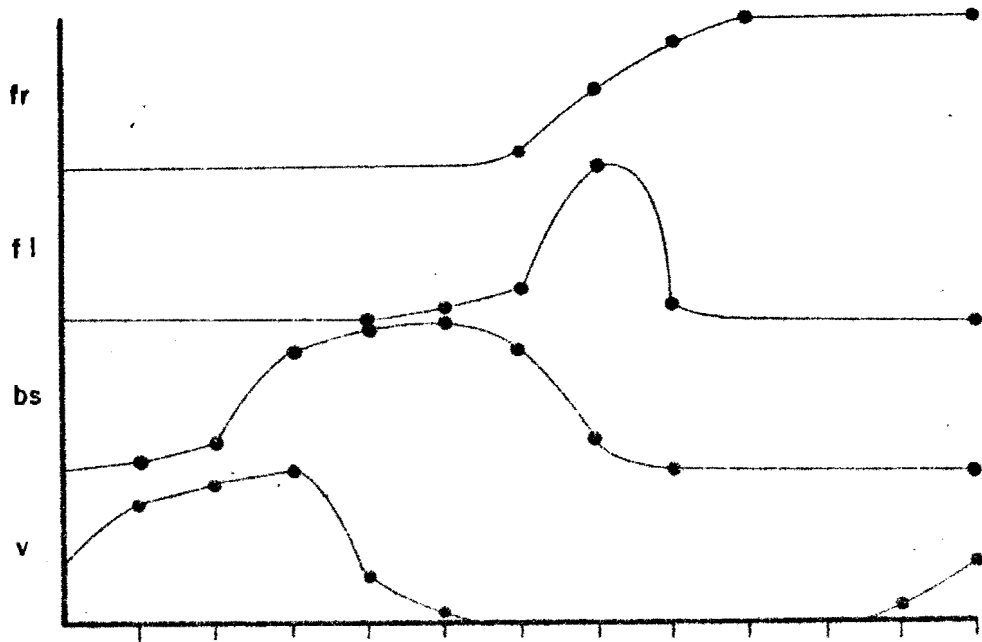
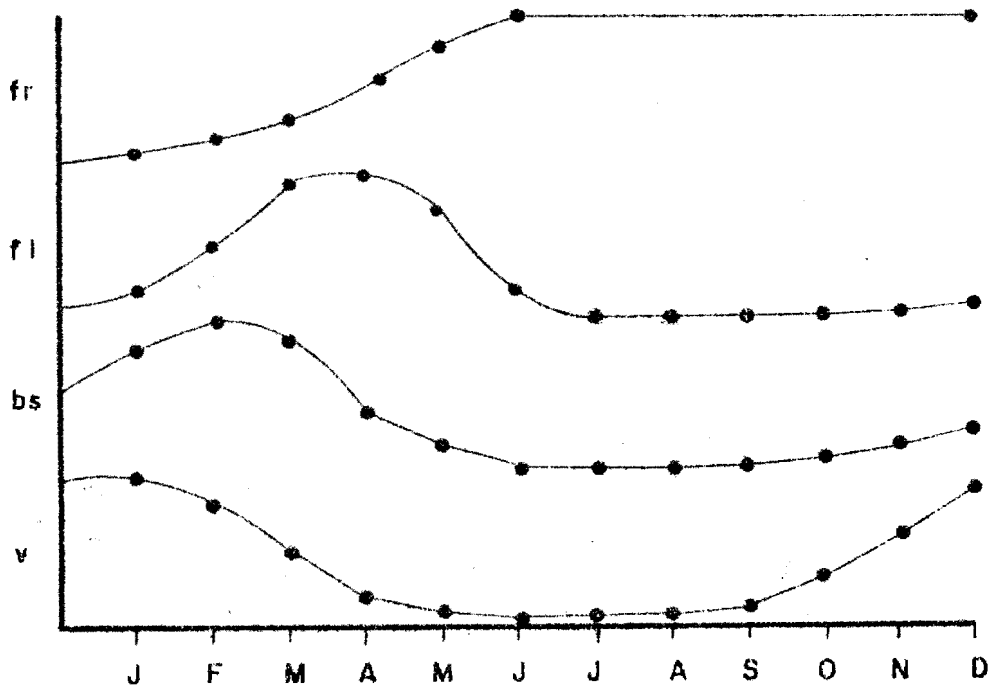


Fig. 52. Phenograms for S. articulata and E. pulchella.

LEUCADENDRON LAUREOLUM



RESTIO EGREGIUS

Fig. 53. Phenograms for *L. laureolum* and *R. egregius*.

Phenological observations were carried out approximately in the middle of each month (14th - 16th) as part of an experiment to determine the long-term response of selected fynbos species to fire. The species were Leucadendron lauratum (Lam.) Fourcade, Erica pulchella Houtt. Sympieza articulata (Thunb.) N.E.Br, Restio egregius Hochst, Phaenocoma prolifera (L.) D. Don, and Dilatis viscosa L. Ten individuals of each species were marked to monitor their phenology. In addition notes were kept of general observations in the field and these ultimately aided in the interpretation of results. For instance, it was noticed that seedlings of Ericaceae, Restionaceae and even Proteaceae appeared in the mature vegetation in bare patches after the winter rains. In all the dioecious species the male plants started flowering ahead of the female plants.

Some of the Restionaceae with relatively small fruits that occur on the experimental plots can be dispersed by wind because the inner perianth of the flowers adpress firmly to the fruit and are persistent (Fig. 50).

Flowers of specifically Erica pulchella apparently yield very little seed in the mature fynbos as they are predated heavily by tiny beetles. The beetle was not collected but approximately ninety percent of the flowers had holes eaten in the corolla tubes and the gynaecia or developing fruits are then destroyed.

Due to irregular and sometimes long intervals between visits to the research area accurate phenograms can not be drawn for the species investigated. The phenograms in figs. 51-53 for the above mentioned species are inaccurate in that change-over times for the different phenophases are approximations only (the stated time-table could not always be adhered to). The species were selected to point out the effective

partitioning of resources by species within a fynbos community.

Although a large number of species flower in spring, all of them do not actively grow at the same time. The dominant species Leucadendron laurifolium (Lam.) Fourcade for example flowers from July to early September, but starts active growth only in late November, Restio egregius Hochst, a monocotyledonous tussock forming plant must grow vegetatively (flowers are initiated on terminal growth points) before it can flower. The main growth flush started in December-January followed by the flowering phase in April-May.

Apparently the season in which a fire occurs can affect the first flowering date of vegetatively regenerating species. Pillansia tempelmannii (Bak.) L. Bol., a geophyte, skipped the first flowering season after a burning treatment in spring. A Homeria sp. (not identified because the genus is under revision) flowered within two months after a summer burn. The Homeria sp. flowered after the spring burn of the previous year towards the end of the flowering phase in the summer burn experiment. However, the flowering response to the summer burn was forty times greater than the belated response to the spring burning treatment. In the experiments conducted by Wicht (1948) he noted that sprouting species might miss the flowering season in spring if the vegetation is burned in late summer or autumn. Alternatively flowering could be delayed considerably. Burning in summer generally promotes the flowering of geophytes and probably some therophytes. According to Wicht (1948) burning in summer and autumn will prevent the flowering, for one season at least, of many perennial shrubby species, especially those that redevelop from seed. He concluded that burning in autumn was more unfavourable than burning in summer.

Observations in the Kogelberg State Forest experimental area confirm most of Wicht's findings. According to observations in the Kogelberg a spring burn was also "more unfavourable" than burning in summer. Proteaceous species that regenerate from seed take up to six years before they flower so that retardation of flowering by one season is difficult to prove or disprove. Almost all the sprouting species had flowered one season after the spring burn. The summer burn vegetation grew so vigorously that if the species did not flower in the next season it could be because of the vigorous growth and not a retardation effect of the fire. All indications are, however, that an autumn burn retards the redevelopment of the vegetation more than either a summer or a spring burn.

6.5 SURVIVAL OF SPECIES AFTER FIRE

6.5.1 SPROUTING

A number of species that are known to regenerate vegetatively after a fire were marked to determine their rate of survival. The rate of survival is high in all but one species (Table XXV)

It is evident that some species are less resistant to fire than others. R. bifarius would only survive in great numbers after very mild fires. In hot fires R. bifarius can only survive if its physical location and environment is conducive to survival, for example, when the rootstock is protected by a rock. All the other species exhibited a high level of tolerance to fire. In the few cases where survival was not 100% the explanation may be two-fold. One possibility is that the species were subjected to a fire that locally

Table XXV A list of vegetative regenerating species and their survival rates after a fire.

Family	Species	* %Survival
Restionaceae	<i>Restio bifarius</i> Mast.	13,0
	<i>R. egregius</i> Hochst.	90,9
Cyperaceae	<i>Tetraria thermalis</i> (L.) C.B.CL.	100,0
Haemodoraceae	<i>Dilatris viscosa</i> L.	100,0
Iridaceae	<i>Nivenia stokoei</i> N.E. Br.	100,0
	<i>Pittansia tenpelmannii</i> (Bak.) L. Bol.	100,0
Penaeaceae	<i>Salterna sarcocolla</i> (L.) Bullock	100,0
Ericaceae	<i>Erica corifolia</i> L.	98,6
Compositae	<i>Corymbium cynosum</i> E.Mey. ex DC	97,8

* a hundred individuals of each species were marked.

exceeded their resistance to fire. The other explanation is that so called "hot spots" occur in all fires and even the most tolerant species will not survive such temperatures for any length of time. Table XXVI summarises the rates of survival after a fire for a few non-sprouting species that are totally dependant on regeneration by seed.

A completely different picture emerges with the non-sprouting species. Some species can not tolerate fire at all, in the case of the species that did survive, though at a very low level,

Table XXVI List of non-sprouting species and their rates of survival after an experimental fire.

Family	Species	% Survival
Ericaceae	<i>Erica pulchella</i> Houtt.	2, 5
	<i>E. gysbertii</i> Guthrie & Bolus	2, 3
	<i>Sympieza articulata</i> (Thunb.) N.E.Br.	0, 0
	<i>Blaeria dumosa</i> Wendl.	2, 2
Proteaceae	<i>Serupia inconspicua</i> (L.) Guthrie & Salter	0, 0
	<i>Leucadendron laureolum</i> (Lam.) Fourcade	0, 0

the explanation is again twofold. This time the boot is on the other foot. Species showing a very low survival rate could have been subjected to a fire of such a mild intensity that it did not completely exceed their threshold for surviving a fire. Microtopography, physical location and environment of the individual plant must have an effect on the survival or death of any individual plant in the event of a wild or experimental fire. Again protection by rocks and large stones is probably responsible for the survival of many species that can not normally survive fires.

6.5.2 SURVIVAL THROUGH SEED

Many changes in environmental and edaphic factors are induced by fire (Brown and Davis, 1973; Wright and Heinzelman, 1973).



Fig. 54. Gnidia pinifolia, an example of a species that sprout after a burn.

Changes that occur during, after and as a result of the fire often affect seed germination and seedling survival. The high rate of seedling mortality during the first months after germination reflects the vulnerability of the seedling phase in the life cycle of plants (Harper and White, 1974). There are a number of studies that confirm this statement (Specht et. al., 1958; Marshall and Jain, 1970; Hull 1974; Christensen and Muller, 1975). Seedling predation, fungal disease and water stress appear to be the chief causes of mortality (Purdie, 1977). In the fynbos context another factor is nutrient deficiencies that seemed to occur toward the end of the rainy season. Factors such as toxic substances and competition, which are difficult to identify, can cause heavy seedling losses.

Soil samples were collected before and after experimental burns to determine the post-fire viability of soil stored seed. After the winter rains initiated a flush of seed germination, surveys were carried out in the field to assess seedling numbers, diversity and vitality.

Field counts of the number of L. laurignum seedlings were carried out six months after the onset of the winter rains.

The experiment with soil stored seed yielded interesting results (Table XXVII).

E. L. L. L.

Table XXVII Mean number of seedlings per tray for the different treatments.

	Season of burn					
	Spring		Summer		Autumn	
Not burnt	(2, 1)	2, 2	(5, 9)	4, 1	(2, 4)	17, 9
Burnt	*(3, 3)	1, 9	(24, 6)	13, 6	(2, 9)	4, 5

* Figures in brackets are for surveys conducted two months after sowing. Unbracketed numbers are the mean numbers of species counted six months after the rainy season commenced. That is in November, because the rainy season started at the end of May.

An analysis of variance showed significant differences at $p = 0,05$ confidence limits, and this demonstrated that by not burning in autumn and by burning in summer a positive seed regeneration response can be achieved in rynbos. In none of the other treatments significant responses were obtained. The Tukey test was applied to the data to test the responses of the different treatments against each other.

Spring	Spring	Summer	Autumn	Summer	Autumn
Burnt	Not burnt	Not burnt	Burnt	Burnt	Not burnt
<u>1, 9</u>	<u>2, 2</u>	<u>4, 1</u>	<u>4, 5</u>	13, 6	17, 9

* Figures connected by a line are not significantly different from each other.

In order to get some measure of the diversity of species associated with the regenerative effort, the mean number of different species in each treatment was calculated (Table XXVIII).

Table XXVIII Mean number of different seedling species per tray for the different treatments.

	Season of burn		
	Spring	Summer	Autumn
Not burnt	(0, 8) 1, 8	(1, 5) 3, 0	(1, 9) 4, 1
Burnt	*(0, 5) 1, 2	(1, 5) 3, 3	(0, 6) 2, 2

* Figures in brackets are for surveys conducted two months after sowing. Unbracketed numbers are the mean number of seedlings counted six months after the commencement of the winter rains.

According to the Tukey test there were significant differences among the treatments at $p = 0,05$.

Spring	Spring	Autumn	Summer	Summer	Autumn
Burnt	Not burnt	Burnt	Not burnt	Burnt	Not burnt
1, 2	1, 8	<u>2, 2</u>	<u>3, 0</u>	<u>3, 3</u>	4, 1

*Figures underlined are not significantly different from each other.

It is interesting to note that the autumn nonburning treatment again yielded the best results followed by a summer burn, summer non burn and an autumn burn

Surveys conducted on the experimental plots revealed that the regeneration by seed is best in the first few months after the winter rains. (Table XXIX). The death rate and germination rate is in a continual flux for several months. With the onset of the dry summer months

Table XXIX. Mean number of seedlings and species, three and four months after the first winter rains.

	Season of burn		
	Spring	Summer	Autumn
No. Seedlings			
at 3 months (August)	106,2	50,8	88,4
at 4 months (September)	46,0	51,8	41,2
No. of species			
at 3 months (August)	9,4	9,6	5,2
at 4 months (September)	6,4	9,0	5,0

germination ceases and the death rate slowly diminishes as the selected few seedlings become temporarily established.

Seedling species could be identified to family and genus level and in a few cases to species level. Erica pulchella Houtt. could be identified positively. Seed regeneration of E. pulchella comprised up to 56,9% of all the seedlings found in the soil stored seed experiment (Table XXX).

Evidently a fire in either spring or autumn is not conducive to regeneration by seed for E. pulchella. In the soil stored seed collected with the spring burn E. pulchella was present in the initial regeneration response, but none of the seedlings survived to the next spring.

Surveys conducted in the spring burnt plot a year after the experimental burn showed that 30,1% of the seedlings that germinated after the winter rains were E. pulchella. Two salient points arise from these observations. The one is that a burn in autumn does not stimu-



Fig. 55. Above: Regeneration
by seed, 3 months old.

Left: Seedling of
L. laureolum.



Fig. 56. Micro-weirs are easily identifiable on gently sloping ground.

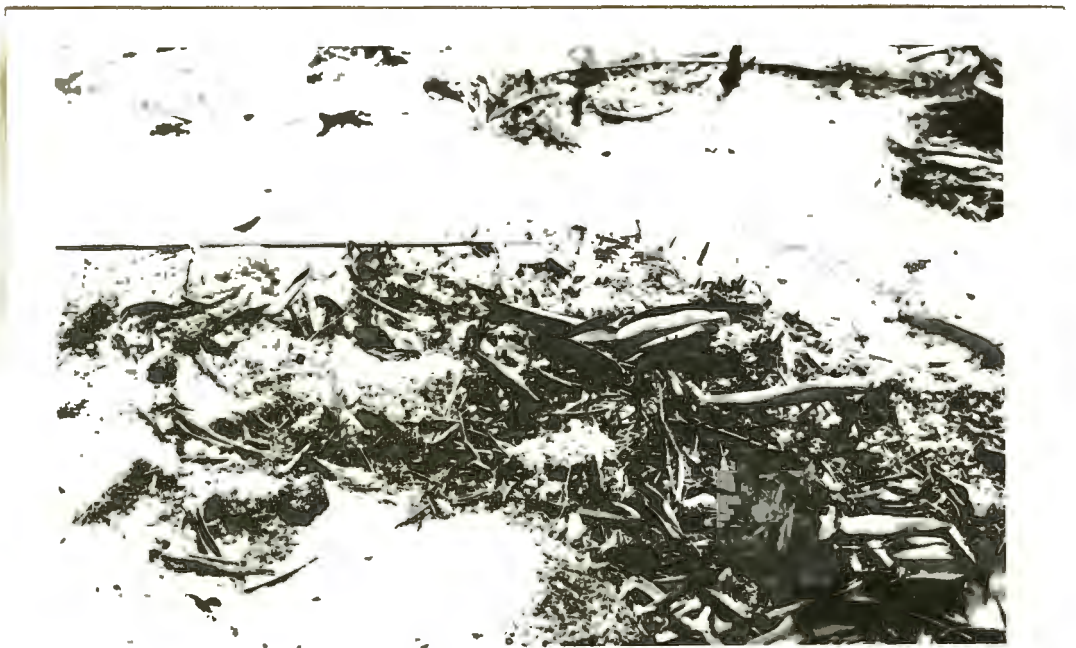


Fig. 57. "Mud-flow" can be seen as the whitey shaped stretch of sand originating top left and right and flowing to the middle righthand side of the photograph.

Table XXX

Number of	Spring		Summer		Autumn	
	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt
Erica seedlings	0	0	10	41	102	2
			(24, 4%)	(30, 1%)	(56, 9%)	(4, 4%)

late seed germination to the same extent as a summer burn. When burnt in spring the seedlings that emerge do not all survive until the rainy season whereafter the normal germination of seed takes place as in any naturally bare area (dormant seed or seed carried in from outside is responsible for the second response). The next point is that the natural time for seed to germinate is during or directly after the rainy season. Seedlings of the summer burnt exhibited very vigorous growth and a much larger size than seedlings of the other treatments and specifically the autumn non burn treatment. Therefore, though seedlings naturally germinate during or directly after the rainy season, a summer burn positively stimulates seed germination and establishment of seedlings.

Seedlings are very much dependent on the micro-environment for survival. Much greater germination and establishment of seedlings were seen on the sides of micro-weirs (Fig. 56) formed by erosion of higher lying soil during heavy rains, than in the bare sand centres of micro-weirs or on micro slopes and micro-rises. Large numbers of seedlings may be buried in "micro-mudflows" (Fig. 57) during heavy rains. In this way the initial regeneration pattern fades



Fig. 58. An example of severe sheet erosion on the research site exposing and undermining the roots of active growing plants.

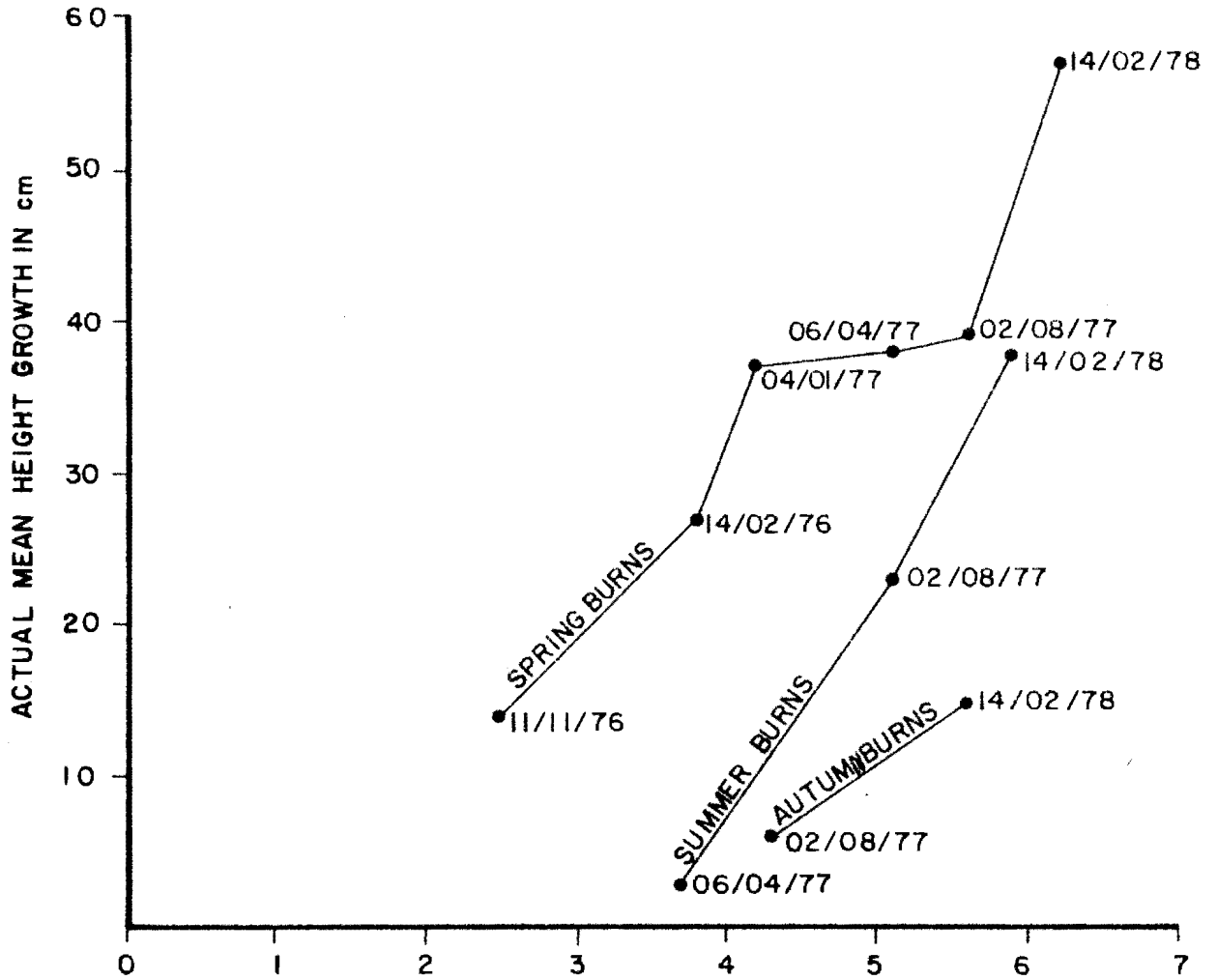


Fig. 59. Growth of *R. egregius* after fires in different seasons.

during subsequent community development. Sheet erosion is severe in burnt areas when heavy rains fall. Fig. 58 is a photograph of living roots exposed after a "normal" rainy season on one of the burning experimental plots.

One L. laureolum seedling germinated after the spring burn. In the other two burning treatments L. laureolum seedlings appeared for the first time after the onset of the winter rains.

Six months later (December) all the L. laureolum were counted on the three plots (Table XXXI).

Table XXXI Numbers of L. laureolum seedlings that germinated in the experimental plots after burning treatments in different seasons.

	Season of burn		
	Spring	Summer	Autumn
	0, 20 ha	0, 25 ha	0, 20 ha
Before rain	1	0	0
7 months after	440	873	1204
the first rains (December)	*(352)		(963)

* Numbers in brackets are the actual number of seedlings counted. Because plot sizes differed the counts were adjusted to be directly comparable. Plot sizes (and with that the numbers) were adjusted to 0,25 ha, the size of plot 2, the summer burn.

6.6 GROWTH OF RESTIO EGREGIUS AFTER A FIRE

The effect of fire on the resprouting of vegetative regenerating species is dramatically illustrated in Fig. 59. Rate of height

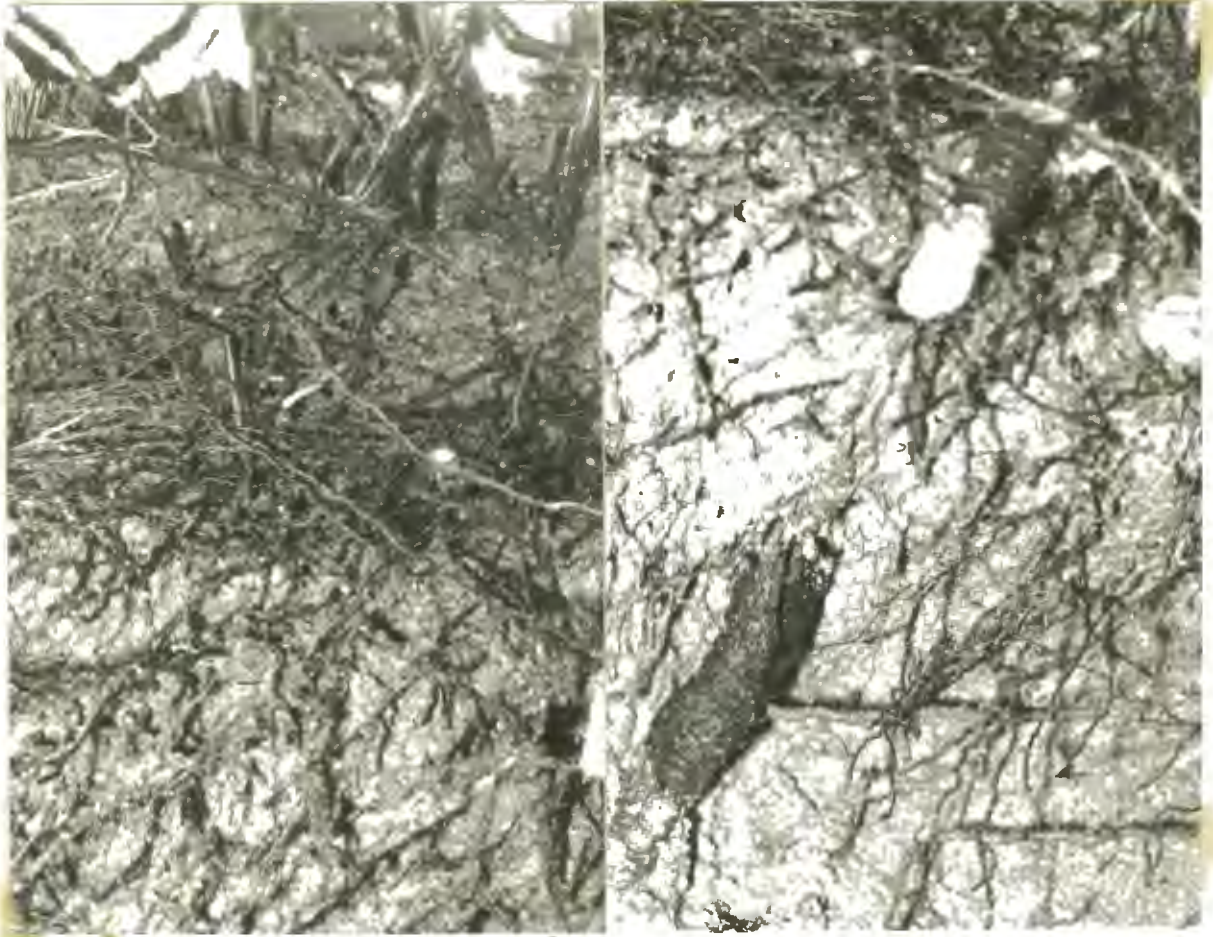


Fig. 60 Effective root depth is approximately 20cm with a great concentration near the soil surface (left photograph). In the righthand photograph is an example of "sinker" roots as found in L. laureolum.

growth for the tussock-forming restioid species reduced appreciably from springtime to autumn. The post-fire regeneration of the spring-burn was monitored the longest and two fast growing periods can be identified in the growth curve. Height growth is plotted against the natural logarithm of the number of days after burning. The natural logarithm was used to make a graphical representation possible. Both the summer and the autumn burning treatments were monitored well into summer and active growth was observed over the same period as for the spring burn. Initial growth directly after the fire was out of phase until springtime. The growth phases of R. egregius monitored in all three plots were in phase again by mid-summer though the growth rates differed.

6.7 WATER RELATIONS

Most true fynbos species have evergreen sclerophyllous leaves and therefore do not wilt when they experience water stress. Sclerophylly could be an adaptation which protects the plants from possible sunburn damage on larger branches when they are under water stress. It could also be an adaptation to utilize favourable conditions for normal photosynthesis whenever that occurs. Vegetation in mediterranean type climates are adapted to survive the hot dry summer seasons and the concomitant high radiation loads (Poole and Miller, 1975). At the end of summer, available moisture in the very sandy soils is greatly depleted (Fig. 61). Similar observations in other mediterranean climates were reported by Kramer (1952) and Pillsbury et. al., (1963). Direct comparison of the magnitude of water stress in deep rooted species and shallow rooted species was

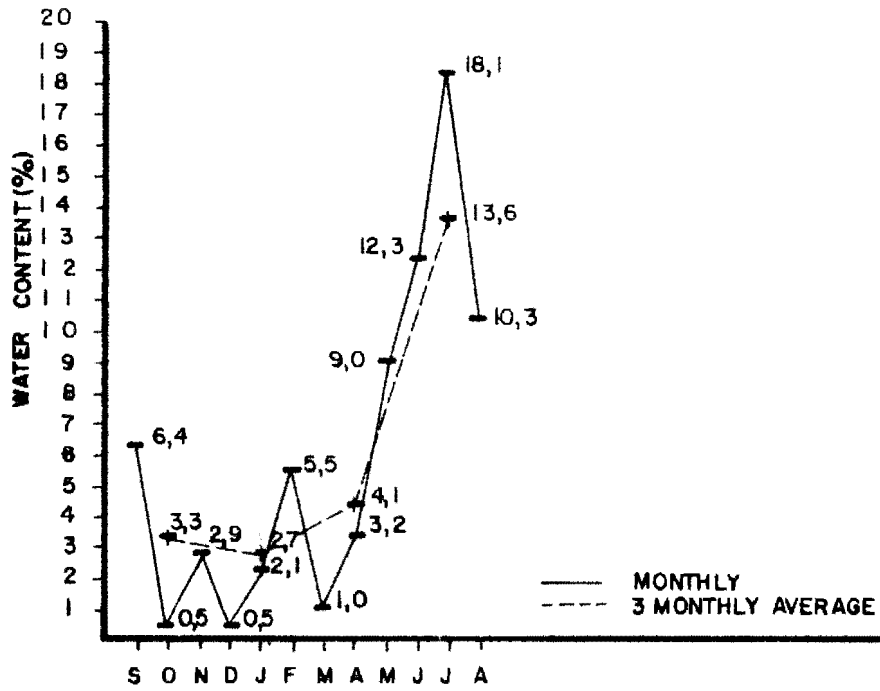


Fig. 61. Plot of monthly and three monthly mean soil water

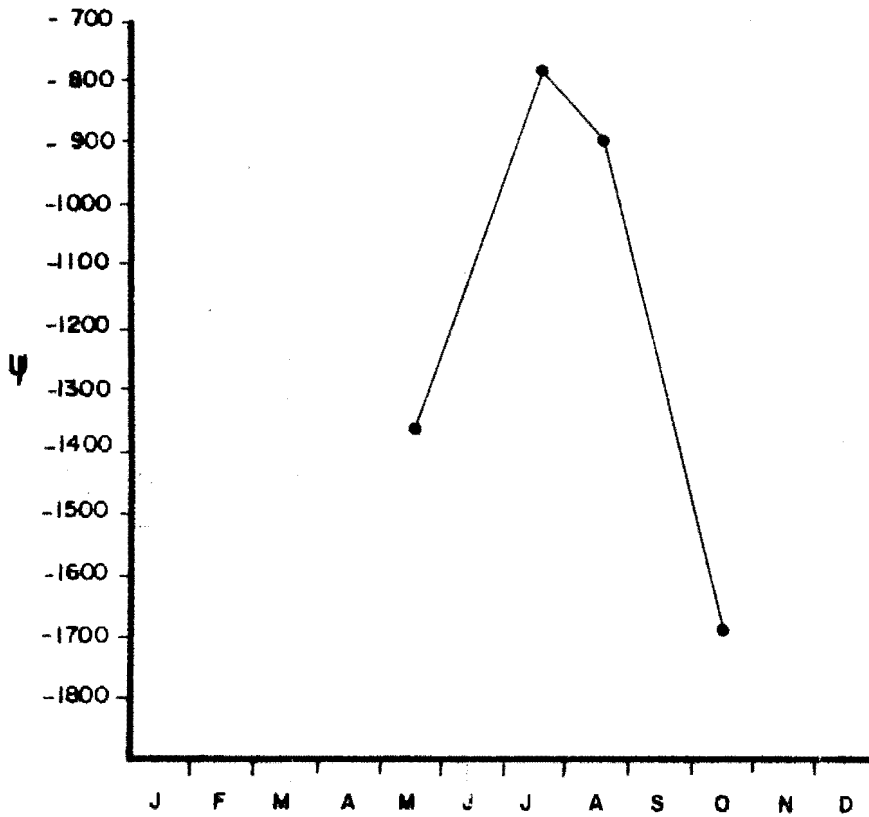


Fig. 62. Variation of L. laureolum water potentials for a number of months.

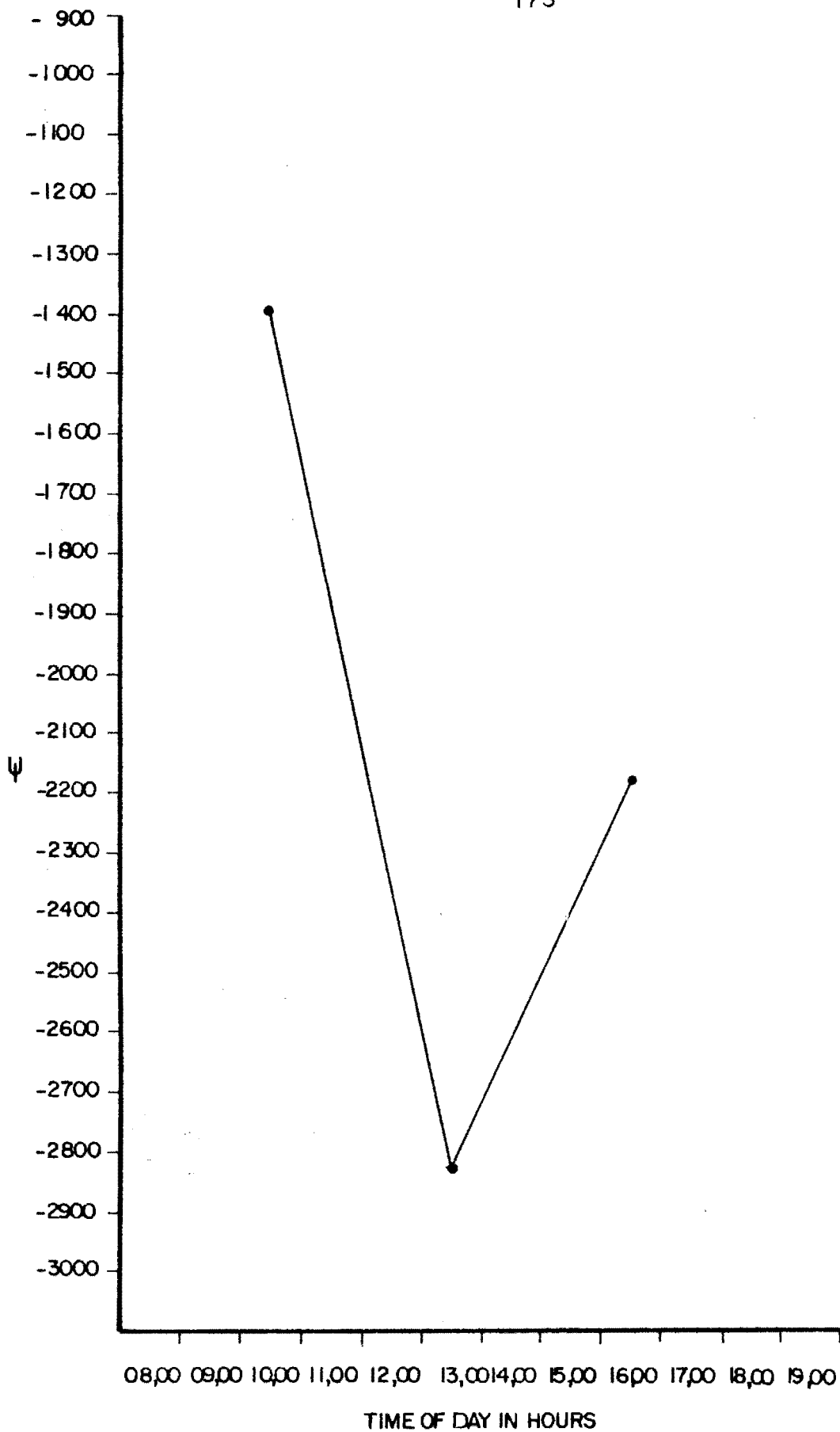


Fig. 63. Advance of *R. egregius* water potentials during one day in August.

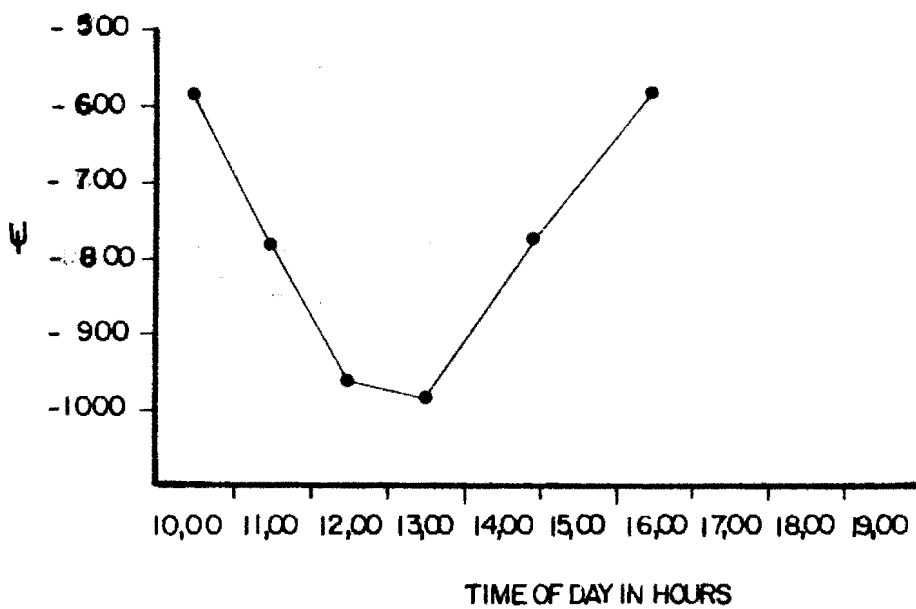
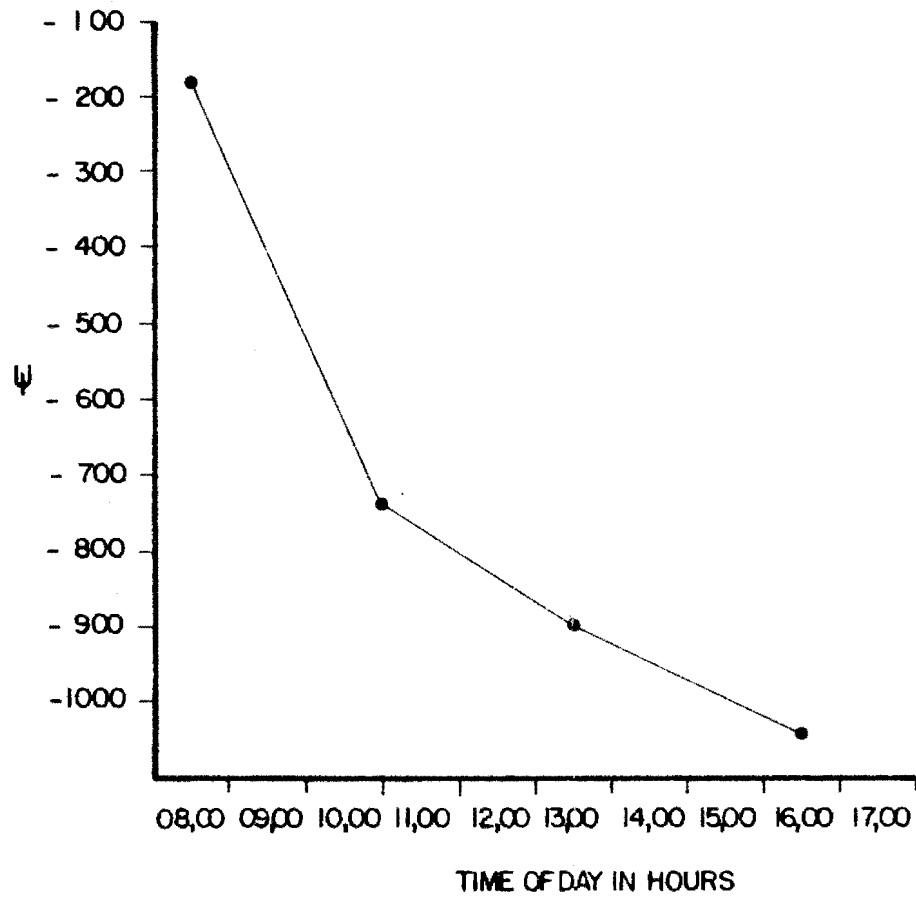


Fig. 64. Advance of *L. laureolum* water potentials during one day in August (top) and a day in July (below).

possible. L. laureolum is the dominant shrub of the community and is characterized by two types of root systems. The "feeder root" system is shallow and does not extend deeper than 20cm (Fig. 60). "Water roots" penetrate deep into the soil and the deeply cracked parent rock material. R. egregius is a tussock forming hemicryptophyte with a shallow adventitious root system that does not extend deeper than 10 - 20 cm.

Water potential measurements of the two species at the same time of day indicates that R. egregius is subjected to a much more severe water stress than L. laureolum (Fig. 63 & 64 top).

Water potential varies approximately inversely with the rainfall pattern of the region (Fig. 62). It is obvious that water stress increased as the day advanced until approximately 13h00 after which the water potential of L. laureolum increased rapidly.

The minimum water potential measured for L. laureolum was - 3100 Kpa (-31 bars) in October, the last month of spring. R. egregius had a minimum water potential reading of -3200 Kpa (-32 bars) in August the first month of spring. L. laureolum had a minimum water potential of -1250 Kpa (-12,5 bars) in August when water potentials tended to decrease to much later in the day than in July the last month of winter (Fig. 63).

Cape fynbos species are comparable with species in the Californian chaparral. Larrea tridentata (D.C.) Cov. exhibited minimum water potentials in autumn of approximately -5800 Kpa (-58 bars) (Syvertsen, et. al., 1975). In November, just before the winter rains, the minimum water potential exhibited by a Californian chaparral species Adenostoma fasciculatum Lindl. was a value below -6500 Kpa

(-65 bars) (Poole and Miller, 1975). The autumn water potential measurements taken in the fynbos were measured after the first rains and is therefore not directly comparable. The minimum value of -3200 Kpa obtained for R. egregius was near the minimum water potential that could be measured with the specific model of the Scholander bomb that was employed.

Evergreen sclerophyllous shrubs tolerate summer droughts through physiological means of controlling water loss (Mooney and Dunn, 1970). From the data presented it is clear that L. laureolum is able to withstand severe water stress as well as any similarly adapted plants. The difference between water potentials observed for L. laureolum and R. egregius is a function of the effective root depth of the species. R. egregius is a shallow rooted plant while L. laureolum have additional deeply penetrating tap roots.

6.9 FIRE INTENSITY

Very little attention has thus far been devoted in South Africa to the different intensities of fires and their effect on the vegetation. The lack of information is even more acute in the fynbos region than for the grasslands of South Africa. Experiments to determine fire temperatures of grassland-savanna have been conducted successfully in Kruger National Park (van Wyk, 1971).

The experimental burns were conducted in exactly identical manner so that if there should arise doubts as to the validity of the formula employed for calculating fire intensity the relative intensities for each burn still remain valid. Except for the values obtained for the mass of material that did not burn, all the other

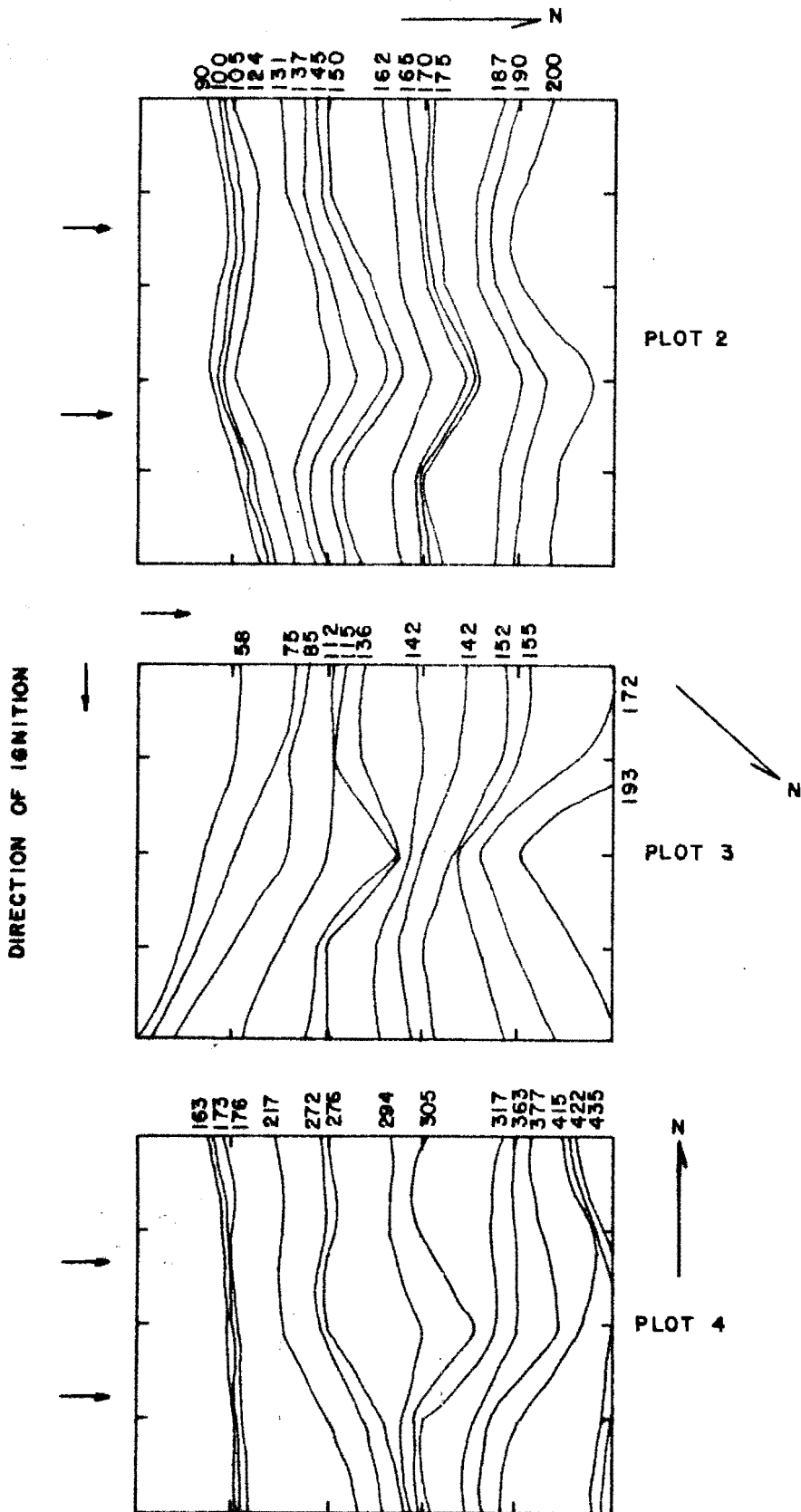


Fig. 65. Isolines of the movements of the fire fronts in seconds during experimental burns. Fires were lit on the hand side of the figure and as indicated by small arrows.



Fig. 66. Aerial photograph of the experimental plots showing where the summer burn had jumped the fire break (top middle of photograph). Plot 3 = spring burn, Plot 2 = summer burn, Plot 4 = autumn burn. (Plot 5 is a spring burn but is not considered in this thesis).

parameters collected for the formula is acceptably accurate to lend the calculated fire intensities credibility. In Fig. 65 the movements of the fire fronts are portrayed. The sizes of the plots were large enough to represent "natural" burns and some weight is added to this statement by the fact that the summer burn gathered enough momentum (Fig. 66) to jump a firebreak around plot 2.

Combustion heat of fynbos fuel ranged from 18225J/g - 20677J/g as compared to grasslands with values of 17992J/g - 19254J/g (Iwanami, 1973). The average heat value of fynbos is therefore in the region of four percent higher than that for Japanese grasslands. In the calculation of fire intensities for Australian grasslands a heat value of 17000J/g is generally used (McArthur and Cheney, 1972). Fynbos restioid-veld has an average heat value of thirteen percent higher than the value quoted for Australian grasslands. Under identical conditions a fynbos fire could therefore yield hotter fires than either the Japanese or the Australian grasslands.

Summer burns with higher initial temperatures and perfect environmental conditions for fire should be intenser than either spring or autumn burns (Byram, 1958). Fire intensity is also very dependent on the type of veldfire i.e. headfire or backburn (Byram, 1958).

A comparison of the statistics of each plot and the differences in fire intensities and concomitant environmental factors is given in table XXXII.

Table XXXII Characteristics and parameters measured of similar experimental burns in three different seasons.

Parameters	Plot 2 (summer burn) 23 February 1977.	Plot 3 (spring burn) 28 September 1976.	Plot 4 (Autumn burn) 20 May 1977.
Mean no. of spp. per 4m ²	19,5 (57)	21,0 (50)	20,28 (50)
Index of Beta diversity	2,61	2,71	2,47
Pre fire biomass litter kg/ha	11304	10430	13804
Post fire biomass and litter kg/ha	1341	1098	1468
Duration of burn min/sec.	3,50	4,42	7,40
Fire intensity: KJ/m	3033,894	2878,412	2326,613
<u>Observations before fire</u>			
Soil water content %	3,9	4,5	8,3
Vegetation water content %	125,6	137,6	147,8
Litter water content %	8,8	10,3	12,4
<u>Observations during the burn</u>			
Mean temperature °C	23,97	25,43	26,55
Mean relative humidity %	53,2	19,0	83,3
Mean wind speed m/s	5,67	5,00	10,00
Mean Rate of spread of fire m/s	0,155	0,157	0,096
CONSTANT			
Heat yield KJ/kg	19646,2	19646,2	19646,2

7. RESULTS

Historically the fynbos vegetation of the Kogelberg State Forest is the result of some natural evolution and a great deal of disturbance by human intervention over the past three hundred years. In the last few decades the pressure has increased dramatically. Only a few isolated spots have escaped fire in the last twenty years and it is probable that no true climax vegetation exists in the area.

The research site was approximately twenty years old at the beginning of the experimental burning programme and is considered to be a mature fynbos stand. The results of the surveys and burning trials can be divided into two categories. Firstly a descriptive model of mature fynbos structure (see under structure) and secondly an evaluation of the short-term response of the fynbos vegetation to fire in different seasons.

Structural Model:

In the experimental area fynbos vegetation is characterised by a canopy stratum with a height of 2,0 - 2,5 m and consists almost wholly of Proteaceae. Undergrowth consists of hemicryptophytes (Restionaceae) and members of the Ericaceae (nanophyllous nanophanerophytes) that dominate the seasonal aspect and the physiognomy for the first few years after a burn. The restioid-ericoid stratum is the second most important structural layer from a vertical distribution viewpoint. Species diversity and horizontal structure, or pattern, is most prominent in the lower strata.

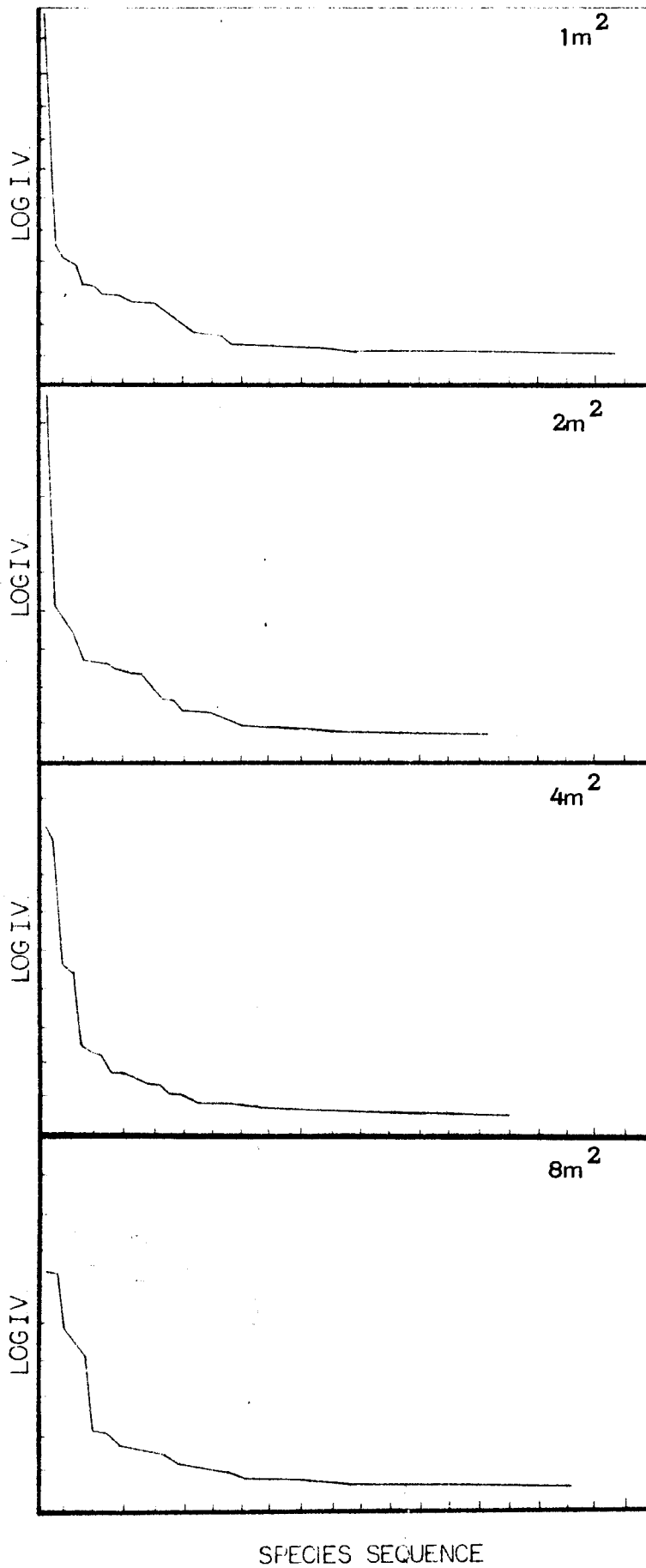


Fig. 67. Species importance value curves for the different quadrat sizes.

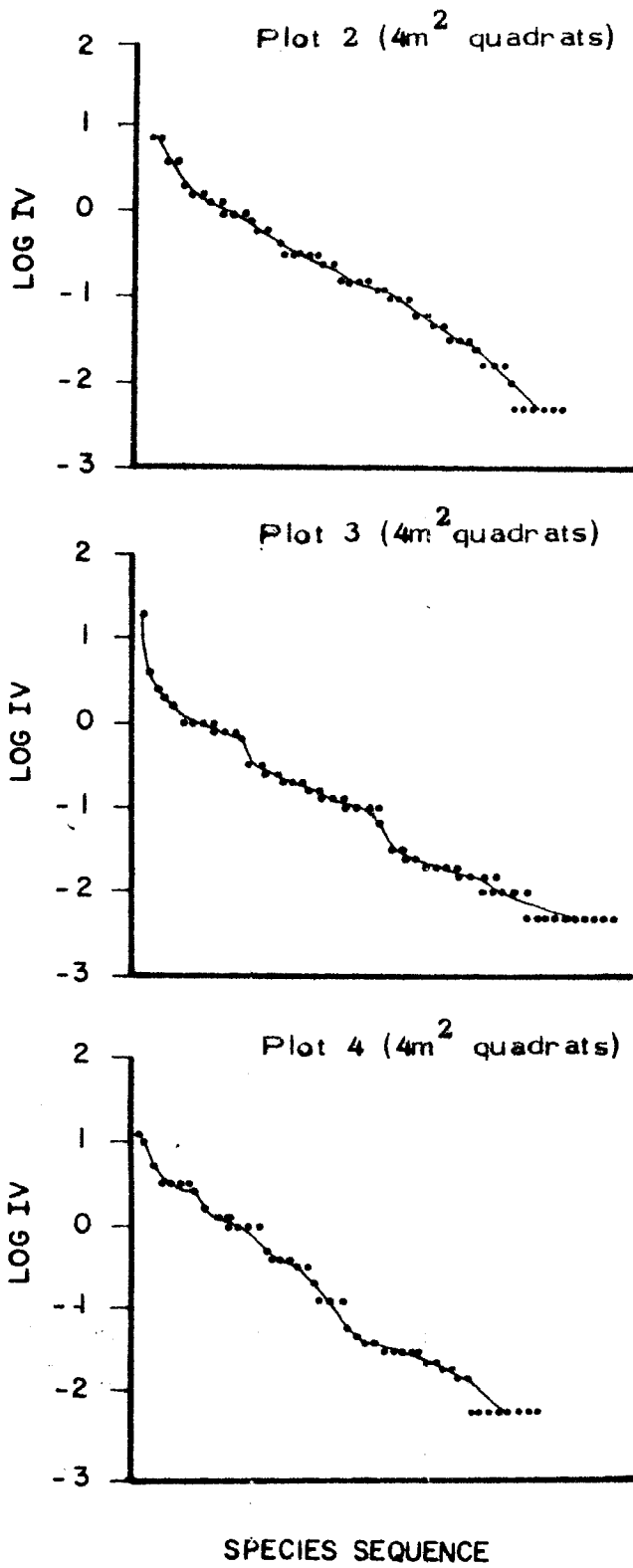


Fig. 68. Species importance value curves for the three experimental burning plots

Species differ in their ability to occupy and utilize the available niche hyperspace and the community resources (Whittaker, 1972). Species of the tree experimental plots were ranked according to their percentage cover values to form importance value or dominance-diversity curves. According to Whittaker (1972) the forms of importance-value curves do not permit strong inference about resource division, but their expression of species relationships are of interest.

Fig. 67 shows that the size, shape and number of quadrats do not have any appreciable influence on the shape of the importance-value curves. They also correspond well with the curves for the three experimental plots (Fig. 68). It is important to note that although Leucadendron laureolum is the dominant shrub of this particular fynbos community, it does not overshadow the next species in the importance-value sequence to any marked degree. An exception is plot three where L. laureolum (nanophanerophyte) exhibits a definite superiority over its closest rival which is R. egregius a hemicryptophyte. This can be attributed to the dense stand of small leucadendron shrubs with relatively large canopies. In the other two plots the dominant shrub L. laureolum has an importance value that is readily matched by R. egregius (Plot 2) and Erica pulchella (Plot 4). The fact that there is very little difference in importance-values of successive species indicates that the fynbos vegetation does not have single clear dominant species, even on such a small scale as the experimental plots.

Equally important to niche pre-emption is the way in which species are complementary to each other in their seasonal development. In chapter six, under phenology it was pointed out that although most species flower in spring there are always some species flowering at any time of the year. Two times of seed-shed was observed

by Levyns (1929b) namely summer- and winter seed-shedders. Vegetative growth is also subject to partitioning by species. Under the phenology heading the active growth stages of L. lauroleum and R. egregius was discussed. Kruger (1977) takes observations in this regard a step further by stating that shoot-growth tends to be correlated with life- or growth-form. Therefore herbs would grow from late winter to early summer and shrubs tend to initiate growth during spring and summer. All the data gathered on seasonal growth patterns support this viewpoint.

SHORT-TERM RESPONSE OF FYNBOS TO FIRE:

Fluctuation of environmental factors influence the development of vegetation, both mature and developing vegetations. There is therefore no guarantee that post-fire regeneration will lead to exactly the same community as that what came before. Flower and seed predation by insects as was discussed for Erica pulchella can have a marked effect on the eventual community composition if the pre-fire predation is resumed immediately in the post-fire development of the vegetation.

Fungal root pathogens such as Phytophthora cinnamomi Rands which is known to be a pernicious killer of Proteaceae, can change the community structure and composition permanently under certain conditions. Pressures exerted on developing vegetation caused by the grazing of animals can have unestimable repercussions. For example a lone grysback regularly visited the experimental burns and grazed resprouting Restionaceae and Leguminosae seedlings (Aspalathus sp.). Baboons and hedgehogs dug out the bulbs of flowering geophytes fairly regularly. The damage caused by the animals was in no way extensive but under different environmental



Fig. 69 Seedling in a mature fynbos community.

circumstances all these factors add up to environmental pressure that could force the vegetation into a different avenue of development,

Some characteristics of the regeneration methods of species are of prime importance to ensure that the community retains its species richness. Different requirements for regeneration can only be effective in maintaining species-richness or diversity if the adult plants of the many different species are reasonably evenly balanced in competition (Grubb, 1977). With rare exceptions it is the nutrient poor soils rather than fertile soil types that host the greater species diversity (Grubb, 1977). The potential for continued co-existence by differentiation in requirements for regeneration is much greater in communities with nutrient resource limitations than for communities with less restrictions on potential growth opportunities. It is important to note that regeneration in fynbos is a continuous process. It is prominent in "gaps" created by the death of individual species. L. laurosum seedlings and seedlings of Restionaceae and Ericaceae were observed in larger and smaller gaps that appear regularly in a mature vegetation (Fig. 69). Seedlings of L. laurosum were found under the canopy of parent shrubs and they have the potential to supercede the niche of the parent plant in the case of the parent plant's demise. Restionaceae and Ericaceae seedlings colonise the gaps in the centres of old restioid tussocks and in bare patches originating spontaneously. It is therefore evident that the relationship, between regeneration and succession is largely dependent on the extent of the

bare area. Fire usually creates vast bare areas where regeneration occurs according to the strategies of each species and is the first step in succession. "Succession" on naturally occurring bare areas as described for Proteaceae and Restionaceae is recognised to be primarily regeneration with a limited potential for successional development. Niche differentiation is intricately concerned with gap quality (Grubb, 1977).

On the germination requirements of the vast numbers of fynbos species very little is known. Jordaan (1949, 1965) came to the conclusion that fire can stimulate the germination of certain species regenerating from seed but that there are "safe" and "unsafe" periods regarding fire. He came to the conclusion that fire frequency is of the utmost importance for the maintenance of specific species in the community, notably species of the dominant shrub growth form. The results of the germination trial of soil stored seed are for one season and therefore only applicable to one set of environmental conditions. Generalizations on the short-term effect of fire on the regeneration of the community are consequently untenable.

Under the specific set of conditions however, it was found that Erica pulchella and various species of the Restionaceae responded well to burning treatments in summer. Leucadendron laurum responded very well to a burn in summer but even better to an autumn burn. However, although the ground layer species responded very well to an autumn burn, the survival rates of the seedlings were poorer than that for the summer burn. The spring burn had a better

initial germination of seed regenerating species than either the summer or the autumn burn in the field surveys. Even though the regeneration after a spring burn was very good, the survival rate of the seedlings was poorer than that of a summer burn and comparable to that of an autumn burn. The "number of seedling species" follow a slightly different pattern than the "number of seedlings". Results of the soil stored seed germination trial contradict those of the field surveys. For the soil stored seed the spring burn had the lowest regeneration and survival rate whereas the autumn burn had the highest of both with the summer burn somewhere in the middle. Species composition was highest for the summer burn followed by the autumn and spring burns. In the field surveys the summer and spring burns were on a par with the autumn burn performing poorer both with respect to the number of seedlings and the number of species.

Since the soil stored seed germination trial was subject to a regular watering and an artificial fertilizer programme the trial indicated potential regeneration and survival rates. Under ideal conditions an autumn burn would ensure the highest revegetation rate but under field conditions, as the field surveys indicate, the picture is rather different. It is not clear why the survival of different seedling species in the germination trial was so low in the spring burn. The cause may be attributed to a longer seedling growth period before fertilizer was applied for the first time, than in the other treatments. Other factors can however not be excluded.

Seedlings of a summer burn were larger, grew more vigorous and

exhibited the highest survival rate of all the treatments. The number of different species were also the highest.

All being equal, an autumn burn remains an attractive management burning time. However, the growth rate for Restio egregius was slower after an autumn burn than for any of the other treatments and almost all the species except for a few geophytes missed the first flowering season for the vegetative regenerating species. The following list of species are of the species that were flowering and had flowered at the time of the final survey approximately seven months after the winter-rains had started (Table XXXIII). That is 15 months after the spring burn, 10 months after the summer burn and 7 months after the autumn burn.

As the list indicates the autumn burn had a depressing effect on flowering of sprouting species. The summer burn exhibited a slightly better flowering response than the autumn burn.

An inhibition of flowering in the summer burn is attributed to very vigorous vegetative growth and development of the sprouting species. There is of course a time difference between the growth-after-fire periods between the different seasons of burn, but there was sufficient vegetative growth on for example Phyllica lasiocarpa after the autumn burn for it to be able to flower. The difference in the summer burn revegetation vigour compared with the other treatments is stressed because of the markedness of the response.

Table XXXIII

<u>Spring burn</u>	<u>Summer burn</u>	<u>Autumn burn</u>
Homeria sp.	Homeria sp.	Homeria sp.
Aristea oligocephala	A. oligocephala	A. oligocephala
Spiloxene curculigoides	S. curculigoides	S. curculigoides
Pillansia tempelmannii	P. tempelmannii	P. tempelmannii
Drosera trinervia	D. trinervia	D. trinervia
Zygophyllum fulvum	Z. fulvum	
Oxalis purpurea	O. purpurea	
O. luteola	O. luteola	
Gnidia pinifolia	G. pinifolia	
Aspalathus microphylla	A. linearis	
Merxmuellera rufa	M. rufa	
Romulea gracillima	R. gracillima	
Euryops abrotanifolius	E. abrotanifolius	
Corymbium cymosum		
Staberoha cernua		
Phyllica lasiocarpa		
Phyllica imberbis		
Ficinia indica		
Ficinia filiformis		
Ficinia levynsae		
Hypodiscus argenteus		
Thamnochortus dichotomus		
Willdenowia lucaeana		
Erica corifolia		
Lobelia coronopifolia		
Hypodiscus aristatus		

Table XXXIII (continued)

Restio cuspidatus

Dilatris viscosa

Nivenia stokoei

Restio egregius

Lanaria lanata

Selago spuria

8. DISCUSSION AND CONCLUSIONS

Fynbos species can and do regenerate successfully in a mature community, but at a very slow rate compared to a non competitive situation such as after a fire. The real crux of maintaining a maximum species diversity in managed fynbos is to establish that any combination of species may co-exist indefinitely on the basis of differences in their regeneration niches. Grubb (1977) cites two major conditions for indefinite co-existence. The first is that species B must be able to persist in the community as long as the mean time between those events which cause either the creation of a gap of a kind which favours the establishment of species B more than species A, or the creation of a gap at a place where species B has propagules and species A has not. The second condition is that sufficient gaps that are relatively more suitable for one or the other species must continue to arise in the area concerned. A major determinant of the relative abundance of the species in the community will be the exact proportion of gaps with the potential to ensure the survival of either species in the example mentioned. Persistence of certain species in the presence of different species may not necessarily be in the form of seedproducing adults, but may be as dormant soil-stored seed or as plants in an adjacent community (Grubb, 1977).

Sprouting species are far less sensitive to adverse environmental conditions than seed regenerating species in accomplishing successful regeneration and continued presence of species in a plant community. Furthermore sprouting species have a back-up

seed regenerating system while for species that regenerate by seed only, it is a vital last resort for continuing their existence in that community.

The intensity of a fire determines the survival rate of both sprouting and seed regenerating species. In comparing fynbos fire intensities with those of two different grassland types the results showed clearly that the average fire in fynbos has a higher intensity than the grasslands. Unfortunately no comparable data could be found for analogous vegetation types which would have been a much more valid comparison. If the mediterranean type vegetations in the other parts of the world (Australia, California, Chile and the Mediterranean countries) are comparable with the grassland as regards fire-intensities, fynbos may have the unique problem of having fires with the highest intensities.

Kruger (1977) reports that a growth rate of 2500kg/ha per annum in the first two years after a burn in the fynbos may be a reasonable average. This will depend on the timing of a burn as indicated by the growth rates of Restio egregius after burns in different seasons (Fig. 59). A summer burn exhibited the fastest growth rate and an autumn burn the slowest. The spring burn had a growth rate between the summer and autumn burn rates, but it is interesting to note that the second period of active growth exhibited a much faster growth rate than the first period. It may be assumed that the same phenomenon can be expected for the summer and autumn burns. What is relevant at this point, however, is that the regeneration-rate in the first year after a burn is relatively slower than in succeeding years. The short-term effect of a fire is therefore a general

depression of regeneration and the extent of the regeneration is totally dependent on the prevailing environmental conditions of that first year.

Clearly a project to establish the frequency of the appearance of gaps suitable for the regeneration of one or more species to the exclusion of other species with different sets of requirements, will entail a long-term and detailed study of considerable magnitude. The only meaningful way that such a complex set of results can be interpreted will be to build a computer model of the regeneration niche hyperspace of the community.

The ideal way of conducting research into the maintenance of the species diversity and structure of plant communities is to build simple models of survival and proceed to complex models of indefinite co-existence of the species complement. Unfortunately time is the limiting factor and researchers in nature conservation need the results of such longterm projects before they even start. For the sake of expedience the burning trials and parallel research projects were conducted in such a way that data could be accumulated over a broad spectrum of related problems without bogging down into too much detail.

Observations in the field during the surveys and experiments together with all the data and results obtained from the study have led to the following conclusions:

- (i) Climatically the South-Western Cape is comparable with all the other regions with mediterranean type climates.

- (ii) The structure of fynbos communities range from fairly simple to very complex, at different stages of development and at different localities. Vertical structure is simple and needs no further elaboration. In contrast pattern in fynbos communities is very complex. Pattern is controlled by climatic and edaphic factors on a regional, topographical and site bound scale. On the small scale that pattern was investigated no definite results emerged. Virtually no species associations or vegetation trends could be identified. The only trend detected was on plot 3 and that is associated with shallow soils, rockyness and consequently dryness. This is most probably partially responsible for the low survival rate of seedlings on the spring burn plot.
- (iii) Since abundant numbers of seedlings appeared in the soil stored seed experiment, seeding of burnt areas from outside sources can only be considered as complementary to the vital soil stored seed supply. Fynbos regenerate therefore primarily from its soil stored seed reservoir.
- (iv) Regrowth and the establishment of vegetation cover after a fire proceed slowly in the first season after a fire. Depending on the season of the burn the rate of regrowth is depressed to a greater or lesser degree. A burn in summer has the least retarding effect on regrowth-rate whereas an autumn burn has the greatest retarding effect on the rate of regrowth of the emerging vegetation. This depressing effect of an autumn burn is probably closely associated with the effective growth temperature requirement of fynbos vegetation.

- (v) Seedlings that appeared after the experimental burns could not all be identified at such an early stage in their development. The dominant species such as Erica pulchella regenerated successfully from seed. The numbers of different seedlings that could be distinguished were virtually equal to the number of species that occurred on the plots before the experimental burns. Several new species that were not recorded in the pre-fire vegetation were present in the post fire vegetation. Notably most new species were geophytes. Species such as the Homeria sp. Aristea oligocephala, Spiloxene curculigoides and Romulea gracillima were new additions to the species list of the plots. All the new species were also under the first species that flowered suggesting that they occur primarily in the initial stages of a pyric succession in fynbos.
- (vi) The soil stored seed germination trial showed that the season of burn had an influence on the number of species that manage to regenerate from seed. Both a spring and summer burn exhibited the same seedling diversity but the autumn burn had a lower species richness in the field surveys. The soil stored seed trial indicated that species diversity declined from a summer burn to an autumn, and then a spring burn. Taking all the factors into consideration the results indicate that a summer burn results in the best regeneration of species and number of species, compared to an autumn and spring burn where either growth rate or the number of species that regenerate successfully are depressed. However, since the field survey of the seedling status of each plot indicated a species diversity for the spring burn that equals that of the summer

burn the contention is that a spring burn yields more species and numbers of different species than an autumn burn.

Management of fynbos catchments and reserves should be conducted according to practices that will work with nature to accomplish the desired affect and not against it. According to the results presented a summer burn results in a vigorous and well balanced community regeneration with the highest diversity and growth rate when compared with other treatments. A spring burn is equally well balanced although with a lower diversity and growth-rate but with a higher initial number of sprouting and seedling species that achieve flowering maturity within six to nine months after a burn. Spring is most probably the only practical period to burn from a management point of view.

Although an autumn burn is attractive from a management point of view the effect of such a burn is a general depression of post fire vegetative and seed regeneration and retards flowering maturity of the first flowering species in the pyric succession. Maintenance of species diversity will be endangered if a permanent autumn burning season cycle is adopted.

Under a summer or spring burning régime certain species may be endangered but it is not apparent now. A monitoring program for all management programmes is recommended to detect problem areas.

9. SUMMARY

An example of a physiognomically homogeneous fynbos vegetation

is analysed and described. Experimental burns were carried out in different seasons and their short-term effects on the vegetation were assessed and evaluated.

The fynbos vegetation on the research site in the Kogelberg State Forest is typical in that all the characteristic growth-forms are represented. Proteaceous shrubs dominate the community while the undergrowth is typified by Ericaceae and Restionaceae, without which the term fynbos would not apply. Structurally the Proteaceae dominate in height and cover. The Ericaceae and similar growth-forms from other families locally dominate in cover and biomass over Restionaceae but are overall usually less prominent. All other growth-forms are less prominent and approximately equal in importance.

The phenology of fynbos species and growth-forms exhibit an integrated and complex nature that optimise resource partitioning to a greater or lesser degree in the different seasons. In spring a larger complement of species flower than in any of the other seasons with a concomitant greater drain on community resources at one time. By separating flowering time and the active growth phase as in the case of Leucadendron laurifolium as opposed to the active growth phase immediately followed by flowering as in Restio egregius, resource partitioning in seasonal cycles are effected. Distribution of seed is spread in the same manner and evidence of delayed seed release is prominent especially in the dominant growth-forms.

Little information was gained in the study of the temperature profile in fynbos vegetation. Of importance is the fact that during the day the soil temperatures are always lower than ambient temperature

and the difference is greatest from midday to approximately 14h00. The highest temperatures were recorded 25cm above ground level in the densest undergrowth layer.

A study on the water relations of L. laureolum and R. egregius confirmed assumptions that the growth-forms can tolerate very low water potentials and still grow and flower actively. Soil water content followed the general rainfall régime and underlined the low water holding capacity of the sandy soils. High water tables during the rainy season confirmed soil profile analyses in that the relatively impermeable deeper horizons and shallow bedrock formations prevented deep percolation of water in the short-term. Water logged sandy soils are subject to "mud-flows" during rain and many emerging seedlings are uprooted or buried by them. Micro weirs form on land with sufficient slope to drain excess water and the walls of these micro weirs are the centres of primary seed regeneration in those areas. The initial vegetation pattern is dictated by the intensity of micro weirs and micro relief on the soil surface.

Survival of sprouting species is not very critical under all but the most extreme conditions. The rate of survival of sprouting species was found to be very high. Opportunistic resprouters occur such as R. bifarius where the survival of a tussock depended on the local intensity of the experimental burns to a very large degree. Species that regenerate from seed depend wholly on favourable environmental and edaphic conditions for their successful germination and establishment. Here the very low nutrient status of the soils is of primary importance. Burns in different seasons

affected seed regeneration in both positive and negative ways. Summer and spring burns, in that order, are more favourable for species diversity and seedling establishment than autumn burns.

The growth of sprouting species was affected similarly by fire in different seasons. In the first few months after a fire a summer burn responded with a relatively high growth-rate followed by spring and then an autumn burn.

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APPENDIX I. PROVISIONAL LIST OF THE FLORA ON THE RESEARCH SITE IN THE KOGELBERG STATE FOREST.

The flora of the research site was collected as intensively as possible. Specimens are stored in the Wicht Herbarium at the Jonkershoek forest Research Station. It was duplicated as far as possible in the National Herbarium at the Botanical Research Unit in Stellenbosch.

Specimens were identified at the National herbaria in Stellenbosch and Pretoria, at the University of Cape Town and the Compton Herbarium, National Botanic Gardens, Kirstenbosch.

The species are arranged according to the Wettstein system of classification.

Pteridophyta

Schizaeaceae.

Schizaea pectinata (L.) Smith

Angiospermae

Class: Dicotyledones

Subclass: Choripetalae.

A: Monochlamydeae

Order: Proteales

Family: Proteaceae.

Aulax cneorifolia Knight.

Diastella fraterna Rourke.

Leucadendron gandogerii Schinz. ex Gandoger

L. laureolum (Lam.) Fourcade

L. Salignum Berg.

Leucospermum oleifolium (Berg.) R. Br.

Mimetes cucullatus (L.) R. Br.

L. truncatulum (Salisb. ex Knight) Rourke

L. cordifolium (Salisb. ex Knight) Fourc

Protea scabra R. Br.

Serruria elongata R. Br.

S. inconspicua (L.) Guthrie & Salter

Spatalla mollis R. Br.

Order. Tricoccae

Family Euphorbiaceae

Euphorbia tuberosa L.

E. Silenifolia (Haw.) Sweet

Euphorbia sp. Dur. (no)

B. Dialypetaleae

Order. Parietalis:

Family: Droseraceae

Drosera trinervia Spreng.

Order: Rosales

Family: Papilionaceae

Argyrolobium filiforme Eckl. & Zeyh.

Aspalathus abientina Thunb.

A. ciliaris

A. linearis (Burm. f.) Dahlgr.

A. microphylla D.C.

A. retroflexa

A. stenophylla Eckl. & Zeyh.

A. tridentata L.

Indigofera sp. cf. *I. digitata* Thunb.

Psoralea pinnata L.

P. rotundifolia L. f.

Order: Myrtales

Family: Penaeaceae

Penaea cneorum Meerb. ssp. *lanceolata* R. Dahlg.

P. mucronata L.

Saltera sarcocolla (L.) Bullock

Family: Thymelaeaceae

Gnidia galpinii C.H. Wr.

G. juniperifolia Lam.

G. oppositifolia L.

G. pinifolia L.

G. viridis Berg.

Struthiola ciliata (L.) Lam

S. ciliata (L.) Lam. ssp. *angustifolia* (Lam) B. Peters

Order: Gruinales

Family: Oxalidaceae.

Oxalis luteola Jacq.

O. purpurea L.

/231 Family:

Family: Geraniaceae

Pelargonium angulosum (Mill.) Ait.

Family: Zygophyllaceae

Zygophyllum fulvum L.

Z. flexuosum Eckl. & Zeyh.

Z. sessilifolium L.

Order: Terebinthales:

Family: Rutaceae

Agathosma bifida Bartl. & Wendl.

A. imbricata Willd.

Coleonema juniperum Sond.

Diosma hirsuta L.

D. oppositifolia L.

Euchaetis elata Eckl. & Zeyh.

E. linearis Sond.

Family: Polygalaceae

Polygala garcini D.C.

Order: Rhamnales:

Family: Rhamnaceae

Phyllica imberbis Berg.

P. lasiocarpa Sond.

Order: Umbelliflorae

Family: Umbelliferae (Apiaceae)

Centella glabrata L.

C. virgata (L.f.) Drude

Thumbergiella filiformis (Lam.) Wolff.

Sub class: Sympetalae

Order: Bicornes

Family: Ericaceae

Anomalanthus scoparius Klotzsch

Acrostemon stokoei (L.) Guthrie

Blaeria ericoides L.

Blaeria dumosa Wendl

Erica articularis L.

E. campanularis Salisb.

E. cerinthoides L.

E. corifolia L.

E. cristata Dulfer

E. gysbertii Cuthrie & Bolus

E. hipidula L.

E. imbricata L.

E. pectinata

E. perspicua Wendl.

E. pulchella Houtt.

E. squarosa Salisb.

Nagelocarpus serratus (Thunb.) Bullock.

Scyphogyne divaricata Benth.

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

Order: Tubiflorae

Family: Scrophulariaceae.

Selago spuria L.

Agathelpis dubia (L.) Hutch.

Family: Labiatae

Stachys reticulata Codd

Order: Contortae

Family: Gentianaceae

Chironia tetragonia L.F.

C. jasminoides L.

Order: Rubiales

Family: Rubiaceae

Anthospermum lichtensteinii Cruse

Order: Synandreae

Family: Campanulaceae

Cyphia volubilis (Thunb.) Willd.

Roella ciliata L.

R. incurva D.C.

Family: Lobeliaceae

Lobelia coronopifolia L.

L. linianis

L. tomentosa L.F.

Family: Compositae (Asteraceae)

Berkheya barbata (L.F.) Hutch.

B. herbaceae (L.F.) Druce.

Corymbium africanum L.

C. cymosum E. Mey. ex D.C.

C. glabratum L. sensu Levyns, Adams & Salter

C. scabridum L.F. forma *filiforme* (L.F.) Thunb.

Disparago ericoides Gaertn.

Euryops abrotanifolius (L.) D.C.

Helipterum canescens (L.) D.C.

Helichrysum metalasiodes

H. sesamoides (L.) Willd.

H. vestitum (L.) Shrank.

Lachnospermum umbellatum (D. Don.) Pillans

Metalasia sp. cf. *M. tenuifolia* D.C.

Othonna bulbosa L.

O. heterophylla L.F.

Phaenocoma prolifera (L.) D. Don.

Senecio arenarius Thunb.

S. pinifolius

S. triqueter Less.

S. umbellatus L.

Stoebe cinerea Thunb.

Ursinia crithmoides (Berg.) Poir.

U. quinquepartita (D.C.) N. E. Br.

Class: Monocotyledones

Order: Liliiflorae

Family: Liliaceae

- Albuca cooperi* Bak.
Bulbine favosa (Thunb.) Roem. & Schult.
Bulbinella triquetra (L.F.) Kunth.
Eriospermum pumilum Jacq.
Urginia filifolia (Jacq.) Steinh.

Family: Haemodoraceae

- Dilatria corymbosa* Berg.
 D. pillansii Barker
 D. viscosa L.
Wachendorfia paniculata Burm.

Family: Amaryllidaceae

- Lanaria lanata* (L.) Dur. & Schinz

Family: Hypoxidaceae

- Spiloxene curculigoides* (N. Bol.) Garside.

Family: Iridaceae

- Aristea oligocephala* Bak.
Aristea racemosa Bak.
Bobartia gladiata. (L.F.) Ker-Gawl.
 B. indica.
Geissorhiza humilis Ker-Gawl.
 G. juncea
 G. ovata (Burm. F.) Aschers & Graebn.

Gladiolus bullatus Thunb. ex Lewis

G. brevifolius Jacq.

Homeria sp.

Ixia micrandra Bak.

Lapeyrousia micrantha

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

Nivenia stokoei N.E. Br.

Pillansia tempelmanii (Bak.) L. Bol.

Romulea gracillima Bak.

Watsonia pyramidata (Andr.) Stapf.

Family: Juncaceae

Juncus capensis Thunb.

Order: Enantioblastae

Family: Restionaceae

Chondropetalum hookerianum 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. thyrsefera Pers.

E. vaginulata

Hypodiscus albo-aristatus Mast.

H. aristatus nees

H. argenteus Mast.

Hypolaena digitata Pillans

H. filiformis Mast.

Leptocarpus distichus Pillans

L. hyalinus Pillans.

Restio bifarius Mast.

R. bifidus Mast.

R. curviramis Kunth.

R. cuspidatus Thunb.

R. egregius Hochst.

R. filiformis Poir.

R. pedicellatus

R. pupurascens Nees ex Mast.

R. triticeus Rottb.

Staberoha cernua Dur. & Schinz.

Thamnochortus dichotomus R. Br.

T. fraternus

T. guthrieae Pillans

T. pulcher Pillans

Willdenowia humilis Mast.

W. lucaeana Kunth.

Order: Cyperales

Family: Cyperaceae

Ficinia albicans Nees

F. dunensis Levyns

F. filiformis (Lam.) Schrad.

- F. indica* (Lam.) Pfeiffer
- F. lateralis* (Vahl.) Kunth.
- F. levynsae* Arnold MS.
- F. minutiflora*
- F. monticola* Kunth.
- F. zeyheri* Boeck.

Scirpus ecklonii Steud.

Tetraria compar (L.) Iestib.

- T. cuspidata* (Rottb.) C.B. Cl.
- T. exilis* Levyns
- T. fasciata*. (Rottb.) C.B. Cl.
- T. flexuosa* (Thunb.) C.B. Cl.
- T. microstachys* (Vahl) Pfeiffer
- T. thermalis* (L.) C.B. Cl.

Order: Glumiflorae.

Family: Graminae (Poaceae)

Erharta bulbosa Sm.

Erharta ottonis Kunth.

Merxmuellera rufa (Nees) Conert.

Pentaschistis steudelii (Nees) Mc Clean

APPENDIX II. LIST OF AVIFAUNA OBSERVED IN KOGELBERG
STATE FOREST AT THE RESEARCH SITE AND
IMMEDIATE VICINITY.

Arranged according to Roberts (Mclachlan & Liversage, 1971).

Family: Threskiornitidae

Platalea alba Scopoli	Spoonbill
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Family: Anatidae

Alopochen aegyptiacus Linnaeus	Egyptia goos
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Anas sparsa Eyton	Black duck
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Family: Falconidae

Falco tinnunculus Linnaeus	Rock kestrel
----------------------------	--------------

Family: Aquilidae

Aquila verreauxi Lesson	Black eagle
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Buteo ruffofuscus Forster	Jackal buzzard
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Family: Phasianidae

Francolinus africanus Stephens	Grey-wing francolin
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F. levaillantii Valenciennes	Red-wing francolin
------------------------------	--------------------

Coturnix coturnix Linnaeus	African quail
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Family: Burhinidae

Burhinus capensis Lichtenstein	Cape dikkop
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Family: Laridae

Larus dominicanus Lichtenstein

Southern black-backed gull

L. hartlaubii Bruch

Hartlaub's gull

Family: Columbidae

Columba guinea Linnaeus

Rock pigeon

Streptopelia capicola Sundevall

Turtle dove

Stigmatopelia senegalensis Linnaeus

Laughing dove

Family: Alcedinidae

Megaceryl maxima Pallas

Giant kingfisher

Family: Timaliidae

Chaetops fraternus Temminck

Rock jumper

Family: Turnidae

Monticola rupestris Vieillot

Cape rock-thrush

Sixicola torquata Linnaeus

Stone chat

Cossypha caffra Linnaeus

Cape robin

Family: Sylviidae

Sphenoeacus afer Gmelin

Grass bird

Family: Motacillidae

Motacilla capensis Linnaeus

Cape wagtail

Macronyx capensis LinnaeusOrange throated
long claw

Family: Lanidae

Lanius collaris Linnaeus

Fiscal shrike

Telophorus zeylonus Linnaeus

Bokmakirie

Family: Turnidae

Onychognathus morio Linnaeus

Redwinged starling

Family: Buphagidae

Promerops cafer Linnaeus

Cape sugarbird

Family: Nectariniidae

Nectarinia famosa Linnaeus

Malachite sunbird

Anthobaphes violacea Linnaeus

Orange-breasted sunbird

Family: Ploceinae

Ploceus capensis Linnaeus

Cape weaver

Coliuspasser capensis Linnaeus

Cape widow (Cape bishop
bird)

Sub family: Estrilidinae

Estrilda astrild Linnaeus

Common waxbill

Family: Fringillidae

Serinus canicollis Swainson

Cape canary

Fringillaria capensis Linnaeus

Cape bunting

APPENDIX III. LIST OF MAMMALIA FOUND IN THE KOGELBERG
STATE FOREST ON THE RESEARCH SITE.

The animal names are arrange alphabetically.

<i>Aethomys namaquensis</i>	Namaqua rock rat
<i>Histrix africae-australis</i>	Porcupine
<i>Oreotragus oreotragus oreotragus</i>	Klipspringer
<i>Papio urinus ursinus</i>	Cacma baboon
<i>Pelea capreolus</i>	Grey-rhebuck
<i>Raphicerus melanotis</i>	Grysbuck
<i>Rhabdomys pumilio</i>	Striped mouse (Four-striped rat)
<i>Sylvicapra grimmia grimmia</i>	Common duiker

APPENDIX IV. LIST OF AMPHIBIA FOUND IN AND AROUND THE
RESEARCH SITE IN THE KOGELBERG STATE
FOREST.

Amphibians are listed alphabetically.

Breviceps montanus

Rain toad

Rana fasciata-montana

Long toed rana

Rana fasigula

Common rana

APPENDIX V. LIST OF REPTILIA FOUND IN THE KOGELBERG
STATE FOREST, ON THE RESEARCH SITE.

1. *Bitis arietans*
2. *Pseudaspis cana* (young)

Dr. E. Moll,
Dept. of Botany,
University of Cape Town,
University Private bag,
Rondebosch. 7700.

44 Acacia crescent,
West Acres,
Nelspruit. 1200.

27th June, 1981.

Dear Eugene,

Please pardon the delay in answering your letter. Your letter arrived on Monday the 15th June and by then I had just returned from hospital. Earlier in the year my left sinus above the eye was operated on and this time it was the other side. It would have been ideal for me to get the information you require as I was at home until this weekend. Unfortunately the operation involves removing the eye from its socket and the result is double vision for quite a while after the operation. That was the biggest stumbling block for except for the pain there was a drainage pipe up my nose.

Enough of that, herewith the information you asked for in the same order:

P. 29 Table I CEC units = $\text{me}/100\text{g}$.

P. 33 All climatic data in the thesis were gathered in the period from June, 1976 to May, 1977. After the last date there is a long period with fragmentary records because of problems with the recording apparatuses.

P. 84 There are a number of mistakes in this graph (Fig. 24), the worst being that the area is actually the number of quadrats and the numbers given there are only applicable to the 2m^2 quadrats. The other mistake is that I have never done 3m^2 quadrats, they are supposed to be 8m^2 quadrats.

I am replacing the graph with a more appropriate one which will be included with this letter.

At the end of this letter I shall try and explain why the thesis is of such mediocre quality. ^②

P.86. Braun-Blanquet cover estimates.

P92 Fig.26 y axis = Oven dry mass in kilogram
x axis = stem diameter in centimeter.

P93 Fig.27 y axis = Natural logarithm of mass in kilogram (ODW)
x axis = Natural logarithm of stem diameter in cm.

P94 Fig.28 The units are:

y axis = residuals of the natural logarithm of mass (ODW) in kilogram ($X - \bar{x}$).

x axis = residuals of the natural logarithm of stem diameter in cm ($X - \bar{x}$)

81/06/30

Unfortunately I do not have access to the original computer programme that calculated and drew the graphs. The printouts have already been returned to Tonkershack. The axes have subdivisions of

2 1 0 -1 2 which would suggest that the graduations are in Standard Deviation units but it is basically the same thing.

P124. Block or quadrat sizes are correct and the peak at 1 m^2 is also correct because we never used quadrat sizes other than 1 m^2 , 4 m^2 and 8 m^2 . Two meter square blocks were computer created by lumping successive pairs of 1 m^2 quadrats. All the larger sizes were also created by lumping smaller quadrat sizes. In the cases of Table XVIII and the graph (Fig. 37) I used all the Braun-Blanquet data available for the research area.

The reasons for this are that the vegetation was selected for its homogeneity and the other reason is that with the 1 m^2 quadrats that were contiguous only 3 blocks of 32 m^2 could be compiled. The variance on three blocks would be too large. The great variance is a problem in the

64 m² blocks but I^③ accepted that the last quadrat or rather block size would always have that problem.

The data for the graph and the table were processed approximately 3 and 4 years ago and the difference came with more data being available at the last calculation. Unfortunately that data is also at Jankershoek and I shall have to obtain it from them to check the validity of both the table and the graph.

P.126 para 2. "It is clear from table XVIII". At the time of writing that section of the thesis I did not have the raw data any more and I could not even attempt to carry out the procedure as suggested by Dr Lubke. I have the article that he refers to and I shall try to validate my statement when I have the raw data available again.

P.168 Fig 59. The x axis was not labeled because I dated all the data points. The actual scale is the Natural logarithm of {the number of days after each burn less 31 days}. The 31 days were subtracted because of the frequency of my visits to the plots. My first burn was visited 31 days after the burn for the first time and at that stage there was no response. Twelve days later I made the first measurements. Because the data were recorded that way I used it that way. The natural logarithm was employed to compress the time period to get it all on one graph.

p.172, 173 + 174 Figs 62, 63 + 64. y units are in Kilopascals or Kpa (Kpa ÷ 100 = bar).

p. 212 Jordaan 1941 + Jackson⁽⁴⁾ 1976 referred to on page 149.

Jackson, W.P.U. 1976. Fire and flora on Constantra Ridge, Table Mountain. Veld + Flora 62 (1), 24-27

Jordaan, P.G. 1949. Aantekeninge oor die voortplanting en brand periodes van Protea mellifera Thunb.
(Notes on the propagation and fire period of Protea mellifera Thunb.). Journal of South African Botany 15, 121-125

P. 228. Voucher specimen numbers of plants in check list.
I can let you have my numbers but some of the numbers are in Fred Kruger's, Brian van Wilgen's and Ross Haynes's collection books because we all collected during the duration of the experiments. Collection is still being carried out. The list of plants that was compiled for the Kogelberg by ~~the~~ the Wicht herbarium did not contain any numbers and I did not bother about them from Nelspruit.

I shall need a little more time to gather all my numbers from my collection book. There are, however, also a number of plant names that were sent to me from Tankershoek without the collection numbers that still have to be filled into my collection book.

⑤

As you can see the letter was written in a serial fashion because I was interrupted by visitors and family. There were also meetings etc. to be attended and today was the first time that I had the time to write seriously again.

At present I am feeling much better and have started to work again. From the onset there were meetings to be attended such as one for the organizing of the Howveld Farmer's Association's exhibition this year. Since I shall not be replaced while I am in Israel I have to do two years planning in advance and try and finish off all projects in different committees that I am a member of.

You normally have a busy schedule and I can now appreciate it thoroughly. Before the news of the Israel bursary became known I had started planning the building of a house. The house may just be finished before I leave but it is improbable, with the result that I have to plan to make the move, that my wife will have to conduct, as easy as possible.

In the meantime I am still trying to follow the Fynbos Ecosystem Project's progress in the Cape. There seems to be much more funds available to do proper research.

Herewith I wish you well and may your research and projects all be a resounding success!

Ben.

N.B.: The graphs that I include may be inserted in the thesis by tearing out the page and pasting in the new one. I hope it does not cause any embarrassment.

81/07/01

⑥

2 As I promised, here follows an explanation for some of the major mistakes except the writing:

My typist was leaving for Sasolburg at the end of April and I had to get it typed before she left. They went on two weeks holiday before leaving cutting down my time even more. Her typewriter had characters that are not easily matched in Nelspruit and her speed and accuracy of typing is vastly superior, therefore I was not prepared to change to another typist at the end.

The girl that did my graphs, maps and other drawings took all the work I gave her to her home. She then developed a cancerous tumour behind her one eye and left for Pretoria without returning my work. She delivered the graphs etc. at number 99 and I did not check the work very well because most of the work was just copying. A mistake like fig 24 came in when she misread my 8 for a three and rearranged the sequence of small graphs. The graphing error was mine, I plotted the data incorrectly.

Towards the end the thesis was just one big rush and I apologize for obvious mistakes.

Dr. Lubke's remark about "running out of steam" is generally correct because I am drifting away from pure ecological thought as my work is agricultural and very economically orientated.

My time is limited but if possible I shall try and draft one or two possible publications so that the data in the thesis do not get "lost".

Thank you for your patience and perseverance.

Ben.