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Description of a proteoid-restioid stand in Mesic Mountain Fynbos of the south-western Cape and some aspects of its ecology

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Keywords: *Chondropetalum hookerianum*, duplex soil, *Erica cristata*, Fynbos Biome, *Leucadendron xanthoconus*, mediterranean-type climate, Mountain Fynbos, soil nutrients

ABSTRACT

A description of the community and its climatic and edaphic environments is given for a stand of Mountain Fynbos vegetation codominated by *Leucadendron xanthoconus* and *Chondropetalum hookerianum*. The paper categorizes aspects of the study site either according to existing classifications, or by comparison with other fynbos systems. Comparison of rainfall and temperature data with those collected at an agricultural research station in the region indicated high variability in the spatial and temporal pattern of precipitation, and an air temperature regime which was influenced by the topography. Analysis of vegetation data revealed a species richness lower than other fynbos communities, but a species turnover of similar magnitude. A list of flowering plants and ferns found in the stand is appended. The soil of Table Mountain Group origin comprised a colluvial A–E horizon with a well defined stone-line, and residual B and C horizons of shale origin. It had low pH and nutrient status, with a high measured concentration of aluminium, especially in the B horizon.

UITTREKSEL

'n Bergfynbos-plantegroeigemeenskap met *Leucadendron xanthoconus* en *Chondropetalum hookerianum* as dominante plantsoorte, asook die klimaats- en edafiese omgewing daarvan, word beskryf. Die artikel kategoriseer aspekte van die studieterrein òf volgens huidige klassifikasies òf deur vergelyking met ander fynbossisteme. Reën-val- en temperatuurdata is met dié van 'n landbounavorsingstasie in dieselfde streek vergelyk. Hierdie vergelykings het aangetoon dat die neerslag binne die streek baie veranderlik ten opsigte van ruimte en tyd was, en dat temperatuur deur die topografie beïnvloed is. Ontleding van die plantegroeidata het aangetoon dat die spesierykheid laer as dié van ander gemeenskappe in die fynbos was, maar dat die spesieomset ongeveer dieselfde was. 'n Lys van blomplante en varings wat in die stand aangetref word, word bygevoeg. Die grond van Tafelberggroep-oorsprong het uit 'n kolluviale A–E-horison met 'n duidelike kliplyn, en residuele B- en C-horisonne van skalie-oorsprong bestaan. Die pH- en voedingstofstatus was laag, met 'n hoë aluminiumkonsentrasie, veral in die B-horison.

INTRODUCTION

Mountain Fynbos is the best preserved vegetation type in the Fynbos Biome of the Cape (Moll & Bossi 1984). The poor, highly leached soils of these upland sites (Kruger 1979) have proved unsuitable for conventional agriculture, and direct commercial utilization is restricted almost entirely to silviculture and the wildflower industry. As a large-scale international trade, the latter is relatively young, and production techniques are in many instances still experimental (Davis 1984). It is expected that wildflower producers will increasingly favour cultivation over the traditional veld-harvesting method of floricultural production to assist in controlling product quality (Brits *et al*. 1983). Those parts of the relatively unutilized Mountain Fynbos which contain the preferred habitats of many of the showy proteaceous species, are seen as the logical locations for this branch of agricultural development. This article is based on observations made during the first phase of a study into the possible effects of physical disturbance by agricultural tillage on natural Mountain Fynbos.

The primary objective of this paper is to describe the chosen study site in terms of the existing classifications and other frames of reference normally used for fynbos systems. Where this is not possible, or is not appropriate, comparison with data from other fynbos studies is attempted. The rationale for these exercises is two-fold. Firstly, recognition of common sets of attributes, especially ecologically functional ones, is a necessary basis for formulating the management strategies required for utilization and conservation of Mountain Fynbos vegetation. Secondly, where the classifications used to describe Mountain Fynbos systems are incomplete, the task of workers motivated to update them, is facilitated by available quantitative data. This paper endeavours also to be a small part of that accessible repository.

STUDY AREA

The chosen site is on the south edge of the Grabouw Basin, Caledon District, within a region where quartzite, sandstone and thin bands of shale and conglomerate of the upper Table Mountain Group outcrop, as documented on the 1:125 000 geological map of the area (Government Printer 1966). It lies on a gentle slope of approximately 8%, with an aspect of 246° and at an altitude of 375 m. It is 10,5 km from the sea on the landward side of a ridge which rises to a maximum height of approximately 500 m. The grid co-ordinates of the site are: 34° 15' 38"S and 19° 6' 38"E. Until March 1987, the area in which the study site is located was managed by the Directorate of Forestry (Department of Environment Affairs) as a mountain water catchment area. It is

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now under the control of the Department of Nature and Environmental Conservation (Cape Provincial Administration).

METHODS

Development of the study site

An experimental plot 50 x 50 m was delineated at the site during 1984. Sample quadrats (2 x 2 m) were delineated at 28 regularly spaced stations, providing a sampling intensity of 4% for the major components of the vegetation. As part of the long-term experimental design the site was cleared by means of a controlled burn in February 1985.

Climatic data

A weather station was set up on the cleared area and a data-logging device (MC Systems, Cape Town) installed. This monitored a set of environmental parameters, including precipitation and air temperature. Regional long-term precipitation data were obtained from records of the Weather Bureau (1985), and from a statistical report issued by the Soil and Irrigation Research Institute (Agrometeorological Division 1983) for the following stations respectively: Highlands Forest Station (34° 17'S; 19° 6'E; 426 m) over the period 1938–1984; and the experimental farm of the Fruit and Fruit Technology Research Institute in Elgin (34° 8'S; 19° 2'E; 305 m) over the period 1963–1983. As an estimate of the long-term mean air temperature at the study site, long-term data from the Elgin Station (Agrometeorological Division 1983) were adjusted by the differences recorded for this same parameter at the two stations during the period July 1985–June 1986 (see Results).

For periods when the data-logging equipment was non-functional (a total time of approximately six weeks during the sample period of July 1985–December 1986), precipitation data recorded at the Highlands Forest Station, 2,5 km to the south-west, have been used. Means of the monthly totals at these two stations during 1986 agreed to within 1,3%. Temperature data were not augmented in this way.

Vegetation

Mature vegetation was sampled at the 28 stations mentioned above. A 1 x 1 m subquadrat was used for close inspection of the less conspicuous species. A list of all identified species of ferns and flowering plants observed on random scans of the plot and its immediate surroundings (a total area of ± 0,65 ha) is given in the Appendix. Further species recognized as distinct are not recorded because the material found was such that it could not be identified.

A single set of nested quadrats (after Whittaker *et al.* 1979) was marked out in veld adjacent to the study plot for the construction of a species-area curve to permit comparison of the site with data from other studies. The number of different species was measured in quadrats of: 1 m² (10 replicates); 10 m² (2 replicates); 100 m² and 1 000 m² (no replication).

Age of the stand was estimated by counting the number of nodes on the largest individuals of the dominant shrub species, *Leucadendron xanthoconus* (Kuntze) K. Schum., and cross-checking against aerial photographic records of the Department of Surveys and Mapping.

Soil

Description of the soil profile was provided by three shallow soil pits (approximately 0,8 m deep), and a single deeper one (1,8 m). For analysis of the physical and chemical characteristics of the soil, samples were taken from the A horizon, the top of the B horizon, and a single sample from saprolitic parent material at 2 m. Each of these samples was air-dried and sieved to 2 mm. Nutrient analyses were performed by the regional Soil Analytic Laboratory of the Department of Agriculture and Water Supply (Winter Rainfall Region) at Elsenburg using methods described by Jackson (1958), Hesse (1971), the Fertilizer Society of South Africa (1974), and Moore & Chapman (1986). Bulk density and field capacity were determined on undisturbed soil cores, and texture on 2 mm sieved samples.

As possible factors influencing pedogenesis at the site, incidental observations of plant or animal interactions with the soil were noted; the most apparent of these was the presence of a number of termite mounds.

RESULTS

Climate

The climatic diagram (after Müller 1982), derived for the study site from the adjusted data of Highlands Forest Station and Elgin Experimental Farm, is given in Figure 1. Figure 2 shows the total monthly rainfall measured at the study site (with adjustments for missing data — see Methods), together with concurrent and long-term data from other sites. Figure 3 demonstrates that on a weekly basis during the sample period the rainfall was very unevenly distributed between the Highlands study site and Elgin, although total precipitation received during 1986 at each station was similar (Highlands, 1 110 mm and Elgin, 1 090 mm). The weekly Highlands total of 123,4 mm in this latter figure comprises precipitation recorded by the Highlands Forest Station during a single

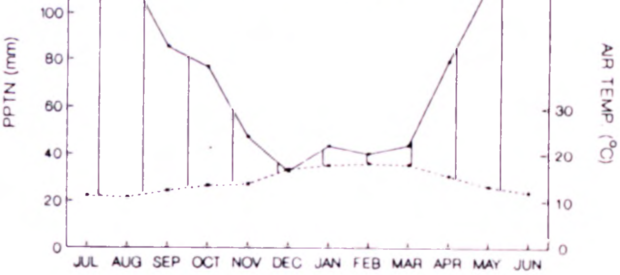

FIGURE 1.—The derived climate diagram for the Highlands study site. The broken line depicts mean monthly air temperature, while the solid line is total monthly precipitation (after Müller 1982).

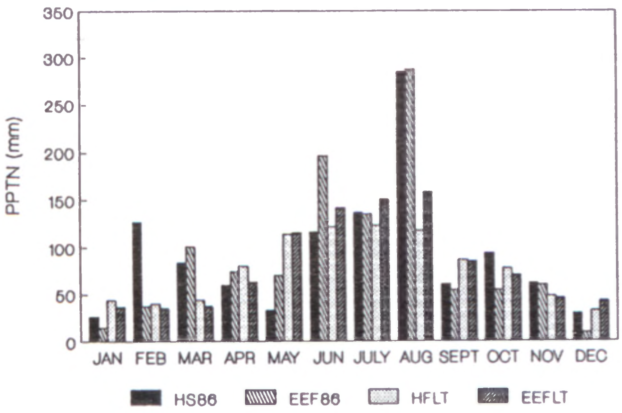

FIGURE 2.—Total monthly precipitation during 1986, and long-term averages for sites in Highlands and Elgin. Legend symbols are as follows: HS86 = Highlands study site, 1986; EEF86 = Elgin Experimental Farm, 1986; HFLT = Highlands Forest Station (1938–1984); and EEFLT = Elgin Experimental Farm (1963–1983).

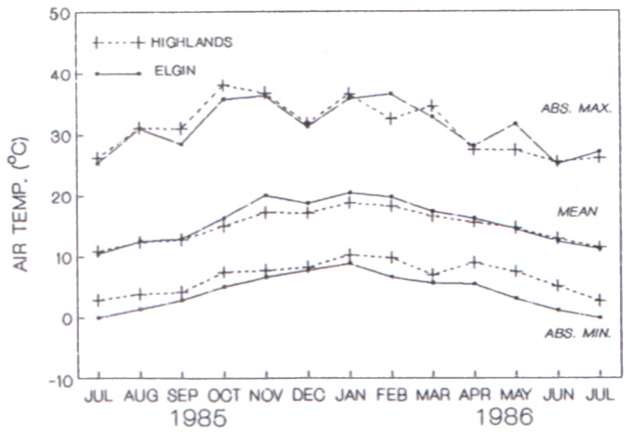

FIGURE 4.—Mean monthly temperature measures recorded at the Highlands study site and the Elgin Experimental Farm during the period July 1985 to July 1986. February values for Highlands include a 10-day period of missing data, which could cause the extreme values during that month to be unrepresentative.

24 h period in February 1986 when the data logger system at the study site was not functional. An accumulation type rain gauge at the study site confirmed rainfall in excess of 100 mm for the month of February.

For reasons dictated by the completeness and reliability of the data, air temperature regimes are given for the period July 1985 to June 1986 (see Figure 4). The most noticeable differences between these two locations are the consistently warmer mean temperatures during the spring and summer months, and the year-round colder minima at the Elgin Station. A 10-day period of missing logged data at the study site during February may cause the reported extreme values to be inaccurate for that month.

Vegetation

Vegetation at the site was estimated to be 12 years old. Aerial photographs taken in 1973 (Department of Surveys and Mapping) indicated that the area had been recently burned. This agreed with the Highlands Forest Station records documenting an accidental fire during the same year. The plant community was characterized by a shrub layer largely comprising *Leucadendron xanthoconus*, and a dense restioid component dominated by *Chondropetalum hookerianum* (Masters) Pill. The mean measured density of *L. xanthoconus* on the plot was 1,7 mature plants per m² (1,23 S.D.) with a mean height of 0,80 m (0,155 S.D.). Approximate projected cover of live restioid shoot material (mostly *Chondropetalum hookerianum*) was 39%, and that of accumulated dead tissue added a further 35%. A third species which was abundant throughout the site was *Erica cristata* Dulfer. This species had a frequency of occurrence of 93%, but probably contributed little to the aboveground biomass of the system owing to its sparse and rangy habit. Another conspicuous shrub species at the site was *Erica longifolia* Ait., which was thinly and unevenly distributed (0,48 mature plants per m²; 1,2 S.D.) with individual heights of up to 1,4 m.

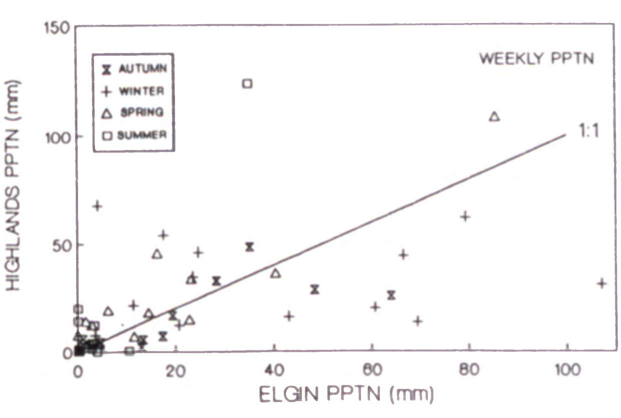

FIGURE 3.—Comparison of weekly precipitation totals recorded at Highlands (combined forest station and study site data), and the Elgin Experimental Farm during 1986.

The mean species richness in the set of twenty-eight 1 m² quadrats was calculated to be 7,7 species per m² (1,7 S.D.), whereas the 1 m² quadrats of the nested set afforded a slightly higher value of 8,6 species per m² (1,7 S.D.). The overall mean for these two sets is 7,9 species per m². The larger quadrats of the nested set contained 19 (mean of 2); 37; and 56 species in 10 m², 100 m², and 1 000 m² respectively. A linear regression between the number of species (S), and the $\log_{10}$ of the quadrat area (LogA) gave the following relationship:

$$S = 6{,}12 + 16{,}02 \text{ LogA} \quad (r^2 = 0{,}984)$$

The species list (see Appendix) contains the names of all taxa recorded at the site both before the experimental burn in 1985, and for two subsequent seasons.

Soil

Soil at the site was duplex, a category found throughout the south-western Cape (Schloms *et al.* 1983). It comprised a dense underlying stratum of saprolitic shale with a shallow (150–800 mm) colluvial overburden of predominantly quartzitic material. The top stratum consisted of an orthic A horizon, a leached E horizon, and a basal stone-line (commonly 150 mm thick) of quartz and sandstone rock fragments. In places, the topsoil contained more fine shale-derived material, while in others the sandy surface layer was missing entirely, leaving a lithosolic A/E horizon. Rock particles varied

TABLE 1.—Chemical and physical properties of soil at the Highlands study site. Mean values are given for each parameter, followed by the standard deviation of the mean. Values for the C horizon represent a single sample only, and bulk density of the B horizon a set of 2 values

Parameter	Units	A horizon	B horizon	C horizon
N (Kjeld)	$\mu g.g^{-1}$	453 (155)	192 (53)	–
P (Bray 2)	$\mu g.g^{-1}$	7,3 (0,6)	6,3 (3,1)	8
K (Bray 2)	$\mu g.g^{-1}$	79 (18)	59,3 (32,3)	18
Exch. cations:				
Na^+	me/100 g	0,62 (0,11)	0,36 (0,15)	0,42
K^+	me/100 g	0,19 (0,02)	0,1 (0,05)	0,08
Ca^{2+}	me/100 g	1,04 (0,28)	1,07 (0,35)	0,35
Mg^{2+}	me/100 g	0,75 (0,12)	1,29 (0,65)	0,39
C.E.C.	me/100 g	3,54 (1,92)	8,82 (1,04)	0,2
Al	me/100 g	0,44 (0,08)	10,8 (2,93)	–
C	%	3,32 (0,51)	1,08 (0,49)	<0,05
Resistance	ohms	747 (116)	3687 (1494)	520
pH		4,3 (0,1)	3,9 (0,2)	3,9
Texture:				
Clay	%	7,4 (4,1)	27 (3,6)	–
silt	%	8,1 (2,1)	50 (3,0)	–
sand	%	85 (6,1)	17 (7,2)	–
sand texture		medium	medium	
Bulk density	$mg.mm^{-3}$	1,23 (0,1)	1,45 (–)	–

in the size of their largest dimension from less than 10 mm, to more than 300 mm, and were usually heavily ferruginized. The B horizon was composed exclusively of the shale-derived material, showed weak structure, and tended to be gleycutanic. The deeper soil pit which was dug outside of the study plot and adjacent to an area with outcropping sandstone, revealed in the subsoil horizon a layer of pre-weathered sandstone approximately 1,2 m thick, bounded above and below by shale-derived material. This band dipped at an angle of approximately 45°, and it is thought that the C horizon throughout the study plot was effectively within the upper shale stratum. With regard to the classification system developed by MacVicar *et al.* (1977), the soil could be placed in the Kroonstad Form (Mkambati or Avoca Series), although where the B horizon displayed more prismatic structure and darker cutans, association with the Estcourt Form was stronger (Uitvlugt or Estcourt Series). Identification of the soil series was equivocal on account of the variability of the clay content of the E horizon, a diagnostic feature of both forms.

Results of the physical and chemical analyses performed on samples taken from the site are summarized in Table 1. In terms of the textural classification included by MacVicar *et al.* (1977), soil of the A horizon lies on the border between loamy sand and sandy loam. Field capacity of the top layer of soil, expressed as gravimetric water content, was measured as 22,5% (3,57 S.D.).

The following features which might influence profile development were observed at the site: 1, surface soil movement under the influence of winter runoff; 2, waterlogging of the colluvial stratum, but not the B horizon during winter; 3, the presence of termite colonies (*Amitermes sylvestris*) whose mounds were present with a mean density of 120 per ha, and a mean height of 350 mm; 4, the occurrence of earthworms (infrequently observed); 5, occasional mole or mole rat activity; and 6, the penetration of roots into the dense B horizon. This latter phenomenon was limited to structural faults and was noted as occurring to the maximum investigated depth of 1,8 m. These roots probably belonged to *Leucadendron xanthoconus* individuals, the only species whose roots were positively identified as penetrating into the B horizon. Fungal hyphae were also observed in old root channels in this horizon.

DISCUSSION

Climate

The climate diagram (Figure 1) based on long-term data depicts a typical humid mediterranean-type with winter half-year rainfall (May to October) exceeding 65% of the 928 mm annual total, and a distinct winter with at least one mean monthly temperature less than 15°C (Aschmann 1973). As described by Fuggle & Ashton (1979), the climates of the Fynbos Biome form a 'spatially diverse mosaic' on account of its mountainous topography. Comparison of the observed climatic parameters at the study site and at the Elgin Experimental Farm illustrates this diversity, with precipitation patterns in the region being especially non-uniform (Table 2).

TABLE 2.—Long-term annual precipitation at various stations within the Grabouw Basin

Station	Altitude (m)	Ann. pptn (mm)	Source
Elgin FS	281	1120	Fuggle 1981
Elgin EF	305	978	Agromet. 1983
Lebanon FS	351	675	Fuggle 1981
Highlands FS	426	928	WB 1985
Nuweberg FS	650	1499	Fuggle 1981
Jakkalsrivier – 1	655	824	Kruger 1979
Jakkalsrivier – 2	817	956	Kruger 1974

EF, experimental farm; FS, forest station; Agromet., Agrometeorology Division; WB, Weather Bureau.

The heterogeneity of the rainfall may also play a critical role in the fire ecology of these seasonally flammable areas. The single highest rainfall event at the Highlands Forestry Station during the sample period occurred in February, the height of the fire season. Such temporal and spatial patchiness of rainfall acting over the millennia of fynbos evolution could have contributed significantly to a patchy fire history, and hence to the heterogeneous mosaic of the present-day vegetation.

Regional patterns of ambient air temperature appear to be more predictable than those of precipitation (Figure 3). The warmer spring and summer mean air temperatures, and the colder year-round minima of the Elgin Experimental Farm relative to the Highlands study site, can probably be explained by the location of the former station. Elgin almost certainly experiences more restricted air movement during the windier spring and summer period than the study site (partly supported by unpublished data from this study); and perennial nocturnal drainage of cold air (Barry & Chorley 1982) from the large mountains of the Hottentots Holland and Franschhoek to the north. See Davis (1987) for a brief discussion of wind at the study site.

Vegetation

The criteria established by Taylor (1978) for the definition of fynbos are amply satisfied by vegetation at the study site, and the species which characterize it, all have distributions restricted to the Fynbos Biome as delineated by Moll & Bossi (1984).

Species richness at the site was lower than the much quoted fynbos figure of 121 flowering plant species within an area of 100 m^2 (Taylor 1972). Unfortunately this figure has been quoted in the literature as a benchmark of species richness in fynbos (e.g. Bond 1983; Jarman 1982; and Taylor 1978), when, in fact, it is given in a semi-popular article in which descriptive details are omitted. Better documented figures are presented by Bond (1983), who reports a maximum figure of 104 species in an area of 1 000 m^2 in a Jonkershoek stand of *Protea nitida* (waboomveld), the extrapolation of which on the log-scale would agree well with the total of 126 species recorded at the Highlands study site in an area of approximately 0,65 ha. In the same paper, Bond presents a synoptic species-log area curve for fynbos vegetation in the southern Cape mountains. For the formulation $S = b + d\log_{10}A$, where S is the number of species in an area A, he found b = 16,4 and d = 15,8. These constants of the linear equation represent 'point diversity' and species turnover (or community patchiness) respectively (Bond 1983). Highlands data indicate a significantly lower point diversity (t-test; $p < 0{,}001$), but a similar patchiness for the community at the study site. They are more similar to those obtained by Whittaker *et al.* (1979) for mallee vegetation in New South Wales, Australia (b = 5,3 and d = 15,3). Based on a sample area of 100 m^2, Cowling (1983) reported species-richness of 26,5 for Mountain Fynbos in the south-eastern Cape. This is lower than the Highlands figure, while on the other hand the mean of his 'point diversity' (*sensu* Bond 1983) for fynbos shrubland sites was twice that of the study site. The measures of diversity discussed above lend a valuable perspective to the description of the Highlands study site, but as yet the body of available information is insufficient for this parameter to be used as an accurate classifier.

According to the description of post-fire succession in fynbos by Kruger & Bigalke (1984), as summarized by Rutherford & Westfall (1986), the 12-year post-fire stand of the study site was in an early stage of maturity, a phase during which the codominance of phanerophytes, chamaephytes, and hemicryptophytes is best developed. However, the abundance of restioid shoot tissue and the consequent build-up of a dense mat of litter may effectively advance the maturation process in the site community by causing premature reduction in species richness.

Subjectively, the mature vegetation of the study site was best described as a *Leucadendron xanthoconus* stand, with an understorey dominated by *Chondropetalum hookerianum* and *Erica cristata*. These species have distributions as follows: *L. xanthoconus* and *C. hookerianum* occur from the Cape Peninsula eastward as far as Bredasdorp (Vogts 1982) and Riversdale (Linder 1985) respectively, while *E. cristata* is restricted to the area between Sir Lowry's Pass and the Klein River Mountains (Baker & Oliver 1967). Grobler (1964), Boucher (1972, 1978), Kruger (1974), and Durand (1981) have all conducted vegetation surveys within a 15 km radius of the study site, and although they cite some species conspicuous in the Highlands vegetation, none of their community descriptions characterize it. Inspection of Boucher's (1978) data for the occurrence of the above three species in his study area between Cape Hangklip and the Palmiet River revealed a pattern (Figure 5), which suggests that the convergence of all three at Highlands may be a characteristic feature of the site. In two of the three instances where this occurred in Boucher's study, soil was of the duplex Estcourt Form. (It is possible that *E. cristata* and *C. hookerianum* form a commensalistic association, in which physical support of the trailing ericoid by the erect restioid may be an element, a phenomenon observed in the mature vegetation at the study site.)

Comparison of the Highlands species list (see Appendix) with those of Boucher (1978) and Kruger (1974)

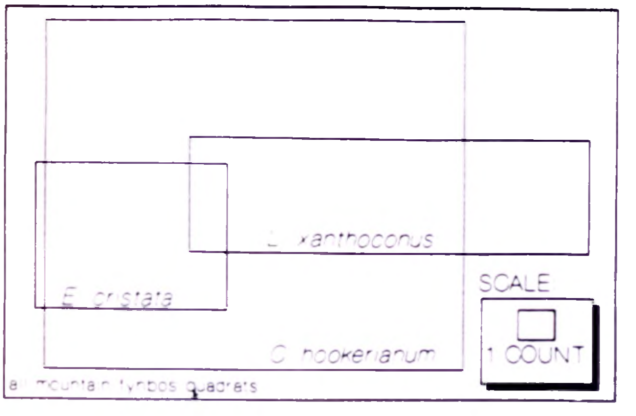

FIGURE 5.—Frequencies with which the three species *Leucadendron xanthoconus*, *Chondropetalum hookerianum* and *Erica cristata* occurred at Mountain Fynbos sample plots in the Cape Hangklip area, and their degree of distributional overlap. Drawn from the data of Boucher (1978).

confirmed the small degree of overlap at the species level. Of the Highlands species, approximately one third of the total number was contained in each of the other lists, while less than 20% were common to all three. Kruger & Taylor (1980) have previously demonstrated that a 60% difference in species composition exists between Cape Hangklip and Jakkalsrivier.

The above discussion suggests that while many phytosociological elements of the region are represented at the study site, regional patchiness might easily make manifestation of a previously recognized community unlikely. In an attempt to improve upon the phytosociological approach to classification of Mountain Fynbos vegetation, Campbell (1985, 1986) invested considerable effort in constructing a structural classification with *a priori* rules for classifying communities. He pointed out (Campbell 1985), using stands dominated by *Leucadendron gandogeri* as an example, that some assemblages of plant life will necessarily defy classification by that particular system. Interpretation of the Highlands vegetation according to the key of structural features affords it a similarly equivocal position. Careful consideration of the Highlands vegetation may offer additional information to resolve that particular shortcoming of the structural classification.

Soil

As with the composition of plant communities, soil is a characteristically variable component of the Fynbos Biome (Moll & Jarman 1984). Boucher (1978) counted eight soil forms (14 series) in his study area of 115 km², but some of his classified mountain plant communities included up to six of these. Estcourt, one of the forms identified at the Highlands site, occurred at 15% of his mountain relevés as the Soldaatskraal Series, while Kroonstad was not listed at all. Kruger (1974), noted six forms within the 1,58 km² Jakkalsrivier catchment, none of which was in common with the Highlands site. Campbell (1983), in his extensive survey of montane environments in the Fynbos Biome also encountered none of the forms identified at the study site, although the Highlands data are consistent with the generalized gradients which summarize his work. Considering the shale-derived component of the Highlands soil, his warning against equating non-quartzitic origin in Mountain Fynbos soil with nutrient-richness is borne out.

In the broad context of fynbos soils, topsoil at the study site is typical in that it is acid, leached, and nutrient poor (Kruger 1979). Being duplex in nature, however, the dense B horizon acts as an impediment to the vertical loss of many of the soil constituents that might normally be removed from the system during the podzolization process, although throughflow (Trudgill 1977) may account for loss via seeps. (The working definition of nutrient-poorness supplied by Campbell (1983) is easily met for both A and B horizons.)

Apart from some intensive studies on lowland systems with narrowly defined objectives (e.g. Low 1983; Mitchell *et al.* 1984; Stock 1985; Witkowski & Mitchell 1987), published data which describe the nutrient status and cycling processes in fynbos soils are limited. Information on nutrients in mountain systems is sporadic in the literature, and usually incidental to broader ecological studies. Comparison of the Highlands data with those describing other Mountain Fynbos sites (Low 1983), indicated that total N in the Highlands topsoil was greater than at these other sites by factors of between 1,1 and 3,2. The measured available P was comparable to the values of between 2,5 and 4,5 $\mu g.g^{-1}$ reported by Read & Mitchell (1983) for coastal fynbos. The C.E.C. measured at the Highlands site fell into the wide range of values measured by Kruger (1974) for soils at Jakkalsrivier (0,5 to 44,0 me/100 g), while it was appropriately lower (for an oligotrophic soil) than the approximate mean of 14 me/100 g given by Tucker (1983) for a range of non-carbonate soils in Australia and the USA.

Accumulation of clay particles at the top of the B horizon clearly increased the measured C.E.C. at this level (Table 1), but parallel concentration of aluminium may outweigh the advantage of this to plants by reducing the availability of phosphorus under the inherently acid conditions (White 1979). The ability of Scottish heathland plants to survive on soils with high Al content is demonstrated in a study cited by Woolhouse (1981) where concentrations of 0,17% (18,9 me/100 g) are reported for the B_1 horizon. These figures are somewhat greater in magnitude than those obtained for soil of the Highlands study site. It would be reasonable to suppose that the toxic effects of Al are countered either edaphically (Norrish & Rosser 1983), or physiologically within heathland and fynbos systems, where this element is liable to be common (Hesse 1971).

The observed downhill movement of topsoil during the rainy season at the Highlands site implies that the process of soil creep responsible for the formation of this duplex soil is still in progress. However, root penetration, together with some activities of the soil fauna, may be acting to ameliorate and stabilize the soil in local patches.

Synthesis

The data which describe phenomena of the Highlands study site are valuable to the ongoing study by providing a base-line for the investigation of ecosystem functions. The immediate objective, however, is to place that information in a general descriptive context which relates to other Mountain Fynbos systems. This is attempted in Table 3.

TABLE 3.—A summary description of the Highlands study site with regard to the climate, vegetation and soil

Feature	Description
Climate	Humid mediterranean-type with spatial and temporal stochasticity of precipitation
Vegetation	Proteoid-restioid (*Leucadendron xanthoconus-Chondropetalum hookerianum*) with species turnover typical of Mountain Fynbos, but with low point diversity
Soil	Of Table Mountain Group origin with a quartzitic and shale-derived colluvium (probably mobile) overlying weathered shale; acid, nutrient-poor and seasonally waterlogged

CONCLUSION

As human demands inevitably increase with time, conservation and effective utilization of natural resources such as Mountain Fynbos vegetation will depend greatly on the extent to which managers are able to identify and predict responses of ecosystems to the impacts of exploitation. Classification of ecosystem attributes is an important step in establishing a means to extrapolate knowledge of specific sites to larger managerial units. Treating the Highlands site as a test case, we have seen above that hopes for the development of a classification which encompasses the functional complexity of Mountain Fynbos are justified. This is especially true considering the large body of information which has accumulated over the past decade under the co-ordination of the Fynbos Biome Project of the CSIR (see Moll & Jarman 1984).

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APPENDIX

A provisional list of the species occurring at the Highlands study site in the Caledon District. The alphabetical arrangement of Bond & Goldblatt (1984) is used here for ease of access, but nomenclature and authorship are according to Gibbs Russell *et al*. (1985) and Gibbs Russell *et al*. (1987), except for the Restionaceae, where Linder (1985) has been used.

SCHIZAEACEAE
Schizaea pectinata *(L.) Swartz*

PINACEAE
Pinus pinaster *Ait.*

CYPERACEAE
Chrysithrix capensis *L.*
Ficinia
 albicans *Nees*
 bolusii *C.B. Cl.*
 capensis *L.*
 ecklonea *(Steud.) Nees*
 fascicularis *Nees*
 lateralis *(Vahl) Kunth*
 paradoxa *(Schrad.) Nees*
Tetraria
 brachyphylla *Levyns*
 capillacea *(L.) C.B. Cl.*
 compar *(L.) Lestib.*
 cuspidata *(Rottb.) C.B. Cl.*
 fimbriolata *(Nees) C.B. Cl.*
 ustulata *(L.) C.B. Cl.*

HAEMODORACEAE
Dilatris pillansii *W.F. Barker*
Lanaria lanata *(L.) Dur. & Schinz*
Wachendorfia paniculata *Burm.*

IRIDACEAE
Anapalina triticea *(Burm. f.) N.E. Br.*
Aristea
 juncifolia *Bak.*
 oligocephala *Bak.*
 spiralis *(L. f.) Ker-Gawl.*
Bobartia
 filiformis *(L. f.) Ker-Gawl.*
 gladiata *(L. f.) Ker-Gawl.*
Gladiolus maculatus *Sweet*
Ixia micrandra *Bak.*
Micranthus junceus *(Bak.) N.E. Br.*
Thereianthus bracteolatus *(Lam.) G.J. Lewis*
Tritoniopsis parviflora *(Jacq.) G.J. Lewis*

LILIACEAE
Eriospermum sp. *Jacq. ex Willd.*

ORCHIDACEAE
Ceratandra atrata *(L.) Dur. & Schinz*

POACEAE
Ehrharta longifolia *Schrad.*
Merxmuellera rufa *(Nees) Conert*

RESTIONACEAE
Calopsis
 hyalina *(Mast.) Linder*
 membranacea *(Pillans) Linder*
Cannomois virgata *(Rottb.) Steud.*
Ceratocaryum decipiens *(N.E. Br.) Linder*
Chondropetalum hookerianum *(Mast.) Pillans*
Elegia filacea *Mast.*
Hypodiscus
 albo-aristatus *(Nees) Mast.*
 argenteus *(Thunb.) Mast.*
 aristatus *(Thunb.) Krauss*
 laevigatus *(Kunth) Linder*
 willdenowia *(Nees) Mast.*
Ischyrolepis caespitosa *Esterhuysen*
Mastersiella digitata *(Thunb.) Gilg-Ben.*
Restio
 filiformis *Poir.*
 similis *Pillans*
 triticeus *Rottb.*
 verrucosus *Esterhuysen*
Staberoha cernua *(L. f.) Dur. & Schinz*
Thamnochortus lucens *(Poir.) Linder*
Willdenowia sp. cf. arescens *Kunth*

APIACEAE
Centella restioides *Adamson*
Lichtensteinia trifida *Cham. & Schlechtd.*
Peucedanum ferulaceum *Thunb.*

ASTERACEAE
Berkheya
 barbata *(L. f.) Hutch.*
 herbacea *(L. f.) Druce*
Corymbium africanum *L.*
Elytropappus rhinocerotis *(L. f.) Less.*
Gerbera linnaei *Cass.*
Helichrysum
 cymosum *(L.) D. Don*
 pandurifolium *Schrank*
 teretifolium *(L.) D. Don*
Lachnospermum umbellatum *(L. f.) Pillans*
Osteospermum tomentosum *(L. f.) T. Norl.*
Othonna quinquedentata *Thunb.*
Phaenocoma prolifera *(L.) D. Don*
Senecio
 pubigerus *L.*
 triqueter *DC.*
Stoebe
 capitata *Berg.*
 plumosa *(L.) Thunb.*
Ursinia paleacea *(L.) Moench*

BALANOPHORACEAE
Mystropetalon thomii *Harv.*

BRUNIACEAE
Berzelia lanuginosa *(L.) Brongn.*
Brunia
  laevis *Thunb.*
  neglecta *Schltr.*

CAMPANULACEAE
Lightfootia unidentata *(Thunb.) A. DC.*
Lobelia tomentosa *L. f.*
Roella ciliata *L.*

CRASSULACEAE
Crassula ericoides *Haw.*

DROSERACEAE
Drosera
  cistiflora *L.*
  trinervia *Spreng.*

EBENACEAE
Diospyros glabra *(L.) De Winter*

ERICACEAE
Erica
  coccinea *L.*
  corifolia *L.*
  cristata *Dulfer*
  cruenta *Soland.*
  longifolia *Ait.*
  nudiflora *L.*
  pulchella *Houtt.*
  spumosa *L.*

EUPHORBIACEAE
Euphorbia silenifolia *(Haw.) Sweet*

FABACEAE
Argyrolobium filiforme *Eckl. & Zeyh.*
Aspalathus sp.
Otholobium rotundifolium *(L. f.) C.H. Stirton*
Rafnia sp.

GENTIANACEAE
Chironia linoides *L.*

GERANIACEAE
Pelargonium ellaphiae *E.M. Marais*

LOBELIACEAE
Cyphia volubilis *(Burm. f.) Willd.*
Merciera leptoloba *A. DC.*

OXALIDACEAE
Oxalis polyphylla *Jacq.*

PENAEACEAE
Penaea mucronata *L.*

POLYGALACEAE
Polygala bracteolata *L.*

PROTEACEAE
Aulax umbellata *(Thunb.) R. Br.*
Diastella thymelaeoides *(Berg.) Rourke*
Leucadendron
  salignum *Berg.*
  xanthoconus *(Kuntze) K. Schum.*
Leucospermum truncatulum *(Salisb. ex Knight) Rourke*
Protea
  cordata *Thunb.*
  longifolia *Andr.*
  scabra *R. Br.*
Serruria
  barbigera *Knight*
  elongata *R. Br.*
Spatalla racemosa *(L.) Druce*

RHAMNACEAE
Phylica
  atrata *Licht. ex Roem. & Schult.*
  ericoides *L.*
  imberbis *Berg.*

ROSACEAE
Cliffortia complanata *E. Mey.*

RUBIACEAE
Anthospermum galioides *Reichb.*

RUTACEAE
Diosma oppositifolia *L.*

SELAGINACEAE
Selago scabrida *Thunb.*

STILBACEAE
Campylostachys cernua *(L. f.) Kunth*
Stilbe ericoides *(L.) L.*

THYMELAEACEAE
Gnidia anomala *Meisn.*
Struthiola eckloniana *Meisn.*

ZYGOPHYLLACEAE
Zygophyllum fulvum *L.*