Distinguishing features of forest species on nutrient-poor soils in the Southern Cape

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ABSTRACT

Soils of the indigenous forest-fynbos interface in the Southern Cape were sampled for chemical and physical analyses and compared by means of anlyses of variance. Correlations among soil variables were investigated by subjecting the correlation matrices to cluster analysis. Soil data were compared with that of fynbos and tropical forest areas.

Morphological and physiological features of the forest vegetation, such as evergreenness, sclerophylly, phenolic compounds in the leaves, mast fruiting (i.e. gregarious fruiting) and root mat, were correlated with the soil nutritional status.

INTRODUCTION

The Afromontane forests of the Southern Cape are surrounded by fynbos. Schimper (1903) postulated that the distribution of the forest is controlled by soil moisture. Neethling (1970) showed that forest occurs on soil types as shallow, highly leached and infertile as those on which fynbos occurs. Kruger (1979) mentioned that seasonally severe soil moisture deficit, together with periodic fires might, by and large, preclude the growth of native trees. Van Daalen (1980) postulated that the poor nutrient status of the forest soils might prevent the regeneration of trees when the forest has been destroyed.

Jordan & Herrera (1981) proposed two types of nutrient cycling strategies for tropical forests, i.e. an oligotrophic strategy, which occurs on nutrient-poor soils, and an eutrophic strategy occurring on nutrient-rich soils. The majority of the tropical forests are, however, oligotropic ecosystems (Janzen, 1974; McKey *et al.*, 1978), susceptible to leaching loss of nutrients as the result of rapid decomposition of litter and heavy, frequent rains (Jordan & Herrera, 1981).

Are the Southern Cape forest soils richer in nutrients than the surrounding fynbos soils? Or do the forests grow on nutrient poor soils, where an oligotrophic strategy applies? If so, what are the distinguishing features of the forest species on these poor soils?

In an attempt to answer these questions, available data on the morphology and physiology of the forest species are correlated with results obtained from soil analyses from the forest-fynbos interface.

METHODS

Soils within and outside the forest were described and sampled for chemical and physical soil analyses. Five study areas were sampled: parts of Kleineiland (33°58'S, 23°13'E) and Grooteiland (33°57'S, 23°13'E) at Kaffirkop State Forest, Dirk se

Eiland (33°56'S, 23°13'E) at Diepwalle State Forest, and Forest Creek Concession area (33°54'S, 22°52'E) and Ratelbos Island (33°53'S, 22°53'E) at Goudveld State Forest (Fig. 1). The former three sites are on the 220 m coastal plateau, whereas the latter two are in the foothills of the Outeniqua Mountains.

The following chemical and physical soil analyses were made (see Appendix for the description of analytical methods):

(a) pH in H_2O and $CaCl_2$.
(b) Particle size analyses.
(c) Organic carbon of the A_1 horizon.
(d) Exchangeable cations (K, Ca, Mg, Na).
(e) Exchangeable acidity and aluminium.
(f) Available phosphorus.
(g) Total phosphorus.
(h) Total nitrogen.

Accuracy of determinations were checked by including laboratory standard samples for each element and calculating coefficients of variation of the results.

The chemical and physical features of soils under forest and fynbos, and of soils on different study sites were compared by means of analyses of variance for each element and ratios of different elements separately (Table 1). Homogeneity of variance was assumed.

The correlations among the different chemical elements and particle sizes were investigated by calculating Pearson's correlation coefficient for the variables of the A_1 and B_{21} horizons separately, except for C/P (perchloric acid), C/K, C/Ca and percentage base saturation. The two correlation matrices were subjected to cluster analyses (Orlóci, 1975; Campbell, 1978 and Webster, 1979) using a cluster procedure of group average sorting to construct the dendrogram (Pritchard & Anderson, 1971) (Figs 2 & 3).

Elemental concentrations of the A_1 horizon were compared with available elemental information from selected tropical and fynbos surface soils (Table 2).

Specific leaf mass (dry mass/unit area) was

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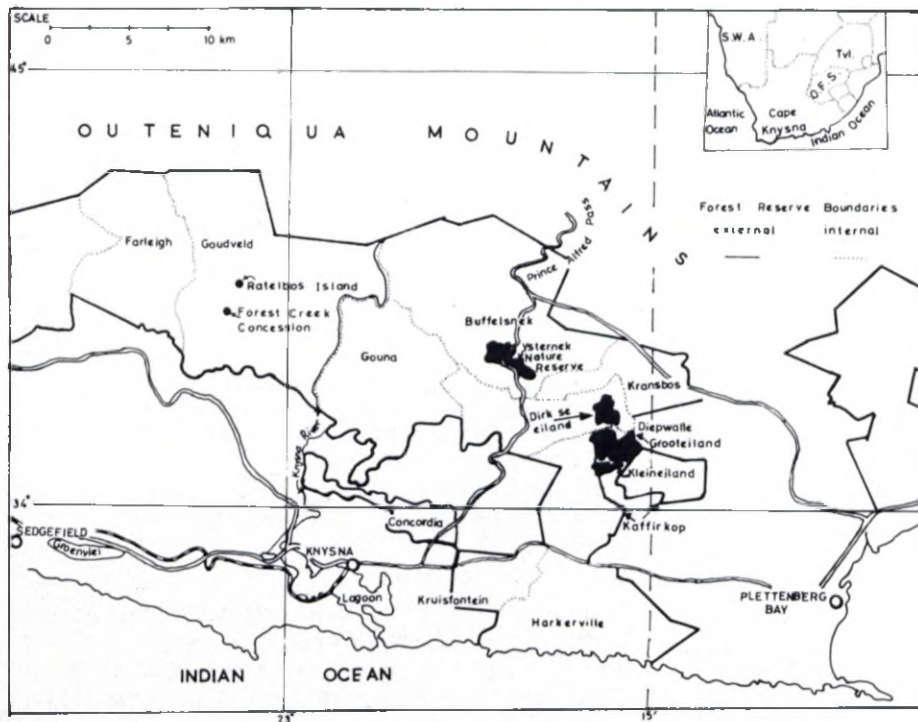
FIG. 1.—Map of study areas.

determined for seventeen selected forest species (Table 3). Leaf area of adult leaves ($\frac{1}{2}$ to 1 year old) was measured and the samples were then dried and the mass determined.

RESULTS

Analyses of variance

No major differences between the morphology of forest and fynbos soils were noticed on any single site. Where differences did occur, they did not coincide with the forest edge, indicating that the forest-fynbos edge was artificially induced in these cases* (Van Daalen, 1980). Differences between sites were found; soils of the mountain foothills were without any E (A_2) horizons, whereas the plateau soils had pronounced E horizons and heavy subsoils.

Only mean pH, and potassium, calcium and aluminium concentrations showed significant differences between forest and fynbos. Mean pH (in H_2O and $CaCl_2$) of the B_{21} horizons of the forest was lower than that of the fynbos B_{21} horizons. pH was negatively correlated (p <0,01) with aluminium. The forest B_{21} horizons had 65% higher aluminium compared to the fynbos B_{21} horizons, thus decreasing the pH through increased hydrolysis associated with an increase in aluminium (Etherington, 1975). There was a 55% decrease in aluminium of the A_1 horizon from fynbos to forest with no noticeable effect on pH.

Although aluminium was positive correlated with percentage cla in the A_1 and B_{21} horizons (see below), no significant difference in clay content could be found between forest and fynbos sites in both A and B horizons.

The pH of fynbos B_{21} horizons was significantly higher than that of fynbos A_1 horizons, whereas the pH of both the forest and fynbos A_1 horizons of the plateau sites was significantly higher than that of the mountain foothill sites.

Potassium of both A and B horizons decreased by 50% from forest to fynbos, and also from the A_1 to the B_{21} horizons in both forest and fynbos.

Calcium decreased from forest to fynbos only in the A_1 horizon.

When standardized per unit clay, all the cations, except sodium, decreased significantly from the A_1 to the B_{21} horizon (Table 1). With the exception of two values, all the S-values/100 g clay for the B_{21} horizons were in the mesotrophic range. The S-values for the A_1 horizons varied widely, especially where the clay content was low.

Percentage base saturation decreased significantly from the A_1 to the B_{21} horizons in the forest. Due to large variation in the values for fynbos the decrease from fynbos A_1 to B_{21} horizons, and the decrease from forest to fynbos A_1 horizons, were statistically insignificant (Table 1).

Organic carbon was consistently higher in the forest than in the fynbos, although not statistically significantly so. A larger sample will be needed to confirm this result.

No significant differences in nitrogen, and total or available phosphorus between forest and fynbos sites could be found (Table 1). The nitrogen content of the B_{21} horizon was significantly lower than that of the A_1 horizon, both in the forest and fynbos. In the B_{21} horizons of the mountain foothill sites it was about three times higher than in the dense clayey B_{21}

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* The present study was limited to the coastal plateau and the southern mountain foothills. On the more northern foothills on the southern side of the Outeniqua Mountains, i.e. on the northern boundary of the main forests, the distribution of forest seems to be controlled by soil moisture to a greater extent than that of the main plateau forest.

Source of variation		F	df[1]		F	df[1]		F	df[1]
B_{21} hor.	4,4/4,8	19,58**	1:33	3,8/4,0	8,33**	1:33	1232/714	2,67	1:33
Forest : A_1/B_{21} hor.	4,1/4,4	3,76	1:25	3,6/3,8	1,02	1:24	3233/1232	15,28**	1:24
Fynbos : A_1/B_{21} hor.	4,1/4,8	36,39**	1:49	3,4/4,0	34,59**	1:49	2457/714	38,32**	1:49
Between Sites:									
[2] Kaffirkop/Goudveld:									
Forest A_1 hor.	4,3/3,8	6,92*	1:12	3,8/3,2	10,32*	1:12	2964/3906	1,61	1:12
B_{21} hor.	4,4/4,2	2,76	1:10	3,8/3,8	0,20	1:10	740/2707	8,29*	1:10
Fynbos A_1 hor.	4,3/3,6	19,64**	1:26	3,6/3,1	10,53**	1:26	2273/3008	1,87	1:26
B_{21} hor.	4,9/4,4	8,60*	1:21	4,0/4,0	0,22	1:21	541/1535	18,64**	1:21

Source of variation	Org. Carbon (%)			C/P (perchloric acid) (%/%)			K (ppm)		
	mean	F	df[1]	mean	F	df[1]	mean	F	df[1]
Forest/Fynbos									
Kleineiland A_1 hor.	4,6/3,6	2,56	1:6	249,9/ 164,4	0,77	1:6			
B_{21} hor.									
Grooteiland A_1 hor.	5,9/4,5	2,54	1:8	776,7/ 683,6	0,50	1:8			
B_{21} hor.									
Dirk se Eiland A_1 hor.	3,7/3,4	0,39	1:11	672,8/ 736,3	0,13	1:11			
B_{21} hor.									
Forest Creek A_1 hor.	5,5/5,3	0,03	1:4	1325,4/1272,6	0,08	1:3			
Ratelbos A_1 hor.	4,6/4,0	0,06	1:3	787,7/ 689,3	0,07	1:3			
B_{21} hor.									
Combined A_1 hor.	4,8/4,0	3,22	1:40	683,9/ 693,0	0,01	1:39	111/54	8,67*	1:18
B_{21} hor.							45/27	7,63*	1:16
Forest : A_1/B_{21} hor.							111/45	7,19*	1:14
Fynbos : A_1/B_{21} hor.							54/27	27,67**	1:20
Between Sites:									
[2] Kaffirkop/Goudveld:									
Forest A_1 hor.	4,7/5,0	0,10	1:12	534,8/1056,6	4,94	1:12	87/198	11,12*	1:7
B_{21} hor.							46/42	0,07	1:5
Fynbos A_1 hor.	3,8/4,7	2,90	1:26	610,7/ 981,0	6,90*	1:25	52/64	1,08	1:9
B_{21} hor.							25/36	6,44	1:9

Source of variation	% clay			% N/100g clay			Al (ppm)		
	mean	F	df[1]	mean	F	df[1]	mean	F	df[1]
Forest/Fynbos									
Combined A_1 hor.	10/11	0,13	1:18	4,492/2,206	4,34	1:17	161/250	6,86*	1:18
B_{21} hor.	21/19	0,46	1:18	0,377/0,416	0,05	1:16	318/192	8,78*	1:18
Forest : A_1/B_{21} hor.	10/21	9,66*	1:14	4,492/0,377	11,28*	1:13	161/318	15,23**	1:15
Fynbos : A_1/B_{21} hor.	11/19	6,73*	1:22	2,206/0,416	14,68**	1:20	250/192	2,60	1:20
Between Sites:									
[2] Kaffirkop/Goudveld:									
Forest A_1 hor.	12/7	0,74	1:6	3,705/6,854	1,55	1:6	152/102	0,35	1:7
B_{21} hor.	21/22	0,01	1:6	0,270/0,646	85,75**	1:5	342/248	2,01	1:6
Fynbos A_1 hor.	12/10	0,16	1:10	1,832/3,885	4,06	1:9	253/237	0,07	1:9
B_{21} hor.	21/9	4,09	1:10	0,248/1,170	28,43**	1:9	191/196	0,00	1:9

Source of variation	S (m.c.%)/100g clay			C/Ca (%/%)			% K/100g clay		
	mean	F	df[1]	mean	F	df[1]	mean	F	df[1]
Forest/Fynbos									
Combined A_1 hor.	67,86/36,28	5,19	1:17	92,1/154,3	3,76	1:18	0,159/0,062	4,59	1:17
B_{21} hor.	12,09/ 9,93	0,53	1:17				0,020/0,019	0,02	1:16
Forest : A_1/B_{21} hor.	67,86/12,09	13,69**	1:14				0,159/0,020	6,50*	1:13
Fynbos : A_1/B_{21} hor.	36,28/ 9,93	24,66**	1:20				0,062/0,019	11,59**	1:20
Between Sites:									
[2] Kaffirkop/Goudveld:									
Forest A_1 hor.	62,74/83,23	0,33	1:6	90,0/100,1	0,07	1:8	0,096/0,347	11,52	1:6
B_{21} hor.	10,17/17,87	1,11	1:6				0,020/0,018	0,20	1:5
Fynbos A_1 hor.	36,28/36,32	0,00	1:9	118,2/298,7	20,15**	1:8	0,054/0,100	2,54	1:9
B_{21} hor.	9,51/11,85	0,67	1:9				0,014/0,042	67,59*	1:9

Source of variation	Ca (ppm)			Mg (ppm)			% Base saturation [3]		
	mean	F	df[1]	mean	F	df[1]	mean	F	df[1]
Forest/Fynbos									
Combined A_1 hor.	701/289	16,40**	1:18	166/153	0,74	1:18	66,7/52,2	4,18	1:18
B_{21} hor.	110/131	1,17	1:17	82/78	0,04	1:17	33,8/44,0	1,14	1:17
Forest : A_1/B_{21} hor.	701/110	28,57**	1:15	166/82	17,29**	1:15	66,7/33,8	19,01**	1:15
Fynbos : A_1/B_{21} hor.	289/131	16,09**	1:20	153/78	24,50**	1:20	52,2/44,0	0,89	1:20
Between Sites:									
[2] Kaffirkop/Goudveld:									
Forest A_1 hor.	731/596	0,27	1:7	179/118	5,38	1:7	68,6/59,8	0,50	1:7
B_{21} hor.	117/91	3,04	1:6	99/32	7,49	1:6	37,9/21,6	1,70	1:6
Fynbos A_1 hor.	326/126	7,22*	1:9	157/133	1,36	1:9	55,7/36,2	2,75	1:9
B_{21} hor.	140/89	1,86	1:9	88/33	3,42	1:9	48,2/25,5	1,64	1:9

% Ca/100g clay	% Mg/100g clay

horizons of the plateau sites. Root penetration into the more sandy B_{21} horizons of the mountain foothill sites was much better than in the plateau B_{21} horizons. Nitrogen could therefore be added to these sandy horizons much more efficiently.

No significant differences in the carbon/potassium, carbon/calcium and carbon/total phosphorus ratios between forest and fynbos sites were found. The A_1 horizons of the mountain foothills fynbos sites had significantly lower (more favourable) carbon/calcium and carbon/total phosphorus ratios than that of the plateau fynbos sites.

Cluster analyses

Fig. 2 shows the strong positive correlations among the standardized S-value, nitrogen, cation (except sodium) and carbon values for the A_1 horizon. For the B_{21} horizon these relations were much weaker (Fig. 3), possibly as a result of a lower carbon content.

Sand content (especially in the A_1 horizon), silt content and pH were relatively independent. Strong positive correlations between clay content and aluminium, both in the A_1 and B_{21} horizons were observed.

Comparison of elemental concentrations

1 Phosphorus and carbon/phosphorus ratio

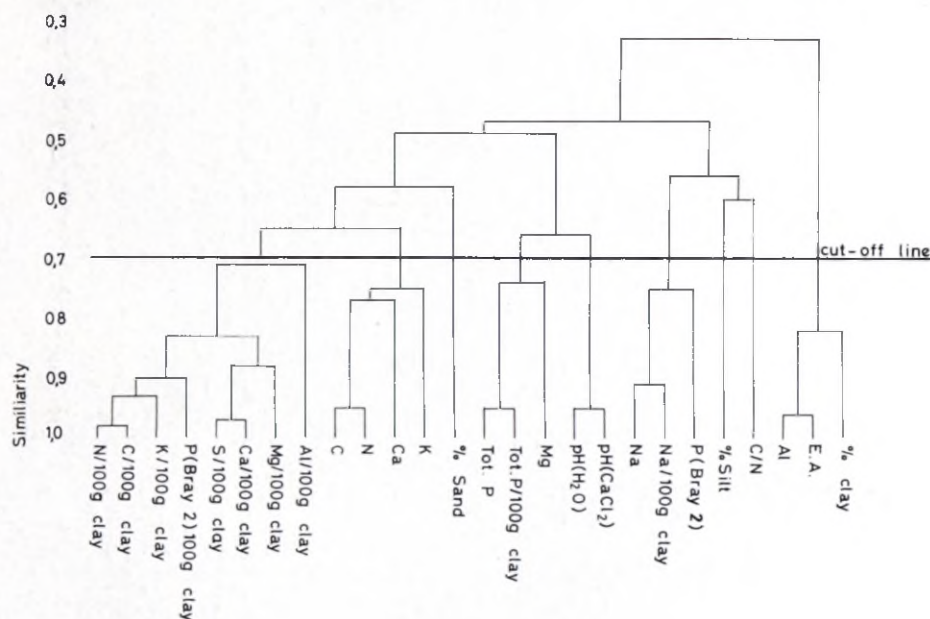Available phosphorus values for this study, and those of tropical forest and fynbos areas, were in the

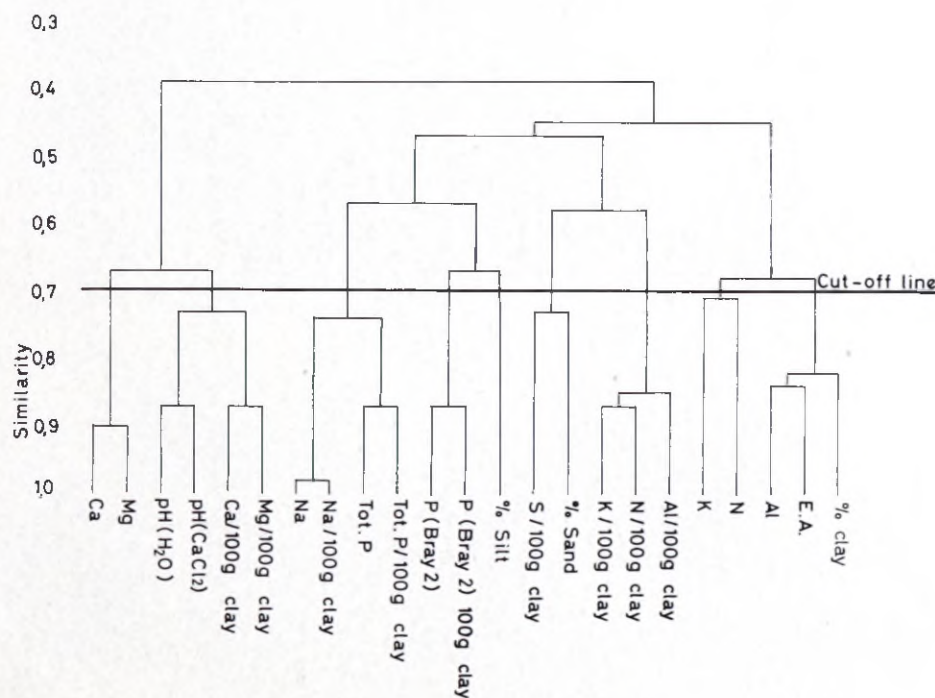FIG. 2.—Dendogram for A_1 horizon variables using Pearson's correlation coefficients as similarity indices.

FIG. 3.—Dendogram for B_{21} horizon variables using Pearson's correlation coefficient as similarity indices.

TABLE 2. — Elemental concentrations (ppm) in surface soils (A₁ horizons) of selected tropical forest and fynbos areas

etation	Location	P*	P	N	K*	Ca*	Mg*	Na	C/N	C/P	C/K*	C/Ca*	Reference
ry to Moist													
	Southern Cape	9	117	3233	111	701	166	81	15,53	683,9	605,5	92,1	} This study
	Southern Cape	7	80	2457	54	289	153	67	17,08	693,0	674,0	154,3	
Forest	Panama	7,7	–	–	527	4873	1217	–	–	–	–	–	Gamble et al., 1969
Forest	Panama	1,7	–	–	606	7880	1144	–	–	–	–	–	Blue et al., 1969
Forest	Costa Rica	1,1	–	–	82	1534	600	85	–	–	–	–	Holdridge, 1971
t	Panama	6,3	–	–	103	4400	600	–	–	–	–	–	Gamble et al., 1969
t	Panama	1,6	–	–	389	6710	1513	–	–	–	–	–	Blue et al., 1969
t	Costa Rica	2,4	–	–	58	1120	379	58	–	–	–	–	Holdridge, 1969
et Forest	Costa Rica	0,9	–	–	27	246	71	51	–	–	–	–	Holdridge, 1969
h Forest	Guatemala	5,2	–	–	195	3440	1824	–	–	–	–	–	Tergas, 1965
Forest	Thailand	–	–	–	86	120	22	25	–	–	–	–	Tsutumi et al., 1967
Forest	Ghana	–	–	–	109	360	133	–	–	–	–	–	Nye & Greenland, 1964
Forest	India	–	–	–	1271	2340	780	–	–	–	–	–	Singh, 1968
Forest	Jamaica	–	–	6940	203	348	400	57	14,9	–	750	2251	Tanner, 1977
e Rain Forest	New Guinea	–	–	–	–	–	–	–	1,0	–	481	72	Edwards, 1973 ex Tanner, 1977
	Australia	–	2784	4083	182	2402	316	16	8,9	13,3	295	36,1	} Brasell et al., 1980
est	Australia	–	2600	3667	196	2782	328	17	10,2	14,5	359	19,6	
	South Australia	–	260	1270	2659	14870	2296	575	–	–	–	–	} Specht et al., 1961 ex
	South Australia	–	70	740	1095	6172	1677	345	–	–	–	–	} Groves, 1980
s	Western Cape	44	–	2600	–	–	–	–	16,7	–	–	–	} Kruger, 1979
bos	Western Cape	8	–	1440	–	–	–	–	19,0	–	–	–	
bos	Southern Cape	–	–	1100	–	–	–	–	16,9	–	–	–	Lambrechts, 1964 ex Kruger, 1979
bos	Southern Cape Swartberg S. aspects	8,7	133	833	58	130	58	30	19,8	183,9	320,1	141,1	} Bond, 1981
bos	Southern Cape Outeniqua Mountains S. aspects	5	24	1439	23	73	67	47	23,0	3314,3	1380,3	549,5	

le concentration. All other values are total concentrations.

same range. Total phosphorus and carbon/total phosphorus values were, however, in the range of the fynbos site values (Table 2).

2 Nitrogen, cations and carbon/nitrogen, carbon/potassium and carbon/calcium ratios

On the whole, these values were higher (lower in the case of the ratios) than those of the fynbos sites and lower (higher in the case of the ratios) than those of tropical forest sites (Table 2).

DISCUSSION

Differences between forest and adjacent fynbos sites

The higher aluminium content of the forest B_{21} horizons compared to forest A_1 horizons might reflect a more effective podzolisation under forest than under fynbos because of a different organic composition. Usually the aluminium-pH relation in the A horizon is complicated by litterfall, nutrient circulation, decomposition rate and the type of vegetation (D. C. Grey, personal communication, 1980). This can mask any aluminium-pH correlation.

As mentioned before, all the study sites had artificially induced forest-fynbos edges; therefore the differences in nutrients are probably vegetation induced. A possible explanation for the decrease in potassium from forest to fynbos is that most of it is locked up in the vegetative biomass. The forest, with a higher biomass will keep more potassium than the fynbos. Alternatively, the fynbos might take up less potassium per biomass unit. When a forest is destroyed, more potassium is available than can be utilized by the invaders, in this case fynbos, with a consequent leaching of this mobile element (Etherington, 1975). This theory is confirmed by the strong positive correlation between potassium and organic carbon (Fig. 2) and the results of Brasell, Unwin & Stocker (1980). They found a higher potassium content in the litter of the more fertile rain forest and Araucaria cunninghamii plantation sites in tropical Australia than on the less fertile forest and plantation sites.

The same arguments as for potassium can be applied to explain the decrease in calcium from forest to fynbos A_1 horizons. Again, bio-cycling of calcium is important in restricting leaching loss by returning calcium to the soil surface (Etherington, 1975). As with potassium, Brasell et al. (1980) found a higher calcium content in the litter of the more fertile sites. Although calcium is not immobilized in organic matter, it does show chelation with a number of organic acids, for example citric and gluconic (Stevenson, 1967 ex Etherington, 1975). (Also see the strong positive correlation between calcium and organic carbon in Fig. 2.) This can restrict leaching of calcium out of the soil profile.

The higher cation content of the A_1 horizon compared to that of the B_{21} horizon can be attributed to the greater number of exchange sites associated with a higher carbon content in the A_1 horizon than in the B_{21} horizon (see Fig. 2 for positive correlation between standardized cations and standardized carbon content).

Correlations between elements

The positive influence of standardization for clay on the correlations among different elements, including organic carbon (Fig. 2), emphasizes the importance of the organic carbon in maintaining the nutritional status of the A_1 horizon.

Comparison with fynbos and tropical forest areas

Unlike Brasell et al. (1980), who found significantly higher concentrations of total phosphorus and nitrogen in the litter of tropical rain forest in Australia than in that of adjoining Araucaria cunninghamii plantation, the differences in nitrogen and total or available phosphorus between forest and fynbos sites were very small and insignificant. On the whole, the elemental concentrations of the forest horizons were in the range of concentrations of fynbos and heathland sites in South Africa and Australia (Table 2). Total phosphorus, in particular, was much lower than that of savanna and tropical forest areas.

Evers (1967) used carbon-based ratios to characterize the nutritional status of spruce (Picea excelsa) sites. Large ratios implied unfavourable nutritional conditions. He suggested the following limiting values for these forests:

C/N 24–26
C/P 350–450
C/K 400–500
C/Ca—uncertain, but preferably less than 100.

He found the C/P ratio a particularly good indicator of the general nutritional status, in contrast to the C/N ratio.

C/P ratios of this study were very high (Table 2). This implies poor nutritional status. Generally, the southern Cape indigenous forests are growing on fynbos soils. As a result of this, certain distinguishing features of the forest species can be observed.

Distinguishing features of forest species

1 Evergreenness and sclerophylly

Evergreen sclerophylls could be related to low nutrient availability. These leaves are longer lived, have relatively thick cuticles and wax cover and may be more resistent to nutrient loss by parasites and herbivores than mesophytic leaves (Grubb, 1977). Loveless (1961 & 1962) regarded the sclerophyllous leaf as the expression of a metabolism found in plants that can tolerate low levels of phosphate. He suggested that a phosphorus content of leaves below about 0,3% resulted in sclerophylly. Cowling & Campbell (1980) demonstrated that the higher degree of evergreenness and sclerophylly in the South African fynbos compared to shrublands in Chile and California is related to low soil nutrient levels, rather than winter rainfall and summer droughts, as suggested by Schimper (1903).

In Table 3 some forest species are listed in a decreasing order of specific leaf area of adult leaves. By comparing these values to those of Sobrado & Medina (1980) for the scleromorphic low-tree forest on sandy podzolised soils of Amazonas (which vary

between 455 for old *Mouriri uncitheca* leaves to 89 for young *Catostemma* sp. leaves) and by using Schimper's (1903) and Bond's (1981) guidelines for the field recognition of scleromorphic leaves (i.e. non-succulent leaves which break when folded, they are leathery and tend to maintain their shape on drying), the species with a specific leaf mass of 140 and more can be regarded sclerophyllous. These species form 66% of the total forest tree composition (Geldenhuys, 1975; Geldenhuys, 1980). Leaf analyses for some of these species yielded phosphorus levels of 0,08% and lower (Table 3).

TABLE 3. — Specific leaf mass, and percentage P and total phenol content in leaves of some forest species

Species	Specific[1] leaf mass g/m^2	%p[2]	Total[3] Phenols mg/g
Sclerophyllous			
Podocarpus latifolius	196	–	78,5
Rapanea melanophloes	179	0,08	50,8
Pterocelastrus tricuspidatus	179	0,07	50,0
Olea capensis subsp. *capensis*	179	–	–
Podocarpus falcatus	169	–	–
Curtisia dentata	164	0,06	54,3
Cassine papillosa	154	–	67,9
Olea capensis subsp. *macrocarpa*	154	–	44,8
Diospyros whyteana	152	–	–
Olinia ventosa	145	–	–
Cassine peraqua	143	–	71,3
Mesophytic			
Apodytes dimidiata	123	–	33,0
Nuxia floribunda	100	–	53,5
Ocotea bullata	84	–	29,2
Trimeria grandifolia	79	–	29,2
Trichocladus crinitus	70	0,08	51,3
Halleria lucida	39	–	27,5

[1] Specific leaf mass determined on fully grown leaves ($\frac{1}{2}$ –1 year old.
[2] Average of all seasons (Koen, J.H., 1981).
[3] Average of determinations made by J.H. Koen (personal communication, 1981) and A.H.W. Seydack (1981).

Although *Trichocladus crinitus* (Thunb.) Pers., the dominant ground layer shrub in the forest, did not fit the pattern of sclerophylly associated with low leaf phosphorus levels (Table 3), in general sclerophylly seems to be related to low soil phosphate levels in the southern Cape.

The following benefits of evergreenness on nutrient poor soils have been suggested:

(i) Evergreens have a higher nutrient use efficiency than deciduous plants, i.e. higher carbon gain per unit of nutrient used in leaf construction (Small, 1972).

(ii) If the evergreen leaves are retained for more than one year, they have a lower annual nutrient requirement and loss (Monk, 1971; Chapin *et al.*, 1980).

(iii) Chapin *et al.* (1980) suggested that evergreens have a reduced annual cost of translocation of nutrients from senescent leaves, and of synthesis and breakdown of nutrient storage compounds. However, when leaves are shedded, large proportions of especially P, N and K are retranslocated to the twig before abscission (Small, 1972).

(iv) Evergreens have a year-round abscission and production of new leaves so that nutrients are retained in leaves rather than in soil and thus fewer nutrients are lost to the system by leaching (Monk, 1966; Thomas & Grigal, 1976).

Goldberg (1982) proposed that evergreen plants would grow and survive at least as well on fertile as on infertile soils in isolation. As a result of lower photosynthetic rates and larger amounts of structural carbon per leaf (Grime & Hunt, 1975), and a higher investment in anti-herbivore compounds (see below), they have a lower maximum growth rate and therefore a lower competitive ability than deciduous plants on fertile soils.

Deciduous tree species present in the Southern Cape forests occur mainly on the few shale bands and other more fertile sites. Very few occur on the nutrient poor sandstone derived soils (C. J. Geldenhuys, personal communication, 1981).

2 *Phenolic compounds in leaves*

Janzen (1974) postulated that the vegetation on tropical poor, leached soils is protected against herbivory by exceptionally high levels of toxic phenolics and other secondary compounds. In a habitat with extremely low primary productivity, yet a climate favourable to animals year round, there should be strong selection for plants that are exceptionally rich in chemical defenses. This is so for the following reasons:

(a) In infertile habitats it is costly to replace nutrients of consumed and damaged vegetative parts.

(b) In a habitat with low productivity and evergreen plants, proportionally more of the plant's resources are expected to be spent on defenses to prevent herbivore damage before the leaf must be replaced for internal economic reasons.

Determinations of total phenols in leaves of some of the sclerophyllous species in Table 3 yielded values of more than 50 mg/g dry leaf material, except for *Olea capensis* L. subsp. *macrocarpa* (C. H. Wr.) Verdoorn, which had a phenol content of 44,8 mg/g. These values are in the same order as those for some African rain forests (McKey *et al.*, 1978). Some values for the mesophytic species in Table 3 were above 50 mg/g too, but the average of the sclerophyllous species was 59,6 mg/g compared to 38,9 mg/g for the mesophytic species.

3 *Mast fruiting*

Mast fruiting (i.e. gregarious fruiting) in Dipterocarpaceae has been observed in South-East Asia, where trees have population- and community-level fruiting that is synchronized at intervals greater than one year. The adaptive significance of synchronous fruiting on habitats with low primary productivity is the advantage of saturating seed predators, thereby increasing the

probability of reproductive success. Furthermore, large population buildups of seed predators are prevented due to the lack of food between fruiting years (Janzen, 1974).

Fruiting intervals of more than one year are well-known for many forest species in the Southern Cape, for example *Olea capensis* subsp. *macrocarpa*, *Podocarpus latifolius* (Thunb.) R.Br. *ex* Mirb., *P. falcatus* (Thunb.) R.Br. *ex* Mirb., *Rapanea melanophloeos* (L.) Mez, *Apodytes dimidiata* E. Mey. *ex* Arn. and *Olinia ventosa* (L.) Cufod. (Phillips, 1926; F. von Breitenbach, 1965). The release of mature seed of all these species seems to be synchronized to a certain extent, although it can take several months before all seed of a species has been dropped (Phillips, 1926).

4 Root mat

According to Jordan & Herrera (1981) the root mat on the soil surface is one of the most important mechanisms for direct nutrient cycling and nutrient conservation in the Amazonian rain forest. They found that the gradient of decreasing thickness of the root mat paralleled the gradient of increasing soil fertility. Stark & Jordan (1978) showed that 99,9% of all ^{45}Ca and ^{32}P sprinkled on these root mats was immediately absorbed and only 0,1% leached through the mat. Rapid growth of small roots is another nutrient conserving mechanism (Jordan & Escalante, 1980), and Herrera *et al.* (1978) demonstrated the rapid colonization of a fallen leaf by small roots and its rapid decomposition.

Dense root mats on and in the surface soil layer occur in the Southern Cape indigenous forests (Van Daalen, 1980). Small roots that have colonized decomposing logs above the root mat and humus layer have been observed in the forest (Fig. 4).

Plant litter falling on the floor, is decomposed and nutrients that become available are utilized immediately. Disturbance of the root and litter layers will have significant negative effects on forest nutrition, and implicitly will effect forest regeneration and development.

CONCLUSIONS

Apart from some higher elemental concentrations in forest than in fynbos A_1 horizons due to a higher carbon content, forest soils in the Southern Cape are not richer in nutrients than the surrounding fynbos soils. Distinguishing features of the forest species on these soils are evergreenness and sclerophylly, high levels of phenolics and other secondary compounds, fruiting intervals of more than one year and dense root mats on and in the surface soil layer.

This has several implications for the management of these forests:

(a) During exploitation the root mat and soil surface must be left intact as far as possible. The more this is disturbed, the more difficult it will be to restore the closed nutrient cycle of the forest.

(b) The smaller the gap created in the canopy when felling trees, the more likely it will be that plant litter reaches the opened forest floor and that the nutrient conserving mechanisms can be maintained.

(c) Assuming a positive relation between forest growth and soil nutrient status, organic carbon can be an indicator of the potential of a site for forest growth (Ojeniyi & Agbede, 1980). Exploitation should then be limited to sites with high organic carbon in the A horizon.

(d) Forest edges should be left undisturbed. The better nutrient conserving mechanisms and nutrient cycles can be maintained, and the healthier and more vigorous the ecotone vegetation is, the better

Fig. 4.—Roots colonizing a decomposing log above the root mat and humus layer in the southern Cape indigenous forest.

these edges can tolerate negative external influences, like disturbances through fire or exploitation of adjoining plantation.

(e) When re-establishing forest, the re-establishment of the soil nutrient status is of great importance. Re-establishment should be done with species that can tolerate low nutrient levels, i.e. the most sclerophyllous species.

Further studies are needed concerning the relation between nutrient status and forest regeneration, growth and distribution of species, on mast fruiting, phenolic compounds in leaves, sclerophylly and nutrient cycling in the forest.

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UITTREKSEL

Gronde van die inheemse woud-fynbos-skeidingsvlak in die Suid-Kaap is bemonster vir chemiese en fisiese grondontledings en deur middel van variansie-analise vergelyk. Korrelasies tussen grondveranderlikes is ondersoek deur die korrelasiematryse aan klont- (= 'cluster') analise te onderwerp. Die gronddata is vergelyk met dié van fynbos en tropiese woudareas.

Morfologiese en fisiologiese eienskappe van die woudplantegroei, soos bladhoudendheid, sklerofillie, fenoliese bestanddele in blare, gesamentlike saadlewering en die wortelmat, is met die voedingstatus van die grond gekorreleer.

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APPENDIX

ANALYTICAL METHODS USED FOR THE PHYSICAL AND CHEMICAL SOIL ANALYSES

(a) pH in H_2O and $CaCl_2$ (O,O1M) was determined by means of a 1: 2 soil: liquid ratio, measured in the supernatant after one hour, using a combination glass electrode.

(b) Particle size analyses were made using the hydrometer method (Day, 1965). All soils were pretreated by H_2O_2 to remove the organic matter.

(c) Organic carbon of the A_1 horizon was determined by the Walkley–Black method (Allison, 1965), using a correction factor of 1,33 for recovery.

(d) Exchangeable cations (K, Ca, Mg, Na): The determination was made on a 1N NH_4Cl extract of the less than 2 mm fine earth by atomic absorption spectrophotometry. The S-value per 100 g clay was calculated.

(e) Exchangeable acidity was determined on a 1N KCl extract (extraction time = 4 minutes) by titration with NaOH. After addition of NaF exchangeable Al was determined by back titration using HCl.

(f) Available phosphorus was determined colorimetrically by the molybdenum blue procedure on a Bray No. 2 extract.

(g) Total phosphorus: After digestion with perchloric acid, the colour development was determined spectrophotometrically using ammonium vanadate.

(h) Total nitrogen was determined by a modified micro-Kjehldahl method. After digestion with H_2SO_4, the ammonia was determined by titration with HCl.