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

J. C. VAN DAALEN*

Keywords: evergreenness, forest, fynbos, mast fruiting, nutrition, phenolic compounds, roots, sclerophyll, soils

ABSTRACT

Soils of the indigenous forest-fynbos interface in the Southern Cape were sampled for chemical and physical analyses and compared by means of analyses 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, sclerophyll, 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, oligotrophic ecosystems (Jenzen, 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, Dirkse 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 H₂O and CaCl₂.
(b) Particle size analyses.
(c) Organic carbon of the A₁ 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 A₁ and B₃ 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 A₁ horizon were compared with available elemental information from selected tropical and fynbos surface soils (Table 2). Specific leaf mass (dry mass/unit area) was
determined for seventeen selected forest species (Table 3). Leaf area of adult leaves (1 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$_2$O 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 $B_2$ 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 clay 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 $B_{21}$

* 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.

Fig. 1.—Map of study areas.
Between Sites:

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Org. Carbon (%)</th>
<th>C/P (perchloric acid) (%)</th>
<th>K (ppm)</th>
</tr>
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<tr>
<td></td>
<td>mean F df</td>
<td>mean F df</td>
<td>mean F df</td>
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<tr>
<td>Forest/Fynbos</td>
<td>4.6/3.6</td>
<td>2.56 1:6</td>
<td>249.9/164.4 0.77 1:6</td>
</tr>
<tr>
<td>Combined A hor.</td>
<td>4.8/4.0</td>
<td>3.20 1:2</td>
<td>683.9/693.0 1.40 1:2</td>
</tr>
</tbody>
</table>

% clay % N/100g clay Al (ppm)

Source of variation
mean F df
Forest/Fynbos
Combined A hor. 10/11 0.13 1:18 4.492/2.206 4.34 1:17 161/250 6.86 1:18
B21 hor. 21/19 0.46 1:18 0.377/0.416 0.05 1:16 318/192 8.78 1:18
B21 hor. 11/19 6.7/1 1:12 2.226/0.416 14.68 1:12 250/192 2.60 1:18

Base saturation

% Ca/100g clay

Source of variation
mean F df
Forest/Fynbos
Combined A 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
B21 hor. 12.09/9.93 0.53 1:17 4.492/0.377 11.23 1:17 0.159/0.020 6.50 1:17
Fynbos: A1/B2 hor. 36.28/9.93 24.66 1:20 0.248/1.170 28.43 1:20 0.062/0.019 11.59 1:18

% Mg/100g clay

Source of variation
mean F df
Forest/Fynbos
Combined A hor. 701/129.9 18.00 1:18 166/153 0.74 1:18 66.7/52.2 4.18 1:18
B21 hor. 110/131.7 1.71 1:17 82.78 0.04 1:17 33.8/44.0 1.14 1:17
Fynbos: A1/B2 hor. 701/110 28.57 1:15 166/82 17.29 1:15 66.7/33.8 19.01 1:15

% Base saturation

Source of variation
mean F df
Forest/Fynbos
Combined A hor. 701/289 16.40 1:18 166/153 0.74 1:18 66.7/52.2 4.18 1:18
B21 hor. 110/131 1.71 1:17 82.78 0.04 1:17 33.8/44.0 1.14 1:17
Fynbos: A1/B2 hor. 289/131 16.09 1:20 153/78 24.50 1:20 52.8/44.0 0.89 1:20

% Ca/100g clay

Source of variation
mean F df
Forest/Fynbos
Combined A hor. 731/56 0.27 1:17 179/118 5.38 1:17 68.6/59.8 0.50 1:17
B21 hor. 117/91 3.04 1:16 99/32 7.49 1:16 37.9/21.6 1.70 1:16
Fynbos: A1/B2 hor. 326/126 7.22 1:19 157/33 1.36 1:19 35.7/36.2 2.75 1:19
B21 hor. 140/89 1.86 1:19 88/33 3.42 1:19 48.2/25.5 1.64 1:19
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

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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.
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Table 2. Elemental concentrations (ppm) in surface soils (A1 horizons) of selected tropical forest and fynbos areas. All values are total concentrations. Reference for Continental areas: ex Golley et al., 1975.
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 A1 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 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 sclerophyll

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 resistant 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 sclerophyll. Cowling & Campbell (1980) demonstrated that the higher degree of evergreenness and sclerophyll 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 uncinethaca* 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). Analyses for some of these species yielded phosphorus levels of 0.08% and lower (Table 3).

Leaf phosphorus levels of 0.08% and lower (Table 3). (Geldenhuys, 1975; Geldenhuys, 1980). Leaf are leathery and tend to maintain their shape on non-succulent leaves which break when folded, they do not fit the pattern of sclerophyllous leaves (i.e. 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).

Although *Triocladus crinitus* (Thunb.) Pers., the dominant ground layer shrub in the forest, did not fit the pattern of sclerophyll associated with low leaf phosphorus levels (Table 3), in general sclerophyll 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. 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 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* subsp. *macrocarpa* (C. H. Wr.) Verdooorn, 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. falcatius (Thunb.) R.Br. ex Mirb., Raphanea 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 45Ca and 32P 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 A1 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, sclerophyll and nutrient cycling in the forest.

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UITTREKSEL

Grond van die inheemse woud-synbosseidingvlok in die Suid-Kaap is bemonster vir chemiese en fisiese grondonledings en deur middel van varianstie-analise vergelyk. Korrelasies tussen grondveranderlikes is ondersoek deur die korrelasieparameter aan klont- (= ‘cluster’) analise te onderwerp. Die gronddata is vergelyk met dié van Stellenbosch en Mr. F. J. Kruger of the South African Forestry Research Institute, due to Messrs C. J. Geldenhuys, W. J. Bond and D. C. Grey of the Saasveld Forestry Research Station.

REFERENCES


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**APPENDIX**

**ANALYTICAL METHODS USED FOR THE PHYSICAL AND CHEMICAL SOIL ANALYSES**

(a) pH in H$_2$O and CaCl$_2$ (O.01M) 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$_2$O$_2$ 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$_4$Cl 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-Kjeldahl method. After digestion with H$_2$SO$_4$, the ammonia was determined by titration with HCl.