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Autor:	Theron, G.K.
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The distribution of the summer rainfall zone Protea species in South Africa with special reference to the ecology of *Protea caffra*

G. K. THERON

SUMMARY

The author presents distribution maps of the 16 summer rainfall species of *Protea* occurring in South Africa. A special stress is laid upon the ecological distribution of *Protea caffra* and of 19 other tree species in the Loskop Dam Nature Reserve, Transvaal. For these taxa, species position indices were established, and principal component as well as multiple regression analysis of the ecological factors were carried out.

RÉSUMÉ

L'auteur présente des cartes de distribution des 16 espèces de *Protea* de la zone des précipitations estivales de l'Afrique du Sud. Une étude approfondie porte sur la distribution écologique de *Protea caffra* ainsi que de 19 autres espèces arborescentes de la Réserve naturelle du "Loskop Dam", Transvaal. Les indices de position ont été établis et les facteurs écologiques analysés.

The *Proteaceae* is not only a family famous for brilliance and beauty but it is also steeped in history, the descendants of *Glossopteris*, which flourished more than 200 million years ago (Palmer & Pitman, 1972). The family is also of interest as it is cited as evidence of the existence of Gondwanaland which linked the continents of the southern hemisphere. The occurrence of large numbers of representatives of the *Proteaceae* in South Africa and Australia is regarded as being particularly important in this regard.

There are 60 genera and about 1300 species in the family, most of which occur in the southern hemisphere and a few in the northern hemisphere. At least 14 genera and well over 300 species are found in South Africa, and although they are widely distributed—usually in mountainous areas—they are most abundant in the south western Cape Province. Here they often grow on the poorest soils on rocky ridges or on bare mountains, as shrubs or as trees.

Protea is the largest genus in the family with over 100 species in South Africa alone. According to Beard (1958) the genus *Protea* is distributed throughout Africa south of the Sahara with two main centres of distribution, the Cape macchia and the Central African *Brachystegia* woodland which stretches from Angola and the Congo through Zambia, Zaïre, Rhodesia, Malawi, Mozambique into Tanzania.

The Cape macchia contains more than 70 species and there are about 50 species in the *Brachystegia* woodland with four other species occurring further north bringing the total for the tropics to about 54 species (Beard, 1958). In the summer rainfall zone of South Africa, which may be designated as a subtropical belt linking the tropical and Cape centres of distribution, 13 endemic species occur, as well as three other species with a wider distribution. Of the three, *Protea lacticolor* is essentially a Cape macchia species which extends into the North Eastern Cape Province, while *P. gaquedi* and *P. welwitschii*, both tropical species of very wide distribution, extend into Natal (Beard, 1958).

Of the endemics *Protea subvestita* and *P. roupelliae* are of Cape affinity belonging to sections *Exsertae* and *Ligulatae* of the genus, otherwise only found in the Cape macchia. The other species either belong to the typically tropical sections *Lasiocephala* and *Leiocephala* or to the *Patentiflorae* (Beard, 1958).

The summer rainfall zone of South Africa with its 16 *Protea* species is therefore much poorer in species than the main centres to the north and the south. This area is essentially a transition zone for *Protea* species and ecologically of special interest.

Distribution

The distribution of the *Protea* species as given here is based on the work of Beard (1958) while Veld Types are based on the vegetation map of Acocks (1953). The distribution maps (Figs. 1, 2 and 3) have been compiled from records of the National Herbarium, Pretoria¹ and the Herbarium, in Durban, Republic of South Africa.

The true macchia, the centre of distribution of the Cape species of *Protea*, is confined to the winter rainfall area west of Knysna. *Protea* species also occur in the "False macchia" of the various mountain ranges in the Uniondale, Humansdorp and Port Elizabeth Divisions with a constant rainfall through the year. The "False macchia" is extended in a narrow strip along the Zuurbergen, around Grahamstown and at Riebeeck East.

North of the "False macchia" summer rainfall vegetation appears in the form of various types of grassland, forests and savannas (bushveld). Here the *Protea* species are much more restricted and only occur in localised patches of suitable habitat. Many of the summer rainfall zone *Protea* species are found in similar localities to evergreen forests (Natal, Eastern Transvaal) but never as constituents of the forests. In those areas where they occur in high mountain grassland as an open *Protea* woodland they probably indicate that forest has been more extensive in the past (Beard, 1958). In the Central and Western Transvaal the pattern changes and becomes much more suggestive of the tropics. Here most of the summer rainfall zone species occur in the Sour Bushveld, Sourish Mixed Bushveld and the Bankenveld (Acocks, 1953). In the Sour and Sourish Mixed Bushveld their occurrence is widespread and in the Bankenveld (Fire climax grassland) they occur in the woodland which covers rocky knolls, in both cases helping to make up a type of savanna woodland of distinctly tropical appearance.

¹ Botanical Research Institute, Private Bag X101, Pretoria, 0001, Republic of South Africa.

In general, however, the *Protea* species occupy poor rocky ground in the areas of highest rainfall (Beard, 1958). Adamson (1938) on the other hand is of the opinion that e.g. *Protea caffra* occurs on the ecotone between a shrubsavanna and grassland, in those areas with cold winters.

According to Beard (1958) the summer rainfall zone *Protea* species occur in the following veld types (Acocks, 1953):

- (a) Coastal Forest and Shrub;
- (b) Pondoland Coastal Plateau Sourveld;
- (c) Highland Sourveld;
- (d) North-east Highland Sourveld;
- (e) Ngongoni veld of the Natal Mistbelt;
- (f) Piet Retief Sourveld;

and in the savanna in the following veld types (Acocks, 1953):

- (g) Sour Bushveld;
- (h) Sourish Mixed Bushveld;
- (i) Bankenveld (Fire climax grassland).

Of the sixteen summer rainfall zone *Protea* species, *P. roupelliae* has the widest distribution, ranging from the North Eastern Cape Province through Natal and Swaziland to the Transvaal where it is widely distributed (Fig. 1). *P. roupelliae* occurs from sea level to an altitude of approximately 2000 m.

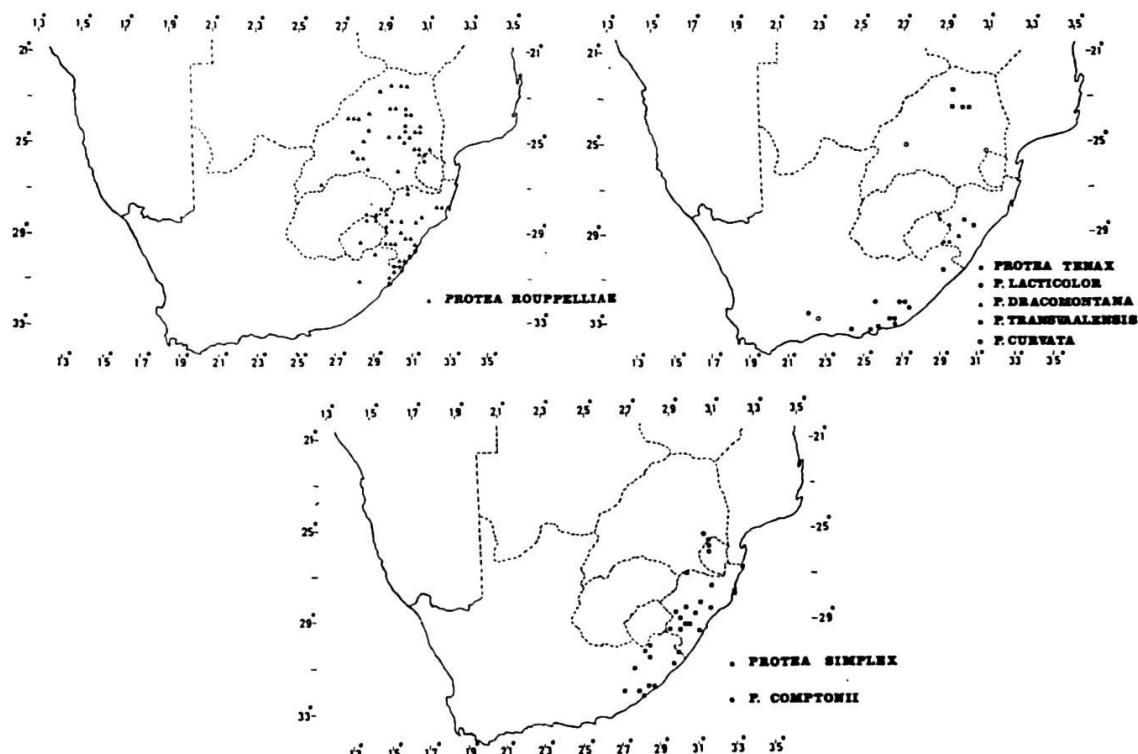
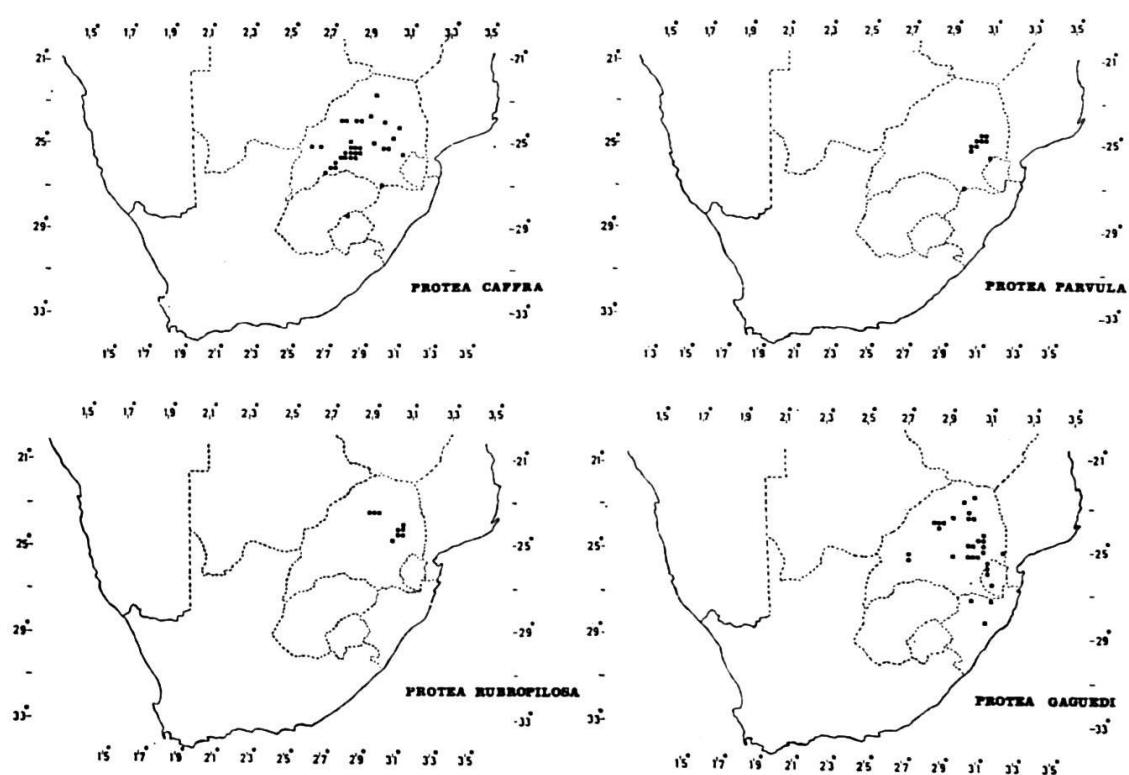
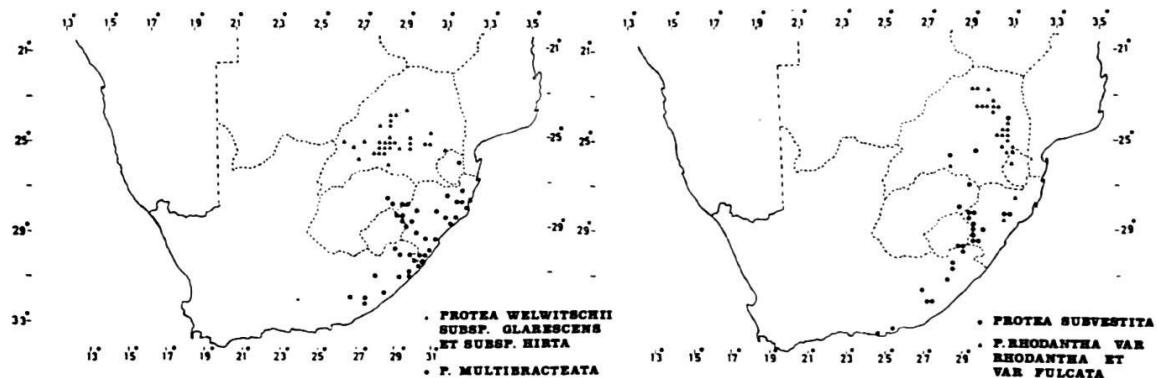


Fig. 1. — The distribution of *Protea roupelliae*, *P. tenax*, *P. lacticolor*, *P. dracomontana*, *P. transvaalensis*, *P. curvata*, *P. simplex* and *P. comptonii* in the summer rainfall zone of South Africa.

P. tenax and *P. lacticolor* (Fig. 1) occur mainly in the "False macchia" of the Eastern Cape Province, although the distribution of *P. tenax* extends through the North Eastern Cape Province into Natal and *P. lacticolor* is essentially an inhabitant of the Cape macchia.

P. simplex (Fig. 1), *P. multibracteata* and *P. subvestita* (Fig. 2) are mainly found from the North Eastern Cape Province through Natal and with the exception of *P. subvestita* into Swaziland. *P. subvestita* and *P. multibracteata* are also found in Lesotho and the Eastern Orange Free State, while the distribution of *P. subvestita*



extends into the Southern Transvaal. Although these species occur from the coast to the high mountains they are more often found in mountainous areas in the eastern parts of South Africa.

The distribution of *P. dracomontana* (Fig. 1) is restricted to the Drakensberg from Underberg in the Natal to Leribe in Lesotho.

Protea comptonii (Fig. 1) is only known from the mountains around Baberton in the Eastern Transvaal. The distribution of *P. curvata* (Fig. 1) is very localised and is found near Rustenburg and Barberton in the Transvaal and Oudtshoorn in the Cape Province.

Protea transvaalensis (Fig. 1), *P. parvula* and *P. rubropilosa* (Fig. 3) are the only summer rainfall zone *Protea* species which are restricted to the northern and eastern mountainous areas of the Transvaal. Although *P. welwitschii* (Fig. 2), *P. rhodantha* (Fig. 2), *P. caffra* and *P. gaguedi* (Fig. 3) are more common and widely distributed in Transvaal, *P. caffra* is also found in the Eastern Orange Free State and the other three species in the northern areas of Natal.

The ecology of *Protea caffra*

Study area

The study area is the Loskop Dam Nature Reserve, centred on 25°50'S, 29°50'E, in the Transvaal, Republic of South Africa. The nature reserve covers an area of approximately 16 148 ha of mountainous terrain around the dam. The vegetation is predominantly Sourish Mixed Bushveld and Mixed Bushveld (Acocks, 1953). These veld types are a dry open savanna. They are very heterogeneous and according to Acocks (1953) "... are a more than Dadaelion maze of variations and transitions". Nearly a 1000 species of flowering plants occur in the reserve, grouped into a great variety of different plant communities (Theron, 1973).

The reserve lies in a summer rainfall area with mild to very hot summers with temperatures varying from 9°C at night to 39°C in the day. Winters are mild and frost occurs on hill tops and in low-lying valleys, with temperatures varying from -2°C at night to 29°C in the day. The average rainfall for the reserve is 720 mm which falls mainly as showers and thunderstorms of short duration and high intensity.

*The distribution of *Protea caffra* in the reserve*

One of the most conspicuous features of this area is the great difference in the vegetation between the north and south facing slopes (Pl. Ia). *Protea caffra* is one of many species in the reserve that occurs on south, south-east and south-west facing slopes and on the mountain plateaux, but is rarely found on the north and north-west facing slopes (Pl. Ib).

Methods

The ecological position of *Protea caffra* was determined along an ecological gradient by means of index iteration (Goff & Cottam, 1967). The ecological distribution of species was determined by means of principal component analysis of stands (Gittins, 1969). Importance values of the different species used in these procedures were determined by means of the quarter method (Cottam & Curtis, 1956) as adapted for South African savannas (Louw & Grunow, 1969). Importance values were

calculated as the sum of relative percentage frequency, relative percentage density and relative percentage dominance. Relative percentage dominance was derived from the expression:

$$\text{Relative percentage dominance} = \frac{2 \times \text{Relative \% Canopy diameter} + \text{Relative \% tree height}}{3}$$

A total of 123 stands were sampled. The stands were subjectively distributed over the reserve after an assessment of the overall species composition and habitat conditions had been made. Uniformity of stands was considered to be most important and this was subjectively assessed using all the properties of the vegetation and sites that could be directly observed. To ensure that stands included in the data would be homogeneous, a Chi-square test for homogeneity of the plant species present was also conducted (Curtis, 1959). For the same reason and in the same way as Curtis & McIntosh (1951), only those species with a relative percentage frequency of 25 percent and above were tested for homogeneity at the 5 percent level of significance.

Trees were present in only 111 of the stands and only 103 of these were found to be homogeneous. Only those species which occurred in at least 25 of the stands, with the exception of *Protea caffra* which only occurred in 16, were used in the index iteration and principal component analysis.

To determine the ecological behaviour of the individual species the following environmental characteristics were determined by means of standard methods (Theron, 1973): Altitude, angle of the slope, aspect, geological formation, soil texture, soil depth, soil colour, soil resistance, infiltration time of water, available water, soil pH, and the presence of Na^+ , Ca^+ , K^+ , Fe^+ , Zn^+ , Co^+ , Cu^+ , P, C, N.

The environmental factors (independant variables) and the vegetation (importance values, dependant variables) after standardization were subjected to multiple regression analysis (Draper & Smith, 1967; Snedecor & Cochran, 1968) as applied by Stephenson (1971).

Index iteration, principal component analysis and multiple regression analysis were carried out by an IBM 360/40 Digital Computer at the Computer Centre, University of Pretoria.

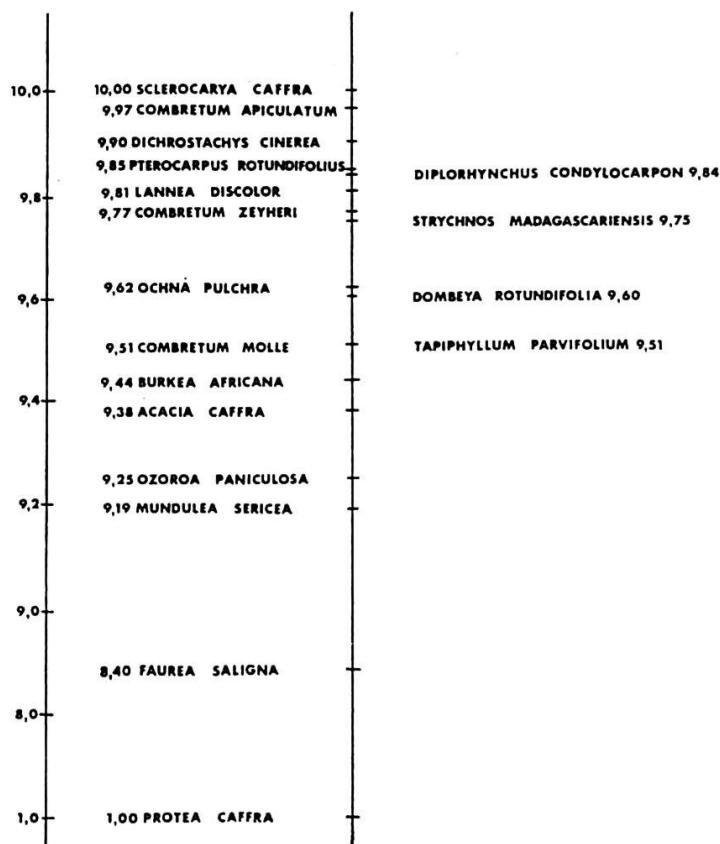


Fig. 4. — Species position indices (SPI) for tree species occurring in at least 25 stands in the Loskop Dam Nature Reserve.

Results

Index iteration

The species position indices (SPI) for 19 of the species that occurred in the 103 stands are shown in Figure 4.

The high SPI-values of *Sclerocarya caffra* and *Combretum apiculatum* indicate the low ecological status of these species in the reserve. These species are associated with the warm, dry conditions prevailing on the north and north-west facing slopes of the reserve.

The low SPI-value of *Protea caffra* on the other hand indicates the high ecological status of this species in the reserve. *Protea caffra*, as previously stated, is common on south, south-east and south-west facing slopes and on the mountain plateaux. The plateaux and especially the south facing slopes are cooler (Theron, 1973) and the soil probably has a higher moisture content than the other slopes or on the flats (Aitken, 1922; Bews, 1925; Roberts, 1966; Walter, 1971). *P. caffra* is regarded as a species ecotonal between a shrubsavanna and grassland in the cool to cold areas (Adamson, 1938). *P. caffra* is therefore probably representative of the more mesophytic conditions in the xerarchal succession in the reserve.

The absence of any intermediate values on the SPI-scale (Fig. 4) between those species with a low ecological status and *Protea caffra* with a high ecological status can probably be explained by the restricted distribution of *P. caffra* in the reserve and the more specific habitat in which it occurs.

It is therefore possible to identify an ecological gradient from the drier and warmer sites, where *Sclerocarya caffra*, *Combretum apiculatum* and *Diplorhynchus condylocarpon* are the dominant species, to moister and cooler sites where *Protea caffra* is the dominant species.

Principal component analysis (PCA)

The distribution of *Protea caffra* as plotted in relation to the first two components of the PCA are shown in Figure 5. The importance values have not been plotted directly but have been grouped, each group designated by a symbol (Table 1). Isolines have been drawn to highlight aspects of the species behaviour and do not convey precise quantitative information nor do they necessarily imply that no alternative isoline patterns could be found (Fig. 6).

Symbol	Importance value group
—	Absent
○	0.6 - 29.9
▽	60 - 69.9
△	120 - 149.9
■	210 - 239.9
★	270 - 300.0

Table 1. — Symbols assigned to groups of importance values used for *Protea caffra* in Figure 7.

The main centres of distribution of several other species in relation to the first two axes, also indicated by isolines, are shown in Figure 6.

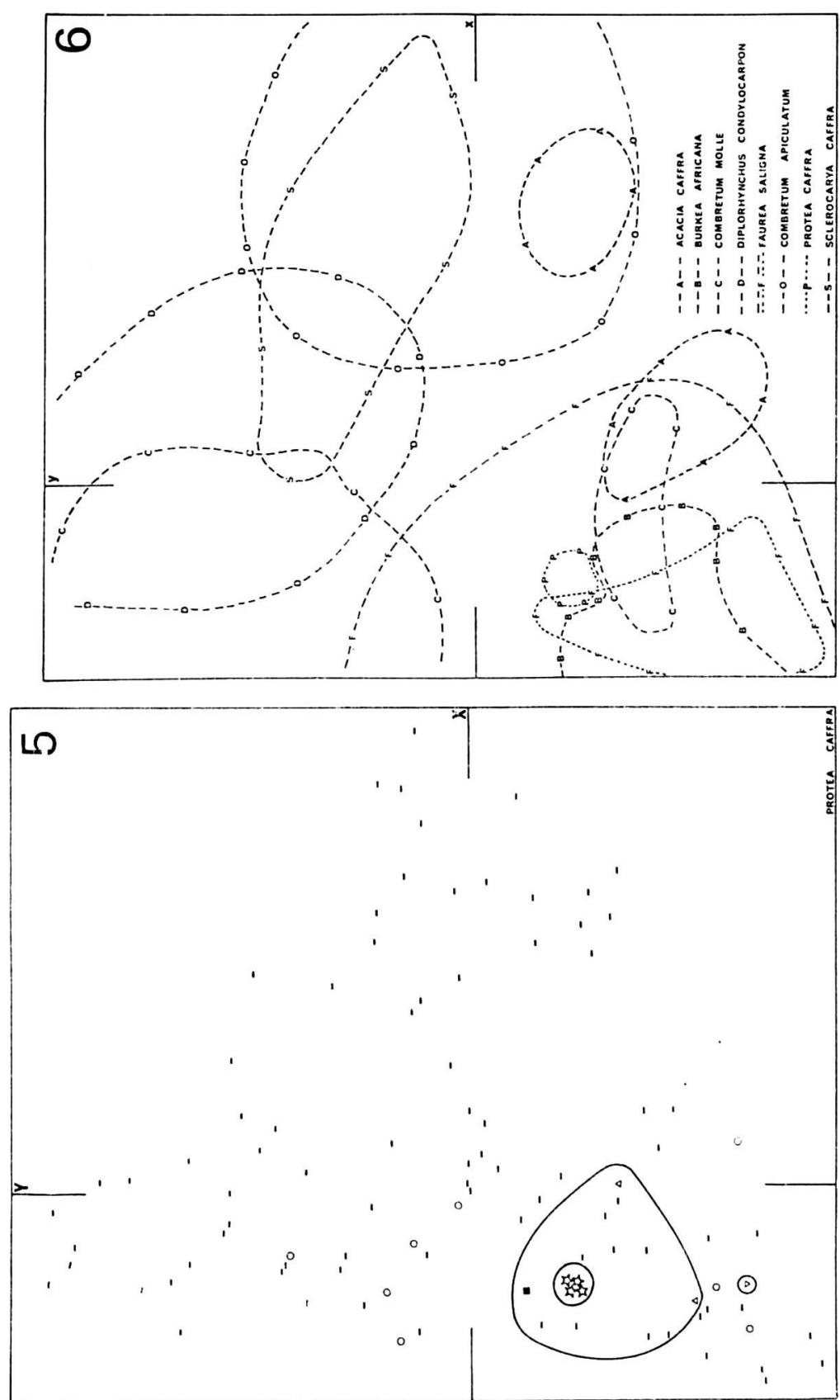


Fig. 5. — The distribution of *Protea caffra* in the Loskop Dam Nature Reserve in relation to the x- and y- axes of the ordination (cf. Table 1.)
 Fig. 6. — The distribution of selected tree species in the Loskop Dam Nature Reserve in relation to the x- and y- axes of the ordination.

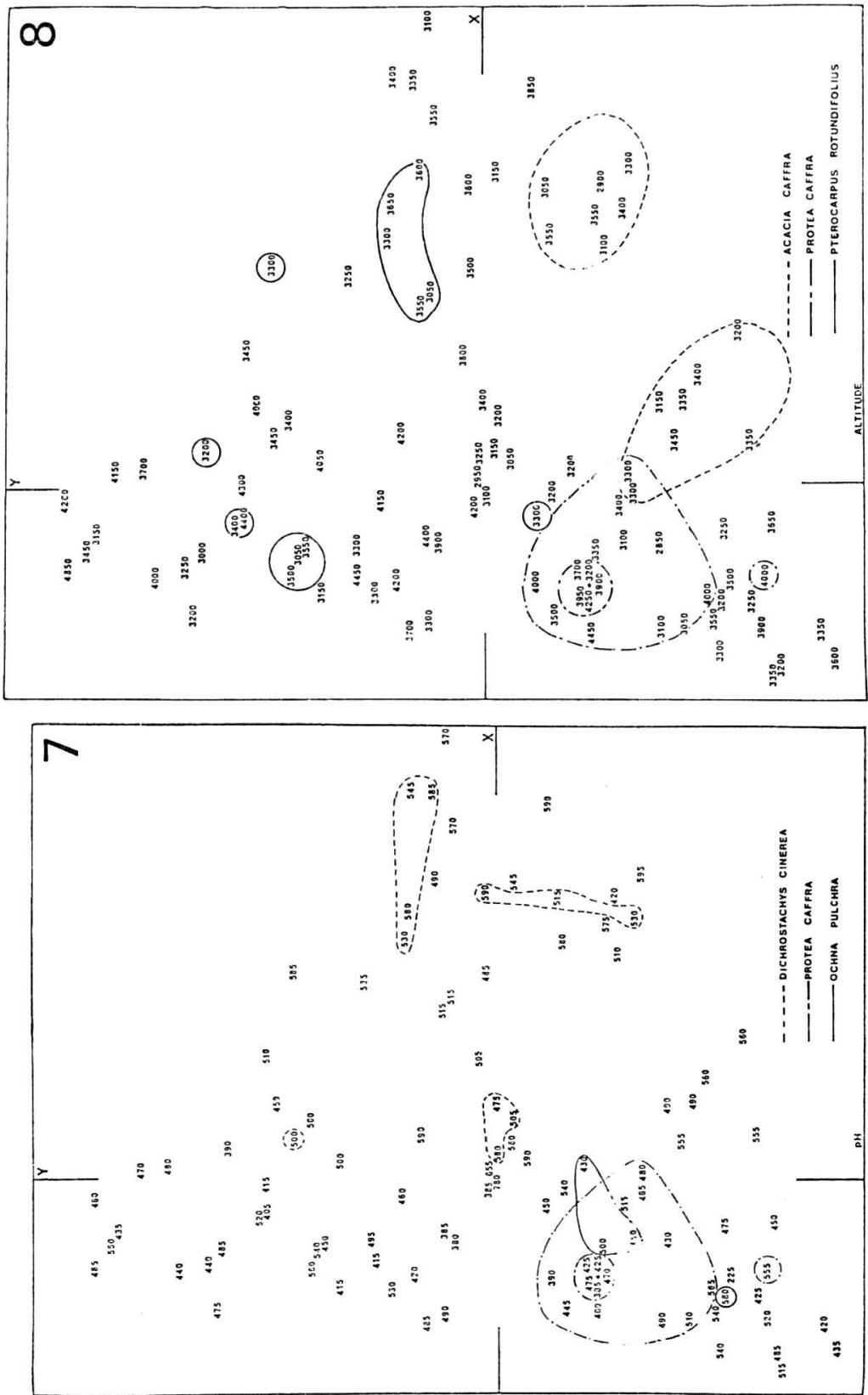


Fig. 7. — The distribution of *Protea caffra* and the pH-values of the soils in the different stands, in relation to the x- and y-axes of the ordination.
 Fig. 8. — The distribution of *Protea caffra* and the altitudes of the different stands, in relation to the x- and y-axes of the ordination.

Although the distribution patterns differ from species to species (Fig. 6) those of e.g. *Faurea saligna*, *Burkea africana* and *Protea caffra* correspond. It is also clear that *Protea caffra* has a narrower ecological amplitude and that it occurs in a more restricted habitat. The overlapping in the distribution pattern of the different species is indicative of a gradient along the diagonal from the lower left to the upper right of Figure 6. Those species with their main distribution centre to the lower left and with low SPI-values (Fig. 4) represent more mesophytic conditions and occur either on:

- (a) south, south-east and south-west facing slopes and the plateaux e.g. *Protea caffra*, or
- (b) the above sites, and on the flats e.g. *Faurea saligna*, *Burkea africana* and *Acacia caffra*.

The species having high SPI-values (Fig. 4) and with their main centres of distribution more to the upper right of Figure 6, e.g. *Diplorhynchus condylocarpon*, *Sclerocarya caffra*, *Combretum apiculatum* and *Acacia caffra* occur on the more xerophytic north, north-east or north-west facing slopes.

Those species with more than one main centre of distribution occur under varying conditions on both north and south facing slopes, e.g. *Combretum molle*, or on both south and north-west facing slopes, e.g. *Acacia caffra*.

Of all these species *Protea caffra* has the most restricted distribution and is confined to the cooler and moister habitats in the reserve.

Multiple regression analysis

Those environmental factors which were significantly correlated with the importance values (distribution) of *Protea caffra* in the reserve, were plotted on the first two axes of the PCA. The isoline signifying the main distribution centre of *Protea caffra* was drawn in (Figs. 7, 8, 9, 10).

It can be seen that *Protea caffra* is negatively correlated with high or increasing pH and grows on soils with a pH-value as low as 3.85 (Fig. 7). *P. caffra* shows a positive correlation with altitude and occurs mostly higher up on the slopes and on the plateaux (Pl. Ib, Fig. 8) in the reserve. When *P. caffra* is found on north facing slopes it is usually under cooler conditions at altitudes above 2000 m.

Although the zinc and sodium content of the soils on which *P. caffra* grows are respectively high and low (Figs 9, 10) the positive correlation that was found with multiple regression analysis can not be accounted for.

Conclusion

From the distribution maps for the different summer rainfall zone *Protea* species, it is clear that they occur at higher altitudes and in the cooler and higher rainfall zones of the country. Most of the species occur in the Transvaal and in the Drakensberg area of Natal.

Of the nineteen tree species in 103 stands studied in the Loskop Dam Nature Reserve, *Protea caffra* is probably the most mesophytic species. It prefers cooler and moister conditions and is usually found on south facing slopes and on the plateaux.



However, it also occurs on north facing slopes at high altitudes. Although *P. caffra* is a summer rainfall zone species it seems to prefer more temperate conditions such as are found in the winter rainfall areas of the South Western Cape Province where most of the *Protea* species occur. Not only does *Protea caffra* prefer a temperate climate but also soils with a low pH, the same as many of the *Protea* species from the winter rainfall areas (Vogts, 1971).

This preliminary account of the distribution and ecology of *Protea caffra* indicates that more research is necessary to determine the precise ecological requirements of this species.

Acknowledgement

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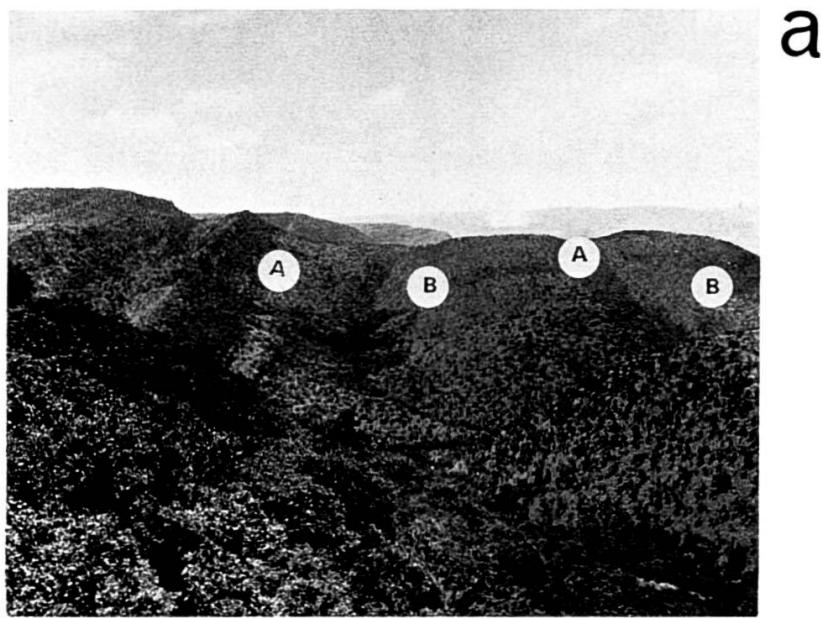
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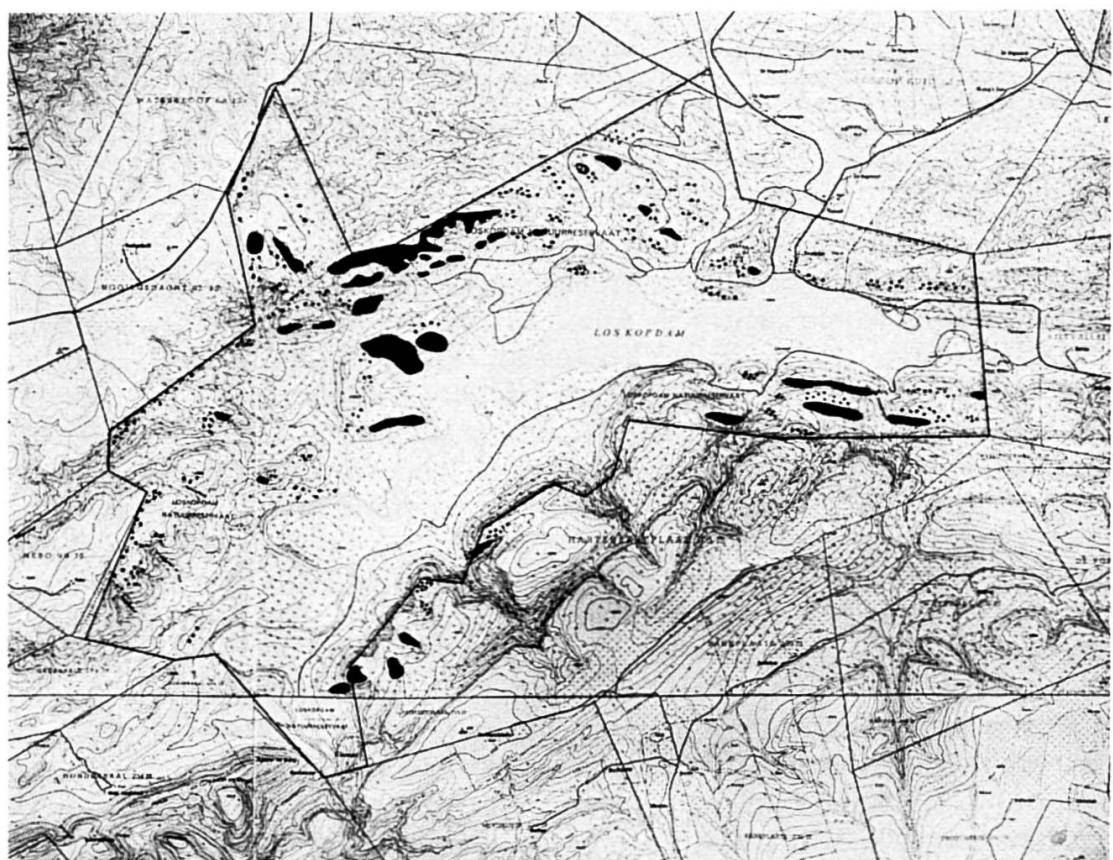
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a

b



a, physiognomically different plant communities against north (A) and south (B) facing slopes in the Loskop Dam Nature Reserve.

b, the distribution of *Protea caffra* in the Loskop Dam Nature Reserve.