Fungal populations associated with root systems of proteaceous seedlings at a lowland fynbos site in South Africa

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Fungi were isolated from rhizosphere and non-rhizosphere soil from root systems of *Leucospermum parile* and *Hakea sericea* seedlings growing in sand plain lowland fynbos. Deuteromycotina were most prevalent; *Penicillium, Aspergillus* and *Trichoderma* were the main genera. The root systems supported a more varied mycoflora than the non-rhizosphere soil but were non-mycorrhizal. A number of fungi, including representatives of the Ascomycotina, were found almost exclusively in the root region. The proteoid and non-proteoid regions of the roots of both species contained similar fungal populations. Nine fungal species and the genus *Helicoon* were recorded for the first time in South Africa.

Grondfungi is van die risofeer van *Hakea sericea* en *Leucospermum parile* wat in laaglandfynbos groei geïsoleer. Soorte behorende tot die Deuteromycotina het die algemeenste voorgekom. Hiervan was die genera *Penicillium, Aspergillus* en *Trichoderma* die belangrikste. Die wortelstelsels het 'n groter verskeidenheid mikoflora ondersteun as die omringende grond, maar het geen mikorrisale assosiasies gehad nie. 'n Aantal fungi, insluitende soorte behorende tot die Ascomycotina was byna uitsluitlik in die wortelstreek aangetref. Daar is geen verskil in die funguspopulasies van die proteoïede en nie-proteoïede wortels gevind nie. Nege fungussoorte en die genus *Helicoon* is vir die eerste keer in Suid-Afrika aangetoon.

Keywords: Fynbos, Proteaceae, proteoid roots, soil fungi

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Introduction

Shrubs of the Proteaceae dominate the fynbos vegetation of the south-western Cape Province of South Africa and characteristically produce proteoid roots (Lamont 1983a). Proteoid roots are densely packed clusters of short-lived rootlets arising along the lateral roots, and play a special role in nutrient uptake (Lamont 1983b), but are non-mycorrhizal in some members of the Australian Proteaceae (Malajczuk *et al.* 1981).

In this study, fungal populations were identified in the rhizosphere and root tissue of proteoid and non-proteoid roots of members of the Proteaceae growing in an acidic sandy soil (Mitchell *et al.* 1984) and were compared with the mycoflora of the non-rhizosphere region. Soil fungi are frequently in a dormant state and the rhizosphere is likely to be one of the few sites in the soil where active microbial growth occurs (Robinson *et al.* 1968; Barber & Lynch 1977). Rhizosphere and rhizoplane saprotrophic fungi have mainly been studied in economically important plants (Newman 1978) whereas this paper reports on micro-organism/root interactions in a natural vegetation.

Materials and Methods

Plant material and study site

Two species of Proteaceae were selected: *Leucospermum parile* (Salisb. ex J. Knight) Sweet which is endemic to the sand plain lowland fynbos, south-western Cape and *Hakea sericea* Schrad. which was introduced to the Cape Province from Australia during the 19th century (Annecke & Neser 1977). Seed of *H. sericea* was germinated in sterile acid-washed sand. During April 1982 5-week-old seedlings were transplanted to Clovelly sand, at the Pella study site (33°31′S, 18°32′E; 160 – 220 m altitude; 294 ha; 62 km north of Cape Town, South Africa). Seedlings of *L. parile* were naturally growing at the same study area.

The soil is classified as the Clovelly form, Geelhout series according to MacVicar *et al.* (1977) and is a medium sand aeolian in origin, well drained with pH 4,6 – 4,8 and has an organic matter content of 1,8% (Mitchell *et al.* 1984; Brown & Mitchell 1986). The vegetation is sand plain lowland fynbos (Moll *et al.* 1984) dominated by evergreen sclerophyllous shrubs and rush-like plants belonging to the Restionaceae. The climate is mediterranean with a mean annual rainfall of 400 mm falling mainly between May and October. The site had been burnt during November 1980.

Isolation of fungi

The root systems of seedlings of *L. parile* (one year old) and *H. sericea* (five months old) were collected during winter (late May to September) 1982 in soil blocks which were transported to the laboratory in sterile polythene bags. The roots were dissected under aseptic conditions leaving undisturbed soil adhering to them. The fungi were isolated within 24 h of collection.

The rhizosphere fungi were isolated by the serial root washing technique (Harley & Waid 1955). One proteoid root complex or a 5-cm length of non-proteoid root from both *H. sericea* and *L. parile* were used for each washing series and ten replicates of each were washed 25 times in 5 cm^3 of sterile distilled water. The rhizosphere fungi were isolated by plating aliquots of water from the first and 25th washing in 15 cm^3 of cool Rose Bengal chloramphenicol agar (Lab M, Salford, U.K.). To isolate the fungi attached to the root systems after 25 washings, four serially washed proteoid and non-proteoid roots of each species were macerated. A few drops of macerate were spread over Rose Bengal chloramphenicol agar. Plates of the first and 25th washing and macerate were replicated four times.

The non-rhizosphere soil fungi were sampled by collecting soil free of roots and away from the canopy of any plants. Soil cores were collected 5 cm below the surface in sterile test tubes. Soil fungi were isolated using the soil plate technique (Warcup 1950) and five replicates of 10 soil samples were prepared.

Plates were examined after 3 – 5 days in the dark at 25°C. Representatives of all species were transferred to Potato Dextrose agar (PDA) and identified after they had sporulated.

Penicillium spp., *Eupenicillium* spp., *Scopulariopsis* spp. and *Talaromyces* sp. were grown on media described by Pitt (1979). *Aspergillus* spp. were grown on Czapek Dox agar and Malt Extract agar (Raper & Fennell 1965). *Trichoderma* spp. were grown on Malt agar (Rifai 1969) and *Chaetomium* spp. were grown on cellulose-amended PDA or sterile carrot plugs (Ames 1963). The histochemical technique of Phillips & Hayman (1970) was used to detect vesicular-arbuscular (VA) mycorrhizal fungi on the root systems. Live cultures of all fungi were deposited in the fungal collection of the Department of Botany, University of Cape Town.

Results

In the serial washing procedure of Harley & Waid (1955), the first three washings removed most of the rhizosphere fungi and after the fifth washing, a low but constant number of fungi were isolated (Figure 1).

A total of 61 species were identified from 380 isolates of the non-rhizosphere Clovelly sand (Table 1) and rhizospheres of *H. sericea* (Table 2) and *L. parile* (Table 3). The rhizospheres of the two plant species supported a more varied fungal flora than the non-rhizosphere region. Members of the Deuteromycotina were commonly isolated and the most frequent genera were *Aspergillus, Penicillium* and *Trichoderma*. The common species isolated in descending order of frequency, were: *Aspergillus fumigatus, Penicillium restrictum, Scopulariopsis brevicaulis, P. novae-zeelandiae, A. duricaulis, Scopulariopsis* sp., *Trichoderma viride, P. verruculosum, T. pseudokoningii* and *Eupenicillium hirayamae*. Of these, *Scopulariopsis* sp. and *E. hirayamae* were absent from the non-rhizosphere region. Other species only colonizing the root zones were *P. restictum, P. janczewskii, P. funiculosum, A. unilateralis, E. pinetorum*, and *Periconia digitata*. Representatives of the Ascomycotina with the exception of three isolates from the soil, were restricted to the rhizospheres of *H. sericea* and *L. parile*.

The rhizosphere and macerate of washed roots of both *H. sericea* (Table 2) and *L. parile* (Table 3) contained 67 and 62% respectively of the total species isolated. None of the common species were specifically associated with either the root systems of *H. sericea* and *L. parile* or the soil. There were no differences in the fungal populations associated with the proteoid and non-proteoid roots. The populations of the first and 25th washing and the macerate were similar. Only five species (*A. flavus, A. niger, Apiospora montagnei, Botryotrichum* sp. and *Drechslera* sp.) were restricted to the non-rhizosphere soil but none were common.

No VA mycorrhizal fungi were detected in the roots of either *H. sericea* or *L. parile*.

Table 1 Soil fungi isolated from non-rhizosphere Clovelly sand at Pella, South Africa, by the soil plate method. Figures represent the presence of each species in ten separate soil samples

Mortierella vinacea Dixon-Stewart	1
Mucor hiemalis Wehmer	1
Apiospora montagnei Sacc. (*Arthrinium* anamorph)	1
Neosartorya fischeri (Wehmer) Malloch & Cain	2
Phoma sp. 1360	1
Aspergillus duricaulis Raper & Fennell	2
Aspergillus flavus Link	1
Aspergillus fumigatus Fr.	10
Aspergillus niger v. Tieghem	1
Botryotrichum sp. 1308	1
Curvularia sp. 1316	1
Drechslera sp. 1318	1
Fusarium spp. 1321 – 23	3
Harzia sp. 1324	2
Penicillum novae-zeelandiae v. Beyma	5
Penicillium raistrickii G. Smith	7
Penicillium restrictum Gilman & Abbott	1
Penicillium verruculosum Peyronel	2
Scopulariopsis brevicaulis (Sacc.) Bain.	4
Trichoderma harzianum Rifai	1
Trichoderma koningii Oudem.	1
Trichoderma pseudokoningii Rifai	3
Trichoderma viride Pers. ex Gray	5
White Sterile	1
Black sterile 1359	1

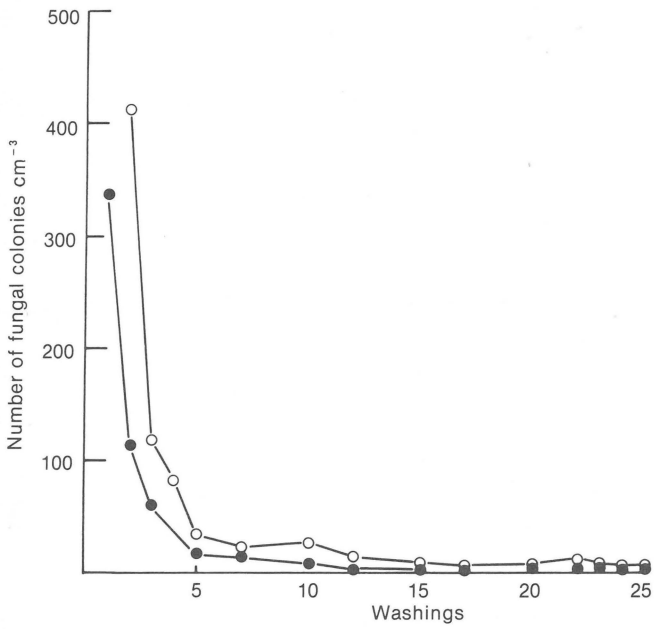

Figure 1 Number of fungal colonies isolated from 1 cm^3 of each washing of one proteoid (○) and one non-proteoid (●) root of *Hakea sericea* growing in Clovelly sand at Pella.

Discussion

The fungal populations of sand plain lowland fynbos resemble those reported from tropical, desert and other warm regions where the genus *Aspergillus* tends to be abundant (Warcup 1951; Barron 1968). *Aspergillus fumigatus* is the most frequent species isolated in the present study but is rare or absent in other South African soils, viz. Zululand forest soils (Eicker 1969), Transvaal savanna (Eicker 1974) and a western Transvaal *Acacia karoo* community (Papendorf 1976). This species is common in Australian heathlands as are *A. duricaulis* and *A. unilateralis* (McLennan & Ducker 1954) which occur on the root systems of both *H. sericea* and *L. parile* but have not been reported elsewhere in South Africa. pH has been implicated as a major determinant of soil mycofloral populations (Jensen 1931; Warcup 1951; Singh 1980). The Clovelly sand at Pella and Australian heathlands soils have a pH less than those of the Transvaal savanna which have fungal populations dominated by *P. multicolor* (= *P. slerotium* v. Beyma) and *Gliocladium roseum* not present at Pella (Eicker 1974).

Members of the Zygomycotina are less frequent in the Clovelly sand of this study compared with other soils of Australian heathlands (McLennan & Ducker 1954) and Californian chaparral (Cooke 1970). Sandy soils in warm dry regions generally contain low Zygomycotina populations (Nicot 1960; Wohlrab & Tuveson 1965; Papendorf 1976) and

Table 2 Fungi isolated from the 1st and 25th washing of serially washed roots, and macerate of washed roots of *Hakea sericea*. Figures denote the number of samples in which each species occurred from 10 of each washing and four macerated root systems

	Proteoid			Non-proteoid		
Species	1st wash	25th wash	Macerate	1st wash	25th wash	Macerate
Mortierella vinacea Dixon-Stewart	1	1	2			
Mucor hiemalis Wehmer	1	1		1		2
Byssochlamys nivea Westling			1			
Chaetomium cochliodes Pall.	1					
Chaetomium funicolum Cooke				1		
Eupenicillium hirayamae Scott & Stolk	2	1	1	1		2
Eupenicillium pinetorum Stolk	1					
Microascus triganosporus Emmons & Dodge			1			
Talaromyces wortmanii (Klöcker) C.R. Benjamin			1			
Unidentified Basidiomycete 1358					1	
Phoma sp. 1361			1	1	1	
Dark Coelomycete 1315		1				
Aspergillus duricaulis Raper & Fennell	2	4		3		2
Aspergillus fumigatus Fr.	2	2	1	7	2	2
Aspergillus unilateralis Thrower			1	1		
Curvularia sp. 1316				1		
Fusarium spp. 1321 – 23	1	2	1	2	1	
Harzia sp. 1324		1	1			
Helicoon sp. 1325				1		
Paecilomyces marquandii (Massee) Hughes				1		
Paecilomyces variotii Bain		1				
Penicillium funiculosum Thom				1	1	
Penicillium janczewskii Zaleski				1		
Penicillium melinii Thom			2	1		
Penicillium novae-zeelandiae v. Beyma	3	1	1	1		3
Penicillium raistrickii G. Smith			2	2		1
Penicillium restrictum Gilman & Abbott	4	5		2	3	3
Penicillium verruculosum Peyronel	2	1	1	1		
Periconia digitata (Cooke) Sacc.				2		1
Scopulariopsis brevicaulis (Sacc.) Bain.	4	1		3	3	3
Scopulariopsis sp. 1348 *S. brumptii* series	1	1		2	1	1
Trichoderma harzianum Rifai	1					
Trichoderma koningii Oudem.			1		1	
Trichoderma pseudokoningii Rifahi				1	1	2
Trichoderma viride Pers. ex Gray	3		1	3		1
Trichoderma sp. 1355						1
Torulomyces lagena Delitsch	1	1	1			
Ulocladium atrum Preuss		1				
Wardomyces anomalus Brooks & Hansf.			1			
Unidentified Porospore 1362					1	
Black sterile 1359		2	1			1

this group may prefer moister soils with a higher organic matter content as in the forest soils of Zululand (Eicker 1969). The absence of Oomycetes may be ascribed to low soil moisture and high summer temperatures (Papendorf 1976).

The species recorded for the first time in South Africa are *A. duricaulis, A. unilateralis, Eupenicillium pinetorum, Mortierella vinacea, P. novae-zeelandiae, Periconia digitata, Talaromyces wortmanni, Trichoderma harzianum* and *Wardomyces anomalus*. The genus *Helicoon* has not been isolated previously. This isolate was similar to *H. ellipticum* Peck. The most common isolate which may represent a new species is *Scopulariopsis* sp. with features similar to *S. croci*. Isolates from the genera *Chaetomium, Trichoderma* and *Penicillium*, and a fungus with non-septate porospores may represent new species.

There is generally a greater diversity of fungal species in the root zone compared with the soil (Thrower 1954; Jalaluddin 1975; Odunfa & Oso 1979). The Clovelly sand at Pella is of a low phosphorus status (Mitchell *et al.* 1984), which would limit fungal growth in the non-rhizosphere region (Warcup 1951; Brian 1960; Robinson *et al.* 1968; Barber & Lynch 1977). Active plant roots exude metabolites which may stimulate spore germination and supply nutrients for fungal growth (Rovira 1979; Barber & Martin 1976). Any similarities between the soil and root zone may be ascribed to the fact that the soil contains a species reservoir which colonizes new substrates e.g. growing roots. However, some fungal species were absent or rare in the non-rhizosphere soil e.g. *A. unilateralis, P. restrictum, Scopulariopsis* sp. and members of the Ascomycotina. Roots may provide a relatively permanent habitat in which fungal metabolism can continue and perhaps provide the specialized nutritional needs of some fungi

Table 3 Fungi isolated from 1st and 25th washings of serially washed roots, and macerate of washed roots of *Leucospermum parile*. Figures denote the number of samples in which each species occurred from 10 of each washing and four macerated root systems

	Proteoid			Non-proteoid		
Species	1st wash	25th wash	Macerate	1st wash	25th wash	Macerate
Mortierella isabellina Oudem.					1	
Mucor hiemalis Wehmer				1		
Mucor plumbeus Bonord			1			
Chaetomium funicolum Cooke						1
Chaetomium humicolum v. Warmelo	1	1	1			
Chaetomium sp. 1313	1					
Eupenicillium hirayamae Scott & Stolk	1		1			1
Eupenicillium pinetorum Stolk	2	1		2	1	1
Neosartorya fischeri (Wehmer) Malloch & Cain	4	2		1		
Pale coelomycete 1314			1			
Aspergillus duricaulis Raper & Fennell	1	3		1	2	2
Aspergillus flavipes (Bain & Sart.) Thom & Church	1					
Aspergillus fumigatus Fr.	8	2	3	1		1
Aspergillus unilateralis Thrower	2	2		2	1	
Aspergillus versicolor group (Vuill.) Tiraboschi						1
Cladosporium herbarum (Pers.) Link ex Gray	1					
Fusarium spp. 1321 – 23	1	1				
Penicillium citrinum Thom	1					
Penicillium funiculosum Thom	1	1	1			
Penicillium glabrum (Wehmer) Westling		2	1			
Penicillium janczewskii Zaleski	1			2	2	
Penicillium miczynskii Zaleski		1		1		
Penicillium novae-zeelandiae v. Beyma	4	2	1	1		2
Penicillium purpurogenum Stoll	1	1				
Penicillium raistrickii G. Smith	4	3	3	4	2	1
Penicillium restrictum Gilman & Abbott	7	3	1	2	2	1
Penicillium verruculosum Peyronel	1			2		1
Penicillium sp. 1. 1344	1					
Penicillium sp. 2. 1345			1			
Periconia digitata (Cooke) Sacc.					2	
Scopulariopsis brevicaulis (Sacc.) Bain.	2	1	3	2	1	2
Scopulariopsis sp. 1348 *S. brumptii* series	3	1	1	1		1
Torulomyces lagena Delitsch	1			1	1	
Trichoderma pseudokoningii Rifai	1	1				1
Trichoderma viride Pers. ex Gray	1					
Ulocladium atrum Preuss						1
White sterile	1	3				
Black sterile 1359	1		1			

(Robinson *et al.* 1968; Barber & Lynch 1977).

The roots of *H. sericea* and *L. parile* do not possess VA mycorrhizal fungi, agreeing with the study of Malajczuk *et al.* (1981). The fungal flora of the proteoid roots of *L. parile* was more diverse than that of the non-proteoid regions. Proteoid roots occur in regions of high organic matter (Purnell 1960; Lamont 1981), where a more diverse fungal population may be present (Bisset & Parkinson 1979). The similarity of the fungal flora of the root systems of *H. sericea* and *L. parile* growing in the same soil agrees with the studies of Thrower (1954), showing that six Australian heathland plant species supported similar rhizosphere fungal populations. *H. sericea* is an aggressive alien in the SW Cape (Fugler 1982) and one possible reason for its success is the ability of its root systems to accommodate the indigenous soil mycoflora.

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References

AMES, L.M. 1963. A monograph of the Chaetomiaceae. U.S. Army Research and Development Series, No. 2, U.S.A.

ANNECKE, D.P. & NESER, S. 1977. On the biological control of some Cape pest plants. In: Proceedings of the Second National Weeds Conference of South Africa, A.A. Balkema, Cape Town.

BARBER, D.A. & LYNCH, J.M. 1977. Microbial growth in the rhizosphere. *Soil Biol. Bioch.* 9: 305 – 308.

BARBER, D.A. & MARTIN, J.K. 1976. The release of organic substances by cereal roots into soil. *New Phytol.* 76: 9 – 80.

BARRON, G.L. 1968. The genera of hyphomycetes from the soil. Williams & Wilkins, Baltimore.

BISSET, J. & PARKINSON, D. 1979. The distribution of fungi in some alpine soils. *Can. J. Bot.* 57: 1609 – 1629.

BRIAN, P.W. 1960. Antagonistic and competitive mechanisms limiting survival and activity of fungi in soil. In: The ecology of soil fungi. eds Parkinson, D. & Waid, J.S. pp. 115 – 129, Liverpool University Press, Liverpool.

BROWN, G. & MITCHELL, D.T. 1986. Influence of fire on the soil phosphorus status in sand plain lowland fynbos, south-western Cape. *S. Afr. J. Bot.* 52: 67 – 72.

COOKE, W.B. 1970. Fungi in burned and unburned Chapparal soils. *Sydowia* 24: 164 – 168.

EICKER, A. 1969. Microfungi from surface soil of forest communities in Zululand. *Trans. Brit. mycol. Soc.* 53: 381 – 392.

EICKER, A. 1974. The mycoflora of an alkaline soil of the open-savannah of the Transvaal. *Trans. Brit. mycol. Soc.* 63: 281 – 288.

FUGLER, S.R. 1982. Infestations of three Australian *Hakea* species in South Africa and their control. *S. A. For. J.* 120: 63 – 68.

HARLEY, J.L. & WAID, J.S. 1955. A method of studying active mycelia on living roots and other surfaces in the soil. *Trans. Brit. mycol. Soc.* 38: 104 – 118.

JALALUDDIN, M. 1975. Study of micro-organisms from root regions of rice. *Pl. Soil* 43: 337 – 345.

JENSEN, H.L. 1931. The fungus flora of the soil. *Soil Sci.* 31: 123 – 158.

LAMONT, B. 1981. Specialised roots of non-symbiotic origin in heathlands. In: Heathlands and related shrublands. 9B. Analytical studies, ed. Specht, R.L. pp. 183 – 195, Elsevier, Amsterdam.

LAMONT, B. 1983a. Proteoid roots in the South African Proteaceae. *J. S. Afr. Bot.* 49: 103 – 123.

LAMONT, B. 1983b. Strategies for maximising nutrient uptake in two mediterranean ecosystems of low nutrient status. In: Mediterranean-type ecosystems — the role of nutrients, eds Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. pp. 246 – 273, Springer-Verlag, Berlin.

MACVICAR, C.N., DE VILLIERS, J.M., LOXTON, R.F., VERSTER, E., LAMBRECHTS, J.J.N., MERRYWEATHER, F.R., LE ROUX, J., VAN ROOYEN, T.H. & HARMSE, H.J. VON M. 1977. Soil classification: A binomial system for South Africa. Department of Agricultural Technical Services, Pretoria.

MALAJCZUK, N., LINDERMAN, R.G., KOUGH, J. & TRAPPE, J.M. 1981. Presence of vesicular-arbuscular mycorrhizae in *Eucalyptus* spp. and *Acacia* sp., and their absence in *Banksia* sp. after inoculation with *Glomus fasciculatus*. *New Phytol.* 87: 567 – 572.

McLENNAN, E.I. & DUCKER, S.C. 1954. The ecology of the soil fungi of an Australian heathland. *Aus. J. Bot.* 2: 220 – 245.

MITCHELL, D.T., BROWN, G. & JONGENS-ROBERTS, S. 1984. Variation of forms of phosphorus in the sandy soils of coastal fynbos, south-western Cape. *J. Ecol.* 72: 575 – 584.

MOLL, E.J., CAMPBELL, B.M., COWLING, R.M., BOSSI, L., JARMAN, M.L. & BOUCHER, C. 1984. A description of major vegetation categories in and adjacent to the Fynbos biome. South African National Scientific Programmes Report 84, CSIR, Pretoria.

NEWMAN, E.I. 1978. Root microorganisms: their significance in the ecosystem. *Biol. Reviews* 53: 511 – 554.

NICOT, J. 1960. Some characteristics of the microflora in desert sands. In: The ecology of soil fungi, eds Parkinson, D. & Waid, J.S. pp. 94 – 97, Liverpool University Press, Liverpool.

ODUNFA, V.S.A. & OSO, B.A. 1979. Fungal populations in the rhizosphere and rhizoplane of cowpea. *Trans. Brit. mycol. Soc.* 73: 21 – 26.

PAPENDORF, M.C. 1976. The soil mycoflora of an *Acacia karoo* community in the western Transvaal. *Bothalia* 12: 123 – 127.

PHILLIPS, J.M. & HAYMAN, D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Brit. mycol. Soc.* 55: 158 – 160.

PITT, J.I. 1979. The genus *Penicillium* and its teleomorphic state *Eupenicillium* and *Talaromyces*. Academic Press, London.

PURNELL, H.M. 1960. Studies of the family Proteaceae. I. Anatomy and morphology of the roots of some Victorian species. *Aus. J. Bot.* 8: 38 – 50.

RAPER, K.B. & FENNELL, D.I. 1965. The genus *Aspergillus*. Williams & Wilkins, Baltimore.

RIFAI, M.A. 1969. A revision of the genus *Trichoderma*. *Mycol. papers* 116: 1 – 56.

ROBINSON, P.M., PARK, D. & GARRETT, M.K. 1968. Sporostatic products of fungi. *Trans. Brit. mycol. Soc.* 51: 113 – 124.

ROVIRA, A.D. 1979. Biology of the soil – root interface. In: The soil – root interface, eds Harley, J.L. & Scott Russell, R. pp. 145 – 160, Academic Press, London.

SINGH, K.G. 1980. Rhizosphere and root surface fungi of some heath plants and the role of dark sterile forms. *Pl. Soil* 54: 185 – 193.

THROWER, L.B. 1954. Rhizosphere effect of heathland plants. *Aus. J. Bot.* 2: 246 – 267.

WARCUP, J.H. 1950. The soil plate method for isolation of fungi from soil. *Nature* 166: 117.

WARCUP, J.H. 1951. The ecology of soil fungi. *Trans. Brit. mycol. Soc.* 34: 376 – 399.

WOHLRAB, G. & TUVESON, R.W. 1965. Distribution of fungi in early stages of succession in Indiana dune sands. *Amer. J. Bot.* 52: 1050 – 1058.