AN ECOLOGICAL STUDY OF THE SOIL FUNGI OF SOME BRITISH SAND DUNES

by

Juliet C. Brown

Royal Holloway College,
University of London.

A thesis submitted for
the Ph.D. Degree in the
University of London.

February, 1957.

Abstract

The distribution of soil microfungi in the successive ecological zones of eight dune systems on the British coast was investigated with special reference to the acid system at Studland and the alkaline system at Sandwich. A number of direct and indirect fungal isolation methods were used and a new modification of the soil impression technique was developed for a comparative estimate of the amount of mycelium in dune soils. Qualitative and quantitative changes in the fungal population were studied in relation to the soil type, the soil profile and the vegetation.

A succession of species was found to occur across the dune systems from the pioneer communities of the foreshore to the climax or sub-climax communities of the fixed dunes. The existence of distinct mycofloras in the acid and alkaline soils and the development of a microfungal profile were also demonstrated.

The root surface fungal floras of Ammophila arenaria and Carex arenaria were examined at various stages of the dune succession and found to vary with soil type, reflecting the succession of "free" soil fungi.

The dune soil fungal flora appeared from this investigation to be an active and relatively rich community, exhibiting an ecological succession and species associations on a scale comparable with that of the higher plants.

CONTENTS

1. Introduction and Historical Review

The ecology of soil fungi was described by Garrett in 1952 as a study "still in its veriest infancy", half a century after the pioneers in this field, Adametz (1886) and Oudemans and Koning (1902) had isolated several soil fungi and attempted to relate them to their environment. Soil mycology has, nevertheless, received much attention in the last 50 years and many aspects of its problems have been attacked, as shown by the wealth of literature and the number of reviews of the subject (Burges 1939; Waksman 1932, 1944; Chesters 1949; Garrett 1952, 1955).

In 1916, Waksman demonstrated that fungi do actually live in the soil; this was followed by attempts to enumerate and separate their active and non-active components (McLennan 1928), by many investigations of their physiological and biochemical activities, and by suggestions for their classification into broad ecological groups. Waksman (1917), for example, distinguished between soil inhabitants and soil invaders, Winogradsky (1925) between autochthonous and zymogenous soil microorganisms, and others between nutritional types (Thom and Morrow 1937; Burges 1939; Garrett 1950). At the same time there were numerous studies involving the mass isolation and description of species and floristic lists for soils in all parts of

the world were compiled. They were mostly, however, until recently, the work of systematists rather than ecologists and added little to the general conclusion drawn by Waksman in 1917, namely, that there was a basic and cosmopolitan fungus flora of the soil, though the relative importance of different groups might vary with latitude and soil type.

Many of these early floristic studies are difficult to interpret or compare because the habitats investigated were insufficiently described; selective isolation techniques lacked uniformity; samplings were not replicated and the relative frequencies of species were not estimated. They brought out, however, the very widespread distribution of many soil fungi and the major variations in the populations such as the replacement of Penicillium species common in temperate zones by species of Aspergillus in warmer regions.

Conclusions as to the variation in fungus floras with soil type were often conflicting and inconclusive. Werkenthin (1916) and Brierley (1928) from a comparison of cultivated and uncultivated soils found no evidence of distinct fungus associations conditioned by edaphic factors. Some variations between soil types in this respect were reported, however, by Swift (1929) and Jensen (1931) and in 1933 Bisby, James and Timonin from their investigation of 75 Manitoban soils claimed that there were definite

differences in the fungus flora of distinct soil types, but the differences were not defined.

The investigations of the soil micro-fungi of natural and semi-natural soil types were few in comparison with those of agricultural soils, but a relatively wide range of habitats have been examined including, among others: woodlands (Paine 1927; Jensen 1931; Ellis 1940); moorlands (Dale 1914, Jensen 1931); saltmarsh (Bayliss-Elliott 1930; Sabet 1935); bogs (Boswell and Sheldon 1951); deserts and sand dunes. Recognisable fungal communities corresponding with these vegetational units were not, however, revealed and few generalizations can be made other than that members of the Mucorales are more frequent in forest soils than in grassland soils, where, especially in acid types, Penicillium and Trichoderma are common (Chesters 1949).

More detailed studies of the ecological distribution of soil fungi have been made in the last six years, initiated by that of Warcup (1951) on five natural grasslands. He investigated a range of soils varying from a highly alkaline type to a highly acid podsol, and showed that by precise definition of the sampling sites and repeated sampling over the same areas, definite species combinations could be distinguished. Investigations of similar intensity have been made on heathlands by Jefferys et al (1953) and

Sewell (1954) in the British Isles and by McLennan and Ducker (1954) in Australia. These revealed a marked similarity between the fungus floras of acid podsols in various localities and a relatively high degree of constancy of occurrence for a number of species.

The recent successional study by Tresner, Backhus and Curtis (1954), with its attempt at a closer synthesis of the ecology of soil fungi and of higher plants, is of particular interest. These workers related the distribution of soil microfungi to a hardwood forest continuum, sampling sites being defined by "continuum index" figures based on the relative density, frequency, dominance and shade tolerance of higher plants. It was found that the soil fungi were distributed in patterns remarkably similar to some shown for the higher plants of the area in question, and that a series of progressively changing species combinations, including "pioneer", "climax" and "indicator" species, occurred along the gradient of the forest continuum.

These intensive inquiries into the ecology of soil fungi, though few as yet, indicate the valuable information still to be gained by relating soil fungal communities with their macro-habitats, and should when extended to more soil types provide a firm foundation for the detailed analysis of their microhabitats advocated by Chesters (1949) and Garrett (1955).

This thesis attempts to define as closely as possible the microfungal soil floras of some British sand dunes and to relate their successional development and variations to the dune macrohabitat. The experimental evidence is based on a study of the influence of soil type, soil horizon, vegetation and locality on the distribution of fungi in the various ecological zones of dune systems.

The dune habitat with its display of development both in time and space provides exceptional scope for the study of plant colonisation and succession. Marked changes in soil type and vegetation are to be found within relatively small areas of a dune system - sometimes over a distance of only a few feet - and the successional stages from pioneer to climax communities can often be dated on historical evidence with some accuracy. The pioneer phase is of particular ecological interest, for here is a natural soil in the making where conditions fluctuate between the two extremes of aridity and submersion by sea water and the biological community probably presents a less confused ecological picture for interpretation than more highly developed ecosystems.

Many aspects of the dune xerosere have been described (Salisbury 1952) and the zonation of its angiosperm and bryophyte flora is a classic example of ecological

succession. However, detailed investigations of the ecology of the soil microfungi of maritime dunes have not hitherto been made and information on the distribution of soil fungi in relation to dune type and dune succession has been fragmentary. The microfungal flora of the soil is an important component of most plant communities and its neglect has given a one-sided picture of the dune ecosystem.

Historical Review of Investigations on the Soil Microfungi of Sand Dunes

There are early reports of the existence of fungi in sandy soils of very low organic content. Waksman (1922) recorded the presence of fungal mycelium in a nearly pure siliceous sand and Snow in her comparative study of the bacterial flora of wind-blown desert and dune sands (1926-33) determined the number of fungal colonies developing from the sand in culture. She concluded that sand was unfavourable to fungal growth and that bacteria and actinomycetes predominated over fungi, but gave no evidence that the fungi were active. The microflora of the desert steppe zones, including mobile sand hills, of Central Asia were investigated by Sabinin and Minina (1930); biologically active soil layers were stated to occur, but their experimental procedure and floristic data were not given. Killian and Fehér's (1935) work on the microflora of inland dunes is more noteworthy. They found that the sand hills of the Sahara, in spite of their low water content and the high temperatures to which they are exposed, were by no means sterile; soil respiration was used as a measure of microbiological activity and the relative frequencies of fungal species were estimated, which showed that Mucor, Trichoderma and Aspergillus occurred most constantly.

The first ecological study of the soil microfungi of

maritime dunes appears to be that of Duché and Heim (1931) on the French coast. Ten species were isolated by a dilution plate technique from various sites on a calcareous dune system, but they were not related to dune development or the soil profile and no estimate was made of their frequency of occurrence in a given soil type. It was concluded, however, that the density and nature of the vegetation had no influence on the fungal population and that coastal sands though relatively poor in fungi contained a remarkable mycoflora.

The soil fungi of French dunes were further investigated by the Moreaus in 1940. Their survey was, however, of a preliminary and cursory nature and only tentative conclusions could be drawn from their findings. Thirty species of microfungi were isolated by the direct inoculation of the culture medium with sand grains. Hyphomycetes, including a number of dematiaceous forms, predominated; a few were found near the sea so that they were assumed to be capable of withstanding high salinities as was confirmed experimentally. An attempt was made to relate the fungus flora with the dune succession, but again frequency estimates were not made and specific associations between fungi and higher plants could not be distinguished. There were, however, indications that the microflora changed with dune development and the authors suggest that there may be

species of microfungi as constant in and characteristic of dune soils as are certain members of the higher plant communities.

More recently, observations by the Japanese on dune soil fungi have been reported. Ikeda (1954) claims that Penicillium and Aspergillus are the commonest fungi in dune soils and Saitô (1952) states that there is no essential difference between the sand dune habitat and other habitats with respect to the fungus flora, Penicillium and Trichoderma being principal constituents of the alkaline dune he examined. The latter also deduced from counts of fungal colonies developing in culture that the dune habitat was unfavourable to fungal growth. In further investigations Saitô (1955) found a marked rise in fungal numbers as soon as vegetation colonizes the sand of a dune system and an increase in fungi with dune succession.

Quantitative estimates of the fungal content of acid dunes in Scotland have been made by Eastwood et al (1950) and more extensively by Webley et al (1952). The latter related numbers of fungi to the dune succession and found, as did Saitô, a marked increase in numbers of bacteria and fungi as soon as vegetation colonized the sand, continuing with dune development. Colonization by heather was accompanied by a fall in the numbers of bacteria while the fungus population continued to increase.

Here again, the estimates of fungal numbers were made from counts of colonies on dilution plates - a technique which is unsatisfactory both because of its selectivity and because of its reflection of sporing capacity rather than of active fungal content. The figures quoted by these authors can therefore be taken only as indicators of the general trend and not as absolute values. The examination of the root region floras of dune plants by these authors is discussed elsewhere (Section III).

Apart from a short list of Mucorales isolated by Campbell (1938) from a few random samples of dune sand, floristic data for the soil microfungi of British dunes does not appear to have been published.

From the foregoing it can be seen that there is some past evidence for the existence of an active population of dune soil microfungi increasing in size with dune development, but what had not been discovered was, at what stage fungal colonization begins, whether there is a definite succession of species and how this population varies with soil horizon, vegetation, dune development and type of dune system.

2. The Dune Habitats

Two dune systems were chosen for a detailed study of their soil microfungal population, namely the calcareous dune system at Sandwich, Kent, and the acid dune system at Studland, Dorset.

It was considered that two extreme types of dunes, such as these are, would elucidate most clearly the ecological fungal patterns associated with dunes. Moreover, the ecological zonation of these sands in certain localities is relatively distinct, so that the soil fungi can be related to the successional development of the whole dune complex.

The investigations were restricted in general to the dune ridges and dune lows were not examined in any detail. The term "low" is used as by Salisbury (1952) for hollows between ridges which do not normally contain standing water. A small number of soil profiles in sandy lows at Studland and Blakeney, Norfolk, were compared with those of adjacent dune ridges and are briefly referred to in the discussion on the effects of salinity on the dune microflora. A water table was not encountered in any of the dune ridges examined. The foreshore is perhaps not strictly part of a dune system, but as dunes are formed from the sand of this zone it has been included in the investigation.

Much is known about the history and higher plant ecology of the Studland dunes from the work of Diver (1933) and Good (1935) and general ecological studies on the Sandwich dunes are in progress (Rose - unpublished data). For this reason detailed descriptions of the higher plant vegetation are omitted in the following account of the habitats.

The Sandwich Dune System

The dunes at Sandwich face east and extend for about 5½ miles from Deal to Shellness Point as long low ridges parallel to the sea from 1/4 mile to 1 mile in width. They show little active growth and sandhills and slacks are very local. The system is, however, an excellent example of mostly old, calcareous dunes with a rich angiosperm flora.

Golf courses cover much of the fixed dunes and there is a certain amount of chemical spraying, burning, cutting and artificial draining in these areas. Sampling sites were chosen carefully to avoid localities where there was evidence of such biotic activities. Rabbit grazing appeared to be slight at the time of sampling.

An area, a mile south of Shellness Point and approximately 1/4 mile square, where the stages of dune succession are most distinct, was selected for this study. The 5 zones investigated were:-

(1) the open sand of the tide-washed beach OS
(2) fore dunes FD
(3) semi-fixed "yellow" dunes YD
(4) semi-fixed to fixed "grey" dunes GD
(5) old fixed dune pasture DP

(1) The Open Sand

Soil samples were collected approximately mid way

The Sandwich Dune System

Scale: 2½ inches = 1 mile. * Sampling area.

between high and low water mark of ordinary tides.

(2) The Fore Dunes

The fore dune ridge is straight, approximately 30 feet in width and 2 - 4 feet high. The habitat is mobile and relatively open, vegetation covering 50% or less of the ground surface.

The principal angiosperms are:-

Agropyron junceiforme	a - f
Ammophila arenaria	a - o
Festuca rubra v. arenaria	a
Eryngium maritimum	f
Euphorbia paralias	f
Honkenya peploides	f

(3) Semi-fixed or "Yellow" Dunes

There is no succession to high white Ammophila dunes, typical of many dune systems. Instead the ground behind the fore dunes is occupied by a community on flattish ground dominated by Ammophila arenaria with a rich associate flora.

The following species are frequent:-

Calystegia soldanella

Eryngium maritimum

Euphorbia paralias

Festuca rubra var. arenaria

Melilotus alba

M. officinalis

Ononis repens

Trifolium arvense

Some dune ephemerals have been omitted from this and succeeding lists.

A marked feature of this zone is the presence of mat-forming bryophytes - Brachythecium albicans, Camptothecium lutescens, Tortula ruralis and Tortula ruraliformis. Moreover a relatively tall and close growth of Ammophila and Melilotus affords considerable ground shelter, so that stabilization of the dune is at an advanced stage at a distance of only a few feet from the fore dunes.

(4) Fixed or "Grey" Dunes

Behind the yellow dunes and separated from them by fairways are low fixed dune ridges covered by a relatively short close turf of the co-dominants Carex arenaria, Festuca rubra v. arenaria and Koeleria albescens.

Frequent associates in the sampling areas included:

Cochlearia danica

Erodium cicutarium

Ranunculus bulbosus

Saxifraga tridactylites

Sedum acre

Lichens, absent from the younger zones, are occasional on the grey dunes; the commonest are species of Cladonia

and Peltigera canina.

Ammophila arenaria, the dominant of the semi-fixed dunes, occurs occasionally, but is in a somewhat stunted form.

(5) Dune Pasture

The zone of dune pasture at the rear of the dune system differs from the previous zone mainly in its greater abundance of pasture grasses. Koeleria and Festuca remain dominants, but Carex arenaria is less abundant.

The Soil Profiles

Open Sand.

The beach profiles were not visibly differentiated into horizons.

The sand is pale yellow, relatively coarse grained and mixed with considerable amounts of comminuted shells.

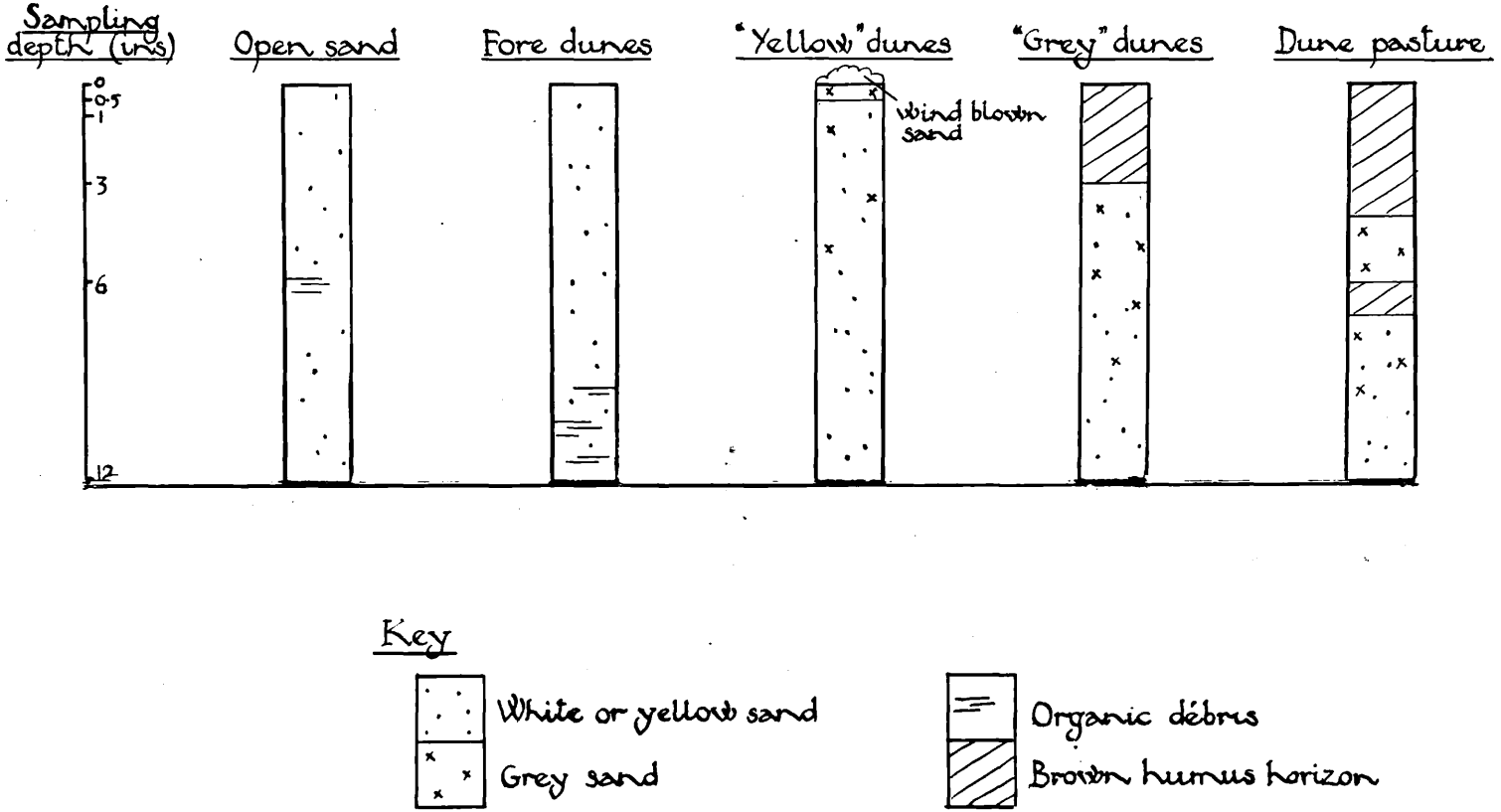
The sand of the foreshore and fore dunes is considered as a very immature soil.

Fore Dunes.

A surface humus layer was not distinguishable in the fore dunes either and the top 2"- 3" of sand was usually loose and dry. The sand is coarse and shingle was often encountered at a depth of about 18".

Yellow Dunes.

A light grey to dark brown sandy humus horizon 0.5"- 3" in thickness was usually present at the surface below a thin



Soil profiles typical of the Sandwich dune system

litter layer, grading into clean yellow sand which extended to an indefinite depth. Sometimes a thin layer of wind-blown sand was found above the humus horizon. In summer months the sand was loose and dry at the surface, but it was usually compact and damp at a depth of 3" - 6". The sand is still rather coarse in this zone and mixed with much grit and comminuted shells.

Grey Dunes.

Although the surface humus layer was rarely more than 3" in depth in the grey dunes, the transition through grey humus stained sand often extended to a depth of 1 foot, i.e. much deeper than in the profile described above, and dark coloured sub-surface humus horizons were sometimes encountered at varying depths. The humus horizons are very friable, but the degree of compacting is greater and the texture of the sand considerably finer than in the semi-fixed dunes.

Dune Pasture.

The soil profile in the dune pasture zone appears to be maturer than the above and consists of the following horizons:

(i) Sandy humus layer 0.5 - 4 inches thick. Friable.

(ii) A grey or slightly reddish bleached horizon 0.5 - 3 inches thick.

(iii) A compact humus horizon with a well defined upper limit 0.5 - 3 inches thick.

(iv) Transition zone to clean yellow sand at a depth of 6 - 12 inches.

Distinct humus bands occurred in some profiles at depths of 6 - 12 inches.

The Studland Dune System

The Studland dunes are based on a low-lying peninsula running N.-N.E. to South Haven Point forming the southern arm of the entrance to Poole Harbour. These so called Eastern Sands are composed of sand ridges running roughly north and south parallel with the sea. The oldest ridges are about 250 years old and growth continues to occur eastwards. The area exhibits a very complex mosaic of successional states of both wet and dry habitats, but the present investigation was restricted almost entirely to an area in the south where there is a relatively straightforward succession from Ammophiletum to dry heath and where the ecological zones follow closely upon one another and are little complicated by sand erosion or slack and bog formation.

Areas obviously disturbed by war manoeuvres were avoided. There was no evidence of cutting and burning of the vegetation in the vicinity, but rabbit pressure was relatively heavy at the time of sampling. Myxomatosis was reported on South Haven Peninsula in 1955.

The detailed investigation of the soil fungus population was carried out about 1½ miles south of South Haven Point over an area approximately 1/4 mile square.

The following six ecological zones were investigated:

(1) the open sand of the tide washed beach OS

The Studland Dune System

Scale: 2½ inches = 1 mile. * Sampling area.

(2)	fore dunes	FD	
(3)	semi-fixed dunes or "dune grass" (Good 1935)	DG	
(4)	semi-fixed to fixed dune heath	DH	
(5)	the "Southern Heath" Callunetum	SH	2 facies of dry dune heath developed on the oldest dunes
(6)	Pteridium - Betula heath	BH	

(1) The Open Sand

As at Sandwich, samples were taken from the open sand between the normal low and high tide marks.

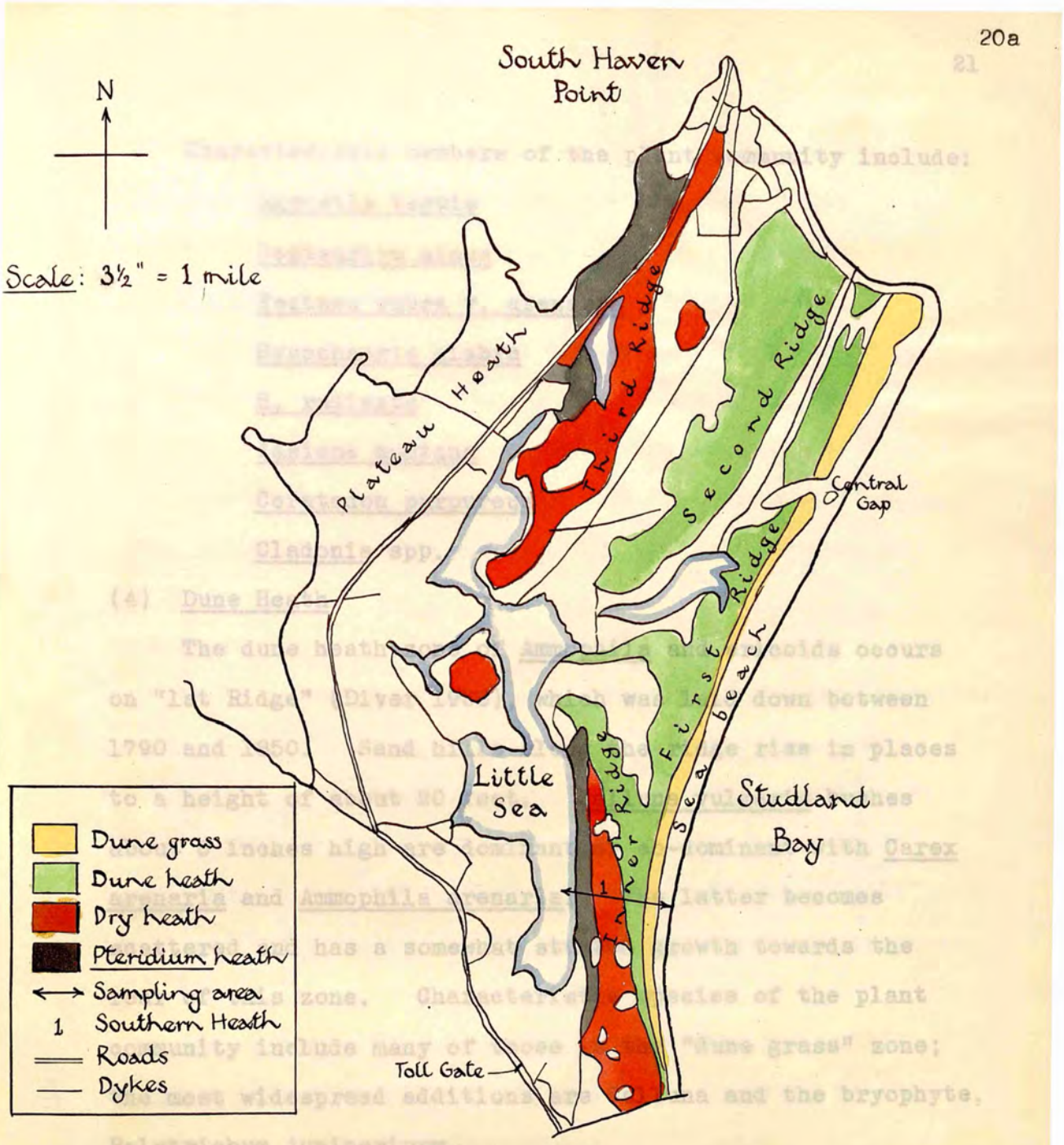
The zone of strand plants and embryo dunes is incomplete and was not included in the detailed survey.

(2) The Fore Dunes

The mobile fore dunes extend about 30 feet back from the shore and rise to a height of about 12 feet. The higher plant community is an almost pure Ammophiletum. Agropyron junceiforme and Elymus arenarius are occasional associates of Ammophila in this open habitat.

(3) Semi-fixed Dunes or "Dune Grass"

The "dune grass" zone, using Good's terminology, occurs as an undulating ridge about 60 feet wide between the fore dunes and the ericoid vegetation. It is readily distinguished from the younger zones by its grey colour and by the presence of Carex arenaria, a co-dominant with Ammophila, and lichens and bryophytes.



The Studland Dune System

(after Good, 1935)

Characteristic members of the plant community include:

Agrostis tenuis

Centaurium minus

Festuca rubra v. arenaria

Hypochaeris glabra

H. radicata

Jasione montana

Ceratodon purpureus

Cladonia spp.

(4) Dune Heath

The dune heath zone of Ammophila and ericoids occurs on "1st Ridge" (Diver 1933), which was laid down between 1790 and 1850. Sand hills along the ridge rise in places to a height of about 20 feet. Calluna vulgaris bushes about 6 inches high are dominant or co-dominant with Carex arenaria and Ammophila arenaria. The latter becomes scattered and has a somewhat stunted growth towards the rear of this zone. Characteristic species of the plant community include many of those in the "dune grass" zone; the most widespread additions are Calluna and the bryophyte, Polytrichum juniperinum.

(5) "Southern Heath"

Southern Heath is a dry heath more than 200 years old. It occurs on flattish ground behind the high ridge of the last zone described above. The dominant Calluna has an

extremely poor associate flora and the ground between the Calluna bushes (c. 6" in height) is occupied almost exclusively by a thin mat of lichens and bryophytes.

(6) Pteridium - Betula Heath

Pteridium - Betula heath occurs in a narrow zone on the western side of Southern Heath bordering Little Sea. It dates from about 1700. The vegetation is characterised by the dominant Pteridium aquilinum and small stands of Betula. Carex arenaria and Calluna vulgaris are also abundant.

The Soil Profiles

Open Sand.

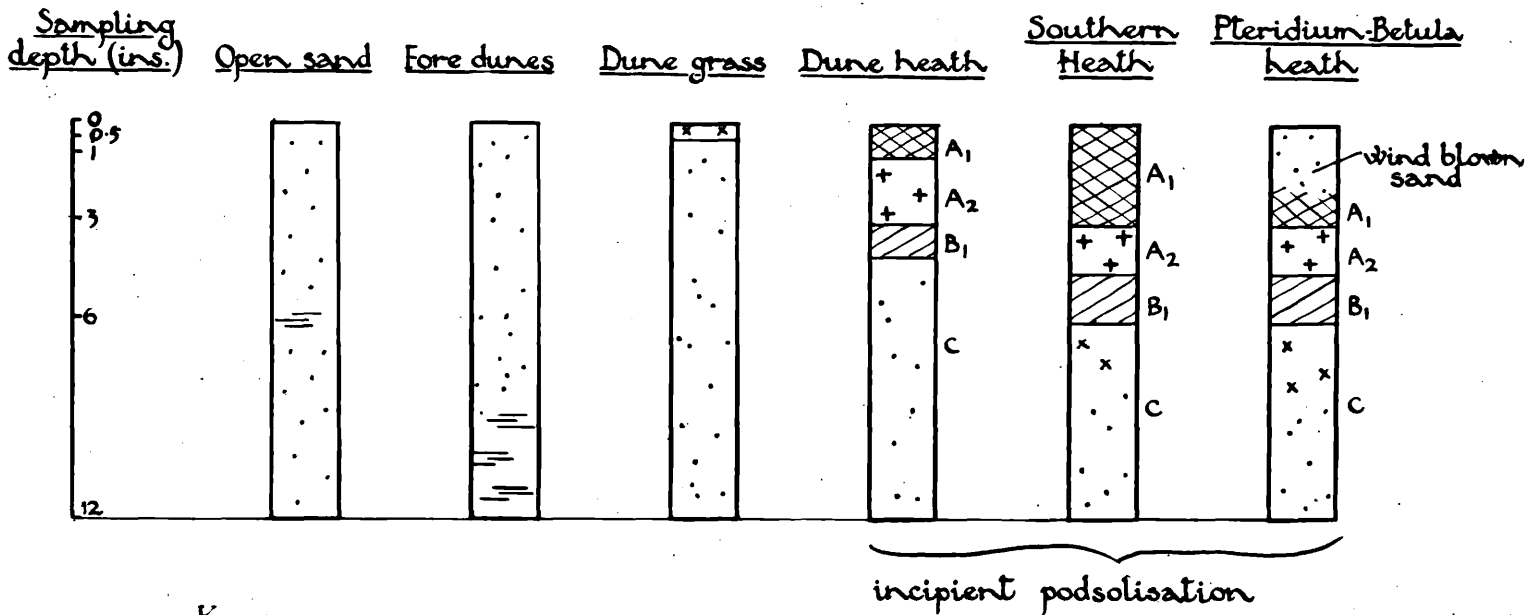
As at Sandwich no horizons were visible in the intertidal zone. The sand is almost white, relatively fine and homogeneous in contrast to that at Sandwich. It consists almost entirely of silica and contains very small amounts of calcium. Good considers that there is little doubt that it is derived from the denudation of Bagshot beds elsewhere.

Fore Dunes.

The soil profile of the fore dunes remained undifferentiated into horizons and the upper 2 - 3 inches of sand was usually dry and shifting.

Semi-fixed Dunes or "Dune Grass".

In this zone and in older dunes early stages of podsolisation were sometimes evident, and the following horizons occurred in some profiles:



Soil profiles typical of the Studland dune system

A_0 Litter layer of *Ammophila* 0 - 1 inch deep

A_1 Humus-rich sand 0 - 0.25 inches (maximum 1 inch deep)

A_2 Leached horizon

B_1 Indistinct humus pan at a depth of c. 3 inches

C Gradual transition to white sand.

Usually, however, the A_1 horizon graded straight into the C horizon.

Dune Heath.

Early stages of podsolisation were observed throughout the dune heath zone and were similar to the above, i.e. a leached horizon usually occurred below the very thin surface humus layer and a soft humus pan occurred at a depth of 1 - 4 inches. Humus bands and iron mottling were sometimes found at lower depths.

Southern Heath.

The soil profile in Southern Heath was typically as follows:

A_0 Thin *Calluna* litter layer

A_1 Well developed. Dark brown, sand speckled peat 1 - 3.5 inches deep

A_2 Leached horizon. 1.5 - 3 inches deep) Sometimes absent or indistinct

B_1 Humus pan. 1.5 - 3 inches deep → grey transition zone.)

C Silverwhite sand.

Pteridium - Betula Heath

The soil profile in the oldest zone of dunes investigated

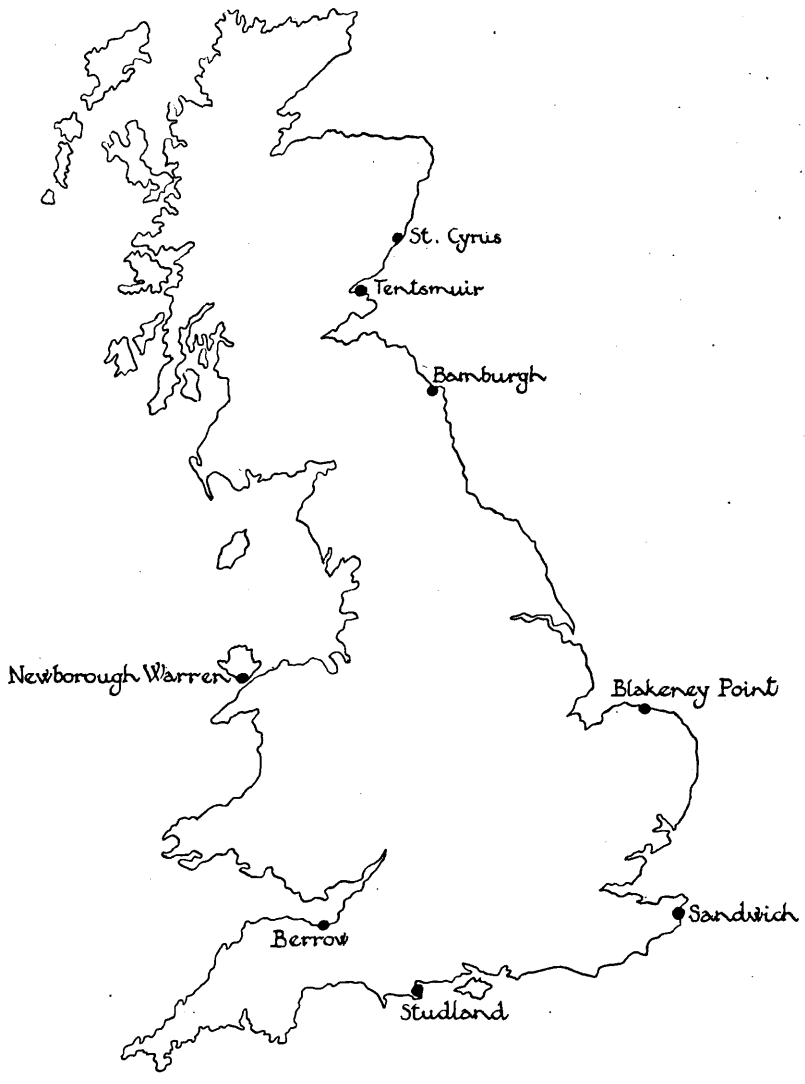
resembled that of Southern Heath, but the litter layer was usually deeper and it was often complicated by the fact that miniature blow outs are formed around decaying Pteridium plants so that the upper horizons were eroded or covered by a layer of wind blown sand.

Six other dune systems of various habitat types and in widely dispersed localities of the British Isles were chosen for an investigation of their microfloras by the soil plate method, in order to obtain supporting evidence for the findings from the intensive study of the Sandwich and Studland dunes.

Both acid and alkaline, calcareous and non-calcareous dunes are represented, some approach the conditions of the extreme types, others are of a more intermediate nature, as is indicated by the soil pH range in the areas sampled. When considered as a whole these dune systems may be classed broadly as either "alkaline" or "acid", although the foreshore and fore dune sand is usually alkaline and the final zone of the dune succession may be acid even in an otherwise typically alkaline system.

	Location of Dune System	Soil pH Range
Alkaline types	Sandwich, Kent	6.5 - 9.9
	Berrow, Somerset	7.5 - 8.6
	St. Cyrus, Kincardineshire	7.0 - 7.9
	Bamburgh, Northumberland	7.0 - 7.5
	Newborough Warren, Anglesey	5.5 - 8.7
Acid types	Blakeney Point, Norfolk	4.9 - 6.8
	Tentsmuir, Fife	4.9 - 8.0 (transect B) 4.2 - 7.0 (transect A)
	Studland, Dorset	3.1 - 7.5

Dune systems of a type at all comparable with the acid Studland system with its succession to dry dune heath are



Dune systems investigated

represented elsewhere in Britain only in Scotland. The principal examples are the Tentsmuir and Culbin Sands. The latter probably approximate most closely in soil type to that of Studland but were considered unsuitable for the present investigation owing to their extreme mobility and to the recent extensive afforestation of the area.

A brief account of these dune habitats follows. As before, subjective estimates of the most frequent members of the surface flora are given in order to typify the areas sampled.

The Berrow Dunes, Somerset

The calcareous dunes at Berrow form part of the dune system facing W.-S.W. which runs for about 5 miles between Burnham and Brean Down and extends about 3/4 mile inland. These sands laid down over tidal mud are believed to be of comparatively recent origin (Moss 1907). Some anomalous features of the higher plant succession in its early stages occur and are probably related in part to the admixture of mud and sand. The angiosperm flora is rich and includes a number of calcicoles; it has been described by Moss (1907); Watson (1918) and Stuart Thompson (1922; 1930).

The transition from Agropyron mobile dune through semi-fixed dune to fixed dune of the grassland type occurs in some parts over a distance as short as 50 - 100 yards.

The system as a whole has a somewhat damper facies than that at Sandwich, but the two systems have many features in common. The average calcium carbonate content of the sand at Berrow is 3% (Hepburn 1944) and the organic content 1 - 3.4% (Salisbury 1952).

The following stages in the dune succession were sampled along 2 line transects A and B approximately ½ mile apart.

		Transect
1.	Agropyron junceiforme embryo dune	A
2.	Open beach sand	A + B
3.	Agropyron junceiforme fore dune	A + B
4.	Mobile "Yellow" dune	A + B
5.	Ammophila semi-fixed dune	A + B

		Transect
6.	Fixed "Grey" *Carex* dune	B
7.	Dune Pasture	A

The open sand zone lay between the embryo dunes and the continuous fore dune belt, which is a low sand ridge about 12 yards wide. Apart from an occasional *Atriplex*, the higher plant community of the fore dunes is a pure Agropyronetum and the plant cover is $\leq$ 100%. The abundance of snails in the area was particularly marked.

Erratum

Page 28. Continued on Page 37 at Line 12 to the end of Page 38

The St. Cyrus Dunes, Kincardineshire

The St. Cyrus sand dunes on the east coast of Scotland run as a single ridge for approximately $1\frac{1}{2}$ miles facing south-east. The sand is mainly non-calcareous (mean 1.75% $CaCo_3$) but it is alkaline or only slightly acid in the oldest dunes.

The general plant ecology of the area has been described by Gimingham (1951). The vegetation of these relatively sheltered dunes is rich. The rabbit population appeared to be large at the time of sampling.

The following zones in the dune succession were sampled (notation of zones after Gimingham):

1. Mobile dunes "C".
2. Young fixed dune "C" - "D".

The mobile dunes are dominated by relatively dense stands of Ammophila arenaria. Abundant associates include Cirsium arvense, Festuca rubra, Senecio jacobaea, Cerastium tetrandrum, Bryum pendulum and Ceratodon purpureus.

Ammophila arenaria is still dominant in the fixed dunes, but the community is more or less closed. The bryophytes Tortula ruraliformis, Brachythecium albicans, and Rhytidiadelphus squarrosus are prominent in this zone. The profile was prepared below Ammophila arenaria and Tortula ruraliformis.

Figures for the $CaCo_3$ content and loss on ignition are given by Gimingham for these two zones.

	Mean $CaCO_3$ content (g. per 100 g. air dried sand)	Loss on ignition (g. per 100 g. oven-dry soil)
Mobile dunes	1.59	0.2 (surface) 0.1 (12")
Young fixed dune	1.59	0.2-1.3 (surface) 0.1-0.3 (12")

The Bamburgh Dunes, Northumberland

Investigations on the Bamburgh dunes were limited and restricted to the semi-fixed *Ammophila* dominated zone and the fixed dune pasture, both of which had a slightly alkaline reaction. Rabbits infected with myxomatosis were seen on the area.

Sparse associates of *Ammophila* on the semi-fixed dunes are *Senecio jacobaea* and *Carex arenaria*. The profile was prepared below *Ammophila* and *Tortula ruraliformis* which forms local swards.

On the fixed dune pasture *Ammophila* is co-dominant with other grasses and *Brachythecium albicans* and *Rhytidiadelphus triquetrus* are abundant.

The Newborough Warren Dune System, Anglesey, N. Wales

The Newborough Warren dunes extending over an area of 8 square miles in the south of Anglesey, are formed from blown sands overlying rocks of Pre-Cambrian origin.

The range of soil reaction is wider than that of either Sandwich or Studland. Soil pH values recorded for the young dunes are as high as 8.5, but those for the surface soil of the fixed Calluna dunes are as low as 5.5.

The calcium carbonate content of the soil is relatively low 0.5 - 2.0% (E.J. Salisbury).

A soil profile was sampled in each of the following successive dune zones:-

1. Ammophila embryo dune.
2. Ammophila fore dune.
3. Late "Yellow" dune.
4. Fixed "Grey" dune.
5. Salix - Calluna - Caricetum.

Frequent associates of Ammophila on the "yellow" dunes are:- Agrostis tenuis, Carex arenaria, Galium verum, Ononis repens, Sedum acre, Thymus serpyllum. Ammophila is also dominant on the "grey" dunes and associated with Agrostis tenuis, Carex arenaria, Senecio jacobaea, Brachythecium species, Tortula ruraliformis, Cladonia and Peltigera species.

The Caricetum behind the "grey" dunes occupies a narrow zone intermediate between slack and fixed dune. The plant association is relatively complex and closely grazed by sheep and rabbits. The profile was prepared below Calluna

which was locally dominant with Salix repens as a sub-dominant.

The water table reaches to the surface in winter months, but at time of sampling was at a depth of 22 inches below the surface.

The Blakeney Point Dune System, Norfolk

Detailed studies of the topography, vegetation and pedology of the Blakeney Point dune system have been made by Oliver and Salisbury (1913) and Salisbury (1922; 1925).

The dune succession is somewhat incomplete in that a transition to dune heath is absent, but earlier stages in the succession are well represented.

These dunes are mainly acidic and their calcium carbonate content is relatively low even in the young stages of development. (Soil pH range: 5.5 - 7.4; av. calcium carbonate content: 0.3%, Salisbury.)

2 soil profiles were prepared and sampled in each of the following dune zones.

1. Agropyron embryo dunes.
2. Semi-fixed "yellow" Ammophila dunes.
3. Fixed "grey" Carex dunes.

The following vegetation was adjacent to the profile pits:-

"Yellow" dunes	"Grey" dunes
Ammophila arenaria	Carex arenaria
Festuca rubra	Cladonia species
Sedum acre	
Senecio jacobaea	
Brachythecium albicans	

The Tentsmuir Sands, Fife

The Tentsmuir Sands, on the east coast of Scotland just south of the Tay Firth, consist of a series of dune ridges running roughly parallel with the coast and cover an area of about 10 square miles. The region is low-lying, rather poorly drained and relatively sheltered from the prevailing west winds so that sand stabilisation is rapid. Afforestation is extensive and sampling was restricted to the unplanted area at the northern end of the dune system, where a complete sequence from embryonic dunes through to old dune heath occurs over a relatively short distance.

The vegetation has been described by Smith (1905) and Shaw (1935). Ovington (1951) in a study of soil changes affected by afforestation gives detailed information on the pedology of an area of unplanted, fixed Calluna dune in close vicinity to the profile sampled in this investigation (transect A).

The sands are mainly acidic except in the youngest zones of the system.

Samples were taken along two transects A and B approximately 1 mile apart.

Transect A ran through Forestry Commission territory north of Scots craig and transect B was situated in the Nature Conservancy reserve.

A soil profile was prepared and sampled in each of the

following dune zones:-

Transect A. (Soil pH range 7.0 - 4.2)

1. Fore dunes.
2. Semi-fixed - fixed "grey" dunes.
3. Fixed dune heath.

Transect B. (Soil pH range 8.0 - 4.9)

1. Open sand of the foreshore.
2. Fore dunes.
3. Semi-fixed - fixed dunes.
4. Fixed dune heath.

The fore dunes were highly mobile. At A they drop steeply by an eroded face to the open shore and are dominated by Ammophila arenaria with Festuca rubra an occasional associate. At B Elymus arenarius and Agropyron junceiforme are co-dominant and Ammophila only occasional on a more gently sloping ridge.

The "grey" dunes (A) form a low ridge behind the high Ammophila dunes, Ammophila arenaria and Carex arenaria are co-dominant with a rich association of lichens (Cladonia species) and bryophytes (Rhytidiadelphus squarrosus; Dicranum scoparium).

The 3rd zone of semi-fixed - fixed dunes in transect B differs from that in A in the absence of Carex as a dominant and in the richness of the angiosperm flora. Ammophila is dominant and the most prominent members of the rich associate flora include Hieracium pilosella, Luzula campestris, Thymus serpyllum, Cladonia species, Ceratodon purpureus and Brachythecium albicans.

The fixed dune heath zone at A is a somewhat indistinct ridge of Calluna dominated hummocks behind the "grey" dunes and near the forward limit of an old established pine plantation. Ammophila arenaria appears to be a relict member of the plant community. Mats of the bryophytes, Pleurozium schreberi, H. cupressiforme, and Polytrichum juniperinum are extensive.

The heath zone at B is also dominated by low Calluna bushes and has a similar plant community to the latter, but as will be seen profile development is more advanced in this area.

The mobile "yellow" dune ridge rises to a height of about 20 feet and extends 20 - 30 yards inland behind the

Erratum

Page 37. Line 12 to the end of Page 38 is a continuation of the account of the Berrow dune system on Page 28.

~~Ammophila arenaria-locality d.~~

and the frequent associates:

Hypochaeris radicata

Senecio jacobaea

Plant cover is only c. 50%. Rabbit pellets were frequent. Profiles were prepared below Ammophila.

The later semi-fixed zone is characterised by the entry of bryophytes and the plant cover has risen to nearly 100%. Ammophila arenaria is dominant throughout. In transect A,

The fixed dune heath zone at A is a somewhat indistinct ridge of Calluna dominated hummocks behind the "grey" dunes and near the forward limit of an old established pine plantation. Ammophila arenaria appears to be a relict member of the plant community. Mats of the bryophytes, Pleurozium schreberi, H. cupressiforme, and Polytrichum juniperinum are extensive.

The heath zone at B is also dominated by low Calluna bushes and has a similar plant community to the latter, but as will be seen profile development is more advanced in this area.

The mobile "yellow" dune ridge rises to a height of about 20 feet and extends 20 - 30 yards inland behind the fore dunes. The relatively rich flora includes:

Vulpia membranacea d.

Euphorbia paralias co-d.

Ammophila arenaria locally d.

and the frequent associates:

Hypochaeris radicata

Senecio jacobaea

Plant cover is only c. 50%. Rabbit pellets were frequent. Profiles were prepared below Ammophila.

The later semi-fixed zone is characterised by the entry of bryophytes and the plant cover has risen to nearly 100%. Ammophila arenaria is dominant throughout. In transect A,

the profile was prepared below Ammophila arenaria, Arenaria serpyllifolia, Hypochaeris radicata, Tortula ruraliformis and Camptothecium lutescens. In transect B the profile was prepared below an association of Ammophila and Tortula ruraliformis.

The "grey" dune ridge rising to a height of about 30 - 40 feet is characterised by the entry of lichens and Carex arenaria into the plant succession. The vegetation above the sampling pit included Ammophila arenaria (d); Carex arenaria; Festuca rubra (c-d) and Tortula ruraliformis.

Dune grassland occupies a low undulating region behind the high dune ridges described above. The soil profile was prepared below Ammophila arenaria (d) and Carex arenaria (sub-dominant).

Chemical Properties of the Dune Soils Investigated

Soil reaction was measured at all seasons of the year on every sample examined for microfungi. Measurements were made also of the total organic, salt and calcium carbonate contents of the Sandwich and Studland soils.

Soil Reaction

As Pearsall (1952) has pointed out, the pH value of natural soil may be related to four other soil properties: base status, water content, soil metabolism and vegetation. "Because of these correlations and if their existence is appreciated it may safely be said that soil pH remains as the most useful single measurement that can be made for ecological purposes."

Soil pH values were determined electrochemically using a Cambridge bench meter. The samples were saturated in the field with glass distilled water + toluene (to check biological activity) or with saturated potassium chloride solution (see Puri and Ashgar, 1938). Measurements were made, if possible within 24 hours of collection, on a soil-water mixture (soil : water = 1 : 1). Standardisation of the method was considered to be of especial importance if the measurements were to have any comparative and reproducible value.

The range of pH values obtained is given in Table where it is related to soil depth only owing to the

variability and indistinctness of the soil horizons.

The pH values of soils from closely adjacent sites differed as much as those obtained from soils at the same site at different seasons of the year.

Total Organic Content

The total organic content of the soil was estimated as % loss on ignition in a muffle furnace. Corrections were made for loss of hygroscopic moisture and of carbon dioxide from carbonates.

Salinity

Soil salinity was estimated as the % total chlorides by a silver nitrate titration method (Piper 1950). The estimations were made on the extract obtained by shaking 200 gm. samples of air-dry soil with 1 litre distilled water on a mechanical shaker for one hour.

Soil Sample	Soil Depth (ins.)	% Chloride in air-dry soil (maximum values)
SANDWICH		
Open sand	1"	0.38
Fore dunes	1"	0.07
" "	12"	negligible*
Semi-fixed "yellow" dunes	1"	0.03
" " " "	12"	0.01
Fixed "grey" dunes	1"; 12"	negligible
Dune pasture	1"; 12"	negligible
STUDLAND		
Open sand	1"	0.95
Fore dunes	1"	0.01
" "	12"	negligible
"Dune grass"	1"; 12"	negligible
"Dune heath"	1"; 12"	negligible

* < 0.001

Water Sample

STUDLAND	% Chlorides
Temporary lagoon in sandy low	1.43

The values obtained for the soil salt content indicate that the dune ridges are not usually "saline" habitats, as has been found by Salisbury (1952) and Oosting and Billings (1942).

A small number of salinity determinations were made on sand from the lows at Blakeney using the above method and are given here for comparison, although no account can be made of the periodic fluctuations in the salinity.

Salisbury found that salinities as high as 3 - 5% may occur in dune lows and that a salinity up to 1% is not uncommon.

Blakeney (Sept. 1953)

Soil Sample	Soil Depth	% Chlorides/ air dry soil
Glaux Low A	1"	0.01
" " "	6"	0.01
Semi-fixed "Yellow" Dune adjacent to Low A	1"	$\leq$ 0.01
	6"	negligible
Glaux Low B	1"	$\leq$ 0.01
" " "	6"	0.02
[Subterranean water	$>$ 17"	0.71]
Semi-fixed "Yellow" Dune adjacent to Low B	1"	$<$ 0.01
	6"	negligible

Calcium Carbonate Content

Approximate estimates of the calcium carbonate content of the soil were made by comparing the effervescence produced when the soil was treated with dilute hydrochloric acid. The figures for % calcium carbonate content quoted in table 1 were determined by a titration method using HCl and NaOH (Piper, 1950).*

* I am indebted to Dr. D. Parkinson for these $CaCO_3$ determinations.

The following table summarises some of the features of the Sandwich and Studland dune systems with their diversity of sandy habitats to be correlated with a soil microflora.

It can be seen that the soil pH range is wide. The dunes at Sandwich are mostly highly alkaline (pH values $\leq$ 9.9 obtained) in the youngest stages of the succession and when fixed are neutral to slightly acid (pH $\geq$ 6.5) at the surface. The dunes at Studland, on the other hand, even in the youngest zones, although sometimes having a slightly alkaline reaction, are more frequently on the acid side of neutrality and become rapidly more acid with fixation, the lowest pH value recorded being 3.1 at the surface of fixed Pteridium dune heath. The change in soil reaction with dune development is more clear cut on the acid dunes of Studland than on the alkaline dunes of Sandwich; this may be due partly to the difficulty of obtaining accurate values for the reaction of highly calcareous soils. However, in the present study, in which the correlations between soil reaction and biological differences are to be drawn, it is to be remembered that from theoretical considerations changes at the acid end of the soil reaction range are likely to be of the greater significance.

Except in the fore dunes and in the most mobile semi-fixed dunes, the pH value of the soil increased steadily with depth and was about 1 unit higher at a depth of 12 inches

TABLE 1

	DUNE ZONE	STATE OF FIXATION	DOMINANT HIGHER PLANTS	SOIL pH. SOIL DEPTHS 0"-1"	2"-3"	5"-6"	11"-12"	SOIL ORGANIC CONTENT - % Loss on Ignition - SOIL DEPTHS 0"-1"	2"-3"	5"-6"	11"-12"	CALCIUM CARBONATE CONTENT (%) SOIL DEPTH 0"-12"
SANDWICH	OS OPEN SAND	Mobile	-	7.7-9.1				1.3				
	FD FORE DUNES	Mobile	Agropyron junceiforme Ammophila arenaria Festuca rubra v. arenaria	7.4-9.1	7.7-9.7	7.6-8.9	7.5-8.8	0.8	0.7	0.7	0.8	8.5-14.5
	YD "YELLOW DUNES"	Semi-Fixed (Entry of Bryophytes)	Ammophila arenaria	6.8-9.9	7.4-8.5	7.4-8.6	7.4-9.2	1.5	1.2	0.7	0.8	6.0-9.0
	GD "GREY DUNES"	Fixed (Entry of Lichens)	Carex arenaria Festuca rubra v. arenaria Koeleria albescens	6.8-7.6	7.2-8.0	5.6-8.8	7.4-8.3	2.2	0.9	0.8	0.6	0.0-4.0
	DP DUNE PASTURE	Fixed	Festuca rubra v. arenaria Koeleria albescens	6.5-7.7	7.0-7.7	6.9-7.8	7.2-8.4	3.2	2.6	2.0	1.0 (- 4.5)	
STUDLAND	OS OPEN SAND	Mobile	-	6.4-7.3				0.2				
	FD FORE DUNES	Mobile	Ammophila arenaria	6.6-7.0	6.8-7.2	6.1-7.5	6.2-7.5	0.2	0.2	0.2	0.2	0.0-2.5
	DG "DUNE GRASS"	Semi-fixed (Entry of Bryophytes & Lichens)	Ammophila arenaria Carex arenaria	4.3-5.3	4.6-5.8	4.7-5.8	5.4-6.6	0.7	0.2	0.3	0.2	
	DH DUNE HEATH	Semi-fixed-Fixed	Ammophila arenaria Carex arenaria Calluna vulgaris	3.7-4.3	3.4-4.2	4.0-4.6	3.8-4.9	2.0	A_2 0.3 B_1 9.2	0.7	0.3	0.0
	SH "SOUTHERN HEATH"	Fixed	Calluna vulgaris	3.5-4.2	3.2-4.0	3.5-4.7	4.1-4.6	11.9	2.3	0.8	0.3	
	Bh PTERIDIUM-HEATH	Fixed	Pteridium aquilinum	3.1-4.0	3.2-4.3	3.7-4.6	4.0-5.0	2.2	0.5	0.2	0.2	

than at the surface. In general the lowest values were recorded from surface humus-rich horizons, but sometimes the soft humus pans of soils showing early stages of podsolisation were slightly more acid than the surface horizons.

The organic content of the soil of the young dunes is very low especially at Studland (fore dunes 0.2%), but there is a definite increase with dune development, the maximum value recorded at Sandwich being 3.2% at the surface of fixed dune pasture and 11.9% in the surface peaty horizon of dune heath at Studland. The low value of 2.2% for the surface of Pteridium heath dune is correlated with the pockets of wind blown sand that occur in this zone. In the absence of sub-surface humus-rich horizons or pans the organic content of the soil usually dropped sharply below the A_1 horizon to values approximating to those of the open shore and fore dune sands.

3. Methods Used to Investigate the Distribution of Microfungi in Dune Soils

The following methods were selected for the investigation of the distribution of fungi in dune soils:-

1. Cultural Methods
   - (i) The soil plate technique (Warcup 1950) for mass isolations.
   - (ii) The water and hemp seed baiting technique (Butler 1907), for the selective isolation of Phycomycetes (p.64).
2. "Traps"
   - (i) Slide-traps (Sewell 1954; 1956)
   - (ii) Contact slides (Rossi-Cholodry, 1930)
3. Direct Soil Examination
   - (i) Soil crushes
   - (ii) A new modification of the soil impression technique (Section II.d.)

A number of methods were used together in order to counter their selectivity. Some of their merits and limitations and the procedure adopted in their application to dune soils are described in this section.

The Soil Plate Technique

Preliminary direct microscopic examination of the sand showed that living fungal mycelium was present in even the youngest dunes. This observation could give little information on the nature of the indigenous fungus flora, but it did vitiate the argument that this was a study of fungal spores alone which were contaminating the dunes, and it warranted further investigations.

The first aim was to obtain a general picture of the entire microfungal component of the soil, whatever its morphological or physiological state. The Warcup (1950; 1955[b]) soil plate technique was employed for this purpose. The following considerations led to the choice of this method.

By the soil plate technique, in which the soil is distributed throughout a thin layer of the culture medium, the whole soil sample is retained and the floristic lists of mycologists who have used this method indicate that it is, in general, less selective than the classic methods of direct inoculation (Waksman, 1916) and dilution (Waksman, 1917). McLennan and Ducker (1954) concluded that there was no advantage to be gained by its use. They found soil plates unsatisfactory because they were quickly overrun by numerous fungal colonies. This criticism could be applied also to the dilution technique and the defect was overcome

to a large extent in this investigation by reducing the size of the soil inoculum and by excising young colonies from the culture plates. Soil plates share with dilution plates the disadvantage that they do not reveal directly whether the fungal colonies have developed from spores or from mycelium and they, therefore, tend to exaggerate the importance of heavily sporing fungi. Unlike dilution plates (Brierley, Jewson and Brierley, 1928), however, they are quick and simple to prepare and easily standardised.

As Garrett (1951) points out, Warcup's technique "as a non-selective method for general isolation of soil fungi.... probably represents the best compromise so far evolved."

Field Sampling Procedure

Sand samples were collected at approximately monthly intervals from November 1952 - January 1955. On each sampling date a pit (approx. 24" square and 18" deep) was prepared towards the centre of each ecological zone under investigation. The pits were dug along a single line transect stretching inland from the open beach across the dune system. Successive monthly transects were distributed randomly over the sampling areas.

A vertical profile was prepared on one side of each pit and some of the exposed soil removed with a sterile scalpel to prevent contamination of one soil horizon by another. In the youngest and most mobile fore dunes it was sometimes

difficult to prepare a profile without contaminating sand. This difficulty was overcome to some extent by inserting sterile glass plates horizontally at various depths to support the sand and to protect exposed surfaces from falling sand grains. The likelihood of there being a biological profile closely related to depth in the upper regions of these continually shifting dunes was considered to be too slight to warrant more elaborate precautions to prevent contamination.

As soil horizons varied considerably in distinctness and position if present at all, certain soil depths rather than horizons were sampled each time. Sampling depths of ½", 1", 3" 6" and 12" were chosen after preliminary samplings had shown that differentiation of the profile usually occurred only in the top few inches and that the sand was generally sterile as regards fungi below a depth of about 12" or less. Extra samples were taken if these arbitrary depths did not coincide with any marked features of the profile. Only surface soil was sampled in the foreshore zone owing to the mobility of the habitat and sporadic occurrence of fungi.

One sample at each depth was taken in a sterile 2½" x ½" glass tube plugged with cotton wool. The mouth of the tube was flamed just before it was inserted horizontally into the sand for the withdrawal of the sample.

Preparation and Examination of Soil Plates

Soil plates were prepared in an inoculating room within 24 hours from the time of field sampling. The general procedure described by Warcup (1950) was followed. A tool found more suitable than a flattened needle for the transference of soils of this loose sandy type was a metal spatula with a small depression at one end which could be filled with the soil to the same level each time. The minimum number of plates prepared from any one sample with a given culture medium was 3, i.e. not less than 15 plates were prepared for each soil profile examined. Each soil plate contained approximately 0.002 - 0.005g of soil and 8 - 10 mls of agar medium.

2 isolation media were used:

1. Czapek-Dox agar (with the substitution of glucose for sucrose, Hawker, 1950) + 0.5% yeast extract + rose bengal (1 : 15,000 medium) + phosphoric acid or sodium hydroxide for adjustment of the pH to that of the soil in the respective dune zones.
2. A weak soil extract agar, with the addition of glucose, 5g/L, sodium nitrate 0.5 g/L, potassium phosphate (K_2HPO_4) 0.5g/L and rose bengal (1 : 15,000 medium).

The pH of the medium was not adjusted.

Separate soil extracts (soil : water = 1 : 3) were prepared for each dune zone with soil from the sampling sites.

All media contained 2.5% agar, so that they were relatively stiff, which facilitated excision of colonies.

Preliminary experiments had shown that growth of bacteria and actinomycetes on soil plates prepared from calcareous sands was heavy and seriously impeded fungal growth and its isolation. The use of acid media for the inhibition of bacteria and actinomycetes irrespective of the soil reaction, as by Warcup (1951) and Stenton (1953), is inadvisable since some fungi are particularly sensitive to hydrogen-ion concentration. For this reason the bacteriostatic dye, rose bengal, was incorporated into the media (Smith and Dawson, 1944; Dawson and Dawson, 1946). Parallel experiments were run to compare fungal growth on media with and without rose bengal. The numbers of fungal species and colonies were not noticeably reduced by the dye, but the growth of certain spreading fungi, in particular Absidia glauca, A. spinosa and Mucor hiemalis was restricted which was an added advantage.

Five parallel sets of soil plates were prepared with the soil extract and Czapek-Dox agar media.

It was found that "common" species occurred on both culture media, but the following figures show that in general more species were isolated by the use of Czapek-Dox agar than by soil extract agar.

Total Number of Species Isolated in 5 Monthly Samplings
(75 plates/dune zone/culture medium)

	Soil Extract Agar (S)	Czapek-Dox Agar (C)	Ratio C/S
SANDWICH			
Open Sand	4	13	3.3
Fore Dunes	14	9	1.4
Semi-fixed "Yellow" Dunes	28	35	1.3
Fixed "Grey" Dunes	25	32	1.3
Dune Pasture	25	36	1.4
STUDLAND			
Open Sand	0	5	-
Fore Dunes	30	23	0.8
Semi-fixed "Dune Grass"	36	40	1.1
Dune Heath	36	42	1.2
"Southern Heath"	30	37	1.2
Pteridium Dune Heath	29	32	1.1

All the species isolated by one medium only were "casuals", but it is noteworthy that over 60% of the Ascomycetes were recorded on the Czapek-Dox agar. Sporulation sometimes occurred more readily on soil-extract agar, but colony characteristics were usually less clearly defined so that more isolations had to be made for identification purposes. Moreover the less discrete nature of the colonies with their thin spreading type of mycelial growth on the soil medium frequently made isolation difficult. The Czapek-Dox agar was therefore considered to be the most suitable medium and was used in all routine isolations by the soil plate method.

The plates were kept at room temperature for one month. After the first 2 - 4 days fast-growing fungi such as

Trichoderma and Mucor were subcultured for identification purposes and then excised or, if they were particularly abundant, the slower growing species in their path were subcultured. The plates were then left undisturbed for 3 - 4 weeks to allow the development of slow growers and to reduce the risk of aerial contamination. In the final examination the plates were scanned with a wide field binocular microscope (x 24). All known species on each plate were recorded and colonies of unknown identity were subcultured on to potato dextrose agar for further study. Approximately 2,700 fungal colonies were subcultured during the examination of soil plates. All species of Mortierella, Mucor and Penicillium had to be subcultured so that they could be compared under more uniform conditions. Identification of Mortierella species was facilitated by floating them on tap water which often favoured sporulation (Warcup, 1951).

In all experiments control plates without soil inocula were prepared and species believed to be laboratory contaminants were excluded from the floristic lists of dune fungi. Penicillium cyclopium and Cladosporium herbarum were among the supposed aerial contaminants, but their occurrence and distribution on soil plates strongly suggested that they were often present in the soil. Warcup (1951) and Jefferys et al (1953) have held this view with regard to Cladosporium and it is supported by the fact that in the

present investigation the above species were found to have grown from the soil into slide traps.

Warcup's (1951) steaming method for the selective isolation of Ascomycetes was applied to a small number of soil (and Ammophila root) samples, but steam treatment did not appear to increase the ascigerous component of the plate populations.

Terms used in Recording the Isolation Data

The ecological techniques of soil mycology do not permit the use of such terms as "dominant" in the analysis of a species population. At present, the life form of a soil microfungus is, in general, known on the culture plate alone, and, as direct examination of the soil sometimes indicates, the fungal "trees" and "shrubs" of laboratory media are not necessarily those of the soil. Furthermore a satisfactory quantitative estimate of the soil fungal population cannot be made from counts of colonies developing in culture, if these reflect sporing capacity. Several workers, including Oudemans and Koning as early as 1902, have pointed out that such quantitative determinations are of little value, a fact ignored by an army of mycologists in the last half century.

In the present investigation of fungal populations, it is not the biotic status nor the abundance, but the dispersion or distribution of species within the community that has been determined. "Frequency" of occurrence is used in the

analysis of constancy and it was determined by recording the presence and absence of species in samples taken repeatedly at intervals. Thus, a high frequency or constant species is considered to be widespread, but not necessarily dominant in a particular habitat.

In the determination of the % frequency of occurrence of species in the Sandwich and Studland dune systems, a fungus was given a positive record if it occurred on one or more of 3 replicate culture plates. In recording the data from other dune systems, where only one or two soil profiles were examined, only subjective estimates of frequency are given.

The Slide Trap Technique

The soil plate method, although it provides valuable information on the fungal complement of the soil as a whole, concerning the activity state of the several species leaves much to guess work. Fungal traps (immersion tubes: Chesters 1940, 1948, Nicot and Chevaugeon, 1949; immersion plates, R. Thornton, 1952; slide traps: La Touche 1949; Sewell 1954) isolate, it is hoped, only those fungi existing as active mycelium in the soil. It must be borne in mind that the immersion in the soil of any form of fungal trap introduces artificial conditions (Chesters, 1948), but it would be difficult, if not impossible, to devise any isolation method that did not do so to some extent.

The Sewell slide trap, which consists of a Perspex chamber filled with a thin layer of agar and covered by a glass microscope slide, was used to investigate the dune mycoflora because it is simple to construct and use and undesirable factors such as competition, anaerobism and contamination of the agar surface are less evident than in the earlier techniques. Claims that the range of species isolated by this slide trap is greater than or compares favourably with those obtained by other trap methods have been substantiated by the results of the present investigation, in which the trap has been used in a wider range of soil types than hitherto.

Procedure

The procedure adopted by Sewell (1954) in the construction, preparation and immersion of the slide traps was followed closely, but for the purpose of comparison with the soil plate experiments, the modified Czapek-Dox agar, with its pH adjusted to approximate to that of the soil under investigation, was employed instead of tap water agar.

Tap water agar was used in a supplementary experiment to determine whether the medium had any marked effect on the number and types of fungi isolated by slide traps. Rather more fungi were isolated by the use of Czapek-Dox traps than by the use of tap-water agar traps. Mucor hiemalis appeared to be favoured by Czapek-Dox agar (cf. Sewell 1954). The general composition of the isolated population on the two media was, however, similar and the colonies were more discrete on the nutrient medium. Tap water agar, therefore, seemed to have no advantage over Czapek-Dox agar for the present study.

The incubation period in the soil varied from 4 days in the summer to 3 weeks in the winter. Extra traps were incubated in sand both near the laboratory and on the dunes in order to follow the progress of infection, but the most suitable incubation period was best judged by attention to weather conditions and experience.

Control traps, which were not immersed in soil, all remained sterile.

The trap technique was restricted to 3 dune zones in each dune system: fore dunes, semi-fixed dunes and fixed dunes and to 2 soil depths in each zone: surface soil (0-2") and subsurface soil (5-6"). Not less than 10 traps were immersed in a given soil type at any one depth and time. Traps which had been invaded by nematodes, as sometimes occurred in calcareous sand, were ignored to avoid the risk of isolating contaminants. Two hundred and ninety traps were successfully incubated at different seasons of the year over the period November 1954 - August 1955.

The traps were examined under a wide-field binocular microscope and each group of hyphae, which could be seen to have grown into the trap between the glass and the Perspex, was marked and isolated for identification on potato dextrose agar.

Estimates of % frequency i.e. the % number of traps colonised by a certain species were found to be of little comparative value since they took no account of the fact that a single trap might be invaded at a number of points along its perimeter, each colony, unlike those on soil plates, representing an activity centre in the soil. Counts of the total number of colonies in each set of traps were therefore made and expressed as a relative % frequency.

The relative % frequency of species x =

$$\frac{\text{The total no. of colonies of species x}}{\text{The total no. of colonies of all species.}} \times 100$$

The Rossi-Cholodny Contact Slide Technique

The simple Rossi-Cholodny (1930) technique of burying a clean glass slide in the soil and examining the fungi *in situ*, which have grown over and adhered to the glass surface, was used as a supplementary method of studying the dune flora. Local soil conditions, such as aeration and moisture, must be affected when these slides are introduced into the soil, but considering the variety of natural surfaces to be found in any soil, the glass surface is perhaps not such an artificial microhabitat as it appears. Several aspects of the soil mycoflora can be studied by the use of contact slides. Identification of the mycelium is often impossible, but some species which sporulate freely over the slides are easily recognised, so that the presence of species isolated by other methods can be confirmed. The existence in the soil of species which never appear in culture media is also often demonstrated and the distribution of active mycelium whatever its identity can be followed. Further, the relationship between the fungi and their substrates or other organisms can often be seen and the morphological characters assumed by fungi growing on contact slides are likely to approximate more closely to their natural soil forms than do those of cultural growths.

Procedure

The slides were handled in the field according to the

procedure described by Cholodny (1930). Ten slides were buried, so that their long edges lay parallel to the surface, at three depths (0-1"; 5-6"; 11-12") in each dune zone on any one date. Each set of slides was buried in 2 groups of 5. The slides were incubated in the soil during September - November 1954 and February - March 1955 for a period of 1 - 3 weeks.

The preparations were dried in air, then fixed by heating, washed under a jet of water to remove coarse soil particles, stained for one hour in phenolic aniline blue (Jones and Mollison 1948) and mounted in lactophenol. 200 contact slides were successfully prepared in this way.

Direct Soil Examination

There have been several attempts to study soil micro-organisms in their natural environment by direct and instantaneous examination of the soil, without the use of selective media. Use has been made of wet and dry soil preparations (Conn 1916, 1918, 1922), "soil chambers" (Cholodny 1934, 1936), refined optical equipment for micro-dissection of the soil *in situ* (Kubiena 1932, 1938) and soil slicing techniques (Kubiena 1938; Alexander and Jackson 1952; Haarløv and Weis-Fogh, 1952; Hepple and Burges, 1956).

All these direct methods of investigation provide restricted information and the more elaborate are unsuitable for routine soil examinations. Undue disturbance of the soil is often a major defect or, if the natural spatial arrangements of soil and organisms are maintained, the three dimensional pattern of the mycelium is difficult to decipher.

Direct examination of dune soil organisms was made, therefore, using only the simple soil crush and soil impression techniques (Rossi et al, 1936).

Soil crushes were prepared by crushing small quantities of soil between two glass slides and staining them with cotton blue in lactophenol. The method was of use in the preliminary survey for the quick location of fungi.

The more refined soil impression technique, which,

unlike Rossi-Cholodny slides, indicates the status quo of the mycelial component of the soil, was adapted for quantitative purposes and is described in a later section.

4. Experimental Analysis

Section I. The Range of Taxonomic Groups and Species Isolated from Dune Soils.

Fungi Imperfecti

Over 80% of the species isolated were Fungi Imperfecti. Many of them figure frequently in lists of soil fungi isolated from other habitats and they include well-known saprophytes and some plant parasites (e.g. *Fusarium* spp; *Myrothecium roridum*). A number of rare species were also isolated, but some of these may, with further mass isolations of soil fungi and improvements in the isolation techniques, be found to be more widespread.

Penicillium, *Cephalosporium* and *Coniothyrium* were the commonest genera of imperfect fungi both as regards frequency and number of species.

Ascomycetes

Twenty-four species of Ascomycetes were isolated. From a survey of the literature on soil fungi, this number appears to be relatively high for one habitat; the individual species were mostly, however, of sporadic occurrence. Their frequency in dune soils may be associated with the presence of rabbit dung, for many Ascomycetes are known to be coprophilous. *Gelasinospora retispora*, *Sordaria destruens* and *Sporormia intermedia* occurred on both soil plates and dung

plates prepared from surface sterilized rabbit pellets.

Phycomycetes

The Phycomycetes were represented by several Zygomycetes, Mortierella was the commonest throughout the range of dune soil types and Absidia was also frequent, but of more local distribution. No Oomycetes were isolated, although the selective water and hemp seed baiting technique for the isolation of water moulds (Butler 1907) was applied in August and again in October. Saproleginales have, however, been isolated from a number of soil types (Ivimey, Cook and Morgan, 1934). Their absence from the dune flora may be associated with the dryness of the habitat, but the dune habitat, except at the surface of the dunes, is not generally very dry as is often supposed.

Basidiomycetes

None of the mycelia isolated on soil plates or in slide traps from dune soils were known to be those of basidiomycetes, although the fruit bodies of agarics and gasteromycetes were frequent within the dune sampling areas. Mycelia bearing clamp connections were, however, seen occasionally on soil impressions and contact slides.

No satisfactory explanation has yet been given for the infrequent isolation of basidiomycetes from soils of all types. Some species have been shown to form definite mycelial zones in the soil (Warcup 1951[c]; Stenton 1953)

and others are known to inhabit the litter zone and plant debris rather than mineral soil layers. The apparent absence of basidiomycetes in samples of dune soil, although taken in close proximity to sporophores, may be due to such a localisation of the vegetative mycelium, if not to experimental technique. Warcup (1955[a+b]) found that many hyphae on a soil plate failed to grow in the agar medium and that several basidiomycetes absent from dilution plates could be isolated by a direct hyphal isolation method. This suggests that the environment of the culture plate is uncongenial for these fungi which are known to be often nutritionally exacting and slow-growing and it would explain their demonstration in this investigation by direct non-cultural methods only. Competition on the plates prepared from sand of the young dunes, where sporophores of Psilocybe ammophila were particularly abundant, was very slight, so that some direct nutritional factor is more likely to have been a check to growth.

Sterile Mycelia

As with several other soil types, a number of light and dark coloured mycelia which remained sterile in culture were isolated. The majority were septate and formed numerous chlamydospores. All were of sporadic occurrence and few were recorded more than once.

Actinomycetes and Bacteria

No attempt was made to study the associate flora of actinomycetes and bacteria, and for practical reasons culture media were used which inhibited the growth of these organisms. It was noted that they were more frequent in alkaline dunes than in acid dunes and that the population was most dense in the fixed dune pasture. One actinomycete was commonly associated with Mucor ramannianus and Penicillium restrictum in the subsoil of acid dune heath at Studland, but actinomycetes and bacteria were otherwise rare in these most acid sands. Bacteria were often aggregated around living and dead fungal hyphae on Rossi-Cholodny slides and a few fungi, Coniothyrium S10, for example, were characteristically associated with bacteria when growing on soil plates.

Section II. The Distribution of Microfungi in the Dune Soils

(a) The general distribution of species and the demonstration of an "acid" and "alkaline" dune mycoflora.

Soil Plates

Ninety-five species of fungi including sterile mycelial forms were isolated on soil plates from the Sandwich dunes and ninety-nine from the Studland dunes. Only 28% of these species were common to both dune systems. The number of individual species encountered was therefore relatively high as was to be expected in a macro-habitat of so many facets, and where, except in the oldest seres, the soil is continually being opened up to the opportunist fungus. In table 2 the numbers of species which occurred in each % frequency class are recorded. This illustrates a frequency pattern in which there is a preponderance of species in the lowest of frequency class ($< 20\%$) and a relatively small number in the intermediate and high % frequency classes.

Species of apparently very local distribution form a considerable proportion of the total number; of these many were observed only once, and probably include both the contaminant with no, or a very restricted, active stage in the soil, and the "casual" active in the soil but of low ecological status in the fungal community; others appeared in "flushes" where local conditions had perhaps favoured the competitive advance of a species. The apparent absence of

TABLE 2

The total number of species in each % frequency of occurrence class.

	% Frequency of Occurrence				
STUDLAND	0-20	21-40	41-60	61-80	81-100
Open Sand	12	0	0	0	0
Fore Dunes	28	4	1	1	0
Semi-fixed "Dune Grass"	36	9	2	0	1
Semi-fixed-Fixed Dune Heath	37	8	3	4	1
Old Fixed Dune "Southern Heath"	29	7	5	3	0
Old Fixed Dune Pteridium Heath	23	7	4	4	0
SANDWICH					
Open Sand	12	1	0	0	0
Fore Dunes	32	3	2	1	0
Semi-fixed "Yellow" Dunes	38	6	6	1	2
Fixed "Grey" Dunes	29	6	5	4	1
Dune Pasture	35	2	6	1	3

certain species with a low frequency of occurrence from other dune systems may be entirely fortuitous and more extensive sampling or more favourable experimental conditions might have altered the general distribution picture somewhat. It cannot be hoped, as yet, that all the fungal species present in a given soil sample will develop on a culture medium; as will be shown, mycelium can be seen in dune soils where cultural treatment has failed to reveal its presence. The ecological status of the apparently infrequent fungus may not be as low as it appears to be, for as an associate of the more widespread species it may have some important biotic influence on the structure of the population. Moreover the infrequent fungus of the young dunes may be of interest when its possible pioneer as opposed to contaminant nature and its increase or decrease with closure of the community is considered.

In spite of the large number of infrequent species encountered in these dune sands, various fungal associations were clearly distinguishable and typified by their small number of characteristic or constantly occurring species.

The results of the mass isolations of microfungi by the soil plate technique are recorded in tables 3 - 13. The data obtained from 10 profiles in each dune zone in ten different months of the year - (November 1952 - January 1955) have been condensed; this was considered permissible because

the soil plate populations did not appear to vary with season. The occurrence records do not indicate how abundant a species was throughout a single profile or on individual soil plates.

Tables 3 - 13

The % Frequency of Occurrence of Microfungi at Various Soil Depths in the Successive Zones of the Sandwich and Studland Dune Systems as Determined by the Soil Plate Isolation Technique.

TABLE 3

OPEN FORESHORE SAND - STUDLAND

% Frequency of Occurrence at a depth of 1 inch in 10 profiles

Asteromyces cruciatus	10
Botrytis cinerea	10
Gliomastix convoluta v. *felina*	10
Papularia sphaerosperma	10
Penicillium nigricans	10
Penicillium sp. (D1078)	10
Pyrenochaeta sp. (D40)*	10
Tilachlidium sp. (S546)*	10
Verticillium nigrescens (?)	20
1 sterile hyaline mycelium	10
2 sterile dark-coloured mycelia	10 ea.

Footnote:

* The type culture number (S/C) is given if the identification of a species has not been completed or if it is doubtful.

TABLE 4

FORE DUNE - STUDLAND

% Frequency of Occurrence in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.6 - 7.0		6.8-7.2	6.1-7.5	6.2-7.5
S/C No.	Species					
	Chaetomium cochliodes	-	-	10	-	-
	Sporormia intermedia	-	-	10	-	-
D1132	Unidentified Ascomycete	-	-	-	10	-
	Botrytis cinerea	-	-	10	10	-
	Cephalosporium acremonium	-	10	-	-	-
S1325	Cephalasporium sp.	10	-	-	-	-
	Cladosporium herbarum	10	-	10	20	10
D20	Coniothyrium sp.	-	-	10	10	-
D402	Helminthosporium sp.	-	-	-	-	10
	Papularia arundinis	-	-	10	-	-
	Papularia sphaerosperma	-	10	-	-	-
	Penicillium adametzi	-	-	-	10	-
	P brevi-compactum (?)	-	10	-	-	-
	P. cyclopium	10	10	-	10	-
	P. decumbens	-	10	-	-	-
	P. nigricans	20	50	20	10	-
	P. piceum	10	-	-	-	-
	P. thomii	10	-	-	-	-
	Penicillium digitatum	-	-	10	-	-
D273	P. terlikowskii (?)	-	-	10	-	-
D1501	Piricularia sp.	-	-	-	10	10
D40	Pyrenochaeta sp.	-	30	10	20	20
D73	Stemphylium sp.	-	20	-	-	-
S546	Tilachlidium sp.	-	20	-	-	-
	Trichoderma viride	-	20	10	10	-
	Trichosporium cerealis	-	-	-	10	-
	4 sterile dark coloured mycelia	-	-			
	4 sterile hyaline mycelia	-	-			

TABLE 5

SEMI-FIXED 'DUNE GRASS' - STUDLAND

% Frequency of Occurrence of Fungi in 10 Soil Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	4.3 - 5.3		4.6-5.8	4.7-5.8	5.4-6.6
S/C No.	Species					
	Mortierella alpina	-	-	-	-	10
	Mortierella isabellina	10	-	-	-	-
	M. parvispora	10	20	-	-	-
	Mucor hiemalis	10	10	-	-	-
	M. ramannianus	20	-	10	-	-
	Chaetomium cochliades	-	10	-	-	-
	Gelasinospora cerealis	10	-	10	-	-
D128	Unidentified Ascomycete	10	-	-	-	-
D1038	Cephalosporium sp.	-	-	10	10	10
	Cladosporium herbarum	20	-	10	10	-
D20	Coniothyrium sp.	10	10	-	10	10
	Fusarium oxysporum	10	-	-	-	-
	Gliomastix convoluta v. felina	-	-	10	20	10
	Papularia arundinis	20	10	-	-	-
	Papularia sphaerosperma	10	-	-	-	-
	Penicillium cyclopium	-	-	-	10	-
	P. decumbens	10	-	-	-	-
	P. lapidosum	-	-	-	-	10
	P. lividum	-	10	10	-	-
	P. melinii	20	10	-	10	-
	P. namyslowskii	20	-	-	-	-
	P. nigricans	80	70	60	60	30
	P. paxilli	-	-	-	10	-
	P. restrictum	-	10	10	-	-
	P. spinulosum	-	10	10	10	-
	P. viridicatum	10	-	-	-	-
D273	Penicillium terlikowskii(?)	20	-	-	-	-
D 381	Penicillium sp.	-	-	-	10	-
	P. simplicissimum	-	-	-	-	10

TABLE 5

SEMI-FIXED 'DUNE GRASS' - STUDLAND

% Frequency of Occurrence of Fungi in 10 Soil Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	4.3 - 5.3	4.6-5.8	4.7-5.8	5.4-6.6	
S/C No.	Species					
	Mortierella alpina	-	-	-	-	10
	Mortierella isabellina	10	-	-	-	-
	M. parvispora	10	20	-	-	-
	Mucor hiemalis	10	10	-	-	-
	M. ramannianus	20	-	10	-	-
	Chaetomium cochliades	-	10	-	-	-
	Gelasinospora cerealis	10	-	10	-	-
D128	Unidentified Ascomycete	10	-	-	-	-
D1038	Cephalosporium sp.	-	-	10	10	10
	Cladosporium herbarum	20	-	10	10	-
D20	Coniothyrium sp.	10	10	-	10	10
	Fusarium oxysporum	10	-	-	-	-
	Gliomastix convoluta v. felina	-	-	10	20	10
	Papularia arundinis	20	10	-	-	-
	Papularia sphaerosperma	10	-	-	-	-
	Penicillium cyclopium	-	-	-	10	-
	P. decumbens	10	-	-	-	-
	P. lapidosum	-	-	-	-	10
	P. lividum	-	10	10	-	-
	P. melinii	20	10	-	10	-
	P. namyslowskii	20	-	-	-	-
	P. nigricans	80	70	60	60	30
	P. paxilli	-	-	-	10	-
	P. restrictum	-	10	10	-	-
	P. spinulosum	-	10	10	10	-
	P. viridicatum	10	-	-	-	-
D273	Penicillium terlikowskii(?)	20	-	-	-	-
D 381	Penicillium sp.	-	-	-	10	-
	P. simplicissimum	-	-	-	-	10
D1152	Phialophora sp.	-	-	-	10	-
	Pullularia pullulans	-	10	10	-	-
D40	Pyrenochaeta sp.	10	10	-	-	-
	Septonema chaetospira	-	-	-	10	-
S546	Tilachlidium sp.	10	-	-	-	-
	Trichoderma viride	20	10	-	10	10
D1038	?	-	-	-	10	-
	[6 sterile hyaline mycelia]					
	[6 sterile dark coloured mycelia]					

TABLE 6

SEMI-FIXED - FIXED DUNE HEATH, STUDLAND

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	3.7 - 4.3		3.4-4.2	4.0-4.6	3.8-4.9
S/C No.	Species					
	Absidia spinosa	10	10	10	10	10
	Haplosporangium decipiens	-	10	-	-	-
	Mortierella isabellina	10	10	10	-	-
	M. marburgensis	10	10	10	-	-
	Mucor hiemalis	20	-	-	-	-
	Mucor ramannianus	10	-	10	20	30
	Zygorrhynchus vuilleminii	-	-	-	-	20
	Gelasinospora cerealis	-	10	-	-	-
	G. retispora	-	10	-	-	-
	Sporormia intermedia	10	-	-	-	-
D128	?	-	10	-	-	-
D1236	Aspergillus sp.	-	-	-	10	10
	Beauveria bassiana	-	-	10	-	-
	Botrytis cinerea	-	-	-	-	10
D1038	Cephalosporium sp.	-	-	-	10	-
D1391	" "	-	10	-	-	-
D1732	" "	-	-	10	-	-
	Cladosporium herbarum	20	-	-	-	10
D20	Coniothyrium sp.	-	-	10	-	-
D1793	" "	-	-	-	-	10
	Fusarium culmorum	10	-	-	-	-
	Gliomastix convoluta v. felina	-	10	20	20	10
D127	Monotospora sp.	-	10	-	-	-
	Papularia arundinis	10	-	-	10	-
	Penicillium adametzi	20	30	40	40	20
	P. brevi-compactum	-	20	20	-	10
	P. cyclopium	20	10	10	10	10
	P. decumbens	10	-	-	-	-
	P. lapidosum	20	-	-	-	-

continued

Table 6 - contd.

Semi Fixed - Fixed Dune Heath, Studland

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	3.7 - 4.3		3.4-4.2	4.0-4.6	3.8-4.9
S/C No.	Species					
	Penicillium melinii	60	60	40	40	20
	P. namyslowskii	40	-	-	10	10
	P. nigricans	60	30	30	20	20
	P. paxilli	-	-	-	-	20
D461	P. raistrickii series	10	-	-	-	-
	P. restrictum	10	10	40	50	50
	P. spinulosum	20	50	20	40	30
	P. thomii	10	-	-	-	-
D1030	Penicillium sp.	10	-	-	-	-
	P. martensii	10	-	-	-	-
D919	Penicillium sp.	10	-	-	-	-
D1051	Piricularia sp.	-	10	10	-	-
	Pullularia pullulans	10	-	-	-	-
D509	Sarcinella sp.	-	10	-	-	-
	Trichoderma viride	90	80	60	40	10
	Trichosporium cerealis	-	-	-	-	10
	Verticillium nigrescens (?)	-	10	-	-	10
	3 sterile hyaline mycelia					
	4 sterile dark coloured mycelia					

TABLE 7

FIXED DUNE - "SOUTHERN HEATH" - STUDLAND

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	3.5 - 4.2		3.2-4.0	3.5-4.7	4.1-4.6
S/C No.	Species					
	Absidia orchidis	20	-	-	-	-
	Absidia spinosa	20	10	-	-	-
	Mortierella isabellina	10	20	20	10	10
	M. marburgensis	10	-	-	-	-
	M. parvispora	-	-	-	-	10
	Mucor ramannianus	-	10	10	20	50
D1019	Piptocephalis sp.	-	-	-	-	10
D274	Syncephalastrum sp.	10	-	-	-	-
	Gelasinospora cerealis	10	10	-	-	-
	G. retispora	-	10	-	-	-
	Beauveria bassiana	-	-	-	10	-
	Cladosporium herbarum	20	20	-	-	-
	C. macrocarpum	-	-	-	10	-
D20	Coniothyrium sp.	-	10	-	-	-
	Gliomastix convoluta v. felina	10	-	-	-	-
	Papularia arundinis	-	-	10	-	-
	Penicillium adametzi	10	40	30	40	30
	P. cyclopium	-	10	-	10	20
D1050	P. cyclopium series	10	-	-	-	-
	P. decumbens	10	-	-	-	10
	P. lapidosum	10	-	-	-	-
	P. lividum	-	-	10	10	10
	P. melinii	30	30	20	10	10
	P. namyslowskii	10	20	20	-	-
	P. nigricans	30	40	10	30	30
	P. paxilli	10	-	10	10	-
	P. restrictum	-	10	40	50	30
	P. spinulosum	30	30	-	10	-
	P. thomii	20	20	10	-	-
D28	P. thomii series	-	10	-	-	-
D273	Penicillium terlikowskii (?)	20	10	10	-	-
D919	Penicillium sp.	-	10	-	-	-
D990	" "	-	10	-	-	-
	P. simplicissimum	10	-	-	-	-
	P. martensii	-	-	-	10	10
D357	Sarcinella sp.	-	10	-	-	-
	Trichoderma viride	90	80	20	10	-
	Verticillium nigrescens (?)	10	10	10	-	-
	4 sterile hyaline mycelia					
	2 sterile dark coloured mycelia					

TABLE 8

FIXED DUNE, PTERIDIUM-HEATH - STUDLAND

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	3.1 - 4.0		3.2-4.3	3.7-4.6	4.0-5.0
S/C No.	Species					
	Haplosporangium decipiens	-	-	10	-	-
	Mortierella isabellina	20	-	10	20	10
	M. parvispora	20	10	10	10	-
	Mucor ramannianus	30	20	30	60	40
D1091	Piptocephalis sp.	10	-	-	-	-
	Rhizopus nigricans	-	10	-	-	-
	Gelasinospora cerealis	-	-	10	-	-
	Botrytis cinerea	-	-	-	10	10
	Cladosporium herbarum	10	-	10	-	10
	Papularia arundinis	-	10	-	-	-
	Penicillium ademetzi	40	20	60	20	-
	P. brevi-compactum (?)	10	-	-	-	10
	P. cyclopium	20	20	10	20	20
D1605	P. cyclopium series	-	-	-	10	-
	P. decumbens	30	10	10	-	-
	P. lividum	10	20	-	20	-
	P. melinii	20	30	-	-	-
	P. namyslowslii	30	30	-	-	-
	P. nigricans	30	30	-	20	40
	P. paxilli	20	10	-	-	-
	P. restrictum	-	-	-	10	-
	P. spinulosum	50	50	50	20	20
D28	P. thomii series	30	-	-	-	-
D273	Penicillium terlikowskii (?)	30	10	-	-	-
D476	" sp	20	10	20	10	-
D990	" "	10	-	10	-	-
D1701	" "	10	-	-	10	-
D20	Pestalotia sp.	-	10	-	-	-
D105	" sp.	-	10	-	-	-
	Pullularia pullulans	10	10	10	20	-
D1077	Sarcinella sp.	-	10	-	-	-
	Trichoderma viride	60	60	70	20	10
	Verticillium nigrescens (?)	20	-	20	30	20
	1 sterile hyaline mycelium					
	4 sterile dark coloured mycelia					

TABLE 9

OPEN FORESHORE SAND - SANDWICH

% Frequency of Occurrence at a depth of 1 inch in 10 profiles

Mortierella alpina	10
Alternaria sp. (S301)	10
Asteromyces cruciatus	10
Cladosporium herbarum	20
Gliomastix convoluta v. felina	10
Helminthosporium sp.	10
Penicillium brevi - compactum	30
P. cyclopium	10
P. restrictum	10
P. spinulosum	10
Tilachlidium sp. (S546)	10
2 sterile dark-coloured mycelia	10

TABLE 10

FORE DUNES - SANDWICH

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	7.4 - 9.1		7.7-9.7	7.6-8.9	7.5-8.8
S/C No.	Species					
	Mortierella alpina	-	10	20	-	10
	Mucor hiemalis	-	10	-	-	-
	Chaetomium cochliodes	-	20	-	-	-
S318	Sporomia sp.	-	-	10	-	-
S996	?	-	10	-	-	-
	Botrytis cinerea	-	-	-	10	-
S33	Cephalosporium sp.	-	10	-	-	-
S1396	" "	-	10	-	-	-
S1397	" "	-	-	10	-	-
	Cladosporium herbarum	30	10	10	-	30
	Gliomastix convoluta v. felina	-	-	-	10	20
S1381	Nematogonum sp.	10	-	-	-	-
	Papularia arundinis	-	20	-	-	10
	Penicillium brevi-compactum (?)	10	10	10	-	10
	P. cyclopium	10	-	-	-	20
	P. cyaneo-fulvum	-	-	-	10	10
	P. melinii	10	10	10	-	10
	P. restrictum	20	10	30	20	10
	P. spinulosum	10	-	-	-	10
	Penicillium miczynskii	10	-	-	-	-
D40	Pyrenochaeta	-	10	10	-	10
	Scopulariopsis brevicaulis	-	-	-	-	10
S402	Sporotrichum sp.	-	-	10	10	-
S23	Stemphylium sp.	10	10	10	-	-
S546	Tilachlidium sp.	20	40	30	50	20
	Verticillium nigrescens	-	-	10	-	-
S46		-	-	-	10	10
	[6 sterile hyaline mycelia]					
	[5 sterile dark coloured mycelia]					

TABLE 11

SEMI-FIXED "YELLOW DUNE" - SANDWICH

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.8 - 9.9		7.4-8.5	7.4-8.6	7.4-9.2
S/C No.	Species					
	Absidia glauca	40	10	-	-	-
	A. spinosa	10	-	-	-	-
	Mortierella alpina	70	60	50	60	-
	Mucor hiemalis	40	20	10	-	-
S15	Thamnidium sp.	-	-	10	-	-
	Chaetomium murorum	10	10	-	-	-
	Gelasinospora retispora	10	-	-	-	-
S362	Unidentified Ascomycete	20	-	-	-	-
S1326	" "	10	-	-	-	-
S1392	" "	-	10	-	-	-
B101	Aspergillus sp.	-	10	-	-	-
B138	Cephalosporium sp.	-	-	-	-	10
S33	" "	-	10	-	-	-
S1325	" "	-	-	-	20	-
	Cladosporium herbarum	40	-	-	-	10
S10	Coniothyrium sp.	50	50	40	20	-
	Fusarium culmorum	40	10	-	-	-
	Fusarium oxysporum	40	30	-	-	10
S371	Fusarium sp.	20	-	-	-	-
S752	" "	-	-	10	-	-
	Gliomastix convoluta v. felina	10	-	10	20	10
S451	Humicola sp.(?)	10	10	-	-	-
	Myrothecium roridum	-	-	10	-	-
	Papularia arundinis	-	-	-	10	-
	Penicillium adametzi	-	10	-	-	-
	P. cyaneo-fulvum	-	20	10	-	-
	P. cyclopium	-	-	10	10	20
	P. lividum	-	-	10	10	-

continued

Table 11 - contd.

Semi-Fixed "Yellow Dune" - Sandwich

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.8 - 9.9		7.4-8.5	7.4-8.6	7.4-9.2
S/C No.	Species					
	Penicillium melinii (?)	20	10	-	-	-
	P. nigricans	40	20	20	20	10
	P. raistrickii	20	10	-	-	-
	P. restrictum	30	70	50	40	10
	P. spinulosum	20	-	-	-	-
D28	P. thomii series	10	-	-	-	-
D1030	Penicillium sp.	10	-	-	-	-
	Periconia igniaria	10	-	-	-	-
D40	Pyrenochaeta sp.	-	10	-	10	10
	Scopulariopsis brevicaulis	10	-	-	-	-
	Spicaria violaceae	10	-	-	-	-
S25	Stemphylium dendriticum	-	10	-	-	-
S546	Tilachlidium sp.	20	20	-	20	10
	Trichoderma viride	10	10	20	-	-
D784	Verticillium sp.	10	-	-	-	-
S2	?	10	-	10	10	-
S46	?	-	-	-	-	-
S27	?	-	10	-	-	-
	1 sterile hyaline mycelium					
	6 sterile dark coloured mycelia					

TABLE 12

FIXED "GREY DUNE" - SANDWICH

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.8 - 7.6		7.2-8.0	5.6-8.8	7.4-8.3
S/C No.	Species					
	Absidia glauca	20	10	10	20	-
	A. spinosa	20	50	70	40	20
	Mortierella alpina	50	60	60	50	30
	Mucor hiemalis	20	-	-	-	-
	Gelasinospora retispora	10	-	-	-	-
	Sporomia intermedia	10	-	-	-	-
S30	Sporomia sp.	-	-	-	10	-
B125	Cephalosporium sp.	-	-	-	10	-
B132	" "	10	-	-	-	-
S33	" "	-	10	30	10	-
	Cladosporium herbarum	30	-	20	-	10
S10	Coniothyrium sp.	70	70	40	20	10
S1389	Dicoccum sp.	-	-	-	10	-
	Fusarium culmorum	30	50	-	-	-
	F. oxysporum	30	60	-	-	-
S371	Fusarium sp.	-	20	-	-	-
	Gliomastix convoluta v. felina	-	10	10	20	10
S890	Harposporium sp.	10	-	-	-	-
S984	Microdiplodia sp.	-	-	10	-	-
S1373	Monotospora sp.	-	10	-	-	-
	Myrothecium roridum	20	20	-	-	-
	Penicillium adametzi	-	10	10	-	-
	P. cyclopium	-	-	10	-	10
D1605	P. cyclopium series	-	-	-	-	10
	P. cyaneo-fulvum	-	10	-	-	-
	P. nigricans	30	70	40	60	40
	P. restrictum	70	70	70	70	40
	P. spinulosum	20	-	-	-	-
S324	Penicillium sp.	-	-	-	-	10
D40	Pyrenochaeta sp.	30	-	-	-	-
	Stemphylium dendriticum	10	20	-	-	-
S1384	" "	10	-	-	-	-
S546	Tilachlidium sp.	-	-	-	10	-
	Trichoderma viride	-	-	-	10	-
B139	Verticillium sp.	10	-	-	-	-
S312	?	-	10	10	40	20
S2	?	-	-	-	-	10
	5 sterile hyaline mycelia					
	3 sterile dark coloured mycelia					

TABLE 13

DUNE PASTURE - SANDWICH

% Frequency of Occurrence of Fungi at 5 Soil Depths in 10 Profiles

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.5 - 7.7		7.0-7.7	6.9-7.8	7.2-8.4
S/C No.	Species					
	Absidia glauca	60	40	40	50	10
	A. spinosa	50	70	10	10	-
	Mortierella alpina	70	50	20	40	10
S1158	Mortierella hygrophila (?)	10	-	-	-	-
S1316	Mortierella sp.	-	-	-	10	-
S1357	" "	-	10	-	-	-
	Mucor hiemalis	40	20	-	-	-
	Gelasinospora cerealis	10	-	-	-	-
	Gelasinospora retispora	-	20	-	-	-
	Gymnoascus sp.	-	-	10	-	-
	Botrytis cinerea	10	20	-	-	-
B125	Cephalosporium sp.	-	-	-	20	-
S33	" "	-	10	-	-	-
	Cladosporium herbarum	10	-	-	-	-
S10	Coniothyrium	30	30	40	30	-
	Fusarium culmorum	50	10	10	-	-
	F. oxysporum	-	10	20	-	20
	Gliocladium roseum	-	10	10	-	-
	Gliomastix convoluta v. felina	-	-	-	10	10
	Microdiplodia sp.	10	-	-	-	-
S1317	Monosporium sp.	-	-	-	10	-
	Papularia arundinis	-	10	-	-	-
	Penicillium cyaneo-fulvum	-	10	-	-	-
	P. cyclopium	20	-	10	10	-
D1605	P. cyclopium series	-	-	-	10	10

continued

Table 13 - contd.

Dune Pasture - Sandwich

	Sampling Depth	½"	1"	3"	6"	12"
	Soil pH Range	6.5 - 7.7		7.0-7.7	6.9-7.8	7.2-8.4
S/C No.	Species					
	Penicillium decumbens	10	-	-	-	-
	P. melinii (?)	10	10	-	-	-
	P. nigricans	50	30	40	30	20
	P. restrictum	80	70	60	40	10
	P. spinulosum	-	10	10	-	10
	P. thomii	10	-	-	-	-
S1377	*Penicillium* sp.	-	-	-	10	-
	Spicaria violaceae	-	30	-	10	-
S402	*Sporotrichum* sp.	-	10	-	-	-
S25	*Stemphylium dendriticum*	10	-	-	-	-
S1292	" "	-	-	-	-	10
	Stysanus stemonites	-	-	-	10	-
	Trichoderma viride	10	10	-	-	-
B139	*Verticillium* sp.	-	-	-	-	10
S2	?	20	10	-	-	-
S312	?	10	-	10	40	50
S400	?	10	-	-	-	-
	[3 sterile hyaline mycelia]					
	[2 sterile dark coloured mycelia]					

It can be seen from the foregoing isolation data that the microfungal populations of the two extreme types of dune system are remarkably distinct, as is the surface vegetation. Of the species common to the Sandwich and Studland dunes only three have a frequency of occurrence of 50% or more in both systems, namely, Penicillium nigricans, P. restrictum and Cladosporium herbarum. Penicillium nigricans seems to be the most widespread member of the microfungal population of dune soils in Britain considered as a whole, being the commonest isolate from 6 out of 8 dune systems investigated. Warcup (1951) found this species was also the commonest microfungus in both alkaline and acid sandy grasslands. Penicillium restrictum has a high frequency in both acid and alkaline sands, but the isolates from the respective dunes were morphologically distinct and those from Studland restricted almost entirely to the subsurface of fixed dune heath. The widespread distribution of Cladosporium herbarum is well known and the doubts concerning its activity in the soil have already been pointed out.

A comparison of the distribution range of various

species reveals three components of the population. Firstly, there are those species restricted to the alkaline system, secondly, those restricted to the acid system and, thirdly, those with apparently a broader tolerance of soil conditions. In table 14, members of the 3 groups: Phycomycetes, Penicillia and Fungi Imperfecti other than Penicillia which occurred in more than 1 soil profile are arranged according to their distribution in the 2 dune systems to illustrate this division of the flora into an "acid" and "alkaline" component and the existence of "tolerant" species. Although a number of Ascomycetes were isolated, individual species were sporadic so that their distribution could not be correlated with dune type.

Some of the most common species which appeared to be characteristically associated with acid or alkaline dunes respectively are listed below:

Acid dunes	Alkaline dunes
Mortierella isabellina	Absidia glauca
M. parvispora	Mortierella alpina
Mucor ramannianus	Cephalosporium S33
Coniothyrium D20	Coniothyrium S10
Penicillium adametzi	Fusarium culmorum
P. melinii	F. oxysporum
P. restrictum (form B)	Myrothecium roridum
Trichoderma viride	Penicillium restrictum (form A)
Verticillium nigrescens(?)	S312 (unidentified species)

Evidence that the differences in the distribution

TABLE 14

THE 'ACID', 'ALKALINE', AND COSMOPOLITAN COMPONENTS OF THE DUNE MICROFUNGAL FLORA

% Frequency of Occurrence of Species in 10 Soil Profiles/Dune Zone

OS = Open Sand
FD = Fore Dune
YD = Semi-Fixed 'Yellow' Dune
GD = Fixed 'Grey' Dune
DP = Fixed Dune Pasture
DG = Semi-Fixed 'Dune Grass'
DH = Fixed Dune Heath
SH = 'Southern Heath' (old fixed dune heath)
BH = *Pteridium* Dune Heath

(Species which occurred in only one profile have been omitted)

DUNE SYSTEM	SANDWICH					STUDLAND					
DUNE ZONE	OS	FD	YD	GD	DP	OS	FD	DG	DH	SH	BH
Soil pH Range	7.7-9.1	7.4-9.7	6.8-9.9	5.6-8.8	6.5-7.8	6.4-7.3	6.1-7.5	4.3-6.6	3.4-4.9	3.2-4.7	3.1-5.0
PHYCOMYCETES											
Absidia glauca	-	-	50	50	70	-	-	-	-	-	-
Mortierella alpina	10	30	90	100	90	-	-	10	-	-	-
Mucor hiemalis	-	10	60	30	50	-	-	10	10	-	-
Absidia spinosa	-	-	10	70	100	-	-	-	30	30	-
Mortierella parvispora	-	-	-	-	-	-	-	30	-	20	50
Mucor ramannianus	-	-	-	-	-	-	-	30	60	50	70
Mortierella isabellina	-	-	-	-	-	-	-	10	30	30	50
Mortierella marburgensis	-	-	-	-	-	-	-	-	40	-	-
Zygorrhynchus vuilleminii	-	-	-	-	-	-	-	-	20	-	-
Haplosporangium decipiens	-	-	-	-	-	-	-	-	10	-	10
Absidia orchidis	-	-	-	-	-	-	-	-	-	10	-

continued

Table 14 contd.

DUNE SYSTEM	SANDWICH					STUDLAND					
DUNE ZONE	OS	FD	YD	GD	DP	OS	FD	DG	DH	SH	BH
Soil pH Range	7.7-9.1	7.4-9.7	6.8-9.9	5.6-8.8	6.5-7.8	6.4-7.3	6.1-7.5	4.3-6.6	3.4-4.9	3.2-4.7	3.1-5.0
PENICILLIA											
Penicillium restrictum (A)	10	60	80	80	90	-	-	-	-	-	-
P. cyaneo-fulvum	-	20	30	20	10	-	-	-	-	-	-
P. miczynskii	-	10	10	-	-	-	-	-	-	-	-
P. raistrickii	-	-	40	-	-	-	-	-	-	-	-
P. brevi-compactum	30	10	-	-	-	-	10	30	10	10	-
P. spinulosum	10	10	20	20	20	-	-	20	60	60	80
P. cyclopium	10	30	20	20	30	-	30	10	20	30	30
P. melinii	-	20	10	10	10	-	-	30	80	50	40
P. nigricans	-	-	40	80	60	20	70	100	70	50	70
P. lividum	-	-	20	-	-	-	10	10	-	10	20
P. thomii series D28	-	-	10	-	10	-	-	-	-	10	20
Penicillium D1030	-	-	10	-	-	-	-	-	10	-	-
P. adametzi	-	-	-	20	-	10	-	-	80	70	50
P. decumbens	-	-	-	-	10	-	10	30	30	40	20
P. thomii	-	-	-	-	-	10	-	-	20	30	-
P. terlikowskii (?)	-	-	-	-	-	-	10	30	30	40	20
P. namyslowskii	-	-	-	-	-	-	-	20	30	30	40
P. restrictum (B)	-	-	-	-	-	-	-	10	70	70	10
P. raistrickii series D461	-	-	-	-	-	-	-	10	10	-	-
P. simplicissimum	-	-	-	-	-	-	-	10	-	10	-
P. lapidosum	-	-	-	-	-	-	-	10	20	10	-
P. paxilli	-	-	-	-	-	-	-	10	10	10	30
Penicillium D919	-	-	-	-	-	-	-	-	10	10	-
P. martensii	-	-	-	-	-	-	-	-	10	10	-
Penicillium D990	-	-	-	-	-	-	-	-	-	10	20
Penicillium D476	-	-	-	-	-	-	-	-	-	-	40

continued

Table 14 contd.

DUNE SYSTEM	SANDWICH					STUDLAND					
DUNE ZONE	OS	FD	YD	GD	DP	OS	FD	DG	DH	SH	BH
Soil pH Range	7.7-9.1	7.4-9.7	6.8-9.9	5.6-8.8	6.5-7.8	6.4-7.3	6.1-7.5	4.3-6.6	3.4-4.9	3.2-4.7	3.1-5.0
FUNGI IMPERFECTI other than Penicillia											
Stemphylium S23	-	20	-	-	-	-	-	-	-	-	-
Cytoplea S46	-	20	20	-	-	-	-	-	-	-	-
Cephalosporium S33	-	10	50	10	-	-	-	-	-	-	-
S 402	-	20	-	-	10	-	-	-	-	-	-
Spicaria violacea	-	-	10	30	-	-	-	-	-	-	-
Fusarium oxysporum	-	-	90	70	60	-	-	-	-	-	-
Coniothyrium S10	-	-	90	80	50	-	-	-	-	-	-
Stemphylium dendriticum	-	-	10	40	10	-	-	-	-	-	-
Coniothyrium S2	-	-	10	20	20	-	-	-	-	-	-
Myrothecium roridum	-	-	10	40	10	-	-	-	-	-	-
S 312	-	-	-	60	60	-	-	-	-	-	-
Microdiplodia D388	-	-	-	10	10	-	-	-	-	-	-
Cephalosporium B125	-	-	-	-	20	-	-	-	-	-	-
Asteromyces cruciatus	10	-	-	-	-	10	-	-	-	-	-
Gliomastix convoluta v.felina	10	20	40	40	20	10	-	30	60	20	-
Cladosporium herbarum	20	60	40	60	20	-	40	50	30	10	20
Cephalosporium S1325	-	20	10	-	-	-	10	-	-	-	-
Tilachlidium S546	-	80	50	10	-	10	20	-	-	-	-
Pyrenochaeta D40	-	20	20	30	-	10	50	40	-	-	-
Papularia arundinis	-	20	20	-	10	-	10	10	20	10	-
Verticillium nigrescens ?	-	10	10	-	-	20	-	-	10	50	60
Trichoderma viride	-	30	10	-	-	-	10	20	90	80	80
Fusarium culmorum	-	-	50	60	50	-	-	-	10	-	-
Botrytis cinerea	-	-	-	-	30	10	20	-	10	-	30
Papularia sphaerosperma	-	-	-	-	-	10	10	20	-	-	-
Stemphylium D73	-	-	-	-	-	-	20	-	-	-	-
Piricularia D1051	-	-	-	-	-	-	10	10	-	-	-
Pullularia pullulans	-	-	-	-	-	-	-	20	10	-	30
Trichosporium cerealis	-	-	-	-	-	-	10	-	10	-	-
Coniothyrium D20	-	-	-	-	-	-	30	50	10	10	-
Cephalosporium D1038	-	-	-	-	-	-	-	30	-	-	-
Beauveria bassiana	-	-	-	-	-	-	-	-	10	20	-

ranges of the various species are in great part correlated with soil type is given by the distribution data obtained from other localities in the British Isles (see tables in Appendix). The similarities between the fungal communities of the dunes of similar soil type investigated are striking. Of the high frequency members of the Sandwich flora all but Absidia spinosa have a similar distribution elsewhere. For example, Mortierella alpina (< 100% frequency), Coniothyrium S10 (< 90% frequency) and Penicillium restrictum form A (< 90% frequency) were isolated in abundance from the alkaline dunes at Bamburgh, Berrow and St. Cyrus and from the young alkaline or only slightly acid zones of the Blakeney, Newborough Warren and Tentsmuir dunes. Similarly, characteristic and constant species of the acid Studland dunes, for example, Trichoderma viride (< 90% frequency) and Mucor ramannianus (< 70% frequency) were common isolates from one or more of the most acid dune zones at Blakeney, Newborough Warren and Tentsmuir but were absent or rare elsewhere.

Slide Traps

Fifty-eight species of fungi were isolated by using the slide trap technique including:-

11 Phycomycetes
3 Ascomycetes
27 Fungi Imperfecti (10 Penicillium species)
17 Sterile mycelia.

The range of species isolated was relatively wide and included all but 5 of the species shown by use of the soil plate method to have a frequency of occurrence of 50% or more. The 5 species - Cephalosporium S33, Gliomastix convoluta var. felina, Penicillium adametzi, P. restrictum (form B) and Verticillium nigrescens (?) are all rather slow growing in culture and their absence in slide traps may have been due to failure to compete with faster growing species. Nevertheless a number of slow growers, for example Mucor ramannianus, Penicillium species, Pyrenochaeta D40 and sterile dark coloured mycelia were isolated by slide traps.

Species isolated by slide traps only were of relatively rare occurrence; the most frequent was Mortierella hygrophila.

Species Isolated by use of the Slide Trap Technique

Absidia glauca
A. spinosa
Haplosporangium decipiens
Mortierella alpina
M. hygrophila
*M. hygrophila ?
M. parvispora
Mucor hiemalis
M. ramannianus
*M. strictus
Thamnidium sp.
Chaetomium pannosum
Gelasinospora cerealis
G. retispora
*Aspergillus sp. D2088
Botrytis cinerea
Cladosporium herbarum
Coniothyrium sp. S10
Coniothyrium sp. D20
Fusarium culmorum
F. oxysporum
Fusarium sp.
Fusarium S752
Papularia arundinis
Penicillium cyclopium
P. decumbens
P. melinii
P. namyslowskii
P. nigricans
P. restrictum (form A)
P. raistrickii series
P. spinulosum
P. thomii
*Penicillium sp. D946
*Phoma sp. D1801
*Phomopsis sp. D1800
Pyrenochaeta sp. D40
*Sporotrichum sp. D1807
Tilachlidium sp. S546
Trichoderma viride
S312

13 sterile hyaline mycelia

4 sterile dark coloured mycelia

* species which were not isolated by the soil plate technique.

If the species distribution patterns revealed by the use of the two isolation methods, soil plates and slide traps, are considered merely in terms of "presence" and "absence" of species there is some correlation between them. Thus the "acid" and "alkaline" flora already described is reflected by the slide trap isolation analysis. The latter indicates, for example, the preferential association of certain Fusaria with alkaline sands and of Trichoderma viride with acid sands (see table 15). It is the proportional composition of the fungal populations and not the species composition which differs most widely when the isolations by the two methods are compared. Slide trap isolates include a relatively high preponderance of a few fast-growing species, Fusarium culmorum, Mucor hiemalis and Trichoderma viride in particular. A preponderance of species of this growth type seems a likely failing inherent in the trap technique, but the number of Mucor hiemalis isolations from acid soils appears excessively high in comparison with the findings of the soil plate analysis. It is interesting to consider in this connection Sewell's observation (1954) that Mucor species other than M. ramannianus and including M. hiemalis were never isolated from acid Calluna heath soils on soil plates although their presence was shown by other techniques. It was suggested that this lack of isolation was due to limited sporulation in the soil and

TABLE 15

Relative % Frequency of Isolation of Species of Fungi from Surface Soils by the Slide Trap Technique

		SANDWICH			STUDLAND		
	DUNE ZONE	FD	YD	GD	FD	DG	DH
	Soil pH Range	7.4-9.1	6.8-9.9	6.8-7.6	6.6-7.0	4.3-5.3	3.7-4.3
	Absidia glauca	-	-	<5	-	-	-
	Haplosporangium decipiens	-	-	-	-	-	<5
	Mortierella alpina	22	-	-	-	-	-
	Mortierella hygrophila	-	-	-	-	6	-
	Mucor hiemalis	11	30	26	65	50	21
	M. ramannianus	-	-	-	-	<5	-
	M. strictus	-	-	-	<5	<5	-
	Thamnidium sp.	-	-	-	-	<5	-
	Chaetomium pannosum	-	-	7	-	-	-
	Gelasinospora cerealis	-	-	-	-	-	<5
	G. retispora	-	-	-	-	-	<5
D2088	*Aspergillus* sp.	-	-	-	-	<5	-
	Botrytis cinerea	-	<5	-	-	<5	-
	Cladosporium herbarum	-	-	-	-	<5	-
D20	*Coniothyrium* sp.	-	-	-	-	<5	-
	Fusarium culmorum	-	49	47	<5	6	-
	F. oxysporum	11	-	<5	-	-	-
	Fusarium sp.	-	<5	7	-	-	-
S752	*Fusarium* sp.	-	<5	-	-	-	-

continued

Table 15 - contd.

		SANDWICH			STUDLAND		
	DUNE ZONE	FD	YD	GD	FD	DG	DH
	Soil pH Range	7.4-9.1	6.8-9.9	6.8-7.6	6.6-7.0	4.3-5.3	3.7-4.3
	Papularia arundinis	-	-	-	-	<5	-
	Penicillium cyclopium	-	-	-	<5	<5	-
	P. melinii	-	-	-	-	-	<5
	P. namyslowskii	-	-	-	-	-	<5
	P. nigricans	-	-	<5	-	<5	-
	P. restrictum	11	-	<5	-	-	-
	P. raistrickii series	11	-	<5	-	-	-
	P. spinulosum	-	-	-	-	<5	-
	P. thomii	-	-	-	-	-	<5
D1801	Phoma sp.	-	-	-	-	-	<5
D1800	Phomopsis sp.(?)	-	-	-	-	-	<5
D40	Pyrenochaeta	11	-	-	-	<5	-
D1807	Sporotrichum sp.	-	-	-	-	<5	-
S546	Tilachlidium sp.	-	-	-	-	<5	-
	Trichoderma viride	-	<5	<5	20	16	67
S312	?	<5	-	-	-	-	-
	Sterile hyaline mycelia	<5	<5	<5	<5	<5	-
	Sterile dark coloured mycelia	-	<5	-	<5	<5	-
D1673	" " " "	-	-	-	-	<5	13

inadequate amounts of mycelium in the soil plate inocula. In the present investigation M. hiemalis was certainly a rare soil plate isolate from acid soils but frequent among the alkaline soil isolates. This difference is perhaps connected not with actual distribution but with the vegetative state and spore yield of the fungus in the various types of soil. It is perhaps noteworthy that the vegetative growth of Mucor hiemalis in artificial culture was found to be more vigorous in media of slightly acid reaction.

Thus although the use of the trap technique may exaggerate the importance of certain members of the soil fungal community it may also counteract shortcomings of the plate technique as perhaps in the specific case of Mucor hiemalis.

The most important contribution of this slide trap analysis to the general picture of the fungus population of the dunes under investigation is probably the confirmatory evidence that many of the species isolated on soil plates are active in the soil.

Contact Slides

The general distribution and quantity of mycelium in the soil as deduced from isolations made by the use of soil plates and slide traps was reflected closely by the fungal growth obtained on Rossi-Cholodny contact slides. Much of

the mycelium, which included septate and non-septate light and dark coloured types was sterile and could not therefore be identified, but a few species sporulated on the slides and, as far as can be said without cultural evidence, were the following:-

SANDWICH

Beauveria bassiana. Fore Dunes.
Cladosporium herbarum " "
C. macrocarpum " "
Penicillium sp. (monoverticillate) Fore Dunes & Semi-fixed Dunes.
Stemphylium sp. Semi-fixed Dunes.
Cephalosporium sp. Semi-fixed and Fixed Dunes.
Mortierella alpina " " " "
Mortierella sp. " " " "

STUDLAND

Mortierella marburgensis. Dune heath
M. parvispora " "
Penicillium sp. (monoverticillate) "

All the above species were isolated also by the cultural techniques. Mortierella was the only genus which spored frequently on contact slides and it often formed extensive growths over the glass surface. The Penicillia also exhibited a widely spreading type of growth on these slides in contrast to the restricted colonies formed on culture media.

Many of the thick walled dematiaceous hyphae did not stain with aniline blue so that living and dead material could not be distinguished from one another, but whatever the vitality of the mycelium its presence indicated fungal

activity at some point in time and probably during the slide incubation period.

Fungal spores of various types occurred occasionally on most of the slides. Some were quite unlike those of species isolated by cultural techniques.

The type of microhabitat with which the mycelium was associated could often be seen. Hyphae were frequently twined closely around sand grains where there was little visible organic matter and the grains sometimes appeared to form an anchoring base for a spore-bearing organ. The sporangiophores of the unidentified Mortierella species in particular appeared to be associated with the presence of sand grains. The vegetative mycelium of this species grew freely over the glass surface but sporangiophores were seen only on sand grains, to which they were attached at their base by a rhizoid-like growth or hold-fast. Fungal mycelium was most prolific on plant and animal debris and particularly on insect material. Dark thick walled mycelium appeared to be most abundant in the presence of humus particles and predominated over hyaline mycelium in the peaty dune heath horizons, but both types of mycelium often spread out from their local nutritive sources over relatively wide areas of the open glass surfaces.

Note on the Seasonal Variations in the Fungus Population

The soil environment may be climatically less variable than the subaerial habitats, but conditions are far from constant and the existence of a seasonal periodicity in the vegetative growth and sporulation of soil fungi seems probable. Past evidence of seasonal fluctuations in the size of soil populations is conflicting (Brierley 1928; Vandecaveye and Katznelson 1938) and there have been few demonstrations of the seasonal activities of individual species, which is due partly to the use of unsuitable cultural techniques. Seasonal effects on the isolation of certain Pythium species have been reported by Meredith (1940) and Warcup (1952) and more recently Sewell (1954) showed using the immersion tube isolation method that the activity of Trichoderma viride was closely related to the prevailing temperature, this species being virtually absent from immersion tubes buried in heathland soil during the winter months.

The slide trap experiments on dune soils, although they extended over a period of only one year, also indicated that the activity of Trichoderma viride is reduced during the winter.

% Number of Slide Traps invaded by Trichoderma viride in surface soils of the Studland Dune System.

	Nov.54	Dec.54	Feb.55	Jun.55	Aug.55
	24	14	0	31	38
*(Mean Max.Temp.°F	52	49	40	63	72
(" Min. " "	40	40	30	49	54
(No.of days with ground frost	10	6	20	0	0

* Data obtained from the Metereological Station, Poole.

The soil plate analysis made over a 2-year period failed to reveal any periodicity in the fungal population, but considerable seasonal differences in the rate of linear spread of many species was evident from the length of incubation period required in order to obtain fungi in slide traps, or on Rossi-Cholodny slides.

Section II

(b) The Succession of Dune Soil Fungi

The most widespread species of each dune zone are listed in table 16 to illustrate that there is a succession across a dune system and a build up of a more and more stable population from a pioneer to a climax or sub-climax community.

In the open sand of the foreshore and in the fore dunes where there is a constant change of substrate it was to be expected that the analyses at monthly intervals would show many variations. "Common" species were not in fact recorded from the open sand and only two or three occurred in the fore dunes. As the dunes become more stable and the environment becomes more favourable for those fungi not adapted to the extreme conditions of the foreshore both the number of constant species and the total number of species increases rapidly. The total number of species was actually greatest in the semi-fixed zones, partly due, it would seem, to over-lapping of the ranges of some pioneer and climax species within these intermediate habitats. Tresner, Backus

and Curtis (1954) found that a similar phenomenon occurred in the succession of soil fungi in a forest continuum.

Numbers of Species Isolated from 10 Soil Profiles in each Dune Zone

Dune Zone	SANDWICH OS.	FD.	YD.	GD.	DP.	STUDLAND OS.	FD.	DG.	DH.	SH.	BH.
Total number of species isolated	13	38	53	45	47	12	34	48	53	44	38
% number of species isolated from only 1 profile	92	53	51	47	53	91	73	63	61	43	37
% number of species isolated from 5 or more profiles	0	8	17	22	19	0	6	6	15	18	21

From the above figures it can be seen that as the fungal population becomes more well defined the percentage number of "rare" or sporadic species decreases and the percentage number of constant or widespread species increases. For example, at Sandwich the percentage number of species encountered in only one soil profile falls from 92% in the open sand to 53% in fixed dune pasture and the percentage number of species isolated from five or more soil profiles rises from 0% in open sand to 22% in fixed "grey" dune.

In the semi-fixed dunes, the pioneer species which were widespread in the more mobile dunes are associated with or replaced by a number of other common species. Some of these disappear with dune development but many remain relatively constant and as a more balanced state of equilibrium in the fungus population is approached the number of new entrants

TABLE 16

THE SUCCESSION OF "COMMON" SPECIES IN 2 DUNE SYSTEMS

Species are written in red in the zone in which they first enter the succession as widespread members of the flora i.e. the first time they attain a % frequency of 50 or more.

CALCAREOUS DUNES. SANDWICH		ACID DUNES. STUDLAND	
OPEN SAND	-----	OPEN SAND	------
FORE DUNES		FORE DUNES	
(% freq.)		(% freq.)	
80%	Tilachlidium S546	70%	Penicillium nigricans
60	Cladosporium herbarum	50	Pyrenochaeta D40
60	Penicillium restrictum (form A)		
SEMI-FIXED "YELLOW DUNES"		SEMI-FIXED "DUNE GRASS"	
90	Mortierella alpina	100	Penicillium nigricans
90	Coniothyrium S10	50	Cladosporium herbarum
80	Penicillium restrictum (form A)	50	Coniothyrium sp. D20
60	Mucor hiemalis	SEMI-FIXED - FIXED DUNE HEATH	
60	Fusarium oxysporum		
50	Absidia glauca	90	Trichoderma viride
50	Cephalosporium S33	80	Penicillium adametzi
50	Tilachlidium S546	80	P. melinii
50	Fusarium culmorum	70	Penicillium nigricans
		70	Penicillium restrictum (form B)
FIXED "GREY DUNE"		60	Mucor ramannianus
		60	Gliomastix convoluta v. felina
100	Mortierella alpina	60	Penicillium spinulosum
80	Coniothyrium S.10		
80	Penicillium nigricans	OLD FIXED DUNE - "SOUTHERN HEATH"	
80	Penicillium restrictum (form A)		
70	Absidia spinosa	80	Trichoderma viride
60	Cladosporium herbarum	70	Penicillium adametzi
60	Fusarium oxysporum	70	Penicillium restrictum (form B)
60	Fusarium culmorum	60	Penicillium spinulosum
60	S312?	50	Mucor ramannianus
50	Absidia glauca	50	Penicillium melinii
		50	Penicillium nigricans
DUNE PASTURE		50	Verticillium nigrescens (?)
100	Absidia spinosa	OLD FIXED DUNE - PTERIDIUM-HEATH	
90	Mortierella alpina		
90	Penicillium restrictum (form A)	80	Penicillium spinulosum
70	Absidia glauca	80	Trichoderma viride
60	Fusarium oxysporum	70	Mucor ramannianus
60	S312?	70	Penicillium nigricans
60	P. nigricans	60	Verticillium nigrescens (?)
50	Mucor hiemalis	50	Mortierella parvispora
50	Coniothyrium S10	50	Penicillium adametzi
50	Fusarium culmorum		

For complete lists of species isolated from each zone see Tables 3-13

falls. Thus, in the oldest fixed dune zones all but one of the common species - Mortierella parvispora - were encountered frequently at some earlier stage in the dune succession.

The simpler microflora of the early stages, in contrast to the more balanced population of the later stages of the succession, may be compared with the conditions prevailing in a sterilized and recolonizing soil, where it has been shown that the fungus flora may be dominated by a single organism (Garrett, 1956). As Garrett points out: "This contrast between the population spectra of recolonizing soils and soils in microbiological equilibrium is strikingly reminiscent of the similar contrast between the population spectra of higher plant species in the early and climax stages, respectively, of succession in a habitat above ground....."

The Successive Fungal Associations

The Open Sand of the Fore Shore (OS)

All fungi isolated from the open sand of the fore shore, at sites well in front of the forward limit of higher plant colonization and between the normal high and low tide marks, were of sporadic occurrence, the majority being encountered in only one soil sample. Moreover, the number of colonies of any one species that developed on a soil plate was usually relatively small and in 61% of the plates fungi were entirely

absent, but small "oases" of fungi were sometimes found to coincide with pockets of extraneous organic material, incorporated into the otherwise practically sterile sand. Slide traps could not be used satisfactorily in this tide washed zone and fungal mycelium did not develop on Rossi-Cholodny slides, but small amounts of mycelium were observed in sand crushes and impressions indicating that certain fungi have a period of active, even if short, existence in the shore sand.

Most of the species isolated from the foreshore are members of the communities found in the dunes proper. The most noteworthy exception is Asteromyces cruciatus, a new British record. Although this fungus was isolated from only one sample of sand at both Sandwich and Studland, the colonies developing on soil plates were numerous. It was originally isolated by Moreau (1940) in France from Agropyron and Ammophila sand dunes. Colon (see Moreau 1940) reports that this species is very resistant to desiccation, is able to develop on media of low nitrogen content; withstands alternate immersions in fresh and salt water and is exceptionally tolerant of high concentrations of sodium chloride. The latter observation was confirmed in the present investigation (Section IV), supporting the view that Asteromyces cruciatus is a true pioneer colonist of marine sands. Two other open sand isolates, Gliomastix convoluta

v. felina and Pyrenochaeta D40 were found to be fairly tolerant of high salt concentrations, but not strikingly so, as in the case of Asteromyces. Gliomastix convoluta v. felina is a widespread soil fungus, but is perhaps one of the characteristic members of saline habitats. Bayliss Elliott (1930) isolated this species frequently from salt marsh soils and it appears to be common in the saline lows at Studland and Blakeney. / Höhnk (1954) has recently described two maritime Ascomycetes which fruit on the quartz grains of coastal sands in Germany. Direct examination of foreshore sand was made for fungi of this type without success.

Truly marine species, which have been recorded from wood and plant remains permanently or temporarily submerged in sea water and which are often characterised by their elaborate spores and other morphological features apparently associated with their aquatic habitat (Barghoorn and Linder 1944; Wilson 1951), were also not encountered.

The Fore Dunes

The soil fungi of the fore dunes also appeared to be sparse, as expected in the exacting conditions of this arid and mobile habitat subject to extreme variations in humidity and temperature and perhaps temporarily exposed to high salinities. The number of soil plates which remained sterile, as regards fungi, when prepared from fore dune sand indicates the open nature of the fungus community.

Percentage Number Soil Plates Prepared from Surface Soil (0 - 0.5") of Successive Dune Zones which remained Sterile.

SANDWICH

Open Sand	Fore Dunes	Semi-fixed "Yellow" Dunes	Fixed "Grey"Dunes	Dune Pasture
69	50	10	17	3

STUDLAND

Open Sand	Fore Dunes	Semi-fixed "Dune Grass"	Fixed Dune Heath	Pteridium Dune Heath
53	73	17	0	0

The fore dunes were, however, the first stage in the dune xerosere with a recognisable soil microfungal community, that is, certain species were sufficiently widespread for the soil plate analysis to reveal a distribution pattern. The repeated isolation of a few species including, for example, Tilachlidium S546 at Sandwich and Pyrenochaeta D40 at Studland suggested that these were not accidental invaders of the sand but characteristic members of its flora, tolerant of the extreme conditions and perhaps "escapers" of the intenser competition in older dune soils. These species were found to be active on root surfaces (p.126) from which numerous spores may have been shed into the surrounding sand, but extensive development of fungal mycelium sometimes observed on Rossi-Cholodny slides buried in fore-dune sand was evidence of fungal activity in the "free" soil of this zone. The possibility that fungal growth was stimulated by the introduction of these slides cannot be ruled out, but, as has been pointed out, glass surfaces are perhaps not

unlike other surfaces occurring naturally in the soil and equally favourable for fungal growth; furthermore mycelium was observed on soil impression slides to which the arguments against the use of artificial substrates do not apply. A species resembling Beauveria, colonizing a nematode and a monoverticillate Penicillium were observed on Rossi-Cholodny slides, but the identity of the mycelium was otherwise unknown. Antecological studies are required to determine to what extent the various species do colonize the open sand. Many of the sporadic associates of the more constant species are no doubt contaminants or restricted to very local centres of activity around roots and pockets of organic debris.

As Salisbury (1952) has pointed out dunes are not usually saline habitats despite their proximity to the sea. The salt from sea spray is quickly washed down through the sand by rain or diluted by dew so that the salt content of even the fore dunes is often negligible as was found in this investigation and there was no evidence for the existence of a specifically halophytic fungal community. Isolates of Penicillium nigricans and Pyrenochaeta D40 from fore dunes were to some extent salt tolerant in artificial culture, but what might be termed truly maritime fungi, such as Asteromyces cruciatus, were not encountered in these dunes. The majority of the species isolated belong to the Fungi Imperfecti, and

Phycomycetes, more prominent at later stages of dune development, were of rare occurrence. A number of Tilachlidium and Pyrenochaeta colonies sometimes developed on a single soil plate but other species including Penicillia were usually represented only by isolated colonies.

The preponderance of fast growing species such as Trichoderma and Mucor among slide trap isolates has already been pointed out. It was especially striking in the fore dune zone because of the rarity of these species on soil plates, but the discrepancy between the findings obtained by the two isolation methods is not as great as appears at first sight, when it is remembered that the volume of soil tapped by a slide trap is considerably larger than that used as a soil plate inoculum, and although most of the traps were invaded the number of hyphae penetrating each trap was relatively small.

The fore dunes of the other dune systems examined also appeared to be sparsely colonized by soil microfungi. The densest population occurred at Berrow where there was a relatively close cover of vegetation and considerable admixture of silt and sand. Tilachlidium S546 and Pyrenochaeta D40 were both isolated from the young dunes at Berrow, but it was not obvious, from analysis of the limited number of samples taken, which were the most constant species in the various localities. The populations were, however, of the

same general type with Fungi Imperfecti predominant and Phycomycetes rare.

The Semi-Fixed Dunes

The soil microfungal populations of the semi-fixed dunes where a thin surface humus horizon first becomes visible, are quite distinct from those of the fore dunes, and there is a marked increase in the number of colonies developing on the soil plates and in the amount of mycelium in the soil to be correlated with, among other factors, the greater stability of the habitat and increased supply of nutrients and moisture.

Of the supposed fore dune pioneers, Tilachlidium and Pyrenochaeta show a decline in frequency but Penicillium nigricans and Penicillium restrictum increase to a maximum in this zone. Mucorales, Coniothyria and Fusaria which did not feature in the fore dunes also become prominent (table 16).

The Sandwich plates were characterised in general appearance by the presence of numerous colonies of Mortierella alpina; Coniothyrium S10; Penicillium nigricans and Penicillium restrictum, as were also the soil plates of the semi-fixed dunes of the Bamburgh, Berrow, Blakeney, St. Cyrus and Newborough Warren systems.

The fungus flora of the acid semi-fixed dunes at Studland was less rich than the above, possibly due to a relatively

low soil organic content - 0.7% compared with 1.5% at Sandwich. The soil plates of these dunes were characterised by abundant colonies of Penicillium nigricans which was often isolated in pure culture on a soil plate and found in every soil profile examined. Occasional associates here were species such as Mortierella isabellina and Mucor ramannianus typical of the more acid and peaty dune zones that follow in the succession. A similar picture was presented by the semi-fixed dunes of the Tentsmuir system when acid, but when alkaline or only slightly acid there appeared to be an overlap of the "acid" and "alkaline" population types.

The Fixed Dunes of the Calcareous System

In the succession at Sandwich from semi-fixed "yellow" dunes to fixed "grey" dunes the most notable changes were: the increased frequency of Absidia spinosa and Penicillium nigricans; the first appearance of an unidentified species S312 with a frequency of 60%, and the decline of Tilachlidium S546 and Cephalosporium S33 to rarity.

The climax (or sub-climax) population of the dune pasture, the final stage of the xerosere, does not differ greatly from that of the previous "grey" dune stage. 90% of the "grey" dune species remain of "common" rank. The frequency of Cladosporium herbarum fell from 50% to 20%, but this reduction is perhaps due to the fact that aerial contamination in this closed community with its dense vegetational cover

is here at a minimum. The Tilachlidium member of the pioneer communities was no longer among the isolates.

The microfungal association of the Sandwich dune pasture soil resembles that of other alkaline sandy grasslands. Most of the more constant species were isolated also from the dune pasture at Berrow (Somerset) or Bamburgh (Northumberland) and five were found by Warcup to be constant in the inland alkaline sandy grasslands (A + B) of the Brecks (Norfolk).

The Fixed Dunes of the Acid System

In the development of the Studland dunes from semi-fixed "dune grass" to fixed dune heath, over a period of approximately twenty years, a marked change occurs both in the macrohabitat and in its associated soil microflora. In the heath zones, characterised by the presence of Calluna and a peaty A_1 soil horizon with a pH value < 5, the number of common species of microfungi rose from 3 to 8 and with the closing of the community the number of sterile soil plates fell from 17% to 0%. Penicillium adametzi entered the community with a frequency of 80% and there was a sharp rise in the frequency of some of the former members including Trichoderma viride (20 $\longrightarrow$ 90%), Penicillium melinii (30 $\longrightarrow$ 80%) and Penicillium restrictum form B (10 $\longrightarrow$ 70%).

The three stages of fixed dune heath investigated - Dune Heath, Southern Heath and Pteridium Heath - differ in their respective ages and higher plant dominants, but are

fundamentally similar as regards soil type and their micro-fungal populations do not diverge greatly. Verticillium nigrescens (?) becomes more widespread in Southern Heath and Mortierella parvispora in Pteridium Heath than in the younger dunes, but otherwise the composition of the high frequency component of the fungus flora alters only slightly.

It is interesting to compare this dune heath community with that of Western Plateau Heath investigated by Sewell (1953). Western Plateau approximately half a mile from the dune sampling sites is an old slightly damp podsolised heath on Bagshot beds with a climatic climax type of vegetation dominated by Calluna and Erica. Good (1935) suggests it is the ultimate vegetational equilibrium to which the successive dune trends are converging, although a state of equilibrium already seems to have been reached in the older zones of dune heath. Comparison of species lists shows that those for the surface soils are practically identical but on Western Plateau there is a greater development of the subsurface population correlated with the maturer soil profile.

The only other comparable dune heath examined was that of the Tentsmuir system in Fifeshire. The fungal association found in the 2 profiles sampled was very similar to that of Studland, and most of the species widespread in the southern locality were isolated. The floras of the 2 dune heaths

are compared below together with data obtained for inland heath soils (Sewell 1954).

	CALLUNA HEATH SOILS			
	MARINE DUNES. STUDLAND.		INLAND HEATHS TENTSMUIR	
	% Frequency	+Present	-Absent	% Frequency
Trichoderma viride	90	+		97*
Penicillium adametzi	80	-		87*
P. melinii	80	+		15 (?)
P. nigricans	70	+		41*
P. restrictum	70	-		10
Mucor ramannianus	60	+		82*
Gliomastix convoluta v. felina	60	+		8
Penicillium spinulosum	60	+		82*

* "Abundant" or "frequent" in dry sandy Callunatum.

Sewell found that eleven species were of more or less constant occurrence in Calluna heathland soils: namely Absidia orchidis, Mucor ramannianus, Mortierella isabellina, Zygorrhynchus vuilleminii, Beauveria bassiana, Penicillium adametzi, P. namyslowskii, P. nigricans, Pullularia pullulans, Trichobotrys sp. and Trichoderma viride. All of these except Trichobotrys were isolated from dune heath soils in the present investigation. Trichobotrys and Beauveria rare in dune soils were primarily members of the subsurface flora of inland heaths which in dunes, as will be shown, are poorly developed.

Further evidence that the above dune heath mycoflora is relatively typical for the soil type is given by McLennan

and Ducker's (1952) investigation of the distribution of Penicillium species in Australian soils. They found that Penicillium adametzi, P. nigricans, P. restrictum and P. spinulosum were among "the most abundant" species of sandy podsols.

In the Newborough Warren system the alkaline or only slightly acid fixed grey dune fungus flora was of the alkaline type, but it was replaced by a more acid type in the nearby Callunetum intermediate between fixed dune and slack. The latter association was, however, unlike that of the dry dune heaths described above in that it was characterised by the presence of an unidentified Penicillium N58, not encountered elsewhere, which formed numerous colonies on soil plates, whereas Penicillium adametzi, P. nigricans, P. melinii, P. restrictum and Mucor ramannianus were rare or absent. This change in the community pattern may be associated with the high soil water content. Mucor ramannianus has been found to be invariably absent from inland heath soils if constantly wet and inadequately drained and Penicillium nigricans declines under these conditions (Sewell 1954).

At Blakeney, where there is no succession to dune heath, the population of the grey fixed dunes (pH 4.9 - 6.6) was of an intermediate type and included both "acid" species, such as Trichoderma viride, Mortierella isabellina and Mucor

ramannianus (rarely), and "alkaline" species, such as *Myrothecium roridum*, *Mortierella alpina* and *Coniothyrium* S10, but *Trichoderma* predominated on soil plates.

It can be seen that the succession of soil fungi from shore to fixed dune culminates in a community relatively typical of acid heathland or alkaline grassland. The several species combinations which lead to this climax each possess a certain individuality and although there is considerable overlap the distribution range and zone of maximum frequency of the more widespread species is usually clearly defined. There are, therefore, in the successive zones of a dune system distinct associations of both higher plants and soil fungi.

Section II

(c) The development of a microfungal profile in dune soils and vertical distribution patterns of dune soil fungi.

Most of the species isolated occurred in surface soil (0" - 1") and a general decrease in the number of species, species frequency and number of colonies on soil plates was found to occur with increase in soil depth (table 3 - 13). Slide traps and Rossi-Cholodny slides also indicated a decrease in the amount of active mycelium down the soil profile. Mycelium was observed on contact slides from all the soil zones and depths sampled except those of the open foreshore, but, although it was prolific on slides from surface humus horizons, it always became sparse on slides buried at depths of 6 - 12 inches. These decreases suggested a rapid reduction in the size of the fungus population down the soil profiles, although variations in the numbers of colonies on soil plates do not necessarily parallel variations in the mycelial content of the soil. Changes were usually most rapid in the surface three inches of soil and a marked differential distribution of species could sometimes be detected within even the first inch of soil. The depth at which the sand was sterile as regards fungi, when a surface population was present, varied from about 1 inch in young dunes to about 12 - 18 inches in old fixed dunes.

Development of a microfungal profile

In the fore dunes, where soil horizons were not visible

and where the upper layers of sand were frequently disturbed, the vertical distribution of fungi varied considerably and when considered as a whole showed no clearly defined population gradient with soil depth. Sometimes pockets of buried organic debris, usually in the lower regions of the profile, were found to be associated with local increases in the fungus population, so that the microfungal profile was the reverse of that usually found in a more mature soil. Moister conditions and a greater abundance of roots in the subsurface sand probably also played a part in this reversal.

The first well defined microfungal profile of the dune succession was found in the semi-fixed zone, that is, in the "yellow" dunes at Sandwich and in the "dune grass" zone at Studland. In the calcareous "yellow" dunes a downward gradient in the size of the fungal population was indicated by the decrease in the total number of species isolated, from 29 at 0.5 inches to 9 at 12 inches, and by the increase in the number of sterile soil plates, from 10% at 0.5 inches to 69% at 12 inches (tables 17, 18).

The number of colonies on soil plates always dropped abruptly below the A_1 horizon. Species such as Fusarium culmorum which were restricted to surface soil and others, such as Mortierella alpina with a continuous but more gradual decline in frequency with depth were found in these "yellow" dune profiles, but a subsurface population was not distinct

TABLE 17

THE % OF THE TOTAL NUMBER OF SOIL PLATES PREPARED WHICH REMAINED STERILE AS REGARDS FUNGI

Soil Depth (ins.)	0.5	1.0	3.0	6.0	12.0
SANDWICH					
Open Sand	69				
Fore Dunes	50	43	36	46	46
Semi-Fixed "Yellow" Dunes	10	13	10	26	69
Fixed "Grey" Dunes	17	0	3	7	36
Dune Pasture	3	0	17	13	33
STUDLAND					
Open Sand	53				
Fore Dunes	73	43	69	50	79
Semi-Fixed "Dune Grass"	17	13	26	40	36
Semi-Fixed - Fixed Dune Heath	0	13	10	7	30
"Southern Heath"	0	10	43	26	40
Pteridium Dune Heath	0	0	13	23	46

TABLE 18

TOTAL NUMBER OF SPECIES OF FUNGI ISOLATED FROM VARIOUS DEPTHS OF THE PROFILE

(10 profiles/dune zone examined)

Soil Depth (ins.)	0.5	1.0	3.0	6.0	12.0
SANDWICH					
Open Sand	11				
Fore Dunes	10	14	12	7	14
Semi-Fixed "Yellow" Dunes	29	22	14	12	9
Fixed "Grey" Dunes	20	17	13	14	12
Dune Pasture	22	22	13	16	11
STUDLAND					
Open Sand	9				
Fore Dunes	6	10	11	11	4
Semi-fixed "Dune Grass"	20	13	10	14	8
Semi-fixed - Fixed "Dune Heath"	25	21	17	14	20
"Southern Heath"	22	22	14	14	12
Pteridium Dune Heath	23	20	15	16	10

from that of the surface, formed as it was by "sporadics" and species at their lower limit of vertical distribution. A well-defined subsurface population was not in fact found in any of the calcareous dunes.

In the acid semi-fixed dunes at Studland, the vertical distribution of fungi was more restricted than in the comparable zone at Sandwich which can be correlated perhaps with the lower organic content of the soil at Studland. Where the A_1 horizon was very thin or absent, the micro-fungal profile was of the fore dune type. Even in the presence of an A_1 horizon the fungus flora was sparse below a depth of about 0.5". For example, in one profile where the A_1 horizon extended to a depth of 0.5", the average number of colonies on plates prepared from soil at this depth was 21, whereas plates of soil from a depth of 1" remained practically sterile (i.e. 2 - 3 colonies/plate); such a decrease in the colony numbers, even if partly a reflection of a reduction in the sporing capacity, indicates some marked change in the flora.

The most notable feature of the microbiological profile of the fixed "grey" dunes at Sandwich, when compared with that in the younger dunes of this system, was its further downward extension. Whereas in the "yellow" dunes total sterility in a profile sometimes occurred at a depth of 1", in the "grey" dunes such conditions were not found above a

depth of 6". A certain amount of sterility occurred at a depth of 0.5", but this was associated with the presence of an overlay of wind blown sand.

In the "dune pasture" - the final stage in the Sandwich succession - a still further downward extension of the microfungal profile appeared to be associated with the greater depth of humus-rich soil. The size of the fungal population sometimes became unexpectedly small at depths of 3" - 6"; this was possibly related to a marked increase in the bacterial population noted at this level. A secondary increase of fungi was found in the streaks of humus running through the subsoil. An unidentified species, S312*, appeared, from its distribution in the fixed dunes, to be typically a member of the subsurface flora rather than of the surface flora, which indicated a further development of the microbiological profile.

The microfungal profile, like the soil profile, was found to be most highly differentiated in the zones of fixed dune heath where incipient podsolisation occurred. Here, in the maturer profiles, fungal horizons could sometimes be distinguished below that of the A_1. There was, for instance, a sparse flora in a leached A_2 horizon compared with that of a peaty A_1 horizon followed by a slight secondary increase of fungi below the A_2. A B_1 humus pan was rarely clearly delimited if present at all, so it was difficult

---

* possibly a species new to science.

to assess its effect on the fungus community without more selective sampling of this and adjacent horizons. Numbers of species and colonies showed a marked increase in the B_1 horizon over those in the A_2 in only one profile, and they never exceeded those of the A_1.

The most interesting feature of the dune heath profiles was the presence of the first distinct subsurface flora. Two species of fungi, Mucor ramannianus and Penicillium restrictum (form B) and an actinomycete were characteristically associated together at soil depths of 6" - 12", often to the apparent exclusion of other species. The maximum development of this subsurface flora appeared to be always in relatively clean sand below the organic horizons. Sterile mycelia were not characteristic members of the subsoil association and they were only sporadic at other levels of the profile. The fungus flora of more mature inland podsols has been shown (Sewell, 1954) to include a sterile mycelial component associated in particular with the illuviated horizons and parent clayey sands. Its absence from the dune soils examined is related perhaps to the relatively shallow and well-aerated nature of the soil.

It can be seen that the development of the microfungal profile in the fixed dunes, in spite of the lack of definition in the pedological profile, shows a considerable advance over that of the young mobile dunes which indicates the importance

of stability and a higher plant cover in the formation of a definite pattern in the vertical distribution of soil fungi.

Vertical distribution patterns

As in other habitats (Bisby, James and Timonin 1935; Warcup 1951; Burges and Fenton, 1953) 3 vertical distribution types were recognisable in the dune mycoflora.

The first and largest group of species was restricted to or more common in the surface soil; the second was found throughout the soil profile and was not associated with any particular soil depth or horizon, and the third was most widespread at subsurface levels. Explanations for these differences in the vertical distribution pattern of soil fungi have been put forward, but there is little certainty in most cases as to the effect of such factors as aeration, organic content and water movements in the soil.

(i) Surface species.

The first group in dune soils included Mucor hiemalis and Fusarium culmorum. These two species were most frequent in the upper 0.5 inches of soil and rarely isolated below a depth of 3 inches. The distribution of F. culmorum, in particular, was sharply defined, for example, in the "grey" fixed dunes at Sandwich; it was present in 50% of the profiles at a depth of 1 inch, but it was not isolated from soil at lower depths. The range of these species did not always extend to the lower limit of a surface humus horizon,

nor did they appear in subsurface accumulations of humus; aeration or moisture may therefore be one of the major factors involved. Bisby et al (1935) and Warcup (1951) found that Mucor species were more common in surface soil than at lower levels.

Other members of the surface group, such as Absidia glauca, Coniothyrium (S10), and a number of Penicillia showed a continuous but more gradual decrease in frequency down the soil profile. Their actual distributions may have been obscured by a downwash of spores and filtering actions by the sand should also be taken into account. Burges (1950) has demonstrated a rapid downward movement of fungal spores through sandy soil, but he has shown that wet spore types are more easily washed through soil than dry spore types such as Penicillia.

Penicillium nigricans and Trichoderma viride, also found to be characteristically surface soil dwellers, appeared to be more closely related in their distribution to the organic matter gradient than the above species. Burges (1953) found that P. nigricans was restricted to the upper two inches of certain Breckland soils and suggested this was an aeration effect. In dune soils, however, there were indications that the frequency of this species reached a secondary maximum in subsurface humus-rich soil at depths of 6 - 12 inches. Trichoderma was not uncommon below the

A_1 horizon of acid soils as shown also by Warcup (1951) and Jefferys et al (1953). 61 isolations of Trichoderma were made from soil of the semi-fixed and fixed dunes at a depth of 0 - 2 inches using slide traps compared with 26 at a depth of 5 - 6 inches, but its spread often appeared to terminate abruptly at the limit of an organic horizon. Its appearance in subsurface soil was usually associated with concentrations of organic matter and it was among species found in pockets of organic matter buried in the otherwise rather arid sands of the foredunes. This species has been shown to be fairly tolerant of high concentrations of carbon dioxide (Burges, 1953), so its vertical distribution may, it seems, be determined by the nutrient status of the available substrates rather than by aeration.

The distribution of Mortierella alpina was somewhat irregular. Its frequency usually decreased with depth, but occasionally, as at Blakeney, it was isolated from only the deepest parts of the profile. A possible explanation is that it was ousted either in the soil or in culture by a competitor. It is noteworthy that Trichoderma was infrequent at those profile levels at which M. alpina was common.

(ii) Ubiquitous species.

Species of the second group, which occurred throughout the profile without an obvious gradient in their vertical

distribution, appear to be tolerant of a relatively wide range of conditions in their environment. Gliomastix convoluta v. felina, which Burges found was "intermediate" in its reaction to carbon dioxide, was a member of this group.

(iii) Subsurface species.

The maximum frequency of Mucor ramannianus and Penicillium restrictum (form B)* usually occurred, as shown below, in subsurface soil.

		% Frequency of Occurrence				
	Soil Depth	0.5"	1"	3"	6"	12"
STUDLAND						
Dune Heath	M. ramannianus	10	0	10	20	30
	P. restrictum	10	10	40	50	50
"Southern Heath"	M. ramannianus	0	10	10	20	50
	P. restrictum	0	10	40	50	30
Pteridium Heath	M. ramannianus	30	20	30	60	40

The vertical soil range of Mucor ramannianus has been commented on by several workers. Jefferys et al (1952) found M. ramannianus was most frequent in the lower levels of the A horizon and in the B horizon of acid podsols, and they considered that the absence of this species from a particular profile might be associated with the absence of a well

---

* A strain resembling Aspergillus sydonis (Raper and Thom, 1949), and readily distinguished from the strain common in alkaline dunes by its colony characters.

defined pan. McLennan and Ducker (1954) found some evidence in support of this view. Sewell (1954) found, however, that it was most frequent in the leached A_2 horizon and least frequent in the B_2 iron pan and he showed it was sometimes frequent in profiles without a pan. In dune soils the frequency of M. ramannianus appeared to be unrelated to pan development. In the three zones of dune heath examined the frequency increased down the profiles to a maximum in humus-poor sand in the presence or absence of a pan. It may be argued that the apparent reduction in frequency at surface soil levels is an effect of competition in culture. Early excision from the soil plates of species with a spreading type of growth did not, however, result in an increase in the number of M. ramannianus colonies.

The lower limit of the vertical range of M. ramannianus was often clear cut although the sand above and below it appeared to be similar. This phenomenon was possibly caused by a downwash of spores with a well-marked advance front. Ovington (1950) and Wright (1955) noted that moisture falling on a dune moves down the profile as a compact mass under the influence of gravity, its upper and lower boundary remaining sharply defined when the sand is texturally uniform.

At Studland and Tentsmuir the distribution of M. ramannianus was somewhat anomalous, as it was isolated from only the surface soil of the semi-fixed dune zone - the stage before dune heath in the succession. The fungus

perhaps migrates to lower depths with profile development and entry of more competitors, but at Tentsmuir it appeared to be restricted to the A_1 horizon, not only of the semi-fixed dunes, but also of the dune heath, in contrast to the findings at Studland. A strain difference may be involved; it was noted that surface isolates spored more prolifically in culture than those from subsoil. The vegetative growth and sporulation of P. restrictum (form B) was also relatively restricted in culture compared with that of strains inhabiting surface soil.

Bisby et al (1935) after an investigation of sub-surface populations suggested that "physiological and morphological strains may develop during a long sojourn deep in the soil."

Section II

(d) A Comparative Estimate of the Quantity of Fungal Mycelium in Dune Soils by the use of a New Modification of the Impression Slide Technique.

A satisfactory method for the quantitative estimation of soil fungi has not as yet been devised. In fact, it is doubtful whether it will ever be possible to determine the "number" of fungi in a given quantity of soil, for, as Burges (1939) pointed out, the expression "individual fungus" has no real meaning in the sense that we may talk of individual bacteria. Without such a precise fungal unit, estimates have been made of colony numbers in culture and of the length, coverage or number of mycelial fragments in microscopic fields - quantities which within the experimental limits are far from critical. The problem of the determination of the total weight of viable fungal mycelium in a given amount of soil is also unsolved, since the complete separation of fungus material from soil, from other groups of micro-organisms with which it is associated, and from its own non-viable component has not been achieved.

Most attempts at the quantitative estimation of soil fungi have entailed the removal of the mycelium from the coarser soil fractions by shaking, grinding and centrifuging processes, and the preparation of a soil suspension. The fungi in this suspension have then been examined by a direct observational method (Winogradsky 1925 - primarily a bacteriological technique; Jones and Mollison 1948) or have been cultured before enumeration (Waksman, 1922; Brierley, Jewson and Brierley, 1927).

Cultural techniques, including the widely used dilution plate technique, have already been referred to and their short-comings as quantitative methods have been pointed out.

Jones and Mollison's direct method is ingenious. The soil suspension is diluted with melted and cooled agar and films of constant thickness prepared from it with the aid of a haemocytometer slide. The length or number of mycelial fragments in random microscope fields are then determined on a soil weight basis. This method was applied in the present investigation to sand dune soils, but its use was discontinued when it was found that the removal of the coarse sand fraction

resulted in the virtual absence of mycelium from the final preparations of young dune soils. Mycelium was known to be present in these soils from preliminary examinations, which showed that the hyphae were often closely wrapped around the sand grains. Even if the removal of mycelium was more complete, the method would be of doubtful quantitative value because of the unsatisfactory method of standardising the amount of soil used. A quantitative comparison of mycelium in various soil types on a soil weight basis is not justifiable, even on a single dune system, where the range of soil type as regards soil particle dimensions is considerable - a criticism which applies to all the above methods.

The Rossi-Cholodny (1930) slide technique has been used by some workers for quantitative or semi-quantitative purposes. Jensen (1935) divided the slides into microscopic quadrats and determined the percentage number of fields showing the presence of fungal hyphae. King, Hope and Eaton (1934) made subjective estimates of the approximate area of the slides occupied by various taxonomic groups of the soil population and Verplancke (1932) attempted to

relate population counts to soil weight by weighing the slides before and after preparation. This method does not, however, lend itself to quantitative analyses, since the estimations are made of mycelium which has grown over the artificial habitat of the slides after a period of incubation, and not of mycelium present at any one moment in the soil.

With the above considerations in mind, it was felt that some direct method of examining the soil, which did not involve the removal of the coarser sand grains, and which would yield quantitative results on a comparative rather than a finite basis, would be the most promising line of approach to an estimate of the variation in the total amount of fungus mycelium from one dune type to another and at different stages of dune development. A modification of Rossi and Riccardo's (1927) impression slide technique for the examination of soil micro-organisms was therefore adopted.

Rossi obtained soil films or "impressions" by pressing clean glass slides, or slides smeared with agar or gelatin, momentarily against a prepared soil surface; the micro-organisms which adhered to the slides were then fixed and stained. It was found in the present investigation that the amount of material which adheres to a clean glass slide in this way was too small and variable for quantitative

purposes. If, however, a fairly strong adhesive was smeared over the slides, relatively even soil films could be obtained during brief contact with the soil. The adhesive must spread evenly over the glass; be semi-transparent to allow the passage of light during microscopic examinations, and not take up fungal stains or mix readily with water. After preliminary trials with various adhesives, nitrocellulose thinned to a convenient consistency with amyl acetate was found to be suitable in these respects and was used throughout the following experiments.

The difficulty of examining the soil films at high magnifications without the removal of the coarse mineral particles, as is usual in the preparation of impression and contact slides, was overcome by the use of a metallurgical objective which, with its relatively long working distance, permitted the examination of the unmounted soil films at all depths of focus.

Satisfactory impressions of soils with a relatively high organic content, such as the peaty surface horizons of old dune heath, were sometimes difficult to obtain because of clumping of the rather sticky soil aggregates. Further, a certain amount of mycelium within the humus particles was probably obscured from view and the figures given for these organic layers may be somewhat low. This impression technique is thus primarily a method for the examination

of soils of the dune type with a low humus status, and of special value in coarse grained sands.

Variations in the adhesive powers of the soil constituents and in the amount of pressure applied when the impressions are taken may alter the denseness of the soil films. It is, therefore, important to standardise the procedure as far as possible; to spread the adhesive thinly and evenly, and to press lightly so that most of the material which adheres is that originally flush with the soil surface. With careful attention to such details good replicate slides could usually be obtained which appeared to reflect closely the normal spatial arrangements of the soil particles. The heterogeneous nature of the soil and the irregular distribution of its micro-organisms probably does not warrant greater precision in the preparation of these films for comparisons of total mycelium in equivalent areas of soil.

A disadvantage shared by other direct observational methods is that the fungi cannot in general be identified on their natural vegetative characters alone, so that the quantitative estimates must be of total mycelium. Features such as the septation, branching and colouring of the hyphae were, however, often clearly visible, and conidiophores occasionally distinguishable.

An important merit of the technique is that it is both quick and simple to apply. Large numbers of slides can

be prepared at a time and, since the preparations are permanent, the final recordings can be made and repeated at leisure. Furthermore, the soil is disturbed relatively little so that the mycelium, including that of species which have not been isolated in artificial culture, is seen in its natural relationship to the soil.

Procedure:

Sterile glass slides were smeared evenly over a central area (2" x 1") with nitrocellulose in amylacetate immediately before contact was made with the soil. The adhesive was applied with a brush. Preparations were made both from soil removed from the field and from the vertical face of soil profiles in situ; numerical results for the latter only are recorded here. The slides were pressed against the soil for approximately 20 seconds and then left to dry in covered containers. When dry, excess material not touching the adhesive could be removed by gently tapping the slide. The soil films were then stained for one hour in phenolic aniline blue (Jones and Mollison 1948), quickly rinsed in sterile distilled water and dried. The dry mounts were examined by reflected and transmitted light using a combination of an 8 mm. metallurgical objective, bloomed and corrected for uncovered mounts, and a (x 25) compensating ocular eyepiece.

Comparative quantitative estimates of the amount of

mycelium on these slides were made by recording the presence and absence of mycelium in microscopic quadrats (side length 55 μ). A thousand quadrats were examined for any one soil type and for any one soil depth, distributed over five replicate slides. Ten random microscope fields each divided into twenty quadrats were analysed on every slide. The quadrats were delimited by inserting in the eye piece a glass disk ruled in squares. The films were focussed at all depths before the recordings were made.

Comparative estimates of total mycelium by means of impression slides were made for all dune zones and soil depths included in the detailed soil plate investigation at Sandwich and Studland. Very fine mycelium believed to be that of actinomycetes was not included.

The figures given in table 19 represent the percentage number of microscopic quadrats (side length 55 μ) in which mycelium was present i.e. % frequency of occurrence of mycelium. A thousand quadrats were examined for each sample.

The values given for the soil pH and organic content are average figures for the dune systems.

TABLE 19

% FREQUENCY OF OCCURRENCE OF FUNGAL MYCELIUM IN DUNES SOILS - ESTIMATED BY AN IMPRESSION SLIDE TECHNIQUE.

STUDLAND

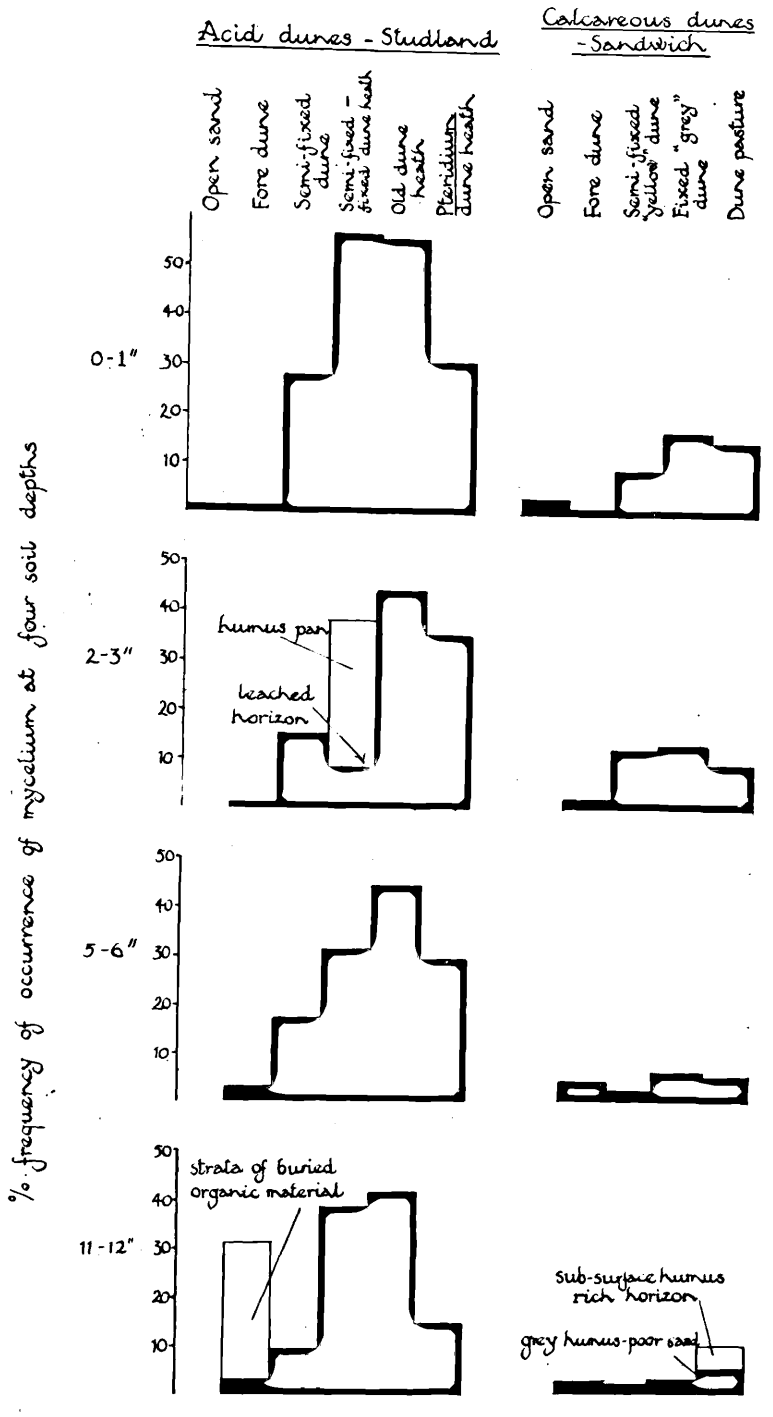
DUNE ZONE	Soil Depth	% frequency of Mycelium	SOIL PROFILE FEATURES	Soil pH Range	Soil Organic Content (% Loss on Ignition)
OPEN SAND (OS)	0-1"	1		6.4-7.3	0.2
FORE DUNES (FD)	0-1"	1)		6.6-7.0	0.2
" "	2-3"	1)	Undifferentiated	6.8-7.2	0.2
" "	5-6"	3)		6.1-7.5	0.2
" "	11-12"	3)		6.2-7.5	0.2
" "	11-12"	31	Pockets of buried organic material	-	-
SEMI-FIXED "DUNE GRASS" (DG)	0-1"	28	Humus horizon	4.3-5.3	0.7
" " " "	2-3"	15	Transition to white sand	4.6-5.8	0.2
" " " "	5-6"	17	↓	4.7-5.8	0.3
" " " "	11-12"	9	↓	5.4-6.6	0.2
FIXED DUNE HEATH (DH)	0-1"	57	Humus horizon	3.7-4.3	2.0
" " "	2-3"	8	Leached horizon	3.6-4.0	0.3
" " "	2-3"	38	Indefinite humus pan	3.5-4.0	9.2
" " "	5-6"	31	Transition to grey sand	4.0-4.6	0.7
" " "	11-12"	38	with bands of humus	3.8-4.9	0.3
OLD FIXED DUNE - SOUTHERN HEATH	0-1"	56	Sandy peat horizon	3.5-4.2	11.9
" " " " (SH)	2-3"	44	Transition to grey sand	3.2-4.0	0.5
" " " " "	5-6"	44	↓	3.5-4.7	0.2
" " " " "	11-12"	41	↓	4.1-4.6	0.2
PTERIDIUM DUNE HEATH (BH)	0-1"	31	Sandy peat horizon with	3.1-4.0	2.2
" " "	2-3"	35	pockets of wind-blown sand	3.2-4.3	0.5
" " "	5.6"	29	Transition to grey sand	3.7-4.6	0.2
" " "	11-12"	14	↓	4.0-5.0	0.2

continued

Table 19. contd.

SANDWICH

DUNE ZONE	Soil Depth	% frequency of Mycelium	SOIL PROFILE FEATURES	Soil pH Range	Soil Organic Content (% Loss on Ignition)
OPEN SAND (OS)	0-1"	3		7.7-9.1	1.3
FORE DUNES (FD)	0-1"	1	Undifferentiated profile	7.4-9.1	0.8
" "	2-3"	2	↓	7.7-9.7	0.7
" "	5-6"	4	↓	7.6-8.9	0.7
" "	11-12"	3	↓	7.5-8.8	0.8
SEMI-FIXED "YELLOW" DUNES (YD)	0-1"	9	Sandy humus horizon covered with wind blown sand	6.8-9.9	1.5
" " " "	2-3"	12	↓	7.4-8.5	1.2
" " " "	5-6"	2	Transition to clean yellow	7.4-8.6	0.7
" " " "	11-12"	2	sand	7.4-9.2	0.8
FIXED "GREY" DUNES (GD)	0-1"	17	Humus horizon	6.8-7.6	2.2
" " "	2-3"	13	↓	7.2-8.0	0.9
" " "	5-6"	6	Transition to yellow	5.6-8.8	0.8
" " "	11-12"	3	sand	7.4-8.3	0.6
DUNE PASTURE (DP)	0-1"	15	Humus horizon	6.5-7.7	3.2
" "	2-3"	9	↓	7.0-7.7	2.6
" "	5-6"	5	Transition to grey sand	6.9-7.8	2.0
" "	11-12"	5	↓	7.2-8.4	1.0
" "	11-12"	10	Subsurface humus bands	-	4.5



Percentage frequency of occurrence of fungal mycelium in dune soils estimated by an impression slide technique.

Three points stand out from the above analysis, namely that the mycelial content of these dune soils differs widely with dune type, increases rapidly with dune development, and in general decreases with increasing soil depth.

The difference between the two dune systems is striking. Except in the open sand and fore dunes where soil conditions in the two systems are most alike, the acid dunes contain about 2 - 4 times as much mycelium as the alkaline dunes, the highest frequency figure for Studland being 57% (fixed dune heath) and for Sandwich only 17% (fixed "grey" dune). It is widely held that acid soils contain a richer fungus flora than alkaline soils where bacteria are more common (Waksman 1924). Warcup (1951) pointed out that this view was based mainly on counts of fungal colonies in culture, which might reflect the high sporing capacity of a few fungi rather than a high level of fungal activity in the soil. Jensen (1931), however, concluded from direct microscopical examinations that larger amounts of mycelium occur in acid than in alkaline or nearly neutral soils, and the above results to some extent confirm this observation. Whether or not soil reaction is directly responsible for this differential distribution of mycelium is uncertain and many factors including bacterial competition and attack may be involved.

The mycelial content of the open shore and fore dunes

of both systems is very low, except in the vicinity of pockets of buried organic material, but rises rapidly when the dunes become semi-fixed, reaching a maximum in the surface soils of the fixed dunes. Frequencies below the maximum in the Pteridium-heath dune may be correlated with the presence in this zone of miniature blow-outs and pockets of wind blown sand round decaying Pteridium plants. A slight decrease in the amount of mycelium occurs also in the dune pasture zone of the calcareous system. This possibly reflects a decrease in aeration or an increase in the bacterial population. The vegetational cover is more dense, the soil profile is more compact and bacteria appeared from their growths on soil plates to be more prevalent here than in the preceding zone of "grey" fixed dune.

The amount of mycelium at various levels of the soil profile appears to depend both on soil depth and on soil organic content. Thus although there is a general tendency for the amount of mycelium to decrease with depth from a maximum at the surface, a subsurface increase in organic content is often paralleled by a rise in mycelial content.

An interesting reversal of the normal biological profile occurs in the fore dunes. Here the humus-rich A_1 horizon is absent, and the upper layers of sand are unstable and often dry, but at lower depths moisture increases and pockets of buried organic material occur. Correlated with these

profile features is the slight general increase in mycelial content with depth and the presence of subsurface flushes (see table 19). Similarly where the A_1 horizon is often covered by wind blown sand, as on the semi-fixed dunes at Sandwich, the maximum quantity of mycelium occurs just below the surface. Again, in the dune pasture zone a secondary rise occurs where humus-bands traverse the subsurface sand, and in the podsolised dune heath soils a marked fall in mycelial content from 57% at the surface to 8% in the leached A_2 horizon is followed by a rise to 38% in the B_1 humus pan, confirming earlier reports on the nature of the micro-biological profiles of podsols (Gray and Taylor 1935; Jefferys et al 1953).

The amounts by which the mycelium content of these subsurface humus horizons rises is not as great as might be expected from a consideration of the organic content alone and is a further illustration of the fact pointed out by Timonin (1935) and Stenton (1954) that micro-organisms decrease with depth despite high concentrations of organic matter.

Little attempt was made to classify the mycelium into types, but dematiaceous hyphae (D) appeared to be more closely associated with humus particles than the hyaline or light coloured hyphae (H), which often occurred as extensive branching growths between the sand grains, and

the ratio D : H sometimes tended to be higher in the humus-rich horizons. Some error in the figures must be assumed due to the probable inclusion of a certain amount of non-viable dematiaceous mycelium in the estimates.

Ratio of Dematiaceous : Hyaline or Light Coloured Hyphae in Fixed Dune Heath Soil, Studland.

Soil Horizon.	A_1	A_2	B_1	C
D : H	2.4	0.0	0.8	1.0

In general the number of colonies on the soil plates reflected the variations in the size of the fungus population shown by this impression slide technique. There was, however, rather more mycelium at the lower depths of the acid dunes than expected from the soil plate examinations; this is possibly correlated with a decline in sporing capacity with depth. Mycelium was, however, sometimes frequent in soil which appeared to be practically sterile when cultured, suggesting an incomplete isolation of the soil fungal component by cultural techniques.

Spores appeared infrequently on the impression slides and no estimate was made of their numbers.

Section III. The Fungal Populations on the Surface of the Rooting Systems of *Ammophila arenaria* (L.) Link and *Carex arenaria* L. and their Relationships with the "Free" Soil Mycoflora.

A definite line cannot be drawn between the fungus populations of the "root region"* and the surrounding "free" soil because their microhabitats merge. It was felt, therefore, that some investigation of the dune root region fungi was warranted since they might have a considerable influence on the establishment and succession of fungi in dune soils.

The relatively simple ecosystem of the young dunes in particular, and the presence of *Ammophila* as a dominant in a number of different dune soil types, provided a unique opportunity for such a study of the possible correlations between the root and soil distribution of fungi in a natural habitat.

Root region fungi have been the subject of extensive researches, but these will not be referred to in any detail as they have been comprehensively reviewed by Garrett (1938); Burges (1939); Katznelson, Lochhead and Timonin (1948); Harley (1948) and Clark (1949).

The congregation of soil micro-organisms that occurs on

---

* The term "root region", as applied by Harley (1948), includes two zones influenced by the root, these being the root surfaces and the rhizosphere soil.

and around root systems is a phenomenon which has been demonstrated by a number of research workers, since Hiltner in 1904 recognised and defined the rhizosphere as: the zone of enhanced microbiological activity immediately around a root. The nature of this root region fungal community has been studied more from the quantitative than from the qualitative aspect. Evidence of preferential stimulation of certain fungi by plant roots is inconclusive (Katznelson et al, 1948), but Thom and Humfeld (1932) and Kürbis (1936) have shown, in attempts to determine the relative importance of "host" plant and soil type, that there is a certain uniformity among the root fungus floras of a species growing under various soil conditions. It will be seen that such a uniformity is not apparent in the dune ecosystem.

Qualitative studies have been made of the distribution of fungi on the root systems of a few specific plants, including wheat (Simmonds and Ledingham 1937) and beech (Harley and Waid 1955), but as regards the relationship between the spatial distribution of fungi of the free soil and of the root region down a soil profile little is known.

Ammophila arenaria and Carex arenaria were the "host" plants chosen for the present investigation because they are among the dominants of both the acid and alkaline dune systems, and the former species occurs both as a pioneer colonist of the youngest dunes, and as a member of the fixed

dune flora, so that it offered possibilities of following changes in the root microflora with dune development.

Nicolson (1955) studied the vesicular-arbuscular endophyte "infecting" Ammophila arenaria roots in relation to dune succession. The incidence of "infection" was found to vary according to the vegetation zone and soil depth. Mycorrhiza were not observed in the present investigation.

The root microfloras of Agropyron junceum, Ammophila arenaria and Atriplex babingtonii growing in the foreshore zone of the St. Cyrus dune system were investigated by Webley, Eastwood and Gimingham (1952). The existence of a relatively dense rhizosphere flora round the root systems of these species was demonstrated using a dilution technique and differences in the bacterial root floras of Ammophila and Agropyron were indicated, but the fungus floras were apparently relatively uniform. However, the floristic data given by these authors was scanty and comparisons between root and soil fungal populations were made on a generic basis only.

Webley et al attempted to investigate both the root surface and the rhizosphere microflora of these dune plants and claimed to be able to separate one from the other by a washing technique. The root system was subjected to two washing processes, the first of which was continued until

all adhering sand had been removed and provided the source of their rhizosphere fungi and the second of which provided the source of their so-called "root surface" fungi. The point at which separation is assumed to have occurred seems purely arbitrary, and the "root surface" fungus flora as defined by these authors must be considered as a mixed population of rhizosphere fungi and true root surface fungi. As Harley and Waid (1955) have pointed out, there is probably little information to be gained by a study of such a mixed population derived from a variety of microhabitats.

The following study was restricted as far as possible to the active root surface fungi, that is, to those fungi believed to be closely adhering or actually attached to the root surface and with, therefore, a relatively well defined microhabitat. These fungi were examined in situ after removal of the rhizosphere micro-organisms by washing with sterile water. Similar techniques have been used by Simmonds and Ledingham (1937); Kürbis (1931); Robertson (1954) and Harley and Waid (1955). Repeated washings in sterile water appear to be an efficient means of cleansing roots and preferable to the more drastic and less easily controlled treatments with poisonous surface sterilising agents as used by Glynne (1939). The complete removal of spores clinging to the root surfaces is not ensured by these cleansing methods, but there was no evidence for

their presence in any number.

Procedure

Adventitious roots and rhizomes were collected from the following dune zones and soil depths:

Species	SANDWICH			STUDLAND		
	DUNE ZONE	SAMPLING DEPTH	Soil pH	DUNE ZONE	SAMPLING DEPTH	Soil pH
AMMOPHILA ARENARIA Adventitious roots only	FORE DUNE (Ammophila dominant)	0-6") Soil horizons 6-12") not visible	7.4-9.1 7.5-8.9	FORE DUNE (Ammophila dominant)	0-6") Soil horizons 6-12") not visible	6.1-7.5 6.2-7.5
	SEMI-FIXED DUNE (Ammophila dominant)	0-3" A_1 humus horizon 3-6") "Humus-poor" 6-12") Subsoil	6.8-8.5 7.4-8.6 7.4-9.2	SEMI-FIXED "DUNE GRASS" (Ammophila and Carex co-dominant)	0-3" A_1 humus horizon 3-6") "Humus-poor" 6-12") subsoil	4.3-5.8 4.7-5.8 5.4-6.6
	SEMI-FIXED -FIXED DUNE (Carex dominant)	0-3" A_1 humus horizon (Material below 3" was insufficient to make collection practicable)	6.8-7.6	FIXED DUNE HEATH (Ammophila and Calluna co-dominant)	0-3" A_1 "Humus-rich" horizon 3-6") "Humus-poor" 6-12") subsoil	3.7-4.3 4.0-4.6 4.0-4.9
CAREX ARENARIA Adventitious roots and rhizomes	SEMI-FIXED -FIXED DUNE (Carex dominant)	0-6" (most roots located at a depth of 2-4" in and just below A_1 horizon)	5.6-8.8	SEMI-FIXED "DUNE GRASS" (Ammophila and Carex co-dominant)	0-6" (most roots located at a depth of 2-4" in and just below A_1 horizon)	4.3-5.8

The rhizome surface investigations were unfortunately restricted and made only on Carex arenaria because of limited time, and will not be discussed in detail.

Small quantities of Ammophila roots collected from the fore dunes of the Berrow and Tentsmuir dune systems were also examined for comparison with the findings at Sandwich and Studland.

Full scale collections of material were made in the spring of 1954 and repeated in the autumn of 1954. The plants selected for sampling appeared to be fully grown and were as widely separated as possible within the experimental area - the choice was otherwise arbitrary. 6 plants per dune zone were sampled on each occasion. The roots from each sampling depth were excavated and collected separately but were always traced to the parent rhizone in order to verify their origin. The material was transported to the laboratory in sterile containers and, unless it could be examined within 24 hours, was stored in a refrigerator. Roots with obvious lesions were discarded.

The main aim of this analysis was the determination of the composition of the root surface fungal flora as a whole within certain soil habitats rather than the demonstration of the pattern of distribution of fungi along an individual root. For this reason the root material was classified into 3 groups according to root diameter ($\leq$ 0.5 mm; 0.5 -

1 mm. and 1 - 2 mm.) so as to include roots of all types and ages and little attempt was made to relate the fungal distribution to root development.

The roots were rinsed in sterile water and cut into approximately 2 mm. long segments which were washed in 4 changes of water for 20 minutes by means of a device described by Simmonds (1930). This device includes an aerator system for agitation of the material during washing and enables repeated and rapid changes and drainage of water to be made under sterile conditions. During preliminary trials dilution plates were prepared from the separate washings after they had been centrifuged and it was found that, whereas the fungal content of the first washings was relatively large, that of the third and fourth washings was negligible. Microscopic examination of squashes of root fragments washed by the above process, and stained with cotton blue in lactophenol showed the presence of fungal hyphae on the root surface, but fungal spores were not observed.

The washed root segments were blotted free of surplus water on sterile filter paper to prevent excessive growth of bacteria and were then plated in agar by gently pressing them below the surface of the medium. 5 segments were arranged equidistantly from one another in each petri-dish. Warcup's (1950) modified Czapek-Dox agar with the addition

of rose bengal (1 : 15,000) was used in all the root experiments as for soil plates and the pH of this medium was adjusted by the addition of sodium hydroxide or phosphoric acid to approximate to that of the soil from which the roots had been excavated.

The root plates were incubated at room temperature and examined for the isolation and identification of fungi over a period of 3 weeks. Recordings were made for every root segment of the occurrence of species and not less than 100 segments of any one size group and from any one soil sampling depth were examined in this way. Competition between species developing from the same segment was an inevitable source of error, but it was overcome to some extent by isolating the majority of the more restricted growth types during the first few days of development before they had been overgrown.

Control experiments with sterilised root segments were run and water from the washing apparatus was examined from time to time for the presence of fungal contaminants.

The Carex rhizomes were, after the removal of leaf sheaths, treated in the same way as roots. No attempt was made to relate the fungal population with the presence or absence of a leaf sheath. In the following discussions rhizomes are included under the general term of "root" unless otherwise stated.

Section III.

(a) The range of species isolated and their general distribution on the root surfaces.

60 spore-forming species and 22 sterile mycelial forms were isolated from the root surfaces of Ammophila arenaria and Carex arenaria. These are listed in table 20 with their source of isolation. The majority were typical soil fungi. Only 9 of the spore-formers were not obtained from the free soil of the dunes and these, including species of Alternaria, Camarographium, Fusarium and Hendersonia, genera often found as parasites or saprophytes of plant tissues, were of sporadic occurrence. Of species with a frequency of occurrence of 50% or more in the free soil, only three, Cephalosporium S33, Verticillium nigrescens (?) and the unidentified species S312, were not encountered on the root surfaces of either Ammophila or Carex, possibly because these species of relatively restricted growth failed to compete with neighbouring species when provided with an artificial nutrient medium.

Carex arenaria was examined from only one soil zone in each dune system; its investigation was, therefore, more limited than that of Ammophila, but it showed that the root surface fungus floras of these two species growing in the same soil do not differ strikingly. The four species isolated most commonly from the Carex - Absidia spinosa;

TABLE 20

SPECIES OF FUNGI ISOLATED FROM ROOT SURFACES

A - isolations from Ammophila arenaria
C - " " Carex arenaria
S - " " free soil

Species	A	C	S
Absidia glauca Hagem	+	+	+
A. spinosa. Lendner	+	+	+
Mortierella alpina. Peyronel	+	+	+
M. isabellina. Oud	+	-	+
M. marburgensis. Linn	+	-	+
M. parvispora. Linn	+	-	+
Mucor hiemalis. Wehmer	+	-	+
M. piriformis. Fischer	+	-	-
M. ramannianus. Moller	+	-	+
M. sylvaticus. Hagem	+	-	-
Gymnoascus sp. S947	-	+	+
Sporomia intermedia. Auerswald	-	+	+
Alternaria sp. S910	+	-	-
Alternaria sp. S943	-	+	-
Botrytis cinerea. Persoon	+	-	+
Camarographium sp.	+	-	-
Cephalosporium sp. D1776	+	-	+
Cephalosporium sp. D1391	+	-	-
Cladosporium herbarum (Persoon). Link	+	-	+
C. macrocarpum. Preuss	+	+	+
Coniothyrium sp. S10	+	-	+
" " D20	+	+	+
Fusarium culmorum. (W.G.Smith) Saccardo	+	+	+
F. oxysporum. Sensu Snyder & Hansen	+	+	+
Fusarium sp. S497	+	+	-
Gliomastix convoluta v. felina. (Harz) Mason	+	-	+
Harposporium. S890	+	+	+
Hendersonia sp. S937	-	+	-
Microdiplodia sp. D388	-	+	+
Papularia arundinis. (Corda) Fries	+	+	+
P. sphaerosperma. (Pers. ex. Fr.) von Höhnel	+	-	+
Penicillium adametzi. Zaleski	+	+	+
P. brevi-compactum. Dierckx	+	-	+
P. cyaneo-fulvum. Biourge	+	+	+
P. cyclopium. Westling	+	+	+
P. decumbens. Thom	+	-	+
P. lividum. Westling	+	-	+
P. melinii. Thom	+	+	+
P. namyslowskii. Zaleski	+	-	+
P. nigricans. Bainier	+	+	+

Table 20 contd.

Species	A	C	S
Penicillium restrictum. Gilman & Abbott (Form A)	+	-	+
" " " " (Form B)	+	-	+
Penicillium spinulosum. Thom	+	+	+
P. terlikowskii. Zaleski	+	-	+
P. thomii. Maire	+	-	+
P. thomii series. D28	+	-	+
Penicillium sp. D381	+	-	+
" " D946	+	-	+
" " D1030	+	-	+
Penicillium sp. D1070	+	-	-
Phomopsis sp. D1800	+	-	+
Pullularia pullulans. (De Bary) Berkhout	+	-	+
Pyrenochaeta sp. D40	+	+	+
Stemphylium sp. S23	+	+	+
Tilachlidium sp. S546	+	+	+
Trichoderma viride. Pers. ex. Fr.	+	+	+
Verticillium sp. D784	+	-	+

3 unidentified sporing species)
)
1 mycelium bearing clamp connections)
) root
14 dark coloured sterile mycelia) isolates
)
7 hyaline or light coloured sterile mycelia)

Harposporium S890; Penicillium nigricans and P. restrictum were all common on Ammophila. Five species were restricted to Carex, but these were all of rare occurrence and there was no evidence of a preferential stimulation of fungi by either plant.

The figures obtained for the frequency of occurrence of fungi on the root surfaces (table 21, 22) cannot be directly compared with those for the free soil, but from the amount of mycelium that grew from the roots it appeared that Fusarium species, Penicillium cyclopium and Trichoderma viride were more abundant on the root surfaces than in the soil. This seems all the more certain when it is remembered that the advantage given to heavily sporing hyphomycetes on dilution and soil plates is not operative on the root plate, where it is thought that the majority of the colonies develop from active mycelium or from resting bodies of the chlamydospore and sclerotial type rather than from conidia, most of which it is hoped have been removed by washing.

One of the most striking features of the root surface fungus population was the discontinuous distribution of some of its members. Several species, Coniothyrium S10; Fusarium culmorum; F. oxysporum; Penicillium cyclopium; P. nigricans; P. spinulosium; and Trichoderma viride in particular, often occurred in runs or "flushes" along a root over a distance of several millimetres, although they were

TABLE 21

% FREQUENCY OF OCCURRENCE OF SPECIES OF FUNGI ON THE ROOT SURFACE OF AMMOPHILA ARENARIA

Figures based on the analysis of 300 root segments at each depth

		SANDWICH					STUDLAND					
	DUNE ZONE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	
	SOIL DEPTHS & HORIZONS SAMPLED	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	Sand 6-12"
	Soil pH	7.4-9.1	7.4-8.9	6.8-8.5	7.4-9.2	6.8-7.6	6.1-7.5	6.2-7.5	4.3-5.8	4.7-6.6	3.7-4.3	4.0-4.9
Culture No.	Species											
	Absidia glauca	-	-	8	-	6	-	-	-	-	-	-
	A. spinosa	-	-	-	-	18	-	-	-	-	2	3
	Mortierella alpina	1	6	-	2	4	-	-	-	-	-	-
	M. isabellina	-	-	-	-	-	-	-	-	-	7	2
	M. marburgensis	-	-	-	-	-	-	-	-	-	1	-
	M. parvispora	-	-	-	-	-	-	-	-	7	<1	2
	Mucor hiemalis	1	-	6	1	5	4	8	-	-	-	-
	M. piriformis	-	-	-	-	-	5	1	-	-	-	-
	M. ramannianus	-	-	-	-	-	-	-	-	3	25	50
	M. sylvaticus	-	-	-	-	-	1	-	-	-	-	-
S910	Alternaria sp.	-	-	-	-	2	-	-	1	-	-	<1
S943	" "	-	1	-	-	-	-	-	-	-	-	-
	Botrytis cinerea	-	-	-	1	-	-	-	1	<1	-	-
D1629	Camarographium sp.	2	-	-	-	-	-	-	-	-	-	-
	Cephalosporium acremonium	-	-	-	-	-	5	2	-	-	-	-

continued

Table 21 .
contd.

	DUNE ZONE	SANDWICH					STUDLAND					
		FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	
	SOIL DEPTHS & HORIZONS SAMPLED	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	Sand 6-12"
	Soil pH	7.4-9.1	7.4-8.9	6.8-8.5	7.4-9.2	6.8-7.6	6.1-7.5	6.2-7.5	4.3-5.8	4.7-6.6	3.7-4.3	4.0-4.9
Culture No.	Species											
D1776	Cephalosporium sp.	-	-	-	-	-	-	-	-	-	-	-
D1391	" "	-	-	-	-	-	1	-	-	-	-	-
	Cladosporium herbarum	4	6	2	5	2	6	1	1	-	2	<1
	C. macrocarpum	-	-	-	1	-	-	-	-	-	-	-
S10	Coniothyrium sp.	1	4	18	17	-	1	1	-	-	-	-
D20	" "	-	-	-	-	-	-	6	-	<1	-	-
	Fusarium culmorum	1	-	8	1	2	3	6	1	1	-	-
	F. oxysporum	4	2	21	9	4	-	-	-	-	-	-
S497	Fusarium sp.	-	-	-	-	-	2	-	-	-	-	-
	Gliomastix convoluta v. felina	1	3	-	-	-	-	-	-	<1	<1	-
S890	Harposporium sp.	16	-	1	4	6	11	1	-	-	-	-
	Papularia arundinis	11	1	1	1	-	2	1	2	-	-	<1
	F. sphaerosperma	-	-	-	-	-	-	1	-	-	1	-
	Penicillium adametzi	-	-	-	-	-	-	-	-	<1	18	-
	P. brevi-compactum	-	-	-	1	-	-	-	-	-	-	-
	P. cyaneo-fulvum	<1	-	1	-	-	-	-	-	-	-	-
	P. cyclopium	11	-	-	-	-	24	45	14	9	15	4
	P. decumbens	-	-	-	-	-	-	-	-	<1	-	-

continued

Table 21
contd.

		SANDWICH					STUDLAND					
DUNE ZONE		FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	
SOIL DEPTHS & HORIZONS SAMPLED		0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	Sand 6-12"
Soil pH		7.4-9.1	7.4-8.9	6.8-8.5	7.4-9.2	6.8-7.6	6.1-7.5	6.2-7.5	4.3-5.8	4.7-6.6	3.7-4.3	4.0-4.9
Culture No.	Species											
	Penicillium lividum	3	-	2	3	2	-	1	2	<1	1	-
	P. melinii	2	-	-	-	-	<1	-	1	7	2	1
	P. namyslowskii	-	-	-	-	-	-	-	-	-	1	-
	P. nigricans	-	-	-	-	1	<1	7	80	42	<1	-
	P. restrictum (form A)	1	16	10	32	15	-	-	-	-	-	-
	" " (form B)	-	-	-	-	-	-	-	-	-	2	1
	P. spinulosum	-	1	6	3	-	1	2	5	6	26	15
	P. terlikowskii	-	-	-	-	-	<1	-	-	-	-	-
	P. thomii	<1	2	-	-	-	-	-	-	-	2	-
D28	*P. thomii* series	1	-	-	-	-	-	-	-	-	-	-
D381	*Penicillium* sp.	-	-	-	-	-	-	-	-	1	-	-
D946	" "	-	-	-	-	-	-	-	-	1	-	-
D1030	" "	1	-	-	-	-	-	-	-	<1	-	-
D1070	" "	-	-	-	-	-	-	-	-	1	-	-
D1800 ?	*Phomopsis* sp.	-	-	-	-	-	-	-	-	-	1	-
	Pullularia pullulans	1	-	-	-	-	1	-	-	-	-	-
D40	*Pyrenochaeta* sp.	-	-	-	-	-	4	5	1	<1	1	-
S23	*Stemphylium* sp.	-	2	-	-	-	4	-	-	-	-	-
S546	*Tilachlidium* sp.	22	4	1	-	-	1	3	-	-	1	-

continued

Table 21
contd.

		SANDWICH					STUDLAND					
	DUNE ZONE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	FORE DUNE		SEMI-FIXED DUNE		FIXED DUNE	
	SOIL DEPTHS & HORIZONS SAMPLED	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	0-6"	6-12"	Surface Humus Horizon	Sand 6-12"	Surface Humus Horizon	Sand 6-12"
	Soil pH	7.4-9.1	7.4-8.9	6.8-8.5	7.4-9.2	6.8-7.6	6.1-7.5	6.2-7.5	4.3-5.8	4.7-6.6	3.7-4.3	4.0-4.9
Culture No.	Species											
	Trichoderma viride	27	19	9	16	1	62	50	19	22	31	57
D784	*Verticillium* sp.	-	-	-	-	-	-	1	-	-	-	-
D701	?	-	-	-	-	-	1	1	-	-	-	-
D729	?	-	-	-	-	-	<1	-	-	-	-	-
S1049	?	-	-	-	1	-	-	-	-	-	-	-
D1795	Mycelium bearing clamp connections	-	-	-	-	-	1	-	-	-	-	-
D766	Sterile dark coloured mycelium	<1	-	-	1	-	-	2	1	4	-	-
	13 other dark coloured mycelia	2	-	-	1	-	-	1	1	8	<1	-
	7 sterile hyaline or light coloured mycelia	1	-	-	1	2	-	<1	-	<1	<1	-

TABLE 22

% FREQUENCY OF OCCURRENCE OF SPECIES OF FUNGI ON THE SURFACE OF THE ROOTING SYSTEM OF CAREX ARENARIA

(Figures based on analysis of 100 rhizome segments and 200 root segments in each zone)

		SANDWICH		STUDLAND	
	DUNE ZONE	SEMI-FIXED - FIXED "GREY" DUNE		SEMI-FIXED "DUNE GRASS"	
	SOIL DEPTH	0 - 6"		0 - 6"	
	Soil pH	5.6 - 8.8		4.3 - 5.8	
	Rooting System	Rhizomes	Roots	Rhizomes	Roots
Culture No.	Species				
	Absidia glauca	-	1	-	-
	A. spinosa	2	13	-	-
	Mortierella alpina	-	2	-	-
S947	Gymnoascus sp.	-	1	-	-
	Sporormia intermedia	-	-	-	1
S910	Alternaria sp.	1	1	-	-
	Cladosporium herbarum	7	9	-	2
S10	Coniothyrium sp.	5	7	-	-
D20	" "	-	-	4	2
	Fusarium culmorum	-	2	2	2
	Fusarium oxysporum	2	3	-	-
S497	Fusarium sp.	-	1	-	-
S890	Harposporium sp.	3	21	-	-
S937	(?) Hendersonia sp.	-	1	-	-
D388	Microdiplodia sp.	-	-	-	2
	Papularia arundinis	-	-	2	8
	Penicillium adametzi	-	-	8	4
	P. cyaneo-fulvum	-	7	-	-
	P. cyclopium	3	1	-	-
	P. melinii	-	-	4	4
	P. nigricans	-	-	82	80
	P. restrictum	63	44	-	-
	P. spinulosum	27	17	1	2
D40	Pyrenochaeta sp.	-	-	-	2
S23	Stemphylium sp.	-	-	-	-
S546	Tilachlidium sp.	-	-	4	-
	Trichoderma viride	1	6	6	-
D766	Sterile dark coloured mycelium	-	2	-	-
	4 other sterile dark coloured mycelia	-	5	-	-
	4 sterile hyaline or light coloured mycelia	-	2	4	-

absent from similar sites on other roots. The results of the analyses are percentaged to give an overall picture of frequency, but with the result that these local preponderances of species are obscured.

Marked variations in the size or nature of the fungal population with change in root size were not apparent, but this may have been due to the fact that the collective root samples contained roots of various ages.

The number of species that developed from a root fragment was usually 2 or 3, the maximum number being 6, and on only 19% of these approximately 2 mm. long segments was no fungal growth observed. Rather more sterility as regards fungi occurred in the $<$ 0.5 mm. diameter group, which included the finest lateral rootlets, i.e. 27% sterility as opposed to 12% in the 0.5 - 1 mm. diameter group.

The distribution of Harposporium S890 and of Tilachlidium S546 was possibly correlated with age and size of root. Harposporium was most abundant on Ammophila roots of 1 - 2 mm. diameter whereas Tilachlidium was most abundant on Ammophila roots of $<$ 0.5 mm. diameter.

% Frequency of Occurrence

Soil Type: Fore Dune Sand, Sandwich	Root Diameter (mm.)		
Sampling Depth 0 - 6"	$<$ 0.5	0.5-1	1-2
Harposporium S890	2%	5%	42%
Tilachlidium S546	38%	22%	7%

In a subsidiary experiment whole lateral roots of Ammophila were excavated from the fore dunes and cut up after washing so that each segment could be related exactly to its original position on the root system and the distribution of fungi from the apices back along the root mapped. It was found that the number of fungi tends to increase with root age but even the extreme apex of the root was often colonized. However, a definite succession of species along the roots was not discernible nor were sterile forms more prevalent at the tips as shown by Harley and Waid (1955) for beech. Waid (unpublished data) reports the absence of a species succession along roots of rye grass (Lolium perenne) and suggests that it is the secondary thickening of a dicotyledon root which results in a succession.

Section III

(b) The distribution of the root surface fungi of Ammophila in relation to soil depth and horizon.

The number of species on the root surfaces and the degree of root colonization did not appear to vary significantly with sampling depth or soil horizon. Thus the decrease in the size of the fungus population which was found to occur down the soil profiles was not reflected by the root surface population as a whole, probably because the latter is linked by a continuous food base. There were, however, variations in the frequency of a few individual species which could be

correlated with sampling depth.

The frequency of occurrence of Mucor ramannianus on Ammophila roots in the acid fixed dunes was 25% in the A_1 horizon and 50% in the subsurface sand. The vertical distribution of this species on roots is of interest, especially in the light of its soil distribution and the suggestions that its apparent preponderance in subsurface horizons is due to the downward flow of water washing the spores from the surface down the profile and depositing them at lower levels. Sewell (1954) found M. ramannianus to be sparse on Calluna roots in the A_1 horizon but common on roots of the A_2 and B_1 horizons. It seems, therefore, that the subsurface environment may well be more favourable than that of the surface horizons for the growth of this species, but the possibility that the degree of root "infection" varied with the spore content of the surrounding soil cannot be ruled out.

Fusarium oxysporum was more common on roots in the surface humus horizon (0 - 3") than on those in the subsurface sand - a distribution which corresponds with that in the soil, where this species was found to be relatively rare below the A_1 horizon. Simmonds and Ledingham (1937) in their study of the fungus flora of wheat roots found that Fusarium oxysporum, among other Fusaria, was infrequent below the first foot of soil. A similar relationship between

the root and soil distribution was shown by some of the Penicillia and by Penicillium nigricans in particular.

Distribution of Penicillium nigricans in the Semi-fixed dunes (DG), Studland

% Frequency of Occurrence

	Ammophila Roots		Soil				
Sampling Depth	0-3"	3-12"	½"	1"	3"	6"	12"
	80	42	80	70	60	60	30

(Number of colonies on a soil plate decreased from about 30 at ½" to 2 at 12".)

Vertical distribution patterns such as the above appear on comparison to be governed by some factor other than the organic content of the habitat, although it is possible that the reduced root population at the lower depths is a direct result of a limited number of "infection sites" in the humus-poor subsurface sand.

The soil organic content is more obviously a factor limiting the spread of a fungus down the soil profile in the case of Trichoderma viride. This species was present in much reduced numbers in the lowest regions of the soil investigated but on the roots it showed no constant variation in frequency with depth. The migration of the fungus into "humus-poor" subsurface soil via the root system is here envisaged.

Although, in the sand dune habitat, the influence of

soil depth and soil horizon on the vertical distribution of root surface fungi does not appear great, that of the roots on the vertical distribution of the free soil fungi may be considerable especially in the more arid regions because the roots are not only a source of nutrients but also a centre for potential "soil" fungi. Sabinin and Minina (1930) in a study of the microflora of the desert steppe soils of Central Asia showed how closely the micro-biological profile was related to root distribution in sand dunes when they found an anomalous increase in the number of micro-organisms down the soil profile and correlated it with the root systems present and their deeply penetrating type of growth.

Section III

(c) The distribution of the root surface fungi in relation to dune development and soil type.

(i) The successive root surface populations of Ammophila arenaria.

The succession of soil fungi which has been shown to occur across a dune system is reflected relatively closely by the root surface floras examined. The fungal communities on the root surfaces of the same "host" species growing in different dune zones and in different dune systems are thus by no means the same, but vary both quantitatively and qualitatively, paralleling changes in the surrounding soil

communities.

The greatest divergence between the Ammophila root surface and free soil populations occurs on the fore dunes. Here the root surface flora is almost as rich and constant as that on the plants of the fixed dunes whereas the fore dune soil community is sparse and indefinite. Soil plates were practically sterile even if prepared from sand grains picked off the roots - a method used by Rokitskaya (1935) in the study of the rhizosphere. Sabinin and Minina (1930) noted that the mobile sandhills of the steppes were sterile a short distance from roots and the quantitative estimate of foreshore microfungi made by Webley, Eastwood and Gimingham (1952) are clear evidence of the same phenomenon.

There seem to be in the desert-like habitat of the fore dunes oases of active root surface fungi already in relatively well defined communities before a really distinct and definable soil population has been established.

The most frequent members of the root surface populations of the successive dune zones are listed in table 23. All species with a frequency of occurrence of 10% or more at any one soil level are included. From a comparison of this list with that showing the succession of fungal communities in the soil (table 16) it can be seen that in general at any particular stage of dune development, although the soil population is richer, most of the commonest root surface

TABLE 23

THE SUCCESSION OF AMMOPHILA ROOT SURFACE POPULATIONS WITH DUNE DEVELOPMENT

(Compare Table 16)

CALCAREOUS DUNE SYSTEM, SANDWICH

FORE DUNES

ƒ*Harposporium* sp. S890
**Papularia arundinis*
**Penicillium cyclopium*
Penicillium restrictum
Tilachlidium S546
**Trichoderma viride*

SEMI-FIXED "YELLOW" DUNE

Coniothyrium S10
Fusarium oxysporum
Penicillium restrictum
**Trichoderma viride*

FIXED "GREY" DUNE

Absidia spinosa
Penicillium restrictum

ACID DUNE SYSTEM, STUDLAND

FORE DUNES

ƒ*Harposporium* sp. S890
**Penicillium cyclopium*
**Trichoderma viride*

SEMI-FIXED "DUNE GRASS"

**Penicillium cyclopium*
Penicillium nigricans
Trichoderma viride

FIXED DUNE HEATH

Mucor ramannianus
Penicillium adametzi
**Penicillium cyclopium*
Penicillium spinulosum
Trichoderma viride

ƒ Not isolated from the soil of this zone

* Infrequent in the soil of this zone

dwellers are also prominent members of the associated free soil flora.

Harposporium S890, Penicillium cyclopium and in some cases Trichoderma viride were the only common root species which were not also common in the surrounding soil and of these only the Harposporium of the fore dunes appeared to be restricted to the root region.

The frequency of Trichoderma viride on roots of both dune systems is possibly a reflection of more acid conditions in the root region for, as has been shown, this species was relatively rare in the soil of the alkaline dune systems, although common in the acid types.

Of the species common in the soil, but not on the roots, Mortierella alpina with a frequency of 100% in the soil of the "grey" fixed dunes was the most striking example. Thrower (1954) in a study of the rhizosphere of Australian heath plants recorded that Absidia spinosa and Mucor ramannianus were predominantly inhabitants of the free soil and infrequent in the root region. This was not confirmed in the present investigation as both these species were among the common root surface fungi.

(ii) Variations in the root surface populations of Ammophila arenaria with soil type.

Comparing the Ammophila root surface floras of the two dune systems, they appear to diverge more and more from one

another with dune development, that is, as the soil type becomes more and more distinct and approaches the extremes of fixed acid and fixed calcareous dune. Between the fore dune root surface floras there is a general similarity about 50% of the species being common to the Sandwich and Studland sites as compared with 20% in the semi-fixed or fixed dunes - habitats which vary far more from one locality to another than fore dunes, and hence might be expected to harbour a greater range of root microfloras. Examination of small quantities of Ammophila root material from the fore dunes at Berrow in Somerset and at Tentsmuir in Fife-shire gave further evidence that the species composition of these fore dune root floras does not vary greatly with locality, as is shown below,p.136. There were, however, considerable variations in the relative frequency of individual species, but this was no doubt due partly to limited sampling, the "flush" phenomenon and competition on the root plates.

THE FORE DUNE ROOT SURFACE FUNGI OF AMMOPHILA ARENARIA

Only species which were common or occurred in more than one dune system are included.

"Common" species: frequency of occurrence $>10\%$

"Infrequent" species: " " " $<10\%$

Sampling Depth 0-6"

	SANDWICH	STUDLAND	BERROW	TENTSMUIR
"Common" Species	Fusarium S890 Papularia arundinis Penicillium cyclopium Tilachlidium S546 Trichoderma viride	Fusarium S890 Penicillium cyclopium Trichoderma viride	Fusarium culmorum Penicillium spinulosum	Cephalosporium D1971 Fusarium S890
"Infrequent" Species	Cladosporium herbarum Coniothyrium S10 Fusarium culmorum Penicillium lividum Penicillium melinii Penicillium restrictum Penicillium spinulosum Stemphylium S23	Cladosporium herbarum Coniothyrium S10 Fusarium culmorum Penicillium lividum Penicillium melinii Penicillium nigricans Penicillium spinulosum Stemphylium S23	Cladosporium herbarum Penicillium restrictum	Cladosporium herbarum Fusarium culmorum Papularia arundinis Penicillium lividum Penicillium nigricans Stemphylium S23

/Webley, Eastwood and Gimingham (1952) recorded a Cephalosporium species as the most frequent member of the root surface flora on the Ammophila of the St. Cyrus fore dunes in Kincardineshire. Cephalosporium D1971 was the most frequent species (48% frequency) on the Tentsmuir root samples but was not encountered elsewhere./

Although, as has been pointed out, certain species, such as Trichoderma viride, as root surface inhabitants are more evenly distributed over the dune range than as free soil inhabitants, the fixed dune root surface flora can be classed as "acid" or "alkaline" in type. Mucor ramannianus, a possible calcifuge, is thus a prominent member of the dune heath root surface flora but absent from the calcareous system where Fusaria characteristic of the more alkaline soils are a feature. Ammophila arenaria is therefore an example of a plant with a root surface fungus flora which varies with the soil environment.

The habitat range of Carex arenaria was small in comparison with that of Ammophila, but there were indications that the root surface flora of this species also varies with soil type.

Webley et al (1954) suggested that the successive higher plant dominants might influence the general soil microflora by their own typical root region flora. Without a study of a wider range of dune plants it cannot be said with any surety that this is not so. It does seem, however, from the above evidence that the association between dominant plant and general soil microfungi is not a highly selective one, and that the nature of the several soil fungal communities

is governed by a multiplicity of factors, those of soil type being all important, except perhaps in the very earliest stages of dune development. Here the root region fungi probably play a key rôle in the initial establishment of a free soil community.

Section IV. Physiology.

Experiments and Further Observations on the Relationship between the Distribution of Dune Soil Fungi and the Salinity and Hydrogen-ion Concentration of the Soil.

The effects of variations in the salinity and hydrogen-ion concentrations of the culture medium on the growth of a small number of fungal species isolated from dune soils were investigated. The experiments were of a limited nature, but some of the results are recorded here as of interest, as far as they go, in the light of the foregoing distribution data. Pure culture studies cannot give direct evidence for the factors controlling the distribution of a species in complex natural habitats and must therefore be interpreted with caution.

Salinity

The following species were selected for a study of their growth on salt-enriched media:

	Origin of Isolate Tested
Asteromyces cruciatus	Open tide-washed sand, Sandwich.
Pyrenochaeta sp. (D40)	Fore dunes, Studland (50% frequency).
Tilachlidium sp. (S546)	Fore dunes, Sandwich (80% frequency).
Gliomastix convoluta v.*felina*	Sandy low, periodically flooded with sea water. Studland.
Penicillium nigricans	Semi-fixed dune, Studland (100% frequency).
Trichoderma viride	Inland *Calluna* heath, Chobham, Surrey.

These fungi were grown on Czapek-Dox agar + 5% yeast extract made up with various concentrations of an artificial sea water. A relatively rich medium was used so that growth might not be limited by lack of nutrients.

The sea water was made up according to the formula given by McLean and Cook (1941):

sodium chloride	29.429 gms.
magnesium chloride	3.22 "
magnesium sulphate	2.40 "
potassium chloride	0.59 "
sodium bromide	0.569 "
calcium carbonate	0.11 "
ferric oxide	0.003 "
distilled water	to 1000 mls.

Four media were used in parallel treatments:

(1) Modified Czapek-Dox agar with a base of full strength sea water

(2) Modified Czapek-Dox agar with a base of full strength x2 sea water

(3) Modified Czapek-Dox agar with a base of full strength x0.5 sea water

(4) Modified Czapek-Dox agar with a base of distilled water only.

The media were initially slightly acid - neutral in reaction.

3 plates/medium/species were prepared. Each plate was inoculated centrally with a mycelial disk 3 mm. in diameter, cut by means of a sterile cork borer from the submarginal non-sporulating zone of a young colony (12 - 72 hours old according to the species) growing on Czapek-Dox agar + 0.5%

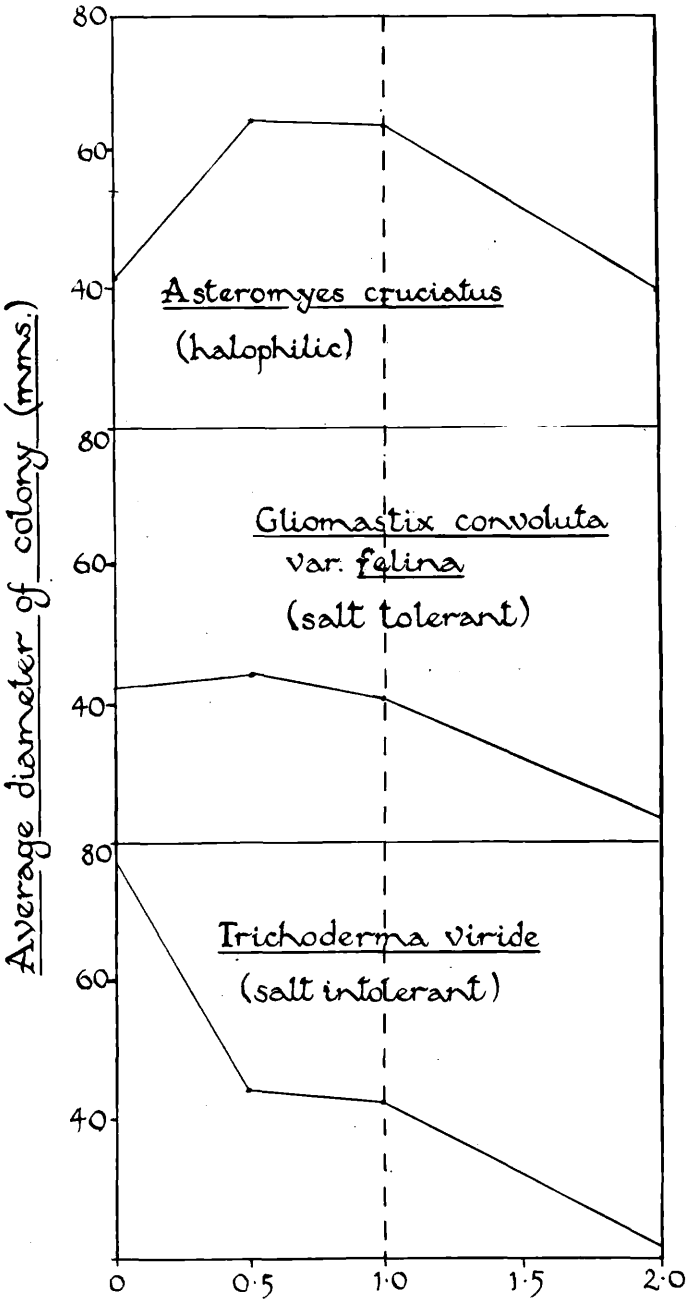
yeast extract.

The cultures were incubated at 25°C. The linear growth of each colony was measured daily along two diameters at right angles to each other, so that six growth measurements were obtained for each species at any one time and on any one medium, from which average values were derived. Some of the results are presented graphically.

Asteromyces cruciatus was the only species which appeared to be truly "halophilic". Its rate of linear growth, amount of aerial mycelium and degree of sporulation were all at a maximum on media containing full or half strength sea water. Linear growth was approximately 60% more on these saline media than on the controls. Even on the saline medium x2 the normal concentration linear growth was for the first seven days only slightly less than that on the non-saline medium, although further growth was of the staling type and sporulation was reduced. This "pioneer" of the dune succession is, therefore, apparently favoured by the presence of excess salts in the medium including approximately 3% sodium chloride, and is to some extent tolerant of even higher concentrations, so it may be expected to be better adapted to its maritime habitat than many more cosmopolitan soil fungi.

The effect of saline media on the growth of Trichoderma viride, isolated from an inland heath soil, was in marked

Growth of 3 soil fungi on a salt enriched culture medium



contrast to that of the above. Linear growth was checked on all the salt enriched media and the cultures on the normal and more concentrated sea water agar failed to sporulate. This species, which does not appear frequently at early stages of the dune succession, appears, therefore, to be of the "halophobic" type, although maritime salt-tolerant strains may exist. Saitô (1952) grew Trichoderma liquorum (T. viride) in saline solutions of varying concentrations and found similarly that growth was at a maximum in the absence of sodium chloride, slightly inhibited in 1% NaCl and much reduced in 5% NaCl; spore germination was less affected by the presence of salt. Trichoderma appeared to be less frequent in the saline lows at Blakeney than in the adjacent "yellow" dunes, but Bayliss-Elliott 1930 recorded it quite frequently in salt marsh soils.

Growth of the Tilachlidium species was also much reduced on sea water agar, but as has been pointed out (p. 41) the fore dunes where it was encountered most frequently did not at the time of sampling contain significant amounts of chlorides.

The other species examined showed less extreme growth variations on the different media. Growth of Pyrenochaeta (D40), another member of the fore dune flora, was relatively normal on all media at first, but tended to stale after a week on salt-enriched agar. Penicillium nigricans, the

commonest dune soil microfungus, showed healthy growth on all media without marked differences in linear growth, amount of aerial mycelium, nature of the colony margin or amount of sporulation. There was perhaps slight stimulation of growth in the presence of sea water at all the concentrations applied, but the reactions of species of such a restricted growth habit are not easily assessed by linear measurements.

Gliomastix convoluta v. felina also showed a certain tolerance of high salt concentrations. Growth was stimulated slightly by the addition of diluted sea water (x0.5) to the culture medium and was little affected by the full-strength sea water, although sporulation was somewhat reduced; on the most concentrated medium, however, only sterile mycelium with little aerial development was formed.

Among this small number of species examined there are, therefore, considerable differences of response, as regards vegetative growth and sporulation, to variations in the salt content of the immediate environment, some of which may well occur in the natural medium of the soil. Such factors as the hydrogen-ion concentration of the medium and staling phenomena may mask the direct effects of salinity, but these cultural studies indicate three species types - the truly halophilic or maritime such as Asteromyces cruciatus; the "salt-tolerant" such as Gliomastix convoluta v. felina and Penicillium nigricans and the "salt-intolerant" such as

Trichoderma viride and the Tilachlidium species (S546). Further investigations are required to show whether or not these physiological differences are associated with only certain strains.

Since the dunes proper are not usually saline habitats, it is in only the earliest stages of dune development that ability to tolerate high salt concentrations is likely to aid the fungal colonist. A more halophilic fungus flora is to be expected in the dune lows periodically flooded by sea water, than in the dune ridges, or at least one which can tolerate wide fluctuations in soil salinity unless there is within this community a continuous cycle of destruction and recolonisation.

Four soil profiles in the Blakeney and Studland lows were sampled and their fungus flora compared with that of adjacent dune ridges. Several species were found to be common to both habitats, but there was a definite divergence of the community pattern in the lows from that typical of the dune ridges. The most noteworthy feature of the dune low flora was the relatively rare occurrence of Mortierella alpina and Coniothyrium S10, the preponderance of Penicillium janthinellum in the Studland profiles - a species not encountered elsewhere in the dune system, and the restricted vertical distribution of the population as a whole. Cultural studies on the salt tolerance of the above species would be

of interest. Both the "salt-tolerants" Gliomastix convoluta var. felina and Penicillium nigricans were frequent isolates from the Blakeney and Studland lows whereas the "salt-intolerant" Trichoderma was less common here than in adjacent dunes. This differential distribution between dune low and dune ridge is not, without further study, easily correlated with the habitat factors, since there are a number of variables, including vegetation type, soil organic content and aeration, besides salinity, but it does accentuate the pattern of distribution which has been described for the xerosere.

Hydrogen-ion Concentration

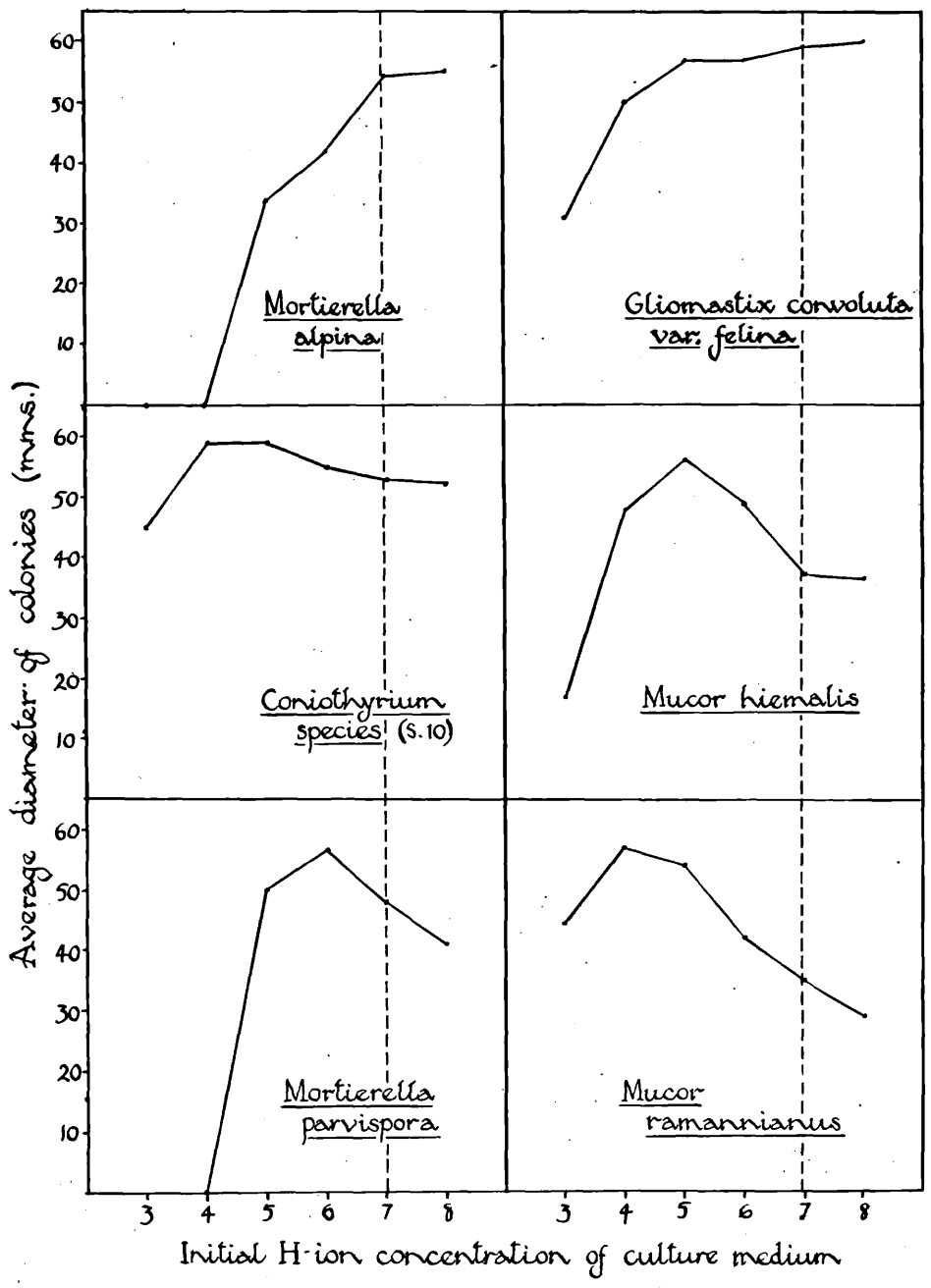
The following species were selected for an investigation of the effect of variations in the hydrogen-ion concentration of the culture medium on their growth and sporulation; they include members of both the "acid" and "alkaline" dune floras:-

		Distribution in Dune Soils
1.	Coniothyrium S10	Maximum frequency in slightly acid, highly alkaline soil.
2.	Mortierella alpina	" " " " "
3.	Mortierella parvispora	Restricted to acid soil.
4.	Mucor ramannianus	" " " "
5.	Mucor hiemalis	Widespread (see p. 75)
6.	Gliomastix convoluta var. felina	"

The medium used was Czapek-Dox agar + 0.5% yeast extract buffered at pH 3, 4, 5, 6, 7 and 8 by the addition of McIlvaine's standard buffer solutions of sodium phosphate (Na_2HPO_4) and citric acid. The method of inoculation, experimental conditions and number of replications were the same as in the salinity experiments. Measurements of linear growth were made daily, or more frequently if the growth changes were particularly rapid as in the case of Mucor hiemalis.

There was, in general, a relationship between the soil distribution of a species and its relative growth rate on the various media and a correspondence between the range of pH for optimum growth in culture and maximum frequency in dune soil. Certain divergences, however, did occur. These probably reflect both the fact that mycelial vigour and frequency in the soil are not necessarily related and also that the hydrogen-ion concentration is not always an all-important factor when variables such as nutrient supply and biological competition are involved.

The tolerance of a relatively wide range of hydrogen-ion concentration in the medium; the inhibition of growth in some cases at rather sharply defined limits of this range and a less clearly defined optimum, as shown by the growth curves (p.146a), are phenomena typical of many fungi (Hawker 1950). Investigation of a wider range of reactions would



Growth of 6 dune soil fungi on a buffered medium (Czapek-Dox agar + 0.5 % yeast extract) with various initial H-ion concentrations

probably have revealed further growth inhibition and more clearly defined optima for the "alkaline" species.

The growth curve of Mortierella alpina shows an optimum at pH8, rapid decline on the acid side of neutrality and inhibition at pH4 and is therefore a close reflection of the soil distribution. pH6 was, on the other hand, the optimum value for growth of Mortierella parvispora. The inhibition of the latter in media of pH4 and less is somewhat surprising in the light of the distribution data. It may be that the pH values obtained for the gross soil samples are not strictly comparable with those of the microhabitats in which this species occurs.

Linnemann (1941) and Warcup (1951) have also noted that different species of Mortierella occur in soils of different pH. Their findings for Mortierella alpina and Mortierella isabellina are in agreement with the data obtained in this investigation. The occurrence of Mortierella alpina in very acid soils as reported by Jefferys et al (1953) does not appear to be usual.

Soil pH Range

	Linnemann (1941)	Warcup (1951)	Jefferys et al (1953)	Sand Dunes
Mortierella alpina	7.6-6.5	8.6-6.0	4.6-3.9	(9.9)8.8-6.1(5.4)
Mortierella isabellina	4.2-3.8	4.5-3.8	4.5-4.1	(7.3)4.9-3.5

Myrothecium roridum was another member of the alkaline dune flora with a distribution resembling that of Mortierella alpina. Preston (1943), in a study of this plant parasite, found its growth in culture was definitely favoured by alkalinity and was a maximum at pH8.

The linear growth rate of both Mucor species reached a maximum in acid media, but Mucor hiemalis appeared from its aerial growth and sporulation to be tolerant of a wide range of reactions. The anomalies associated with the isolation of this species from various soil types have already been discussed. Mucor ramannianus, common only in the most acid dunes and never isolated from alkaline soil, showed the most marked preference for acid conditions and intolerance of alkalinity in culture. Vigorous sporulation, easily assessed by eye from the coloration of the colonies by the pink sporangia, occurred over a particularly narrow range of pH. Spore production was a maximum at pH3 and 4 but at pH7 was sparse. Jensen (1931) has also noted that acid media (pH4 - 6.6) are optimum for the growth of M. ramannianus. This species has however been recorded from alkaline or only slightly acid fen peat (Stenton 1953).

The widely distributed species, Gliomastix convoluta var. felina, was relatively tolerant of both acid and alkaline media, but so also was Coniothyrium S10, common only in alkaline soil. The distribution of the latter does not,

therefore, appear to be directly related to the hydrogen-ion concentration of the soil, although it may well be determined by the presence of species that are themselves exacting for alkaline or acid conditions.

These cultural studies support the evidence of the comparative isolation data for the existence of two distinct dune fungus floras - the acid and the alkaline - which are characterised by the presence of certain "indicator" species associated with tolerant and cosmopolitan species.

5. Discussion

The picture of the soil microfungal flora of the dune xerosere, which can be drawn from this survey, is one of an active and relatively rich population, originating under the exacting conditions of the foreshore and developing through a successional series of fungal communities. Two community patterns can be recognised, one typical of acid dunes and the other typical of alkaline dunes on the British coast.

By the use of a number of sampling techniques, direct and indirect evidence of fungal activity has been found throughout the dune systems studied. Indirect evidence was provided by the constant or frequent occurrence of certain species on soil plates from all soils except that of the open tide-washed foreshore. It seems unlikely that a species will occur repeatedly on soil plates from a wide area of a particular ecological zone and not from an adjacent zone unless it is, or has been, active in that soil. The presence of a number of colonies of a single species on a plate, even if it is a reflection of sporing capacity, also suggests previous activity of the fungus in the soil, if allowance is made for aerial contamination. Mycelial growth into slide traps, over contact slides, and in soil impressions and crushes gave further and direct evidence of fungal

activity in even the most barren of the dune soils investigated.

The dune soil mycoflora, made up as it is of a range of communities, cannot be closely defined when it is considered as a single unit. It can be said, however, that as a whole it is rich as regards numbers and range of active species, although only a small proportion of these are "constants" or have a high frequency of occurrence. Fungi Imperfecti predominate and Penicillia are particularly common, but most groups of soil fungi are represented. Many of the species are cosmopolitan soil forms and only a few are possibly obligate sand fungi or exclusive to the dune habitat. The dune soil mycoflora is therefore recognisable, not so much by its component species as by its species associations and the numerical composition of these associations when compared with the soil floras of other habitats.

Origin of the Fungal Colonists

Primary colonisation of the sand by fungi appears to begin at a very early stage in dune development. The presence of scattered pioneers was indicated in the foreshore sand even before the establishment of higher plants, although it seems that organic sources such as plant roots are major centres of colonisation and the widespread establishment of microfungi in the open soil is probably a secondary

development from these centres.

The primary fungal colonists of dune sands have no doubt a variety of origins and dispersal agents. Root surface fungi of the young dunes may be conveyed to the site on plant propagules or may be soil borne and already present as inactive contaminants in the sand through which the roots are growing. Nicolson (1955) found indications that an endophyte of Ammophila arenaria was soil borne, spreading on plant debris to the drift line sand in advance of the colonising grasses. Wind and water dispersal is probably particularly prevalent in this unstable and unsheltered maritime habitat. Many fungi have been shown to occur in the "air spora" and the chances are that a wide range of them will reach the young dunes, although they may fail to become established. Only 5 species were in fact found to occur in the fore dunes with a frequency of 50% or more and several fungi in the older but adjacent dunes were never encountered; this indicates the selective nature of the habitat.

The Succession

The main discovery of this ecological investigation is the existence of a primary succession of soil fungi within the dune habitat. The pioneer invaders are replaced with dune development not by a haphazard assemblage of species but by a distinct series of communities.

The salient features of the succession may be briefly summarised as follows. (For a complete list of "common" species in the succession at Sandwich and Studland see table 16.) In the open foreshore sand, where the most maritime conditions occur, fungi are sporadic and distributed irregularly, but they include what appear to be littoral types such as Asteromyces cruciatus which is probably specific to the habitat. In the adjacent fore dunes the distribution pattern of the fungal community is more clearly defined and is characterised by a small number of Fungi Imperfecti, including, for example, Penicillium, Pyrenochaeta and Tilachlidium which are of more than sporadic status. The most marked increase in the richness of the fungal flora occurs with the further development of the dunes to the semi-fixed stage. Here, Phycomycetes, previously rare or absent, Coniothyria and, in alkaline dunes, Fusaria become prominent. In the final stages of dune fixation the species association of the semi-fixed dunes is replaced by a community containing, in general, a greater preponderance of Phycomycetes and a greater variety of Penicillium species and, if the soil is acid, characterised by the almost constant presence of Trichoderma viride, a species which is infrequent or absent in young dunes. Comparison of fixed dunes of various ages indicates the attainment of a certain equilibrium in this climax or sub-climax fungal population

which resembled that of similar but non-maritime grassland or heathland soils.

Although the substrate pattern was destroyed by the soil sampling procedure so that the distribution mosaic within each dune zone was obscured, the fact that a succession of distinct fungal communities was recognisable suggests a remarkable homogeneity in the overall population of each ecological zone, especially when it is remembered that reproducible isolation data were obtained from soil inocula weighing only 0.005 g. collected from over an area of 1/4 mile square.

Parallel with the succession of species are quantitative changes in the dune fungal population which indicate its increasing closure and stabilisation with dune development. The total number of species in the oldest fixed dunes was found to be about three times greater than that in the pioneer phases. The percentage number of common species also increased (0% - 20%) with dune fixation and in the final stages of the sere, where habitat differences from one ecological zone to another are less extreme, the number of species which appeared for the first time in the succession with a high frequency status ($>$ 50% frequency of occurrence) decreased, so that the community pattern became less variable. Similar quantitative changes were shown by the rapid increase in the number of colonies on soil plates and by the increase

in the number of "infections" in slide traps with dune development. More direct evidence of the increase in the total fungal content of the soil was given by an assessment of mycelial abundance using the modified slide impression technique. This indicated that the quantity of mycelium in surface soil was small in the foreshore and fore dunes, but that it had increased by over 50% in the acid fixed dunes and by 15% - 20% in the calcareous fixed dunes.

The qualitative and quantitative features described above apply primarily to surface soils where the micro-organisms are concentrated, but it has also been shown that the horizontal sequence from the sea inland to fixed dunes is accompanied by a marked vertical development of the fungal population, culminating in a stratified microfungal profile with characteristic subsurface species associations.

The microfungal succession of the Studland dune system can be related to the time factor giving some idea of the age limits of the various fungal communities. On historical evidence (Diver, 1933) the ages of the dunes sampled are approximately: semi-fixed dunes (DG) 80 - 100 years; fixed dune heath (DH) 100 - 150 years; old fixed dune of "Southern Heath" (SH) $\geq$ 200 years. It can be inferred, therefore, that the semi-fixed "dune grass" community with a surface horizon of fungi, containing a predominance of Penicillium nigricans and relatively few associate species, has evolved

from the pioneer colonising associations in less than 100 years. In less than a further 20 years it has been replaced by another community, characteristic of heath soil, in which Mucor ramannianus, Trichoderma viride and various Penicillia are common. During this latter period both the number of species occurring with $\geq$ 50% frequency and the mycelial content of the soil have more than doubled. A further 100 years of dune development appears, in the case of "Southern Heath" to have been accompanied by less radical changes in the fungal community, which may be related to the similarities in dune stability, vegetation and soil pH of the DH and SH zones.

Causal Factors

The salt, water and organic matter contents of the sand are probably, initially, the most important factors controlling the nature and distribution pattern of the fungal flora of a dune system. Salinity does not appear to be significant in the dunes proper, but it is doubtless a limiting factor in the intertidal zone, where fungi were very sparse and included salt-tolerant and halophilic species.

In the upper layers of the fore dunes establishment and spread of fungi appear to be severely restricted by lack of moisture and organic matter, and incessant disturbance of the substrate adds to the rigours of the habitat. The fungal concentration closely paralleled the visible moisture

gradient and was sharply delimited wherever the sand had dried out. At moister levels a few species were widespread, but most of the fungi isolated from the fore dune zone, including common soil forms and species prominent in the older dunes, occurred only in the vicinity of buried organic debris and on plant roots.

The frequency of several species characteristic of the final stages in the dune succession, Trichoderma viride for example, appeared to be governed by the amount of organic matter in the dunes, that is, frequency maxima occurred in zones and horizons which were richest in organic matter. Some related factor may, however, have been more directly involved. Confinement of Mucor ramannianus to the dune heath zones is possibly related to the presence of heath vegetation and to the dependence of this species on an external supply of thiamine or its derivatives, arising from litter and root material (Müller and Schopfer, 1937). It has been shown (Newman and Norman, 1943) that subsoil populations of micro-organisms are less versatile than those of surface soil where greater fluctuations in the energy supply occur. A similar nutritional differentiation of the fungal population may occur across a dune system, the young open dunes, where the energy source is added most sporadically, supporting the most versatile population and the fixed dunes containing more exacting species, such as M. ramannianus. A closer

analysis of the nutritional requirements of the successive fungal colonists of a dune sere in relation to nutrient turnover at the various stages of dune development, would be of considerable interest.

As has been shown, the fungal succession is typical of the dune habitat in general, but varies characteristically with dune soil type. From a comparative study of a number of dune systems the soil pH appears to be a key factor controlling these differences, and cultural work gave further evidence for the existence of "acid" and "alkaline" species in the dune mycoflora.

The higher plant cover and the soil microflora are so closely interdependent in any habitat that it is difficult, in a general study, to separate out vegetational factors having a decisive and specific influence on the fungal distribution pattern. The limits of the successive dune communities of higher plants coincided with those of the soil fungi, emphasising the fact that these two groups are two aspects of the same sociological unit. In the dune habitat, the general soil microflora is probably most selectively affected by higher plants at the initial stages of the succession. Here isolated plant colonists, such as Ammophila arenaria, stabilizing the sand and ameliorating the nutrient and moisture status of the soil, form centres of fungal activity. In the dune systems examined, Ammophila

arenaria continued to dominate some of the later stages of the succession, but its root surface flora varied with the habitat and there was no evidence that it influenced the general soil microflora by possessing a characteristic root flora of its own. Thus the majority of the fungi isolated from root surfaces were also obtained from the free soil and the successive root surface floras reflected the general succession of free soil fungi.

Many aspects of the soil fungal component of the dune habitat have not been mentioned. Among these is the part played by soil fungi in dune development and stabilisation. Only the effects of dune maturation on the fungal population have been described, but the soil microflora is both a cause and an effect of the process. Aggregation of sand grains by fungal mycelium was often observed on contact and impression slides, but it was not further investigated. A comparison of the relative aggregating powers of the various colonists in relation to their position in the succession would be interesting.

Another untouched problem concerns the microhabitats and microseres, which require examination by more selective techniques with a more autecological approach. The young dunes, where mycelia are widely dispersed, would provide an exceptional opportunity for such a study of microhabitats, with the possibility of correlating substrate spatial relation-

ships with the macro distribution patterns described in this investigation.

For several years emphasis has been laid on the uniformity and cosmopolitanism of the ecological communities of soil fungi. Stanier (1952) states: "As far as free-living micro-organisms are concerned, a very broad ecological classification into terrestrial, marine and fresh-water forms is generally possible, but localization on a macro-scale can go no further," but he adds that this statement may not be wholly valid for fungi. From quite recent ecological studies it can be concluded that associations of soil fungi on the macro-scale equivalent to those of higher plants and corresponding with certain vegetational units such as grassland (Warcup 1951) and heathland (Sewell 1954) can be discerned, although floristic differences and geographical limits are less well defined in the case of the fungi. The findings of this investigation of the soil fungi of the dune ecosystem support this conclusion.

Summary

1. The distribution of the dune soil mycoflora was studied with special reference to succession in an acid dune system (Studland) and an alkaline dune system (Sandwich) and in less detail in six other British dune systems.

2. Among the isolation methods used was a modified soil impression technique which was developed particularly for quantitative studies.

3. A relatively rich and active fungal population was found, but it contained few species which appeared to be confined to dunes.

4. The acid and alkaline dune mycofloras were found to be distinct from one another. Fungal mycelium was more abundant in the acid dunes.

5. A succession of species was shown to occur across the dune systems from the foreshore to the fixed dunes. The fixed dune flora resembled that of inland soils.

6. The development of the microfungal profile was studied. In general the number of species, species frequency

and amount of mycelium decreased with increasing depth.

7. The root surface fungal floras of Ammophila arenaria and Carex arenaria were investigated and found to vary with soil type.

8. Cultural experiments suggested the existence of acid and alkaline "indicators" and of both halophilic and salt-tolerant fungi among the members of the dune mycoflora.

9. This investigation showed that in the dune xerosere there is a succession of soil fungi on a scale comparable with that of higher plants.

ACKNOWLEDGEMENTS

I am most grateful to Professor F.W. Jane and Dr. M.P. Topping for supervising this research. I also wish to thank Dr. A.W. Apinis, Dr. M.B. Ellis, Dr. W.L. Gordon, Mr. A.E. Mason, Mr. G. Smith and Mrs. M. Turner who kindly examined cultures of some of the fungi and I am indebted to Mr. A. Dibdin, C.I.E., and Mrs. S. Martin for their help in collecting slide-traps and to Miss J. Raven for technical assistance with the diagrams.

This investigation was carried out during the tenure of a postgraduate Driver Scholarship awarded by Royal Holloway College, University of London, a State Research Scholarship and Surrey County Exhibition and later a Nature Conservancy Research Studentship.

APPENDIX

1. Biological Notes

1. Beauveria bassiana, an animal-parasite, was isolated occasionally from dune heath soil, and a fungus believed to be the same species was observed colonizing a nematode on a Rossi-Cholodny slide, which had been incubated in fore dune sand. Sewell (1954) recorded B. bassiana frequently from Calluna heath soils and also observed it growing on a nematode. Previous reports of this species among isolates of soil fungi appear to be rare and insects are the hosts usually quoted. It would be interesting to know to what extent its association with heaths is related to the fauna and soil type.

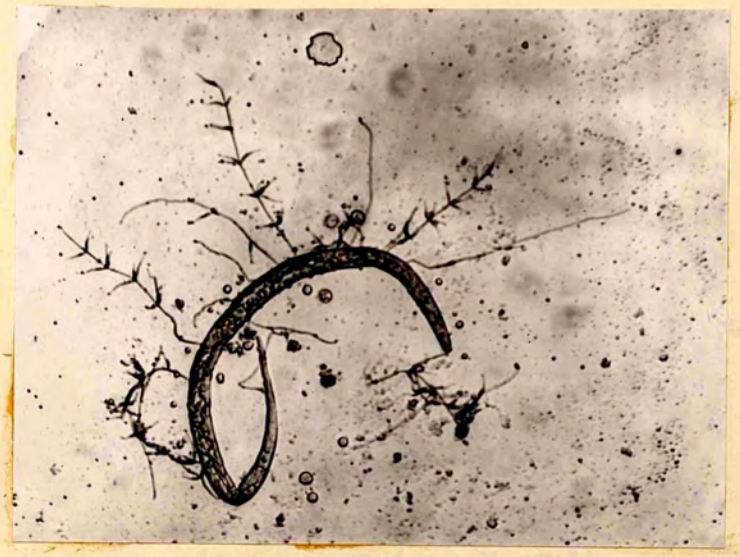
2. Gelasinospora cerealis and G. retispora appeared to be widespread in acid and alkaline dunes. Warcup (1951)[b] isolated G. cerealis from a steam-treated soil and Sewell (1954) found these species were locally common in acid Calluna soils and that they occurred in rabbit dung. These appear to be the only previous reports of their isolation from soil, although their distribution in relation to soil type does not seem from the present investigation to be particularly narrow. Evidence for their existence in the soil was obtained by the use of 3 isolation techniques. The

ascospores with their characteristically sculptured walls were often observed on Rossi-Cholodny slides from calcareous dune pasture and acid peat soils of fixed dune. Ascomycetes have rarely been isolated by the methods designed to trap only actively growing mycelium, but both G. cerealis and G. retispora were isolated by slide traps. Both species formed abundant penthecia on soil plates and G. cerealis was among the few species observed sometimes to antagonise the growth of Trichoderma viride in culture. Of the two species only G. retispora was isolated from rabbit dung collected from the dunes.

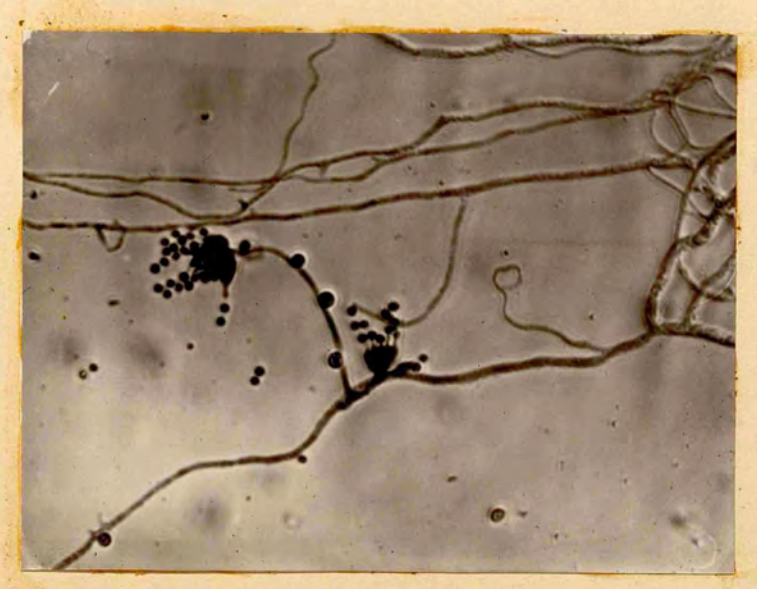
3. Two mucorine parasites developed on the soil plates, a Syncephalastrum species on a Mortierella host and Piptocephalis xenophila (?) on Penicillium spinulosum. Piptocephalis xenophila, described by Dobbs and English (1954) as a new species, was first found on a Penicillium isolated from sandy soil near Bristol and is the only mucorine parasite known to form haustoria in a host of another order of fungi.

4. An interesting feature of the Phycomycete population was the formation of zygospores by heterothallic species on the soil plates, although it is widely held that the two strains of a heterothallic species do not occur together in nature. Zygospore formation in Absidia glauca and A. orchidis was particularly common and occasional in Mucor hiemalis.

Microphotographs of Rossi-Cholodny soil slides from the fore dunes, Sandwich



A fungus (Beauveria bassiana ?) colonising a nematode worm (x 180)



A monoverticillate Penicillium species sporulating on the slide surface (x 750)

APPENDIX

2. The Distribution of Microfungi at Various Soil Depths in the Successive Zones of the Dune Systems at

Berrow, Somerset
St. Cyrus, Kincardineshire
Bamburgh, Northumberland
Newborough Warren, Anglesey
Blakeney Point, Norfolk
Tentsmuir, Fife.

Subjective estimates of frequency made from soil plate isolations

*** common
** frequent
* occasional
absent

BERROW

The Soil Profiles

1. Agropyron junceiforme embryo dune.
   No visible horizon differentiation of the soil profile.
   Sand mixed with a considerable amount of silt and mottled with iron coloured stains.

2. Open Sand.
   High proportion of silt in the sand as above.

3. Agropyron fore dunes.
   Litter layer of Agropyron and washed up Ascophyllum relatively thick.
   A_1 horizon indistinguishable.
   The whole profile consisted of a relatively dark coloured sand incorporated with a fine black material in transect A. and of a relatively clean sand in transect B. (These differences were reflected by the microfungal content of the sand.)

4. Mobile "yellow" dunes.
   Litter layer sparse.
   Soil horizons not visible.

5. Semi-fixed dunes.
   A. The surface humus layer was not distinct, but the top 1/4" of sand was slightly darker in colour than at greater depths.
   B. 0 - 1 inch: light brown humus stained sand.
      1 - 12 inches: relatively clean sand.

6. Fixed "grey" dune.
   0 - 2 inches: brown sandy humus horizon; relatively loose and dry; lower margin indefinite. Fine rootlets formed a dense interwoven mass.
   2 - 12 inches: yellow sand.

7. Dune Pasture.
   0 - 1 inch: dark brown humus horizon.
   1 - 12 inches: yellow sand.

   An interwoven growth of fine rootlets from 0 - 3 inches gave the soil a loose structure, whereas from 3 - 12 inches the sand was relatively compact.

BERROW, SOMERSET. /TRANSECT 'A'/ JUNE 1954		Open Sand	Agropyron Fore Dune					Mobile Dune					Semi-Fixed Ammophila Dune					Dune Pasture				
	Sampling Depth	1"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	8.6	7.7		7.8	8.2	8.4	7.9		7.9	8.3	7.8	7.7		7.5	7.7	7.8	7.5		7.6	7.8	7.8
S/C No.	Species																					
	Absidia glauca																	***				
	Mortierella alpina							**					**	**					**	*	*	
S301	Alternaria sp.		*																			
S1130	Aspergillus sp.											***										
	Botrytis cinerea			*					*													
	Cephalosporium acremonium																					
B138	Cephalosporium sp.								*													
D18	" "	*	**	**	*	***																
	Cladosporium herbarum		***					*	**													
S10	Coniothyrium sp.												***	*	**	**		***	**			
	Fusarium culmorum			**																		
	Gliomastix convoluta v. felina													*	**		***			*	*	
S890	Harposporium sp.		*																			
	Myrothecium roridum														*	***						
	Papularia arundinis						*															
	Penicillium cyaneo-fulvum		**	*																		
	P. melinii (?)																	***				
	P. nigricans														*				**	*		
	P. paxilli						**															
	P. raistrickii																	*				
	P. restrictum	*				*		**	*				***	***	***	**	*	***	*	***		
	P. rubrum		*																			
D40	Pyrenochaeta sp.		**	*	*							***					***					
	Septonema chaetospira			*	*																	
	Stachybotrys atra		*																			
?S546	Tilachlidium sp.															**		*				
	Trichoderma viride														*							
S312	?																				*	
	7 sterile dark coloured mycelia		*					*			*				*						*	
	1 sterile hyaline mycelium														*							

BERROW, SOMERSET /TRANSECT'B'/ JUNE 1954		Open Sand	Agropyron Fore Dune					Mobile Dune					Semi-Fixed Ammophila Dune					Fixed "Grey Dune"				
	Sampling Depth	1"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	8.5	8.1		7.9	8.4	8.3	7.9		8.1	8.1	8.1	8.1		7.7	7.8	7.6	7.7		8.0	8.1	7.8
S/C No.	Species																					
	Absidia glauca																	*				
D527	Cunninghamella sp.																	**				
	Mortierella alpina								**				*		**			***	*			
	Mucor hiemalis												*	*								
S1065)													*									
S1125)	Unidentified Ascomycetes																*					
S1326)									**													
	Botrytis cinerea														*							
	Cephalosporium acremonium		*	**																		
B138	Cephalosporium sp.									*												
	Cladosporium herbarum								*			**			**			*				
S10	Coniothyrium sp.												***	*				***	***			
	Fusarium culmorum																	*				
	Gliomastix convoluta v. felina													*	***						*	
S890	Harposporium sp.								**													
	Penicillium cyaneo-fulvum	*																				
	P. cyclopium																	*				
	P. lividum												*									
	P. melinii (?)																	***	*			
	P. nigricans																	***	***			
	P. paxilli	*																				
	P. restrictum												**	***	***			***	***	**	*	
	P. rubrum																	*				
D40	Pyrenochaeta sp.		*	*				***	***								**					
	Spondylocladium sp.				**																	
S25	Stemphylium dendriticum												*									
S546	Tilachlidium sp.							**	*	*												
	3 sterile dark coloured mycelia												*									
	2 sterile hyaline mycelia												*									

ST. CYRUS

The Soil Profiles.

1. Mobile dunes.

No horizon development.

2. Young fixed dunes.

The only sign of profile development was a very indistinct surface horizon of humus stained sand (0 - 2 inches).

ST. CYRUS, KINCARDINESHIRE

APRIL 1955

		Mobile Fore Dune					Semi-Fixed Dune				
	Sampling Depth	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	7.0		7.7	7.5	7.9	7.2		7.4	7.1	7.7
S/C No.	Species										
	Absidia glauca								*		
	Mortierella alpina						***	***	**	**	
	Mucor hiemalis						*	*		*	
	Beauveria bassiana		*								
	Cephalosporium acremonium	*	***				*	*	*		
	Cladosporium herbarum						***	*			
S10	Coniothyrium sp.						***	***			*
D1957	" "						***	***	*		
D1964	" "						**	**			
	Gliomastix convoluta v. felina									**	
D1906	Hendersonia sp.						*	*			
	Myrothecium roridum						*	*	*		
	Penicillium restrictum						**	**	***	**	
S25	Stemphylium dendriticum						*	*			
D1953	Sterile dark coloured mycelium		*								

BAMBURGH

The Soil Profiles.

1. Semi-fixed dune.

The soil profile had no horizons other than a very thin surface humus layer.

2. Fixed dune pasture.

0 - 3 inches: dark brown humus horizon; somewhat clayey.

3 - 12 inches: humus stained sand.

BAMBURGH, NORTHUMBERLAND

APRIL 1955

		Semi-Fixed Dune					Fixed Dune Pasture				
	Sampling Depth	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	7.5		7.0	7.1	7.3	7.1		7.1	7.2	7.1
S/C No.	Species										
	Absidia glauca						**	***			
	Mortierella alpina	*	***	***			*	***			
	Mucor hiemalis						*				
	Sporormia intermedia		*								
	Penicillium adametzi							*			
	P. cyaneo-fulvum			*							
	P. cyclopium	*									
	P. lividum						***	*			
	P. nigricans			*							
	P. restrictum	*	**	***	***	*		***	**		
D461	Penicillium sp.						***	*			
D1881	Aspergillus sp.		*								
S301	Alternaria sp.	*									
S33	Cephalosporium sp.	*			***	*		*	***	*	
S10	Coniothyrium sp.	*	*	**						*	
D1964	" "	***	***				*				
	Cladosporium herbarum		*						***	*	
D1877	Cladosporium sp.	*									
	Fusarium culmorum	*									
	Gliomastix convoluta v. felina					**		**		*	*
	Papularia arundinis		*								
D1889	Phialophora sp (?)							*			
D1966	Sterile hyaline mycelium		*								
D1872	Sterile dark coloured mycelium			*							
D1919	" " " "										*

NEWBOROUGH WARREN, ANGLESEY
MAY 1953

S/C No.	Species	Ammophila Embryo Dune					Ammophila Fore Dunes					Late "Yellow Dune"					Fixed "Grey Dune"					Salix-Calluna-Caricetum Inter. between Stack and Fixed Dune				
	Sampling Depth	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH						8.5			8.7		8.6			8.5		6.6-7.2			8.3		not sampled	5.5	5.6	6.1	7.9
	Absidia orchidis																						*			
	Mortierella alpina												**		*	*	*	***	**							
	M. parvispora																						***			
	Mucor hiemalis			**																			**			
	Chaetomium cochliodes											*														
N94	Chaetomium sp.					***																				
N63	Thielavia sp.																						***			
	Beauveria bassiana																						*			
S33	Cephalosporium sp.																		***					*	*	
	Cladosporium herbarum		*											*					*				*			*
S10	Coniothyrium sp.				*			*		*		***	***	**	*		*	**					*			
	Fusarium culmorum												*	**			**									
	Gliomastix convoluta v. felina														*								*			
S890	Harposporium sp.											**														
N50	(Melanconiales)													**												
	Myrothecium roridum												*	***												
	Papularia sphaerosperma		*				*	*															*			
	Penicillium melinii																						*			
	P. nigricans							*									***	***	***	**					*	
	P. paxilli		**	**			*																			
	P. restrictum												*	***	*		**	*	*	*						
	P. spinulosum			*	*			*																	*	*
	P. thomii																						***			
N58	Penicillium sp.																		*					**	***	*
N67	" "															*										
	Pullularia pullulans																						*			
	Trichoderma viride							*										*					***			
	Trichosporium cerealis													***												
	3 sterile dark coloured mycelia)																									
	6 sterile hyaline mycelia)																									

BLAKENEY POINT

The Soil Profiles

1. Agropyron embryo dune.

   Profile undifferentiated.

2. Semi-fixed "yellow" dune.

   A very thin surface humus layer above a uniform profile of yellow sand.

3. Semi-fixed - fixed "grey" dune.

   0 - 2 inches: A_1 humus-rich horizon.

   2 - 12 inches: yellow sand.

BLAKENEY POINT, NORFOLK		Semi-Fixed "Yellow Dune"					Semi-Fixed - Fixed "Grey Dune"				
SEPT. 1953	Sampling Depth	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	6.3		6.3	6.6	6.8	4.9		-	6.6	6.1
S/C No.	Species										
	Mortierella alpina		*	*	***	***					**
	Mortierella isabellina						*	**			
	Mucor hiemalis	*									
	M. ramannianus								*		
	Sordaria minuta							*			
B101	Aspergillus sp.						*				
	Botrytis cinerea						*				
B132	Cephalosporium sp.				**	***					
B138	" "						*				
	Cladosporium herbarum	**				*			*		
S10	Coniothyrium sp.	***	***	***	***	*	*	*	*		
B69	" "							*			
	Fusarium culmorum	***	***				**	**			
	Gliomastix convoluta v. felina				***						
	Myrothecium roridum									*	
	Penicillium namyslowskii								*		
	P. nigricans	***	***	***	***	*	*	**	*		
	P. restrictum	*									
	P. spinulosum	*									
	Trichoderma viride	***	***	*	*		***	***	***	***	
	Verticillium nigrescens (?)						*				
B139	Verticillium sp.				*						
B96	Sterile dark coloured mycelium						*				
B111	" " " "				*						

TENTSMUIR

The Soil Profiles

Transect A

1. Fore dunes.

   No profile development visible.

2. Semi-fixed - fixed "grey" dune.

   0 - ½ inch: light grey humus horizon.

   ½ - 12 inches: clean sand.

3. Fixed dune heath.

   0 - 1½ inches: brown humus horizon.

   1½ - 12 inches: transition to clean sand.

   No evidence of podsolisation.

Transect B

1. Open Sand.)
) No profile development
2. Fore dunes.)

3. Semi-fixed - fixed dune.

   0 - ½ inch: light grey humus horizon.

   ½ - 12 inches: clean sand.

4. Fixed dune heath.

   0 - 2 inches: brown humus horizon.

   2 - 3 inches: leached horizon.)
) horizons
   3 - 6 inches: humus pan.) indefinite
)
   6 - 12 inches: transition to clean sand.)

TENTSMUIR, FIFE /TRANSECT A/
APRIL 1955

		Mobile Fore Dune					Semi-Fixed Dune					Calluna Fixed Dune				
	Sampling Depth	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	6.7		7.0	6.5	6.9	4.2		5.8	6.2	6.6	4.5		5.3	6.3	5.6
S/C No.	Species															
	Mortierella isabellina						***	**								
	M. parvispora						***						*			
	Mucor hiemalis				*											
	M. ramannianus											***	***	**		
S33	Cephalosporium sp.								**							
	Cladosporium herbarum															*
	Gliomastix convoluta v. felina													*	*	
	Penicillium cyaneo-fulvum													*		
	P. cyclopium													**		
	P. nigricans							***	*		*	**	***	***	*	
D461	P. raistrickii											*				
	P. spinulosum						***					***	*			
D946	Penicillium sp.						***					*	*			
D1855	" "											***				
D1866	Penicillium miczynskii						***									
D1948	Scopulariopsis sp.											***		*		
	Trichoderma viride			*								**	***			
	Trichosporium cerealis													*		

XX

TENTSMUIR, FIFE /TRANSECT B/ APRIL 1955		Open Sand	Mobile Fore Dune					Semi-Fixed Dune					Calluna Fixed Dune				
	Sampling Depth	1"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	Soil pH	7.6	7.4		8.0	7.0	7.0	6.8		7.3	7.3	7.5	4.9	6.1	7.0	6.9	7.7
S/C No.	Species																
	Mortierella alpina		*			***	*				*						
	Mortierella isabellina							*		*			**	*	*		
	M. parvispora													*			
	Mucor ramannianus							***					***				
	Gelasinospora cerealis												**				
	Beauveria bassiana													*	*		
	Botrytis cinerea													*			
	Cephalosporium acremonium	*															
S33	Cephalosporium sp.		*	*													
D1918	" "						**										
	Cladosporium herbarum		**								*						
D1933	Cladosporium sp.													*			
S10 ?	Coniothyrium sp.					*		**									
D1920	Hormiscium sp.											*					
D1917	Paecilomyces sp.						**										
	Penicillium cyclopium							**									
	P. melinii												***	*			
	P. nigricans							***	***	***	*		***	***	*		
	P. spinulosum												*	*	**		
D946	Penicillium sp.														*		
	Trichoderma viride							**		*			**	*	**		
D1928	Sterile hyaline mycelium							*									
D1919	Sterile dark coloured mycelium											*					

THE DISTRIBUTION OF MICROFUNGI IN 2 SOIL PROFILES OF A DUNE LOW AT BLAKENEY POINT, NORFOLK

Subjective estimates of frequency from soil plate isolations
*** common
** frequent
* occasional

Sept. 1953.

		GLAUX LOW, PROFILE 'A'					ADJACENT "YELLOW" DUNE				
	SAMPLING DEPTH	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	SOIL pH	6.6		6.5	6.8	6.6	6.8		-	6.6	6.5
	SALINITY (% total chlorides)	0.01			0.01		<0.01			-	
S/C No.	Species										
	Mortierella alpina		*						*	***	**
	Mucor hiemalis						*				
	Sporormia intermedia		*								
B 101	Aspergillus sp.					*					
B 132	Cephalosporium sp.				*					**	**
B 138	" "				*						
	Cladosporium herbarum	*	*		*		***				*
S 10	Coniothyrium sp.	*					***	***	***	***	*
	Fusarium culmorum		**	***			*				
	Myrothecium roridum				*						
S 1091	Oospora sp.	*									
	Penicillium nigricans	***	*	*			**	***	***	***	*
	Penicillium spinulosum						*				
S 25	Stemphylium sp.	*									
	Trichoderma viride	*					*	**	**		
B 139	Verticillium sp.									*	
	Verticillium nigrescens (?)			*							
	Sterile dark coloured mycelium						*				

continued

THE DISTRIBUTION OF MICROFUNGI IN 2 SOIL PROFILES OF A DUNE LOW AT BLAKENEY POINT, NORFOLK

Subjective estimates of frequency from soil plate isolations

*** common
** frequent
* occasional

		GLAUX LOW, PROFILE 'B'					ADJACENT "YELLOW" DUNE				
	SAMPLING DEPTH	½"	1"	3"	6"	12"	½"	1"	3"	6"	12"
	SOIL pH	6.4		6.7	6.8	6.8	6.3		6.3	-	6.8
	SALINITY (% total chlorides)	<0.01			0.02	¥	<0.01			-	
S/C No.	Species										
	Mortierella alpina							*		***	***
B 101	Aspergillus sp.		*								
B 125	Cephalosporium sp.			**							
	Cladosporium herbarum	***			*						
S 10	Coniothyrium sp.	**					***	***	***	**	*
	Fusarium culmorum						***	**			
	Gliomastix convoluta v. felina	***	**								
	Penicillium nigricans	***	*	*			***	***	***	***	
	Trichoderma viride	*					*	**	*	**	
	Verticillium nigrescens (?)	*	***	*	*						
	Sterile hyaline mycelia	*	***	*							
	Sterile dark coloured mycelium									*	*

¥ Salinity of water table at a depth of 17" = 0.71%

The lows were sampled several months after they had been flooded by sea water.

APPENDIX

3. Species of Microfungi Isolated from Dune Soils

PHYCOMYCETES

MUCORALES

Absidia glauca Hagem
A. orchidis (Vuillemin) Hagem
A. spinosa Lendner
Cunninghamella sp.
Haplosporangium decipiens Thax.
Mortierella alpina Peyronel
M. hygrophila Linneman
M. isabellina Oud.
M. marburgensis Linn.
M. minutissima van Tieghem
M. parvispora Linn.
M. spinosa Linn.
Mucor hiemalis Wehmer
M. spinescens Lendner
M. strictus Hagem
M. ramannianus Moller
Piptocephalis xenophila Dobbs ?
Rhizopus nigricans Ehrenberg
Syncephalastrum sp.
Thamnidium sp.
Zygorrhynchus vuilleminii Namyslowskii

ASCOMYCETES

EUROTIALES

Gymnoascus sp.
2 *Thielavia* spp.

SPHAERIALES

Chaetomium cochliodes Palliser
C. murorum Corda
C. pannosum Wallr.
Chaetomium sp.
Gelasinospora cerealis Dowding
G. retispora Cain
Sordaria destruens (Shear) Hawker
Sordaria minuta (?)
Sporormia intermedia Auerswald
2 *Sporormia* spp.

*10 Unidentified spp.

FUNGI IMPERFECTI

SPHAEROPSIDALES

7 Coniothyrium spp.
? Cytoplea sp.
Hendersonia sp.
2 Microdiplodia spp.
Phoma sp.
Phomopsis sp.
Pyrenochaeta sp.

MELANCONIALES

? Melanconium sp.
2 Pestalotia spp.

MONILIALES

Pseudosaccharomycetaceae

Pullularia pullulans (de Bary) Berk

Moniliaceae

5 Aspergillus spp.
Beauveria bassiana (Bals) Vuill.
Botrytis cinerea Pers. ex Fr.
13 Cephalosporium spp.
Cephalosporium acremonium Corda
Gliocladium roseum Bainier
Harposporium sp.
Monosporium sp.
Nematogonum sp.
Paecilomyces sp.
Penicillium adametzi Zaleski
P. aurantio-candidum Dierckx?
P. brevi-compactum Dierckx
P. cyaneo-fulvum Biourge
P. cyclopium Westling
Penicillium cyclopium series
P. decumbens Thom
P. digitatum Saccardo
P. funiculosum Thom
P. janthinellum Biourge
P. lividum Westling
P. lapidosum Raper & Fennell

P. martensii Biourge
P. melinii Thom
P. miczynskii Zaleski
P. namyslowskii Zaleski
P. nigricans Bainier
P. paxilli Bainier
P. phoeniceum van Beyma
P. piceum Raper & Fennell
P. raistrickii G. Smith
P. raistrickii series
P. restrictum Gilman & Abbott
P. rubrum Stoll
P. simplicissimum (Oud) Thom
P. spinulosum Thom
P. terlikowskii Zaleski (?)
P. thomii Maire
P. thomii series
P. viridicatum Westling
P. wortmanni Klöcker
12 unidentified Penicillium spp.
f* Piricularia sp (?)
Scopulariopsis brevicaulis
Spicaria violaceae Abbott
2 Sporotrichum spp.
* Tilachlidium sp.
Trichoderma viride Persoon ex Fr.
Verticillium nigrescens Pethyb. (?)
2 Verticillium spp.

Dematiaceae

Alternaria sp.
* Asteromyces cruciatus Moreau (new British record)
Cladosporium herbarum Linkex Fr.
Cladosporium macrocarpum Preuss
2 Cladosporium spp.
Dicoccum asperum Corda
Dicoccum sp.
Gliomastix convoluta Harz v. felina Mason
f* ? Gliomastix sp.
Helminthosporium sp.
Hormiscium sp.
* ? Humicola sp.
Monotospora sp.
Papularia arundinis (Corda) Fries
P. sphaerosperma von Höhnel
Periconia igniaria Mason & M.B. Ellis
* Phialophora sp.
2 Sarcinella spp.

Septonema chaetospira (Grove) Hughes
Stachybotrys atra Corda
Stemphylium dendriticum Sousa da Camara
4 Stemphylium spp.
Trichosporium cerealis (Thüm) Sacc.
/ * ? Trichosporium sp.

Stilbaceae

Stysanus stemonites (Pers. ex Fr.) Corda

Tuberculariaceae

Fusarium culmorum (W.G. Smith) Saccardo
Fusarium oxysporum sensu Snyder & Hansen
2 Fusarium spp.
Myrothecium roridum Tode ex Fr.

Unidentified spp. including / * S312

* Deposited at the Commonwealth Mycological Institute, Kew .

/ Species possibly new to science.

REFERENCES

Adametz, L. (1886)
Untersuchungen über die niederen Pilze der Ackerkrume.
Inaug. Diss. Leipzig, 1-78.

Alexander, F.E.S. & Jackson, R.M. (1954)
Examination of soil micro-organisms in their natural environment.
Nature, Lond., 174, 750-751.

Andersson, O. (1950)
Larger fungi on sandy grass heaths and sand-dunes in Scandinavia.
Bot. Notiser Supplement, 2, 1-89.

Barghoorn, E.S. & Linder, D.H. (1944)
Marine fungi: their taxonomy and biology.
Farlowia, 1, 395-467.

Bayliss Elliott, J. (1930)
Soil fungi of the Dovey salt marshes.
Ann. Appl. Biol. 17, 284-305.

Bisby, G.R., James, N. & Timonin, M.I. (1933)
Fungi isolated from Manitoba soil by the plate method.
Can. J. Res. 8(c), 253-275.

Bisby, G.R., James, N. & Timonin, M.I. (1935)
Fungi isolated from soil profiles in Manitoba.
Can. J. Res., 13(c), 47-65.

Boswell, J.G., & Sheldon, J. (1951)
The microbiology of acid soils. II.
New Phytol. 50, 172-178.

Brierley, W.B., Jewson, S.T. & Brierley, M. (1927)
The quantitative study of soil fungi.
Proc. 1st. Int. Congr. Soil Sci., 3, 24.

Burges, A (1939)
Soil fungi and root infection.
Brotéria, Série de Ciências Naturais, 8, 64-81.

Burges, A. (1950)
The downward movement of spores in sandy soil.
Trans. Brit. mycol. Soc. 33, 142-147.

Brierley, W.B. (1928).
The microflora of the soil.
J. Quekett. Micr. Cl., 16, 9-18.

Burges, A. (1953)
Soil fungi and humus decomposition.
Proc. 7th Pacific Sci. Congr. (N.Z.), 6, 47-54.

Burges, A. & Fenton, E. (1953)
The effect of carbon dioxide on the growth of certain soil fungi.
Trans. Brit. Mycol. Soc. 36, 104-108.

Butler, E.J. (1907)
An account of the genus Pythium and some Chytridiaceae.
Mem. Dep. Agric., India, 1, 1-160.

Campbell, M.E. (1938)
An investigation of the Mucorales in the soil.
Trans. Roy. Soc. Edin. 59, 411-436.

Chesters, C.G.C. (1940)
A method of isolating soil fungi.
Trans. Brit. mycol. Soc., 24, 352-5.

Chesters, C.G.C. (1948)
A contribution to the study of fungi in the soil.
Trans. Brit. mycol. Soc. 30, 100-117.

Chesters, C.G.C. (1949)
Concerning fungi inhabiting soil.
Trans. Brit. mycol. Soc. 32, 197-216.

Cholodny, N.G. (1930)
Über eine neue Methode zur Untersuchung der Bodenmikroflora.
Archiv. für Mikrobiologie, 1, 620-52.

Cholodny, N.G. (1934)
A soil chamber as a method for the microscopic study of the soil microflora.
Archiv. für Mikrobiologie, 5, 148-56.

Cholodny, N.G. (1936)
Bodenstaubkulturen und die Mikroflora des Bodens.
Archiv. für Mikrobiologie, 7, 286-96.

Clark, F.E. (1949)
Soil micro-organisms and plant roots.
Adv. Agron., 1, 241-88.

Conn, H.J. (1916)
The relative importance of fungi and bacteria in soil.
Science. 44, 857-8.

Conn, H.J. (1918)
The microscopic study of bacteria and fungi in soil.
N.Y. (Geneva), Agr. Exp. Sta. Tech. Bul., 64, 1-20.

Conn, H.J. (1922)
A microscopic method for demonstrating fungi and actinomycetes in soil.
Soil Sci., 14, 149-51.

Dale, E. (1914)
On the fungi of the soil, II.
Ann. mycol., Berl., 12, 33-62.

Dawson, V.T. & Dawson, R.T. (1946)
Further observations on the use of rose bengal for the enumeration of soil fungi.
Proc. Amer. Soil Sci. Soc., 11, 268-269.

Diver, C. (1933)
The physiography of South Haven Peninsula, Studland Heath, Dorset.
Geogr. J., 81, No. 5.

Dobbs, C.G. & English, M.P. (1954)
Piptocephalis xenophila sp. nov. parasitic on non-mucorine hosts.
Trans. Brit. mycol. Soc., 37, 375-89.

Duché, J. & Heim, R. (1931)
Recherches sur la flore mycologique des sols sableux.
Recueil Travaux mycologiques dédiés à Louis Mangin, Paris, 431-458.

Eastwood, D.J., Fraser, G.K. & Webley, D.M. (1950)
The microbiological factor in the Culbin Sands Afforestation Scheme.
Nature, Lond., 165, 980.

Ellis, M. (1940)
Some fungi isolated from pinewood soil.
Trans. Brit. mycol. Soc., 24, 87-97.

Garrett, S.D. (1938)
Soil conditions and the root-infecting fungi.
Biol. Rev., 13, 159-85.

Garrett, S.D. (1950)
Ecology of the root-inhabiting fungi.
Biol. Rev., 25, 220-54.

Garrett, S.D. (1951)
Ecological groups of soil fungi: a survey of substrate relationships.
New Phytol., 50, 149-66.

Garrett, S.D. (1952)
The soil fungi as microcosm for ecologists.
Sci. Progr., 40, 436-50.

Garrett, S.D. (1955)
Microbial ecology of the soil.
Trans. Brit. mycol. Soc., 38, 1-9.

Garrett, S.D. (1956)
Biology of Root-Infecting Fungi.
Cambridge University Press.

Gimingham, C.H. (1951)
Contributions to the maritime ecology of St. Cyrus, Kincardineshire, II.
Trans. Bot. Soc., Edinburgh, 35, 387-411.

Glynne, M.D. (1939)
Fungal invasion of the roots of healthy wheat plants.
Trans. Brit. mycol. Soc., 23, 210.

Good, R. (1935)
Contribution towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. II.
J. Ecol., 23, 361.

Gray, P.H.H. & Taylor, C.B. (1935)
A microbiological study of podsol soil profiles. II.
Canad. J. Res., 13(c), 251-62.

Haarløv, N. & Weis-Fogh, T. (1953)
A microscopical technique for studying the undisturbed texture of soils.
Oikos, 4, 44-57.

Harley, J.L. (1948)
Mycorrhiza and soil ecology.
Biol. Rev., 23, 127-158.

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, 104-18.

Hawker, L.E. (1950)
Physiology of Fungi.
University of London Press.

Hepple, Shirley & Burges, A. (1956)
Sectioning of Soil.
Nature, Lond. 177, 1186.

Hiltner, L. (1904)
Über neuere Erfahrungen und Probleme auf dem Gebeit der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache.
Arb. dtsch. Landw—Ges., 98, 59-78.

Höhnk, W. (1954)
Studien zur Brack und Seewassermykologie. IV. Ascomyceten des Küstensandes.
Veröffentl. Inst. Meeresforsch, Bremerhaven, 3, 27-33.

Ikeda, S. (1954)
(On the distribution of fungi in sand dune soils).
Jour. Japanese Forest Soc., 36, 221-24.

Ivimey Cook, W.R. & Morgan, E. (1934)
Some observations on the Saprolegniaceae of the soils of Wales.
J. Bot., 72, 345-49.

Jensen, H.L. (1931)
The fungus flora of the soil.
Soil Sci., 31, 123-58.

Jensen, H.L. (1935)
Contribution to the microbiology of Australian soils. III. The Rossi-Cholodny method as a quantitative index of the growth of fungi in the soil, with some preliminary observations on the influence of organic matter on the soil microflora.
Proc. Linn. Soc., N.S.W., 60, 145-54.

Jeffreys, E.G., Brian, P.W., Hemming, H.G. & Lowe, D. (1953)
Antibiotic production by the microfungi of acid heath soils.
J. gen. Microbiol., 9, 314-41.

Jones, P.C.T. & Mollison, J.E. (1948)
A technique for the quantitative estimation of soil micro-organisms.
J. gen. Microbiol., 2, 54-69.

Katznelson, H., Lochhead, A.G. & Timonin, M.I. (1948)
Soil micro-organisms and the Rhizosphere.
Bot. Rev., 14, 543-87.

Killian, C. & Féhér, D. (1935)
Recherches sur phénomènes microbiologiques des sols sahariens.
Ann. Inst. Pasteur, 55, 573-622.

King, C.J., Hope, C. & Eaton, E.D. (1934)
Some microbiological activities affected in manurial control of cotton root rot.
J. agric. Res., 49, 1093-1107.

Kubiena, W.L. (1932)
Über Fruchtkorper bildung und engere Standortwahl von Pilze in Bodenhohl raumen.
Arch. Mikrobiol., 3, 607-42.

Kubiena, W.L. (1938)
Micropedology.
Ames, Iowa: Collegiate Press, Inc.

Kürbis, W.P. (1937)
Mykologische Untersuchungen über den Wurzelbereich der Esche (Fraxinus excelsior L.)
Flora, Jena, 31, 129-75.

La Touche, C.J. (1948)
Slide Traps for soil fungi.
Trans. Brit. mycol, Soc., 31, 281-84.

Linnemann, G. (1941)
Die Mucorincen-Gattung Mortierella Coemaus.
Pflanzenforschung, 23, 1-64.

McLean, R.C. & Ivimey-Cook, W.R. (1941)
Plant Science Formulae.
Macmillan & Co.

McLennan, E.I. (1928)
Growth of fungi in soil.
Ann. appl. Biol., 15, 95-109.

McLennan, E.I. & Ducker, S.C. (1954)
The ecology of the soil fungi of an Australian heathland.
Aust. J. Bot., 2, 220-45.

Meredith, C.H. (1940)
A quick method of isolating certain phycomycetous fungi from soil.
Phytopathology, 30, 1055-6.

Moreau, M. & Mme. F. (1940)
Microflora des dunes.
Rev. de Mycologie, 4-6, 50-94.

Moss, C.E. (1907)
Geographical distribution of vegetation in Somerset, Bath and Bridgwater District.
Roy. Geog. Soc. Supplement.

Müller, W. & Schopfer, W. (1937)
L'action de l'aneurine et de ses constituents sur Mucor ramannianus Möller.
C.R. Acad. Sci., Paris, 205, 687-89.

Newman, A.S. & Norman, A.G. (1943)
The activity of subsurface soil populations.
Soil Sc., 55, 377-391.

Nicolson, T.H. (1955)
The mycotrophic habit in grasses.
Ph. D. Thesis, University of Nottingham.

Nicot, J. & Chevaugeon, J. (1949)
Comparaison des méthodes d'isolement de la microflore fongique du sol.
Bull. Muséum National D'Hist. Natur. 2e Série, 21, 384-92.

Oliver, F.W. & Salisbury, E.J. (1913)
The topography and vegetation of Blakeney Point, Norfolk.
Trans. Norfolk & Norwich Nat. Soc., 9, 485-542.

Oosting, H.J. & Billings, W.D. (1942)
Factors affecting vegetational zonation on coastal dunes.
Ecology, 23, 131.

Oudemans, C.A.J.A. & Koning, C.J. (1902)
Prodrome d'une flore mycologique obtenue par la culture sur gelatine préparée de la terre humeuse du Spanderswond près de Bussum.
Arch. Néerland. Sci. Exact et Nat., Série 2, VII 266-98.

Ovington, J.D. (1950)
The afforestation of the Culbin sands.
J. Ecol., 38, 303-319.

Ovington, J.D. (1951)
The afforestation of Tentsmuir sands.
J. Ecol., 39, 363-375.

Paine, F.S. (1927)
Studies of the fungous flora of virgin soils.
Mycologia, 19, 248-66.

Pearsall, W.H. (1952)
The pH of natural soils and its ecological significance.
J. Soil Sc., 3, 41-51.

Piper, C.S. (1950)
Soil and Plant Analysis.
University of Adelaide.

Preston, N.C. (1943)
Observations on the genus Myrothecium Tode.
Trans. Brit. mycol. Soc., 26, 158-68.

Puri, A.N. & Ashgar, A.G. (1938)
Influence of salts and soil water ratio on the pH value of soils.
Soil Sc., 46, 249-257.

Raper, K.B. & Thom, C. (1949)
A manual of the Penicillia.
Baltimore, Williams & Wilkins Co.

Robertson, N.F. (1954)
Studies on the mycorrhiza of Pinus sylvestris. I.
New Phytol., 53, 253-83.

Rokitzkaya, A.I. (1930)
Soil microflora in the root system zone of plants in the region of forest steppe and chemozem in Ukraine.
Proc. 2nd. Int. Congr. Soil Sci., III, 3, 260-62.

Rossi, G. & Riccardo, S. (1927)
L'esame microscopio e bacteriologica diretto del terreno agrario.
Nuov. Ann. dell Agr., 7, 457-70.

Rossi, G., Riccardo, S., Gesué, G., Stanganelli, M. & Tsu Kao Wang. (1936)
Direct microscopic and bacteriological examination of the soil.
Soil Sci., 41, 53-66.

Sabet, Y.S. (1935)
A preliminary study of the Egyptian soil fungi.
Bull. Fac. Sci. Egypt Univ., No.5, 1-29.

Sabinin, D.A. & Minina, E.G. (1930)
Das Mikrobiologische Bodenprofil als Zonales Kenn zeichen.
Proc. 2nd. Int. Congr. Soil Sci., III, 3, 224-35.

Saitô, Toshi (1952)
The soil fungi of a salt marsh and its neighbourhood.
Ecol. Rev. (Japan), 13, No.2.

Saitô, Toshi (1955)
Soil Microflora of a coastal dune.
The Science Reports of Tôhoku Univ., 21, 2, 145-151.

Salisbury, E.J. (1922)
The Soils of Blakeney Point.
Ann. Bot., 36, 391.

Salisbury, E.J. (1925)
Note on the edaphic succession in some dune soils with special reference to the time factor.
J. Ecol., 13, 322.

Salisbury, E.J. (1952)
Downs and Dunes.
Lond., G. Bell & Sons.

Sewell, G.W.F. (1954)
An ecological study of fungi in Calluna-heathland soils.
Ph.D. Thesis, University of London.

Sewell, G.W.F. (1956)
A slide-trap method for the isolation of soil fungi.
Nature, Lond., 177, 708.

Shaw, R. (1935)
Tentsmuir and its flora.
For. Comm. J., 14, 107.

Simmonds, P.M. (1930)
A washing device for isolation work with plant material.
Phytopathology, 20, 911-13.

Simmonds, P.M. & Ledingham, R.J. (1937)
A study of the fungous flora of wheat roots.
Sci. Agric., 18, 49-59.

Smith, N.R. & Dawson, V.T. (1944)
The bacteriostatic action of rose bengal in media used for the plate counts of soil fungi.
Soil Sci., 58, 467-71.

Smith, W.G. (1905)
Botanical Survey of Scotland, III & IV, Forfar and Fife.
Scot. Geog. Mag., 21, 57-83.

Snow, L.M. (1926-1935)
A comparative study of the bacterial flora of wind blown sand.
Soil Sci., 21, 143-166
24, 39-47; 335-43.
39, 227-31; 233-36.
40, 181-90.

Stanier, R.Y. (1953)
Adaptation, evolutionary & physiological: or Darwinism among the micro-organisms.
Adaptation in micro-organisms, Third Symp. Soc. Gen. Microbiol. Cambridge University Press.

Stenton, H. (1953)
The soil fungi of Wicken Fen.
Trans. Brit. Mycol. Soc., 36, 304-14.

Stuart Thompson, H. (1922)
Changes in the coast vegetation near Berrow, Somerset.
J. Ecol., 10, 53-61.

Stuart Thompson, H. (1930)
Further changes in the coast vegetation near Berrow, Somerset.
J. Ecol., 18, 126-30.

Swift, M.E. (1929)
Contributions to a mycological flora of local soils.
Mycologia, 21, 204-21.

Thom, C. & Humfeld, H. (1932)
Notes on the association of micro-organisms and roots.
Soil Sci., 34, 29-36.

Thom, C. & Morrow, M.B. (1937)
Fungous mycelia in the soil.
J. Bact., 33, 77-78.

Thornton, R.H. (1952)
The screened immersion plate. A method of isolating soil micro-organisms.
Research, V, No. 4.

Thrower, L.B. (1954)
The rhizosphere effect shown by some Victorian heathland plants.
Aust. J. Bot., 2, 246-67.

Timonin, M.I. (1935)
The micro-organisms in profiles of certain virgin soils in Manitoba.
Canad. J. Res., 13, 32-46.

Tresner, H.D., Backus, M.P. & Curtis, J.T. (1954)
Soil microfungi in relation to the hardwood forest continuum in Southern Wisconsin.
Mycologia, 46, 314-33.

Vandecaveye, S.C. & Katznelson, H. (1938)
Microbial activities in Soil, IV.
Soil Sci., 46, 57-74.

Verplancke, G. (1932)
L'examen micro-biologique du sol.
Bull. Inst. Agr. Stat. Rech. Gembloux, I, 35-45.

Waksman, S.A. (1916)
Do fungi actually live in the soil and produce mycelium?
Science, N.S., 44, 320-22.

Waksman, S.A. (1917)
Is there any fungus flora of the soil?
Soil Sci., 3, 565-89.

Waksman, S.A. (1922)[a]
A method of counting the number of fungi in the soil.
J. Bact., 7, 339.

Waksman, S.A. (1922)[b]
The growth of fungi in the soil.
Soil Sci., 14, 153-57.

Waksman, S.A. (1924)
The influence of soil reaction upon the distribution of filamentous fungi in soil.
Ecology, 5, 54-59.

Waksman, S.A. (1932)
Principles of Soil Microbiology. 2nd ed. Lond. Baillière, Tindall & Cox.

Waksman, S.A. (1944)
Three decades with soil fungi.
Soil Sci., 58, 89 - 115.

Waksman, S.A. (1952)
Soil Microbiology, New York: John Wiley & Sons.

Warcup, J.H. (1950)
The soil-plate method for isolation of fungi from soil.
Nature, Lond., 166, 117 - 18.

Warcup, J.H. (1951)[a]
The ecology of soil fungi.
Trans. Brit. Mycol. Soc., 34, 376 - 99.

Warcup, J.H. (1951)[b]
Soil steaming: a selective method for the isolation of Ascomycetes from soil.
Trans. Brit. Mycol. Soc., 34, 515 - 18.

Warcup, J.H. (1951)[c]
Studies on the growth of Basidiomycetes in soil.
Ann. Bot., N.S., 15, 305 - 18.

Warcup, J.H. (1952)
Effect of partial sterilisation by steam or formalin on damping-off of Sitka Spruce.
Trans. Brit. Mycol. Soc., 35, 248 - 62.

Warcup, J.H. (1955)[a]
Isolation of fungi from hyphae present in soil.
Nature, Lond., 175, 953 - 4.

Warcup, J.H. (1955)[b]
On the origin of colonies of fungi developing on soil dilution plates.
Trans. Brit. Mycol. Soc., 38, 298 - 301.

Watson, W. (1918)
Cryptogamic vegetation of the sand-dunes of the west coast of England.
J. Ecol., 6, 126 - 43.

Webley, D.M., Eastwood, D.J. & Gimingham, C.H. (1952)
The development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species.
J. Ecol, 40, 168 - 78.

Werkenthin, F.C. (1916)
Fungous flora of Texas soils.
Phytopathology, 6, 241-53.

Wilson, I.M. (1951)
Notes on some marine fungi.
Trans. Brit. Mycol. Soc., 34, 540-50.

Winogradsky, M.S. (1925)
Études sur la microbiologie du sol.
Ann. Inst. Pasteur, 39, 299-354.

Wright, T.W. (1955)
Profile development in the sand-dunes of Culbin Forest, Morayshire, I. Physical Properties.
J. of Soil Sci., 6, 270-83.