Neth. J. Pl. Path. 75 (1969) 287–295

Cellulose-decomposing fungi in polder soils and their possible influence on pathogenic fungi

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Accepted 21 February 1969

Abstract

For a study of the colonisation of the IJsselmeerpolders by fungi, attention was fixed on the cellulose-decomposing fungi, since these are considered to represent the more stable part of the mycoflora of soils. If one assumes that in the North East Polder, cultivated for approximately 25 years, the fungal population is approaching stability, the progress of colonisation of the younger polders can be judged by comparison of the number of species found and their frequency.

It is shown that the progress of fungal colonisation did not depend only on the time during which a soil has been dry, but also on the use that has been made of it. Of the species known as antagonists of other fungi, *Trichoderma* spp. provided an increasingly larger proportion of the total population as the soils were further from stability.

It is concluded that the increase of fungal antagonists may well be one of the causes of the decline of such parasites as *Ophiobolus graminis* and *Rhizoctonia solani*. Special mention is made of *Gliocladium roseum*, the parasitism of which towards *R. solani* could be demonstrated in paired cultures.

The reclamation of previously submerged land presents an ideal opportunity to study the colonisation of the soil by micro-organisms. In the Netherlands large-scale land reclamation has been proceeding during the last forty years. In 1930 the Wieringermeerpolder was reclaimed from the Zuyderzee. Following the completion of the enclosing dam in 1932, this area of water gradually became a large fresh water lake and was renamed the "IJsselmeer". Three polders have been enclosed and drained since then. This area has a long history of periodic submersion under fresh and salt water, with prolonged intervening periods, when the land was marshy or even quite dry. Consequently, beneath the relatively recent silts are relict clay-loams and peat layers which have been submerged for at least the last 500 years.

During the reclamation of an individual polder an enclosing dam is built and the water is pumped out to reveal the sea bed. Seeds of *Phragmites communis* are then sown from aircraft on the waterlogged, newly exposed mud. The plants, as they grow, have a double function: their rapid transpiration helps to get rid of the excess soil water, and by their prolific growth they exclude the majority of weeds which would be much more difficult to eradicate later. The reclaimed polder is then progressively brought into cultivation over a period of about 10 years, so that there will be a range of conditions, from a short period of reed growth followed by 9 or 10 years of crops on one side of the polder, to the reverse with 10 years of reeds before the first ploughing on the other side. In such regions there is a thick layer of ash built up by the periodic burning of the reeds.

In the early years of cultivation certain soil-borne fungal diseases, notably *Ophiobolus graminis* and *Rhizoctonia solani*, may be extremely active and bring about severe infections, before they decline in importance. Oort (1965) suggested that these pathogens were able to grow rapidly in the new soils before an antagonistic flora developed.[1]

It was therefore decided to survey the abundance of fungi in the IJsselmeer-polders to see if they increased from younger to older soils, and to look for fungi which could adversely affect the pathogens during the first few years of cultivation. This survey concentrated on those fungi which are able to decompose cellulose, because it comprises the bulk of plant remains added to the soil, and it is one of the most abundant organic compounds found in nature. The fungi which can bring about its decomposition probably form part of the autochthonous flora of the soil as they can grow actively, although possibly slowly, over a long period of time. They are therefore likely to be in competition with the pathogens long after the activities of the zymogenous fungi have died down.

Materials and methods

Soil samples were collected in July, 1968 from the three polders reclaimed from the IJsselmeer, to give a range of length of exposure of the soil, from the newly drained South Flevoland to the North East Polder which has been under cultivation for 26 years. Intermediate between these is East Flevoland, which has been drained for 10 years. Here two sites were chosen to compare the effect of 10 years growth of *Phragmites* with 6 years cultivation. Details of the localities are given in Table 1. At each site the sample, containing soil and roots of representative plants, was placed in a new polythene bag for transport to the laboratory.

Inocula, taken from the rhizosphere soil, were plated out on cellulose agar (Eggins and Pugh, 1962) as soon as possible after collection. In case of soil 1, inocula of mud uncolonized by higher plants were taken from 1–2 cm below the surface, and in soil 4a inocula were taken from the surface material. This consisted of a layer of about 2 cm deep, made up of the remains of aerial parts of *Phragmites*, and rhizome and root fragments in a matrix of ash resulting from the periodic burning of the reeds.

Ten plates were prepared from each sample and were incubated at 25 °C. A quantitative assessment of the fungal potential (Pugh, 1963) was made by counting each species which appeared on each plate as one isolate. The results obtained in this way from single soil samples cannot be regarded as being fully comprehensive. Rather, this assessment is used to indicate the distribution and relative abundance of the most common species in these particular samples.

Roots of *Phragmites* and *Senecio* (soils 2 and 3) were plated on Czapek agar to which rose bengal had been added. A total length of 25 cm of roots of three individual plants from each species was used. Wheat seeds were taken from the standing crop on soil 6 and ten were plated on cellulose agar.

[1] A comprehensive account of the occurrence of *Ophiobolus graminis* in the new polders (Gerlagh, 1968) appeared after this paper had been written. In the search for organisms which could be antagonistic to *O. graminis*, Gerlagh found that of the many fungi he examined, only *Gliocladium* spp. could be regarded as possible antagonists.

Table 1. Locality, higher plant cover, drainage and cultivation history, and soil reaction of the sampling sites.

Locality	Details	pH
A. South Flevoland	*Drained in March 1968*	
1. Uncolonised mud		8.0
2. Phragmites communis	Rhizospheres of young plants	8.0
3. Senecio congestus	Rhizosphere	8.0
B. East Flevoland	*Drained in 1958*	
4a. Phragmites communis	Organic litter and burnt debris on surface	
4b. Phragmites communis	Rhizospheres of mature stand	8.2
5. Rape	Rhizospheres of first year crop	8.1
6. Wheat	Rhizospheres of first year crop	7.8
C. East Flevoland	*Drained in 1958*	
7. Mixed grass	Six years cultivation in rotation	7.8
8. Potato	,, ,, ,, ,,	8.2
9. Wheat	Six years continuous cultivation	8.3
D. North East Polder	*Drained in 1941*	
10. Barley	Twenty six years cultivation	8.3
11. Potato	,, ,, ,, ,,	8.1
12. Potato	,, ,, ,, ,,	8.1

Tabel 1. Plaats, begroeiing, ontwatering, voorgeschiedenis en zuurgraad van de monsters.

Results

The distribution of the fungi isolated from the polder soils is given in Table 2, where the species are arranged in alphabetical order. The most frequently isolated fungi, *Fusarium culmorum*, *Gliocladium roseum*, *Plectosphaerella cucumeris*, and *Cephalosporium spp.* were all widespread and occurred in the majority of the soil samples examined. The number of isolates from the rhizospheres in each locality showed a reasonable degree of similarity to each other. However, the overall density of rhizosphere colonisation increased with longer periods of cultivation, which had a much greater effect than length of exposure of the soils. This is illustrated by the samples from the two East Flevoland localities where soils 4b, 5 and 6 have been dry for 10 years (4b was still under reeds, while 5 and 6 were in their first year of cultivation). The rhizospheres yielded a total of 48 isolations, with very little difference between the three plants sampled. Soils 7, 8 and 9 however, which have been dry for the same period, but which have been cultivated for 6 years yielded a total of 119 isolates. Fewer isolates were obtained from the grass crop (soil 7) than from the two cultivated crops at this locality. The North East Polder which was drained in 1941 and has been in cultivation since 1942, had a much more abundant flora, both quantitatively and qualitatively. There were 172 isolates from the rhizospheres of the crop plants studied, representing 27 species. If it can be assumed that the soil mycoflora is approaching stability after 26 years of cultivation, and these totals represent 100% colonisation, then, after 6 years of cultivation the soil, quantitatively, is 69% colonised, with 63% of the species,

Table 2. Distribution of cellulose-decomposing fungi. The figures refer to the number of petri-dishes in which each fungus occurred.

	South Flevoland				East Flevoland					East Flevoland				North East Polder				Total isola-tions
	1	2	3	Total	4a	4b	5	6	Total	7	8	9	Total	10	11	12	Total	
Alternaria tenuis Nees											1	1	2			1	1	3
Aspergillus sp.														1			1	1
Aureobasidium bolleyi (Sprague) v. Arx												7	7	4		2	6	13
Cephalosporium spp.					8			1	1	4	7	3	14	3	4	2	9	32
Chaetomium crispatum Fuckel														3	1		4	4
elatum Kunze ex Fr.														2			2	2
globosum Kunze										1	4	4	9	2	2	1	5	14
Coniothyrium sp.			1	1											1	1	2	3
Doratomyces microsporus (Sacc.) Morton et Smith																1	1	1
Fusarium culmorum (W. G. Smith) Sacc.					2		1	1	2	9	10	9	28	6	7	9	22	54
Fusarium spp.					1						1	3	4	1	5	2	8	13
Gliocladium roseum Bainier					1		1	2	3	4	10	10	24	3	8	9	20	48
Gliocladium sp.												1	1		1		1	2
Gliomastix murorum (Corda) Hughes var. felina (March.) Hughes															1	1	2	2
Humicola fuscoatra Traaen					10	10	1	2	13									23
Humicola grisea Traaen												2	2					2
Ostracoderma state of Peziza					3	1			1									4
Penicillium spp.														1	1	1	3	3
Phoma spp.										1			1		1		1	2
Plectosphaerella cucumeris Kleb. (conidial state)					2		1		1	4	2	3	9	7	6	10	23	35
Stachybotrys atra Corda												2	2			2	2	4
Trichocladium asperum Harz														1		1	2	2
Trichoderma hamatum (Bon.) Bainier						2	3	1	6						2	2	4	10
Trichoderma viride Pers. ex Fr.					5	2	4	2	8	1	3	1	5	1	1	1	3	22
Verticillium nigrescens Pethyb.										1	1		2	5	5	6	16	18
Volutella ciliata Fr.											1		1			2	2	3
Sterile mycelia: hyaline						1	6	4	11		2		2	3		2	5	18
yellow														3	6	4	13	13
+ chlamydospores															4	2	6	6
Rhizoctonia-like						1	1		2	4	2		6	3	3	2	8	16
Number of isolates from each soil			1	1	33	17	18	13		29	44	46		49	59	64		373
Number of rhizosphere isolates from each locality			1				48				119				172			
Percentage colonisation			0.6				28				69				100			
Number of species from each locality			1				10				17				27			
Percentage colonisation			3.7				37				63				100			

Tabel 2. Verdeling van cellulose ontledende schimmels. De cijfers geven het aantal petrischalen waarin de genoemde soorten voorkwamen.

compared with 28% colonisation by 37% of the species after 10 years of reeds and the beginning of cultivation. The South Flevoland muds, which had been dry for less than 4 months when the samples were collected, yielded only a single isolate, which represented 0.6% colonisation by 3.7% of the species and must be regarded as virtually sterile as far as cellulose decomposing fungi are concerned.

An interesting exception to the general paucity of fungi in the uncultivated soils occurred in the surface layers (soil 4a) where there was an accumulation of ash from the burnt *Phragmites*. The isolations from this layer were not included with those from the rhizospheres from this region, but they have been included in the grand total for each species. The 33 isolates from the surface layer greatly exceed the rhizosphere isolations, presumably because of the much more abundant organic matter available and the generally better aerated conditions. While the species isolated were generally widespread, *Humicola fuscoatra* was only found in this locality, where it was present on every petri dish from both the surface litter and the rhizosphere of *Phragmites*. However, it had almost disappeared from the rhizospheres of the two crop plants on the same soil.

In Table 3, the most common fungi have been listed to show their frequency of occurrence expressed as a percentage of the total isolations from each locality. It can be seen that *Cephalosporium* spp., *Fusarium culmorum* and *Gliocladium roseum* all form a greater proportion of the soil flora after 6 years of cultivation than in the other soils; *Plectosphaerella cucumeris* increased in relative abundance with longer periods of cultivation, and that *Trichoderma* spp., while very abundant in the soils just coming into cultivation, form only a small part of the flora after cropping for 6 years. The possible significance of these changes is discussed later in this paper.

Isolations from the roots of *Phragmites* and *Senecio* collected in South Flevoland were very sparse compared with the quantity which can be obtained from roots in older soils. A total of 14 isolates was obtained from 25 cm of *Phragmites* roots, and 11 isolates from a similar length of *Senecio* roots; 23 of these isolates were sterile; the other 2 isolates, both from *Phragmites* were of *Aureobasidium pullulans* and *Cladosporium herbarum*.

Table 3. Frequency of occurrence of the most abundant fungi, expressed as a percentage of the total isolations for each locality.

Fungus	S. Flevoland newly drained	E. Flevoland Reeds	E. Flevoland 6 years cultivation	N.E. Polder 26 years cultivation	British sand-dunes[1]	Greek soils[2]
Cephalosporium spp.	0	2.0	11.8	5.2	5.3	8.1
Fusarium culmorum	0	4.1	23.5	12.8	11.5	18.7
Gliocladium roseum	0	6.2	20.1	11.6	8.0	10.0
Plectosphaerella cucumeris	0	2.0	7.5	13.3	–	–
Trichoderma spp.	0	29.1	4.2	4.1	5.5	3.7

[1] Pugh et al., 1963; [2] Pugh, 1964.

Tabel 3. Frequenties van voorkomen van de meest algemene schimmels, uitgedrukt als een percentage van het totaal der isolaties van ieder monster.

The 10 wheat seeds collected from the standing crop on soil 6, yielded 10 isolates of *Fusarium culmorum*, 3 of an unidentified *Fusarium* sp., 8 of *Cephalosporium* spp. and 1 each of *Acremoniella atra* and *Alternaria tenuis*.

Towards the end of this work, a few dual cultures were set up on cellulose agar, consisting of *Gliocladium roseum* isolated from the polder soils, and of *Rhizoctonia solani* isolated from potatoes. After incubation at 25°C *R. solani* grew more rapidly, but was not able to overgrow the *G. roseum* colony. A microscopic examination of the junction between the two colonies showed that the hyphae of *G. roseum* grew closely adpressed to the surface of the *R. solani* hyphae and although they did not appear to be penetrated, the cells in the hyphae of *R. solani* were seen to be collapsed.

Discussion

A study of soils which have been reclaimed after a long period of submersion provides an interesting comparison with earlier studies of soil fungi in salt marsh muds (Pugh, 1962) and coastal sands (Pugh, 1966), where there was a natural build-up of silt and sand, respectively, which allowed colonisation by higher plants. In each case there was a progressive increase in the fungal potential from the area uncolonised by higher plants to the zone with a closed plant cover. A similar picture is presented for the polder soils, where there is a continuation and acceleration of the increase in fungal potential and in the range of species, when cultivation begins on the reclaimed land. The main difference between the newly exposed muds of South Flevoland and the bare muds of salt marshes is that the new polder muds are almost devoid of cellulose decomposing fungi, while the salt marsh muds have a "transient" fungal flora, probably consisting largely of propagules carried by the sea (Pugh, 1962). However, in both areas the roots of the pioneer plants yielded a number of isolates, and this may provide a clue to possible routes for fungal invasion and colonisation. It has been pointed out by Pugh (1967) that in soils which are relatively unfavourable for fungal growth and contain a sparse mycoflora, the fungi present on the seed coat are able to play a large part in the colonisation of the seedling roots. In this situation they are later ideally positioned to exploit the food reserves on the death of the root, and from this base may be able to grow out into the surrounding soil. *Fusarium culmorum*, which was present on all wheat seeds examined, could quickly build up a large potential in the soil in this way, as it has been shown by Pugh and Williams (1968) to increase rapidly on roots of *Salsola kali* growing on sandy fore dunes.

Other possible sources of fungi capable of colonising the polder soils include air-borne propagules of saprophytes which could grow on the remains of higher plants, and air-borne parasites, some of which are capable of subsequent growth on the dead roots. Birds' feathers have been shown by Pugh (1965) to yield many cellulolytic, and a few keratinophilic fungi. Other animals, including man, are also probable agents of fungal transfer.

As soon as there are some organic substrates present in the soil any fast growing saprophytes should be able to swamp the soil, as has been shown for *Trichoderma viride* in loosely-packed steam sterilised soil by Evans (1955) and in formalin sterilised soil by Warcup (1951). However, just as the pyrophilic discomycetes are able to colonise bonfire sites (El Abyad and Webster, 1968), if they can start growing before their competitors arrive, so here, any parasitic fungi which become established early are in an ideal habitat for an epidemic-type explosion.

The observations on the colonisation of soils which have been sterilised in different ways are of some significance when related to soil 4a. The periodic burning of the reeds must sterilise the uppermost layers of the soil. Six of ten isolates from these layers yielded *Trichoderma viride*, which represented 18% of the isolations. The *Ostracoderma* state of *Peziza atrovinosa* Cooke et Gerard (≡ *Plicaria fulva* Schneider) occurred on three plates, and represented 9% of the isolations. This fungus has previously been reported as extremely common in greenhouses growing in sterilised soil or vermiculite, in pots and flats (see Schneider, 1954 and Barron, 1968). Although it was relatively common in the burnt surface layers, *Ostracoderma* sp. was only recorded once from the rhizosphere regions of plants growing in the same soil. Despite the known ability of species of *Trichoderma* and *Ostracoderma* to colonise sterilised soils, the most frequently isolated species in the surface layers was *Humicola fuscoatra*. Isolates of this species are now being tested as competitive saprophytes, and for their ability to tolerate heat. Of the fungi most frequently isolated from the cultivated soils (Table 3) species of *Cephalosporium*, *Fusarium* and *Gliocladium* formed a larger proportion of the mycoflora after 6 years of cultivation than after 26, by when they had become about of the same relative frequency as in sand-dunes in Britain (Pugh et al., 1963) and in a range of soils in Greece (Pugh, 1964). It is thought possible to establish a "normal" level of occurrence of these fungi in neutral to alkaline soils, from the range of soils studied using the same isolation technique. *T. viride* which was very abundant in soils just coming into cultivation, dropped to about its "normal" level after 6 years of cultivation. The conidial state of *Plectosphaerella cucumeris* (*Cephalosporium ciferii* Verona or *Fusarium tabacinum* (v. Beyma) W. Gams) increased in abundance with greater lengths of cultivation. This species was reported by Domsch et al. (1968) to increase in frequency of occurrence in the soil after two crops of rape, while *Fusarium culmorum* and *Aureobasidium bolleyi* were two of five fungi which they regarded as typical for soils cropped repeatedly with wheat.

The role of *Gliocladium roseum* in the soil has been described by Pugh and Dickinson (1965) who record it as a genuine soil-inhabiting fungus occurring mainly in alkaline soils. It is normally associated with the rhizosphere and root surface. In salt marshes it becomes more common in regions with less frequent inundation by the tides, possibly because of the improved aeration there. The improvement in drainage of the very alkaline polder soils, together with the abundance of roots, could explain the rapid increase of this species in soils 7, 8 and 9. However, after 26 years it has declined to its "normal" level.

The influence of the fungi which have been isolated on soil-borne pathogenic fungi is open to speculation. Obviously they cannot be considered as the only possible competitors or antagonists. Bacteria have been shown to increase in numbers in a maturing polder (van Schreven, 1962) and actinomycetes are of frequent occurrence. It is, of course, appreciated that in a balanced soil the propagules of antagonistic bacteria and actinomycetes will vastly outnumber those of antagonistic fungi, but for the purpose of raising the resistance of an unbalanced soil to parasites, fungi may be more suitable because of their faster growth. Amongst the fungi which are known to be good competitive saprophytes species of *Fusarium* and *Cephalosporium* are common after 6 years of cultivation. *Trichoderma viride* is well known as an aggressive antagonist, but it is abundant in the soils when cultivation begins and has declined after 6 years. If it were active against such pathogens as *O. graminis* and *R. solani*, they should not be able to establish themselves during the first years of cultivation, when *Trichoderma* spp. represented almost one third of the fungal population. *Gliocladium roseum*, on the other hand, was below its "normal" level of occurrence at first, and increased in significance during the early years of cultivation. It is known to be a destructive mycoparasite (Barnett and Lilly, 1962) and has been shown capable of killing hyphae of *R. solani* in paired cultures. However, *R. solani* has a much faster growth rate, and Wastie (1961) showed that colonisation of a agar plate from a mixed inoculum is largely decided by the relative linear growth rates of the competitors, rather than by tolerance of antibiotic substances. This could explain the early rise in importance of fast growing pathogens, but on agar plates *Gliocladium roseum* checks the growth of *R. solani* where the colonies meet. In view of these findings, it could prove profitable to investigate further the potential of *G. roseum* as an agent for biological control of fungal pathogens. It appears worth-while to study the possibility of artificially increasing its abundance during the first 2 years of cultivation of the new polder soils. Garrett (1956) has pointed out that the outcome of the struggle between one particular organism and others will depend on its competitive saprophytic ability and on its inoculum potential. There is no doubt about the former characteristic: something can be done about the latter. From an ecological viewpoint it should be possible to raise the level of *G. roseum* when the soils are first cultivated and in this way perhaps help in overcoming a difficult problem in plant protection.

Acknowledgments

G. J. F. P. is deeply grateful to the Director of the Instituut voor Plantenziektenkundig Onderzoek for his kind invitation to work at the Institute and for his provision of financial assistance, and to Drs H. P. Maas Geesteranus for his hospitality. He also wishes to thank Dr W. Gams and Dr M. Gerlagh for helpful discussions, and the British Council for a grant towards travelling expenses.

Samenvatting

Cellulose afbrekende schimmels in de IJsselmeerpoldergronden en hun mogelijke betekenis als onderdrukkers van planteparasitaire schimmels

Voor een studie van de kolonisatie der IJsselmeerpoldergronden door fungi is de groep der celluloseontleders gekozen omdat deze een meer stabiele populatie vormen dan de zymogene schimmels.

Als men aanneemt, dat in de Noord Oost Polder, thans 25 jaar bebouwd, de schimmelpopulatie een eindtoestand heeft bereikt, kan men de vordering van de kolonisatie der jongere gronden door schimmels daaraan afmeten door vergelijking van het aantal soorten en hun frequentie zoals die met de gevolgde methode worden gevonden.

Het blijkt dat de ontwikkeling van de schimmelpopulatie niet slechts bepaald wordt door de tijd dat de grond droog ligt, maar ook door het gebruik er van.

Van de als antagonisten en parasieten van andere fungi bekende schimmels vormen *Trichoderma* spp. een groter aandeel in de totale schimmelpopulatie naarmate de gronden verder van de eindtoestand af zijn. Hieruit wordt afgeleid, dat soorten van dit geslacht geen functie vervullen bij het terugdringen van parasieten als bijv. *Ophio-*

bolus graminis en *Rhizoctonia solani.* Het parasitisme van de geïsoleerde stammen van *Gliocladium roseum* tegenover *Rhizoctonia solani* kon in het laboratorium worden bevestigd.

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