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Apinis, A. E.

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by

A. E. Apinis

Department of Botany, University of Nottingham (England)

Introduction

The terrestrial biosphere is a relatively thin zone between the earth crust and the atmosphere. Its thickness and physiognomy varies according to prevailing climatic and edaphic conditions but during our present millenium it is also increasingly influenced by the activity of man. The grassland vegetation is an integral part of this biosphere and it may vary from a scanty, dwarf grass turf to the impressive woody bamboos (JAEGER 1945) and, as in the other types of terrestrial vegetation, the growth space (environment) is more or less equally shared between the soil and the adjoining atmosphere. Because of this, the self-imposed limitation to confine this discussion only to the terrestrial activities of fungi is not wholly justified because their biocoenological relationships, including those of other soil microorganisms, extend beyond a grassland soil (cf. APINIS & CHESTERS 1964, APINIS 1965) and, therefore, some reference will be made also to their significance outside their soil environment.

The various grasslands we know, such as the African and Australian "savanna", the Asian "steppe", the Brazilian "kampos", the South American "pampas" and the North American "prairie" as well as coastal reed vegetation, sand dune grasslands and certain alluvial and mountain meadows are mostly types of a natural vegetation or true biocoenoses in a strict sense in which populations of plants and other organisms exist in a dynamic equilibrium based upon abiotic-biotic relationships capable of self-regulation (restoration). In contrast to these natural grasslands, large areas of primary woodlands in Europe, Asia, North America and in other parts of the world are replaced by more or less permanent grasslands, such as meadows and pastures of various patterns in which the change of grassland vegetation into the primary vegetation is prevented by regular cutting, grazing or other agricultural measures. A degree of a natural equilibrium between the various components in such a grassland still persists and it possesses also some degree of self-regulation (restoration) too, and because of this such grasslands are regarded as biocoenoids (SCHWERDTFEGER 1956). On the other hand, the short-lived (artificial) grasslands and the various cereal crops are regarded as technocoenoses in which no ability of self-regulation (restoration) exists and in which the plant growth (monoculture or a simple mixture) is no longer in competitive equilibrium with the other species of the indigenous flora (weeds) and is in contrast to soil microorganisms because of cropping, crop rotation and other agricultural measures; certain temporary microbial equilibria between the soil and vegetation are short-lived and are infrequently in such a technocoenoses variable, if not of a casual nature, with a general microbial activity declining in a relatively short time under continuous cropping coupled with a gradual loss of the original soil fertility. In a permanent grassland (biocoenoid), however, competition between the higher plants and the other indigenious species may still persist and a dynamic equilibrium between the soil organisms and the permanent vegetation could be maintained. Despite the extensive research effort in general on the ecology of various economic grasses and grasslands, including cereals, a good deal of specific fundamental information is lacking concerning biological relationships of grasses and grassland vegetation to certain groups of soil organisms. These problems are also related to soil fertility and productivity of grasslands which, first of all, depends upon climatic conditions, soil and the type of vegetation, but in grasslands used in agriculture also upon the pattern of management. Furthermore, the recent soil biological research have proved beyond any doubt that the soil fertility depends also to a large extent upon soil organisms and their activities in which soil microflora (*algae*, *actinomycetes*, *bacteria* and *fungi)* and soil fauna play a major part.

In these complex soil biocoenotic relationships the populations of fungi play specific parts in a number of phenomena which I am going to discuss below using data from my own work concerning two permanent alluvial pastures studied in England, as well as compare, discuss and mention other published data on the same and related problems of grassland soil biology.

Concerning grassland soil mycoflora

According to estimates made by JAGNOW (1961) the total volume of soil microorganisms (actinomycetes, bacteria and fungi) in a European grassland soil constitute c. 1 to 2% of the soil volume in the turf layer, i. e., 10,000 to 20,000 kg/ha, resp. c. 2000 kg/ha dry matter of which the mass of fungi is estimated 10% to 20%. The relatively low biomass of soil fungi does not deny their biological importance because their relatively high number of species possessing very diverse ecological abilities (cf. HEINTZELER 1939, GARRETT 1951, WARCUP 1957, DOMSCH 1960, APINIS 1960, 1964).

A more or less complete information on soil mycoflora with specific reference to grasslands have been reviewed or reported from Africa by KILLIAN & FEHER (1935), SABET (1935), SAPPA & MOSCA (1954), MOSCA & SAPPA (1956), MEYER (1954), MUSKAT (1955), from Eur-Asia by RANDHAVA & SACHAR (1934), RAYS & BORUT (1958) and DUTTA & GHOSH (1965), review of work in Soviet Union by MISHUSTIN et al. (1961), from Western Europe by DALE (1912, 1914), NIETHAMMER (1937), KREHL-NIEFFER (1951), WARCUP (1951), GUILLEMAT & MONTEGUT (1956, 1957), NICHOLS (1956), APINIS (1958, 1960, 1964, 1967), ŠEBEK (1961) a. o., from Australia and New Zealand by WARCUP (1957), THORNTON (1958) and DI MENNA (1960), from North America by JENSEN (1912), WAKSMAN (1916, 1944), GILMAN & ABBOTT (1927), PAINE (1927), BISBY, JAMES & TIMONIN (1935) and ORPURT & CURTIS (1957), and from South America by BATISTA & UPADHYAY (1965) and UPADHYAY (1967). The higher fungi from various grasslands and their activity have been reported by SCHANTZ (1917), WILKINS & PATRICK (1939), FAVRE (1948), LANGE (1948, 1952), HEINEMANN & DARIMONT (1956), WARCUP (1951, 1959), DENNIS (1955), PARKER-RHODES (1957), KREISEL (1957), ŠMARDA (1964), APINIS (1968) a. o.

These and other investigations show that occurrence of various species of soil fungi is related to certain ecological factors of environment, soil type and the respective kind of vegetation (cf. APINIS 1963) as well as to a certain degree of zonal pattern in their geographical distribution (cf. WAKSMAN 1944 and MISHUSTIN et al. l. c.).

Depth distribution, activity and other biocoenological relationships

The fungal populations in soils depend upon the supply of organic food (energy) sources. This supply is secured mainly by the root system of respective vegetation producing senescent or dead roots, sloughed-off root cell debris, release of soluble organic compounds by the roots, and also by vegetation supplying soil surface debris (litter) which is partially leached or moved into soil by soil fauna, as well as by the debris of soil animals. Formation of new and ageing as well as dead roots, so far we know, is a dynamic phenomenon which depends on climatic and soil conditions, ecological character of the plant species, as well as on biotic factors, such as cutting, grazing or various other harvesting operations. According to Krasilnikov (1958) the dry mass surface yield (shoots) of 2.7 tons/ha in Eastern European meadows corresponds to a root mass of 7 to 11 tons/ha. Konova (1951, cf. Krasilnikov 1958) reports that the grass root yields may reach even 21 tons/ha. In a drier chernozem and steppe surface vegetation yields of c. 7 tons/ha dry matter corresponds to a root yield of c. 25 tons/ha. However, the distribution of the root mass in soil of various kinds of grasslands differ (Linkola & Tiirikka 1936, Klapp 1943, Goedewaagen & Schuurman 1950, Kmoch 1952, Throughton 1957 a. o.). In general, the main root mass is confined to the upper soil layers (Fig. 1). The type of root system produced by a particular grass in a particular soil environment is characteristic but it may vary to a considerable extent (cf. Linkola & Tiirikka l. a. a. o.) influenced by various abiotic and biotic factors (cf. Steen 1957). Thus the average

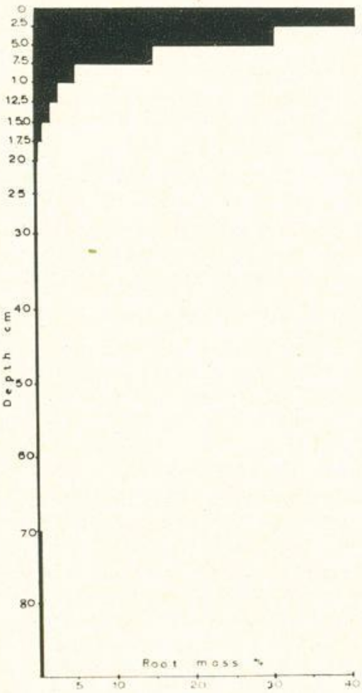

Fig. 1. Root distribution in diluvial Lolieto-Cynosuretum pasture soil

annual amount of roots produced by barley crop is estimated for Netherlands c. 1570 kg/ha dry mass and 3460 kg/ha for rye crop which is usually decomposed in soil until the next crop starts its growth (Goedewaagen & Schuurman l. c.). The above mentioned authors report a higher average root weight in the 20 cm top soil layer of permanent grasslands, i. e., c. 7280 kg/ha which represents c. 87% of the whole root mass. Despite the difficulties in calculating the rate of annual root production, it is estimated to c. 5600 kg/ha which is equal to the approximate annual rate of root decomposition in permanent grassland soils. This higher rate of decomposition, as compared with the annual cereal crops, indicates that the populations of soil organisms are better balanced and less disturbed, and consequently more efficient, in permanent grassland to decompose the soil residues produced by vegetation.

According to Tüxen (1942), Kmoch (1952), a. o. the main mass of roots in the grasslands studied, i. e., c. 87% or so, in a permanent grassland is confined to the upper soil layer of c. 20 to 25 cm and then sharply decreased with the depth in soil (Fig. 1). This distribution of the root mass in soil coincides closely with the general distribution of soil microorganisms (cf. Russell 1923, Waksman 1927) as well as soil fungi in grasslands (cf. Apinis 1958, 1960, 1964). Also the active growth of fungi in the particular permanent grasslands studied, i. e., that of the dry pasture (Lolio-Cynosuretum) on a well drained soil (Fig. 1, Table 1) and the water-logged pasture with distinct A—G soil profile characteristics (Ranunculus repens-Alopecurus geniculatus Ass.), vegetation of which is defined according to Tüxen (1937), show close relationship with the root mass distribution (Apinis 1967). In the waterlogged pasture soil the root mass is much more confined to the upper soil but with roots nearly absent in the G-horizon which is clearly reflected in reduced growth of soil fungi in that horizon (cf. Table 1) too. Furthermore, the number of species of such a growing mycelia in various soil horizons follow exactly the same pattern, i. e., decreasing with increasing depth in soil in the same way as the root mass of the vegetation decreases. This general pattern of active growth of soil fungi equally applies to the distribution of particular groups of fungi, such as thermophilous fungi (Apinis 1963a) and phycomycetes (Apinis 1964). As the redox potential data indicate, the chief cause for this is the soil aeration which is different in various soil horizons.

Table 1. Frequency of growing mycelia and the number of species of fungi in dry pasture (Lolio-Cynosuretum) and water-logged pasture (Ranunculus repens-Alopecurus geniculatus Ass.) soil in the Trent Valley near Nottingham (England) as recorded by immersion tube technique in summer 1952 (Apinis 1967)

Pasture	Depth cm	Frequency	Number of species	Redox potential Eh in mv 20°C	pH
Dry pasture	2 — 5	4.16	24	448	5.3
	20 — 25	2.55	21	414	5.6
	50 — 60	1.90	10	378	6.3
	100 —105	1.13	6	236	6.6
Waterlogged pasture	2 — 5	3.06	27	332	6.3
	20 — 25	1.97	19	342	6.9
	50 — 60	0.40	9	200	6.8

The fungal flora of roots and other underground parts of cereals and grasses is known from the early studies by BECKWITH (1911), SIMMONDS & LEDINGHAM (1937), TYNER (1948) and from the more recent work by WAID (1957), CHESTERS & PARKINSON (1959), CHESTERS (1960), PARKINSON et al. (1963) and others concerning the early stages of colonization and decomposition of roots. Excellent techniques have been worked out by CHESTERS (l. c.), WAID (l. c.) and others for such a study, but so far very limited use of them has been made in the field research of various soils and vegetation. Instead, during the last three decades experimental laboratory work on isolates of soil fungi have been greatly intensified in regard to their correct taxonomic position and their physiological characteristics. Studies on their moisture (cf. APINIS, 1960 & 1964, GRIFFIN 1963) and temperature (APINIS 1963 & 1964) relationships have been carried out to explain their ecological behaviour. A number of interesting results have been produced by the study of their natural substrate relationships in soil (WAKSMAN 1916 & 1944, PAINE 1927, KREHL-NIEFFER 1951, GARRETT 1956, MENON & WILLIAMS 1957, DOMSCH 1960 a. o.) and about their ability to decompose and utilize specific substances within these complex substrata produced by soil fauna and vegetation, such as cellulose, chitin, hemicellulose, lignin, pectin, starch and other carbohydrates, protein including keratin a. o. by production of specific enzymes and in such a way make use of these potentially rich energy sources and satisfy their C, N, S and other requirements. However, the ability of specific fungal species to decompose various organic substrata is restricted because a limited number of enzyme systems is produced by a particular species. Thus the total decomposition of a complex organic substratum in soil is carried out by a number of fungal species and other organisms, and distinct changes take place in populations of decomposing organisms (succession) at the various stages of substrate break down. The end products of this process, besides the substances incorporated into the cells of fungi and other organisms, CO_2 and various inorganic and organic compounds are thus made available to vegetation and other soil life. In this process also humus is produced by soil fungi, as it was recently demonstrated by HAIDER & SCHETTERS (1967) in decomposition of wheat straw lignin by certain sterile mycelia producing phenoloxydases.

In the process of decomposition of complex organic substrata in soil highly active antibiotic substances are released from the plant debris (cf. BÖRNER 1960, DOBBS et al. 1960, WINTER, PEUSS & SCHÖNBECK 1960), especially under insufficient soil aeration (PARTICK & TOUSSOUN 1965) under cereal and other crops which may temporary affect seed germination and plant growth but may in early stages also favour parasitic attack by certain other soil fungi, such as *Fusarium*, *Rhizoctonia* and *Thielaviopsis* species. On the other hand, it is a well known fact that a considerable number of soil fungi produce antibiotic (cf. WEINDLING 1941) as well as toxic substances (cf. MIRCHINK et al. 1962, PIDOPLICHKO et al. 1965) which may not only affect the other fungi and soil microorganisms but also development of higher plants. Recently also favourable effects upon higher plants by certain soil fungi have been confirmed in laboratory experiments (DOMSCH 1965). At present relatively little is known about such interactions under field condition but the evidence mentioned above indicate that a large number of common soil fungi is involved.

Interactions between the various soil fungi, so far as it is known, are based on competition, parasitism and various other kinds of antibiosis (cf.

Garrett 1956 a. o.). However, frequently numerous small niches in the soil are colonized by a few species placed closely together, but such uniform populations on various substrata differ in their species composition. In general, no distinct life forms exist amongst the majority of soil microfungi colonizing plant debris, with some exceptions in lower phycomycetes, in the soils of various grasslands so far investigated. In contrast to this various adaptations of fungi to soil fauna and to the organic debris of animal origin deposited in soil, such as chitin and keratin, are much more distinct. The specialized keratinophilic fungi are known also from certain coastal grasslands (Apinis & Chesters 1964) as well as from pasture soil (Apinis 1964a). Besides the general nonspecific activity of soil fungi upon the easily decomposable animal remains in soil, a highly specialized epiphytic relationship of *Laboulbeniales* exist towards numerous insects, or a distinct parasitism upon insects and their larvae caused by certain ascomycetes and deuteromycetes (cf. Müller & Kögler 1965). Another interesting, specialized case of parasitism is known in certain nematode catching deuteromycetes, i. e., the predaceous fungi (cf. Duddington 1963) and in phycomycetes (*Zoopagaceae*) praying on soil amoebae as well as nematodes; both groups are well represented in permanent grasslands. The latter groups of fungi mentioned have been studied more closely with intent to adopt certain facts in the biological control measures of certain pests attacking plants. Contrary to this, it is known that fungi are consumed as a food by various groups of soil fauna, i. e., the secondary feeders, in a more or less specific way (cf. Kühnelt 1965). This relationship between the saprophytic and plant parasitic soil fungi and the soil fauna, as far as it is known, may be specific in various degrees as it was demonstrated in soil amoeba by Heal (1963) and by Mankau & Mankau (1963) on the feeding habits of the mycophagous nematode *Aphelenchus avenae*.

Relationships of grassland soil fungi and animals may extend even beyond the actual biocoenose (cf. Apinis 1956, Apinis & Pugh 1967). Ajello (1956) have stated already that soil is a considerable source of pathogenic fungi known from various infections in animals and man. This was confirmed by the study of thermophilous soil fungi in the two alluvial pastures mentioned above where such potential pathogens, as *Allescheria boydii*, *Aspergillus fumigatus* and *Mucor pusillus*, were recorded from the top soil layer (Apinis 1963a, 1965).

Relationships to living grass roots

In a grassland soil relations of soil fungi to the growing vegetation, broadly speaking, may be assigned to three major categories: a) rhizospheric relationships, b) parasitism, and c) symbiosis. Rhizosphere relations in cereals and other cultivated plants have been studied extensively during the last three decades and the results of the more recent research have been reviewed by Trolldenier (1961), Gams (1963) and Rovira & McDougall (1967). It is proved that various plant roots release variable amounts of soluble organic substances, such as amino-acids, enzymes, nucleotides, organic acids, sugars, vitamins and other known or unknown compounds, and also inorganic compounds including CO_2 and producing sloughed off root cell debris which all provide an excellent medium around the roots in which various microorganisms can grow including soil fungi (Timonin 1940, Katznelson 1946 & 1965, Krasilnikov 1944 & 1958, Tolle & Rippel-Baldes 1958, Chesters & Parkinson 1959, Rovira & McDougall 1967). The accumulation of microorganisms between the soil surface and the 2 to 3 mm or more thick soil zone around the roots may be very high in bacteria and other microorganisms while this effect is much less distinct in fungi especially those associated with cereals (TIMONIN 1940). The list of fungi isolated from the rhizosphere of wheat, oats and other cereals consists of soil saprophytes and unspecialized root parasites, such as various mucors and species of *Aspergillus*, *Cephalosporium*, *Cylindrocarpon*, *Fusarium*, *Gliocladium*, *Penicillium*, *Phoma*, various sterile mycelia and *Trichoderma*. It appears that this population is less specific for a particular grass species than the fungal population on the root surfaces (MISHRA 1961). In the formation of a grass rhizosphere of seedlings a sequence in colonization by fungi as well as a succession of species have been observed (cf. CHESTERS & PARKINSON l. c.). Furthermore, certain observations indicate that the rhizosphere mycoflora is not a constant phenomenon but is somewhat different in various soil types and different climatic conditions and may change under certain measures in agricultural practice. Experimental research with particular species of fungi isolated confirms this. The fundamental question concerning the significance of particular fungus species isolated from the rhizosphere have been studied recently in laboratory experiments (cf. PIDOPLICHKO et al. 1965). A considerable number of maize rhizosphere fungi representing the common saprophytic mycoflora of soils from the steppe zone of Ukraina have been tested in regard to the influence upon the development of maize seedlings. The majority of the species tested, especially certain *Fusarium* species, had a favourable effect except *F. culmorum* and *F. oxysporum*. Positive results were obtained with culture filtrates of *Fusidium viride*, *Penicillium nigricans*, *P. rugulosum* and other fungi but filtrates of *Penicillium clavigerum*, *P. expansum*, *P. janthinellum*, *P. adametzi* and some other fungi caused inhibition of seedling growth. Using a different laboratory technique DOMSCH (1965) carried out similar experiments using rape and wheat as test plants and the results interpreted in relation to antagonistic and parasitic activity by specific fungi. In general, known toxin producing and parasitic fungi exhibited highest inhibition of seedling development. In the presence of readily available carbohydrate source a number of saprophytic soil fungi which occur also in rhizosphere produce various organic acids which under laboratory conditions favourably influence the availability to higher plants of calcium, potassium and phosphate from certain soil minerals as well as release P, S and other compounds locked up in organic material during decomposition (MÜLLER & FÖRSTER 1964). At present, there is no evidence however how far these interesting laboratory observations apply to a complex soil environment of a grassland (cf. also MIRCHINK & GRESHNYKH 1961).

In the two permanent alluvial pastures mentioned above the turf layer of the top soil up to 15 to 20 cm deep is closely packed with numerous interwoven roots of grasses and roots of other plants thus converting all the upper soil layer into rhizosphere region of the vegetation.

Therefore, the growing soil fungi as recorded by immersion tubes (cf. Table 1) in the upper soil layer partially belong to the rhizosphere mycoflora but for most part represent dead root and soil aggregate flora because the number of the genera present in rhizosphere soil and grass root surfaces is much smaller (Table 2) as the number of genera on soil crumbs and water-stable aggregates (cf. Table 3). A relatively small number of fungal genera is present on actively growing roots which indicates that the part played by fungi at this stage of root development is relatively small (cf. Schönbeck 1958 on antibiotics production by the roots of cereals). However, the generally observed increase of fungi on ageing roots, as well as in the rhizosphere of such roots, indicate a specific stage (brown roots) of their senescence at which the colonization by saprophytic species sets in. Furthermore, the data given in Table 2 indicate that the rhizosphere and root surface mycoflora is influenced by the depth in soil and by the soil type.

Table 2. Number of genera of fungi observed on grass roots with the rhizosphere soil attached and on washed grass roots (root surface fungi) in the dry (Lolio-Cynosuretum) and water-logged (Ranunculus repens-Alopecurus geniculatus Ass.) pasture soils from the soil samples collected July 1949

Pasture and soil horizon	Roots with rhizosphere soil attached	Washed roots	Total number of genera on roots	
			Unwashed	Washed
Dry pasture 0.5 — 2.0 cm .... (A-horizon)	9	4	11	5
Dry pasture 20 — 25 cm .... (A-horizon)	4	3		
Water-logged pasture 0.5 — 2.0 cm .... (A-horizon)	7	5	8	5
Water-logged pasture 20 — 25 cm .... (G-horizon, very few roots present)	1	0		

Interactions of plant pathogenic soil fungi affecting cereal crops and other grasses have been reviewed by Garrett (1950), Sallans (1965) and extensively discussed in a wide context in the book "Ecology of Soil-borne Pathogens" (Ed. by Baker & Snyder 1965). A considerable research effort has been made to resolve the closely related problem regarding mycotrophic relationship of grasses (cf. Nicolson 1960, Boullard 1963), but no answers to certain fundamental questions have been found so far. Endotrophic mycorrhiza is known in cereal crops (Apinis 1940, Strzemska 1953) and in various other grasses in natural grassland communities on dunes (Dominik 1951) as well as in alluvial meadows (Kruger 1957). Results of experimental work on maize mycorrhiza show that such a symbiotic association is beneficial to the plant (Gerdemann 1964). Mycorrhizal associations of a similar type have been found in numerous grasses but the identity of these mycorrhizal fungi has not been established with certainty. In regard to their growth habits in the grass roots, including their ability to produce clusters of characteristic giant cells in soil, they apparently belong to the higher phycomycetes of the genera *Endogone* and *Mortierella*.

Relations to soil structure

It is a known fact that soil fertility depends also on a good soil structure. An improved soil structure frequently has been observed in permanent as well as in temporary grass leys (Berkmann 1913, Martin 1944, McHenry

& Newell 1947, Low 1954 a. o.). Hubbell & Chapman (1946) found that such an improved and maintained soil structure under grass vegetation is not formed by grasses in sterile soil. This biological process in soil aggregate formation appears to be a complex phenomenon involving both vegetation and the soil microorganisms (Krasilnikov 1958) in which a number of actinomycetes, bacteria and fungi take part directly, or indirectly by producing certain metabolites to strenghthen aggregate stability (cf. Griffith 1965). In grassland soils this process is well balanced and is accompanied at first by root exudate utilization but at a later stage of senescent or dead root decomposition at a moderate pace by fungi and other organisms thus resulting in a large complex and smaller granular aggregates formed from alluvial silt, clay and sand (Fig. 2). In both permanent alluvial pasture soils in the Trent Valley the extent of such a biological soil aggregate formation coincides with root mass distribution (cf. Fig. 1). In the turf layer most of the soil is aggregated or in process of aggregation from the soil mineral particles and organic substances left by disintegrating or weak (exhausted) aggregates, whereas in deeper soil few water-stable, granular aggregates are formed because of a lack of root mass and unfavourable physical conditions for such a biological activity. The highest number of very large complex, water-stable aggregates (c. 0.6 to 2.3 cm in diam.) are confined only to the top soil accompanied or interwoven by living, ageing and decomposing roots of grasses often enclosing

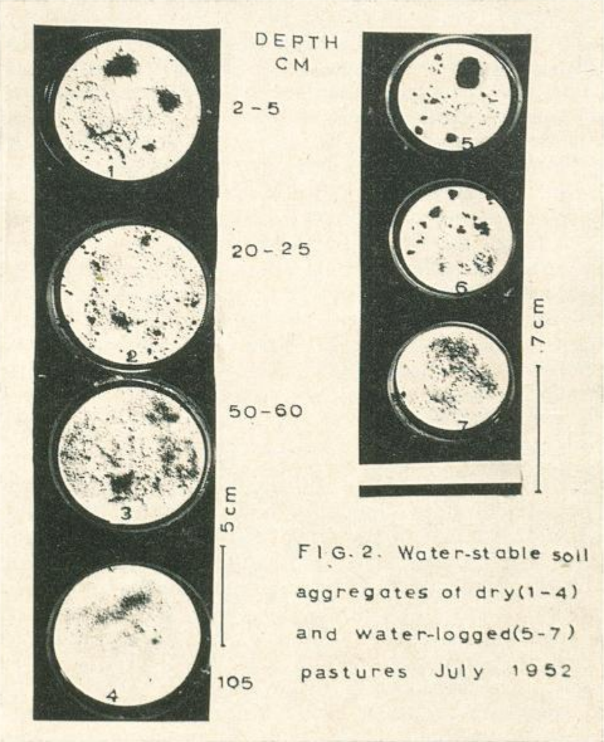

FIG. 2. Water-stable soil aggregates of dry(1-4) and water-logged(5-7) pastures July 1952

both few large (c. 2 to 5 mm) and medium (c. 0.5 to 2 mm) aggregates or small granules which usually lack cellulosic material. In small aggregates (<0.5 mm) no recognizable plant tissue structures were observed.

Such soil crumbs and water-stable aggregates from the top soil horizons were tested on a suboptimal agar medium (washed 2% water agar) in Petri dishes incubated at room temperature (c. 20°C) for growth of fungi and other microorganisms (Apinis 1968). After 5 to 7 days of incubation the very large complex aggregates produced a rich and varied fungal growth accompanied by a number of small colonies of other microorganisms. The large aggregates were similarly efficient in supporting somewhat less rich mycoflora, but on medium aggregates the spreading growth of mucors and other soil fungi were considerably reduced although small colonies of actinomycetes and bacteria were present including colonies of true soil yeasts as well as mycelial soil yeasts (*Candida* and *Trichosporon*). The small aggregates and crumbs usually supported growth of occasional single hyphae with infrequent colony of yeast and some microcolonies of actiomycetes and bacteria. The number of genera of fungi recorded on various crumbs and water-stable aggregates indicate (Table 3) that washed water-stable aggregates produced slightly larger number of genera and species as the untreated crumbs which indicate, probably, that water treatment has removed some of accumulated metabolites from such a substratum. On the other hand, decreased growth of fungi on smaller aggregates and crumbs indicates that their energy source has been exhausted and they are unable to support a varied growth of fungi. The genera of fungi recorded on these soil aggregates belong to the soil saprophytes and are known also from the rhizosphere soil of old roots as well as from decaying grass roots (cf. Beckwith 1911, Tyner 1948), such as *Acrostalagmus*, *Acrospeira*, *Aspergillus*, *Candida*, *Cephalosporium*, *Chrysosporium*, *Cylindrocarpon*, *Dendryphium*, *Gliocladium*, *Gliomastix*, *Fusarium*, *Humicola*, *Mortierella*, *Mucor*, *Oidiodendron*, *Paecilomyces*, *Penicillium*, *Pseudeurotium*, *Pythium*, *Scopulariopsis*, *Stemphylium*, sterile mycelia, *Syncephalis*, *Trichoderma*, *Trichosporon*, *Verticillium* and *Zygorhynchus*. These fungi mentioned indicate that in such a balanced and dynamic population on soil aggregates in the top soil horizons of the permanent grassland the early stages in aggregate formation, obviously,

Table 3. The number of genera of soil fungi growing on large, medium and small soil crumbs and upon the large and medium water-stable soil aggregates from the upper layers of soil in the dry (Lolio-Cynosuretum) and water-logged (Ranunculus repens-Alopecurus geniculatus Ass.) pasture in July 1949 (Apinis 1968a).

Soil / Number of genera of fungi	Soil crumbs		Large and medium water-stable aggregates
	large & medium	small	
Dry pasture 0.5 — 2.0 cm	17	5	20
Dry pasture 20 — 25 cm	16	4	19
Water-logged pasture 0.5 — 2.0 cm	12	3	17
Water-logged pasture 20 — 25 cm	10	3	9

commences with their colonization of senescent grass roots. The population of such fungi increase gradually the peak of which is reached on very large and complex soil aggregates. In case no fresh root material becomes available this population of fungi declines slowly and this consequently leads to aggregate desintegration. In a permanent grassland this desintegration occurs in a relatively minute soil niches, and the growing roots of grasses tend to recolonize such soil spaces and thus provide new energy sources for the soil fungi and other soil organisms.

Summary

In grassland soils various ecological groups of fungi produce distinct mycocoenoses depending upon the type of vegetation, climate, and factors of the soil environment. Above all, the presence of these heterotrophic organisms depend upon a continuous supply of organic energy sources (substrata) which are produced by the roots of the respective vegetation. Consequently, the quantity and quality of a soil fungal population primarily depends upon the distribution and productivity of the root mass in soil. In areas with an oceanic climate (Western Europe) the root production in a permanent grassland may reach 6.000 kg/ha but in semi-arid countries of Eastern Europe grass root yields are reported even as high as 20.000 to 25.000 kg/ha annually. In a balanced environment the amount of organic matter produced annually is more or less the same as the annual rate of decomposition by soil microorganisms including the fungi and the soil fauna. The ecological factors of soil environment, such as soil aeration, are important too in this complex interdependence, as it is clearly shown by the data of root mass distribution and the activity of the respective soil mycoflora (cf. Fig. 1 & Table 1) in the permanent alluvial pasture soils near Nottingham, England.

Various fungi of these grassland soils possess a wide ecological diversity in decomposition of organic matter and display favourable (symbiosis) or unfavourable (parasitism) relationships within the grassland biocoenose but also may influence in one or another way higher plants and other soil organisms by their biosynthetic activity.

According to observations made, the rhizosphere and the root surface mycoflora of the grassland vegetation appears just as an initial phase of root colonization by fungi which increase upon the ageing roots thus initiating biological crumb formation in the turf layer of the top soil. The formation of this highly desirable crumb structure is a complex and dynamic process involving the root systems of various plants and the soil microorganisms in which the population of soil fungi play a distinct part indicating the outset, optimum and the decline of crumb formation and desintegration in a particular microniche of the soil.

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