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## THE ROLE OF FUNGAL GROUPINGS IN THE STRUCTURE OF ECOSYSTEMS

### Abstract

Proceeding from the standpoint of an ecosystem integration level, fungal groupings cannot be regarded as structural elements of a phytocoenosis. The fungal groupings can be considered as a special type of communities — mycocoenoses, which, like phytocoenoses, are components of the biocoenoses.

### Introduction

The modern system approach in ecology is based on distinguishing integration or organization levels. The number of these levels is yet disputable. However, the populational, coenotic and ecosystem levels are most acceptable in ecology ecosystems contain closed cycles of transformation of substances. Instead of the term ecosystem V. N. Sukachev and his school use the term biogeocoenosis. Biogeocoenosis is treated as a system consisting of the living part (biocoenosis) and the corresponding abiotic environment, termed biotope. Biocoenosis is an element of biogeocoenosis, and at the same time a fundamental subject of the next level, of the coenotic one. The structural elements of biocoenoses are numerous coenopopulations of different organisms which form the populational level of organization.

Now the problem is whether the fungal groupings belong to plant communities or phytocoenoses (as synusiae) or they can be treated as relatively independent coenotic systems, so-called mycocoenoses.

Hitherto these problems have been treated on the coenotic integration level. The functional and structural specific features of each system are especially perceptible if observed from a higher level of integration. According to M. I. Setrov (Серпов, 1971), the functional limit between autotrophic and heterotrophic organisms becomes apparent only on the biospheric level of integration. Consequently, in order to solve the problem we must treat it at least on the ecosystem level.

### Fungal groupings in ecosystems

The structure of biocoenosis is defined by the presence of main functional components of an ecosystem, i. e., of producers, macroconsumers (phagotrophic organisms) and microconsumers (saprotrophic organisms) (Odum, 1971). In conformity with their belonging to autotrophic (producers) or

heterotrophic (consumers) organisms, two main elementary energetic blocks are formed in each ecosystem. The main difference in the energy flow through the autotrophic block compared with the heterotrophic one is of principal importance, and therefore the groupings of heterotrophic organisms cannot be placed under the autotrophic ones. In addition, autotrophic and heterotrophic organisms and their activity are usually separated in space and time (e.g., the decomposition by fungi, photosynthesis, etc.) (Odum, 1971). All this points to the relative independence of the groupings of heterotrophic organisms in the structure of ecosystems.

Consequently, proceeding from the ecosystem level of integration, the fungal groupings (as the groupings of saprotrophic organisms) in a biocoenosis cannot be regarded as being subjected to autotrophic coenotic systems.

V. N. Sukachev (Сукачев, 1964) and his school have already acknowledged, besides phytocoenoses in biocoenosis, also the presence of micro-biocoenoses, but V. N. Sukachev himself and several other ecologists, such as B. A. Bykov, N. V. Dylis, T. Lippmaa, H. Trass, a.o., and also many mycologists (J. J. Barkman, I. O. Dudka, M. Lisiewska, B. A. Tomilin, L. N. Vassilyeva, a.o.) are nevertheless of the opinion that fungal groupings — the most important saprotrophic component of an ecosystem — belong to the phytocoenosis, for example as synusiae (cf. Lippmaa, 1935; Трасс, 1970; Barkman, 1973; Дудка et al., 1976). Such a treatment is in contradiction with the theoretical one, taking into account the above-mentioned principles about the function of components of an ecosystem.

Such a contradiction is due to several factors: (1) For a long time, taxonomically, fungi have been considered to be plants. It is not right to locate fungi into the plant kingdom as saprotrophic organisms. Unfortunately, such ideas (Bara, 1952; Whittaker, 1969; Ainsworth, 1971; Тахтаджян, 1973) have not been widely accepted. All the same, to acknowledge fungi as an independent kingdom in the organic nature or in a kingdom consisting of different saprotrophic organisms, is one of the most momentous fixed points to the advantage of the treatment of fungal groupings as a relatively independent component in the structure of a biocoenosis. (2) Phytocoenosis was the first and for a long time the only community studied within the limits of a biocoenosis, and that conditioned the continuous one-sided interpretation of a biocoenosis. The extreme example is to identify the phytocoenosis with the biocoenosis (cf. Быков, 1970), and in that case all the components of the biocoenosis are regarded as structural parts of the phytocoenosis. (3) Due to the strong trophic connections between the saprotrophic and autotrophic organisms, fungi have been regarded with an evident exaggeration «as chained to plants» (Šmarda, 1972).

Of course, no heterotrophic organism can exist without an autotrophic plant, as the latter is a nutritional base for a heterotrophic organism. The autotrophic organisms form a living medium for fungi. H. J. Hueck (1953) and K. Höfler (1955) have referred to the phytocoenosis as a biotic medium at the formation of fungal groupings. J. Westerdijk (1949) points out that in case of fungi the biogenic substrata as a selective medium can be compared with soils at their formation of vegetation of higher plants. Thus, the trophic and topic relations of fungi with the other components of an ecosystem (Harley, 1971) form an essential part in the network of biocoenotic connections. The role of fungi in the functional structure of an ecosystem is studied in consortia. V. V. Masing (Мазинг, 1973) points out that at the treatment of the biogeocoenosis as a

unit of structure and function, the «anatomy» and «physiology» of coenoses cannot be mixed up. Consequently, the presence of biofactors is an inevitable primary condition for the existence of fungi, like the presence of physical factors for autotrophic organisms. This does not mean that in the morphological structure of the biogeocoenosis fungal groupings must also be subjected to the communities of autotrophic organisms.

Thus, fungal groupings cannot be treated as structural elements of the phytocoenosis. Accordingly, at the coenotic integration level the fungal groupings form independent communities — mycocoenoses, which, similar to phytocoenoses, are the main components of the biocoenosis. The fungal groupings as mycocoenoses have been treated by P. Duvigneaud and M. Tanghe (1967), K. Höfler (1955), F. Smarda (1972), H. J. Hueck (1953), H. Kreisel (1961), H. Jahn (1966), M. A. Tcheremissinov (Черемисин, 1971), A. E. Apinis (1972), K. Kalamees (1975), *a. o.*

L. G. Burova (Бурова, 1976) presents arguments in favour of recognizing macromycete groupings as a special self-contained «fungus component» of forest biogeocoenoses. She treats fungal groupings as biogeocoenotic *synusiae*.

According to some researchers, fungi (also mosses and lichens) form independent communities only in such conditions where they are not in competition with the other plants (e.g., on dung and wood), but the groupings of litter saprobionts and mycorrhizal fungi cannot be regarded as independent communities (Pirk, Tüxen, 1957; Tüxen *et al.*, 1957). M. Lisiewska (1974) is almost of the same opinion that the groupings of saprobionts and mycorrhizal fungi as *synusiae* belong to phytocoenoses, but the groupings of wood and debris saprobionts, as well as the groupings of parasitic fungi, are treated as independent associations. These standpoints are likewise not in accordance with the theoretical considerations mentioned above. All fungi have a heterotrophic nutrition, and therefore the coenotic position of fungal groupings in an ecosystem can be defined by one criterion only, which does not depend upon the character of trophical connections of fungi with higher plants (*cf.* Kalamees, 1971b).

### Definition of mycocoenoses

On the basis of nutritional relations which determine the nature of mycocoenoses, it is logical to define mycocoenoses by the peculiarities of the substrate (i.e., by the composition and stage of decomposition of substrate in case of groupings of forest litter, debris and wood saprobionts) or by the influential sphere of a phorophyte (in case of groupings of mycorrhizal fungi and parasitic fungi). Parasites, saprobionts and symbionts, due to the specific nature of their nutritional relations, in principle form different mycocoenoses. The definition of mycocoenoses in that way is often practically more difficult, due to the presence of facultative parasites and symbionts. Fungal symbionts mainly feed on account of mycotrophs, but their mycelium grows in the forest litter horizon where they can also obtain nutrients and water (Шубин, 1973). Thus, they cannot be completely eliminated from the formation of litter fungal communities.

In addition to the peculiarities of the substrate and the sphere of influence of phorophyte, the formation of fungal groupings also depends to a great extent upon the chemical and physical conditions of the environment, on the specific microclimatic features, etc., which form the ecotope by L. G. Ramensky. As can be seen from a great number of

investigations about the mycoecology, a lot of fungi are very sensitive to the factors mentioned above. The especially close contact with the ecotope becomes evident in case of groupings of litter saprobionts and mycorrhizal fungi, fungal groupings on wood and debris; the parasites are also considerably more independent of the ecotope (Nespiak, 1971; Томилин, 1971; Lisiewska, 1974).

Since the distribution of fungal species in ecosystems depends, first of all, on the biogenic factors and only after that on the biotope as a whole, a great number of fungi have a very wide ecological amplitude; due to it, the composition of species in fungal groupings is mostly unstable. Mycocoenoses are essentially more continuous than phytocoenoses. Accordingly, mycocoenoses are relatively less persistent, and in similar conditions the recurrent occurrence of types of coenosis is rather limited.

Therefore mycocoenosis can be defined as a form of coexistence of certain fungal coenopopulations connected with a uniform substrate (according to the composition and the stage of decomposition) or with a phorophyte within the limits of a certain ecotope (or in a part of it). N. A. Tcheremissinov (Черемисинов, 1971) defines the mycocoenosis as a complex of fungal organisms with different biological relations which have a mutual action on themselves and on the other components of biocoenosis. This definition does not include the most essential consideration in determining the mycocoenosis — the connection of fungal groupings with a certain uniform substrate or with a certain phorophyte. According to A. E. Apinis (1972) each mycocoenosis is formed in the boundaries of a plant community of certain sites. This definition is incorrect, since the boundaries of phytocoenosis do not determine the boundaries of mycocoenosis.

### Classification problems

As in case of the other communities, mycocoenoses can also be classified, the types of coenoses can be distinguished and termed. Unquestionably mycocoenoses have their own structure which is probably rather complicated. N. A. Tcheremissinov (Черемисинов, 1971) and A. E. Apinis (1972) differentiate mycosynusiae as structural elements of mycocoenoses.

A number of researchers have attempted to classify mycocoenoses labelling their types mycoassociations. At that only macrofungi have been studied and mycoassociations also called correspondingly, e.g., *Trametes gibbosae* (Pirk, Tüxen, 1957), *Boleto (aerei)-Russuletum luteotactae* (Smarda, 1972), etc.

The differentiation of such types of mycocoenosis is incorrect since saprotrophic microfungi, a lot of which can be found in ecosystems, are completely excluded.

In case of such a nomination of fungal associations there is another danger — the types of mycocoenoses can be mixed up with the seasonal aspects of fungal cover. Several authors (Сукачев, 1964; Мазинг, 1973, a. o.) have referred to the necessity of differentiating the spatial structure of biocoenosis by its seasonal rhythm. In case of fungi it is of great importance to take into consideration this aspect, since fruit-bodies are only a phenophase in the annual life cycle of fungi. We have no good methods to study a more durable phase of the life cycle of fungi — mycelium — from the standpoint of the structure of an ecosystem.

Therefore at present it is too early to differentiate the mycoassociations and mycosynusiae. Although almost half a century has elapsed since the publication of the first mycocoenological reports, mycocoenologists still deal with the research into fungal coenopopulations (Apinis, 1972).

### Methodological aspects

Up to the present time, mycocoenological studies have almost without any exception dealt with the research into the composition of fungal cover of different plant communities or site types, presenting also main coenological characteristics of fruit-bodies. These studies do not solve the main problem of mycocoenology, i. e. defining the actual boundaries of mycocoenoses (and their structural parts). The only mycocoenological investigations are some studies on the communities of wood saprobionts (cf. Pirk, Tüxen, 1957; Kreisel, 1961; Jahn, 1966; Runge, 1967, 1972, a. o.).

Thus, the previous research called «mycocoenology» has rather been mycoecology, which has mainly dealt with the studies on regularities of the distribution of fungi in the biotic environment — in phytocoenoses — vitally necessary for them. The mycocoenologists use the methods taken from phytocoenology and adapted to the peculiarities of biology and dispersion of fungal fruit-bodies in plant communities. In accordance with these methods, an attempt has been made to clarify the specific features of the occurrence of fruit-bodies in plant communities by both route and stationary analyses on sample plots of different shape and size or by transects, at the same time proceeding from the boundaries of a certain plant community or a site type. The author has repeatedly analyzed the hitherto existing field studies methods of mycocoenology (Kalamees, 1971a).

These methods are expedient for clearing up the connection of fungal cover with the site types, with plant associations or their structural parts, etc. In the study of mycocoenoses, their boundaries and structure, such a method is incorrect, since it does not consider the most important factors at the formation of fungal groupings in ecosystems — the character of a substrate and the specific effect of a phorophyte. For example, a horizon of forest litter ( $A_0$ ) consists of a great number of different «litter situations», even in the limits of the same plant community (association) or the forest type. This fact can be seen from the numerous studies by V. Y. Tchastukhin and his collaborators (Частухин, Николаевская, 1969).

Taking into consideration the above-mentioned ideas one can imagine what kind of a «mycocoenological analysis» can be obtained proceeding only from the specific features of plant communities, but not from the most important factors for fungi — the character of a substrate and sphere of influence of a phorophyte. But the mycoassociations distinguished on the basis of such analyses usually represent a mixture of several different types of mycocoenoses (depending on the nature of litter, the occurrence of phorophytes, etc.). Such analysis fulfils the real mycocoenological purpose only in one case — if there is a litter with a completely homogenic composition, and only one species of a phorophyte (e. g., in a pure stand entirely without underforest), but such an occasion is rather rare in plant communities.

To sum up, the real mycocoenological field studies must begin with a precise determination of substrates and the sphere of influence of phoro-

phytae. Sample plots must be selected accordingly. The results may be correct and exact only in case parallel studies are carried out on the decomposition of litter by individual fungal species. L. N. Vassilyeva and M. M. Nazarova (Васильева, Назарова, 1966) are also of the same opinion. Studies on mycorrhizal fungi are also of great importance. Therefore, in the mycocoenological research V. Y. Tchastukhin's methods for studying the litter saprobionts (Частухин, Николаевская, 1969) are at least partially applicable. L. G. Burova has also correctly approached the problem; her studies on mycocoenology are based on the sociation structure of forest communities\* (Бурова, 1968). Sociations as structural components of biogeocoenosis (Дылис et al., 1964) essentially differ in the litter composition and also in that of species of phorophytae. In many cases «the litter situation» formed within the range of a sociation with respect to its composition is evidently the most elementary and homogenic substrate distinguished in the boundaries of a certain forest community.

### Conclusions

To achieve the above-mentioned real mycocoenological purposes, first of all new methods based on the trophic peculiarities of fungi in ecosystems must be worked out. Next to macrofungi, the methods must also include microfungi as they both are equivalent components of an ecosystem. It must be a complex of methods, which besides the solution of mycocoenological objects at the same time also enables to settle the problems of mycorrhizae, decomposition of forest litter and quantitative ecology in connection with the functions of fungi in ecosystems.

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\* The composition of sociations in a certain association has been termed by Dylis as «parcellar structure» and a single sociation as «parcella».

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### SEENERÜHMITUSTE OSA ÖKOSÜSTEEMI STRUKTUURIS

Artiklis on esitatud seisukoht, et lähtudes ökosüsteemi funktsionaalsete komponentide — produtsentide, fagotroofide ja saprotroofide — talitluse printsiipaalsetest iseärasustest ning energiavoo erisuunalisusest ökosüsteemi auto- ja heterotroofses blokis, ei saa seenerühmitusi biotsünoosis vaadelda fütotsünoosi struktuurielementidena, vaid nad moodustavad tsönootilisel organisatsioonitasemel omaette seenekooslusi — mükotsünoose.

Кууло КАЛАМЕЭС

### РОЛЬ ГРУППИРОВОК ГРИБОВ В СТРУКТУРЕ ЭКОСИСТЕМ

Исходя из принципиальных особенностей действия функциональных компонентов экосистемы — продуцентов, фagотрофов и сапротрофов, а также из разнонаправленности энергетического потока в авто- и гетеротрофных блоках экосистемы, грибные группировки в биоценозе нельзя рассматривать как структурные элементы фитоценоза. Они образуют на ценотическом уровне самостоятельные грибные сообщества — микоценозы.