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THEORETICAL ASPECTS OF MYCOCOENOLOGY

Theoretical problems of mycocoenology have been little dealt with in relevant literature. The standpoints of various investigators are rather divergent. Mycologists are agreed only on the question that fungal groupings — which evidently are the subject of study of mycocoenology — are structural elements of biocoenoses, just like phytocoenoses of vascular plants, synusiae of musci and lichens, etc.

First of all, it is necessary to clear up the questions what place fungal groupings occupy in the system of the structural elements of biocoenosis, what they should be called and what are the relationships between them and the other structural elements of a biocoenosis. It is here that the opinions of investigators diverge. Some assert that fungal groupings represent independent communities which must be studied and designated independently of communities of vascular plants. Thence it may be inferred that these investigators place fungal groupings on the same level with phytocoenoses in a biocoenosis. A similar point of view was advanced by K. Höfler (1937) and was shared by F. Shmarda (1948), H. J. Hueck (1953) and G. Ubrizsy in the latter's earlier writings (1941, 1948). These investigators do not completely reject the dependence of fungal groupings on vascular plants, but they see this dependence too one-sidedly, as existing only in nutritional connections (Höfler, 1955), or regard a phytocoenosis from the point of view of fungal groupings merely as a biotic factor (Hueck, 1953). Höfler justifies the treatment of fungal groupings in the capacity of independent communities as follows: 1) similar fungal groupings may occur in several associations of vascular plants; 2) different fungal groupings may be met with in various phytocoenoses of one and the same association. Hueck (1953) adds, besides, further arguments: different research methods in mycocoenology, a different ecological amplitude of fungi, differences in nutritional connections, and an uneven distribution of fungi.

Another group of investigators are of the opinion that, like musci and lichens, fungi constitute independent saprophytic or parasitic communities only at places where they do not compete with other plants, as for instance on dung or wood; saprophytes and mycorrhizal fungi growing on humus, however, cannot be considered to be independent (Meisel-Jahn, Pirk, 1955). According to these investigators, it is possible to find even differential species among mycorrhizal fungi for the characterization of a phytocoenosis. These standpoints can be met with in all the investigations carried out by W. Pirk and his collaborators, who have chiefly dealt with wood-destroying fungi (Pirk, 1948, 1950, 1952; Pirk, Tüxen, 1949, 1957a,

1957b; Tüxen, Hübschmann, Pirk 1957). For the independent fungal groupings they introduce the concept of fungal communities (Pilzgesellschaften), which, in extent, does not coincide with H. Kreisel's concept of a mycocoenosis. H. Kreisel (1957) uses this term as a general notion for designating any kind of fungal groupings.

Part of the investigators belonging to both the above-mentioned groups, particularly Pirk and R. Tüxen, call fungal groupings associations, taxonomically. In practice, a great number of fungal associations have already been established, e. g. *Fometum igniarii*, *Xylarietum hypoxylonis* (Pirk, 1952), *Coprinetum ephemeroeidis*, *Trametetum gibbosae* (Pirk, Tüxen, 1949, 1957a), *Geopyxidetum carbonariae* (Ebert, 1958), *Schizophyllum communis*, *Lepiotetum procerae* (Ubrizsy, 1948), etc. These investigators use the concept of association here entirely in the phytocoenological sense, which has nothing in common with the notion of association introduced by J. Westerdijk (1949) into mycology or more correctly into microbiology. Westerdijk, who studied cultures of moulds, understands by the term "association" a combination of specific microorganisms growing on decaying biological substrata.

The adherents of the third group of investigators in the field of mycocoenology maintain that fungal groups represent structural elements of phytocoenoses — the so-called synusiae. This view is held by A. Shennikov (Шенников, 1943) and Ubrizsy in his later studies (1956, 1959). T. Lippmaa must also be referred to this group who, although he did not make a special study of fungal synusiae, pointed them out in his original classification of synusiae (Lippmaa, 1935; Липпмаа, 1946). He refers fungi to four synusial groups: 1) synusiae in the soil, 2) synusiae of saprophytes on the soil surface, 3) synusiae of parasitic fungi, 4) synusiae on dead and fallen trunks, branches and twigs, at the foot of the trunk of trees, and on stones.

I cannot agree with the adherents of the first two groups who consider fungal groupings to be independent communities. The occurrence of similar fungal groupings in different associations only marks their ability to live in different plant communities, their different vitality in plant communities, as Shennikov (Шенников, 1943) puts it. On the other hand, it is quite natural that individual phytocoenoses of one and the same association may differ with regard to fungal groupings since they always differ to a larger or smaller extent in floristic composition, layer density, soil type, and particularly in the character of humus, etc. It is these circumstances that, above all, determine the distribution of fungi in plant communities. If, for instance, in one phytocoenosis a tree species is missing which necessarily forms mycorrhizae with a certain fungal species, a given fungus cannot occur in that phytocoenosis. In another phytocoenosis of the same association where the given tree species exists, there also occurs the respective fungus (Kalamees, 1960). These small differences undoubtedly bring about some changes in the general ecological state of the community, which in their turn exercise a certain effect on the fungal cover. Pirk and Tüxen (1957a) assert that the climate, the soil and the general character of the forest community do not exercise any effect on the community of wood-destroying fungi, only the species-specific properties of the respective wood are necessary for them. At the same time, Pirk points out that the association of the *Trametetum gibbosae* is not found absolutely anywhere, since it depends on atmospheric moisture and abundance of light in a phytocoenosis. The above microclimatic differences, however, are necessarily linked with the general character of the respective plant community. Hence the said fungal community still somewhat depends on the general character of a given forest community and cannot therefore

be regarded as completely independent. All this strengthens the relationship of fungal groupings to communities of vascular plants and proves the need to study them as the constituent parts of these communities. Ubrizsy (1956) declares that the character of the fungal cover in a phytocoenosis is determined by the organization of the forest community, the level of its development and its synecological state.

Phytocoenology tells us that groupings of vascular plants of the same kind may often be found in different associations. For instance, one and the same kind of moss synusia may be met with in various types of pine and spruce stands. By way of an example, Lippmaa mentions the society of *Hepatica* — *Pulmonaria*, which is distributed all over Europe and can be found in mixed as well as deciduous forests. Yet we do not regard these synusiae as independent plant communities. In forest phytocoenology synusiae truly enjoy a relative independence which also justifies their separate study and classification, as Lippmaa (1940) stresses. All the more can such an occurrence be understood in the case of fungal groupings since the ecological amplitude of fungi is generally wider than that of vascular plants. Kreisel (1957) also points out that fungi are dependent on the substrate, and, in the case of mycorrhizae, more on individual plant species than on the whole vegetation of a phytocoenosis. Hence there is nothing peculiar when the same kind of fungal grouping is present in different associations and when different fungal groupings are found in different phytocoenoses of the same association. In this point, the accentuation by investigators of the first two trends of a certain independence of fungal groupings is fully justified. No doubt, it will be possible in future to study fungal groupings separately and within certain limits even to classify them separately, but we must not regard this independence as completely unrestricted, i. e. we cannot recognize only a close dependence of fungi on vascular plants, at the same time rejecting the retroaction of the community of vascular plants on fungi. Lippmaa always stresses the existence of an exceptionally close ecological relationship between synusiae and phytocoenoses as a whole. One-sided treatment of the above-mentioned problem causes inconsistency even among the adherents of the above-mentioned trend of investigators. Thus Pirk (1948), when analyzing the fungal cover of two *Querceto-Carpinetum* subassociations, lists not only the vascular plants and soil fungi, but also the wood-destroying saprophytic fungi among the differential species. If, however, groups of wood-inhabiting fungi constitute independent associations in a forest, it is impossible to select from them differential species belonging to an association of vascular plants; there is, therefore, no foundation to treat fungal groups as independent communities.

Pirk's suggestions as to the independence of fungal groupings growing on wood and other non-terrestrial substrata are also insufficiently grounded. Unfortunately, Pirk does not say explicitly what he means by competition with other plants. The fungi growing on humus as well as on wood are alike heterotrophs. In the case of humus fungi, therefore, we can hardly speak with greater justification of competition with vascular plants as autotrophs than in the case of wood fungi. If, however, Pirk means by competition relations of dependence on a forest community in general, which seems to be probable, we again arrive at the standpoints which were proved above.

Proceeding from what has been said above, one cannot accept the standpoint from which fungal groupings are regarded as independent associations. H. Trass (1961) also considers it to be unjustified to treat musci and all groupings of lower plants as associations, even if they

occur quite independently of the synusiae of vascular plants, since they differ completely from associations in their genesis, structure and ecology. This principle is also applicable to fungal groupings found on tree-stumps and other substrates outside a forest.

Of the views held by Pirk and his associates one must undoubtedly accept as correct the treatment of fungal groupings growing on wood and other non-terrestrial substrates separately from groupings of humus saprophytes and mycorrhizal fungi. It is indeed impossible to conceive of them as common groupings since in this case one would be able to speak of distinct fungal groupings because of their extraordinarily great variability.

Although we can assert with conviction that fungal groups represent structural elements of a phytocoenosis and not independent communities, we cannot entirely agree with the assertion that they constitute synusiae in phytocoenoses. By a synusia is meant such a structural element of a phytocoenosis as is characterized by a certain specific composition, a certain ecological and biological unity and a certain microenvironment as part of a given ecotype of a phytocoenosis (Лавренко, 1959). A synusia represents a certain closed system. At the same time, the species constituting a synusia must belong to one and the same group of life-forms.

In connection with their wide ecological amplitude, fungi, particularly groupings of terrestrial fungi, can show a considerably greater variability than groupings of vascular plants, on account of which their specific composition in a certain plant community is often rather unstable. This also affects the ecological and biological unity and microenvironment of species. In the case of fungal groupings, therefore, one cannot speak of such a closed system as in the case of synusiae of vascular plants. For instance, on the basis of the author's observations (Каламеев, 1960), *Lactarius subdulcis* is very closely connected with birch-leaf humus and can repeatedly be met with in several different forest communities, depending on the presence of birches in them. It is possible to bring other such instances, particularly of mycorrhizal fungi. The occurrence of certain fungal species in forest communities along with an occasional plant species significantly changes the species composition of fungal groups, as compared with the groups which can be found in another collection of the same forest community where a particular plant species may be lacking. In general, however, it is by far not clear to what extent fungal groupings in reality vary in their species composition since too few studies have been conducted on that problem. Incidentally, due to such a variable species composition of fungal groupings, one cannot consider the separation of differential species of a phytocoenosis from fungi [which can be encountered in Pirk's report (1948)] justified. Neither does Kreisel (1957) find it justified to separate differential species of a phytocoenosis from fungi. For this reason we cannot concur with H. Haas in the opinion that a phytocoenosis can be distinguished on the basis of fungi and that on their basis it is even possible to set up new types of communities.

In addition, one must consider the fact that humus consists of plant remains in various stages of decomposition and that often only a particular group of fungi is able to utilize a given stage of decomposition. We can, therefore, regard only successive fungal groupings of one and the same type of humus at different stages of decomposition as groups more or less invariable in species composition.

It follows from the above that in a biocoenosis fungal groupings constitute structural elements which are considerably more restricted in space and subject to another rhythm in time (e. g. the rhythm of humus

decomposition) than synusiae. It would be wrong to call such structural elements by the name of synusiae and in future one will have to find a more appropriate term for them.

The distinction of such limited structural elements may cause some methodical difficulties since they mostly occur as a mosaic in one and the same phytocoenosis, having become closely interlinked. If it is very easy to distinguish fungal groupings growing on distinct substrates (e. g. on stumps, live trees, decayed tree-trunks, excrements, etc.) from groups of terrestrial fungi, it is often rather difficult to distinguish the latter from groups growing on quickly decaying tiny substrates (such as leaves, needles, grasses, cones, twigs, etc.). In addition, concerning many species it has not been cleared up yet whether they feed symbiotrophically or not. Their inclusion among typical humus fungi renders the fungal groupings very labile in respect to the species composition. The study of mycelia might contribute much to a detailed study of the structural elements of fungal groupings, but at present this is impossible due to the lacking of respective research techniques. It has been repeatedly pointed out by several investigators that the whole of mycocoenology has merely been a coenology of fruit-bodies. The seasonal appearance of fruitbodies depends directly on climatic conditions and never provides a simultaneous perfect picture of the whole fungal cover. Hence the establishment of the structural elements merely on the basis of fruit-bodies is rather difficult.

It is essential to establish if a certain fungal species which is connected with a definite tree species or substrate (including various stages of decomposition of humus) appears in all the forest communities where a tree or a substrate necessary for its existence is present, or if it appears only in certain communities. In other words, it is necessary to determine all the ecological peculiarities of species of fungi. Such studies help to solve the question of to what extent fungal species depend directly on a substrate or a tree species and in what degree on the whole complex of ecological conditions. As it is known, in the study of synusiae, Lippmaa (1933) lays special emphasis on a complex of ecological conditions. He points out that the lower layers in a forest do not often depend on the tree layers as such but need the ecological conditions created by the upper layers. From the point of view of the fungal cover this question is of great importance because fungi undoubtedly belong to one of the lowest forest layers. M. Runge (1960), for instance, refers fungi together with musci to the so-called ground layer. Haas (1953) goes even so far as to speak of a special fungal layer. Although fungi greatly depend directly on substrates and tree species, it appears that many species, in addition, depend on a whole complex of ecological conditions. There is no reason to doubt that the majority of species inhabit definite ecotopes only. On the basis of concrete observations, S. Meisel-Jahn and Pirk (1955) showed that several species which are linked to a certain tree species are met with only in communities growing on a congenial soil and are lacking in others where the soil is not congenial. F. Kotlaba (1953) and A. Nespiak (1959) also arrived at the conclusion that fungi greatly depend on the ecological conditions of an association as a whole. The materials published by the author (Kalamees, 1968) confirm this from the point of view of different forest site types.

A very great difficulty in establishing the structural elements of fungal groupings is the circumstance that studies on the life-forms of fungi are almost completely lacking. The problem of fungal life-forms is also connected with the solution of the problem of "fungal layers".

Alongside of the morphological structure of biocoenosis, the elements

of which have been discussed above, V. Masing (Мазинг, 1966) deals with the functional structure of biocoenosis where primarily trophic and topological relations form the basis of relations between plant groups. A significant functional structural element of a biocoenosis is a consortium. By that is meant a set of all organisms which, in their life activities, are associated with a certain species or sometimes with a whole group of close species from among autotrophic non-epiphytic vascular plants (Мазинг, 1966). Since the relationship of fungi to vascular plants reveals itself vividly in trophic relations, the role of fungal groupings in a biocoenosis can best be characterized by consortia.

However, the concept of consortium mentioned above will have to be somewhat expanded. It seems to us reasonable to think that the central species of a consortium should not include only living plants, but also their decaying remains (e. g. stumps, leaves, needles, twigs, humus, etc.) because the latter serve as a trophic environment for very many organisms as well, primarily for fungi. Non-inclusion of decaying substrates would lead us to an exclusion of all saprophytic fungi from consortia. This, however, cannot be justified since dead plant remains serve as a nutritional medium for saprophytes just as living plants do for parasites or mycorrhizal fungi. Establishment of the belonging of saprophytic fungi to various consortia presupposes detailed investigations into the role that fungi play in the decomposition of humus.

The problem of fungal groupings forming morphological structural elements and the question of their belonging to consortia can be solved only on the basis of stationary long-term observations in different plant communities. Analyses carried out once do not give sufficient material for the solution of those problems due to the peculiarities of the life of fungi. In the first place, it is necessary to clarify the belonging of individual species to definite ecotopes and establish the role of fungal species in the decomposition of humus in forests.

Summary

1. It is not correct to treat fungal groupings in biocoenoses as independent communities or to call them associations. Fungal groupings represent such structural elements of phytocoenoses as do not correspond to the concept of synusia. Fungal groupings constitute spatially considerably more restricted and temporally quite different morphological elements subject to a different rhythm (e. g. that of the decomposition of humus) than synusiae. It is necessary to devise a new designation for such structural elements.

2. The role of fungal groupings in biocoenoses can best be characterized by consortia, i. e. functional structural elements of a biocoenosis, since the relationship of fungi to vascular plants primarily reveals itself in trophic relations.

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MÜKOTSÖNOLOOGIA TEOREETILISED ASPEKTID

Resümee

Mükotsönooloogia uurib seenerühmitusi ning nende seoseid biotsönoosi teiste struktuurielementidega. Küsimuses, milline koht biotsönoosi struktuurielementide süsteemis on seenerühmitustel, esineb kolm seisukohta: 1) seenerühmitused kujutavad endast analoogiliselt füotsöncosidele iseseisvaid ja terviklike kooslusi — mükotsönoose (Höfler, Smarda, Hueck); 2) seenerühmitused moodustavad iseseisvaid kooslusi ainult sellistes

tingimustes, kus nad ei konkureeri teiste taimedega, näiteks sõnnikul ja puidul; kõdul kasvavaid saprofüütidest või mûkoriisaseentest moodustuvaid seenerühmitusi aga ei saa vaadelda iseseisvaina (Meisel-Jahn, Pirk, Tüxen); 3) seenerühmitused kujutavad enesest fütotsõnooside struktuurielemente — sõnuuse (Sennikov, Ubrizsy, Lippmaa).

Seenerühmituste käsitamist iseseisvate kooslustena argumenteeritakse (Höfler, 1937) järgmiselt: 1) ühesugused seenerühmitused võivad esineda paljudes kõrgemate taimede assotsiatsioonides ja 2) ühe ja sama assotsiatsiooni erinevates fütotsõnoosides võib kohata erinevaid seenerühmitusi. Osa uurijaid, eriti aga W. Pirk ja R. Tüxen, peavad seenekooslusi taksonoomiliselt assotsiatsioonideks.

Kahe esimese seisukoha pooltajatega, kes seenerühmitusi käsitavad iseseisvate kooslustena, on raske nõustuda, sest ühesugustesse seenerühmituste esinemine erinevates assotsiatsioonides kajastab ainult nende võimet elada mitmesugustes taimekooslustes, nende erinevat elulisust viimastes (Шенников, 1943). Teisest küljest on täiesti arusaadav, et ühe ja sama assotsiatsiooni eri fütotsõnoosid võivad erineda seenerühmitustele poolest, kuna nad erinevad alati suuremal või vähemal määral ka floristikiliselt koosseisult, rinnete tiheoduselt, pinnase, eriti aga kõdu iseloomult jne. Neist tingimustest aga sõltubki esmajärjekorras seente levik taimekooslustes. Tihe side seenerühmituste ja kõrgemate taimede koosluste vahel tingibki vajaduse uurida neid rühmitusi taimekooslustele osana.

Ka ühesugused kõrgemate taimede rühmitused (näit. sammalde sõnuusid) võivad tihti esineda erinevates assotsiatsioonides, ometi ei loe me neid sõnuuse iseseisvateks taimekooslusteks. Kuid paljudel sõnuusidel on metsafütotsõnoosides töepooltest suhteline iseseisvus, mis iseegi õigustab nende eraldi uurimist. Veelgi enam on selline suhteline iseseisvus mõistetav seenerühmituste puhul, kuna seente ökoloogiline amplituud on enamasti laiem kui kõrgemate taimedel. Selles mõttes on seenerühmituste teatud iseseisvuse toonitamine kahe esimese seisukoha pooltajate poolt täiesti õige, kuid seejuures ei tohi eitada kõrgemate taimede koosluse kui terviku mõju seenkonnale. Pirk pöhjendus, mis käib ainult puidul ja teistel subsitraatidel esinevate seenekooslustele sõltumatuse kohta, on samuti aluseta. Pinnase- ja puuduseened on ühtemoodi heterotroofse toitumisega, mistöttu nii esimeste kui ka teiste konkurentist kõrgemate taimedega kui autotroofidega saab vaevالت rääkida. Eelnevast lähtudes tuleb pidada vastuvõetamatuks seenerühmituste käsitamist omaette assotsiatsioonideka.

Kuigi võime veendunult väita, et seenerühmitused kujutavad enesest fütotsõnoosi struktuurseid osi, mitte iseseisvaid kooslusi, ei ole võimalik nõustuda väită, et nad moodustavad fütotsõnoosides just sõnuuse. Sõnuusi mõiste (vähemalt T. Lippmaa jt. eesti botaanikute järgi) ei sobi hästi seenerühmituste taksonoomilisel piiritlemisel. Seoses seeneliikide ökoloogilise amplituudiga võib seenerühmituste liigiline koosseis erinevates taimekooslustes olla küllaltki erinev, mistöttu nende rühmituste puhul ei saa kaugeltki rääkida. Sellisest suletusest nagu kõrgemate taimede sõnuuside puhul. Tuleb arvestada sedagi, et metsakõdu koosneb kõige erinevamate lagunemisjärkudes olevatest taimjäänustest, millest iga järu on võimeline kasutama sageli ainult teatud seenegrupp. Seepärast saame liigiliselt koosseisult enam-vähem muutumatute rühmitustena käsitada ainult suktsessiivseid seenerühmitusi ühe ja sama kõduliigi erinevat lagunemisjärkudel.

Eelnevast järeldub, et seenerühmitused kujutavad enesest biotsõnoosi ruumiliselt tugevasti piiratuma ja ajaliselt hoopis teistsugusele rütmile (näit. kõdu lagunemise rütmile) alluvaid struktuurielemente, kui seda on sõnuusid. Selliseid struktuurielemente oleks ebaõige nimetada sõnuusideks, sobivat nimetust aga pole neile veel leitud.

Kõrvuti biotsõnoosi morfoloogilise struktuuriga, mille elementidest oli juttu eespool, võib veel rääkida biotsõnoosi funktsionaalsest struktuurist, kus taimerühmitustevaheliste seoste aluseks on eeskätt troofilised suhted. Olulisemaks funktsionaalseteks struktuurielementideks biotsõnoosis on konsortsiumid. Kuna seente seos kõrgemate taimedega avaldub eriti ilmekalt troofilistes suhetes, siis saab seenerühmituste osa biotsõnoosides kõige paremini iseloomustada just konsortsiumide urimise teel.

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КУУЛО КАЛАМЭЭС

ТЕОРЕТИЧЕСКИЕ АСПЕКТЫ МИКОЦЕНОЛОГИИ

Резюме

Микоценология изучает группировки грибов и связь их с другими элементами структуры биоценоза. Существует три точки зрения на вопрос о месте группировок грибов в структуре биоценоза: 1) группировки грибов представляют собой автономные и целостные сообщества — микоценозы, наподобие фитоценозов (Гефлер, Шмарда, Хюк); 2) группировки грибов образуют автономные сообщества только в таких усло-

виях, где они не конкурируют с другими растениями, например на навозе и древесине; тогда как сапрофиты, растущие на лесной подстилке, и грибы-микоризообразователи не образуют автономных сообществ (Майзель-Ян, Пирк, Тюксен); 3) группировки грибов представляют собой структурные части фитоценоза — синузии (Шенников, Убрики, Липпмаа).

Рассмотрение группировок грибов как самостоятельных сообществ обосновывается главным образом следующими доводами (Höfner, 1937): 1) одинаковые группировки грибов могут встречаться во многих различных ассоциациях высших растений, 2) в различных фитоценозах одной и той же ассоциации можно встретить различные группировки грибов. Часть исследователей, в частности В. Пирк и Р. Тюксен, называют типы сообществ грибов соответственно своим взглядам ассоциациями.

Со сторонниками двух первых направлений трудно согласиться. Существование одинаковых группировок грибов в различных ассоциациях свидетельствует лишь об их способности жить во многих растительных сообществах и об их различной жизненности в последних (Шенников, 1943). С другой стороны, вполне понятно, что отдельные фитоценозы одной и той же ассоциации могут иметь разные группировки грибов, так как сообщества всегда в большей или меньшей мере отличаются по своему флористическому составу, густоте ярусов, характеру почвы (особенно лесной подстилки) и т. д. Именно от этих условий в первую очередь и зависит распространение грибов в растительных сообществах. Тесная связь между группировками грибов и сообществами высших растений и доказывает необходимость изучения группировок грибов как основной части сообщества растений.

Однаковые группировки высших растений (например синузии мхов) часто могут встречаться в различных ассоциациях, все же мы не считаем их самостоятельными сообществами. Многие синузии в лесных фитоценозах обладают действительно относительной самостоятельностью, что и оправдывает их разделное изучение. В еще большей мере это относится к группировкам грибов, так как экологическая амплитуда у последних большей частью шире, чем у высших растений. Поэтому определенное подчеркивание самостоятельности группировок грибов вполне понятно. Однако нельзя отрицать влияние сообществ высших растений в целом на грибной покров.

Не имеют оснований и доводы Пирка о независимости группировок грибов, растущих лишь на древесине и других субстратах. Как почвенные, так и растущие на древесине грибы имеют одинаковый гетеротрофный способ питания, вследствие чего о конкуренции с высшими растениями тех или других почти не приходится говорить.

Исходя из вышесказанного, нельзя называть группировки грибов ассоциациями.

Хотя мы достоверно можем утверждать, что группировки грибов представляют собой элементы структуры фитоценозов, а не автономные сообщества, все же нельзя согласиться с утверждением, что именно они образуют синузии в фитоценозах. Группировки грибов по содержанию не соответствуют понятию синузии (в понимании Липпмаа и других эстонских ботаников). В связи с широкой экологической амплитудой отдельных видов состав микрофлоры в различных группировках определенного типа ценозов может быть довольно изменчивым, вследствие чего группировки грибов не обладают такой видовой замкнутостью, как синузии высших растений.

Кроме того, необходимо учесть, что лесная подстилка состоит из растительных остатков, находящихся на различных стадиях разложения; при этом на каждой стадии разложения нередко содействуют различные виды грибов. Поэтому по видовому составу более или менее определенными будут, видимо, только серийные группировки грибов на отдельных стадиях разложения одного и того же типа лесной подстилки одной породы.

Из сказанного следует, что группировки грибов образуют в биоценозе своеобразные структурные части, по времени подчиняющиеся совсем другому ритму развития (например, ритму разложения лесной подстилки), чем синузии в обычном понимании. Для таких типов элементов структуры еще не найдено подходящее общее название.

Кроме морфологической структуры биоценоза, об элементах которой шел разговор выше, можно говорить еще и о функциональной структуре биоценоза, основанной главным образом на трофических взаимоотношениях между организмами. Существенными функциональными структурными элементами в биоценозе являются консорции. Связь грибов с высшими растениями проявляется особенно отчетливо в трофических связях, поэтому именно изучением консорций можно хорошо охарактеризовать группировки грибов, связанные с отдельными видами высших растений в биоценозах.