

EFFECT OF NATURAL AND SYNTHETIC PHYTOHORMONES ON GROWTH AND DEVELOPMENT OF HIGHER BASIDIOMYCETES

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The paper is aimed to analyze the current data on the influence of exogenous growth stimulators on growth and development of higher *Basidiomycetes*. The historical aspects about discovery and role of phytohormones in fungi physiology are reviewed. The taxa of the basidiomycetes, which are capable of synthesizing phytohormones of all known types, including *Aphylllophorales*, *Boletales*, *Agaricales*, *Sclerodermales*, *Hymenogastrales*, *Uredinales*, *Ustilaginales* are described. The data from different sources describing the effects of natural and synthetic growth stimulators on the development of basidiomycetes are summarized and compared. It is noted that various concentrations of phytohormones (auxins, gibberellins, cytokinins) from 0.01 to 400 mg/ml were used in the experiments to study their effects on mycelial growth. Possible causes of conflicting results obtained by different authors, such as application of diverse methods of mushroom cultivation, different media and methods of substrate sterilization, are described.

Key words: higher basidiomycetes, phytohormones, auxins, gibberellins, cytokinins, stimulation of growth and development.

Phytohormones are widely used in modern biotechnologies based on plant cultivation [1]. No less important objects of biotechnology are higher basidiomycetes, which is due to their widespread use in mushroom growing, food production, biologically active substances and medicines. Knowledge of the role of endogenous substances in the growth processes of fungi allows regulating the growth of vegetative mycelium, to influence on the biosynthesis of biologically active substances and the formation of fruiting bodies [2].

The first report on the presence in fungi of substances, similar to plant phytohormones, was made by A. Nielsen in 1930. The growth substance isolated by him during the cultivation of *Rhizopus suinus* Fischer on the glucose medium was later identified as indolyl-3-acetic acid (IAA) [3]. It is now known that more than 100 species of fungi from different taxonomic groups are able to

produce the phytohormones of all known types [4, 5]. Most of the described fungi-producers of phytohormones are phytopathogens [6]. It is believed that the fungus-parasite with the help of phytohormones changes of the hormonal status of the host-plant, which provides for its growth and development more favorable conditions [7, 8].

The role of phytohormones synthesized by saprotrophic and mycorrhizal fungi has not been fully elucidated. Some researchers suggest that mycorrhizal fungi secrete certain metabolites with growth-regulating (gibberellins, IAA, ethylene, vitamins, enzymes, etc.), which are necessary for plants, and plants, in turn, secrete a large number of substances that affect on the growth and morphogenesis mycorrhizal fungi (carbohydrates, cytokinins, M-factor, IAA, jasmonic acid) [8, 9]. For example, it was found that the growth of *Arabidopsis*

sp. and its reproduction is stimulated by endophytic fungi *Piriformospora indica* Verma et Varma, which form many auxins. At the same time this fungus needs cytokinins for its growth synthesized by the plant [10]. As for saprotrophic fungi, it is thought that growth hormones secreted by fungi stimulate plant growth in length. The stems are pulled out and under the weight of their own weight the plants lie down, as a result of which the plant becomes more vulnerable and accessible to saprotrophic fungi. Such action is characteristic, for example, of the known fungus *Gibberella fujikuroi* (Saw.) Wr., which is able to synthesize a large number of different types of gibberellins [6, 11].

Most fungi-producers of phytohormones are representatives of the class *Hyphomycetes*, but they are also found in representatives of the class *Basidiomycetes*, orders: *Aphyllorphorales*, *Boletales*, *Agaricales*, *Sclerodermales*, *Hymenogastrales*, *Uredinales*, *Ustilaginales* [8, 12].

Different types of auxins are able to synthesize species of basidiomycetes such as *Boletus parasiticus* Fr. [13], *Hebeloma cylindrosporum* Romagn., *H. hiemale* Bres. [14], *Pisolithus tinctorius* (Pers.) Cooker et Couch [15], *Phanerochaete chrysosporium* (Fr.) P. Karst. [16, 17], *Trametes versicolor* (L.: Fr.) Quél. [16], species of the genera *Ustilago*, *Puccinia*, *Agaricus*, *Lentinus*, *Amanita*, *Russula*, *Pleurotus*, etc. [18, 19]. IAA was found in the vegetative mycelium of fungi, fruiting bodies and culture fluid [14, 15, 18, 20–23], in uredospores of *Puccinia graminis* Pers. [24], sporocarps of ectomycorrhizal fungi *Paxillus involutus* (Batsch Fr.) Fr. and *Amanita muscaria* (L.) Hook [25]. It is believed that mycorrhizal fungi are more capable of forming auxins than representatives of other ecological groups of higher basidiomycetes [8, 26].

It has been established that phytohormones in the mycelium and basidioms of higher fungi are found in both free and bound forms [27, 28]. In the basidioms of *Agaricus bisporus* (J.E. Lange) Imbach, for example, the level of free form IAA is almost twice that of bound, and in *Pleurotus ostreatus* (Jacq.: Fr.) Kumm. dominated by the bound form of IAA, which is associated with different growth rates of these fungi. It is known that the fruiting bodies of *A. bisporus* grow faster than *P. ostreatus*, which correlates with the amount of free form of IAA, which is more in the basidioms of *A. bisporus* [27, 29, 30].

It is recognized that almost all types of gibberellins can be found in fungal cultures, and each of them has its own specific set of

these hormones [22]. Since for higher plants the metabolism of phytohormones is a species-specific process, Sytnyk, Musatenko and others suggested that this was also characteristic of fungi [8].

About 40 species of mushrooms are now known, which are able to produce 25 types of gibberellins [31, 32]. Unique producers of gibberellins are fungi *G. fujikuroi* [11], *Fusarium moniliforme* Shold. [33, 34]. Substances with the physiological activity of gibberellins form some species of yeast, hyphomycetes [8] and basidiomycetes: *Collybia conigena* Fr., *Hypholoma fasciculare* (Fr.) Kum., *Clitocybe dicolor* (Pers.) Lange [21], *Ustilago zea* (Beckm.) Unger [35], *A. bisporus*, *P. ostreatus* [8, 27], *Laetiporus sulphureus* (Bull.) Murril [12], *Phaner. chrysosporium* [17]. Gibberellins are found in the mycelium, fruiting bodies and culture fluid of fungi. In the fruiting bodies of *P. ostreatus* and *A. bisporus*, insignificant activity of gibberellins was found, which is explained by the main synthesis of these substances mainly in the phase of linear growth of vegetative mycelium, and not during the stage of teleomorph formation [36].

The substances with cytokinin activity have been found in mycelium and culture fluid of more than 35 species of phytopathogenic and mycorrhizal fungi [8, 37]. These are representatives of ascomycetes, hyphomycetes, coelomycetes, basidiomycetes. Among basidiomycetes, the ability to synthesize cytokinins has been found in species of the genus *Puccinia* [38], *Uromyces*, *Ustilago* [39], *Amanita*, *Rhizopogon* [40], *Boletus* [41], *Suillus* [42], *Pleurotus*, *Agaricus* [8, 27, 29], and *Laet. sulphureus* [12], *Schizophyllum commune* Fr. [43], *Phaner. chrysosporium* [17].

The substances with cytokinin activity are found in fungi not only in the free state, but also in the composition of tRNA [44]. Of the large group of natural cytokinins in fungi are mainly zeatin [12], zeatinriboside and N⁶-(Δ^2 -Isopentenyl)-adenine [13].

High content of cytokinins was found in basidiomas of *P. ostreatus* and *A. bisporus* during their differentiation, when spores have already formed in hymenophores [8, 27, 29], which confirms the known literature on the significant accumulation of cytokinins in the germination of fungal spores [38].

It was found that the balance of endogenous phytohormones in the basidiomes of *P. ostreatus* and *A. bisporus* is shifted towards increased synthesis of growth stimulants mainly due to cytokinins.

The growth inhibitor — abscisic acid (ABA) — was first found in phytopathogenic fungi. Now it is isolated in 30 species of fungi of different classes [13], including basidiomycetes: *Polyporus brumalis* (Pers.: Fr.) Fr., *T. versicolor*, *Agrocybe praecox* (Pers.: Fr.) Fay., *Coprinus domesticus* (Bolt.: Fr.) S.F. Gray [8, 45], *Laet. sulphureus* [12], *Schiz. commune* [43], *Phaner. chrysosporium* [17].

The content of the free form of ABA growth inhibitor is increased compared to the conjugated form in basidioms of *P. ostreatus* and *A. bisporus*, which, according to the researchers, is due to changes in the intensity and nature of fungal metabolism at the stage of teleomorphs [8, 29]. These data are consistent with the data obtained for higher plants [46].

The ability to produce ethylene has been established in about 70 species of fungi, most of which belong to phytopathogens [47, 48]. The formation of ethylene by some basidiomycetes — obligate parasites of cereals, legumes, flower crops (*Puc. graminis*, *Puccinia chrysanthemi* Roze, *Uromyces phaseoli* (Rebent.) Wint) [49, 50] and wood-destroying fungi (*Schiz. commune*) [51] was noted.

According to Musatenko, Vasyuk [13], Generalova, Vedenicheva [29], Perepelytsya [27] conjugation of phytohormones in fungi is an adaptive mechanism for neutralization of their free forms, which are not required for growth in certain stages of fungal development. For example, extremely low levels of endogenous phytohormones in the vegetative mycelium of *P. ostreatus* have been noted [8]. Maybe, really, they are not needed there. The correctness of these or other assumptions about the role of growth regulators in the ontogenesis of fungi can be established by studying the effect of exogenous factors (phytohormones) on the growth of vegetative mycelium with the definition of their role on the different stages of morphogenesis of fungi.

The first study of the effects of exogenous growth regulators on the growth and development of fungal organisms appeared in the 30s of the twentieth century. The subjects were mainly zygomycetes, ascomycetes and hyphomycetes. An increase of the mycelial biomass of *Pyronema confluens* Tul in the medium with IAA was shown [52]. Gibberellic acid (GA_3) at a concentration of 50–500 mg/l stimulated the growth of *Cenococcum grandiforme* (Sowerby) Ferd et Winge, but inhibited the development of some mycorrhizal fungi [53]. Mayr et al. (1984) noted a slight acceleration of growth of

Morchella conica Pers. under the action of GA_3 at a concentration of 100–400 mg/l [54]. The stimulating effect of kinetin at a concentration of 21,7–217,0 mg/l on the growth and protein kinase activity of *Verticillium albo-atrum* Reinke et Berth was revealed. [55]. Study of the effect of cytokinins on the growth of *Phycomyces blakesleeanus* Burgeff. showed a stimulating effect, but the magnitude of growth stimulation depended on the structure of the hormone and carbon resources in the culture medium, while increasing the activity of enzymes of the glyoxylate cycle [56].

Studies to establish the presence and nature of the influence of phytohormones on the growth and development of higher basidiomycetes, including mycorrhizal, have long attracted attention of many researchers. As early as 1940, Defago observed an increase of the biomass of several species of the genus *Tilletia* under the influence of IAA [57]. Acceleration of the development of *Psalliota hortensis* (Cooke) Lange (*A. bisporus*) under the action of IAA was noted by Fraser (1953) [62]. Alexandrov (1964) found the effect of cytokinins, auxins and gibberellins on the formation of basidiocarps of higher fungi [58]. The most of the first works related to the effect of plant growth regulators on the growth and development of mushrooms was carried out with *A. bisporus*. Successful experiments on stimulation of *A. bisporus* fruiting in non-sterile conditions by phytohormones and substances of hormonal nature are known (6-methyluracil, 2-chloroethylphosphate, gibberellic acid, diphenylurea, naphthaleneacetic acid) [59–61].

Later, experiments with the use of phytohormones began to be conducted on other species of basidiomycetes: *Lentinus tigrinus* (Bull.) Fr. [63], *Pleurotus* sp. [64]. The positive effect of cytokinins, auxins and gibberellins on the mycelial growth of *A. bisporus* and *Coprinus comatus* Fr. was shown in the work of Hungarian researchers [65]. Volz noted in his work that IAA concentrations of 10–100 mg/l stimulated the growth of *Volvariella* sp. At the same time, these concentrations of IAA did not affect on the growth of *Lepista* sp., *Cantharellus* sp., *Pleurotus* sp., and high concentrations of IAA slowed the development of these species of fungi [66]. In the experiments of Ghosh and Sengypta (1982), IAA stimulated the growth of *Volvariella volvaceae* (Bull.: Fr.) Singer, and kinetin inhibited the development of this fungus [67]. Some authors have found a positive effect of IAA, gibberellic acid, naphthylacetic acid on the development of basidiospores *Pholiota*

destruens (Brond) Gillet, and kinetin, on the contrary, inhibited this process [68]. The positive effect of phytohormones on the growth and yield of *Pleurotus eryngii* var. *nebrodensis* (Inzenga) Quel. was noted [69]. Krasnopolska (1994) showed that the stimulant E-6 (a substance of the steroidal nature) at a concentration of 10^{-11} – 10^{-2} M (optimum — 10^{-4} – 10^{-3} M) stimulated the growth and fruiting of mycorrhizal fungi *Boletus edulis* Bull.:Fr., *Suillus grevillei* (Klotzsch.: Fr.) Sing., as well as *A. bisporus* (the name of the stimulant is not given by the authors) [70].

It was studied that gibberellin increased both biomass and milk-clotting activity of the fungus *Hirschioporus laricinus* (Karst.) RYV, and auxin did not affect on the accumulation of biomass of this basidiomycete and reduced the milk-clotting activity [71]. Scientists have shown the positive effect of gibberellin, β -indolylacetic, indolylbutyric, α -naphthylacetic acids and kinetin on the vegetative growth of *Lentinus squarrosulus* Mont. [72], *Lentinus edodes* (Berk.) Singer [73], *Lentinus connatus* Berk [74], *A. bisporus* ta *P. ostreatus* var. *florida* [75].

Recently, more and more research was devoted to the study of the influence of phytohormones of other groups and growth stimulators of the new generation on the growth and development of cultivated basidiomycetes.

So, Krasnopolska with her co-authors (2014) found the effect of fusicoccin A at a concentration of 10^{-5} and 5×10^{-5} M on the number of fruiting waves, yield and size of fruiting bodies of *A. bisporus*, but no effect on the rate of radial growth was observed [76]. An increase of the crude protein and crude fiber when watering the casing layer with 0.005% aqueous sodium humate solution in the cultivation of *A. bisporus* (strain A-15) has been shown [77]. Polskyh et al. (2007) noted the broad effect of the drug "Humisol Furor" (contains humic acids) on the development of mycelium and fruiting *P. ostreatus*, *A. bisporus*, *Flammulina velutipes* (Curtis) Singer: reduction the maturation of the mycelium, the time of emergence of the first bunches of mushrooms (1.5 times), increasing yields (1.8–2.8 times), reducing the effects of negative climatic factors and the period between waves of fruiting [78]. The use of agrostimulin (containing N-oxide-2,6-dimethylpyridine and Emistim) in concentrations of 0.1, 0.2 and 0.4% helped to increase the yield of enzymes of thrombolytic, milk-clotting activity and caseinolytic enzymes

of the fungus *Irpex lacteus* (Fr.) Fr. [79, 80]. Studies of bioregulators based on arachidonic acid (El-1, Immunocytophyte) showed an increase of the mycelial growth rate, reduced substrate growth time, increased yields of *P. ostreatus* (strain NK-35) and *L. edodes* (strain M 370), and increased cellulolytic activity at a stimulant concentration of 5.2×10^{-5} mg/ml [81–83]. Alekseeva (2002) found a stimulating effect of Epine (group of brassinosteroids) in a concentration of 0.002% on the growth and fruiting of champignon and oyster mushrooms: reduction of fruiting time, increase of the yield by 19.4–20.9% [84]. The stimulation of fruiting of the mushroom *Pleurotus eryngii* var. *ferulae* (Lanzi) Sacc. with *Asafoetida* extract (contains a complex of phytohormones) was shown in [85].

Recently it became known the fact of using of new generation growth stimulants Biolan (contained Emistim C and trace elements) and Emistim C (contained a set of regulators of auxin and cytokinin nature, aminoacids, carbohydrates, fatty acids, trace elements and polysaccharides) in very high concentrations for the increase of yields *A. bisporus* [86]. Our previous studies have shown the positive effect of a complex growth stimulator of biohumate and gibberellin in concentrations of 1–100 mg/l on the lag phase and the rate of linear growth of mycelium, the formation of primordia of some species of the genus *Pleurotus* (Fig. 1–4) [87].

Table summarizes the literature on the effect of natural and synthetic growth stimulants on the growth and development of basidiomycetes. To compare the data obtained by different researchers, the concentrations of phytohormones (Note) are listed by us and given in the same units (mg/l).

Analyzing the data in Table it can be assumed that the nature of the action of phytohormones on the growth of different species of basidiomycetes is probably a special species characteristic and is associated with the own synthesis of these substances by certain species of fungi. For example, IAA at low concentrations of 0.01–100 mg/l stimulated the growth of *P. ostreatus*, reducing the lag phase of growth [88, 90–92], and at concentrations greater than 100 mg/l — inhibited growth [88]. Tan and Chang (1989) showed that IAA concentrations from 5 to 300 mg/l did not affect the growth and fruiting of *L. edodes* [93]. However, Han et al. (1981) noted that the concentration of IAA 0.5–20 mg/l in the nutrient medium increased the biomass of this fungus [94]. At the same time, for

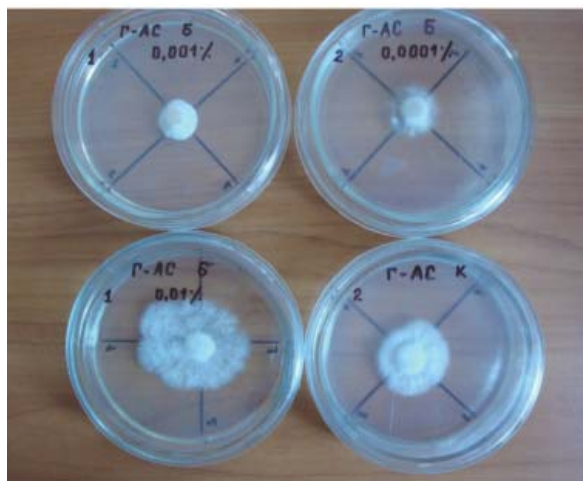


Fig. 1. The effect of biohumate (concentrations 1, 10, 100 mg/l) on the development of mycelium *P. ostreatus* (strain IBK-551) on glucose-asparagine nutrient medium (7th day of cultivation)

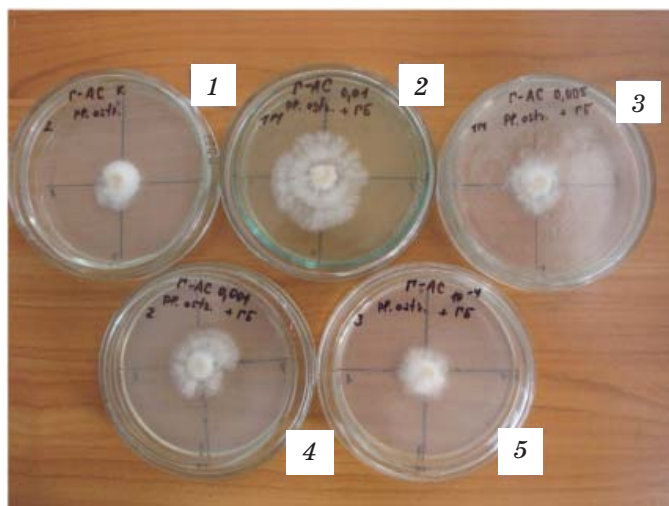


Fig. 2. The effect of gibberellin (GA_3) (concentrations 1, 10, 50, 100 mg/l) on the development of mycelium *P. ostreatus* (strain IBK-551) on glucose-asparagine nutrient medium (G-AS) (7th day of cultivation):
 1 — control; 2 — G-AS + GA_3 100 mg/l;
 3 — G-AS + GA_3 50 mg/l;
 4 — G-AS + GA_3 10 mg/l; 5 — G-AS + GA_3 mg/l



Fig. 3. The effect of biohumate (concentrations 1, 10, 50, 100 mg/l) on the development of mycelium *Pleurotus pulmonarius* (Fr.) Quel. (strain IBK-230) on glucose-ammonium nutrient medium (12th day of cultivation)

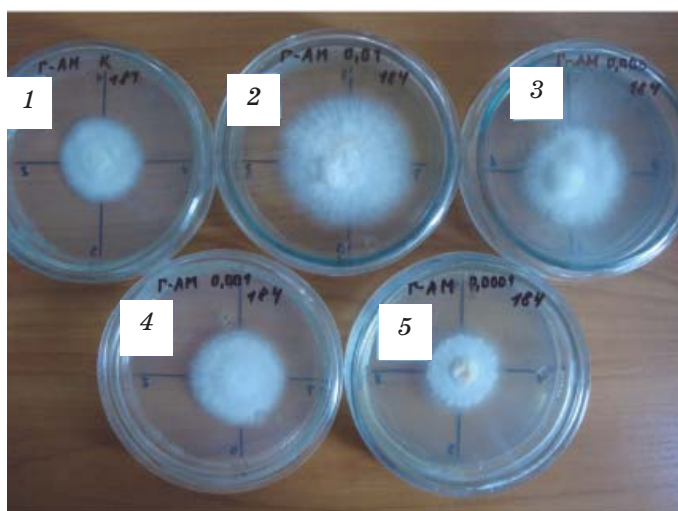


Fig. 4. The effect of biohumate (B) (concentrations 1, 10, 50, 100 mg/l) on the development of mycelium *Pleurotus eryngii* (DC.) Quel. (strain IBK-2011) on glucose-ammonium nutrient medium (G-AM) (14th day of cultivation):
 1 – control; 2 – G-AM + B 100 mg/l;
 3 – G-AM + B 50 mg/l; 4 – G-AM + 10 mg/l;
 5 – G-AM + 5 mg/l

Table. Influence of phytohormones on growth and development of Basidiomycetes

Objects research (species)	Test substances	Concentration (mg/l)	Effect	Source of information
1	2	3	4	5
Auxins				
<i>Pleurotus ostreatus</i> (Jacq.: Fr.) Kumm.	indolyl-3-acetic acid	175 mg/l 1.75 mg/l	Inhibits growth Stimulates growth (reduces the lag phase)	Solomko (1989, 1992) [88, 89]
<i>P. ostreatus</i>	indolyl-3-acetic acid	100 mg/l	Stimulates growth	Vinklarkova, Sladky (1978) [90]
<i>P. ostreatus</i>	indolyl-3-acetic acid	0.01–0.2 mg/l	Stimulates growth	Hong (1978) [91]
<i>P. ostreatus</i>	heteroauxin	20 mg/l	Stimulates growth	Kuzneczova, Zakolesnyk (2006) [92]
<i>Lentinus edodes</i> (Berk.) Singer	indolyl-3-acetic acid	5, 10, 50, 100, 300 mg/l	Does not affect on the mycelial growth and fruiting	Tan, Chang (1989) [93]
<i>L. edodes</i>	indolyl-3-acetic acid	0.5–20 mg/l (optimum — 5 mg/l)	Increases biomass	Han. et al. (1981) [94]
<i>Lentinus tigrinus</i> (Bull.) Fr.	indolyl-3-acetic acid	300 mg/l	Stimulates fruiting	Sladky, Tichy (1974) [95]
<i>L. tigrinus</i>	indolyl-3-acetic acid	100–400 mg/l	Stimulates growth	Mayr et al. (1984) [54]
<i>Phellinus linteus</i> (L.) Qu l.	1-naphthalene-acetic acid	5 mg/l	Stimulates growth, biomass yield and synthesis of exopolysaccharides	Guo, Zou, Sun (2009) [96]
<i>Phel. linteus</i>	indolyl-3-acetic acid	1 mg/l	Stimulates growth	Guo, Zou, Sun (2009) [96]
<i>Phel. linteus</i>	indolyl-3-butyric acid	1.5 mg/l	Stimulates growth	Guo, Zou, Sun (2009) [96]
<i>Agaricus arvensis</i> Schaeff.	indolyl-3-acetic acid	100–400 mg/l	Stimulates growth	Mayr et al. (1984) [54]

Table. (Continued)

1	2	3	4	5
<i>Pholiota destruens</i> (Brond) Gillet	indolyl-3-acetic, naphthyl-acetic acids	0.001 mg/l 10; 1; 0.01 mg/l	Stimulates growth Inhibits growth	Krishna, Sharma (1989) [97]
<i>Calvatia gigantea</i> (Batsch. et Pers.) Lloyd, <i>C. booniana</i> A. H. Smith, <i>C. craniiformis</i> (Schwein.) Fr.	indolyl-3-acetic acid	0.05; 0.5 mg/l 5.0 mg/l	Stimulates growth Inhibits growth	Alexander, Lippert (1989) [98]
Gibberellins				
<i>L. edodes</i>	GA ₃	5 and 100 mg/l	Stimulates growth and fruiting	Tan, Chang (1989) [93]
<i>L. edodes</i>	GA ₃	0.5–20 mg/l (optimum — 10 mg/l)	Stimulates growth and fruiting	Han et al. (1981) [94]
<i>L. tigrinus</i>	GA ₃	300 mg/l	Stimulates fruiting	Sladky, Tichy (1974) [95]
<i>L. tigrinus</i>	GA ₃	100–400 mg/l	Does not affect growth	Mayr et al. (1984) [54]
<i>P. ostreatus</i>	GA ₃	200 mg/l	Stimulates growth	Vinklarkova, Sladky (1978) [90]
<i>P. ostreatus</i>	GA ₃	10–300 mg/l	Stimulates growth	Hong (1978) [91]
<i>P. ostreatus</i>	GA ₃	0.2–2.0 mg/l	Does not affect growth	Jauhri, Sen (1978) [99]
<i>A. arvensis</i>	GA ₃	100–400 mg/l	Does not affect growth	Mayr et al. (1984) [54]
<i>Phol. destruens</i>	GA ₃	10; 1; 0.01; 0.001 mg/l	Stimulates growth	Krishna, Sharma (1989) [97]
<i>Calvatia gigantea</i> , <i>C. booniana</i> , <i>C. craniiformis</i>	GA ₃	0.05; 0.50 and 5.0 mg/l	Stimulates growth	Alexander, Lippert (1989) [98]
Cytokinins				
<i>Calvatia gigantea</i> , <i>C. booniana</i> , <i>C. craniiformis</i>	kinetin	1.0; 20.0 mg/l	Stimulates growth	Alexander, Lippert (1989) [98]
<i>P. ostreatus</i>	kinetin	200 mg/l	Stimulates growth	Vinklarkova, Sladky (1978) [90]
<i>P. ostreatus</i>	kinetin	0.01–0.2 mg/l	Stimulates growth	Hong (1978) [91]
<i>P. ostreatus</i>	kinetin	2.15–215.2 mg/l	Stimulates growth (reduces the lag phase)	Solomko (1989, 1992) [88, 89]
<i>L. edodes</i>	kinetin	5; 10; 50; 100; 300 mg/l	Does not affect on the mycelial growth and fruiting	Tan, Chang. (1989) [93]
<i>L. tigrinus</i>	kinetin	400 mg/l	Stimulates fruiting	Sladky, Tichy (1974) [95]
<i>L. tigrinus</i>	kinetin	100–400 mg/l	Stimulates growth	Mayr et al. (1984) [54]
<i>A. arvensis</i>	kinetin	100–400 mg/l	Stimulates growth	Mayr et al. (1984) [54]

1	2	3	4	5
<i>Phol. destruens</i>	kinetin	0.001 mg/l 10; 1; 0,01 mg/l	Stimulates growth Inhibits growth and biomass yield	Krishna, Sharma (1989) [97]
Complex growth regulators				
<i>A. bisporus</i>	Biolan	10000 mg/l	Increases productivity	Myronycheva, Ponomarenko (2010) [86]
<i>A. bisporus</i>	Emistim C	1000 mg/l	Increases productivity	Myronycheva, Ponomarenko (2010) [86]
<i>P. ostreatus</i> , <i>P. pulmonarius</i> , <i>P. eryngii</i>	Biohumate	1–100 mg/l	Stimulates growth and fruiting	Kuzneczova (2013) [100]
<i>P. ostreatus</i>	Fumar	1–100 mg/l	Stimulates growth	Kuzneczova (2011) [87]

*Note: the data given in concentrations M/l [88, 89], ppm [93–95, 97], % [86, 92] are listed by us and given in the table in the same units — mg/l.

L. tigrinus and *A. arvensis*, high concentrations of auxins — 100–400 mg/l proved to stimulate growth and fruiting [54, 95]. Guo, Zou, and Sun (2009) determined that low concentrations of different types of auxins: from 1 to 5 mg/l stimulated growth, biomass accumulation and synthesis of the exopolysaccharides of *Phel. linteus* [96]. It was also shown that IAA in the amount of 0.001 mg/l stimulated the growth of *Phol. destruens*, and at higher concentrations — inhibited it [97]. For *Calvatia gigantea*, *C. booniana*, *C. craniiformis* the growth stimulation was caused by auxin concentrations of 0.05 and 0.5 mg/l, and a concentration of 5.0 mg/l inhibited the growth of the fungus [98]. Summarizing the above, it can be noted that the effect of auxins on the growth and development of each of these species of basidiomycetes is different and the general patterns of this effect are not observed.

Characterizing the data on the effect on growth and development of different species of basidiomycetes growth stimulators of the gibberellin group, it can be noted that low concentrations of GA₃ — from 0.001 to 50 mg/l — stimulated the growth and fruiting of *L. edodes* [93,94], *P. ostreatus* [91], *A. bisporus*, *B. edulis*, *Suil. grevillei* [70], *Phol. destruens* [97], *Calvatia gigantea*, *C. booniana*, *C. craniiformis* [98]. In contrast to most reports, Jauhri and Sen (1978) showed that GA₃ concentrations of 0.2–2.0 mg/l did not affect on the growth of *P. ostreatus* [99]. High concentrations of GA₃ (100–400 mg/l) as stimulating of growth and fruiting, were

determined for *L. edodes* [93], *L. tigrinus* [95], *P. ostreatus* [90, 91]. At the same time, Mayr et al. (1984) noted that such concentrations of gibberellin did not affect the growth of *L. tigrinus* and *A. arvensis* [54]. That is, it can be stated that different authors provide extremely contradictory information on the effect on the growth of fungi of the same species of different concentrations of GA₃, for example, *P. ostreatus*, *L. edodes*, *L. tigrinus*.

Among the hormones of the cytokinin group, the effect on the growth and development of higher basidiomycetes of kinetin was more often studied. The data in Table 1 show that kinetin at concentrations of 5–300 mg/l did not affect on the growth and fruiting of *L. edodes* [93], inhibited the growth of *V. volucaeae* [67] and at concentrations of 0.01–10 mg/l inhibited the growth and biomass yield *Phol. destruens* [97]. At the same time, it was shown that at low concentrations (0.001–20 mg/l) of kinetin stimulated the growth of *Calvatia gigantea*, *C. booniana*, *C. craniiformis* [98], *P. ostreatus* [88, 89, 91], *Phol. destruens* [97]. High concentrations of kinetin (100–400 mg/l) promoted growth acceleration [90] and reduction of the lag phase of *P. ostreatus* [88, 89], stimulation of growth and fruiting of *A. arvensis* [54], *L. tigrinus* [54, 95]. Thus, information of the effect of kinetin on the growth and development of basidiomycetes does not allow reaching a definite conclusion as well. For example, for *P. ostreatus* the positive effect of kinetin is defined in a wide range: from 0.001 to 200 mg/l [88–91]. *L. edodes*

[93] is generally indifferent to the action of kinetin according to the literature, and on the growth of *L. tigrinus* is affected only by high concentrations of phytohormone [54, 95].

Summarizing the analysis of the literature on the exogenous effects of phytohormones on the growth and development of basidiomycetes, it should be noted that they do not make it possible to identify any regularities regarding the effective concentrations of growth regulators, even for some species of fungi, which have been the subject of many studies. For example, for *P. ostreatus* completely different concentrations of certain phytohormones that stimulate the growth of the fungus are indicated (Table). It remains unclear which hormone and on which phase of the vegetative growth of the fungus it affects: lag phase, exponential growth phase, stationary growth phase — and whether it affects the appearance of primordia, accelerates fruiting, or affects the overall yield.

The reasons for the identified conflicting data may be, in our opinion, the following:

1) the use by researchers of various methods of cultivation of fungi (surface on agar and liquid media, submerged cultivation, solid-phase on the substrate, etc.);

2) the use for the study of different composition of nutrient media (with different sources of carbon and nitrogen);

3) the introduction of growth stimulants into the nutrient medium using various sterilization methods;

4) the determination of stimulation or inhibition of fungal growth by various criteria (mycelial growth rate, biomass accumulation, yield, etc.).

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ДЛЯ ПРИРОДНИХ ТА СИНТЕТИЧНИХ ФІТОГОРМОНІВ НА РІСТ ТА РОЗВИТОК ВИЩИХ БАЗИДІАЛЬНИХ ГРИБІВ

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Проаналізовано дані літератури щодо вивчення впливу екзогенних рiстрегуляторiв на рiст та розвиток вищих базидіоміцетiв. Подано історичні відомості про відкриття фітогормонiв та їхню роль у грибах. Наведено види базидіальних грибiв, здатних синтезувати фітогормони всіх вiдомих типiв. Серед представникiв класу *Basidiomycetes* — гриби порядкiв *Aphyllorphorales*, *Boletales*, *Agaricales*, *Sclerodermales*, *Hymenogastrales*, *Uredinales*, *Ustilaginales*. Систематизовано та зiставлено дані рiзних авторiв стосовно впливу природних i синтетичних стимуляторiв росту на розвиток базидіоміцетiв. Вiдзначено, що науковцi використовували рiзноманiтнi концентрацiї фітогормонiв (ауксинiв, гiберелiнiв, цитокiнiнiв) для вивчення їхньої дiї на мицеліальний рiст: вiд 0,01 до 400 мг/л. Обговорюютьсi можливі причини суперечливих даних, отриманих рiзними дослідникaми, зокрема, застосування рiзних методiв культивування грибiв, живильних середовищ, методiв стерилізацiї субстратiв та iн.

Ключові слова: вищі базидіальні гриби, фітогормони, ауксини, гiберелiни, цитокiнiни, стимуляцiя росту та розвитку.

ДЕЙСТВИЕ ПРИРОДНЫХ И СИНТЕТИЧЕСКИХ ФИТОГОРМОНОВ НА РОСТ И РАЗВИТИЕ ВЫСШИХ БАЗИДИАЛЬНЫХ ГРИБОВ

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Проанализированы данные литературы по изучению влияния экзогенных рострегуляторов на рост и развитие высших базидиомицетов. Представлены исторические сведения об открытии фитогормонов и их роли у грибов. Приведены виды базидиальных грибов, способных синтезировать фитогормоны всех известных типов. Среди представителей класса *Basidiomycetes* — грибы порядков *Aphyllorphorales*, *Boletales*, *Agaricales*, *Sclerodermales*, *Hymenogastrales*, *Uredinales*, *Ustilaginales*. Систематизированы и сопоставлены данные разных авторов о влиянии природных и синтетических стимуляторов роста на развитие базидиомицетов. Отмечено, что ученые использовали различные концентрации фитогормонов (ауксинов, гибберелинов, цитокининов) для изучения их действия на мицелиальный рост: от 0,01 до 400 мг/л. Обсуждаются возможные причины противоречивых данных, полученных разными исследователями, в частности, применение различных методов культивирования грибов, питательных сред, методов стерилизации субстратов и др.

Ключевые слова: высшие базидиальные грибы, фитогормоны, ауксини, гибберелины, цитокинины, стимуляция роста и развития.