Asian Journal of Mycology 9(1): 403–413 (2026) ISSN 2651-1339
www.asianjournalofmycology.org

Article
Doi 10.5943/ajom/9/1/15

Effects of caffeic acid and hispidin on the light emission intensity of mycelia and luminescent systems of the *Neonothopanus nambi* and *Armillaria borealis* basidiomycetes

Ronzhin NO[1], Posokhina ED[1], Le VM[2], Mogilnaya OA[1], Zakharova YuV[3], Baron AV[1], Sukhikh AS[2] and Bondar VS[1]

[1]Institute of Biophysics, Siberian Branch of Russian Academy of Science, Federal Research Center "Krasnoyarsk Science Center SB RAS", 660036 Krasnoyarsk, Russia
[2]Kemerovo State University, 650000 Kemerovo, Russia
[3]Kemerovo State Medical University, 650056 Kemerovo, Russia

Ronzhin NO, Posokhina ED, Le VM, Mogilnaya OA, Zakharova YuV, Baron AV, Sukhikh AS, Bondar VS. 2026 – Effects of caffeic acid and hispidin on the light emission intensity of mycelia and luminescent systems of the *Neonothopanus nambi* and *Armillaria borealis* basidiomycetes. Asian Journal of Mycology 9(1), 403–413, Doi 10.5943/ajom/9/1/15

Abstract

The past decade has seen major advances in research of fungal bioluminescence; however, some biochemical aspects of this phenomenon remain insufficiently understood and need to be studied more thoroughly. In fungi, caffeic acid is a precursor to hispidin, and hispidin, in turn, is a precursor to fungal luciferin. The aim of this work was to study the effects of caffeic acid and hispidin on the intensity of fungal bioluminescence *in vivo* and *in vitro*. *In vivo* experiments demonstrated that caffeic acid stimulates luminescence of mycelia in the basidiomycetes *Neonothopanus nambi* and *Armillaria borealis*, increasing the intensity of light emission by at least one order of magnitude. The rapid increase in the level of luminescence in mycelia upon the addition of caffeic acid suggests that this compound interacts with extracellular fungal enzymes, which are located on the surface or within the surface structures of the basidiomycete cell wall. It is hypothesized that the activation of fungal luminescence *in vivo* may be caused by the oxidation of caffeic acid by ligninolytic oxidases of basidiomycetes (peroxidases, in particular), resulting in the generation of visible light quanta. In contrast, the *in vivo* study showed that the addition of hispidin, a known precursor of luciferin in the light emission reaction in higher fungi, did not change the level of light emission in *N. nambi* and *A. borealis* mycelia. *In vitro* experiments demonstrated that caffeic acid did not affect the intensity of light emission in the enzymatic luminescent systems extracted from *N. nambi* and *A. borealis* mycelia in the presence of NADPH, and considerably inhibited NADPH-hispidin-activated light emission in these systems. Results obtained in the current study give new insights into the mechanisms of light emission in higher fungi and suggest that generation of visible light quanta in basidiomycetes can occur via different biochemical pathways, involving various enzymes and substrates.

Keywords – luminescent higher fungi – mycelium – fungal luminescent systems – caffeic acid – hispidin – reduced pyridine nucleotide – mechanisms of fungal luminescence

Submitted 8 May 2024, Accepted 21 April 2026, Published 18 May 2026
Corresponding Author: Nikita O. Ronzhin – e-mail – roniol@mail.ru

Introduction

The ability to emit visible light is demonstrated by numerous species of higher fungi (Shimomura 2006, Desjardin et al. 2008, Bondar et al. 2012). Over 100 species of basidiomycetes that are capable of bioluminescence – light emission visible in the dark – have been reported by now (Ke & Tsai 2022). Luminescent basidiomycetes have been found in different regions of the world – North and South America, Europe, Asia, Australia, and Africa (Desjardin et al. 2010, 2016, Chew et al. 2014, 2015, Mihail 2015, Puzyr et al. 2016). Yet, luminescent higher fungi occur most frequently in the subtropical and tropical regions – the most favorable environments for their growth and development.

Luminescent basidiomycetes are white-rot fungi capable of lignin degradation (Desjardin et al. 2008) and typically occur as saprophytes, less frequently as pathogens of plants (Shimomura 2006, Ke & Tsai 2022). A number of authors showed that in different stages of their life cycle, basidiomycetes emit greenish light with the emission peak between 520 and 530 nm (Endo et al. 1970, Lavelle et al. 1972, O'Kane et al. 1990, Shimomura 2006, Desjardin et al. 2008, Bondar et al. 2012, Kobzeva et al. 2014). In some of the species of higher fungi, the entire fruiting bodies emit light (Brandl 2011, Vydryakova et al. 2012, Oliveira et al. 2015), while in other species, only the caps or stipes glow (Desjardin et al. 2007, 2008, Teranishi 2016). In *Armillaria* species, only mycelium and rhizomorphs are luminescent (Harvey 1952, Wassink 1978, Desjardin et al. 2008, Mihail 2013, 2015).

The past decade has seen major advances in research of fungal bioluminescence (Bondar et al. 2014, Purtov et al. 2015, Oba et al. 2017, Kaskova et al. 2017, Puzyr et al. 2017, 2019, Teranishi 2017, Kotlobay et al. 2018, Garcia-Iriepa et al. 2020, Ronzhin et al. 2022). Some biochemical aspects of this phenomenon, though, remain insufficiently understood and need to be studied more thoroughly. It is now well established that the precursor of luciferin in higher luminescent fungi is their secondary metabolite – hispidin (Purtov et al. 2015). Purtov et al. (2015) showed that in the presence of oxygen and NADPH, hispidin is hydroxylated by an NADPH-dependent hydroxylase to form luciferin (3-hydroxyhispidin), which is subsequently oxidized by insoluble luciferase, generating a light quantum. This two-step mechanism of luciferin–luciferase reaction, which is responsible for *in vitro* bioluminescence, was originally proposed in the mid-20th century based on experiments with the "cold" and "hot" extracts of luminous fungi (Airth & McElroy 1959, Airth & Foerster 1962, 1964) and has since been confirmed in studies conducted (Oliveira & Stevani 2009, Oliveira et al. 2012).

Despite these advances, it is still unclear what enzyme (or group of enzymes) functions as luciferase in luminescent higher fungi, as it has not been isolated in pure form or fully characterized. Moreover, it remains unclear whether 3-hydroxyhispidin is the only substrate (luciferin) of the bioluminescent reaction and whether the luciferin–luciferase reaction represents the only biochemical pathways responsible for light emission in higher fungi.

Recent studies have suggested the involvement of additional metabolites in fungal bioluminescence. Oxidation of 3-hydroxyhispidin catalyzed by luciferase produces unstable high-energy intermediate emitting a light quantum and yielding oxyluciferin, which is then transformed by caffeylpyruvate hydrolase into 3,4-dihydroxycinnamic (caffeic) acid (Kotlobay et al. 2018). In turn, caffeic acid is converted by hispidin synthase to hispidin – precursor of luciferin (Mitiouchkina et al. 2020). The studies of living pileus gills of the luminous fungus *Mycena chlorophos* revealed two bioluminescence-activating components, trans-4-hydroxycinnamic acid (*p*-coumaric acid) and trans-3,4-dihydroxycinnamic acid (caffeic acid), rapidly increased the intensity of *in vivo* light emission by living pileus gills (Teranishi 2016, 2017). Biotransformation of the bioluminescence-activating components found in pileus gills of the fungus *M. chlorophos* was investigated in ^{13}C- and ^{18}O-labelling studies, which showed that caffeic acid is synthesized from *p*-coumaric acid, but it does not serve as a precursor for hispidin (Teranishi 2017). In that study, additional experiments demonstrated that hispidin supplementation did not affect the intensity of bioluminescence of living pileus gills. Thus, the results of these studies may suggest that the bioluminescence in luminous fungi is realized not only due to the hydroxylase-luciferase

mechanism using hispidin, but also due to some other mechanism using caffeic acid. However, following the published studies on *M. chlorophos* pileus gills, there are currently no follow-up studies investigating whether similar effects occur in other species of luminous fungi or in other parts of luminous fungus. The aim of our work was to study the effects of caffeic acid and hispidin on the bioluminescence in living fungal mycelia of two various species of higher fungi (*Neonothopanus nambi* and *Armillaria borealis*), as well as in enzymatic luminescent systems isolated from them.

Materials & Methods

Materials and reagents

Mycelia of the luminescent basidiomycetes *N. nambi* (strain IBSO 2391) and *A. borealis* (strain IBSO 2328) were used. The strains are maintained in the Collection of Microorganisms CCIBSO 836 at the Institute of Biophysics of the Federal Research Center "Krasnoyarsk Scientific Center", Siberian Branch of the Russian Academy of Sciences (Krasnoyarsk).

Experiments were carried out using spherical mycelial pellets 2–7 mm in diameter, which had been produced by submerged cultivation of the fungi in PDB (Mogilnaya et al. 2017, 2018). Ready-to-use nutrient medium PDB (potato extract 200 g/L, dextrose 20 g/L), which was purchased from HiMedia Laboratory (India), was used to cultivate fungal mycelia. The prepared liquid medium was autoclaved at 120 °C for 15 min before use.

High quality hispidin, NADPH, and caffeic acid (Sigma-Aldrich, USA) were used in the comparative studies *in vivo* and *in vitro*. The 20 mM stock solution of hispidin was prepared in methanol (Serva, Germany); it was stored at a temperature of –20 °C until use. The 33 μM hispidin solution for experiments was prepared *in situ* by successive dilution of the stock solution with deionized (DI) water (Milli-Q system, Millipore, USA). The aqueous solutions of NADPH (5 mM) and caffeic acid (16.5 μM to 1.65 mM) were also prepared *in situ* using DI water.

Bioluminescence measuring

The study of the effects of caffeic acid and hispidin on the light emission of mycelia and luminescent systems of the *N. nambi* and *A. borealis* basidiomycetes was carried out using a Glomax® 20/20 luminometer (Promega, USA). Luminescence signal intensity and dynamics were measured in the mode of one measurement per second. The luminescence values were expressed in arbitrary units. Each measurement experiment (*in vivo* and *in vitro*) was carried out in at least five replicates.

Cultivation and processing

Neonothopanus nambi and *A. borealis* mycelium films grown in Petri dishes on PDA medium for 8–9 days and 14–16 days, respectively, were crushed and used as inoculums for submerged cultivation of the fungi. The volume of the inoculum was 2–5% of the broth volume. The fungi were cultivated in 300-ml flasks containing 100 ml PDB nutrient medium, at a temperature of 25 °C and 27 °C (for *N. nambi* and *A. borealis*, respectively) and continuous agitation at 160–180 rpm using an Environmental Shaker-Incubator ES-20 (Biosan, Latvia). Mycelial biomass of *N. nambi* and *A. borealis* was grown for 7–8 days and 13–14 days, respectively. Then, the mycelial pellets were taken out of the nutrient medium and washed in DI water several times to remove nutrient medium and metabolites. After that, the pellets were placed into a large volume of DI water and incubated at 22–24 °C for 24 h to remove residual nutrient medium and metabolites. After incubation, the pellets of *N. nambi* and *A. borealis* mycelium were used in the *in vivo* study and for preparing "cold" extracts containing enzymatic luminescent systems of the fungi for *in vitro* experiments.

Extracting the enzyme luminescent systems

Extraction of enzymatic luminescent systems was performed at a temperature between 0 and 4 °C. *Neonothopanus nambi* (or *A. borealis*) mycelial pellets were rubbed through a 1-mm mesh metal sieve. The crushed biomass was transferred to a beaker placed in an ice bath, and a cooled 0.1 M phosphate buffer solution (pH 7.0) containing 1% BSA (Serva, Germany) was added at a ratio of 1:5 (biomass volume: buffer volume). The resulting suspension was treated with ultrasound using a Volna USTD-0.63/22 device (U-Sonic, Russia). The sonication was performed thrice, each time for 10 s with 1-min intervals. Then, the homogenate was centrifuged at 40000g for 30 min at 4 °C using an Avanti® J-E centrifuge (Beckman-Coulter, U.S.A.). The sediment was discarded, and the supernatant ("cold" extract) containing the enzymes of the luminescence reaction was collected and used in the study.

Testing the effects of caffeic acid and hispidin *in vivo*

The effects of caffeic acid and hispidin on luminescence of *N. nambi* and *A. borealis* basidiomycetes were estimated *in vivo* as follows: Individual mycelial pellets were placed into 1.5-ml transparent plastic tubes (Eppendorf, Germany) containing 300 µl of DI water each. The tubes were placed into the measuring chamber of a Glomax® 20/20 luminometer, and the initial pellet luminescence level was measured. Then, 5 µl of a caffeic acid (or hispidin) solution was carefully added into the test tubes (without stirring), and the light signal intensity and dynamics were measured again.

Testing the effects of caffeic acid and hispidin *in vitro*

The effects of caffeic acid and hispidin on light emission of the enzymatic luminescent systems extracted from *N. nambi* and *A. borealis* mycelia were estimated in the *in vitro* experiments in the same manner as it was described previously (Ronzhin et al. 2025). Samples of "cold" extracts containing enzymatic luminescent system of *N. nambi* (or *A. borealis*) were transferred to 1.5-ml transparent plastic tubes (Eppendorf) (50 µl per tube). The tubes were placed into the measuring chamber of the Glomax® 20/20 luminometer, and the initial light emission level of the extracts was measured. Then, 5 µl of a NADPH solution was added, and the light emission intensity and dynamics were measured again. The light signals recorded after addition of NADPH show that the samples of the "cold" extracts from the *N. nambi* and *A. borealis* mycelia contain endogenous hispidin, which is utilized in the light emission reaction and is indicative of the functional activity of the enzymes of luminescent systems. After the light signal initiated by the addition of NADPH declined to the stationary level, 5 µl of caffeic acid or hispidin solutions were added to the samples to estimate their effect on the light emission of the luminescent systems. In additional experiments, after light emission of the luminescent systems was activated by the addition of NADPH and hispidin to the samples of "cold" extracts and the light signals reached their maximal levels, 5 µl of a caffeic acid solution was added to the samples, and its effect was estimated from changes in the luminescence intensity and dynamics.

Results & Discussion

The stages of the present study are shown schematically in Figure 1. The major steps were submerged cultivation of the *N. nambi* and *A. borealis* fungi to produce mycelial pellets; washing of the pellets in DI water to remove residual nutrient medium and metabolites; extraction of enzymatic luminescent systems from the mycelial biomass; and a study of the effects of caffeic acid and hispidin on luminescence of the mycelial pellets *in vivo* and the extracted luminescent systems *in vitro*.

Our experiments demonstrated that submerged cultivation of the *N. nambi* and *A. borealis* fungi under the conditions used in this study (the nutrient medium volume, inoculum volume, the velocity of the continuous radial mixing of the culture medium, and cultivation temperature and duration) resulted in the growth of mycelium in the form of 2- to 7-mm-diameter spherical pellets

(Fig. 2). These data are consistent with the results of our previous studies on submerged cultivation of fungal mycelium (Mogilnaya et al. 2017, 2018). The *N. nambi* and *A. borealis* mycelial pellets had rough surface created by numerous hyphae (Fig. 2). Mycelium in the form of spherical pellets has certain advantages as material for *in vivo* studies: individual pellets can be conveniently transferred using a lab spatula from one liquid medium to another and placed into separate test tubes. These manipulations produce very little physical impact on the fungus and do not damage it.

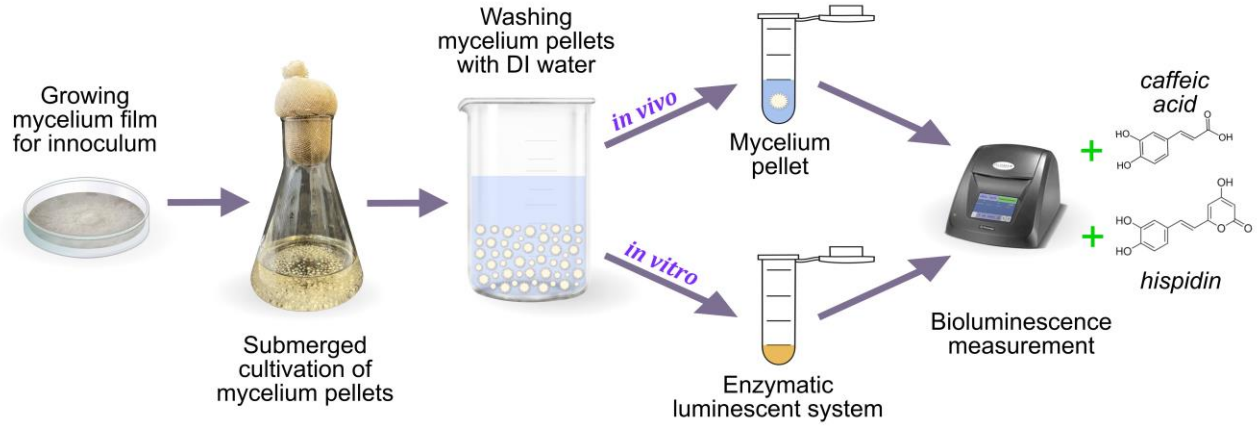

Fig. 1 – A schematic representation of the main steps for producing mycelial pellets and *in vivo* and *in vitro* studies.

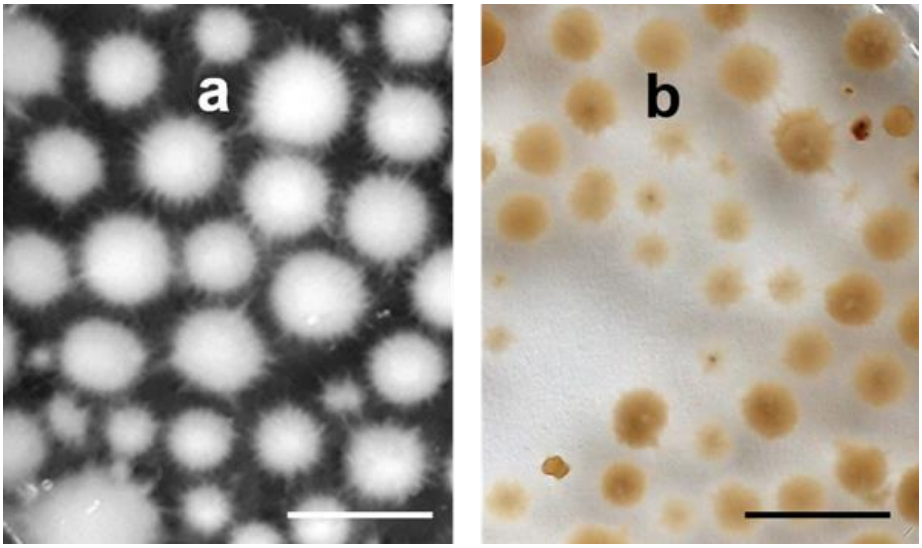

Fig. 2 – Morphology of mycelial pellets of *N. nambi* (a) and *A. borealis* (b) produced by submerged cultivation technology. Bars = 10 mm (a, b).

The *in vivo* study revealed that the addition of caffeic acid to the luminescent mycelial pellets of *N. nambi* and *A. borealis* rapidly enhanced their light emission, which reached levels at least one order of magnitude higher than their initial luminescence (Fig. 3). The increase in the level of luminescence of the pellets was recorded within one minute after the addition of caffeic acid. Our experiments showed that the light-stimulating effect of caffeic acid was dose-dependent, increasing with an increase in the caffeic acid concentration in the sample from 275 nM to 27.5 µM. That was supported by the peak values of pellet luminescence in treatments with different amounts of caffeic acid added to the samples and the areas under the curves of the recorded luminescent signals, which corresponded to the overall quantum yield. At the same time, the *in vivo* comparative experiments demonstrated that the addition of hispidin (at a concentration of 0.55 µM in the samples) to the

luminescent mycelial pellets of the *N. nambi* and *A. borealis* basidiomycetes did not cause any noticeable changes in their light emission (Fig. 4).

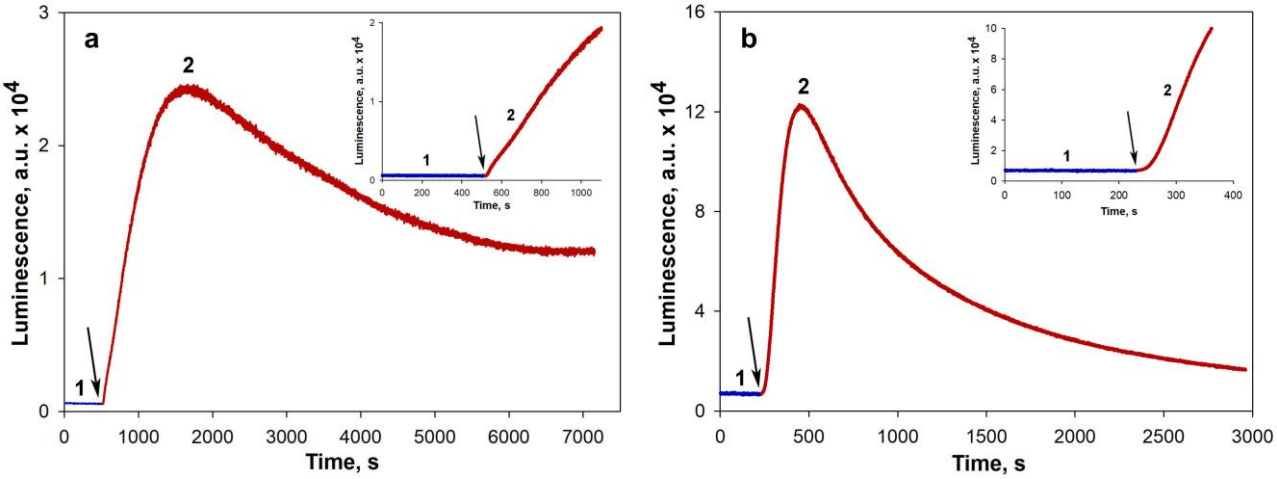

Fig. 3 – Stimulation of luminescence of *N. nambi* (a) and *A. borealis* (b) mycelial pellets by caffeic acid: 1 – initial level of pellet luminescence, 2 – intensity and dynamics of luminescence of the pellets after addition of caffeic acid. Arrows denote time points at which the substance was added to the samples (caffeic acid concentration in the samples 0.55 μM). The insets show the fragments of dynamics of light signals in the initial period of time after addition of caffeic acid.

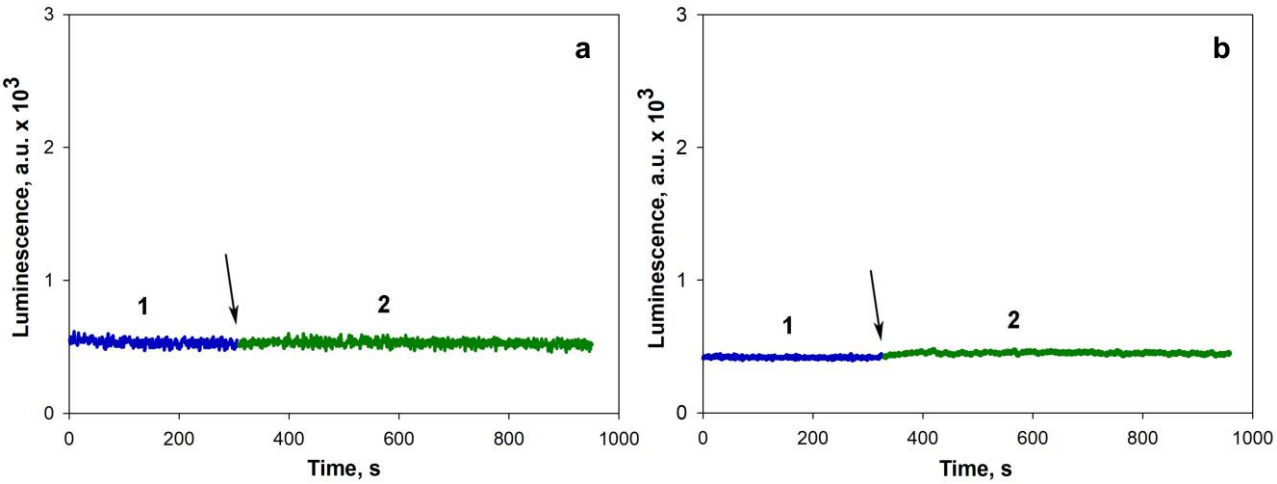

Fig. 4 – Intensity and dynamics of luminescence of *N. nambi* (a) and *A. borealis* (b) mycelial pellets after addition of hispidin: 1 – initial level of pellet luminescence, 2 – the level of light emission by the pellets after addition of hispidin. Arrows denote time points at which the substance was added to the samples (hispidin concentration in the samples 0.55 μM).

The effects of caffeic acid observed in our *in vivo* study with luminescent mycelial pellets of the higher fungi *N. nambi* and *A. borealis* (Fig. 3) are in good agreement with the data on caffeic acid activating light emission of living pileus gills of the fungus *M. chlorophos* (Teranishi 2017). These findings suggest that the luminescence-stimulating effect of caffeic acid may be common to all types of bioluminescent basidiomycetes. The rapid (within one minute) development of luminescent signals upon the addition of caffeic acid to *N. nambi* and *A. borealis* mycelial pellets (Fig. 3) suggests that caffeic acid likely interacts with extracellular enzymes or enzymatic systems, such as ligninolytic oxidases, which are located on the surface or within surface structures of the fungal cell wall. Thus, we propose the hypothesis, which needs to be verified further, that *in vivo* activation of fungal luminescence may result from the oxidation of caffeic acid by ligninolytic

oxidases (peroxidases, in particular) of basidiomycetes, resulting in the generation of visible light quanta. On the other hand, hispidin did not stimulate light emission in *N. nambi* and *A. borealis* mycelial pellets (Fig. 4), suggesting that absence of enzymes involved in the transformation of hispidin into luciferin and its subsequent oxidation with the emission of light quanta, at the cell surface or within the structural elements of the cell wall in these basidiomycetes. The results obtained in the current study (Fig. 3 and 4) indicate that *N. nambi* and *A. borealis* have an additional biochemical mechanism of light emission involving interactions between the extracellular oxidases of the fungi and caffeic acid, which differs from the intracellular fungal luminescence pathway, mediated by the NADPH-dependent hydroxylase–luciferase enzymatic system and hispidin.

In vitro experiments with the "cold" extracts from the biomass of *N. nambi* and *A. borealis* mycelia, which contained the enzymatic luminescent systems of these basidiomycetes, showed that the addition of NADPH led to an increase in the level of the light emission of the extracts (Fig. 5). The light signals recorded after the addition of NADPH indicated that the "cold" extracts contained endogenous hispidin, which is utilized in the light emission reaction catalyzed by the NADPH-dependent hydroxylase–luciferase luminescent system. At the same time, the occurrence of the light signals after the addition of the reduced pyridine nucleotide suggests that the functional activity of the enzymes of both luminescent systems responsible for the light emission reaction *in vitro*. This conclusion is further supported by the levels of light emission observed in extracts supplemented with both NADPH and hispidin, the precursor of the fungal luciferin (Fig. 5). Successive additions of NADPH and hispidin to "cold" extracts caused the generation of luminescent signals with amplitudes at least two orders of magnitude higher than those recorded in extracts supplemented with NADPH alone.

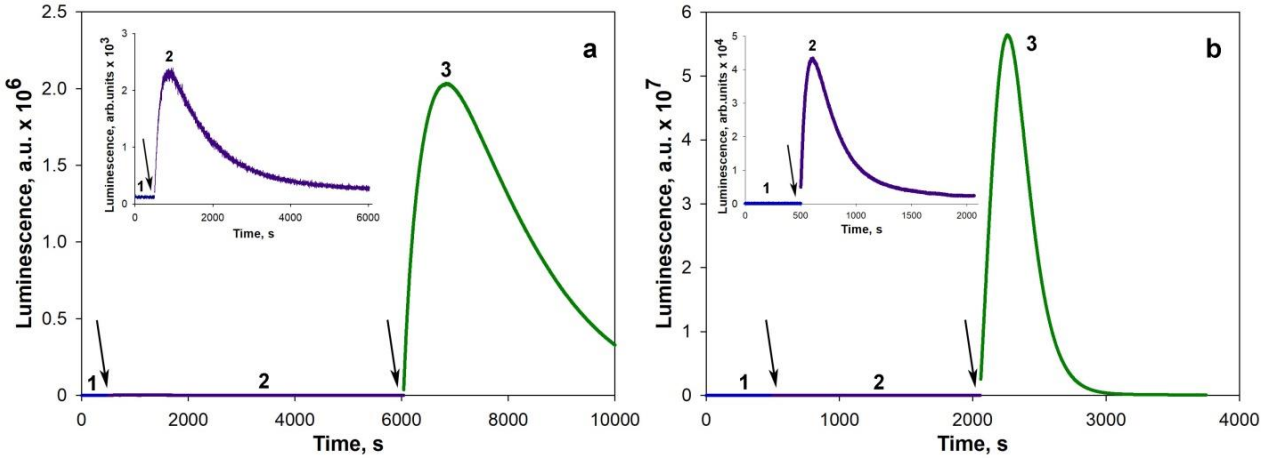

Fig. 5 – Stimulation of light emission of the enzymatic luminescent systems from the *N. nambi* (a) and *A. borealis* (b) mycelia by NADPH and hispidin added successively to "cold" extracts: 1 – initial luminescence level of the systems, 2 – light emission intensity and dynamics after addition of NADPH (at a concentration in the samples of 0.5 mM), 3 – amplitude and dynamics of light signals after addition of hispidin (at a concentration in the samples of 3.3 μM). Arrows denote time points at which NADPH and hispidin were added to the samples. The insets show light signals recorded after addition of NADPH.

Comparative *in vitro* experiments demonstrated that the addition of caffeic acid to "cold" extracts of *N. nambi* and *A. borealis* mycelia that had been preliminarily supplemented with NADPH did not cause any noticeable changes in the levels of light emission of the extracts (Fig. 6). On the one hand, these results suggest that, under the experimental conditions of the present study, caffeic acid is neither transformed into hispidin by the enzymes in the presence of the "cold" extract enzymes nor oxidized to generate light quanta. On the other hand, results of *in vitro* experiments support the hypothesis proposed above that the generation of visible light quanta in

luminescent basidiomycetes may proceed via distinct biochemical mechanisms involving different substrates (caffeic acid and hispidin, in our study) and various enzymes or enzymatic systems.

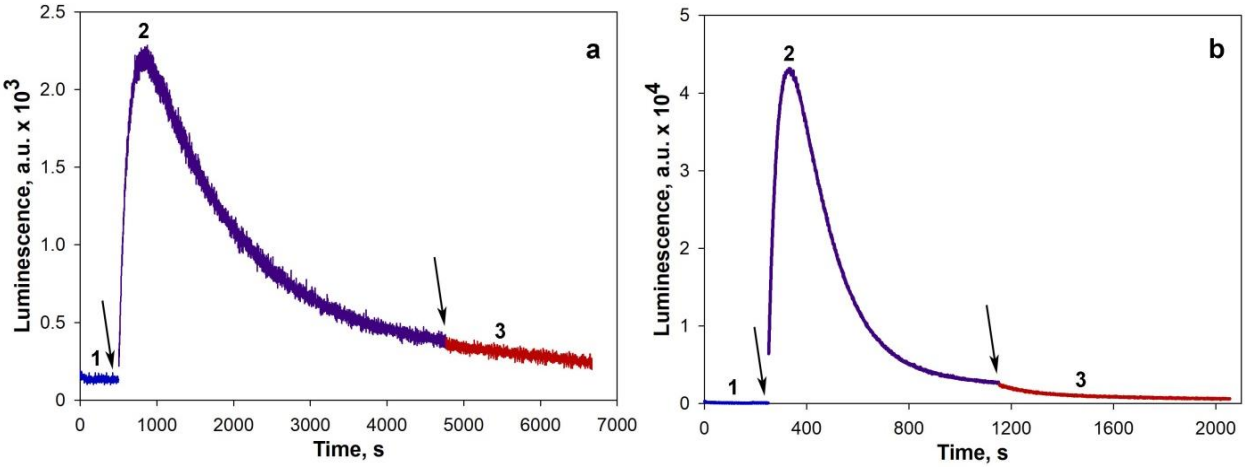

Fig. 6 – Intensity and dynamics of light emission of enzymatic luminescent systems from *N. nambi* (a) and *A. borealis* (b) mycelia under successive supplementation of the "cold" extracts with: 1 – NADPH (at a concentration in the samples of 0.5 mM), 2 – caffeic acid (at a concentration in the samples of 3.3 μM). Arrows denote time points at which NADPH and caffeic acid were added to the samples.

Additional *in vitro* study revealed that caffeic acid considerably inhibited the intensity of light signals from the enzymatic luminescent systems of *N. nambi* and *A. borealis* activated by NADPH and hispidin (Fig. 7). In addition, the inhibitory effect of caffeic acid on light emission was dose-dependent, with increasing concentrations of caffeic acid in the samples leading to progressively lower light emission intensities. Inhibition of light emission from the enzymatic luminescent systems of basidiomycetes can be explained in terms of classical biochemistry, as it is consistent with product inhibition operating through a negative feedback mechanism. This mechanism provides a logical explanation for the effects of caffeic acid observed in the current study, as caffeic acid represents the end product of hispidin transformation during light emission of higher fungi (Kotlobay 2018, Mitiouchkina et al. 2020).

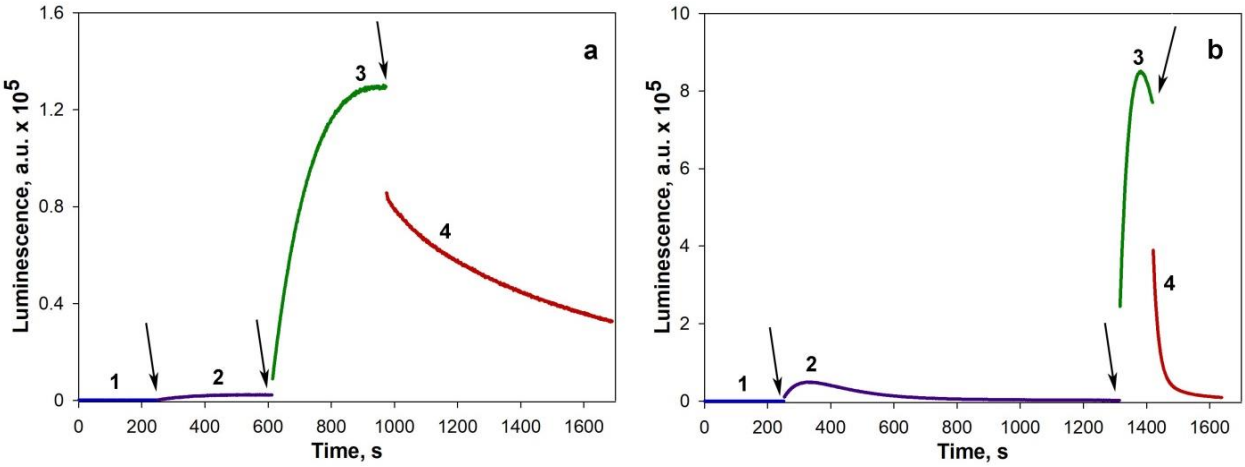

Fig. 7 – Inhibitory effect of caffeic acid on light emission of luminescent systems from *N. nambi* (a) and *A. borealis* (b) mycelia activated by NADPH and hispidin: 1 – initial level of luminescence of "cold" extracts, 2 – the level of light emission after addition of NADPH (at a concentration in the samples of 0.5 mM), 3 – intensity and dynamics of the light signal after addition of hispidin (at

a concentration in the samples of 3.3 μM), 4 – dynamics of the light signal after addition of caffeic acid (at a concentration in the samples of 0.1 mM). Arrows denote time points at which the substances were added to the samples.

Conclusions

The *in vivo* and *in vitro* studies on the effects of caffeic acid and hispidin on the levels of light emission from mycelia and enzymatic luminescent systems of the luminescent basidiomycetes *N. nambi* and *A. borealis* offer a fresh insight into the mechanisms of bioluminescence in higher fungi. Results of the present study suggest that the generation of visible light quanta in basidiomycetes may occur via different biochemical pathways involving various enzymes (and enzymatic systems) and distinct substrates. Specifically, generation of visible light quanta in basidiomycetes can occur due to the functioning of the NADPH-dependent hydroxylase–luciferase intracellular system in the presence of hispidin, and, apparently, from reactions mediated by extracellular ligninolytic oxidase enzymes (peroxidases, in particular) in the presence of caffeic acid. Therefore, the recorded (and visible) luminescence of higher fungi can be considered an integrated indicator of the functional activity of multiple enzymatic systems. Further studies aimed at validating the proposed hypothesis in the present work and identifying the specific ligninolytic oxidases of basidiomycetes responsible for catalyzing oxidation of caffeic acid with the generation of visible light quanta will be a major priority of our future research.

Acknowledgements

The study was funded by State Assignment of the Ministry of Science and Higher Education of the Russian Federation (project No. FWES-2024-0018).

References

Airth RL, McElroy WD. 1959 – Light emission from extracts of luminous fungi. Journal of Bacteriology 77, 249–250.

Airth RL, Foerster GE. 1962 – The isolation of catalytic components required for cell-free fungal bioluminescence. Archives of Biochemistry and Biophysics 97, 567–573.

Airth RL, Foerster GE. 1964 – Enzymes associated with the bioluminescence of *Panus stipticus* luminescens and *Panus stipticus* non-luminescens. Journal of Bacteriology 88, 1372–1379.

Bondar VS, Shimomura O, Gitelson JI. 2012 – Luminescence of higher mushrooms. Journal of Siberian Federal University Biology 5, 331–351.

Bondar VS, Puzyr AP, Purtov KV, Petunin AI, et al. 2014 – Isolation of luminescence system from the luminescent fungus *Neonothopanus nambi*. Doklady Biochemistry and Biophysics 455, 56–58.

Brandl H. 2011 – Luminescent wood in coal and ore mines – A historical review. Fungi Magazine 4, 5–9.

Chew ALC, Tan YS, Desjardin DE, Musa MY, Sabaratnam V. 2014 – Four new bioluminescent taxa of *Mycena* sect. Calodontes from peninsular Malaysia. Mycologia 106, 976–988.

Chew ALC, Desjardin DE, Tan YS, Musa MY, Sabaratnam V. 2015 – Bioluminescent fungi from Peninsular Malaysia – a taxonomic and phylogenetic overview. Fungal Diversity 70, 149–187.

Desjardin DE, Capelari M, Stevani CV. 2007 – Bioluminescent *Mycena* species from Sao Paulo, Brazil. Mycologia 99, 317–331.

Desjardin DE, Oliveira AG, Stevani CV. 2008 – Fungi bioluminescence revisited. Photochemical and Photobiological Sciences 7, 170–182.

Desjardin DE, Perry BA, Lodge DJ, Stevani CV, Nagasawa E. 2010 – Luminescent *Mycena*: new and noteworthy species. Mycologia 102, 459–477.

Desjardin DE, Perry BA, Stevani CV. 2016 – New luminescent mycenoid fungi (Basidiomycota, Agaricales) from São Paulo State, Brazil. Mycologia 108, 1165–1174.
Endo M, Kajiwara M, Nakanishi K. 1970 – Fluorescent constituents and cultivation of *Lampteromyces japonicus*. Journal of the Chemical Society D: Chemical Communications 5, 309–310.
Garcia-Iriepa C, Losantos R, Fernandez-Martinez D, Sampedro D, et al. 2020 – Fungal light emitter: understanding its chemical nature and pH-dependent emission in water solution. The Journal of Organic Chemistry 85, 5503–5510.
Harvey EN. 1952 – Bioluminescence. Academic Press, New York.
Kaskova ZM, Dörr FA, Petushkov VN, Purtov KV, et al. 2017 – Mechanism and color modulation of fungal bioluminescence. Science Advances 3, e1602847.
Ke HM, Tsai IJ. 2022 – Understanding and using fungal bioluminescence – Recent progress and future perspectives. Current Opinion in Green and Sustainable Chemistry 33, 100570.
Kobzeva TV, Melnikov AR, Karogodina TY, Zikirin SB, et al. 2014 – Stimulation of luminescence of mycelium of luminous fungus *Neonothopanus nambi* by ionizing radiation. Luminescence 29, 703–710.
Kotlobay AA, Sarkisyan KS, Mokrushina YA, Marcet-Houben M, et at. 2018 – Genetically encodable bioluminescent system from fungi. Proceedings of the National Academy of Sciences 115, 12728–12732.
Lavelle MMF, Durosay P, Michelson AM. 1972 – Bioluminescence. Luminescence des champignons lumineux. Comptes Rendus de l'Académie des Sciences. Paris. Série D. 275, 1227–1230.
Mihail JD. 2013 – Comparative bioluminescence dynamics among multiple *Armillaria gallica*, *A. mellea*, and *A. tabescens*. Fungal Biology 117, 202–210.
Mihail JD. 2015 – Bioluminescence patterns among North American *Armillaria* species. Fungal Biology 119, 528–537.
Mitiouchkina T, Mishin AS, Somermeyer LG, Markina NM, et al. 2020 – Plants with genetically encoded autoluminescence. Nature Biotechnology 38, 944–946.
Mogilnaya OA, Ronzhin NO, Artemenko KS, Bondar VS. 2017 – Morphological properties and levels of extracellular peroxidase activity and light emission of the basidiomycete *Armillaria borealis* treated with β-glucosidase and chitinase. Mycosphere 8, 649–659.
Mogilnaya OA, Ronzhin NO, Bondar VS. 2018 – Estimating levels of light emission and extracellular peroxidase activity of mycelium of luminous fungus *Neonothopanus nambi* treated with β-glucosidase. Current Research in Environmental and Applied Mycology 8, 75–85.
Oba Y, Suzuki Y, Martins GNR, Carvalho RP, et al. 2017 – Identification of hispidin as a bioluminescent active compound and its recycling biosynthesis in the luminous fungal fruiting body. Photochemical and Photobiological Sciences 16, 1435–1440.
O'Kane DJ, Lingle WL, Porter D, Wampler JE. 1990 – Spectral analysis of the bioluminescence of *Panellus stipticus*. Mycologia 82, 607–616.
Oliveira AG, Stevani CV. 2009 – The enzymatic nature of fungal bioluminescence. Photochemical and Photobiological Sciences 8, 1416–1421.
Oliveira AG, Desjardin DE, Perry BA, Stevani CV. 2012 – Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages. Photochemical and Photobiological Sciences 11, 848–852.
Oliveira AG, Stevani CV, Waldenmaier HE, Viviani V, et al. 2015 – Circadian control sheds light on fungal bioluminescence. Current Biology 25, 1–5.
Purtov KV, Petushkov VN, Baranov MS, Mineev KS, et al. 2015 – The chemical basis of fungal bioluminescence. Angewandte Chemie International Edition 54, 8124–8128.
Puzyr AP, Medvedeva SE, Bondar VS. 2016 – The use of glowing wood as a source of luminescent culture of fungus mycelium. Mycosphere 7, 1–17.

Puzyr AP, Medvedeva SE, Artemenko KS, Bondar VS. 2017 – Luminescence of “cold” extracts from mycelium of luminous basidiomycetes during long-term storage. Current Research in Environmental and Applied Mycology 7, 227–235.
Puzyr AP, Burov AE, Medvedeva SE, Burova OG, et al. 2019 – Two forms of substrate for the bioluminescent reaction in three species of basidiomycetes. Mycology 10, 84–91.
Ronzhin NO, Posokhina ED, Mogilnaya OA, Bondar VS. 2022 – Finding the light emission stimulator of *Neonothopanus nambi* basidiomycete and studying its properties. Doklady Biochemistry and Biophysics 503, 80–84.
Ronzhin NO, Posokhina ED, Mogilnaya OA, Puzyr AP, et al. 2025 – The cytochrome P450 system is involved in the light emission of higher fungi. Asian Journal of Mycology 8(1), 25–36.
Shimomura O. 2006 – Bioluminescence: chemical principles and methods. World Scientific Publishing, Singapore.
Teranishi K. 2016 – trans-p-Hydroxycinnamic acid as a bioluminescence-activating component in the pileus of the luminous fungus *Mycena chlorophos*. Tetrahedron 72, 726–733.
Teranishi K. 2017 – Second bioluminescence-activating component in the luminous fungus *Mycena chlorophos*. Luminescence 32, 182–189.
Vydryakova GA, Van DT, Shoukouhi P, Psurtseva NV, Bissett J. 2012 – Intergenomic and intragenomic ITS sequence heterogeneity in *Neonothopanus nambi* (Agaricales) from Vietnam. Mycology 3, 89–99.
Wassink EC. 1978 – Luminescence in fungi. In: Bioluminescence in Action. Academic Press, London. pp. 171–197.