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REVIEW

Bioluminescent fungi: reviewing nature's riddle!

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Deep down into the woods, certain fungi gleam with streaks of faint green light at night - it is due to a phenomenon called bioluminescence. A recent scientific expedition in West Jaintia Hills, Meghalaya, India, has reported a greenish glow that emerged from dead bamboo sticks that were lustrous with tiny mushrooms. Solely the stalks were lit up. It led to the discovery of a new species that is *Roridomyces phyllostachydis*, which is the first fungus of this genus reported from India. The occurrence of bioluminescence in fungi is rare and confined to basidiomycetes. Bioluminescence is an oxygen-dependent reaction catalyzed by the luciferase enzyme. A few reported species belong to the genus *Mycena*, *Armillaria*, *Omphalotus*, *Pleurotus*, and *Panellus*. DNA-based sequence analysis has brought together these genera in four lineages. ITS sequencing was performed to demonstrate their phylogenetic species. Mushrooms advertise this phenomenon for attracting insects which are hypothesized to help in spore dispersal and for self-defense. Limited studies and experiments have been executed to decipher the biochemical pathways involved under bioluminescence in fungi. This review adds to and updates on the current knowledge of bioluminescent fungi.

Key words: Basidiomycetes, fungus,luminescence, macrofungi, oxyluciferin.

INTRODUCTION

With passing generations, evolutionary diversity has led to progress from darkness towards light. Earlier, we relied upon wood, natural gas, and wax sources for light and cooking purposes. Bogard (2013), a writer from America, illustrates his concern for natural darkness amidst the world lit with faux light sources.

The light at night gets in the way of the body's melatonin production, a hormone that regulates our biological clock. Unilluminated phases are essential to the plants for their proper metabolism and growth. Artificial sources break up the natural circadian rhythm created with the passage of millions of years and not overtime. We have also always heard that light always wins over darkness. There is a world that shines next to the nights with a soft brightness of its own. The first contemplation on the self-luminosity of the bioluminescent organism was imparted to the world by Aristotle, the Greek philosopher (384 to 322 BCE). He even deciphered that this attribute does not go along with heat production. Pliny the Elder, Roman philosopher (23 to 29 CE) narrated bioluminescence in fireflies, jellyfish (*Pelagia noctiluca*), the shining woods, and told that one could grab the slimy secretion of jellyfish on a walking stick and use it as a torch (Lee, 2008). Aristotle and Pliny the Elder, both had shortly remarked on the misty glowing wood that let out a steady light. After many centuries, Robert Boyle showed that oxygen was involved in this procedure in both wood and glow worms.

Bio means "living" (in Greek) and lumen means "light" (in Latin). Bioluminescence is an extremely sensitive phenomenon where conspicuous light is generated by living organisms. The biological constituents working in this process conduct a sequence of reactions that culminate to generate light (Baldwin, 2013). It is more prevalent in oceans than terrestrial areas. A massive number of bioluminescent organisms fall into Bacteria, Porifera, Mollusca, and Diptera. Chemiluminescence has a place in higher plants and bioluminesce-

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nce in the kingdom of Fungi. It is not very comprehensive in fungi but haphazard among the members of Basidiomycota. They are mother nature's enigma and not an effortless phenomenon to spot glowing mushrooms. Most research work rests on their taxonomic relationships. Ecology, spore-dispersal, priority of dispersal is still to be studied widely. So, our aim is to throw some light on these mystical beauties of nature to attract scientists into their in-depth exploration.

DISTRIBUTION OF BIOLUMINESCENT FUNGI

Bioluminescent fungi belong mainly in the Basidiomycota found in a tropical and temperate climate, *Xylaria hypoxylon* being the exception, an ascomycete. They are most prevalent in the dense forests of South America, Europe, and a few Asian countries (Table 1). *Gerronema viridilucens* was reported for the first time from Brazil. There are around 71 known species of luminous fungi (Desjardin *et al*., 2005). There are four definite lineages of bioluminescent fungi. They are a part of Omphalotaceae (*Omphalotus* lineage, twelve species), Physalacriaceae (*Armillaria* lineage, five species), Mycenaceae (Mycenoid lineage, forty-five species), and an unnamed lineage having *Gerronema viridilucens* and *Mycena lucentipes* (Desjardin et al., 2008). Seven novel species of *Mycena* have been outlined as luminescent by Desjardin *et al*. (2010). *Mycena* is a ruling genus exhibiting luminous properties. They have depicted particularly the taxonomy and morphology of the new species collected.

Earlier scientists have described a wood sample from an Indian state that showed luminescence during the monsoons and have studied its requirements for growth by culture samples. Desjardin *et al*. (2005) have characterized a new species of *Gerronema viridilucens* collected from the bark of living *Eugenia* trees from Brazil. They have analyzed it via phenetic studies with similar taxa. The fungus emitted yellowish-green light that appeared bluish to the unaided eye. The mycelium and fruit bodies of the fungus are bioluminescent. Luminescence is generally present in the mycelium. Seas and Avalos (2013) collected samples from litter, decaying trunks, broken branches and found a noticeable relationship between the types of fungi and soil and deciphered that they are affiliated. Chew *et al*. (2014) determined the phylogeny of fifteen surveyed specimens of luminescent fungi from Malaysia using molecular data. Aravindakshan and Manimohan (2015) have given details on *Mycena* genus from India. *Neonothopanus nambi* manifested anticancer effects opposing small lung cancer cell proliferation (Burakorn *et al*., 2015). Capelari *et al*. (2011) have narrated *Neonothopanus gardneri* with the help of molecular data.

FUNGAL PART EXHIBITING BIOLUMINESCENCE

In fungi, the bioluminescent part is sometimes present in the fruiting body though it is restricted mostly either in the mycelium or in the fruiting body (Shih *et al*., 2014). Lack of substrate for luminescence reaction is the principal cause for the absence of luminosity in fruit bodies. Puzyr *et al*. (2017) have studied biochemical changes that followed a non-luminous fruit body in *Armillaria borealis*. A segment of the bioluminescent system in *Mycena chlorophos* is limited to the cell membrane. It gave-off brilliant green light from its pileus for around two days at raised humidity levels (Teranishi, 2016a). Light potency in the cap and upper portion of the gill was substantial than the bottom piece. At microscopic levels, the light is produced from the membrane of hymenium and basidia cells on the gill. Mogilnaya *et al*. (2018) treated mycelium of *Neonothopanus nambi* with beta-glucosidase and found that such treated specimens attained maximum light emission strength shortly. Light emitters from the pileus of *Mycena chlorophos* were investigated. Luminescent gills in pileus had riboflavin, FAD, riboflavin5'-monophosphate as green fluorescent components (Teranishi, 2016b). Flavins are reasonable to be light emitters.

A procedure is to be followed to separate the mycelium culture of glowing mushrooms. Moisture maintenance is the limiting step. Mycelium has everlasting bright luminescence when raised on solid media. High humidity levels are essential for elevated wood luminescence (Puzyr *et al*., 2016). This was confirmed by their work on collected wood samples that inhabited glowing mycelium. *Armillaria mellea* shows limited luminescence as only its mycelium is luminous under natural habitat and on artificial media (Purtov *et al*., 2016). The fruiting body is non-luminous. Set of enzymes and substrates essential for luminosity is rendered only in the mycelium and under the provisions of free oxygen accessibility. The formation of luciferin precursors in fruit bodies was thwarted therefore,

Table 1: Distribution of a few bioluminescent fungi across the globe

Name of Species	Family	Bioluminescent Part-		Distribution	References
		Mycelium	Fruiting Bodies		
Xylaria hypoxylon (L.) Grev.	Xylariaceae	Absent	Present	Ireland, Europe, Britain, North America	Derek et al., 2009; Malakauskiene 2018
Armillaria mellea (Vahl:Fr.) P.Kummer	Physalacriaceae	Present	Absent	North America, Europe	Mihail, 2015
Flammulina velutipes (Curtis) Singer	Physalacriaceae	Present	Absent	Asia, Europe	Desjardin *et al*., 2008
Gerronema viridilucens (Desjardin,Capelari & Stevani)	Marasmiaceae	Present	Present	South America	Mendes *et al*., 2008
Mycena chlorophos (Berk. & M.A. Curtis) Sacc.	Mycenaceae	Present	Present	Japan, Malaysia	Kenichi *et al*., 2011
Mycena galopus (Pers.: Fr.) P. Kumm.	Mycenaceae	Present	Absent	Japan, North America, Europe	Desjardin *et al*., 2016
Mycena lucentipes Desjardin,Capelari & Stevani	Mycenaceae	Present	Present	South America	Bechara, 2015
Mycena luxaeterna	Mycenaceae	Present	Present	America	Desjardin *et al*., 2010
B.A. Perry & Desjardin *Mycena rosea* Gramberg	Mycenaceae	Present	Absent	Europe	Chew *et al*., 2014
Neonothopanus nambi (Speg.) R.H. Peterson & Krisai, Persoonia	Marasmiaceae	Present	Present	Malaysia, South America, Australia	Bondar et al., 2011
Neonothopanus gardneri (Berk. Capelari, Desjardin, B.A. Perry, T. Asai & Stevani)	Marasmiaceae	Present	Present	South America	Capelari *et al*., 2011
Omphalotus nidiformis (Berk.) O.K. Mill.	Marasmiaceae	Absent	Present	Australia, America, Europe, India	Weinstein *et al*., 2016
Omphalotus olearius (DC ex Fr.) Singer	Marasmiaceae	Present	Present	Western Ghats, India	Vrinda *et al*., 1990
Roridomyces phyllostachydis	Mycenaceae	Absent	Present	India	Karunarathna et al., 2020

the formation of luciferin was not supported. Fungal luminescence is a temperature-dependent process.

BIOLUMINESCENCE MECHANISM

There are two basic steps of a BL reaction. They are -

1. The process includes a substrate, luciferin, combined with ATP and oxygen that is run by the luciferase enzyme.

2. The chemical energy in the above step excites a luminescent molecule. The resultant is decay manifested in the form of photon emissions producing light.

The light emitted is a by-product of the chemical reaction and is hence cold light. Raphael Dubois had done a noteworthy experiment and extracted two chief components of BL reaction. He devised the term 'luciferin' from the Latin Lucifer, which means a light carrier, and 'luciferase' from the

French word. The heat-labile enzyme is necessary for light emission (Jacques, 2010). In 2009, Oliveira and Stevani confirmed Airth and Foerster's theory by utilizing warm and cold extracts from luminous fungi indicating that fungal BL confides in NADPH-dependent reductases. It's been clarified that light emission from the combination of the two extracts had the aftermath of a substrate enzyme reaction.

Nevertheless, bacterial BL bears a similar resemblance to fungal about the participation of luciferase and reductase. These enzymes are not alike though they belong to a similar functional class. The luciferase of fungi is related to the membrane-rich fractions this being the difference between fungal and bacterial systems. BL always implies oxidation of a substrate by a luciferase or photoprotein. Oxygen is critical for the bioluminescence as it results in the evolution of oxyluciferin. In fungi and bacteria, NADH/NADPH-dependent reductases are imperative. Auxillary enzymes are needed in changing luciferin into a more reactive form. It will then react with oxygen at the luciferase active site giving away light occasionally (Desjardin *et al*., 2008).

An elementary Bioluminescence formula is - Adenosine Tri Phosphate + Luciferin + Luciferase + Oxygen = Oxyluciferin + Photons
Airth and Foerster's hypothesis (1962) -

$$L + NAD(P)H + H^{+} \xrightarrow{reductase} LH_2 + NAD(P)^{+}$$

$$LH_2 + O_2 \xrightarrow{luciferase} LO + HO + h\nu$$

(Where, LH_2 = Reduced luciferin, LO = Oxyluciferin, L = Luciferin).

FUNGAL BIOLUMINESCENCE MECHANISM

The emission spectra of most fungi lie between 520-530 nm. Some scientists have studied *Panellus stipticus* in both cultures (mono/dikaryotic) and fruit bodies and then analyzed theirs *in vivo* BL emission spectra. It is an economical process. The colour pattern emission differs with organisms as marine organisms, jellyfish, fireflies, and fungi emit blue, green, greenish-yellow, greenish-blue light, respectively. BL occurs within a cell and in spores (Herring, 1978). Various forms of the substrate in creatures produce a gradient of colours as the energy in light particles varies with the frequency. Thus, the beautiful, vibrant colours observed during the night are due to change in frequency.

The effect of abiotic factors on the luminosity of *Armillaria mellea*, *Mycena criticolor*, *Omphalotus olearius*, and *Panellus stipticus* has been studied (Weitz *et al*., 2001). A proper study of the various culture conditions on mycelial development and luminosity index is essential for application as biosensors. Long-term darkness had a positive effect on mycelial luminescence. As per Weitz (2004), the light projected in place of heat in fungi is a by-product of oxidation reactions as in a few BL bacteria. The photon energy differs with the frequency of light therefore, various forms of substrates produce distinct hues in diverse organisms. Fig. 1 shows bioluminescence in fungi during day and at night.

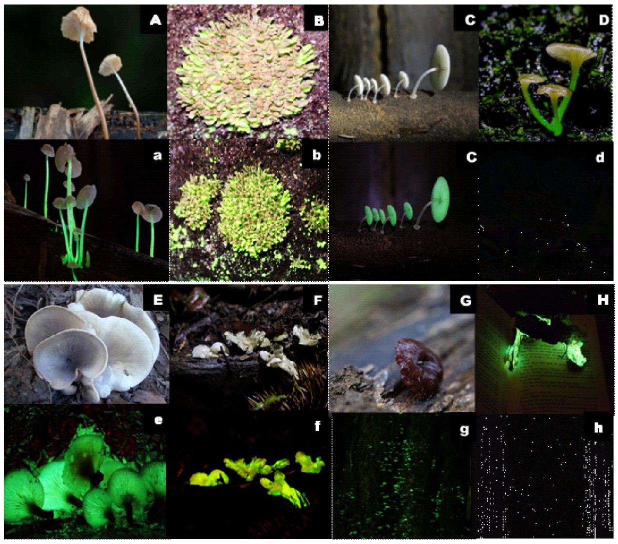

Fig. 1: Fruit bodies and mycelium of a few bioluminescent fungi during day and at night. **A,***Roridomyces phyllostachydis*; **B,b**: *Panellus stipticus*; **C,c**: *Mycena chlorophos*; **D.d**: *Mycena lucentipes*; **E,e**: *Omphalotus nidiformis*; **F,f**: *Neonothopanus nambi*; **G,g**: *Gerronema viridilucens*; **H,h**: Luminescent mycelium of *Armillaria mellea.* (Source: https://www.inaturalist.org/photos/17775684).

Even so, luminescence in fungi is a unique process, sensitivity makes it vulnerable to environmental toxicants. Lead is the ultimate toxic heavy metal to luminescent fungus, *Gerronema viridilucens* (Mendes and Stevani, 2010). A mutually shared BL mechanism is present among the four lineages of luminous fungi. This work has been supported by cross-reactivity between luciferin and luciferase. It occurs in the warm and cold-water extract from each species belonging to the four lineages. Light emission has been perceived in luminous species but no light in non-luminous species (Oliveira *et* *al*., 2012). Stevani *et al*. (2013) assessed that on the exposure of mycelia to toxic substrates, fungal bioluminescence is affected. Not all the fungi show luminescence at night as in a remarkable number, it was detected all over the day. Weinstein *et al*. (2016) had reported that *Omphalotus nidiformis* gleams consistently throughout day and night. According to one hypothesis, bioluminescence in fungi is the impelled action of a detoxification reaction with no major loss. Caffeic acid is an unusual metabolite in the formation of luciferin (Kotlobay *et al*., 2020) (Fig. 2).

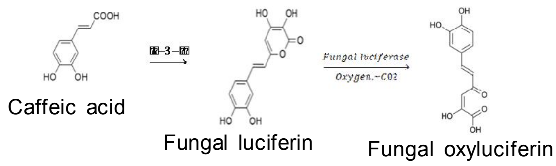

Fig. 2 : Mechanism of Fungal Bioluminescence

By utilizing the mycelia of heterogeneous basidiomycota species, luminescence peak was observed from their cold extracts (Puzyr *et al*., 2017). They incubated live mycelial biomass using deionized water and found that lyophilized specimens have greater thermal tolerance of luminous enzymes when compared with the cooler extract. Hispidin exists as a predecessor of luciferin in bioluminescent mushrooms. Immature, non-luminous fruit bodies showed luminescence after treatment with hispidin only (Oba *et al*., 2017). A mixture of hispidin and NADPH is not crucial to yield bright light in alive gills (Teranishi, 2017). Biochemical methods were involved to find hispidin-3-hydroxylase from *Mycena chlorophos* (Tong *et al*., 2020). It acts as a catalyst to transform hispidin into 3-hydroxy hispidin.

FUNGAL LUCIFERASES

Various assorted experiments have been executed for separating fungal luciferases although they have not given any satisfactory results (Hayashi *et al*., 2012). Cross-reactivity from varying species of basidiomycota proposes a steady BL process in them. Purtov *et al*. (2015) recognized the fungal compound luciferin 3-hydroxyhispidin by chemical tests and postulated it gave rise to bioluminescence. They characterized two bioactive compounds from *Neonothopanus nambi* and found their HRMS spectra identical to hispidin and thus verified hispidin as luciferin precursor. Oxygen is vital for formation of luciferin (Table 2, showing the role of oxygen in mycelia for bioluminescence). Simple synthetic alpha-pyrones have been utilized as luciferin to generate multicolor enzyme chemiluminescence (Kaskova *et al*., 2017). Luciferase promiscuity allows the use of simple alpha-pyrones as chemiluminescence substrates. Luciferase enzyme induces a reaction to generate a clear photon emission using an oxidative procedure. Insects, marine organisms, and certain microorganisms were earlier known as the main sources of discovered luciferase. First come across a wild form of luciferase was from *Photinus spiralis* i.e, firefly. Entire luciferases are mostly distinguished as oxidoreductases. 3-D structure of *Verticillium longisporum* was evaluated and luciferase characterized from this fungus which showed resemblance with other luciferases of bacterial and fungal origin (Yarima *et al*., 2020). Only slight dissimilarities were present in enzyme accuracy, he used different bioinformatics tools.

ECOLOGICAL ROLE OF FUNGAL BIOLUMINESCENCE

Studies on the ecological property of BL have gained momentum for a few decades. On the basis of inquiry performed on the interaction of arthropods and lucent fungi, several hypotheses have been set which may satisfy the ecological implication of fungal luminescence -

1. To engage spore dispersers.
2. To abolish negatively phototrophic fungivores.
3. As an aposematic signal.

Inspection of fungal bioluminescence is no longer thorough without scrutinizing their ecological role and evolutionary steps. Luminescence in *Neonothopanus gardneri* is controlled by circadian rhythm. The substrate (luciferin), reductase, and luciferase engaged in luminescence in fungi are at great heights during the night. Fungi are amid minimally analyzed bioluminescent organisms. He set up artificial mushrooms with an inner LED light source and saw that they fascinated flies, insects, as well as ants in massive numbers since they act in the spore dissemination process in dense forests. It could be queried that the spores produced by basidiomes are in enormous numbers, moreover, are generally wind-dispersed then why there is a need for insects for spore dispersal? Shaw (2004) hypothesized that insects lend a helping hand in this process at places in forests covered by dense canopies where wind cannot

Table 2: Set of enzymes and substrates that aid in the BL mechanism in *Armillaria mellea*. (adapted from Purtov *et al*., 2017)

Armillaria mellea Samples	Hispidin (Substrate)	Hydroxylase (Enzyme)	Luciferin (3-hydroxyhispidin: as Substrate)	Luciferase (Enzyme)
Fruiting bodies	Absent	Absent	Absent	Present
Fresh nonluminous Mycelium	Absent	Absent	Absent	Present
Luminous mycelium exposed to air (O_2)	Present	Present	Maximum Luminescence (hv)	Present

blow with a speed such that it carries along with the spores to distant places. He further hypothesized that fungi need wind for spore dispersal, as a result, it could be speculated that bioluminescence is responsible for the spore dispersal mechanism. They have seen *Neonothopanus gardneri* fruit bodies crowded by beetles (family-Staphylinidae). The mycelia of fungi are also a potential source of food to certain invertebrates and the fruit bodies are sometimes grazed by animals so fungi have evolved these processes to repel these predators (Mamiya, 2006). Night-time clock-controlled luminosity makes it a subject of insects and provides an advantage to it in spore dispersal form. Karunarathna *et al*. (2020) reported that *Roridomyces* genus fungi are moist loving and look as if they have co-evolved with some insects which assist in spore-dispersal.

APPLICATIONS OF BIOLUMINESCENCE

Bioluminescence has revolutionized plant biology and has made it easy the experiments and research on cell biology and immunology. Glowing fungi have been used by tribal communities to light their path through dense forests. Encouraged by such application of luminous fungi, researchers are working on processes to switch artificial light sources with a green light. They have been used as indicator organisms in various bioassays for determining the toxicity of heavy metals and organic compounds (Weitz *et al*., 2002). Earlier, bacterial strains were used to measure contaminants (Elsa *et al*., 2004) but now luminescent fungi have been used for the same. Luminescent molecules are useful in monitoring biological processes such as protein interaction, gene expression. Biosensors have been invented using luminescent molecules at a genetic level owing to the high detectability of luminescent signals (Roda, 2004). Recently, a genetically engineered tobacco plant with a fungal bioluminescent system was created that converts caffeic acid into luciferin and produces luminescence that is visible to with unaided eyes (Mitiouchkina *et al*., 2020). It had advantages over bacterial luminescent methods as they produce very dim light. Bua-art *et al*. (2011) have reported that *Neonothopanus nambi* can act as control agents against parasitic nematodes and soil-borne pathogenic fungi. A self-sufficient luminescence device dependent on the bioluminescence of higher fungi can be established for eukaryotes. This is an exceptionally selective and sensitive quality that has been applied in biomedical and biotechnology fields. Bioluminescence is also used to appraise sanitation efficiency that implicates induction of lux genes into the target and causes their expression (Warriner and Namvar, 2011).

Luciferase reporters have been used in the diagnosis of fungal infections (d'Enfert *et al*., 2014). *Neonothopanus nambi* was applied in imaging experiments It has also been tested as a reporter gene within a range of heterologous systems (Kotlobay, 2018). Fungal biosensors are advantageous over bacterial due to their high specificity and binding capacity. Many yeasts and molds are used as biosensors in ecotoxicity analysis (Singh *et al*., 2020). There are various modes for examining pathogens that evoke allergies and grave illness but they are very expensive and present enormous revenue on poor people but integrating bioluminescence phenomenon to expose, localize and quantify particular immune or pathogen cells can be operative (Suff and Waddington, 2017). Bioluminescence imaging is a non-invasive technique that was used to unmask acute hypoxic (Moon *et al*., 2020). Calcium ion-regulated photoproteins are chiefly obliged for bioluminescence in sea life. Recombinant photo-proteins have their benefits in biomedical examination fields that integrate to quantify calcium in different intracellular divisions of animal cells - which shows an anticipatory role as an analytical tool for *in vitro* and *in vivo* experiments (Sharifian *et al*., 2018). Bioluminescence methods are being leveraged for managing biological processes and not just sensing (Love and Prescher, 2020). Various BL systems have been used to develop bioimaging processes that are used in biomedical research (Mien *et al*., 2020).

CONCLUSION

For light to shine brilliant, there must be darkness. Bioluminescent fungi are a treat for the eyes at night and this phenomenon has been a long evolutionary process. The various results about the bioluminescence mechanism affirm that an elaborate method about the process will be deduced soon. Furthermore, once their distribution will be explored thoroughly, their phylogentic relationships and evolutionary significance could then be associated properly. Bioimaging, biomedical and eco-toxicological processes are new areas and role of luminous fungi are being assessed in them. Diurnal luminescence mechanism in certain fungi need to be studied properly to conclude about their ecological behavior. Ecological aspects, reproductive biology, and explorations on distribution are scattered and need to be focused upon to draw out solid results that may be advantageous to humans.

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