

Naturally bioluminescent fungi

HEDDA J. WEITZ

Department of Plant and Soil Science, School of Biological Sciences, University of Aberdeen, St. Machar Drive, Aberdeen AB24 3UU, UK. E-mail: h.weitz@abdn.ac.uk
The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK.

The natural phenomenon of bioluminescence is the emission of visible light by living organisms mediated by an enzyme-catalysed ('luciferase') reaction of molecular oxygen with a substrate ('luciferin'). Bioluminescent organisms are diverse and widely distributed in nature, for example bacteria, dinoflagellates, fungi and insects. The luciferases show no homology to each other and the luciferins are also chemically unrelated. Molecular oxygen is the only common feature of bioluminescence reactions, indicating that the luminescent systems in most organisms may have evolved independently (Wilson & Hastings, 1998).

In response to the article 'Glowing Report' in *Mycological Dispatches* (*Mycologist* 15/4, pp. 176), this note summarises what is currently known about fungal bioluminescence and what hypotheses have been suggested to explain this phenomenon.

Relatively little research has been carried out on naturally bioluminescent fungi (reviewed by Harvey, 1952; Wassink, 1978; Herring, 1994). There are currently thought to be more than 40 species of bioluminescent fungi within 9 genera, all of which are basidiomycetes (Wassink, 1978; Herring, 1994). Examples of luminescent fungi include *Armillaria mellea* (Fig 1), *Mycena citricolor* (synonym *Omphalia flavida*) and *Omphalotus olearius* (synonym *Pleurotus olearius*, *Clitocybe illudens*). *Panellus stipticus* is unusual in that luminescence is exhibited only by the North American strains of *P. stipticus* and not by the Eurasian strains (Peterson & Bermudes, 1992). Luminescence may occur in both mycelia and fruiting bodies, as for example in *P. stipticus* and *O. olearius*, or only in mycelia and young rhizomorphs as in *A. mellea* (Wassink, 1978). Bioluminescent fungi emit a greenish light with a maximum intensity at 520-530 nm (O' Kane *et al.*, 1990). Some luminescent fungi, for example *A. mellea*, reportedly exhibit diurnal periodicity (Berliner, 1961; Calleja & Reynolds, 1970) and seasonal variation of bioluminescence (Kamzolkina, 1982). It is not known whether the biochemistry of the bioluminescence

system of fungi is the same as that of other known systems (Wilson & Hastings, 1998). Fungal luminescence has been shown to require oxygen and *in vitro* light output has been characterised as an NAD(P)H-dependent luciferin-luciferase system for *A. mellea* and *M. citricolor* (Airth & Foerster, 1962; Kuwabara & Wassink, 1966; Kamzolkina *et al.*, 1984), but not for *P. stipticus* (Airth & Foerster, 1964; Shimomura, 1989).

Numerous reasons for the occurrence of bioluminescence in fungi have been suggested (Bermudes *et al.*, 1992). One hypothesis suggests that the role of luminescence is to attract invertebrates to assist fungal spore dispersal (Sivinski, 1981, 1998). The presence of luminescence most strongly in the gills (e.g. *P. stipticus*) or spores (e.g. *Mycena rorida* var. *lamprospora*) may support this hypothesis (Bermudes *et*

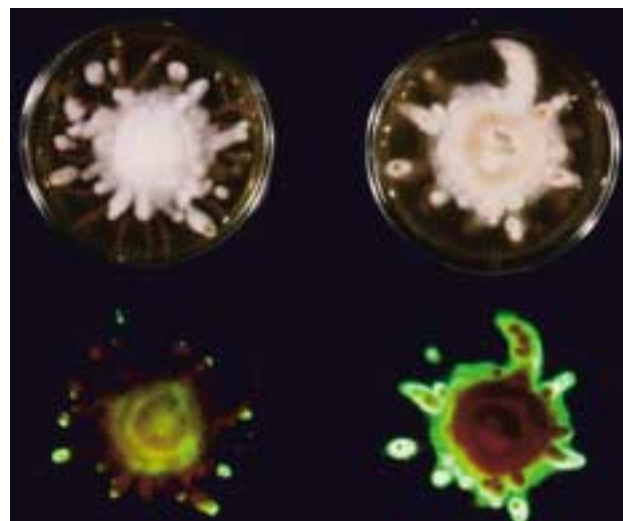


Fig 1 Photographs of *Armillaria mellea* ATCC 1113 grown on YM agar at 22°C in darkness for 3-4 weeks, taken in light (top) and darkness (bottom). The photographs were taken with a Nikon F3 camera and a Micro Nikkor 60 mm lens using a Kodak Ektachome 160T film. For the 'bioluminescence' photograph (bottom), exposure was 16 hours in total darkness. (Photographs taken by David Riley, The Macaulay Institute)

al., 1992). Sivinski (1981) also discusses other possible reasons for luminescence that include the attraction of predators of fungivores, the repulsion of negatively phototropic fungivores, and as a warning signal to nocturnal fungivores. There is some limited evidence to support these hypotheses but overall they remain unproven. Luminescence may not confer a significant selective advantage as there are both luminescent and non-luminescent strains of the same species and species that only have luminescent mycelium (Herring, 1994). Another hypothesis suggests that bioluminescence is a by-product of a biochemical reaction and has no ecological value. Light production has been calculated not to be a significant energetic burden, and bioluminescent fungi may be releasing light (not heat) as an energy by-product of enzyme-mediated oxidation reactions (Herring, 1994; Fox, 2000). For example, a relationship of bioluminescence to lignin degradation has been suggested where it may act to detoxify peroxides that are formed during lignolysis (Bermudes *et al.*, 1992; Lingle, 1993). Many of the bioluminescent fungi are involved in wood and leaf litter decay, for example *A. mellea* and *P. stipticus* are white rot fungi. Cultural factors that have been shown to induce or depress the lignolytic system of other white rot fungi also affect the level of bioluminescence in *P. stipticus* (Lingle, 1993). However, a great deal of additional research still needs to be carried in order to explain the mechanisms and significance of the phenomenon of fungal bioluminescence.

References

- Airth, R. L. & Foerster, G. E. (1962). The isolation of catalytic components required for cell-free fungal bioluminescence. *Archives of Biochemistry and Biophysics* **97**: 567-573.
- Airth, R. L. & Foerster, G. E. (1964). Enzymes associated with bioluminescence in *Panus stypticus luminescens* and *Panus stypticus non-luminescens*. *Journal of Bacteriology* **88**: 1372-1379.
- Berliner, M. D. (1961). Studies in fungal luminescence. *Mycologia* **53**: 84-90.
- Bermudes, D., Petersen, R. H. & Neelson, K. N. (1992). Low-level bioluminescence detected in *Mycena haematopus* basidiocarps. *Mycologia* **84**: 799-802.
- Calleja, G. B. & Reynolds, G. T. (1970). The oscillatory nature of fungal bioluminescence. *Transactions of the British Mycological Society* **55**: 149-168.
- Fox, R. T. V. (2000) Biology and life cycle. In *Armillaria Root Rot: Biology and Control of Honey Fungus*, pp. 3-43. Andover, England: Intercept Ltd.
- Harvey, E. N. (1952) *Bioluminescence*, pp. 96-117. New York, USA: Academic Press.
- Herring, P. J. (1994). Luminous fungi. *Mycologist* **8**: 181-183.
- Kamzolkina, O. V. (1982). Oscillation of bioluminescence in submerged culture of *Armillaria mellea* (Fr.) Kumm. *Mikologiya I Fitopatologiya* **16**: 323-325.
- Kamzolkina, O. V., Bekker, Z. E. & Egorov, N. S. (1984). Extraction of the luciferin-luciferase system from the fungus *Armillaria mellea*. *Biologicheskiiye Nauki* **1**: 73-77.
- Kuwabara, S. & Wassink, E. C. (1966). Purification and properties of the active substance of fungal luminescence. In *Bioluminescence in Progress* (edited by F. H. Johnson & Y. Haneda), pp. 233-245. Princeton, USA: Princeton University Press.
- Lingle, W. L. (1993). Bioluminescence and ligninolysis during secondary metabolism in the fungus *Panellus*. *Journal of Bioluminescence and Chemiluminescence* **8**: 100.
- O'Kane, D. J., Lingle, W. L., Porter, D. & Wampler, J. E. (1990). Spectral analysis of bioluminescence of *Panellus stypticus*. *Mycologia* **82**: 607-616.
- Peterson, R. H. & Bermudes, D. (1992). Intercontinental compatibility in *Panellus stypticus* with a note on bioluminescence. *Persoonia* **14**: 457-463.
- Shimomura, O. (1989). Chemiluminescence of panal (a sesquiterpene) isolated from the luminous fungi *Panellus stipticus*. *Photochemistry and Photobiology* **49**: 355-360.
- Sivinski, J. (1981). Arthropods attracted to luminous fungi. *Psyche* **88**: 383-390.
- Sivinski, J. M. (1998). Phototropism, bioluminescence, and the diptera. *Florida Entomologist* **81**: 282-292.
- Wassink, E. C. (1978). Luminescence in fungi. In *Bioluminescence in Action* (edited by P. J. Herring), pp. 171-197. London: Academic Press.
- Wilson, T. & Hastings, J. W. (1998). Bioluminescence. *Annual Review Cell and Developmental Biology* **14**: 197-230.

Editorial note: Dr Hedda Weitz was awarded the Howard Egging Award for the Best Presentation made by a younger scientist at Basidio 2003, for her talk on bioluminescent fungi.