

European forest fire sites should favour *Neurospora* ascomata. To find them and learn the dynamics of *Neurospora* sexual reproduction will take a concerted effort to survey sites repeatedly through 2004. All mycologists living near or passing through burnt sites are encouraged to search for *Neurospora* perithecia. For additional information on the surveys underway, contact either David Jacobson (djacob@stanford.edu) or Martha Merrow (martha.merrow@imp.med.uni-muenchen.de).

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### PROGRAMMED CELL DEATH ALIVE AND WELL IN FUNGI

The *Oxford Dictionary of Biochemistry and Molecular Biology* (Smith *et al.* 1997) defines apoptosis as ‘cell death ... used broadly to encompass all forms of ... normal or pathological cell death or may be confined to those processes involving morphological changes such as occur in normal animal development’. Fine, but does the lack of mention of fungi or plants mean that they don’t go in for programmed cell death? Or does it reflect that regrettably frequent narrowness of mind that leaves so many people thinking that only animals matter? It’s the latter, I’m afraid, because there’s no doubt at all that plants use programmed cell death (think of all the leaves falling from those deciduous trees. ...); and fungi? Ah well, as you might expect, fungi are well versed in the sophisticated use of programmed cell death (PCD); they’ve been using it for a long time. Some recent papers establish this point, but we can find evidence for it in some of the classic literature, too. Mousavi & Robson (2003), for example, have just demonstrated that cell death of *Aspergillus fumigatus* in the stationary phase depends on caspase-like enzyme activity. This is similar to animal apoptosis, where cysteine-proteinases known as caspases are essential components of the apoptotic pathway. Similarly, Lu, Gallo & Kües (2003) present customarily elegant cytological evidence for apoptotic DNA degradation in basidia of meiotic mutants of *Coprinopsis cinereus* (syn. *Coprinus cinereus*). Again, there is a compelling comparison with animal apoptosis where specific DNA fragmentation is an essential component. As Money (2003) has commented, such a process in a mushroom may well be a matter of resource conservation (the *Coprinopsis* mutants cannot complete meiosis so there is presumably some value in recycling the contents of the defective basidia). However, constant comparison with apoptosis in complex animals may well be diverting us from appreciation of the several roles for programmed cell death in fungi that have been

known for many years. The point is that most research is done (for obvious reasons) on vertebrate animals in which a primary ‘design requirement’ is that as the cell dies release of antigens must be avoided to protect the animal against autoimmunity. This has resulted in development of a highly sophisticated cell destruction process that takes place inside an intact cell membrane, so that the cell remnants remain separated from the immune system until they are engulfed by phagocytes. This seems to be the system with which everything else is compared, but it is a highly adapted system, and even in animals there are many examples of ‘partial apoptotic’ systems which, nevertheless, accomplish programmed removal of cells in a controlled and specific manner (Lockshin, Zakeri & Tilly 1998). So, the message is that a cell death programme will be adapted to its function, and, unless it happens in an organism with an active immune system, it’s unlikely to feature all the events that can be recognised in vertebrates. So where do you look for programmed cell death in fungi? First, look at all those subterminal cells that are sacrificed to release the terminal spore – if their death is not programmed, then what is? Cell death is a common occurrence in various structures starting to differentiate, for example the formation of gill cavities in *Agaricus bisporus* (Umar & van Griensven 1997, 1998). These authors point out that specific timing and positioning imply that cell death is part of the differentiation process and that fungal PCD could play a role at many stages in the development of many species. Individual hyphal compartments can be sacrificed to trim hyphae to create particular tissue shapes. PCD is used, therefore, to sculpture the shape of the fruit body from the raw material provided by the hyphal mass of the fruit body initial and primordium (Moore *et al.* 1998). Several examples detailed by Umar & van Griensven (1998) feature a PCD programme that involves the sacrificed cells over-producing mucilaginous materials

that are released by cell lysis. Evidently, in fungal PCD, the cell contents that are released when the sacrificed cells die could be specialised to particular functions too. But don't run away with the idea that you only have to go back ten years to find examples of PCD in fungi. To my mind, the most obvious example of fungal PCD is the autolysis that occurs in the later stages of development of fruit bodies of many species of *Coprinopsis* and *Coprinus*. So dip into the 30-year old literature and you'll find that autolysis involves specifically-timed production and organised release of a range of lytic enzymes (Iten 1970, Iten & Matile 1970) and is clearly a programmed enzymatic cell death. Allegedly, the phrase programmed cell death was first used in a doctoral thesis dealing with insect development (Lockshin 1963). But over 30 years before that date, Buller (1924, 1931) interpreted autolysis in coprinoid fungi as part of the developmental programme of the fruit body (specifically: autolysis removes gill tissue from the bottom of the cap to avoid interference with spore discharge from regions above). I consider that Reginald deserves a healthy slice of any credit that might be handed out for introducing this concept into biology. He should appear in future editions of the *Oxford Dictionary of Biochemistry and Molecular Biology*.

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## COMPLEX CONIDIA AS BRANCHED HYPHAL SYSTEMS

Bryce Kendrick has been studying hyphomycetes for almost 50 years, since he first discovered several previously undescribed genera and species in the course of his PhD studies at the University of Liverpool in the late 1950s. He was one of the strongest advocates of the need to take a fresh look at approaches to the classification of asexual fungi and their integration into 'whole fungus' systems through the international Kananaskis workshops of 1969 and 1977 of which he was the driving force (Kendrick 1971, 1979). He has now taken a fresh look at the problem, analysing types of conidiophore morphogenesis and conidium types (Kendrick 2003). Most importantly, he endeavours to explain complex conidia, especially staurosporous (e.g. branched) types as condensed or otherwise 'unorthodox' branching hyphal systems (e.g. *Desmidiospora*, *Gyoerffiella*, *Tetracladium*, *Tricladium*, *Uvarispora*, *Varicosporium*), and(or) analogues of colony development (e.g. *Flabelliospora*, *Petrakia*, *Psammia*). More than 150 genera

are considered as forming conidia that are interpretable as branched hyphal systems. This novel approach to the interpretation of complex conidia transcends current thinking (Kirk *et al.* 2001) and demands a re-appraisal of how complex conidia are described and pertinent conidial fungal genera are separated. All concerned with systems of hyphomycetes need to reflect on the fundamental importance of the interpretations suggested here.

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