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FAIRY RINGS OF MUSHROOMS

Much of the mythology and mysticism formerly associated with fairy rings is summed up by the words of Prospero in Shakespeare's *The Tempest*, V.i: "Ye elves of hills. . .that/ By moonshine do the green sour ringlets make,/ Whereof the ewe not bites, and you whose pastime/ Is to make midnight mushrooms. . .". However, in what could be interpreted as a minor triumph of reason over superstition, Prospero's invocation is not to the sorcery that was supposedly imbued in fairy rings, but a declaration that he is giving up magic forever.

Fairy rings are not caused by supernatural beings, witches, moles, snails mating, or lightning—these being some of the early explanations, all the more hilarious *now* for being propounded so seriously back *then*, for the annular rings of dead grass, fringed on both edges by concentric rings of over-lush grass, that are often evident in grassy fields. They are caused by fungi. One of the first scientific investigations to establish this fact was reported by Wollaston (1807), whose explanation of fairy rings is still broadly accepted today. Despite this demystification their appeal to the human imagination remained strong. Kipling (1906) wrote *Puck of Pooks Hill*, a story in which magical manifestations occur when children perform "A Midsummer Night's Dream" in a fairy ring, and Conan Doyle in *The Coming of the Fairies* (1923) only reluctantly admitted that fairy rings were due to fungal growth.

The mode of life involving progressive radial increase from a central point is not unusual among fungi. As pointed out by Ramsbottom (1953), hundreds of fungi grow in circular patterns, including microscopic ones such as *Penicillium* molds as well as those with macroscopic fruiting bodies such as mushrooms and puff-balls. Although the conditions governing initiation of a ring are still obscure, many scientific studies have documented the kinetics of expansion, the species involved, and the biology and ecology of fairy rings. Two excellent and complementary studies are reported in Shantz & Piemeisel (1917) and Dowson et al. (1989).

The underground body of a fairy ring fungus, consisting of a network of filaments called the mycelium, grows radially outwards as it consumes organic matter in the soil. Behind the fungus front the mycelial mass dies, so that the advancing live fungus front is actually a strange sort of disconnected organism. The dead filaments form a dense and water-repellant mat. Grass in this advancing annular region dies, due simply to physiological drought. Inside this bare region, the grass can grow luxuriantly because the dead filaments eventually decay, providing nitrogen-rich fertilizer. In advance of the fungal front, the grass also grows dark and luxuriant because of the peculiar (to us) eating habits of fungi: they exude digestive enzymes into the medium, then absorb this pre-digested food. Left-over digested food stimulates the grass forward of the fungus.

The radial growth rate of grassland fairy rings has been measured between 99 and 350 mm/year (Dickinson, 1979) and diameters of tens and hundreds of meters have been recorded. The obvious but rather awesome conclusion is that fairy rings may be among the world's oldest living organisms, since many rings are estimated to be several centuries old and some are believed to be 600 or 700 years old. It would be a fascinating exercise to obtain supporting evidence, such as historical records or results from scientific dating methods, for the ages of large fairy rings.

At favorable times of the year, fruiting bodies—mushrooms or toadstools—may be put forth around the circumference of a fairy ring. In woodlands these are often the only obvious manifestation of a fairy ring, since leaf-litter usually covers the ground (Figure 1).

Figure 1. A typical fairy ring in grass.

Because they depend on the roots of a tree for nutrient supply woodland fairy rings are referred to as “tethered” rings, whereas those in grassland, for which the nutrient source is spread though the ground, are called “free” rings. The growth of tethered rings is coupled to the radial growth of the host tree roots, and they tend to reach an equilibrium diameter, determined by the mature size of the tree, rather than increase indefinitely (Gregory, 1982).

What happens when two or more fairy rings meet? Usually, the putative intersecting portions of same-species rings are extinguished, because of direct competition for resources or as each reaches the other’s annular dead zone where nutrients and moisture are depleted in any case. Rings of different species either continue growing through each other or only the dominant species may survive. Rings of different species may also form inside one another.

A simple mathematical model for the ecology of fairy ring systems was developed by Parker-Rhodes (1955), from which was derived estimates for the proportion of ground covered by rings at a given time, the age distribution of rings, and for geometric factors affecting inter- and intra-specific competition, such as rate of birth of new rings per unit area and distance between their centers. This model was extended by Stevenson & Thompson (1976) to include boundary effects and a more realistic treatment of the rings as annuli rather than discs. Their conclusions had some interesting implications for the management and control of fairy rings.

Why would anyone want to control them? Some people, sadly, consider fairy rings to be a pathogenic nuisance, a disease to be eradicated, and it is true that they can spoil the appearance and functionality of lawns, golf courses, playing fields, and pastures. The modeling results of Stevenson & Thompson (1976) indicated that if one’s aim is to control a population of harmful rings by using an antagonistic but innocuous species of rings, it is more effective in the long term to choose the *smallest* growth rate available. In their work, the rings’ growth rate was assumed constant.

If we admit, however, that the growth rate is variable, then fairy rings must be modeled as a dynamical system, and since they spread in two spatial dimensions the appropriate dynamical description is a system of partial differential equations. Davidson et al. (1997) modeled the spatiotemporal dynamics of fungal mycelia by nonlinear reaction–diffusion equations describing the coupled evolution of the mycelial biomass and nutrient substrate concentration. They found that qualitative features of the development of fairy rings, such as the annular advancing front, degeneration of colony centers, and extinction of the interface between two colliding fronts, were reflected in the structure of solutions to the equations.

This type of predictive computational modeling and simulation of radial growth patterns is likely to become more important in future—and not only because it gives fairy rings the ultimate modern imprimatur and authority of the computer. Other organisms are known to exhibit the fairy ring habit of growth. In the semi-arid rangelands of Australia, for example, certain species of saltbush grow radially outwards from a central origin forming a slowly increasing ring of foliage, the interior of which is bare ground. The patterns on the landscape formed by these blue-gray saltbush rings on the red soil are very striking from the air. The saltbush is a nutritious food source for sheep; thus one might be interested in management strategies that *increase* the covering fraction of saltbush, and in factors that affect its growth. In this and other similar problems, the results from mathematical modeling of fungus fairy rings will provide valuable insights.

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See also **Growth patterns; Pattern formation; Reaction–diffusion systems**

Further Reading

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