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**RICE BLAST FUNGUS ATTACKS LEAVES AND ROOTS DIFFERENTLY**

Rice blast, the causal agent of which is *Magnaporthe grisea*, is one of the most destructive plant pathogens known. It has been studied in extraordinary detail from almost all conceivable standpoints (Ziegler, Leong & Teng 1994, Tharreau *et al.* 2000, Talbot 2003). The genome has been sequenced, and the infection process on leaves is known to comprise a series of developmental steps involving over 30 genes. The fungus is, however, a member of the same family as the soil-borne take-all pathogen of cereals, *Gaeumannomyces graminis*, which invades through roots. The development of *M. grisea* on roots has now been investigated in detail using strains tagged with a green fluorescent protein (GFP) and chlorazole black E staining (Sesma & Osbourn 2004). It was discovered that on roots the fungus infection developed in a different way to the process on leaves. The melanized appressoria typical of foliar infections and which build up astonishing turgor pressures in order to penetrate leaf surfaces were not developed. Instead, when growing on the root surface, much simpler penetration structures are developed, which take the form of hyphal swellings and in turn give rise to hyphal pegs. The authors refer to these swellings as ‘hyphopodia’, a term better subsumed under ‘appressoria’ as the structures are functionally similar (Mibey & Hawksworth 1995), but it may be more helpful to use the terms ‘functional’ and ‘non-functional’ appressoria. Whatever label is used for the non-functional swellings, the excitement is that these could not form functional appressoria and were unable to penetrate leaves, but could still produce the smaller non-functional appressoria on roots and successfully infect them. The genetic basis for the differences were investigated using an *FOW1* homologue linked with infection processes in *Fusarium oxysporum*, a characteristic root-invader. When the gene was deleted, there was a reduction in root browning. In addition, the authors searched for evidence of gene-for-gene resistance with the host using different rice cultivars, and found some evidence of specific disease resistance to the rice blast fungus in roots.

This is a fascinating story, particularly well-illustrated by colour photographs and also superb confocal microscopy images, and is sure to be something lecturers in plant pathology will wish to include in future courses.


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**WHY PICKING WILD MUSHROOMS MAY BE BAD BEHAVIOUR**

There has been a spectacular increase in mushroom consumption in recent years in North America and western Europe. In the USA, the USDA Economic Research Service estimates that per capita annual consumption of cultivated mushrooms has risen from 0.3 kg in 1965 to 1.8 kg in 2001 (Lucier, Allshouse & Lin 2003). Increasing market acceptance of cultivated fruit bodies has been paralleled by a boost in the popularity of wild mushrooms, and a number of popular species are now harvested on a large-scale...
commercial basis (Schlosser & Blatner 1995). Mushroom hunting, followed by picking, cooking, and eating, has also become a major recreational activity. In addition to their dietary value, a few species are sought for the trip they afford to altered states of perception. But despite its enduring counterculture image, mushrooming has edged its way from a hippy fetish into middle class consciousness. Amateur mycological societies have memberships in the thousands, and the annual Telluride Mushroom Festival in Colorado attracts hordes of fans. Guidebooks for mushroom identification and cookery boast perennially healthy sales, and galleries of colourful images of fruit bodies on the Internet entice armchair mycologists to hunt without fear of a stomach upset. As a commercial and leisure activity, mushrooming bears many similarities to fishing, but differs in one fundamental respect. By comparison with fishing, mushrooming is generally an unregulated endeavour whose environmental consequences have been widely ignored. Another analogy may be useful. Once viewed as dedicated scientists or harmless ‘naturalists,’ oologists who collect bird eggs are reviled today, and, if caught, face significant fines and possible jail time. In this essay, I discuss the possibility that mushroomers, like egg collectors, may jeopardize the objects of their desire.

Assuming that we want wild mushrooms to remain part of our culture and cuisine, I offer the following comments in endorsement of objective appraisals of the long-term effects of harvesting upon this renewable, but highly-sensitive resource. Moreover, though I am particularly concerned about the commercial harvesting of wild mushrooms (because of the scope of the enterprise), my comments are directed toward all mushrooming, even when fruit bodies are picked for personal consumption, or for scientific research and education. Someone must have made a very similar pitch against whalers in the last century (albeit without the issue of recreational whaling). Though a few of the arguments in this essay are novel, there is significant overlap with the voices of other mycologists, including Arnolds (1995), and Leonard (1997). In addition, Kaul (2002) offered a timely overview of research on mushroom conservation. Although this won’t make many mushrooming enthusiasts any happier with my viewpoint, I state, for the record, that I am a fellow practitioner, and am rarely more euphoric than while searching for mushrooms.

Wild mushrooms are an important forest product, whose monetary value sometimes exceeds that of timber (Arnolds 1995). The forests of the Pacific Northwest are prime targets for the commercial exploitation of fungi, accounting for an annual mushroom haul approaching 2 M kg with a value of US$ 41 M (based on decade-old data). Schlosser & Blatner (1995) estimated that fresh weights of 600 000 kg of morels (Morchella spp.), 510 000 kg of chanterelles (Cantharellus spp.), 370 000 kg of American matsutake (Tricholoma magnivelare), and 220 000 kg of boletes were harvested from Idaho, Oregon, and Washington in 1992. The global market for chanterelles is estimated at $ 1.5 billion, and trade in fruit bodies of matsutake at $ 3–5 billion, with most of the West Coast harvest shipped to Japan (Arora 2001). The price for matsutake fruiting bodies paid to ‘professional’ pickers varies greatly from year to year and during a single season (Rowe 1997). Many American pickers, including immigrants from Laos and Cambodia, rely upon the income obtained from mushrooming. In Europe, exports of French and Italian truffles serve as a major pump for regional economies. While the maxim that, ‘ounce for ounce, truffles are more valuable than gold,’ is a fallacy when one compares wholesale pricing, white truffles (Tuber magnatum) sold for more than $ 6000 kg⁻¹ during the hot, dry European summer of 2003 (Sylvers 2003). At more than twice the current value of gold, however, a single 1 kg white truffle sold at a charity auction in 2004 for $ 41000. But returning to less glamorous species, it is clear that lots of people are trampling through the woods in pursuit of fungi.

Field mycologists contend that collecting the fruit bodies of basidiomycetes, and ascomycete fungi like truffles and morels, is a benign activity that causes no damage to the supporting organism. Everyone knows that a plant is destroyed when it’s wrenched from the soil. But picking a mushroom can’t do any harm, mycologists have argued, because the invisible feeding part of the fungus, its soil-bound colony or mycelium, is untouched. After all, colonies can cover monstrous territories and mushrooms shrivel if they are undisturbed. Recollecting the title of Richard Mabey’s classic book Food For Free (Mabey 1972), it might even seem reasonable to assume that it is wasteful to leave mushrooms alone.

Some naturalists speculate that over-harvesting of mushrooms from particular areas is a damaging activity, and signs are posted to discourage collecting from public and private land. The USDA Forest Service administers a programme to manage personal and commercial mushrooming in the Pacific Northwest by granting permits that stipulate the species and quantity that may be harvested, the method of collection (no leafblowers or rakes), and the areas where collecting is permitted. In the UK, The Wild Mushroom Pickers Code of Conduct, published by English Nature in 1998 and endorsed by the British Mycological Society and many other bodies, urges personal collections of ‘no more than 1.5 kg per visit or no more than half of any single species present.’ While I support these efforts, and have lobbied for similar injunctions in Ohio forests, I am troubled by the prevailing justification for these policies. The distinguished mycologist Roy Watling speaks for many in the scientific community when he states that, ‘Picking mushrooms does not generally create a threat to the species as replacement fruit-bodies are already in place under the surface and ready to grow’ (Watling 2003). He continues by promoting limited picking in order ‘to control the
detrimental effects … of soil compaction’ that may crush the mycelium and disrupt the invertebrate fauna. In other words, Watling, and many others who espouse limitations on mushroom picking, view the loss of the fruit bodies themselves as relatively unimportant. It is too early to discern the effectiveness of current conservation efforts, but I suggest that mycologists should consider more direct and potentially more powerful arguments against intensive mushrooming.

By removing mushrooms we lower the spore-releasing capacity of the organism, which is potentially as costly to the fungus as egg collecting is for songbirds. Second, even when the disruption of long-range dispersal of spores is insignificant, the act of picking may impair the health of the colony from which the fruiting body emerged. It seems obvious that the removal of a large enough number of mushrooms, and the attendant decrease in spore release, must sabotage the reproductive success of the fungus (Leonard 1997). But with billions of spores effusing from a single fruit body, optimists have countered, the impact of picking is trivial. As Darwin observed, ‘more individuals are produced than can possibly survive’ (1859: 63). A familiar mycological example is the giant puffball, Calvatia gigantea, a 30 cm diam fruit body of which can produce seven trillion spores (American trillion, $7 	imes 10^{12}$ spores; Buller 1909). If every spore germinated, founded a colony, located a mate, established a dikaryon, and produced at least one fruit body, all of Ohio (almost 45,000 sq. miles, 116,550 km$^2$) could be submerged under a waist-deep pile of puffballs. The probability that any individual spore will escape the puffball, reach fertile soil, survive predation, out-compete the resident microbes, and raise its own family of spores (in cooperation with one or more mates), is very small. There are two valid, and mutually compatible, readings of this reproductive strategy: one dismisses the value of the individual spore, the other celebratess its importance. First, it is clear that any individual, randomly-selected spore is very unlikely to survive. Secondly, puffballs beget puffballs because on billionth or one trillionth of their offspring are ‘successful,’ and there is no way to predict which of the spores will succeed. Frying slices of a puffball in olive oil means that none of them, had they been allowed to develop, stands any chance of producing a new colony. No chance is considerably different from a slim chance. Because mycorrhizal boletes, parasitic and saprobic agarics, wood-decaying brackets, morels, and hypogeous fungi possess distinctive nutritional requirements and reproductive strategies, and respond to different environmental cues for fruiting, they will surely respond differently to intensive harvesting. But I contend that my underlying argument is applicable to all of these organisms.

Besides their importance for establishing new colonies in remote locations, spores can also, at least theoretically, have a profound effect upon fruiting within their birth sites. Basidiospores falling close to their fruit bodies give rise to monokaryons that intermingle with the parent mycelium and with other individuals in the same location. The new colonies can mate with other sexually-compatible monokaryons to form dikaryons that spawn their own crops of mushrooms, or can be ‘fertilized’ by nuclei from an existing dikaryon. The latter mechanism is referred to as the Buller phenomenon, named for its discoverer, the mycological genius, A. H. Reginald Buller (1874–1944). Spores landing beneath the fruit body can therefore enrich the genetic mosaic in the soil by injecting novel combinations of genes, and this may affect subsequent fruiting. The importance of the Buller phenomenon in nature is unknown, but may be a contributing factor to any harm done by mushroom collecting. If a mushroom is removed, there is no opportunity for these local genetic interactions, nor for long-range dispersal of spores.

Mushrooms are often compared to the tips of icebergs, suggesting that the greater mass of the organism remains below ground. The limits of this metaphor are clear, however, from classic experiments on cultured ink-cap mushrooms showing that much of the biomass of the mycelium is transferred to the surface when fruiting occurs (Madelin 1956). It follows, that there is little basis for assuming that picking wild mushrooms removes only a minor part of the whole fungus. Instead, the proportion of the organism that exists within, and above, the substrate varies according to a perpetual cycle of feeding and reproduction. There is another reason that mushroom removal may affect the viability of fungal populations. Like stem cells in human bone marrow, all fungal cells manifest developmental plasticity. Every one of the millions of hyphae that constitute the fleshy tissue of a large mushroom is capable of reverting to invasive growth, penetrating the soil, absorbing nutrients, and producing a new fruit body in a different location (Money 2002). In the laboratory, any piece of fruit body tissue placed on agar will sprout hyphae and plunge into the growth medium. In mushroom farms and in nature, spent mushrooms are often seen sprouting a cobweb of mycelium over the soil surface. Spores retained in the extinguished fruiting body may also germinate and add to the number of cells invading the food source from which the mushroom emerged. Though conjectural, it seems possible that the sterile hyphae that form the mushroom, and spores that become trapped, afford some fungi the opportunity to reenter soil or rotting wood after the fruit body collapses. Picking stops any of these cells from resuming growth.

Given the widespread collecting of mushrooms in some areas, one would anticipate, if there is any merit to my ideas, some data showing the negative impact of mushroomers on natural populations of particular species. Some studies have shown that the number and diversity of fruit bodies of ectomycorrhizal fungi has declined in parts of Europe and Japan (Arnolds 1991, 1992, 1995), but the impact of aerial pollution and insect infestations upon trees are the probable causes of
this ongoing problem. Diminishing hauls of various mushrooms in Europe and the USA, according to anecdotal reports along the lines of ‘they used to grow everywhere around here,’ are perhaps more consistent with the damaging effects of over-harvesting, but the effects of habitat loss, soil pollution due to intensive farming, and other kinds of land development complicate the interpretation of these observations. There have been very few long-term peer-reviewed studies that offer a guide to the impact of mushrooming. The research is tricky, because remarkable genetic diversity can hide in the cells of mushrooms that are classified as the same species. This means that the diversity within a population of a particular mushroom-forming fungus may be severely impaired long before the number of fruit bodies begins to decline. The sporadic fruiting of many species also clouds the apparent losses of particular fungi, and argues for careful monitoring of different habitats to establish reliable benchmarks for fruiting patterns (Straatsma, Ayer & Egli 2001). With this in mind, studies on the harvesting of chanterelles in the North America, and on other edible mushrooms in Switzerland, suggest that extensive collecting of fruit bodies for more than a decade does not necessarily diminish the annual crop (Egli, Ayer & Chatelain 1990, Norvell 1995, Redhead, Norvell & Danell 1997). I use the modifier ‘necessarily,’ because studies have shown that soil-compaction by trampling, and raking of leaf litter, have a negative impact on subsequent fruiting for several years (Arnolds 1995, Molina et al. 2001). A dramatic decline in harvests of the Japanese matsutake (Tricholoma matsutake) appears to have been caused by insect damage to trees rather than over-harvesting, and ongoing research is designed to test the sustainability of commercial harvests of the American matsutake (Hosford et al. 1997, Pilz et al. 1999, Molina et al. 2001, Pilz & Molina 2002). We need more data.

Mycologist David Arora has taken a fervent stand against efforts by the USDA Forest Service, and other agencies, to limit commercial picking (Arora 2001). In defence of people who make their livelihoods by collecting wild mushrooms, he marshals evidence from Europe where the earthly fragrance and nutty texture of Boletus edulis, or porcini, has enlivened Italian cuisine for centuries. Despite relentless picking of porcini, Arora proclaims, bumper crops have been recorded in recent years. I don’t share Aurora’s optimism. I was struck by the story of overexploitation and extinction in Mark Kurlansky’s book, Cod (Kurlansky 1997). Until very recently, Canadian officials treated the fish stocks of the Grand Banks as an inexhaustible resource. In his book, Kurlansky quotes Ralph May, a biologist from Woods Hole, Massachusetts, who suggested that the Canadians were suffering from a perception problem as their fish stocks vanished: ‘You see some cod and assume this is the tip of the iceberg. But it could be the whole iceberg.’ (loc. cit. 185). Readers of this essay should consider the value of substituting ‘mushrooms’ for ‘cod’ in that quote. Population crashes are notoriously difficult to predict (Hutchings 2004).

The proportion of fruit bodies harvested from any area remains the critical consideration for conservation. There are situations in which mushroom collecting is justified. A mycologist can be forgiven for lifting a fly agaric from a cluster to point out the salient features of its amazing structure to a group of students, or to preserve its tissues for taxonomic research. (Having said this, many of my botanist peers go to extraordinary lengths to identify plant species without damaging their flowers.) Collecting a few fruit bodies for personal consumption is a similarly harmless activity. After all, other animals have grazed fruit bodies for tens or hundreds of millions of years. On the other hand, wholesale removal of fruit bodies from a patch of woodland must reduce the probability that individual fungi will survive. As I have said, the variety of breeding systems and nutritional strategies of different fungi means that some species are likely to exhibit far greater resilience than others. But the fact remains that picking a mushroom whose spores are naturally dispersed by anything other than passage through the human digestive tract, is going to impair the distribution of spores from the picked fruit body. Morel collectors have claimed that picking may enhance dispersal by allowing the fungus to distribute spores during transit between its natural habitat and one’s kitchen. This extension of the notion of humankind’s dominion over nature might have a little merit for someone swinging their quarry home in a mesh bag, but undisturbed morels have done very well for themselves long before the evolution of hominid mycophagists. It sounds like wishful thinking to me.

Mushroom guidebooks commonly illustrate species with photographs of hunters surrounded by their bounty. Flipping through two of the best mushroom books on my shelves (Arora 1986, 1991), I find photographs of naturalists buried under white-capped giant horse mushrooms (Agaricus osecanus) and yellow chanterelles, a mycologist proudly holding a giant puffball that will never puff a single spore, and a grinning enthusiast spreading his arms to encompass a table overflowing with ivory-colored umbrellas of prized matsutakes (worth thousands of dollars). Mushrooming societies in my part of the country boast about the tremendous numbers of mushrooms they collect on forays, and even compete with one another for record-breaking harvests. Have mycologists been celebrating something deeply unethical? Imagine a birding book whose jacket displayed an ornithologist holding a basket filled with eggs, or a wild flower guide picturing the author showing a basket brimming with wild orchids.

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past year. I apologize to Michael, and to anyone else, for whom this essay spoils a favorite pastime, and sincerely welcome sensible counter-arguments.


**LIFE-STYLE CHOICES IN LICHEN-FORMING AND LICHEN-DWELLING FUNGI**

Early molecular phylogenetic studies suggested that lichenization had multiple origins in the fungi (Gargas et al. 1995). Indeed, over 100 lichenization events were claimed to have taken place (Aptroot 1998). Yet as sequence data accrued from more fungi, evidence grew that lichenization events had actually been rather few. Lichenization came to be confirmed as the ancestral state in many ascomycete groups which now only include saprobic or plant pathogenic fungi (Lutzoni, Pagel & Reeb 2001). There had been multiple independent losses of the lichen-forming ability amongst ascomycetes, rather than repeated gains. Further, it was suggested that fungi growing on other lichens as pathogens or commensals might have provided a ‘half-way house’ facilitating further adaptations to different habitats (Lutzoni et al. 2001), for instance plant pathogens and saprobes. In contrast, in the case of basidiomycete fungi, lichenization does not appear to be an ancestral state but to have occurred three or four times (Gargas et al. 1995). However, overall at the individual genus level, at least 48 genera are now known to include species some of which are lichen-forming or lichen-dwelling (lichenicolous), and others of which are algalicolous, bryophilous, fungicolous, plant pathogenic, or saprobe (Table 1).

Molecular work is now starting to confirm that genera including species which form or grow on lichens and others which are saprobes or plant pathogens are actually monophyletic. Indeed, the January issue of *Mycological Research* included a paper showing that the conidial basidiomycete genus *Marchantiodimyces*, which had hitherto comprised two species pathogenic to lichens, also contains a third species which grows saprobiically on dead oak (*Quercus*) branches in Virginia, USA (DePriest et al. 2005). However, molecular phylogenetic studies using three parts of the

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