

Presidential Address

Fountains of the forest – the interconnectedness between trees and fungi

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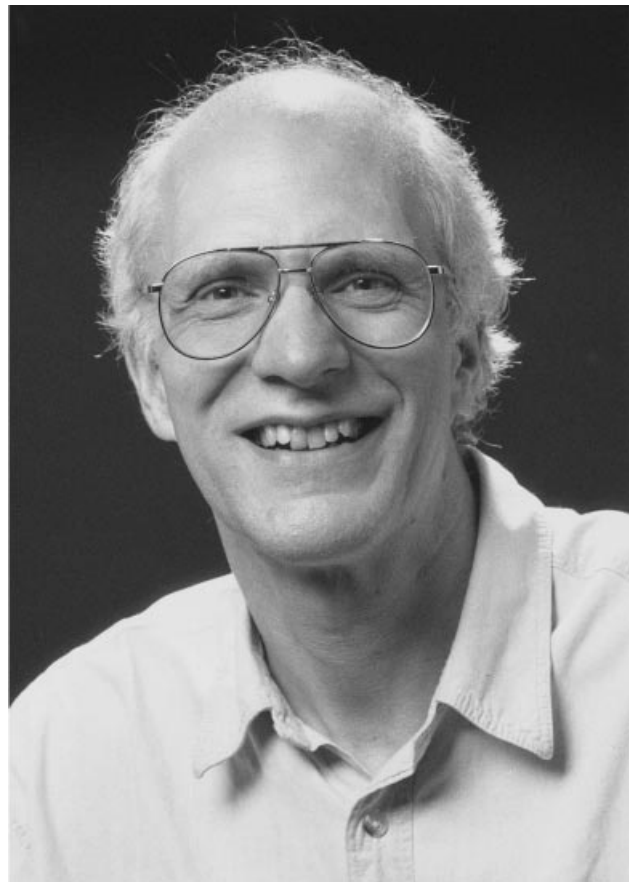
PRELUDE

Perhaps like many other mycologists, my initial encounters with fungi filled me with a desire to engage with mysteries: mysteries embedded in the diversity of form and function in fungi and how this diversity might be related to the life of the forest in which so many of these organisms appear to find their homes. In all good mysteries, the resolution of underlying causes at one level of comprehension only serves to reveal deeper levels for exploration. This can open the way into a cascade that nourishes a growing empathy with fellow beings and so assuages that most fundamental need to have a sense of belonging – to be as one; to be at peace; secure in the knowledge of idiosyncrasies embraced in the fondness of others. I dreamt that fungi would somehow eventually lead me and my fellow travellers down that cascade. I still do.

I was brutally awakened by the stridency of much – though, I hasten to add, not all – current scientific methodology. The stridency of an argumentative approach that interrogates subjects as though they were objects, putting them through their paces, setting them examinations, but never really listening – and treats its own practitioners no better. A purely analytical, calculational approach prescribed and described in desiccating language if not in the ultimately alienating form of numbers. An approach that boils down to statistics deprived of their context. An approach bedevilled with peer rivalry and the need to appease hostility by back-referencing and cross-referencing everything – oblivious of the fact that if a tree clung on to all its branches it would soon become an impenetrable thicket – and so denying the right to forget, overlook, reposition and move on. An approach that, if pursued exclusively, can only sterilize, not fertilize, by driving a wedge between thinking (portrayed as rational calculation) and feeling (portrayed as irrational emotion). An approach which imaginative youth understandably rejects as a dispiriting, despiriting reduction that ultimately only sees life stripped down to its DNA, separated from its dynamic context.

Through engaging with fungi, I have become convinced that such brutality is a form of arrogance, neither necessary nor justifiable in the simple, humble, scientific quest to observe

and interpret reality with the aid of experimentation and measurement. The brutality arises from the widespread ‘discretist’ presupposition that, at least to a good approximation, an absolute demarcation – a complete and fixed boundary – occurs between the inside and outside of any thing. This presupposition is ultimately untenable because it neglects the facts of passing time: the fact that for anything to be dynamic – at least for any living thing to grow, move itself around or multiply – there has to be an input of energy



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Fig. 1. Fountains of the Forest. Oil painting on board by Alan Rayner, especially prepared for and presented to the British Mycological Society on the occasion of his Presidential Address.

in some form that involves a reaction in the boundary of the thing; and the fact that energy supplies vary. Far from passively marking the absolute beginnings and endings of separate objects, the boundaries of life forms are reactive interfaces which differentiate and integrate in ways that alter the dynamic relationship between insides and outsides, at scales ranging from molecular to global, as energy supplies wax and wane. Diversity therefore arises systemically, from the way in which the properties of the changing arenas, the indeterminate dynamic contexts incorporated by the space-time boundaries of life forms, regulate processes of input, throughput and output of energy. Life forms are at least to some degree sensitively moulded through an interplay of expansive and resistive forces rather than constructed solely from fully discrete bytes. Rather than calculating ahead, they feel their way through feedback, in a responsive process that may have as much in common with artistic expression as it does with discretist logic.

It may therefore be helpful to explore more inspirational forms of communication of biological knowledge, including artwork and prose, which emphasize dynamic, interactive qualities as well as technical know how. I now want to take the liberty of trying to describe fungal relationships in this way, based on a painting which I have prepared especially for the British Mycological Society (Fig. 1), in the hope of encouraging deeper appreciation and experience of living systems and their relevance to our own human quality of life.

FIRE, WATER, FUNGI AND TREES

A tree is a solar-powered fountain, its sprays supplied through wood-lined conduits and sealed in by bark until their final outburst in leaves. The leaves assimilate the energy delivered from the sun's fiery integration of hydrogen into helium, and use it to differentiate water into hydrogen and oxygen. The hydrogen is harnessed during the process of photosynthesis to convert carbon dioxide into chemical sources of fuel and structure, in the form of carbohydrates. The oxygen is released but then reabsorbed to sustain the earthly fire of respiration, the slow-burning process that generates the chemical energy which keeps the living alive, at a potential difference from their surroundings. This potential difference enables roots to take in supplies of minerals and water from a current produced when, warmed by the sun and cooled by evaporation, leaves develop a pull of their own which sustains the flow through wood and soil before releasing it to clouds. The fountain rises and falls as boundaries between insides and outsides open and close through day and night, through wet season and dry season, through feast and famine.

In all this, a tree is never alone. Within and upon its branching, enfolding, water-containing surfaces, and reaching out from there into air and soil are branching, enfolding, water-containing surfaces of finer scale, the mycelial networks of fungi. These networks provide a communications interface for energy transfer from neighbour to neighbour, from living to dead, and from dead to living. They maintain the forest in a state of flux as they gather, conserve, explore for and recycle supplies of chemical fuel originating from photosynthesis. Some networks stay on the outside of leaf and bark surfaces;

others penetrate within and either harmonize with or disrupt the tree's functioning. Networks of mycorrhizal fungi form intimate partnerships with the roots of trees and other plants, enhancing uptake of water and minerals, protecting from assault and bringing individuals into communion by bridging gaps between them. Networks of wood decay fungi ramify the tree's core, sometimes emerging out into soil to spread themselves over territories ranging from square metres to perhaps square kilometres in area. Litter-decomposing fungi disintegrate discarded remnants from the extravagance of leafing and flowering. Parasitic fungi hasten demise and consequent re-entry to the system.

The fungal networks produce fountains in their own right: emergent structures that enclose, distribute and liberate their genes within protective envelopes that secure a passage through uncertain space and time. So the fountains of the forest trees are connected and tapped into by the fountains of fungal networks in a moving circulation: an evolutionary spiral of differentiation and integration from past through to unpredictable future; a water delivery from fire to fire and back again, contained within the contextual boundaries of a wood-wide web.

SURFING SURFACES

On the crest of the wave form that comprises a tree are to be found fungi which, as yeasts or mycelia, find sustenance in the flotsam and jetsam arriving upon or ejected from its surfaces. Superficial and exposed though their attachment may be, they can both protect and degrade the tree's boundaries, and serve as vital indicators of the quality of the environment. They are a community that emerges and embellishes as time is translated into the tree's aging. Phyllosphere fungi ride the surfaces of leaves, taking in, amongst other exudates and deposits, the ooze of honeydew and the spatter of pollen dust, whilst abrading the waterproof membrane of cuticle and so opening the way for others to follow in their wake of increased leakiness. Rhizosphere fungi are spurred into action around the surfaces of roots. Caulosphere fungi key onto or into the corky covering of trunks and branches, eking out an existence from a fatty or resinous diet derived from the tree's insulation or growing upon the living or dead remains of other inhabitants such as lichens, bryophytes and scale insects, as do species of *Athelia*, *Galerina* and *Septobasidium* respectively.

PENETRATING DEEPER

Intimacy entails taking the plunge, dipping below the surface. Entry may be forced, stealthy or invited. Once involved in the mainstream, a fungus may assume the role of parasite, passenger or partner, and switch from one role to another in the same way that an actor changes costume when the scenes of circumstance dictate.

Diverting the flow

Some fungi assume the role of biotrophic parasites, infiltrating as forms that escape recognition and often produce specialized

branches, haustoria, that reach like hands in gloves into living cells in foliage or bark and so divert the flow of the tree's fountain to their own ends. The diverted flow both alters and is altered by the developmental course of plant cell boundaries through changes of hormonal balance that result in swellings, brooms and green islands that reflect the tree's subversion. Included here are rust fungi which splash foliage with yellow and brown or erupt as blisters from bark; powdery mildews that dust the surfaces of leaves; Taphrinales which cause leaves to deform and stems to proliferate branches; agarics of *Crinipellis* which infect tropical lianes and cocoa trees; *Rhytisma acerinum*, which causes tar-like spots to form on sycamore leaves, and *Ascodichaena rugosa*, which produces horizontal black stripes on smooth-barked trees such as beech.

Disrupting the flow

Other fungi are necrotrophic parasites, making a living by causing the death of plant cells or tissues and directly or indirectly disrupting the flow. Some species achieve this by smothering host roots with a blanket of mycelium that ramifies over and through the surface in advance of penetrating the interior. In so doing, they obviate the corky or waxy insulation that maintains the root's function and open the way for themselves to invade and exploit the product of past endeavour. *Heterobasidion annosum* and various *Armillaria* species are notorious examples. Though often overlooked, some fungi can operate in much the same way in tree canopies, forming waterproof bridging mycelium that, like a spark crossing a gap, connects infected to uninfected stems where these come into close proximity. Several Hymenochaetales, can do this.

In leaves and needles, necrotrophic fungi produce dead spots. These spots can enlarge and coalesce to cause shrivelling or cut off supplies to distal regions to cause die-backs. The resultant changes from photosynthetic green to dysfunctional browns, reds and yellows can sometimes give the appearance of autumn colours, as when *Guignardia aesculi*, infects horse chestnut leaves.

In bark, necrotrophic fungi produce dead patches, cankers, whose varied shapes depend on how the fungus colonizes and how the tree responds. Colonization from outside-in produces localized cankers that can be diamond-shaped as a consequence of fungal traverses between medullary rays, or target-shaped when the advance of the fungus alternates with the production of boundary-sealing callus. Colonization from inside-out causes strip-cankers – tongues of dead bark that extend, often spirally, along trunks or branches, following the grain of the underlying wood.

In wood, necrotrophic fungi extend their domain by further disrupting the flow, through the production of toxins that disable and enzymes that dissolve the tree's self-protection. Wounds, caused by storm, forester and insects can all provide a base for these fungi to establish themselves. Included here are *Stereum sanguinolentum* and *Heterobasidion annosum*, which infect conifers, and *Chondrostereum purpureum*, which infects angiosperms and causes the leaves of plum trees to silver. *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* are carried by bark

beetles to the crotches in elm branches where the beetles' feeding introduces the fungi into the sap stream. Thereafter, the proliferation of the fungi, in yeast-like form, and the tree's reaction in blocking its own conduits, combine to wilt the tree's canopy, causing the landscape-altering pandemic that has become known as Dutch elm disease. Species of *Fusarium* and *Verticillium* can also cause trees to wilt, though these fungi typically originate in soil and gain access to roots by mechanisms akin to those of biotrophic fungi.

Biding time

The living mainstream of a tree is an inhospitable place, lacking air and/or accessible nutrients, for fungi that are unable to divert or disrupt the flow. Even so, many fungi appear to be able to survive, if not thrive, here, as endophytes. Their life behind the scenes is hard to trace, with little outward sign or symptom to betray their presence. They may, like wilt-causing fungi, be dispersed by the sap stream, they may lie up in recesses or they may infiltrate themselves finely through the system. Only when the flow is disrupted by some outside or inside agent other than themselves, or when some part of the tree becomes detached, do they spring into activity, positioned by biding time to take advantage when the doors of the system's retaining boundaries are unlocked.

Giving and taking

When mycelial networks invade roots in biotrophic mode, they become involved not in parasitism but in mycorrhizal partnership, both part and parcel of an assimilation-distribution system that exchanges photosynthetic fuel for the minerals and water that can be drawn from soil. The partnerships are demanding, accounting for perhaps about a quarter of the tree's production costs, but, unless driven into separation by soils unusually rich in nutrients, are vital to a sustainable, fruitful co-existence. Whilst branches produce the fruit of flowering, roots produce the fruit of their fungal partner's nurture in a many-coloured celebration of fountainous forms that set the forest floor aglow. Here, *Russula*, *Lactarius*, *Amanita*, *Cortinarius* and *Boletus*, to name but a few, are to be found not in splendid isolation but as a multicultural carnival linking root to root, tree to tree and tree to seedling. Not all, of course, are so flamboyant: members of the Endogonaceae fill the cells of their partners with arbuscules – haustoria resembling microscopic bushes; *Cenococcum geophilum* coats roots in fruitless black mycelium. Whether exuberant or drab, however, all take part in the carnival, giving and taking in their own special ways and sometimes invited in, sometimes repelled by the roots' boundary chemistry. Some may fall victim to bandits – non-photosynthetic plants like yellow bird's nest and parasitic fungi like *Cordyceps capitata* – which tap into and drain the networks without giving anything in return. Such intrusions are, as in human societies, an inevitable adjunct of opening communication channels, but in the natural forest their effects are limited by and may enforce the very diversity of a system which tends to repel boarders.

EXPLOITING BREAKDOWN

For many fungi, whether they have been journeying through the wilderness outside, or biding time inside, self-fulfilment only becomes possible when air gets into the system and the tree's fountain ceases to flow. Thereafter, the breakdown of the tree's function is superseded by the fungally-assisted breakdown of the tree's structure in the rendering processes of decomposition and mineralization that return carbon dioxide and water to sky and sea, and soil to soil.

Invading sore points

Death or injury to bark lets air into wood – the more so when higher up than lower down the fountain, and when the stream is under tension rather than pressure. The air spreads more easily with than against the grain, and usually further upwards than downwards, until kept out of the mainstream by self-protective physical barriers, such as pit-closing membranes, within the conduits. In time, these barriers may be reinforced with water-repellent substances, produced by dying wood cells, that seal off the aerated wood and darken upon exposure to oxygen.

Fungi follow the passage of air. Forms that discolour the wood are often prominent before the true rotters set to work degrading the fabric of lignocellulose in the walls of the conduits. As with the air, the spread of the fungi is arrested at seals between functional and dysfunctional conduits, but may extend further if the seals fail.

Profiting from stress

Any condition that impedes flow imposes a stress that can result in deprivation of trunks and branches and consequent aeration of their conduits. Drought, cold, root-disease, defoliation by caterpillars, shade and competition amongst branches can all do this, both on their own and by interacting with one another.

Fungi that have been biding their time as endophytes can then be released, and end their confinement in a flurry of activity that can look for all the world like spontaneous generation out of the tree's dis-integration. Strip-cankers and columns of decay metres-long appear within the space of a growing season. Diamond-cankers may be so prolific as to form a snakeskin-like patchwork. Fruit-bodies erupt out of bark, often in swarms or combined within extensive, crust-like stromata. Characteristically, development of many of these features is arrested at junctions between minor and major branches, in much the same way that traffic on a side road is forced to wait and watch the flow on a main road pass by. In branches that remain partly alive, sealant zones form at the interfaces between functional and dysfunctional wood. These zones may then persist as ridges and flutings, to produce rippling, antler-like, natural sculptures as legacies from a dynamic, interactive past, long after the remainder of the wood has decomposed. The canopies of mature oak trees are a good source of these sculptures.

Many of the fungi show apparently strong preferences for particular kinds of trees, e.g. *Biscogniauxia nummularia*,

Hypoxyylon fragiforme and *Eutypa spinosa* in beech; *Daldinia concentrica* and *Peniophora limitata* in ash; *Stereum gausapatum* and *Peniophora quercina* in oak, and *Piptoporus betulinus* in birch. These preferences may partly reflect the strongly selective conditions imposed when the fountain is active and only the most resilient can manage to pass time. They may, however, also reflect the difference between a covert, endophytic life and the overt self-expression of fruit bodies. *Daldinia concentrica*, for example, can often be detected as an endophyte in trees on which it rarely or never comes to fruition.

These fungi pose a riddle: are they the cause or the effect of the tree's demise? Like the one about the chicken and the egg, this riddle draws attention to the paradoxes produced by asking analytical, either-or questions when the underlying process is both dynamic and interactive.

The true answer can only be 'neither-nor' or 'both-and'. As the fountain begins to lose force, so the enhanced activity of the fungus compounds the dysfunction. In other words, there is a change in dynamic balance between the life forces of the tree and those of its inhabitant fungi, a fact that should not be forgotten when contemplating the future of forests in the face of environmental change.

It should also be recalled that death is part of the life of a tree. Without letting go of some of its past, a tree cannot move on into the future. As its canopy expands and fills, so some branches inevitably become better positioned for gathering and distributing the energy of sunlight than others which become increasingly redundant. If the redundant branches are allowed to be retentive and demanding of resources, they will eventually stifle the system. By succumbing to stress and the effects of internal competition, these branches can detach and decompose in a process of natural pruning that unclutters the canopy and enables resources to be recycled through the medium of fungal fountains.

Disheartening

Old conduits, old pipelines, sooner or later cavitate and fill with air. From then on, like clogged coronary arteries, the embolized pipes must be by-passed if the flow is to continue. Eventually, the embolisms accumulate to the point where all flow ceases and a core of dysfunctional wood begins to form at the heart of the tree's fountain. This core enlarges with the tree's girth and may become coloured by the deposition and oxidation of phenolic and terpenoid compounds, that often strongly inhibit fungal growth, to form a visibly distinct heartwood. Here, it is possible for mycelial networks adapted to the chemically harsh conditions to begin to grow and eventually decompose the wood in a process of heartrot that, sometimes over many decades, ultimately hollows out the tree. These networks can occupy and consume large volumes – cubic metres – of wood, diverting the products of their slow labour to bulky, sometimes perennial fruit bodies that emerge wherever they can escape the confines of living bark and sapwood. Some networks become established via roots, working their way up from the base of the tree to cause butt rots. Others invade trunk or branches to cause top-rots that work their way down the tree. Some may occur in only particular kinds of trees, e.g. the beefsteak, *Fistulina hepatica*

which renders the heart of oak, and occasionally chestnut, into a commercially valuable form for production of veneers. Others, like *Laetiporus sulphureus* on beech, willow, oak, cherry and yew, are more eclectic. Their mechanisms of establishment in the heartwood vary. Some may only be able to colonize wounds large enough to expose the heartwood. Others can be more subtle, like the Indian paint fungus, *Echinodontium tinctatum* which passes time in buried branch stubs until the increasing girth of the heartwood catches up.

A hollow heart may mean loss for the timber merchant, but need not mean loss for the tree or the diversity of community life that develops within its shelter. A hollow cylinder is mechanically strong, providing that its shell is thick enough. A decomposing mulch at the tree's core, enriched as it may be by the droppings of nesting birds and mammals, can provide fertile ground for re-invading roots, mycorrhizas, nitrogen-fixing bacteria, and a host of insects.

Clearing litter

Death in the tree's canopy ends in jettison, so that a rain of remains descends towards the forest floor. Not all these remains complete the fall, but lodge instead in branches – some of which may even have been tied together to form a kind of coarse filter by fungi like *Hymenochaete corrugata*. The mycelial networks – in effect, the filter-feeders – of these fungi may then consume the trapped remains at leisure.

Those remains that do complete the descent vary greatly, with their bulk being roughly inversely related to their frequency but proportional to their residence time at the forest floor. Smaller, more frequent items of foliage or flowering may, if sufficiently palatable – as with elm and ash – rapidly be removed by earthworms and shredded into a mulch of rich mull humus more conducive to bacterial than fungal digestive systems. Alternatively, if lacking nitrogen or embittered with phenolic compounds – as with beech, oak and pine – they may accumulate and form a more or less even carpet that cushions passing feet and rustles in the breeze whilst providing shelter and sustenance for a myriad of fungal networks. Some of these networks may be restricted to individual items of foliage, like *Mycena capillaris* and *Marasmius recubans* whose tiny, hair-like toadstools emerge respectively from the blades and veins of single beech leaves. Others may spread themselves to form dense patches, like *Marasmius wynnei*, or fairy rings, like the clouded funnel cap, *Clitocybe nebularis*.

Larger, more durable items such as woody fruits and cones may likewise harbour specialists, like *Auriscalpium vulgare* on pine and *Xylaria carpophila* on beech, within their physical boundaries or may become interconnected by networks of cable-like aggregations of hyphae. Larger branches and trunks usually only fall naturally once already decayed by an assortment of residents that have benefited from earlier dysfunction of the tree's fountain. These residents may persist long after fall or become replaced as conditions change and/or more combative fungi or other organisms such as arthropods and slime moulds invade their domain. Some may be victims of takeovers, as when *Datronia mollis* is undermined by *Phanerochaete magnoliae* in beech branches.

And so the tree's fallen set the scene for fungal actors who

may, given the opportunity, hog the limelight or make transient appearances in a moving performance. Embedded in this performance are new contexts, new dynamic niches, for all and sundry to occupy, generating diversity over a succession of temporal and spatial scales.

Very different sequences of appearance may occur in the prunings, logs and stumps that result from the cut and thrust of forest management by human beings. The cutting causes sudden exposure of the tree's interior and less chance for those that have been biding time there to fulfil their potential before outsiders arrive. Sequences from less to more actively decay-causing fungi, arriving from air or soil, capitalize on the disruption, in much the same way as those that invade wounds.

EMERGING OUTWARDS

Sooner or later the time comes when a fungus emerges from its feeding or hiding place to spread itself. This is the time when the tree's fountain becomes active, delivering water from sites of gathering to sites of distribution through structures that range over scales of space and time from those of individual hyphal tubes to assemblies of hundreds, thousands, millions, billions ... of tubes.

Dissemination

When the fungal fountain breaks up into droplets, encapsulated in spores, that can be carried by air, water or animals, the end result is dissemination – a far and wide delivery that much more often than not will fall on unreceptive surface. These fountains are the most immediately visible outward signs of underlying fungal networks, and first to attract the attention of human beings partial to their artistry, flavour and potential to deliver death, dreams and drugs. Yet these fountains are also first to deceive, not only because of the difficulty of identifying their multifarious forms as they rise and fall, but also in the extent to which they faithfully represent the efforts of their underlying production team. Like many glamorous icons, they have a fickle nature, subject to the whims of uncertain environmental contexts and prone to flounce out from or burst intrusively upon the scene at the slightest provocation. Some, it's true, like the hardy perennials of some bracket fungi, may be more dependable than others. But, for the casual observer, the overwhelming impression is of impermanence and an attention-seeking sense of occasion – no true reflection of the industry that lies below the surface. They are passed by as objects of little more than transient worth, off the beaten track.

Migration

By remaining coherent rather than breaking up into droplets, a fungal fountain can become nomadic, moving bodily onwards to profit from the serendipity of its own discoveries rather than cast its fate to the lottery of dispersion by outside forces. Some self-determination remains possible as hyphae travel individually or collectively, creating and following

paths of least resistance, dwelling awhile where their environment offers hospitality, moving on where it is unsupportive or even hostile.

This, then, is the hunter-gatherer pattern of many of the most overtly terrestrial and territorial fungi as they forage amongst roots and litter. As with all kinds of expeditionary forces, the way that they distribute themselves depends on the balance between reward and effort embedded in the likelihood of coming across suitable supply depots within relatively long or short range of their current base.

Where supply depots are widely separated, but likely in that very fact to be relatively large, individualistic exploration is favoured. Here, effort is focused along diverging, infrequently branched channels that extend from autonomous growing points potentially capable of being directed, or redirected, towards the scent of their quarry. Depending on their operational scale, these channels may be individual, stolon-like hyphae that can range over up to centimetres, or root-like gatherings of hyphae that can range over up to metres of space. The rhizomorphs of *Armillaria* species are the most extreme example of the latter.

Where depots are smaller, but more plentiful, a more collective organization that spreads itself as a coherent network becomes effective. When supplies are evenly distributed, as in a bed of leaf litter, the network will retain a circular symmetry, as in a fairy ring. When happening across unusually rich or barren locales, however, the network will, if capable of relinquishing its past, redistribute effort from unrewarding to rewarding pathways and so reorganize into arcs or sectors that continue on their way. What was once a single exploration, radiating on a circular front, regroups in much the same way as a bush fire whose flares become isolated by the exhaustion brought about by their own past degradations.

Interconnection

A nomadic life need not be pursued forever, but can itself lead to settlement if systems retain attachments to their past rather than burning their boats. So it is that in many fungal wanderers, especially basidiomycetes, the channels of exploration can, once they have successfully formed links between supply depots, be converted into channels for communication. Initially tenuous connections become reinforced into heavy-duty trunklines that support an ever-increasing flow of traffic along pathways memorized into persistence. The depots then become stations, nodes in self-sustaining fungal networks that become establishments in their own right. Movement in space is superseded by stability through time, as the system becomes a trap rather than a discoverer: resources come to it by entering the confines of its web; it no longer reaches out to find them, but readily accepts donations, wherever they may come from.

In such ways may decomposer fungi such as *Phallus impudicus* and *Tricholomopsis platyphylla* lace together woody debris ranging in scale from small fruits and twigs to tree trunks, the latter like sleeping Gullivers waking to find themselves tied down by mycelial cords to the forest floor. And any fallen remnant from the tree's canopy is destined for

the same fate as contact with the fungal network allows the release of pent-up colonizing power derived from other remnants' disintegration.

Not only the dead find themselves incorporated into a collective recycling system: living roots also are bound into communion by the emergent networks of mycorrhizal fungi. This is a communion of the living which transcends age and species, so that the above-ground superstructure of trees is interconnected by a below-ground fungal infrastructure that mobilizes resources along labyrinthine channels that find their ultimate expression in fruit bodies and a far and wide dissemination of droplets.

LOVING AND CONFRONTING NEIGHBOURS

As fungi surf surfaces, penetrate deeper, exploit breakdown and emerge outwardly, so they are inevitably prone to encounter others of the same or different kinds. Their future then depends critically on whether they react to these others as partners, competitors, subjugates or fellow travellers. Which of these reactions occurs depends, in turn, partly on the genetic make-up of the participants, and partly on the dynamic context of their encounter.

Togetherness

Where the participants belong to the same species, they have the chance, through fusion of their boundaries, to join forces in whole or in part. Such unions may have a sexual end – the love of other-than-self to provide a context for the generation of varied offspring, or a bodily function – the pulling of self together. In many fungi, these contrasting roles are kept separate by confining sexual unions to private parts – specialized cells or organs for the temporary or persistent co-existence of disparate genetic information. Other-than-self can then be rejected bodily but accepted sexually without contradiction: disseminative fountains emerge from sites where mating has occurred whilst the rest of the network sets to work, preserving its individuality. Such is the pattern for many ascomycetes. Many basidiomycetes, however, lack private parts and so negotiate both their sexual and bodily encounters through fusion between unspecialized hyphae. Here, the result of sexual union is the emergence of an independent network, a 'secondary mycelium', containing genetic information from two, potentially disparate and consequently disagreeable sources. All is well, so long as this disparate information complements rather than conflicts, but all the while the secondary mycelium follows a precarious path between love and war, in serious need of marriage guidance from its mating compatibility genes if it is not to disintegrate.

For participants belonging to relatively unrelated species, neither bodily nor sexual union is possible. Nonetheless, their activities and consequent impact on their surroundings may yet be complementary, so that one enhances, or at least does not worsen, conditions for another. They may then be able to co-exist at the same locale, either as a community in space or

as a succession over time. Since all fungi have common needs for sources of organic carbon, water and minerals, however, it is difficult for them, should they be unable to integrate their boundaries, to avoid competing with one another when drawing from the same resource pool.

Separation

When the potential for competition and conflict overwhelms the possibilities of togetherness, the only route to co-existence may be through separation – the assertion of territorial boundaries that divide neighbours into distinct domains or sectors enclosed within some larger boundary such as the perimeter of a woodland or the surface of a log. In such ways, neighbouring fungal networks may emulate the pattern of adjacent river basins that occupy the same landscape whilst being partitioned by their watersheds.

The frontiers between fungal territories are often visible as no-go areas and demarcation zones that map the distribution of individual systems both of the same and of different species over widely ranging scales. In decaying wood, these systems produce colourful three-dimensional mosaics of interlocking, variously outlined, segments with an ornamental quality to delight the observer who cares enough to notice as well as to see. Amongst lichens and within the blades of broad leaves they form two-dimensional, jig-saw-like arrays. As agents of root disease they may lay low patches of forest large enough to be visible from aircraft.

As befits the dynamic, interactive systems that produce them, fungal territorial frontiers are not merely passive barricades, though they can be reinforced by such. Rather, they are sites of considerable tension and upheaval that contain rather than prevent damage.

Where neighbours of the same or closely related species are separated, the tension between them is usually genetic, resulting from the fusion of sexually unspecialized hyphae populated by nuclei containing disagreeable information, and so known as somatic incompatibility. In basidiomycetes, these hyphae usually belong to secondary mycelia in which two disparate kinds of nuclei can be company, but more than two kinds is an unruly, recombinatorial crowd whose disagreement leads to degeneration – the chemical breakdown of protoplasm that is the hallmark of rejecting other-than-self. In ascomycetes, even two kinds of nuclei is a crowd, unless locked in with each other in private chambers of sexual togetherness.

Where disparate species are separated, the warding-off may occur at a distance, through the release of arresting chemicals that diffuse through air or liquid, or only after contact between systems. Where contact is necessary, the engagement that leads to degenerative interference and divorce occurs both at the level of individual troops and massed ranks of hyphae that line up, and often darken in opposition to one another.

As with the poppies that bloomed from the mud of Norman's land in Flanders, there are always some that can benefit from the separation of warring neighbours by sitting on the fence. So it is that in wood containing territories of such decay-causing basidiomycetes as *Coriolus versicolor* and *Stereum hirsutum*, that microfungi with blackened hyphae, such as *Chaetosphaeria myriocarpa*, *Leptodontium* and *Endophragmium*

species, can occupy the war zones, adding their own darkness to the colour of the adversaries' degeneration. In other situations the war zones provide refuge to support the activity of small animals, like springtails and fungus gnats.

Taking over

When other-than-self cannot be warded off, and peaceful togetherness is precluded, a third possible outcome of fungal encounters looms: invasion and consequent disintegration and replacement or subjugation of the self. Within species or between closely related species, the invasion may take place within the hyphal tubes themselves as genetic information contained in nuclei or other packages, including viruses, immigrates through fusions between a system and its neighbour(s). Between disparate species, the invasion may result from the stealthy infiltration of individual hyphae that disrupt or divert the establishment in their own brand of revolutionary guerrilla warfare or parasitism. Alternatively, the invasion may be brought about by massed movements of hyphae organized into coherent expeditionary forces of the same ilk as those that enable migration across all kinds of hostile or unsupportive domain.

MANAGING THE FLOW

So, there is altogether far more to the life of the networks that sustain fungal fountains than the simple exploitative conversion of natural resources into growth. These networks are sophisticated, sensitive, responsive, versatile systems that have much in common with all kinds of social organizations, including human societies, and in which exploitative growth alone detracts in many ways from the qualitative richness and sustainability of life. They live, as we do, in a world in which resource supplies fluctuate and are to some degree unpredictable and non-renewable and so should not be taken for granted. They keep going by managing the flow within their dynamic boundaries to suit the circumstances in which they find themselves, bridging gaps between times and places of plenty and times and places of shortage. Perhaps we can learn from them.

As in a river, whose pattern depends on the dynamic relationship between its ingredients and catchment, the art of managing the flow lies in feedback. Feedback provides the feeling necessary to keep in touch – to generate and respond to local conditions in such ways as to cause a counteraction between the expansive drive that arises from uptake of energy sources and the resistive constraint that results from the containment of energy within a dynamic boundary.

Three basic properties of boundaries – deformability, permeability and continuity – and one basic contextual condition, the relative availability of oxidizing and reducing power, mediate this feedback. With respect to the basic condition, it is vital to recall both that the source of chemical energy for all life forms lies in the giving and taking of electrons, and that one electron taker, in particular, represents the living world's first, most potent, most dangerous addiction – oxygen. By taking electrons one at a time in the course of being reduced,

ultimately, to water, through the burning of respiratory fuel, oxygen releases large quantities of chemical energy. At the same time, however, it forms unstable intermediates – reactive oxygen species – that can disrupt the chemical integrity of protoplasm by reacting with other molecules to generate free radicals with revolutionary inclinations. These reactive species accumulate when the oxygen within cell boundaries is incompletely reduced, due, directly or indirectly, to an insufficiency of fuel, leading to a condition known as oxidative stress.

Living systems in general, and fungi in particular, can respond to the threat and promise of oxygen in contrasting ways. Firstly, where there is plentiful fuel, they can burn it off, using the chemical energy released thereby to support the proliferation of their boundaries. Where there is fuel shortage – or oxygen excess – there are three further options. They may mop up reactive oxygen species internally by producing antioxidant enzymes or compounds, excreting the latter as what have been called ‘secondary metabolites’: this option is only really suitable in watery environments where the movement of oxygen, as with all gases, is relatively slow. They may insulate themselves by incorporating oxygen into an impermeable boundary layer rather than letting it in – an essential feature in terrestrial environments where oxygen in the gaseous phase can diffuse ten thousand times faster than through water. They may actively enable or passively allow degeneration to occur.

These varied responses are linked, in turn, to four fundamental processes of flow management: assimilation, conservation, exploration and recycling.

Assimilation – self-fuelling

Where fuel is plentiful, a system can capitalize, maximizing exploitation regardless of waste by producing boundaries that are both permeable – enabling uptake, but allowing leakage – and deformable – allowing the expansion of uptaking, leaky surface at a compound interest rate. The system uses fuel to gain more fuel. As it does so, the accumulation within its boundaries leads first, as in a swelling, germinating spore, to a symmetrical or isotropic expansion in all directions. Then, once a threshold capacity is reached, polarization and subdivision or branching occurs, in the pattern of the headward-eroding valleys of river tributaries, so increasing the free surface of the system. All is well, until the supplies necessary to sustain the dissipative surface run short, whence, if the system carries on the same way, it will burn itself out.

Conservation – self-containment

By fixing and sealing its boundaries, a system can produce survival structures in which it can conserve what it has already gained, but in so doing enters a self-imposed dormant state that has to be broken if further expansion is to occur. The rigidification, impermeabilization and fusion of boundaries can all play a part in this process, producing, in fungi, such structures as survival spores, sclerotia and pseudosclerotia.

Exploration – self-discovery

By producing an impermeable but deformable boundary, a system can explore hostile or unsupportive environments by channeling, rather than leaking, resources gained in more hospitable places. This is the basis for the ultimate self-expression that lies in the emergence of disseminative and migratory fungal fountains that branch, if they branch, in the pattern of the distributaries within a river delta.

Recycling

By cutting off and feeding from the degenerating remains of its past – a system can free itself to move on from the stranglehold of its own entrenched establishments. Death becomes life, a basis for redeployment from redundancy and protection from takeover, so maintaining a fresh, phoenix-like vitality epitomized in fungi by all kinds of emergent phenomena, from the vacation of a spore to the travelling wave of a fairy ring.

Turning the spiral – the interdependence of self-differentiation and self-integration

As energy supplies wax and wane, so living systems combine processes that maximize the generation of dissipative free surface when there is plentiful fuel with processes that minimize this surface when there is shortage. Boundary-maximizing processes result in the proliferation of the self through expansion and subdivision and so can be thought of as self-differentiation. But as these processes demand more and more fuel, so they in time surrender selves to an incoherent, entropic state in an all-consuming fire from which no thing can emerge. Boundary-minimizing processes of fusion, sealing and redistribution on the other hand prevent this consumption by pulling selves together into more coherent, less dissipative states, and so can be thought of as self-integration. But if taken to completion, these states become more and more constraining until time comes to a standstill. To thrive *and* survive, life forms *both* differentiate into a complex profusion of form *and* integrate into elegant simplifications from which life can not only begin again, but amplify, with the benefit of past experience.

MORAL FROM THE MYCELIUM

Individuality is nurtured, valued, but restrained from running away with itself. Responsibility is shared, collective. Perhaps that is what it really means to belong to a dynamic, evolvable, responsive society.

Thanks to all those fellow travellers who have joined and helped me along some part of the way, often labouring under the misconception that it was *I* who was instructing *them*. I could not have done without their support and guidance.