

PLANT SYMBIOSIS AND PATHOLOGY

Alan Rayner

‘Ecological Relationships – Plants in the Context of Other Organisms’

Aim: *To understand the ecological context in which plants grow and interact with one another, other organisms and their physical surroundings in natural and cultivated environments. Thereby to develop a balanced, all-round perspective of plant health and disease that can inform practical approaches to environmental and crop management.*

Topics: *‘What is a healthy plant? – concepts of plant health and disease’; ‘Modes of interaction between plants and other organisms as complex dynamic systems’; ‘Epiphytes and Endophytes’; ‘Patterns and Processes of Decay in Trees’; ‘Mycorrhizas’; ‘Parasitic Plants’; ‘Human Influences on Plant Health’.*

Outline Notes to accompany Lectures

TOPIC 1: “What is a healthy plant? – Concepts of Plant Health and Disease”

Fundamentally, the Biol0032 course is concerned with two basic issues:

- (i) Through what mechanisms and processes do plants thrive or decline in the presence of other organisms in natural and cultivated environments?
- (ii) How do these mechanisms and processes affect ecological function and our practical approaches to environmental and crop management?

Underlying these issues are the PRESUPPOSITIONS we make when deciding whether a plant should be regarded as healthy or diseased. This decision depends very much on CONTEXTUAL VIEWPOINT or FRAME OF REFERENCE.

For example, people viewing an ancient oak tree with a hollow centre from different perspectives are liable to have different ideas about its health. For example:

- (i) A commercial timber merchant;
- (ii) A Public Safety Inspector;
- (iii) An artist;
- (iv) A conservationist;
- (v) A lover of veteran trees;
- (vi) An evolutionary thinker.

So, which view, if any, is ‘correct’?

Here, we encounter one of the most profound problems affecting human thinking. This is our OBJECTIVE tendency to ‘DEFINE’ or SINGLE ‘THINGS’ OUT from the continuous spatial CONTEXT or DYNAMIC NEIGHBOURHOOD that they both include and are included within.

River systems, which both shape and are shaped by the landscape they flow through, provide a good metaphor for appreciating the one-including-other relationship between content and context, whereby ‘content is contextual’, as epitomized by Pasteur’s dying words: ‘the microbe is nothing, the terrain is all’.

If we truly want to gain an all-round understanding rather than a one-sided view of plant health, should we really view plants or their associated organisms as isolated entities or OBJECTS in discrete snapshots of space and time? Should we not rather view them as EMBODIED WATER FLOWS, fluid dynamic relational PLACES that relate with one another in complex and variable ways, depending on their situation? When we view them this latter way, a variety of DYNAMIC PROPERTIES of plants become apparent that are of considerable relevance to understanding their ecological relationships.

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1. PLANTS ARE, TO A GREATER OR LESSER EXTENT, DEVELOPMENTALLY INDETERMINATE (DYNAMICALLY BOUNDED), VERSATILE SYSTEMS THAT RESPONSIVELY CHANGE THEIR FORM IN ACCORD WITH CHANGING CIRCUMSTANCES

2. PLANTS ARE HYDRODYNAMICALLY PATTERNED

Plants are, in a deep sense, water courses.

As with any water course, the distribution pattern and consequent outward form of a plant depends on three kinds of resistance and associated boundary properties:

- (i) Resistance to expansion – deformability/rigidity
- (ii) Resistance to exchange between inside and outside – permeability/impermeability
- (iii) Resistance to throughput or displacement of contents – continuity/discontinuity.

By varying these resistances/boundary properties according to circumstances, plants can modulate between FOUR FUNDAMENTAL LIVING PROCESSES: CONSERVATION, REGENERATION, EXPLORATION, RECYCLING.

3. DEATH IS A WAY OF LIFE AND NOT NECESSARILY UNHEALTHY

Processes of leaf senescence and abscission, wood formation, branch death and shedding, heartwood formation and decay all play important redistributive roles in plants. In some cases, these processes may be initiated or augmented by other organisms.

4. PLANTS ARE BOTH MEMBERS OF, AND ARE THEMSELVES, DYNAMIC COMMUNITIES

In nature, plants cannot and do not exist in isolation. In a profound sense they are (like us) dynamic 'host spaces' - providers and inhabitants of living space, nested over scales ranging from microcosm to macrocosm.

We cannot, therefore, isolate the question of the individual health of a plant from that of the collective community to which it plays host and that of the collective host community within which it is itself included.

So,

WHAT IS A HEALTHY PLANT?

When we view a plant and ask after its health, what clues should we look for?

Suppose that you see a fungus growing on a dead or dying part of a plant. How do you interpret this situation? It is only too easy to conclude from making the kinds of one-sided definitive assumptions characteristic of 'germ theory' (and certain current 'Heads of State' I can think of) that the fungus is attacking the plant from outside - an 'alien' invader. From here it is a small step to leaping to the defence of the plant, and wanting to *do* something to stop or indeed *eliminate* the fungus, especially if you have some vested interest in the plant.

A moment's reflection will, however, inform you that there could be many, varied and complex explanations for the observed situation. To begin with, the plant might be dead or dying because of the

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presence of the fungus. Or the fungus might be present because the plant is dead or dying for some other reason. You might try to use the definitive set of rules and methodology known as 'Koch's postulates', to discriminate between these alternatives. But then what if the dying of the plant and the activities of the fungus somehow augment each other? And then again, is the death or dying of the plant necessarily a 'bad' thing? Is it an aspect of the natural redistributive processes that are vital to the life of plants (and fungi) both individually and collectively? Is it the result of some externally induced stress or damage, perhaps associated with human intervention?

Clearly, any misreading of the situation is liable to engender inappropriate practice that 'does more harm than good'. The 'art' of balanced practice (what I call 'inclusional' practice) therefore lies in learning how to read the situation in an imaginative yet realistic way, which is open to possibility, through understanding how and why 'context is all'

Our concepts of plant health and disease may therefore differ fundamentally depending on whether we are viewing:

- (i) In the ecological and evolutionary context of the plant, whereby HEALTHY = 'IN PLACE'/IN TUNE WITH CONTEXT and DISEASED = 'DISPLACED' – 'DISSONANT', DIS-EASED
- (ii) From an objective, performance-centred perspective, whereby HEALTHY = PRODUCTIVE, DEPENDABLE, REGULAR and DISEASED = UNPRODUCTIVE, UNRELIABLE, IRREGULAR

TOPIC 2: MODES OF INTERACTION BETWEEN PLANTS AND OTHER ORGANISMS AS COMPLEX SYSTEMS

Just as plants cannot be regarded as discrete, unchanging entities in space and time, so neither can the organisms that they interact with. This is especially true of fungi, arguably the most frequent and intimate associates of plants, which, if anything, are even more developmentally indeterminate, versatile and dynamically responsive – as is evident from the way they grow and interact with one another and their surroundings. Both individually and collectively, fungi can exhibit: i. Diverse spore germination modes; ii. Coenocytic or septate mycelium; tributary or distributary-like branching patterns; dendritic or networked mycelia; assimilative or non-assimilative hyphae; diffuse or aggregated hyphae; generative and degenerative patterns; efficient foraging in heterogeneous environments; capacities for re-organisation in response to interactions with others. Like plants, fungi can be thought of as hydrodynamic systems that modulate between assimilative, conservative, explorative and re-distributive functional roles by varying the deformability, permeability and continuity of their boundaries. Moreover, it seems likely that they do this in fundamentally similar ways to plants, through their responses to availability of reducing power and oxidative stress.

So, given that not only plants, but also the other organisms they interact with are complex dynamic systems whose responses vary according to circumstances, it should be no surprise that the outcome of their interactions may also be complex and varied.

Whilst we should, therefore, be cautious about predicting specific outcomes of interactions between plants and other organisms, this does not prevent us from identifying the various kinds of relationship that are possible. In doing this thoughtfully, the first thing that becomes evident is the *sheer variety of possibilities*, and *different criteria* that can be used in viewing these possibilities. Let's look at some of these criteria.

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1. CLOSENESS OF ENCOUNTER

Interactions occur in three distinctive locations:

- (i) Outside the physical limits of the plant's surface, but within its 'sphere of influence', i.e. in the 'rhizosphere', 'phyllosphere' and 'caulosphere'.
- (ii) At the plant surface, i.e. on the 'rhizoplane', 'phylloplane' or 'cauloplane'.
- (iii) Within the interior of the plant.

2. DURATION OF ENCOUNTER

Here there is a gradation from encounters that may be transient to associations that continue throughout the life span of a plant – and sometimes beyond, as in seed-borne infections. Persistent, intimate associations are often referred to as SYMBIOSES, in the wide sense originally intended by de Bary, who introduced this term during the nineteenth century.

3. OUTCOMES OF ENCOUNTER IN TERMS OF COSTS AND BENEFITS TO PLANT AND OTHER ORGANISM

If net benefit is regarded as positive, net cost negative and no net cost or benefit as zero, then six categories of relationship can be identified:

++ mutualistic

+− parasitic, predaceous, herbivorous, exploitative, [allelopathic, pathogenic]

00 neutral

0+ commensal

0− amensal [allelopathic, pathogenic]

-- competitive

4. MECHANISTIC BASIS OF INTERACTION OUTCOMES

Most emphasis in understanding the mechanistic basis of plant relationships with other organisms has been NUTRITIONAL.

Relationships in which plants are receivers as well as providers, and consequently grow more, as in many mycorrhizal associations, are seen as 'mutualistic'. Relationships in which plants are providers but not receivers, and consequently grow less, are seen as parasitic if the mode of nutrition is absorptive, as with fungi, or as herbivory if it is ingestive, as with many animals. Relationships in which plants are receivers of mineral nutrients but not providers of carbon are regarded as predaceous, carnivorous or more specifically insectivorous where they receive from animals, or as hemiparasitic where they receive from other plants. Relationships in which plants are receivers, but not providers, of both carbon and minerals, as in plants lacking chlorophyll, are regarded as parasitic, but with the plant rather than the other organism as parasite.

But, but, but,...

No consideration is given to indirect effects resulting from the impact of interaction on ecological context, and hence a longer run view.

More generally, there are a vast variety of mechanisms by which organisms can influence one another's lives, besides nutrition:

- (i) Protection from/exposure to pathogens (including physical and chemical factors as well as other organisms).

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- (ii) Developmental
- (iii) Environmental
- (iv) Dispersal, Dormancy and Viability of Propagules

5. NUTRITIONAL MODE

This may be **INGESTIVE** or **ABSORPTIVE**. When absorptive, as with fungi, distinctions are often made between **Biotrophy**, **Necrotrophy** and **Saprotrophy**:

Biotrophy: obtaining nutrients from living cells or tissues, often via specialized transfer organs known as 'haustoria'.

Necrotrophy: Killing cells or tissues in the process of obtaining nutrients from them.

Saprotrophy: obtaining nutrients from non-living substances.

Given the indeterminacy of fungal life styles, there is no theoretical reason why more than one of these modes should not be combined within the life span of an organism, a fact which relates to...

6. DEPENDENCY AND SPECIALISM OF ASSOCIATION

There is a gradation from

| | | |
|--|--------------------------|-------------------|
| FACULTATIVE | OBLIGATE | |
| Which roughly but by no means precisely corresponds with | | |
| UNSPECIALIZED | SPECIALIZED | |
| LESS INTIMATE | MORE INTIMATE | |
| WIDE HOST RANGE | NARROW HOST RANGE | |
| SAPROTROPHIC | NECROTROPHIC | BIOTROPHIC |

So, when we think of the role of relationships with other organisms in the context of plant health and disease, it may be well to keep our eyes and minds open to the implicit possibilities of the wider picture rather than fixed on the immediate view. In a sense, every apparent ending to a discrete, well-defined story makes an opening for another possibility.

TOPIC 3: EPIPHYTES AND ENDOPHYTES

LIVING ON PLANT SURFACES: EPIPHYTES

Plant surfaces can support a wide variety of other organisms, either transiently, as when an animal alights upon the surface, or more persistently, as when the surface provides purchase for colonies of microorganisms, animals and climbing or epiphytic plants. The surface may provide primarily physical support, as with many plants and animals, or it may also serve as a source of nutrients, as with heterotrophic microorganisms. These nutrients may either originate within the plant as secretions and exudations, or they may be deposited onto the plant surface from the atmosphere, e.g. leachates, pollen, 'dirt', pollutants. Surface-inhabiting organisms are of interest in the following ways:

- (i) They occupy a very exposed position, especially those inhabiting aerial as opposed to underground surfaces.
- (ii) Many 'pathogenic and mutualistic' organisms become established via initial colonization of surfaces.
- (iii) Surface-inhabiting organisms can both impede and enhance colonization by others.

LEAF-INHABITING COMMUNITIES – THE 'PHYLLOPLANE/PHYLLOSHERE' MICROFLORA

From their very emergence from the bud, leaf surfaces are covered in assemblages of microorganisms. These organisms can readily be detected by culturing from leaf washings, or by direct observation using light or electron microscopy – whence it is often evident that they tend to concentrate along the

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underside of veins and midribs. The 'mirror yeasts', e.g. *Sporobolomyces roseus* can be detected by suspending a leaf above a nutrient medium.

Characteristically, as the leaf matures, there tends to be a progression from communities dominated by bacteria and yeasts towards a greater abundance of mycelial fungi – e.g. species of *Cladosporium*, *Alternaria*, *Epicoccum*. One fungus in particular, *Aureobasidium pullulans*, is a very common inhabitant, capable of existing both in yeast and in mycelial forms. It is also relatively resistant to heavy metal and sulphur dioxide pollution, so its increased incidence relative to the more sensitive *Sporobolomyces* yeast can be used to measure atmospheric pollution.

The mycelial fungi have better anchorage than the yeasts and are more capable of invading the leaf interior, to which access may be enhanced by the activity of yeasts in eroding waxy cuticle. By the same token, it is widely thought that members of the phylloplane community limit colonization opportunities for leaf parasites.

BARK-SURFACE-INHABITING COMMUNITIES

By comparison with leaf surfaces, bark surfaces are long-lasting interfaces that continue to expand and become topologically more complex as they mature, and which are covered by layers of cork, consisting of dead suberized cells. Bark-inhabiting communities can hence ultimately become highly complex, heterogeneous and elaborately structured assemblages of both autotrophic and heterotrophic organisms.

Carbon sources for heterotrophic bark-inhabiting organisms include:

- (i) Living or non-living tissues or remains of autotrophic colonists;
- (ii) Organic deposits from atmosphere;
- (iii) Sources originating within the tree;
- (iv) Scale insects

LIVING WITHIN PLANT INTERIORS – ENDOPHYTES

A wide variety of organisms find a habitat actually within the interior of plants, including many fungi and animals. Where such organisms are detected in material lacking visible symptoms, then they fall within the narrow definition, which has been used increasingly within recent years, of 'endophytes'.

Endophytic fungi can be found in a variety of forms and locations. Some should perhaps not strictly be regarded as endophytes in that they are present as localized sub-cuticular infections, as with a number of 'latent infections' of fruit, e.g. *Gloeosporium musarum*, which causes banana anthracnose. Others are truly internally located, e.g. *Rhizoctonia parkeri* persists for long periods as hyphae within single epidermal cells of Douglas Fir needles, whilst *Phyllosticta abietis* grows as intercellular hyphae in the mesophyll of these needles.

Over the last 20-30 years, there has been an upsurge of interest, both in their potentially beneficial as well as potentially damaging effects, as well as greater appreciation of their ubiquitous occurrence.

The main beneficial effects that have been envisaged are various kinds of protection against pathogens, e.g.:

Rhizoctonia parkeri infects galls caused by gall midges and induces high larval mortality.

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A *Phomopsis* species deters colonization of dead or dying elm bark by bark beetles, and hence acts as a kind of natural biological control, limiting spread of Dutch elm disease fungus, *Ophiostoma novo-ulmi*, which is carried by these beetles.

A variety of Clavicipitaceous endophytic fungi produce toxins that may deter ingestion of their host plants by herbivores. One of these is responsible for 'ryegrass staggers', which affects sheep and cattle eating infected ryegrass (*Lolium* spp.). The toxin, 'lolitrem', is an example of a tremorgenic mycotoxin. Another member of this group of fungi, *Epichloe typhina*, causes 'Choke' disease of grasses. Symptoms only become evident on flowering stems, where the fungus produces its ascocarps on a thickened segment of stem, at the same time suppressing flowering and hence seed-production by the host. However, the fungus also enhances clonal propagation, in the form of stolon production by the host.

This last example draws attention to the fact that fungi that are symptomless endophytes at one or more phases of their interaction with plants, may give rise to symptoms at other phases or in other circumstances. This may be of especial significance when predicting the possible responses of plants to environmental change, in that plants which co-exist in balance with their endophytic communities under 'normal' circumstances may be overrun by these communities if conditions change; e.g. 'Diamond-bark disease and Sooty-bark disease of sycamore (*Acer pseudoplatanus*) caused by *Dichomera saubinetii* and *Cryptostroma corticale*, respectively, which are induced by 'drought stress'.

TOPIC 4: PATTERNS AND PROCESSES OF DECAY IN TREES

It's one of those facts of life that trees become decayed, in whole or in part, as a result of fungal colonization. They also become decayed in a wide variety of ways: their centres may be hollowed out, from top to bottom or from bottom to top; their roots may rot; whole trunks and branches may die and become decayed throughout their length, finally to become broken or detached; decay may spread from injuries inflicted by animal, human, frost and storm.

How can we make sense of this variety? Can we identify any general patterns – recurrent themes in the manner of colonization and decay that hint at underlying relational processes? How might our presuppositions affect our interpretation of these patterns?

For many years, thinking about decay in trees focused on the explicit destructive action of the decay fungus upon the tree and hence on the underlying notion that the decay fungus is bad for the tree.

This kind of thinking culminated in the 1970s with the emergence of a concept known as 'compartmentalization of decay in trees' (CODIT). This concept, which continues to be influential to this day, effectively explains observed patterns of decay in trees in terms of defensive barricades or 'walls' produced by the tree in order to exclude or confine decay fungi outside or within discrete boundaries.

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CODIT recognised two recurrent themes:

- (i) Zones of fungal colonization from wounds have a characteristic shape, dictated by the nature and location of the wound.
- (ii) Colonized wood becomes discoloured before it becomes decayed, and when and if decay does develop, then it does so initially in regions closest to the wound.

One interpretation of these patterns was that the tree was impeding decay by producing defensive barriers –called ‘Walls 1, 2, 3 and 4’ in order of increasing ‘strength’ – and that the non-decay organisms prepared the way for the decay fungi by breaking down these barriers.

But an alternative interpretation may be possible, based not on the explicit, direct interaction of tree versus fungus, but rather on the implicit, contextual qualities of the tree as A HOST SPACE.

Here, we can recall that a tree can be thought of as a system that connects sites of active uptake of water and mineral nutrients in soil with sites of energy assimilation in a distant, photosynthesizing canopy. Between these sites are annually renewed, axial and radial series of pipelines or conduits in xylem, phloem and medullary rays, insulated by bark. These pipelines are inevitably prone to ‘cavitate’, i.e. become aerated as they get older, and so functionally conductive pipelines tend only to be found in the outermost annual rings. Living cells in aerated older or damaged wood undergo a switchover to secondary metabolic acetate and shikimate pathways associated with oxidative cell death and production and polymerization of hydrophobic and often toxic or inhibitory phenolic and lipid compounds. They may also produce ‘tyloses’. The effect is to generate water-repellent boundaries that seal off conductive from non-conductive tissue, limiting ingress of air.

The wood of a tree is, therefore, a highly heterogeneous, dynamic living space in which the distribution of water is reciprocally related to the distribution of ‘air’ (in the sense of a gaseous phase – the actual chemical composition of this phase may be very different from atmospheric), and where the presence of air can induce secondary metabolism.

Functionally intact, bark-protected, water-filled sapwood is intrinsically inhospitable to active, aerobic, mycelial fungi. Decay and associated active mycelial growth are highly oxygen-demanding processes, and the supply of oxygen through liquid water rather than through a gaseous phase (where diffusion is 10,000 times faster) is insufficient to sustain these processes. So, in order for decay to become established, some kind of dysfunction in the water-carrying capacity of sapwood is required.

FIVE BASIC SCENARIOS LEADING TO THE ESTABLISHMENT OF DECAY-CAUSING FUNGI IN THE WOOD OF TREES

1. Colonization of Heartwood: Heartrot

Loss of conductive function and associated increased gaseous phase enable development of and decay by host-specialized fungi able to tolerate/overcome low oxygen/high carbon dioxide gaseous regimes and the presence of phenolic and terpenoid extractives. Although these fungi are often slow-growing and non-combative, they can over many years establish extensive individual territories and correspondingly produce large, sometimes perennial, fruit bodies.

2. Colonization of Exposed Sapwood: Unspecialized Opportunism

Sudden death of or removal of bark cover, resulting from disease or injury, exposes the underlying sapwood to drying and aeration, enabling colonization by potentially numerous, relatively unspecialized fungi, with non-decay processes and organisms often active prior to establishment of decay processes and organisms. The pattern of dysfunction – and limitation of this dysfunction by boundary-sealing processes – determines the pattern of colonization and depends on circumstances

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both intrinsic and extrinsic to the tree: e.g. wounds inflicted when water columns are under tension allow more colonization than when water columns are under pressure.

3. Colonization of Intact Sapwood in ‘Stressed’ Trees or Parts of Trees: Specialized Opportunism

Many decay fungi establish in apparently intact but dysfunctional sapwood of uninjured trees or parts of trees. They develop rapidly and extensively underlying strips or entire cylinders of dead bark, often show strong host-preferences and are contained at junctions between branches of different order. Important in stressed trees and dysfunctional branches or stems, these fungi probably establish quiescently as ENDOPHYTES in functional sapwood and/or bark (hence ‘specialized’) then become active agents of decay when wood becomes aerated (hence ‘opportunistic’).

4. Colonization of Dead Standing Trunks and Attached Branches: Desiccation-Tolerance

Fungi colonize aerated, dead wood that has lost bark cover, but need to withstand fluctuations of moisture availability associated with varying atmospheric humidity and insolation.

5. Fungally-Induced Dysfunction: Active Pathogenesis

Rather than depending on other factors, true pathogens gain access to wood because of their own ability to cause dysfunction.

TOPIC 5: MYCORRHIZAS

The inclusion, by plant roots, of biotrophic mycelial fungi to form mycorrhizas is an almost ubiquitous feature of terrestrial plant communities, the principal exceptions being in the Cruciferae, Chenopodiaceae, Caryophyllaceae and Cyperaceae.

Mycorrhizal fungi lie at the intimate end of the spectrum of closeness of encounter from the rhizosphere through rhizoplane to root interior. Whereas entry to the root interior by necrotrophic fungi results in root death, mycorrhizas result from biotrophic nutrition. Mycorrhizas are generally regarded as beneficial to the plant, as evidenced by improved growth in the presence of the requisite fungi on nutritionally restrictive soils. However, the kinds of benefit and their relation to potential costs may not be fully understood, and are likely to vary with contextual circumstances. I have already mentioned that whereas the kind of benefit is usually considered to be nutritional, many other possibilities exist, including protective, developmental and environmental effects. Moreover, where the fungus obtains carbon sources from the plant, as in all those mycorrhizal associations assumed to be mutualistic, the scale on which plant resources are diverted can be very large. It has been estimated that fruit body production by ectomycorrhizal fungi may draw off as much as 25 % of a tree’s annual assimilate – notwithstanding that the tree could not produce so much assimilate anyway in the absence of the fungus – at least not on nutritionally restrictive soils. Whilst the tree’s shoots produce their own fruits, the tree’s roots produce fungal fruits by means of supplies diverted from shoots. It is therefore of interest that mycorrhiza formation is less prolific on highly fertile (or fertilized) soils, where the fungal partner is less ‘needed’ than on nutritionally restrictive soils. Another issue that should be borne in mind is that we know very little about patterns of nutrient distribution through mycorrhizas in natural stands of vegetation, since the vast majority of experimental mycorrhizal studies have been made with plants grown outside their natural context, often as seedlings in artificial containers in glasshouses.

TYPES OF MYCORRHIZAL ASSOCIATIONS AND THEIR NATURAL DISTRIBUTION PATTERN

Six main types of mycorrhizas have been distinguished: ectomycorrhizas; arbuscular; ericaceous; arbutoid; monotropoid; orchidaceous. Only the first three of these are generally regarded as MUTUALISTIC, with the plant providing organic carbon and fungus providing inorganic nutrients.

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The distribution of these types varies with altitude/latitude and corresponding soil and vegetation characteristics.

I. Ectomycorrhizas (sheathing mycorrhizas)

These are the predominant mycorrhizal type in boreal and temperate forests, where they are formed by members of the Pinaceae, Salicaceae, Betulaceae, Fagaceae and, in the S. hemisphere, Myrtaceae. They are less frequent in tropical forests, but can occur there, e.g. with Caesalpinoideae. They also extend into non-forest communities including arctic-alpine with dwarf birches and willows and mountain avens (*Dryas octopetala*), and sand dunes with creeping willow (*Salix repens*).

Location and structure Ectomycorrhizas are found in the lowermost litter and uppermost soil horizons, where they are associated with determinate, absorptive short roots that exhibit an increase in diameter, change of colour and distinctive patterns of branching in response to fungal inclusion.

Characteristically, the fungus produces a sheath of compact, sometimes pseudoparenchymatous mycelium around the short root. Some distance behind the root tip, hyphae from the sheath penetrate between the cortical cells to form the 'Hartig Net'. This Hartig net is the communications interface between fungus and host plant, and in mature mycorrhizas the outermost layers of both plant and fungal cell wall merge to form an 'involving layer' consisting of an electron-dense matrix (as viewed by electron microscopy).

Identity and host preferences of ectomycorrhizal fungi A wide range of basidiomycetes (especially Agaricales), some ascomycetes and a few deuteromycetes are considered to be ectomycorrhizal. However, evidence of mycorrhizal association is often indirect, and many fungi considered to be ectomycorrhizal may not rigorously have been shown to be so. Some examples of mycorrhizal genera are:

Agaricales: *Amanita*, *Russula*, *Lactarius*, *Suillus*, *Boletus*, *Cortinarius*

Aphyllorphorales: *Thelephora*

Gasteromycetes: *Scleroderma*, *Rhizopogon*, *Pisolithus*

Ascomycetes: *Tuber*, *Gyromitra*

Deuteromycetes: *Cenococcum*

- Species of these genera often show marked variation in preference for different hosts, some having a wide host range, others a narrow one. E.g. *Russula atropurpurea* occurs with a wide range of coniferous and angiospermous hosts whereas *Suillus grevilleiae* occurs only with larch (*Larix* sp.).
- You might like to think about what mechanisms might underlie these variations and what the ecological implications of these mechanisms might be.

Nutritional exchange between ectomycorrhizal fungi and their hosts Direct evidence for the transfer of carbon sources from host to fungus and of mineral nutrients from fungus to host in ectomycorrhizas was obtained in the 1950s and 1960s using radiolabelling techniques by Melin and Nilsson, and Harley and Lewis and their associates.

With respect to carbon-transfer, an early finding was that the fungus converted sugars from the host into compounds such as mannitol and trehalose that were inaccessible to host metabolism, so that carbon effectively flowed through a 'one-way-door' into the fungus. With respect to phosphorus, an important feature appears to be storage in polyphosphate granules in the fungal sheath as a reserve that can be mobilized at times of high demand. It also appears that many mycorrhizal fungi produce large quantities of surface-bound phosphatases, which enhance phosphate uptake from organic sources in soil. With respect to nitrogen, ammonium absorbed by the fungus is converted into glutamine and glutamic acid, which are transferred to the host. There may also be proteolytic activity, enabling uptake from organic sources in soil.

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Means of arrival and establishment of ectomycorrhizal fungi at host roots, and their ecological consequences

Two basic modes are possible:

- (i) Arrival by spores. Characteristic of 'early phase' fungi colonizing roots of pioneer trees. Establishment may be aided by being able to germinate in response to the presence of exudates from plant roots, i.e. in the rhizosphere. For example, *Suillus* spores have been shown to germinate in response to abietic acid, a diterpene resin acid produced by coniferous trees.
- (ii) Arrival by mycelium. Characteristic of 'late phase' fungi in established stands of trees. Commonly this mode of arrival is accomplished by fungi extending through soil in the form of cable-like mycelial cords. Arrival in this mode has some potentially important implications in that it enables the fungus to form interconnections between different plants, which may, depending on the degree of host preference of/for the fungus, belong to the same or different species. This sets up possibilities for resource-sharing and redistribution via the fungal network amongst members of a stand or community of plants, and between adult plants and seedlings that may in effect be 'nurtured' through 'fungal umbilical cords'.

II. Arbuscular Mycorrhizas

These are extremely widespread, and present in the fossil remains of the earliest known land plants. They occur in many habitats and vegetation types, notably grassland and tropical forest, and are especially important in many agricultural crop plants. They are produced by members of the Endogonaceae (Zygomycotina), which produce diffuse branching systems of coenocytic and also septate hyphae on the outside of roots, and can also interconnect roots of different plants. Within roots, hyphae grow intercellularly and penetrate into host cells as extremely densely and finely branched haustoria, known as 'arbuscules'. In some cases, inter or intra-cellular hyphal swellings known as 'vesicles' are also produced: these may have a storage function. Arbuscular mycorrhizas are generally regarded as extremely important in mineral nutrition of host plants, especially with regard to phosphorus.

III. Ericaceous mycorrhizas

These are found in the fine roots of Ericaceae growing in peaty heathland and moorland soils. The fungus enters cortical cells in which it forms extensive branching systems and may account for as much as 70 % of the root biomass. The external mycelium is diffuse and limited, but there are numerous entry points into host roots. *Pezizella ericae*, an ascomycete, was first shown to be capable of forming these kinds of mycorrhiza. Some Clavariaceous basidiomycetes may also be involved. The fungus is generally held to benefit the plant through improved access to nitrogen, and protection from toxic metal ions in acid soils.

TOPIC 6: PARASITIC PLANTS

MONOTROPOID MYCORRHIZAS

These are formed by chlorophyll-lacking members of the subfamily, Monotropoideae, within the Ericaceae, e.g. *Monotropa hypopitys* (Yellow Bird's Nest), *M. uniflora* (Indian Pipes) and *Sarcodes sanguinea* (Snow Plant). These plants form associations with ectomycorrhizal fungi, which form a living bridge to an autotrophic host. Transfer of carbohydrate from spruce and pine trees to *Monotropa* via ectomycorrhizal mycelium was classically demonstrated in 1960 by Bjorkmann. In effect, these plants 'piratize' the ectomycorrhizal network, tapping in to the 'trade links' between neighbouring trees. Analogous behaviour is shown by some mycoparasitic fungi that parasitize ectomycorrhizal fungi, e.g. *Cordyceps capitata* on truffles.

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Structurally, monotropoid mycorrhizas superficially resemble ectomycorrhizas, having a sheath and limited Hartig Net, but differ in having 'fungal pegs' that intrude from the sheath into the outer cortical cells, causing both the plant cell wall and plasmalemma to invaginate.

ORCHIDACEOUS MYCORRHIZAS

Orchids produce huge numbers of exceptionally tiny seeds, which are unable to germinate without an external source of carbohydrates. In nature, the carbohydrate source is provided by fungal hyphae, which penetrate into the root to form intracellular coils or 'pelotons', that ultimately become digested within the plant cortical cells. Some orchids lack chlorophyll and so are dependent on this fungal source of carbohydrate throughout their lives, e.g. *Neottia nidus-avis* (Bird's nest orchid).

Intriguingly, the fungi involved in orchidaceous mycorrhizas belong to genera more usually regarded as parasitic on plants, e.g. *Rhizoctonia* and, remarkably, *Armillaria*, which forms mycorrhizas with *Gastrodia elata*. Orchids may use such fungi as a bridge to sources of carbon in other plants.

PARASITIC, HEMIPARASITIC AND CARNIVOROUS PLANTS

Whereas orchids and monotropes might be said to parasitize other plants indirectly, through the agency of their fungal associates, there are many plants that make more direct contact with their plant hosts, or indeed in some cases, animal food. Some of the plant parasites and hemiparasites can significantly reduce yields of crop plants and timber, e.g. the tropical 'witchweeds' (*Striga* spp.), the dwarf mistletoes (*Arceuthobium* spp.), and broomrapes, such as *Orobanche crenata*, which affects fields of beans and peas in the Mediterranean region. An interesting feature of the fully parasitic plants, which depend on their hosts for both carbon and mineral nutrients, is the extraordinary degree of convergence in their form with some kinds of fungi.

Hemiparasitic Plants

These characteristically receive mineral nutrients and water from their hosts, but not, or not necessarily, carbon. Well-known examples occur in the Loranthaceae and Scrophulariaceae.

Loranthaceae – Mistletoes Whilst 'leafy' mistletoes such as *Viscum* (Europe) and *Phoradendron* (America) are often considered as more 'decorative' than destructive, extracting water and minerals from their host but producing most of their own carbon by photosynthesis, the 'dwarf mistletoes' are a very different proposition. Although photosynthetic, the dwarf mistletoes are leafless and extract most of their carbon from their host. They are especially important in western North America, on members of the Pinaceae, where they reduce wood production on a very large scale: in 1984 it was estimated that they caused an annual loss of 17 million m³ of wood production.

Scrophulariaceae Whereas the mistletoes are shoot parasites, members of the subfamily Rhinanthoideae, within the Scrophulariaceae, are root hemiparasites on grasses and sedges, and are sometimes regarded as serious weeds in cereal crops. *Rhinanthus minor* (Yellow Rattle) and *Pedicularis sylvatica* (Lousewort) are familiar examples in Europe. The most commercially damaging members of the family occur in the tropical genus, *Striga*: they have no root hairs and rely entirely on their host plant (and presumably associated arbuscular mycorrhizal fungi) for water and mineral nutrition. It is also interesting to note in passing that a related family to the Scrophulariaceae, the **Lentibulariaceae**, supplement their mineral nutrient supply by trapping and digesting arthropods – e.g. Butterwort and Bladderwort. Other carnivorous plants occur in the Sarraceniaceae and Nepenthaceae (Pitcher Plants) and Droseraceae (Sundews and Venus Fly Traps).

Total Parasites

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Totally parasitic plants that lack chlorophyll and so are dependent on their hosts for both carbon and mineral nutrients can, as with hemiparasites, infect both aerial and underground organs.

Well-known examples of purely shoot parasites are provided by the Dodders, species of *Cuscuta* within the bindweed family, Convolvulaceae. It is easy to see how the entwining habit of members of this family, accompanied by a loss of leaves and development of the ability to penetrate host tissues, could lead to parasitism. The habit of dodders is also very parallel to that of some rhizomorphic fungi, especially species of *Marasmius*. Recent studies with *Cuscuta europea* have shown that it produces different frequencies of appressorium-like attachment points on different host species. This frequency increases with 'host quality', suggesting that dodder actively 'forages' for high quality hosts in a heterogeneous plant landscape.

Examples of root parasites are found in the mainly temperate family, the Orobanchaceae, which is closely related to the Scrophulariaceae, and two remarkable, mainly tropical families, the Balanophoraceae and the Rafflesiaceae.

Orobanchaceae Broomrapes and Toothworts. Almost all these plants are rooted in soil, but few form any extensive rooting system. Instead there is either a congested mass of short, thick roots or a large, single or complex, swollen organ. At one or more locations on this underground structure there are connections, via swollen, clamp-like appressoria, with the root of the host plant.

Balanophoraceae These plants infect the roots of various, mostly tree, hosts. The above-ground parts of the plants are usually fleshy, club-shaped inflorescences or 'capitula' that have a very fungus-like appearance and bear many flowers, which are amongst the smallest known. As recently as the early nineteenth century, these plants were actually thought to be fungi. The below-ground part usually consists of a tuber, which may be composed entirely of parasite tissue or, in some cases, of both parasite and host tissue – a chimeric organization unknown elsewhere in higher plants. The inflorescences develop inside the tuber, rupturing it as they emerge, to leave a 'volva' at the base, highly reminiscent of the fungus genus, *Amanita*.

Rafflesiaceae These total parasites include *Rafflesia* itself, which has the largest flowers known, up to 1 metre across. In fact, the reproductive parts are the only parts that are recognizably flowering plant-like. The vegetative tissues consist of a kind of 'mycelium', which ramifies through the host cambium. The flower buds begin development inside the host and then push through the surface. In some species, the mycelium penetrates into the growing points of the host's aerial or subterranean parts and then develops synchronously with the host. A Japanese species of *Mitrastemon* produces its flowers in annual 'fairy rings', corresponding to a zone a few cm within the perimeter of its oak tree host's root system – much like the fruit bodies of many mycorrhizal fungi.

Such striking convergences with fungi may illustrate just how strongly an organism's form is related to its mode of nutrition. Absorptive, heterotrophic nutrition virtually demands a mycelium-like organization and associated apparent simplification of vegetative form.

TOPIC 7: HUMAN INFLUENCES ON PLANT HEALTH

Many of the problems that we attribute to 'pathogenic' organisms, 'causal agents of disease', are problems of our own making, the result of our enormously destabilizing influence on the 'host-space' of plant community life:

1. OUTRIGHT DESTRUCTION

From the time when the nomadic, hunter-gatherer way of life began to be superseded by settlement, agriculture and, ultimately, industry, people have destroyed plant communities in order to clear the way for their own crops, domestic animals and activities.

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The huge impact on the natural landscape of human destruction of plant communities should never be underestimated. Currently, great concern focuses on the destruction of the rain forest, but this is only the most recent episode in a long saga. An indication of the ability of human beings to change things, even with limited technology in early times, is evident in what is known as the 'Elm Decline' – a sudden collapse in the amount of elm pollen present in the palynological record for the most recent post-glacial period. This decline is largely attributable to Neolithic clearance and use of elm foliage as fodder.

2. ALTERATION OF BIOSPHERE CONDITIONS

Destructive and polluting activities associated with the agricultural and industrial revolutions are now widely acknowledged to have had global as well as local effects on atmospheric conditions, soil and water quality etc. At first doubted, global climate change due to greenhouse gases is now widely accepted as a reality. The effects of such changes on the ecological relationships of plants are likely to be both profound and highly unpredictable, operating as they do in complex dynamic systems.

3. MANAGEMENT AND EXPLOITATION OF NATURAL PLANT COMMUNITIES

Natural plant communities are the source of a wide variety of products, from food to sources of pharmaceuticals and materials, such as wood and fibre, for clothing and construction. The harvesting of such products began with hunter-gatherer life styles and with modern machinery and technology can now be practised on very large scales. The way in which this harvesting is done, sustainably in tune or unsustainably out of tune with natural production cycles, can significantly affect the health and structure of plant communities. For example, methods of woodland management known as 'woodmanship' were developed and practised through medieval times until the nineteenth century, were based on the natural ability of hardwood trees to re-grow following cutting, e.g. coppicing and pollarding. More exploitative forms of 'management' treat the natural community as a 'standing crop', to be harvested without regard to its future regeneration.

4. MANAGEMENT AND EXPLOITATION OF CROPS AND PLANTATIONS

Here, the potential for damage and build-up of pathogen inoculum reaches its zenith. Prior to planting of even-aged stands, either the natural plant community that preceded it, or the former crop, is cleared, leaving residues of root systems and rhizosphere soil into which the new crop is introduced. With tree plantations, the trees may be planted deliberately close in order to make them grow straight, so necessitating thinning and exposure of stump surfaces.

Such management practices can result in enormous disease losses. For example, incidence of pathogens like *H. annosum* may be greatly increased as a result of clear-felling and thinning operations in conifer plantations..

Also, in many cases, people actually also play a mechanical part in transferring inoculum in the process of crop planting and harvesting, and can alter soil conditions (affecting, e.g. mycorrhizal production) by application of fertilizers, and environmental quality by application of pesticides.

5. PROPAGATION OF MONOCULTURES

The dangers inherent in growing monocultures on a large scale are well known: monocultures are uniformly susceptible to the same kind of pathogen. To plant a monoculture is an open invitation to whatever pathogen that can infect one of the plants to infect all of them. There are many examples where this invitation has indeed been taken up: e.g. Victoria Blight of Oats; Southern Leaf Blight of Corn; spread of 'physiologic races' of pathogens into cultivars susceptible to those races but bred for resistance to their races.

6. INTRODUCTIONS

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When any plant or associated organism is taken out of its natural context, where it is co-evolutionarily attuned to its neighbours and surroundings, and placed in an effectively new context, the outcome is profoundly unpredictable, but always contains possibilities for going to extremes. The introduced organism can, and sometimes does, overwhelm the resident community as an invasive 'weed' or pathogen.

Some of the most devastating plant disease epidemics have resulted from human introductions. Two kinds of situations can arise:

- (i) A plant is transferred to a context free from its natural co-habitants. It may become rampant, or it may lose natural 'resistance' to pathogens, only to be susceptible to these when they eventually 'catch up' with their host (e.g. *Puccinia polysora* on maize in Africa).
- (ii) A pathogen is introduced to previously unexposed and hence susceptible host population, e.g. Dutch Elm Disease, White Pine Blister Rust, Chestnut Blight, Jarrah Die-back.

Selected References

Books

- Isaac, S. (1992) *Fungal-Plant Interactions*. Chapman & Hall
Rayner, A.D.M. (1997) *Degrees of Freedom – Living in Dynamic Boundaries*. Imperial College Press
Rayner, A.D.M. & Boddy, L. (1988). *Fungal Decomposition of Wood*. John Wiley
Spooner, B. & Roberts, P. (2005). *Fungi*. New Naturalist.
Sinclair, W.A., Lyon, H.H. & Johnson, W.T. (1987) *Diseases of Trees and Shrubs*. Cornell University Press
Smith, S.E. & Read, D.J. (2000). *Mycorrhizal Symbiosis*. Academic Press.

Articles

- Rayner, A.D.M. (1998) Fountains of the forest – the interconnectedness between trees and fungi. *Mycol. Res.* **102**, 1441-1449
Read, D. (1997) The ties that bind. *Nature* **388**, 517-18.
Schulz, B. & Boyle, C. (2005) The endophytic continuum. *Mycol. Res.* **109**, 661-686.