Presidential Address

Fungal succession – unravelling the unpredictable

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The nature and mechanisms of successions of fungi in soil and plant litter are discussed, and an autecological study of a basidiomycete used to illustrate some methods of approach.

This Address was delivered when the British Mycological Society was on the threshold of its Centennial Year, and the President began by reminding her audience of the great sociological changes that had accompanied scientific advances made by mycologists during the last 100 years. Beatrix Potter's paper *On the Germination of the Spores of Agaricinae* was read to the Linnean Society in the same room of Burlington House on 1 April 1897, a year after the founding of the BMS. Not only did the gentlemen prevent her from delivering the paper herself but also did not allow her even to attend the meeting. Instead her paper was read by the first BMS President, George Massee, to a gathering of famous names, including the ecologist A. G. Tansley. Sadly, the paper has been lost, but it is known from her letters that despite her artistic fascination with the fruit bodies of agarics, she was intrigued by what might be their origin, and recognized the importance of the *mycelium*. This she drew in fine and accurate detail, including basidiomycete clamp connections (Jay, Noble & Hobbs, 1992).

Mycelia, their whereabouts, their interactions and their pivotal status, are a recurrent theme in this account of fungal succession from an ecologist's viewpoint, referring in particular to terrestrial saprotrophs.

Plant ecologists have been describing and theorizing about succession since the beginning of the century. The classic volume *Plant Succession. An Analysis of the Development of Vegetation*, published in America by F. E. Clements in 1916 (Fig. 1), was widely read on both sides of the Atlantic. Although he enunciated an exaggerated and untenable theory that a plant community was like an organism that could grow, mature and die, his writings had a major influence on the acceptance of dynamic principles by plant ecologists. Mycologists, however, lagged behind in developing a quantitative and predictive science. For many years they continued to be absorbed in describing and listing species. As late as 1992 it could still be said by Rayner that 'fungi are commonly omitted from the ecological and evolutionary debates of the day'.

Mycologists were hampered until quite recently by a lack of appreciation of the differences between plants and fungi as individuals, and standard texts on plant ecology (e.g. Kershaw, 1964, and later editions) were not matched by the mycological literature. Advances came with the wider recognition of the existence of individual mycelia of indeterminate growth, and landmarks in the progress of fungal ecology were a BMS

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BMS President 1995

PLANT SUCCESSION

AN ANALYSIS OF THE DEVELOPMENT OF VEGETATION

BY

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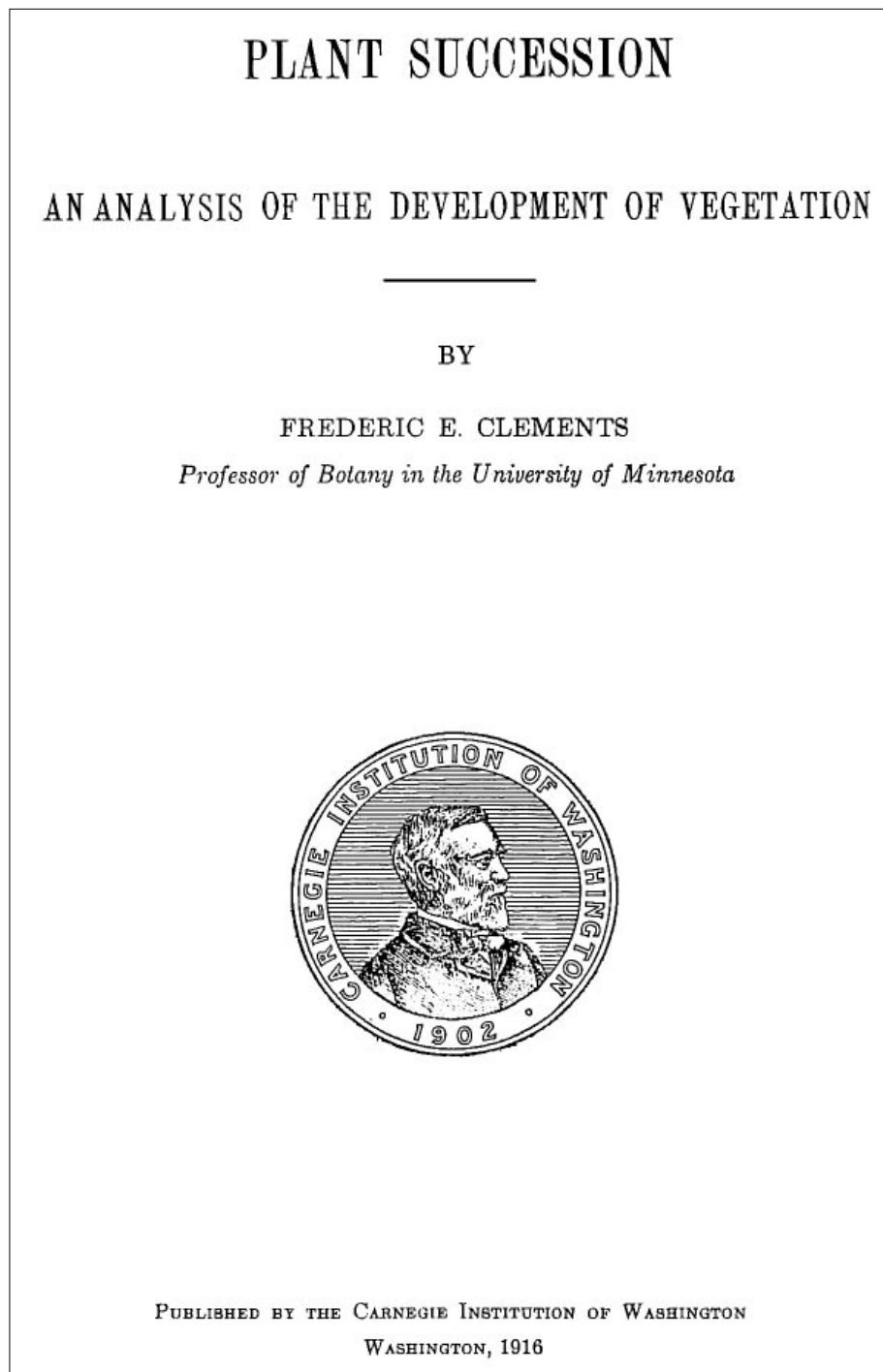PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
WASHINGTON, 1916

Fig. 1. A classic treatise on plant succession widely read by ecologists in the early years of the twentieth century.

Symposium on the mycelium (Jennings & Rayner, 1984) and publication of two editions of *The Fungal Community* (Wicklow & Carroll, 1981; Carroll & Wicklow, 1992), the latter volume described by Rayner in his Introduction as 'richly heterogeneous, as befits a dynamic evolving subject'.
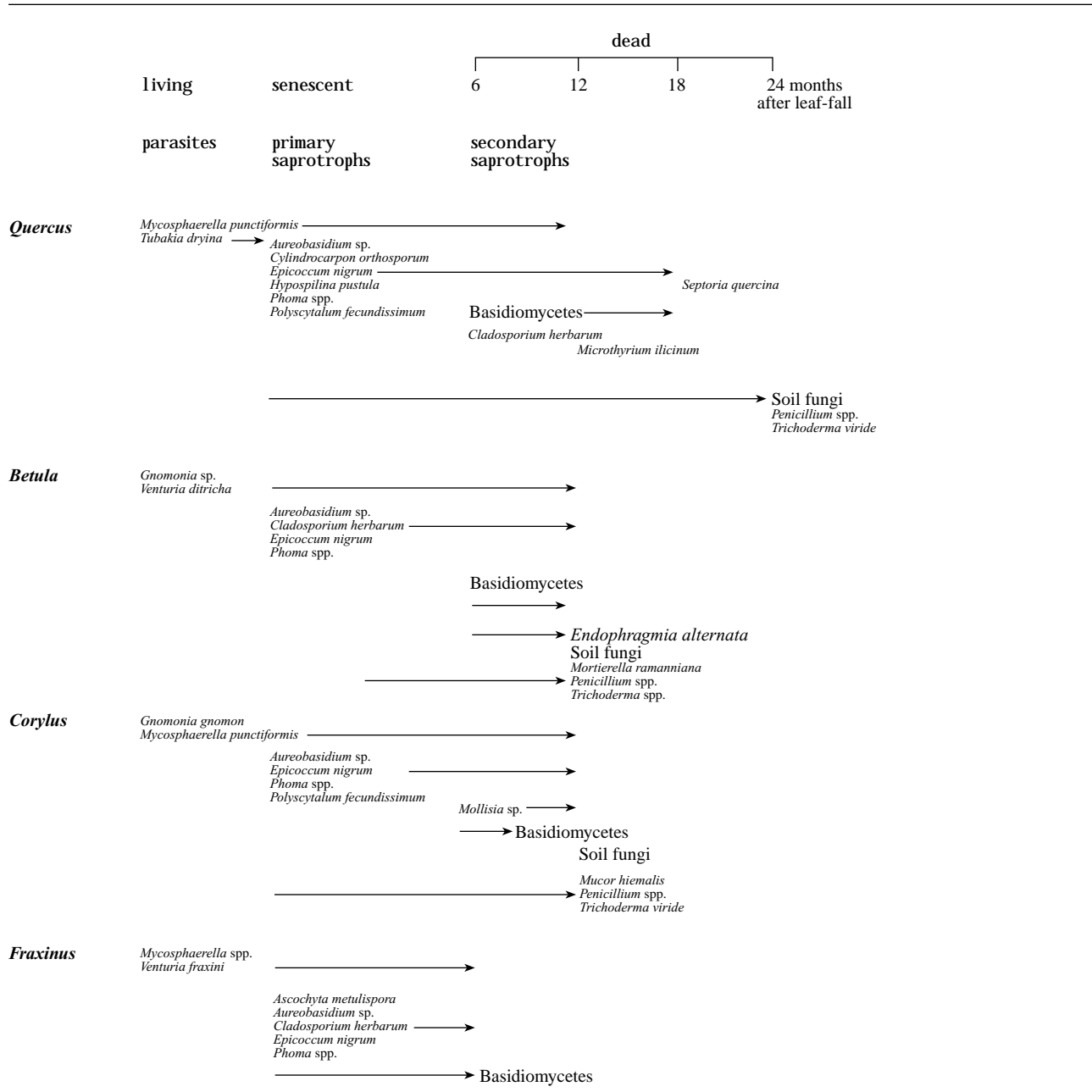
THE NATURE OF FUNGAL SUCCESSIONS

Succession of both plants and fungi can be defined as 'a directional change in the composition, relative abundance and spatial pattern of species comprising communities' (Frankland, 1992). Mycologically, succession is more precisely 'the sequential occupation of the same site by thalli (normally mycelia) either of different fungi, or of different associations of fungi' (Rayner & Todd, 1979). Fungi replace one another as their dynamic communities of mycelia alter in space and time, each species adapted for occupation of particular niches. As Johnson (1979) said: 'The kernel of the idea of succession is obviously evolution.' This fundamental assumption regarding inherited adaptations is often forgotten but underlies the whole subject.

Successional studies have mirrored changes in mycologists' perspectives and techniques of their day. Early workers concentrated on replacement of species in time rather than in

Table 1. Succession of fungi on leaf litter in a temperate woodland on mull humus. Fungi are listed at the first stage in decomposition at which they became 'dominant'. Indicator lines denote presence of a species or fungal group before or after that event.

	living	senescent	dead 6	12	18	24 months after leaf-fall
	parasites	primary saprotrophs	secondary saprotrophs			

Quercus
- *Mycosphaerella punctiformis* ————————→
- *Tubakia dryina* →
  - *Aureobasidium* sp.
  - *Cylindrocarpon orthosporum*
  - *Epicoccum nigrum*
  - *Hypospilina pustula* ————————————————→ *Septoria quercina*
  - *Phoma* spp.
  - *Polyscytalum fecundissimum*
- Basidiomycetes ——————→
  - *Cladosporium herbarum*
  - *Microthyrium ilicinum*
- ——————————————————————————→ Soil fungi
  - *Penicillium* spp.
  - *Trichoderma viride*

Betula
- *Gnomonia* sp. ————————————→
- *Venturia ditricha*
  - *Aureobasidium* sp.
  - *Cladosporium herbarum* ————————→
  - *Epicoccum nigrum*
  - *Phoma* spp.
- Basidiomycetes ——————→
- ——————→ *Endophragmia alternata*
- Soil fungi
  - *Mortierella ramanniana*
  - *Penicillium* spp.
  - *Trichoderma* spp.

Corylus
- *Gnomonia gnomon*
- *Mycosphaerella punctiformis* ————————→
  - *Aureobasidium* sp.
  - *Epicoccum nigrum* ————————→
  - *Phoma* spp.
  - *Polyscytalum fecundissimum*
- *Mollisia* sp. ——→
- ——→ Basidiomycetes
- Soil fungi
  - *Mucor hiemalis*
  - *Penicillium* spp.
  - *Trichoderma viride*

Fraxinus
- *Mycosphaerella* spp. ————————→
- *Venturia fraxini*
  - *Ascochyta metulispora*
  - *Aureobasidium* sp.
  - *Cladosporium herbarum* ————→
  - *Epicoccum nigrum*
  - *Phoma* spp.
- ——→ Basidiomycetes

space, but attempts were made to classify fungal successions and Park's (1968) division into substratum and seral types was widely accepted.

Substratum successions

Numerous successions of the substratum type were described around the middle of the twentieth century. Some were on a single substrate such as a cellulose film (Tribe, 1957, 1961), others on resources that were a complex of substrates, and many on plant litter above ground. A notable example of the latter was followed in a detailed study of a senescing grass, *Dactylis glomerata* L. (Webster, 1956, 1957; Webster & Dix, 1960); most were investigated more superficially. The general features of such successions on plant material have been compared by Hudson (1968) and Dix & Webster (1995). Associations of weak pathogens are followed or overlapped by primary saprotrophs and decomposers of the more recalcitrant substrates. *Alternaria*, *Aureobasidium*, *Cladosporium* and *Epicoccum* occur repeatedly as early colonizers in the published species lists. Nevertheless, each succession is unique, dependent on the 'host' material and its environment.

Usually missing in early descriptions of fungal successions was any mention of the location of the mycelia of the competitors and, except on wood, of the occurrence of basidiomycetes, although with their battery of enzymes they were to be described as 'the major agents of decomposition of plant litter' (Frankland, Hedger & Swift, 1982). In general, there was also scant attempt to relate the successions to any organisms at other trophic levels.

During the International Biological Programme (IBP) of the 1970s, there was a vogue for comparing fungal successions on different types of plant litter. The author, for example, followed succession concurrently on fallen leaves of *Quercus* (oak), *Betula* (birch), *Corylus* (hazel) and *Fraxinus* (ash) in a broad-leaved, U.K. woodland on mull humus (Meathop; National Grid Reference SD 435795) until macroscopic leaf structure was lost. The overlapping waves of fungal species were typical of those described on non-woody plant debris, but there were differences between the four litter types, particularly in duration and in some of the weak parasites of the early stages. The principal colonists, among over 100 species recorded, are shown in Table 1. On *Quercus*, the slowest litter to decay, *Mycosphaerella* was present at leaf-fall and followed by common saprotrophs; basidiomycetes predominated 6 months later and a peak of typical soil fungi occurred after 2 yr. The succession on *Betula* was similar but of shorter duration. *Gnomonia* and *Venturia* replaced *Mycosphaerella* as weak pathogens, and soil fungi peaked after 1 yr. The *Corylus* succession was again similar, but the basidiomycete phase briefer. The *Fraxinus* succession was even more foreshortened; basidiomycetes were found much earlier, and after 6 months most of the leaflets had lost their identity or been drawn down worm burrows. The differences between these successions could be attributed largely to resource quality including nitrogen content and inhibitory tannin concentrations. *Quercus* rich in tannins had the highest C:N ratio (40) at leaf-fall and *Fraxinus* the lowest (23).

The successions recorded by Hering (1965) on the same four litter species but on a moder type humus were similar, except that basidiomycetes were rarely isolated despite the common occurrence of their basidiomata in that woodland. The explanation appears to lie in slight differences of technique. In both studies fungi were isolated from washed fragments of litter plated on agar culture media or by examining them *in situ* on litter incubated in damp chambers (see Frankland, Dighton & Boddy, 1990; Frankland, Latter & Poskitt, 1995). Basidiomycetes tend to be poor competitors in the artificial conditions of the first method, but in the second they are already holding their territory on the litter. In the latter, the moder material was cut into 4 mm discs, whereas the mull litter was left intact and incubated for 12 wk or more until abortive but recognizable basidiomata were produced. As a result, < 89% of the *Quercus* leaves, the principal component of the mull leaf litter, were found to be colonized by basidiomycetes, mostly *Mycena galopus* (Pers.:Fr.) P. Kumm. (Frankland, 1975, 1982). Viable mycelium of basidiomycetes in litter from the moder site was apparently lost by excessive fragmentation. Choice of techniques and a many-sided approach are all-important in successional studies.

The author's investigation of fungal succession on a single species of litter, *Pteridium aquilinum* (L.) Kuhn (bracken), collected from one source but left to decompose in six different but adjacent habitats, highlighted the importance of location and environmental conditions. Decomposition of the frond petioles was followed for 6 yr (Frankland, 1966, 1969, 1974, 1976, 1981). The sequence of events outlined in Fig. 2 was similar on the different sites, but the timing of successional events and state of the petioles each year differed considerably,

the rate of decomposition decreasing in relation to humus type in the order moder > mull > peat. After 5 yr on the moder sites, white rot was visible and the petioles consisted of only loose bundles of fibres and xylem vessels entangled with soil debris and faecal pellets, whereas on peat the outer lignified cylinder was still intact.

The succession on bracken litter, highly lignified (28% O.D.W.) and low in nitrogen (0·24% O.D.W.) before collapse of the fronds, resembled that on woody tissues. Basidiomycetes became prominent in the second year *before* the principal wave of so-called 'sugar' moulds crammed the xylem vessels with hyphae. *M. galopus*, common in many northern temperate forests, was again the most frequent agaric at this location. It bleached the litter and formed 'bore' holes in the fibres as confirmed in axenic cultures on bracken.

Decomposing bracken provided new resources and micro-habitats for small animals. After two or more years, Collembola and Acarina were abundant inside the petioles, grazing voraciously but *selectively* on fungal mycelium and fructifications, pushing the softer tissues aside to form longitudinal channels and adding faeces. Nematodes travelled up into the shelter, and predacious fungi, following in their wake, began to appear among the fungal isolates. Elton (1966) remarked that the fauna was richer in bracken litter than in nearby oak litter during droughts.

Fungal activity had almost ceased by the end of 5–6 yr when bacteria predominated, although 95% loss of dry mass was estimated to take 11–23 yr (Frankland, 1976). The true end-points of fungal successions on the refractory remains of plants have rarely been recorded, but Visser & Parkinson (1975) in their notable quantitative study of *Populus tremuloides* Michaux followed changes in fungal populations and biomass on washed organic particles right into the H humus horizon. Their observations emphasized the significance of fungi in the energy transfer from one trophic level to another.

Frontiers of individual mycelia and their interactions with neighbours in the successions described above were rarely seen. Mycologists of that era seldom homed in at the microscopic level to examine how replacements occurred. The importance of the scale at which observations are needed is highlighted by a single evocative sentence in Kendrick & Burges' (1962) classic account of microfungi decomposing *Pinus sylvestris* L. needles: '*Desmazierella* conidiophores, arising from the substomatal cavities, were unaffected by the distribution of *Helicoma* or *Sympodiella*, but were strongly influenced by the presence of *Lophodermium* diaphragms.' At that date, a full appreciation of fungal individualism was yet to come.

Seral successions

In Park's seral type of succession, a series of fungal assemblages follow successional changes in vegetation. The author's study of the soil microfungi of coastal dunes in the U.K. illustrates one of the few examples (Brown, 1958*a*, *b*; Frankland, 1981).

The occurrence of specific macrofungi fruiting in the different seres of a sand dune system, developing from fore dunes via mobile and semi-fixed dunes to fixed pasture, heath, woodland or as so often now a golf course, is well known to
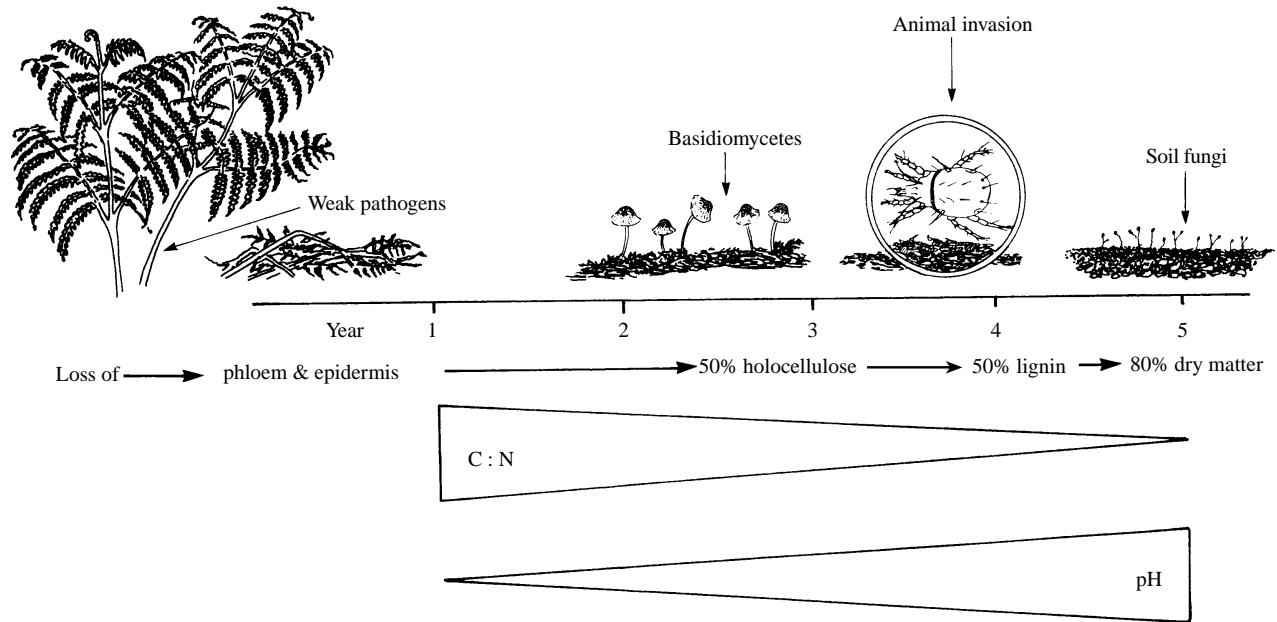
Fig. 2. Generalized succession of fungi on decomposing petioles of *Pteridium aquilinum*.

forayers. Similarly, a dune zone can be distinguished by the predominant soil microfungi as seen on a culture plate inoculated with only a few grains of sand. The assemblage on a plate is, however, only a laboratory artefact that has selected species from a complex of substratum successions, growing on such resources as the dead leaves and roots of *Ammophila* (marram grass), decaying drift wood or perhaps even bracken petioles. In the 'acid' system depicted (Fig. 3), the greatest diversity of fungal species occurred in 100-yr-old semi-fixed

dunes where pioneer and late successional plants overlapped. Further inland, the fungal communities appeared to stabilize as the supply of resources became less variable, and as a soil with well-defined horizons was formed. This apparent state of equilibrium, however, cannot be equated with a Clementsian climax of higher plants, and 'seral' is not ideal in its connotation, but it expresses the interplay between successions at more than one ecosystem level – autotrophic and heterotrophic (Frankland, 1992).
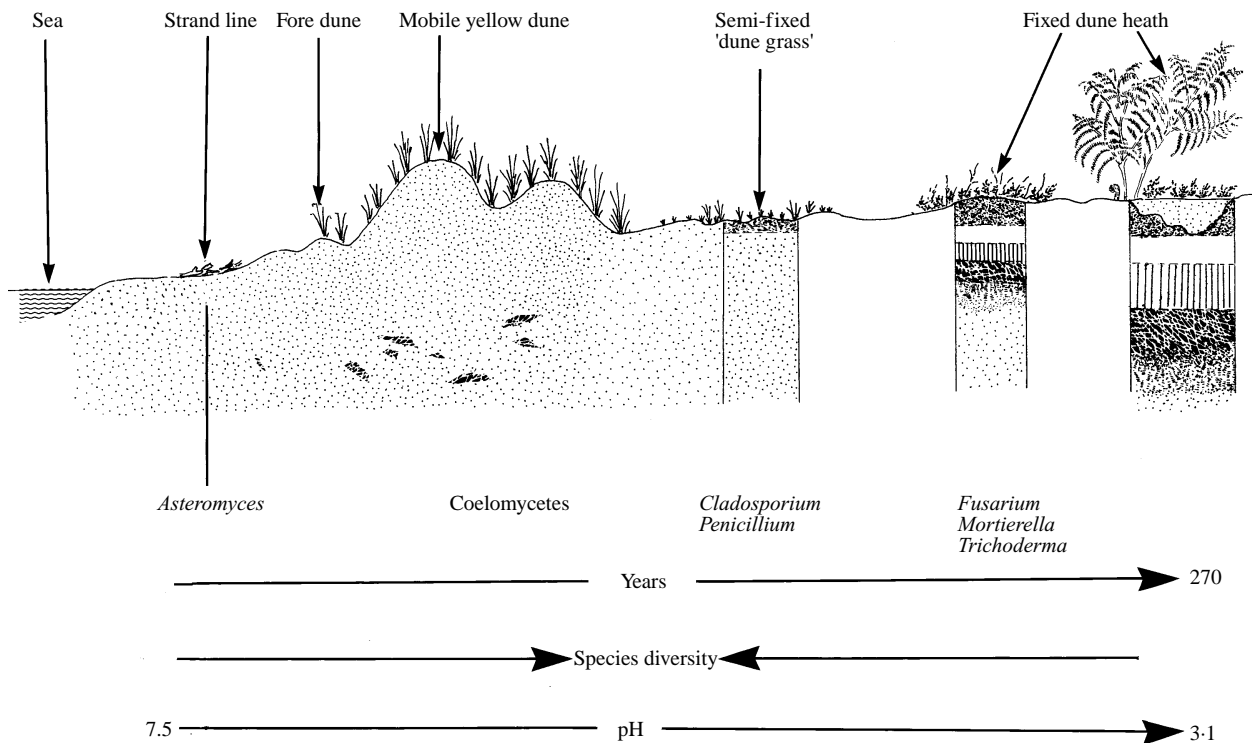
Fig. 3. General features of a succession of soil fungi (characteristic genera only) in an 'acid' sand dune system.
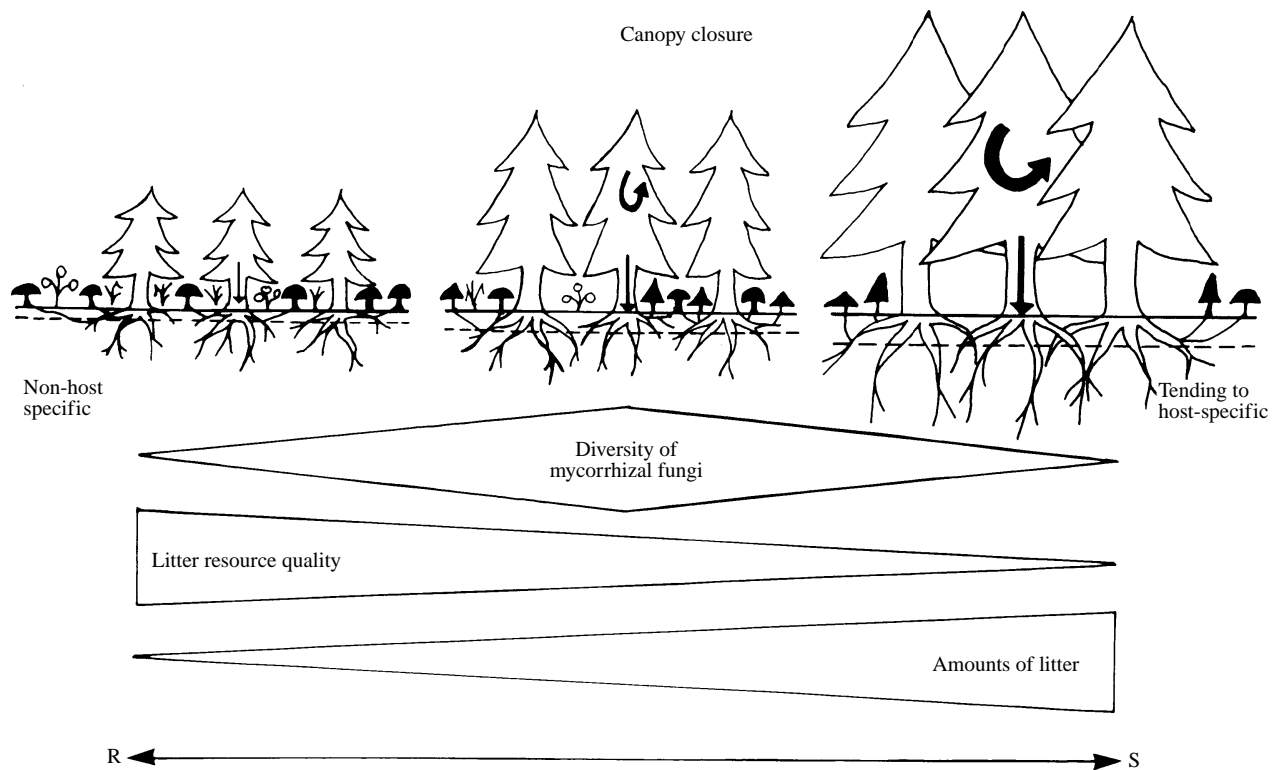
Fig. 4. Succession of mycorrhizal fungi during forest development in relation to R- and S- selection and the litter resource. (After Dighton & Mason, 1985.)

On a much grosser scale, Christensen (1969), in her classic study of soil microfungi along a continuum of 36 dry to mesic conifer–hardwood forests in northern Wisconsin, used mathematical techniques of classification, ordination and regression. From this she was able to describe the species composition of the communities and concluded that the fungi 'exhibited determinable distribution patterns within a multidimensional complex' including vegetation.

Primary and secondary successions

Fungal successions have also been described as primary when pioneers have colonized a virgin surface, or secondary after a major event or 'disturbance' has shifted the course of a succession. The somewhat arbitrary distinction is a useful concept when interpreting complex ecological patterns, but a disturbance can have markedly contrasting consequences. Sand blow on a fixed dune, for example, can destroy primary successions, whereas forest litter-fall enriches them (Pugh & Boddy, 1988). A spectacular example of secondary succession, after fire has reduced competition and soil toxicity so that both ascomycete spores and plant seeds are able to germinate and colonize, has been described by Wicklow (1988, and earlier papers). Less dramatic changes in the micro-environment can activate secondary succession by latent colonizers as in wood (Rayner & Boddy, 1988).

Mycelia may also colonize each other without actual replacement, so the terminology of succession has to accommodate more than just a single linear process (Frankland, 1992).

Mycorrhizal fungi

Both ecto- and arbuscular mycorrhizal fungi by virtue of their intimate relationship with higher plants could play a central role in successions of vegetation and *vice versa*, but there is as yet little direct evidence from the field (Smith & Read, 1997). Apparent seral successions of ectomycorrhizal agarics during the development of temperate forests, particularly those of *Betula*, *Pinus* and *Picea* (Fig. 4), have been described (Dighton & Mason, 1985; Last, Dighton & Mason, 1987). The various assemblages of species under forest stands of different ages were considered to exhibit characters that were adaptations to changes in conditions as the trees matured. Their so-called 'ecological strategies' were defined as ruderal (R), competitive (C) or stress tolerant (S), terms applied to higher plants by Grime (1979) and adapted for fungi by Pugh (1980) in his Presidential Address to this Society. Accordingly, some agarics that were not highly selective of their host trees, reproduced prolifically, possessed relatively small, cordless basidiomata, and occurred under young, first-generation trees were classified as R-selection, for example, *Laccaria proxima* (Boud.) Pat. Species diversity tended then to increase until canopy closure (*ca* 27 yr), but declined when tree litter accumulated with a greater proportion of nitrogen in organic form. More host-selective species, for example, *Amanita muscaria* (L.:Fr.) Hook. with larger, more persistent basidiomata, often corded and possibly more dependent on energy from their hosts (S-selection) typified this later stage. Various anomalies occur within this general picture, but manipulation of the system by transplant, trenching and coring experiments has sometimes provided explanations (Fleming, 1984). Never-

theless, evidence based on the presence of basidiomata above ground without information on the all-important mycelia on the roots can be very misleading. For instance, some common species are known to fruit rarely if at all (Taylor & Alexander, 1989; Smith & Read, 1997), and Visser (1995), by recording ectomycorrhizal morphotypes on roots from an age sequence of *Pinus banksiana* Lamb. (jack pine) and not just fruit body production, found an increase in species diversity between 6 and 41 yr followed by stability, in contrast to the shorter-term investigation by Dighton and co-workers.

Analysis of the relationships between mycorrhizal succession and forest age could become more than just a theoretical exercise, aiding the forester, for example, in choice of inoculants for forest nurseries and spoil heaps. Also, more research is particularly needed in the humid tropics where the presence of vesicular–arbuscular or strictly arbuscular mycorrhizas and ectomycorrhizas may sometimes be crucial for regeneration of trees following deforestation (Janos, 1996).

The rings and spurs of mycorrhizal basidiomata found around individual trees, as distinct from those of saprotrophic agarics, reflect events on the roots, and can be likened to substratum successions despite fundamental differences (Last *et al.*, 1983, 1984; Mason *et al.*, 1988). Once again, succession can be interpreted only by examining the mycelia.

CAUSAL FACTORS

The element of chance in fungal successions – being in the right place at the right time – and the infinite variety of outcomes provide endless Ph.D. studies, but they will be predictable only when the mechanisms are understood and can be related to the multivariate situation. A causal classification, designed for vegetation by Pickett, Collins & Armesto (1987), can, however, provide a framework for clarifying some of the interactions in fungal succession (Frankland, 1992). It depends on three levels of ecological organization:

(1) at the highest level are general causes, e.g. availability of space and species of differential performance;
(2) at the intermediate level are processes and phenomena conditioning the first, e.g. dispersal, competition between species and animal grazing that involve whole communities;
(3) at the most detailed level are inherent characters that define the outcome of the latter and operate between populations and individual mycelia, e.g. differential rates of growth and nutrient uptake.

This causal hierarchy emphasizes our inability to go far in unravelling most fungal successions owing to lack of information. Since Beatrix Potter's time only a very small fraction of identified species, particularly saprotrophs, has been studied ecologically and rarely at the mycelial level. Nevertheless, for the last two decades the focus has been on mycelium rather than spores and there is now much greater understanding of mycelial dynamics. Intermingling, deadlock, 'combat' and actual replacement when two mycelia meet are now well-known features. Again, discovery of such phenomena as: directed growth towards a resource; recognition

responses; flexibility of growth form; ability to behave as a single co-ordinated unit and mycelial interconnectedness (see Cooke & Rayner, 1984; Rayner & Boddy, 1988; Rayner, Griffith & Ainsworth, 1995), together with advances in molecular biology, is revolutionizing our approach to field mycology.

AN AUTECOLOGICAL APPROACH

Turning from fungal succession in general, the need for autecological studies by a variety of methods is illustrated by a long-term investigation of a single saprotrophic member of a succession, *Mycena galopus* on decomposing needles of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) in one locality. It centred on the mycelium and the involvement of a hierarchy of conditioning factors.

M. galopus is common in northern temperate regions. The relatively small fruit body is ephemeral, often surviving for only 2–4 d, but in many angiospermous and coniferous forests it is a major decomposer of plant litter, readily identified when fruiting by white latex in the stipe. As already described in *Quercus* and *Pteridium* successions, it is a secondary colonist. When grown in axenic laboratory systems, it attacked all the major constituents of plant litter, including lignin, α-cellulose, hemicelluloses, protein and soluble carbohydrates, and also purified xylan and pectin (Hintikka, 1961, 1970; Hering, 1967; Frankland, 1969). Enzymes known to be produced include polyphenol oxidases, cellulases and catalase (Lindeberg, 1948; Lamaison, 1976), and it is a particularly vigorous attacker of lignin and cellulose, forming conspicuous patches of white rot on leaf litter (Fig. 5).

The lack of resource specificity is borne out by the distribution of *M. galopus*. As described by Parker-Rhodes (1954), it is a 'quisquilicolous' woodland species growing on a variety of plant litters, including those of trees, herbs, ferns and mosses on a variety of soil types, but rarely on wood of any bulk, probably because it is intolerant of restricted aeration and of various inhibitory chemicals in wood (Hintikka & Korhonen, 1970; Harrison, 1971; Hintikka, 1982).

Steady decomposition rates can be maintained by *M. galopus* over long periods at mean field temperatures in axenic culture, and it has been found to be relatively efficient on *Betula* and *Fraxinus* litter in terms of mycelium produced from unit weight of resource (28–34%; Frankland, Lindley & Swift, 1978). Activity has been recorded even under snow at -2 °C and it can survive at $-12°$ (Hintikka, 1964; Frankland, 1984).

Typically, in a deciduous, mixed woodland in the English Lake District, U.K. (Meathop Wood), with an understorey, ground vegetation and discontinuous resources, only one mycelial genet of the fungus colonized each individual leaf of the dominant *Quercus*. At a later stage, the more exploratory hyphae were able to compact and stabilize the litter. In this type of woodland, the basidiomata, dependent on an adequate build-up of mycelial biomass, are usually solitary. By measuring changes in the biomass and decay rates of tagged mycelium on such leaves, the ratios of basidioma production:vegetative biomass:vegetative production were estimated to be approximately 1:5:10 (Frankland, 1975, 1982). By contrast, in a pure stand of Sitka spruce in the same locality (Grizedale Forest;

Fig. 5. *Mycena galopus* causing white rot of *Quercus* leaf litter. Photo: J. K. Adamson.

National Grid Reference SD 345944), mostly without an understorey or ground vegetation other than occasional patches of moss but with a continuous deep bed of needle litter as resource, the mycelium was produced prolifically and fruited abundantly in troops (Fig. 6). The homogeneity of this site provided substantial advantages over mixed woodland for examining key events in succession – arrival, establishment and replacement of the species.

The arrival of *M. galopus* by air as a colonizer of the spruce litter was investigated by capturing the basidiospore 'rain' (Frankland, Poskitt & Howard, 1995). Homokaryons obtained from both the spruce and oak sites (*ca* 16 km apart), by isolating single basidiospores, were exposed on malt agar in chambers of repli-dishes attached to posts at different levels above ground in the spruce plantation. Dikaryons with clamp connections were formed by < 100% of the mycelia originating from both sites after exposure for 24 h. The supply of viable, aerially dispersed basidiospores appeared, therefore, to be ample and outbreeding between spores from the two forest types to be possible.

With frequent replenishment of freshly fallen needles, space is unlikely to be limiting for the germinating spore despite some colonization by phylloplane organisms before litter-fall, but the persistence of the homokaryons and their ability to decompose the resource among competitors before dikaryotization occurs are not known; their growth in pure culture was very restricted in comparison with that of the dikaryons and heterokaryons.

As a secondary colonist in the succession, major development of the secondary mycelium of *M. galopus* is most likely to occur below the surface litter that has been preconditioned by earlier colonists. The white, non-descript mycelium was visually indistinguishable from that of several other species in the habitat, but its principal niche among black, partially decomposed needles of the F_1 horizon was located by excavating basidiomata to their origins at the base of the stipes (Newell, 1984*a*). After developing a monoclonal antibody (MAb) specific to the mycelium of *M. galopus*, with latex from the stipes as immunogen, another approach using an immunofluorescence technique supported this finding (Fig. 7; Hitchcock, 1992; Hitchcock, Gray & Frankland, 1997).

Basidiomata were also clues to the extension growth of individual mycelia established in the forest floor. The approximate diameters of mycelial genets in a permanent plot (10×4.5 m) were determined by testing for somatic compatibility between paired isolates of mycelium from the stipes (the pilei were too thin a source for inocula). On this basis, relatively large, possibly perennial, mycelia < 2.5 m diam. were detected and also smaller fruiting genets *ca* 0.1 m diam. Intriguingly, many small, incompatible genets were found by the same method in storm- and deer-damaged ground, which suggested recent arrival of a heterogeneous population (Frankland *et al.*, 1995).

Again, evidence for the spatial distribution and persistence of the mycelium in circumscribed areas of the forest was obtained by repeated computer mapping of basidiomata over five years. Remarkable stability was found by determining the number of basidiomata in successive and non-successive years that coincided in position exactly or within 20 mm of a fruiting position that had been recorded in the first year

Fig. 6. Troop of *Mycena galopus* basidiomata on needle litter of *Picea sitchensis* in Grizedale Forest. Photo: A. D. Bailey.
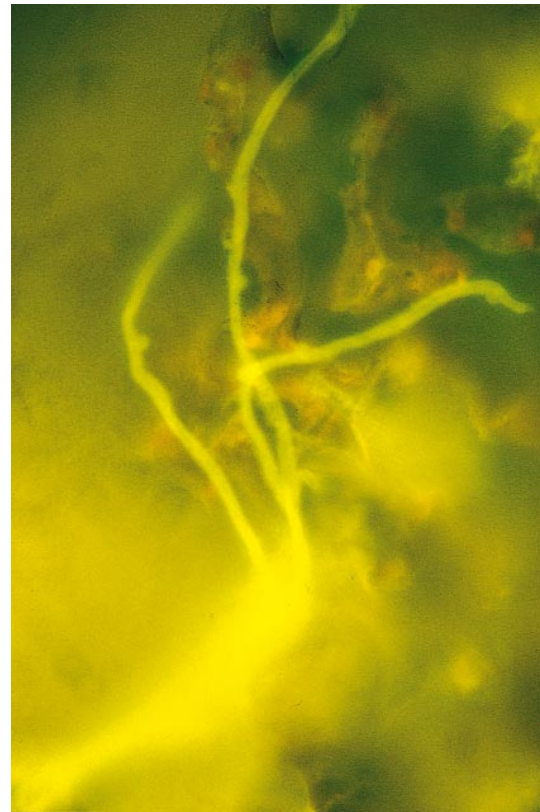

Fig. 7. *Mycena galopus* mycelium in *Picea sitchensis* litter on a membrane filter. Immunofluorescence staining with a specific monoclonal antibody and fluorescein isothiocyanate. Hyphal diam. 2·5 µm. Photo: P. Hitchcock.
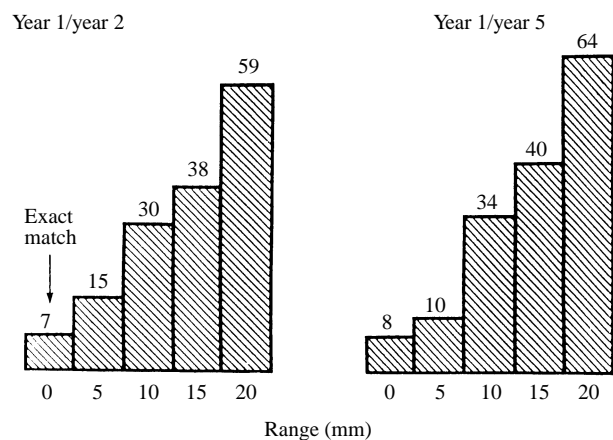

Fig. 8. Numbers of basidiomata of *Mycena galopus* in a $10 \times 4·5$ m *Picea sitchensis* plot over a 5-yr period, with positions that coincided, in successive and non-successive years, exactly or within ranges of 0–20 mm of a position in the first year. (After Frankland, 1984.)

(Frankland, 1984). For example, as shown in Fig. 8, after 4 yr 64 basidiomata occurred within 20 mm and 10 within 5 mm of a position mapped in the first year. The same data showed that the overall distribution was statistically non-random, and revealed arcs or annuli of basidiomata around some of the spruce trees (Fig. 9). In the occasional year when fruiting was prolific, this 'fairy ring' phenomenon was clearly seen without mapping (Fig. 10), and there was an apparent relationship between the tree and reproduction of this non-mycorrhizal fungus. The radial distance of an arc from a tree bole was found to be directly correlated ($P < 0·05$) with the circumference of the bole at breast height (1·5 m) – the larger the tree the further out the ring. Also, unlike a typical 'free' fairy ring, *M. galopus* mycelium, detected again by the specific MAb, occurred throughout the zone between a tree and an arc. Mycelial biomass estimated from hyphal length by this method tended to increase towards the arc where it was significantly greater than near the tree ($P < 0·05$; Fig. 11; Hitchcock, 1992; Frankland *et al.*, 1995).

Many factors related to the architecture and nutrition of the tree might influence the saprotroph's nutrient uptake, build-up of biomass and deceleration of extension growth leading to arc formation. Stemflow, throughfall, drip from overlapping tree canopies and mycorrhizal activity all spring to mind as possibilities. In addition, it is well known that concentric patterns of soil properties occur around individual trees (Zinke, 1962; Hornung, 1985). Variations in some of these have been investigated (and continue to be) on the Grizedale site along radial transects from tree boles of different sizes to arcs of basidiomata (Frankland *et al.*, 1995).

As expected, considering the uneven topography of the forest floor, variability was high. However, extractable ammonium nitrogen (NH_4^+-N) content of F_1 litter was found to be significantly greater in the region of an arc (position
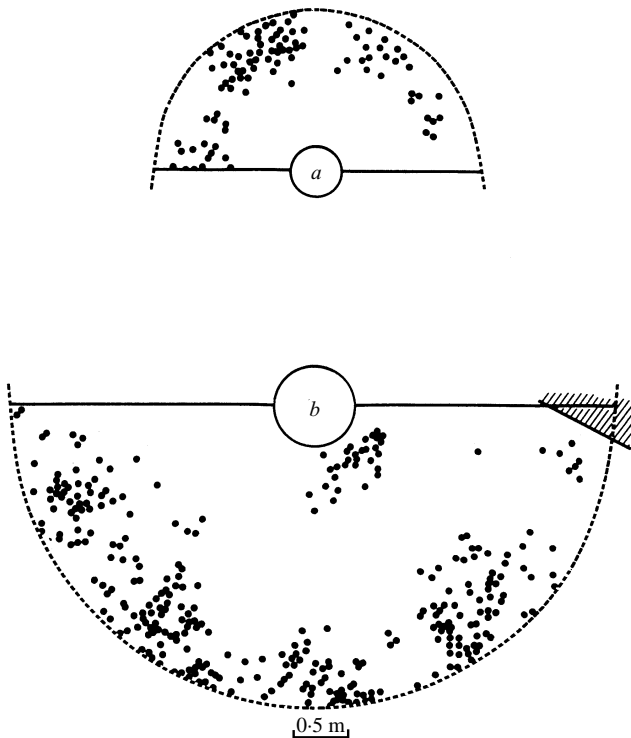
Fig. 9. Arcs of basidiomata of *Mycena galopus* around two *Picea sitchensis* trees (*a* and *b*). Dashed line, arbitrary circular boundary with the tree as centre separating off basidiomata close to neighbouring trees. (From Frankland, 1984.)

Fig. 10. 'Fairy ring' of *Mycena galopus* around a bole of *Picea sitchensis* in Grizedale Forest. Photo: D. Sleep

Fig. 11. Mycelial biomass of *Mycena galopus* in F_1 litter around boles of *Picea sitchensis* in relation to the relative position of basidiomata. Estimates from hyphal length measurements by immunofluorescence. Relative positions: 0%, at the tree; 100%, at a 'fairy ring'. Mean values $\pm$ S.E.M.

relative to the tree, 100%) than the average for relative positions 0 (at the bole), 25, 50 and 150% ($P < 0.01$; Fig. 12), although it might have originated from the basidiomata as they decomposed. Litter pH (4·0–5·2) also attained maximum values in the region of an arc (Fig. 13), but again explanation would require investigation at a microscale level. In contrast, moisture content of the litter measured in winter increased linearly outwards from a tree irrespective of the presence of an arc (Fig. 14). More seasonal sampling of this parameter, including dry summers when moisture could be vital for the very survival of the vegetative mycelium, would be more likely to reveal an arc-related pattern. *M. galopus* is vulnerable to low moisture, fruiting during droughts in the forest only in hollows, under shelter and in stemflow at the foot of tree trunks (see Fig. 9; tree *b*), and its mycelium has been shown to cease growth at 1·0–3·6 MPa (Dix, 1984). The arched root systems of the Grizedale spruce typically formed a terrain of mounds and troughs (Fig. 15), likely to have drained moisture towards the perimeter boundary between neighbouring root systems. Litter also tended to accumulate at a distance from a tree bole, and quadratic curves of litter depth indicated that maxima occurred in the region of an arc and before the zone of overlapping canopies was reached (Fig. 16).

Arrival and establishment of *M. galopus* has so far been considered in isolation, i.e. without regard to how its performance might be conditioned by such processes as competition and grazing – Pickett's intermediate level of ecological organization. On the spruce site, the basidiomata occurred not only in fairy rings but also in discrete clumps, frequently mixed with or e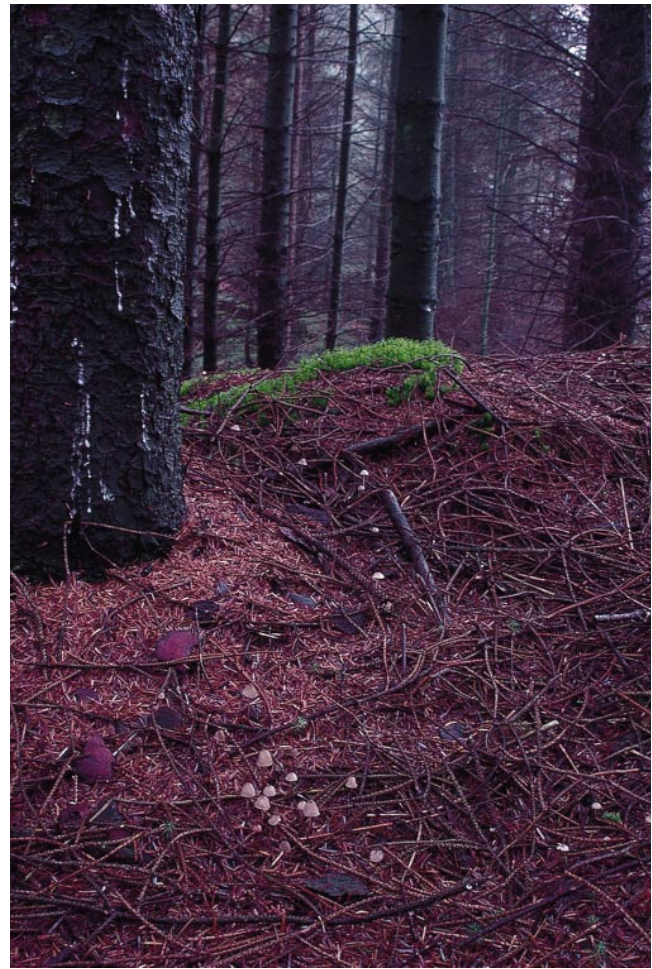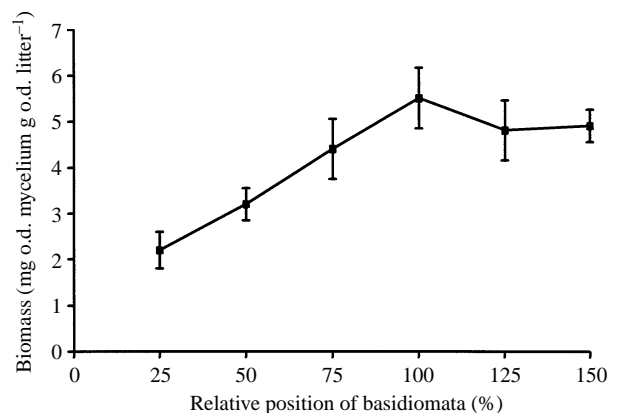ven touching those of other litter-decomposing agarics, particularly *Marasmius androsaceus* (L.:Fr.) Fr.; *Cystoderma amianthinum* (Scop.) Fayod was also common (Fig. 17). An apparent enigma was how the mycelia of these saprotrophs utilizing the same resource could co-exist in such close juxtaposition and produce sufficient biomass to
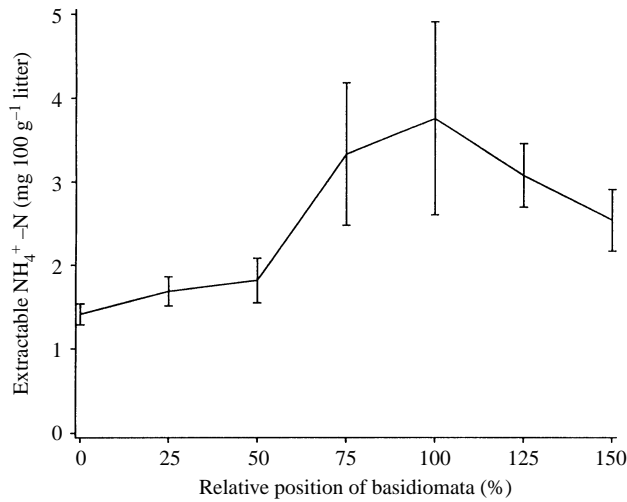
Fig. 12. Extractable NH_4^+-N content of *Picea sitchensis* F_1 in relation to the relative position of basidiomata of *Mycena galopus* (100%). Mean values $\pm$ s.e.m. (After Frankland *et al.*, 1995.)
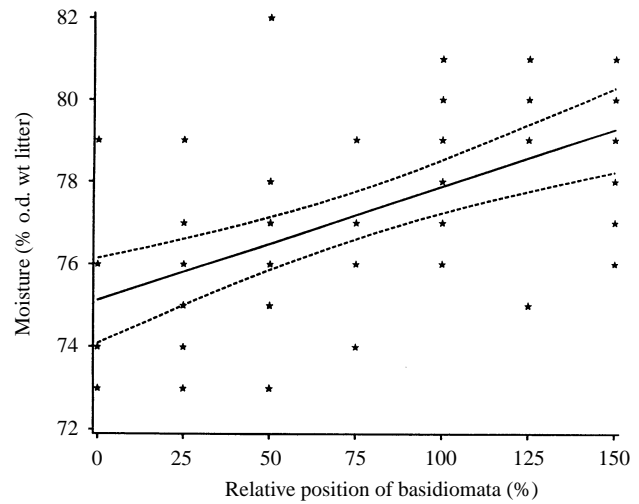

Fig. 14. Moisture content (% o.d.w.) of *Picea sitchensis* F_1 litter in relation to the relative position of basidiomata of *Mycena galopus* (100%). Linear regression line (moisture = $75\cdot1 + 0\cdot028$ position) with 95% confidence limits for mean predicted values.
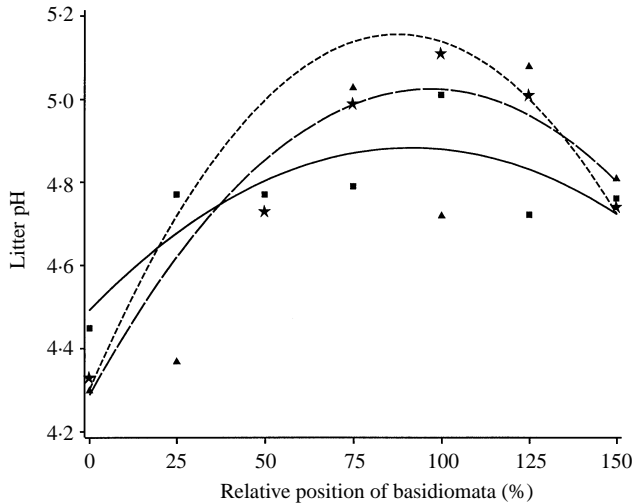

Fig. 13. Quadratic curves of the pH of *Picea sitchensis* F_1 litter in relation to the relative position of basidiomata of *Mycena galopus* (100%) on three radial transects. --- ▲, $R^2 = 66\%$; --- ★, $R^2 = 28\%$; — ■, $R^2 = 33\%$. (After Frankland *et al.*, 1995.)

Fig. 15. Mounding of forest floor formed by arched root systems of *Picea sitchensis* in Grizedale Forest.

reproduce. An exceptional opportunity had arisen for gaining some insight into how competition might operate between *M. galopus* and *M. androsaceus* in the field, albeit at the risk of over-simplifying. After comparing growth characteristics and relative distribution of the mycelia, an hypothesis involving another trophic level was proposed and tested by a variety of laboratory and field experiments (Frankland, 1984; Newell, 1984 *a, b*).

Summarizing, *M. galopus* appeared to be adapted for combative competition. When grown opposite *M. androsaceus*, pigmented interaction zones were formed resulting in deadlock on both laboratory culture media and litter in microcosms. Total biomass of mycelium produced when the two species were grown together in broth culture was less than when they were grown separately ($P < 0\cdot01$), suggesting again that there was some antagonism between them. *Marasmius* was, however, superior in colonizing ability. Its linear growth rate
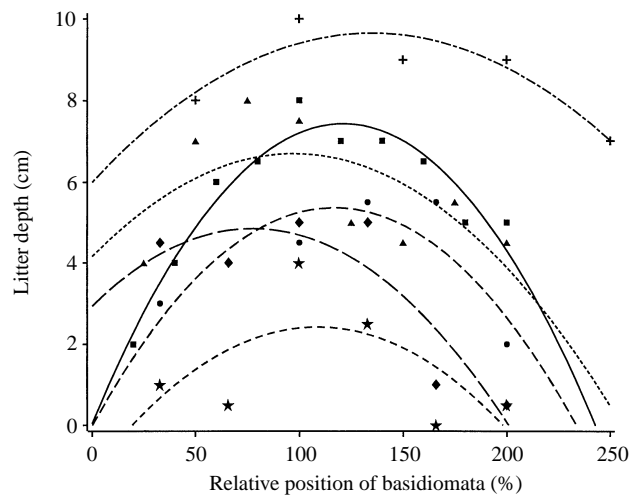

Fig. 16. Quadratic curves of depth of *Picea sitchensis* litter (L + F) in relation to the relative position of basidiomata of *Mycena galopus* (100%) on six radial transects. --- ▲, $R^2 = 14\%$; --- ★, $R^2 = 0\cdot3\%$; --- ●, $R^2 = 57\%$; --- ◆, $R^2 = 67\%$; — ■, $R^2 = 90\%$; —·—·— +, $R^2 = 69\%$.

Fig. 17. Left to right, basidiomata of *Marasmius androsaceus*, *Mycena galopus* and *Cystoderma amianthinum* in close juxtaposition in *Picea sitchensis* litter in Grizedale Forest. Photo: K. Newell.
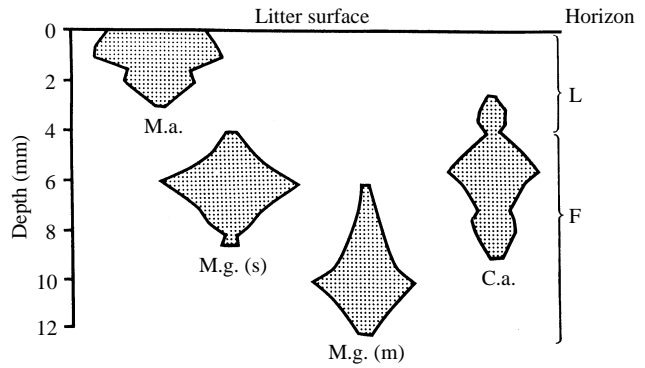

Fig. 19. Fruiting depths of *Marasmius androsaceus* (M.a.), *Mycena galopus* (M.g.) and *Cystoderma amianthinum* (C.a.) in litter of *Picea sitchensis*, Grizedale Forest. The width of each 'kite' at any depth is proportional to the percentage number of basidiomata originating at that depth. s, single-species clumps; m, mixed-species clumps of *M. galopus* with *M. androsaceus*. (From Frankland, 1984.)
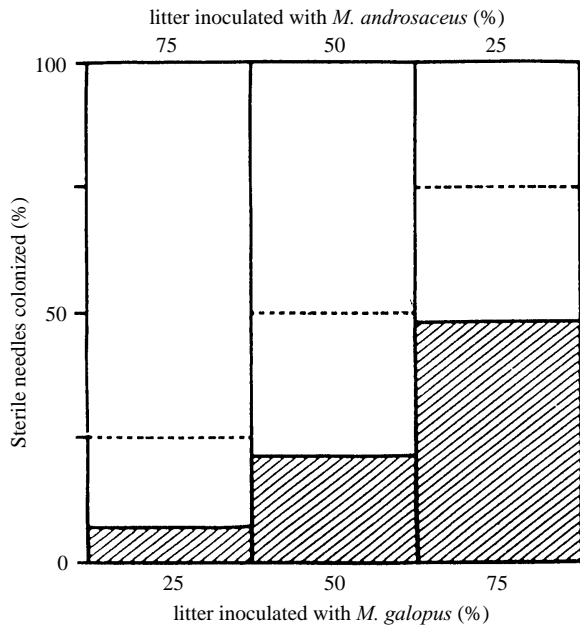

Fig. 18. Colonization of sterile spruce litter after 24 d at 11° by *Mycena galopus* and *Marasmius androsaceus* from litter inoculated with the two species separately and mixed in different ratios. ▨, *M. galopus*; ▢, *M. androsaceus*; ---- expected result if colonizing abilities had been equal. (From Frankland, 1984.)
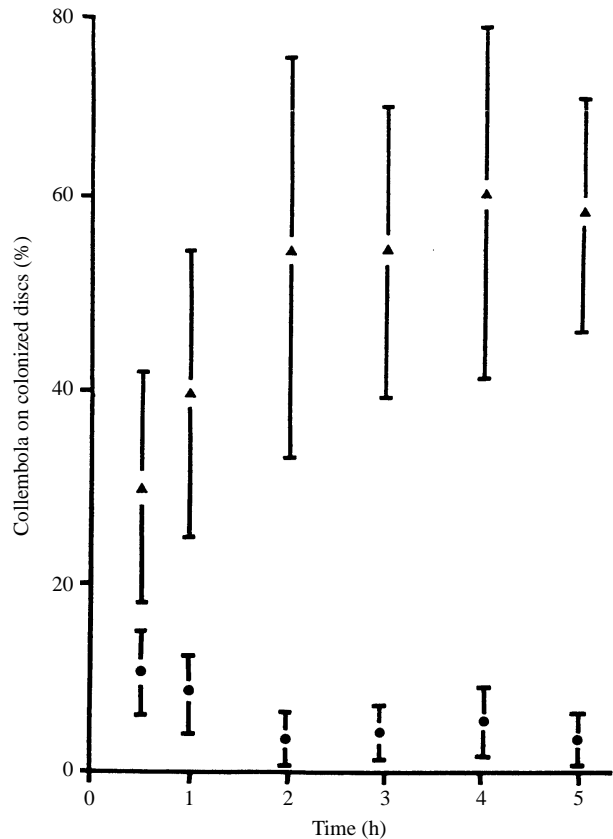

Fig. 20. The percentage number of *Onychiurus latus* that migrated onto agar discs covered with mycelium of *Mycena galopus* (●) or *Marasmius androsaceus* (▲) after increasing time intervals. Error bars are ±s.e.m. (After Newell, 1984a.)

was twice that of *Mycena*, it decomposed more litter and always outcompeted the latter when grown in different ratios on sterile litter (Fig. 18). Acute observation by Newell and repeated practice had enabled her to distinguish the mycelial turfs in the last experiment with 99–100% accuracy. Yet, as pointed out by Rayner & Webber (1984) and Robinson, Dighton & Frankland (1993), the outcome of competition to capture a vacant resource would not necessarily be the same as in a typical field situation.

In the forest, *M. androsaceus* fruited only from the L litter horizon, whereas reproduction of *M. galopus* was restricted to the F_1 horizon. The fruiting depth of *C. amianthinum* was less well defined. The salient discovery regarding the co-existence of *M. androsaceus* and *M. galopus* was the significant displacement of the mean fruiting depth of *Mycena* downwards

when growing with *Marasmius* (Fig. 19). At the time, information on the role of microfauna in decomposition and fungal successions, particularly in coniferous litter, was very limited, but selective grazing by the most abundant myco-phagous collembolan in the Grizedale litter, *Onychiurus latus* Gisin, suggested an explanation. Again, a variety of methods was used to approach the problem, including preference, exclusion and competitive colonization tests.

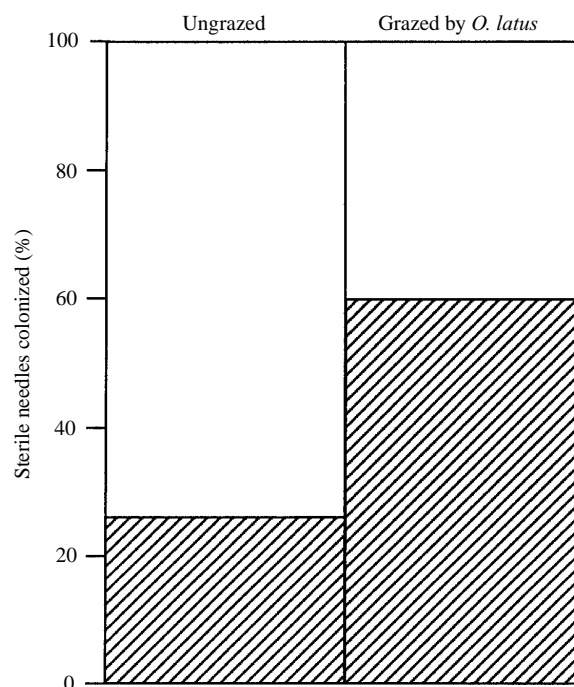*O. latus* in densities of < 600 m⁻² litter and seen to have

Fig. 21. The colonizing abilities of *Mycena galopus* ▨ and *Marasmius androsaceus* ☐ with and without grazing by *Onychiurus latus* after 24 d at 11° in mixed cultures. These initially contained equal quantities of *Picea sitchensis* litter inoculated with each of the two species. (After Newell, 1984*b*.)

basidiomycete mycelium in its gut was in a position to interact with *Mycena* and *Marasmius*. Both species were palatable to it, but the springtail (conveniently a non-jumping species without a furculum!) did show a strong preference for *M. androsaceus* in laboratory (Fig. 20) and field tests. Numbers in litter at the base of *Marasmius* basidiomata were two to three times greater than around the *Mycena* species, and many more, mostly in the feeding state, migrated in the field into bags of litter pre-colonized by *Marasmius* than into bags containing *Mycena* ($P < 0.001$). Moreover, in the laboratory, the relative competitive abilities that had been demonstrated in sterile litter without fauna were reversed by grazing (Fig. 21), and exclusion of *O. latus* from field plots decreased the activity of *M. galopus*.

Microclimate was likely to have had a particularly important influence on the outcome of competition between the two agarics. *O. latus* is prone to desiccation and it migrated up and down the forest floor at Grizedale according to moisture conditions. It moved downwards during the driest periods but usually congregated near the surface in autumn, the percentage number present in the L horizon being directly correlated with the moisture content of the litter ($P < 0.01$).

Taking all the evidence into account, it could be hypothesized that selective grazing allowed *Mycena* to predominate in the F_1 horizon although at a slightly lower level than in its single-species clumps, whereas *Marasmius* with its resistant rhizomorphs could often 'escape' the collembolan during dry periods and build up biomass in the surface litter before initiation of fruit bodies.

Visible mycelium of *M. galopus* reduced rapidly below the F_1 horizon where the spruce needles had collapsed, forming

the amorphous organic matter of the H layer. With depletion and fragmentation of its resource, the cellulolytic and ligninolytic agaric was replaced by *Thysanophora penicillioides* (Roum.) W. B. Kendr. and cosmopolitan soil fungi, including *Mucor hiemalis* Wehmer, potential utilizers of the by-products of cellulose decomposition by *M. galopus* (Frankland, 1974).

This investigation of *M. galopus* led to some unravelling of the processes involved in its establishment and status as a member of a succession on spruce needles in one specific locality. Replaced it was, but while it held its territory it must have been an important cog in the ecosystem, withdrawing, accumulating and releasing vital tree nutrients. In one 10×4.5 m quadrat alone, *ca* 3000 basidiomata (9 kg ha^{-1} O.D.W.) were recorded annually, ten times the quantity quoted for all agaric fruit bodies in a nearby oak wood (Hering, 1966). Extrapolating from the Meathop Wood production data for *M. galopus*, the basidiomata represented approximately 90 kg ha^{-1} O.D.W. vegetative mycelium. Owing to the vagaries of fruiting, this was likely to be a gross underestimate of the true figure.

Questions as to how the distribution of *M. galopus* throughout the forest, with its mosaic of arcs, clumps and scattered basidiomata, had arisen focuses us back to those fundamental causal factors of arrival of species and availability of space, which must encompass the entire biota of a site and its microhabitats. Attainment of the full extent of field knowledge required in answer is a far-off goal, while ecologists are still grappling with the imperfections of 'ecotrons'. To reiterate a well-known comment: succession is the natural integration of all ecosystem processes, and as such is one of the most complex ecological phenomena to unravel (McNaughton & Wolf, 1973).

As the Centenary of the BMS recedes and we approach the Millennium, mycologists are bound to ponder: 'where next?'. Priority is rightly being given by field mycologists to recording the vast diversity of species and to saving some from extinction. At the same time, let us ecologists not neglect to study in greater depth more of the star performers in fungal successions, on which the maintenance of entire ecosystems may depend.

REFERENCES

Brown, J. C. (1958*a*). Soil fungi of some British sand dunes in relation to soil type and succession. *Journal of Ecology* **46**, 641–664.

Brown, J. C. (1958*b*). Fungal mycelium in dune soils estimated by a modified impression slide technique. *Transactions of the British Mycological Society* **41**, 81–88.

Carroll, G. C. & Wicklow, D. T. (ed.) (1992). *The Fungal Community. Its Organization and Role in the Ecosystem*, 2nd ed. Marcel Dekker: New York.

Christensen, M. (1969). Soil microfungi of dry to mesic conifer–hardwood forests in northern Wisconsin. *Ecology* **50**, 9–27.

Clements, F. E. (1916). *Plant Succession. An Analysis of the Development of Vegetation*. Carnegie Institute of Washington Publication No. 242.

Cooke, R. C. & Rayner, A. D. M. (1984). *Ecology of Saprotrophic Fungi*. Longman: London.

Dighton, J. & Mason, P. A. (1985). Mycorrhizal dynamics during forest tree development. In *Developmental Biology of Higher Fungi* (ed. D. Moore, L. A. Casselton, D. A. Wood & J. C. Frankland), pp. 117–139. Cambridge University Press: Cambridge, U.K.

Dix, N. J. (1984). Minimum water potentials for growth of some litter-decomposing agarics and other basidiomycetes. *Transactions of the British Mycological Society* **83**, 152–153.

Dix, N. J. & Webster, J. (1995). *Fungal Ecology*. Chapman & Hall: London.

Elton, C. S. (1966). *The Pattern of Animal Communities*. Methuen: London.

Fleming, L. V. (1984). Effects of soil trenching and coring on the formation of ectomycorrhizas on birch seedlings grown around mature trees. *New Phytologist* **98**, 143–153.

Frankland, J. C. (1966). Succession of fungi on decaying petioles of *Pteridium aquilinum*. *Journal of Ecology* **54**, 41–63.

Frankland, J. C. (1969). Fungal decomposition of bracken petioles. *Journal of Ecology* **57**, 25–36.

Frankland, J. C. (1974). Decomposition of lower plants. In *Biology of Plant Litter Decomposition* (ed. C. H. Dickinson & G. J. F. Pugh), pp. 3–36. Academic Press: London.

Frankland, J. C. (1975). Fungal decomposition of leaf litter in a deciduous woodland. In *Biodégradation et Humification* (ed. G. Kilbertus, O. Reisinger, A. Mourey & J. A. Cancela da Fonseca), pp. 33–40. Pierron: Sarregumines.

Frankland, J. C. (1976). Decomposition of bracken litter. *Botanical Journal of the Linnean Society* **73**, 133–143.

Frankland, J. C. (1981). Mechanisms in fungal succession. In *The Fungal Community. Its Organization and Role in the Ecosystem* (ed. D. T. Wicklow & G. C. Carroll), 1st ed, pp. 403–426. Marcel Dekker: New York.

Frankland, J. C. (1982). Biomass and nutrient cycling by decomposer basidiomycetes. In *Decomposer Basidiomycetes: Their Biology and Ecology* (ed. J. C. Frankland, J. N. Hedger & M. J. Swift), pp. 241–261. Cambridge University Press: Cambridge, U.K.

Frankland, J. C. (1984). Autecology and the mycelium of a woodland litter decomposer. In *The Ecology and Physiology of the Fungal Mycelium* (ed. D. H. Jennings & A. D. M. Rayner), pp. 241–260. Cambridge University Press: Cambridge, U.K.

Frankland, J. C. (1992). Mechanisms in fungal succession. In *The Fungal Community. Its Organization and Role in the Ecosystem* (ed. G. C. Carroll & D. T. Wicklow), 2nd ed., pp. 383–401. Marcel Dekker: New York.

Frankland, J. C., Dighton, J. & Boddy, L. (1990). Methods for studying fungi in soil and forest litter. In *Methods in Microbiology* **22** (ed. R. Grigorova & J. R. Norris), pp. 343–404. Academic Press: London.

Frankland, J. C., Hedger, J. N. & Swift, M. J. (ed.) (1982). *Decomposer Basidiomycetes: Their Biology and Ecology*. Cambridge University Press: Cambridge, U.K.

Frankland, J. C., Latter, P. M. & Poskitt, J. M. (1995). *A Laboratory Guide to Soil Microbiology. Some General Principles and Practice*. Merlewood Research and Development Paper No. 115. Institute of Terrestrial Ecology: Grange-over-Sands, U.K.

Frankland, J. C., Lindley, D. K. & Swift, M. J. (1978). A comparison of two methods for the estimation of mycelial biomass in leaf litter. *Soil Biology and Biochemistry* **10**, 323–333.

Frankland, J. C., Poskitt, J. M. & Howard, D. M. (1995). Spatial development of populations of a decomposer fungus, *Mycena galopus*. *Canadian Journal of Botany* **73**, (Suppl. 1), S1399–S1406.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley: Chichester, U.K.

Harrison, A. F. (1971). The inhibitory effect of oak leaf litter tannins on the growth of fungi in relation to litter decomposition. *Soil Biology and Biochemistry* **3**, 167–172.

Hering, T. F. (1965). Succession of fungi in the litter of a Lake District oakwood. *Transactions of the British Mycological Society* **48**, 391–408.

Hering, T. F. (1966). The terricolous higher fungi of four Lake District woodlands. *Transactions of the British Mycological Society* **49**, 369–383.

Hering, T. F. (1967). Fungal decomposition of oak leaf litter. *Transactions of the British Mycological Society* **50**, 267–273.

Hintikka, V. (1961). Das Verhalten einiger *Mycena* – Arten zum pH sowie deren Einfluss auf die Azidität der Humusschicht der Wälder. *Karstenia* **5**, 107–121.

Hintikka, V. (1964). Psychrophilic basidiomycetes decomposing forest litter under winter conditions. *Communicationes Instituti Forestalis Fenniae* **59:2**, 1–20.

Hintikka, V. (1970). Studies on white-rot humus formed by higher fungi in forest soils. *Communicationes Instituti Forestalis Fenniae* **69:2**, 1–68.

Hintikka, V. (1982). The colonisation of litter and wood by basidiomycetes in Finnish forests. In *Decomposer Basidiomycetes: Their Biology and Ecology* (ed. J. C. Frankland, J. N. Hedger & M. J. Swift), pp. 227–239. Cambridge University Press: Cambridge, U.K.

Hintikka, V. & Korhonen, K. (1970). Effects of carbon dioxide on the growth of lignicolous and soil-inhabiting Hymenomycetes. *Communicationes Instituti Forestalis Fenniae* **69:5**, 1–29.

Hitchcock, P. (1992). Development of an immunological approach to the ecology of a woodland decomposer fungus. Ph.D. thesis, University of Essex.

Hitchcock, P., Gray, T. R. G. & Frankland, J. C. (1997). Production of a monoclonal antibody specific to *Mycena galopus* mycelium. *Mycological Research* **101**, 1051–1059.

Hornung, M. (1985). Acidification of soils by trees and forests. *Soil Use and Management* **1**, 24–28.

Hudson, H. J. (1968). The ecology of fungi on plant remains above the soil. *New Phytologist* **67**, 837–874.

Janos, D. P. (1996). Mycorrhizas, succession, and the rehabilitation of deforested lands in the humid tropics. In *Fungi and Environmental Change* (ed. J. C. Frankland, N. Magan & G. M. Gadd), pp. 129–162. Cambridge University Press: Cambridge, U.K.

Jay, E., Noble, M. & Hobbs, A. S. (1992). *A Victorian Naturalist*. Warne: London.

Jennings, D. H. & Rayner, A. D. M. (ed.) (1984). *The Ecology and Physiology of the Fungal Mycelium*. Cambridge University Press: Cambridge, U.K.

Johnson, E. A. (1979). Succession: an unfinished revolution. *Ecology* **60**, 238–240.

Kendrick, W. B. & Burges, A. (1962). Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia* **4**, 313–342.

Kershaw, K. A. (1964). *Quantitative and Dynamic Ecology*. Arnold: London.

Lamaison, G. (1976). Intérêt chimiotaxonomique de l'équipement enzymatique des macromycètes. *Bulletin de la Société Botanique de France* **123**, 119–136.

Last, F. T., Dighton, J. & Mason, P. A. (1987). Successions of sheathing mycorrhizal fungi. *Trends in Ecology and Evolution* **2**, 157–161.

Last, F. T., Mason, P. A., Ingleby, K. & Fleming, L. V. (1984). Succession of fruitbodies of sheathing mycorrhizal fungi associated with *Betula pendula*. *Forest Ecology and Management* **9**, 229–234.

Last, F. T., Mason, P. A., Wilson, J. & Deacon, J. W. (1983). Fine roots and sheathing mycorrhizas: their formation, function and dynamics. *Plant and Soil* **71**, 9–21.

Lindeberg, G. (1948). On the occurrence of polyphenol oxidases in soil-inhabiting basidiomycetes. *Physiologia Plantarum* **1**, 196–205.

Mason, P. A., Last, F. T. & Wilson, J. (1988). Fruiting and succession of ectomycorrhizal fungi. In *Fungal Infection of Plants* (ed. G. F. Pegg & P. G. Ayres), pp. 253–268. Cambridge University Press: Cambridge, U.K.

McNaughton, S. J. & Wolf, L. L. (1973). *General Ecology*. Holt, Rinehart & Winston: New York.

Newell, K. (1984a). Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. *Soil Biology and Biochemistry* **16**, 227–233.

Newell, K. (1984b). Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. *Soil Biology and Biochemistry* **16**, 235–239.

Park, D. (1968). The ecology of terrestrial fungi. In *The Fungi* **3** (ed. G. C. Ainsworth & A. S. Sussman), pp. 5–39. Academic Press: London.

Parker-Rhodes, A. F. (1954). Deme structure in higher fungi: *Mycena galopus*. *Transactions of the British Mycological Society* **37**, 314–320.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. (1987). A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**, 109–114.

Pugh, G. J. F. (1980). Presidential Address. Strategies in Fungal Ecology. *Transactions of the British Mycological Society* **75**, 1–14.

Pugh, G. J. F. & Boddy, L. (1988). A view of disturbance and life strategies in

fungi. In *Fungi and Ecological Disturbance* (ed. L. Boddy, R. Watling & A. J. E. Lyon). *Proceedings of the Royal Society of Edinburgh* **94B**, 3–11.

Rayner, A. D. M. (1992). Introduction. In *The Fungal Community* (ed. G. C. Carroll & D. T. Wicklow), pp. xvii–xxiv. Marcel Dekker: New York.

Rayner, A. D. M. & Boddy, L. (1988). *Fungal Decomposition of Wood: Its Biology and Ecology*. Wiley: Chichester, U.K.

Rayner, A. D. M., Griffith, G. S. & Ainsworth, A. M. (1995). Mycelial interconnectedness. In *The Growing Fungus* (ed. N. A. R. Gow & G. M. Gadd), pp. 21–40. Chapman & Hall: London.

Rayner, A. D. M. & Todd, N. K. (1979). Population and community structure and dynamics of fungi in decaying wood. *Advances in Botanical Research* **7**, 333–420.

Rayner, A. D. M. & Webber, J. F. (1984). Interspecific mycelial interactions – an overview. In *The Ecology and Physiology of the Fungal Mycelium* (ed. D. H. Jennings & A. D. M. Rayner), pp. 383–417. Cambridge University Press: Cambridge, U.K.

Robinson, C. H., Dighton, J. & Frankland, J. C. (1993). Resource capture by interacting fungal colonizers of straw. *Mycological Research* **97**, 547–558.

Smith, S. E. & Read, D. J. (1997). *Mycorrhizal Symbiosis*, 2nd ed. Academic Press: London.

Taylor, A. F. S. & Alexander, I. J. (1989). Demography and population dynamics of ectomycorrhizas of Sitka spruce fertilised with N. *Agriculture, Ecosystems and Environment* **28**, 493–496.

Tribe, H. T. (1957). Ecology of micro-organisms in soils as observed during their development upon buried cellulose film. In *Microbial Ecology* (ed.

R. E. O. Williams & C. C. Spicer), pp. 287–298. Cambridge University Press: Cambridge, U.K.

Tribe, H. T. (1961). Microbiology of cellulose decomposition in soil. *Soil Science* **92**, 61–77.

Visser, S. (1995). Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist* **129**, 389–401.

Visser, S. & Parkinson, D. (1975). Fungal succession on aspen poplar leaf litter. *Canadian Journal of Botany* **53**, 1640–1651.

Webster, J. (1956). Succession of fungi on decaying cocksfoot culms. I. *Journal of Ecology* **44**, 517–544.

Webster, J. (1957). Succession of fungi on decaying cocksfoot culms. II. *Journal of Ecology* **45**, 1–30.

Webster, J. & Dix, N. J. (1960). Succession of fungi on decaying cocksfoot culms. III. A comparison of the sporulation and growth of some primary saprophytes on stem, leaf blade and leaf sheath. *Transactions of the British Mycological Society* **43**, 85–99.

Wicklow, D. T. (1988). Parallels in the development of post-fire fungal and herbal communities. In *Fungi and Ecological Disturbance* (ed. L. Boddy, R. Watling & A. J. E. Lyon). *Proceedings of the Royal Society of Edinburgh* **94B**, 87–95.

Wicklow, D. T. & Carroll, G. C. (ed.) (1981). *The Fungal Community. Its Organization and Role in the Ecosystem*. Marcel Dekker: New York.

Zinke, P. J. (1962). The pattern of influence of individual forest trees on soil properties. *Ecology* **43**, 130–133.