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Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris

Lynne Boddy

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Decomposition of coarse woody debris (CWD), be it naturally occurring or resulting from forestry activity, begins long before it hits the ground. Obvious and well-known examples of decay in the standing tree result from heartrots, pathogens leading to root, butt and top rots, and wounding, and are only covered briefly here. Even more common, but as yet less well known, is decay developing from fungal propagules latently present within functional sapwood. These propagules do not develop overtly until the high water content stress obtaining in functional sapwood is reduced (e.g. following drought, root damage, light suppression). Which of the several (many) species/genotypes develop depends on temperature, gaseous and drying regime, and host tree species amongst others. Pioneer communities in sapwood, be it in standing trunks, attached branches, felled timber, or windthrown wood, develop from these fungi which are latently present. If dysfunctional wood remains attached to the tree then these fungi develop forming closed communities which can effect substantial decay. Subsequently secondary colonisers may arrive and continue the decay process, until wood becomes sufficiently weakened and falls to the floor where decay of CWD continues. Decay of felled CWD also begins with fungi which develop from latent propagules though they do not always get the opportunity to establish large domains, as other primary colonizers from outside establish rapidly, and both types of primary colonizers are often relatively rapidly replaced by secondary colonizers. On the forest floor later colonizers can arrive as spores or as mycelium, and effects of these different modes of arrival on community development are discussed. Factors affecting community development and species richness are considered, including interspecific interactions and direct and indirect effects of abiotic variables. The mycelium is emphasised throughout, and dangers of overemphasis on carpophores are highlighted.

Decay rate of CWD is commonly approached from an overall process viewpoint, and the effects of abiotic variables on overall decay can be modelled. Ultimately it is the decomposer organisms which effect decay and complex communities can result in extremely heterogeneous decay rates at different spatial and temporal locations within wood. Examples of such differences resulting from presence of different species, interactions between species, and microclimatic variation are presented. Examples are largely taken from temperate angiosperm woodland, but principles are likely to be broadly similar in forests throughout the world, including boreal forests.

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Fungal community development and hence decomposition of coarse woody debris (CWD), be it naturally occurring or resulting from forestry activity, begins long before it hits the ground. Obvious and well-known examples of decay in standing trees result from heartrots, pathogens leading to root, butt and top rots, and unspecialized opportunists causing decay of sapwood following wounding (e.g. Rayner and Boddy 1988, Fig. 1). These will only be considered briefly here, with emphasis on fungal species diversity and specificity. Even more common, but as yet less well known, is the development of decay from fungal propagules latently present within functional sapwood. Following the establishment of these fungi in standing trees, complex communities develop and continually change. Principles of community structure and development are first briefly reviewed and then illustrated with examples in attached branches and felled wood.

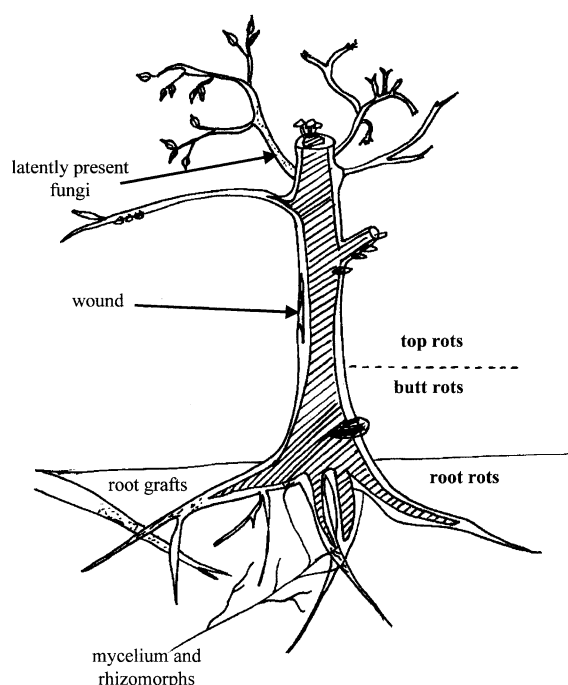


Fig. 1. Diagram illustrating locations of decay in a standing tree. Hatched area represents the region that is subject to heartrot, heartrot fungi being able to gain entry via wounds and broken limbs exposing heartwood, some can become established in dysfunctional sapwood, others become established in twigs and dead stubs which later become buried in heartwood, others establish below ground. The fungi colonizing by active pathogenesis most commonly do so below ground, spreading from tree to tree by rhizomorphs or mycelium or via root grafts. Dysfunctional attached branches are colonized by latently present fungi, and sapwood in the vicinity of wounds is first colonized by species with ruderal characteristics – often non-basidiomycetes initially. (Adapted from Rayner and Boddy 1988.)

To be certain of which fungi are actually present in wood at different stages of decay it is necessary to obtain mycelia from the decay columns in wood, by isolation and/or direct incubation under moist conditions. Many studies, however, rely solely on occurrence of fruit bodies. The relevance of what can be gained from fruit body surveys is debated.

The fungal communities that develop in wood effect decomposition. Thus the factors that influence overall decay do so by the effects which they exert on the fungal decomposers. The major determinants of fungal decomposition of wood are briefly considered, and emphasis is placed on the heterogeneity of the decay processes occurring in wood brought about by the mosaic of different species, variation in microclimate, and interactions between fungi during community development.

Examples are largely taken from temperate angiosperm woodland, but principles are likely to be broadly similar throughout the world, from tropical rainforest to boreal forests, though in the case of latency evidence in conifers is largely lacking.

Origins of decay

CWD arriving at the forest floor is usually already well decayed (e.g. Boddy and Swift 1983, Harmon et al. 1986), the implication being that decay begins in the standing tree. Decay in the standing tree can result from heartrot, pathogens, unspecialized opportunists in wounds/dead wood, and can also originate from fungi latently present in functional sapwood (Fig. 1).

Decay originating from heartrots, pathogens and unspecialized opportunists

In mature standing trees, the inner core has few living cells and a relatively extensive gaseous phase often exists, rendering this region easier for fungi to colonize than functionally intact sapwood where the opposite conditions occur. A wide variety of microorganisms have been found associated with decayed hearts of living trees, though only a relatively few ascomycetes and basidiomycetes are known to cause significant decay (Rayner and Boddy 1988). Both white rot and brown rot is produced. Though easier to colonize than functional sapwood, heartwood is nonetheless a very stringent environment with highly selective conditions resulting from a gaseous environment far removed from atmospheric, and commonly the presence of inhibitory extractives (see below). Heart-rot fungi therefore show a high degree of S-selection (*sensu* Cooke and Rayner 1984), i.e. they have a range of stress-tolerant characteristics. They often grow slowly, lack combative ability and have strong selectivity for particular tree taxa (see below). When mature trees are felled or fall conditions in the

heartwood do not usually alter dramatically, but the sapwood dries, the gaseous regime improves, and living cells die; the sapwood contains fewer inhibitory chemicals than heartwood making the former resource far easier for the majority of wood-rotting fungi to colonize. Sapwood then decays much more rapidly than the heartwood. The S-selected characteristics that fit heart-rot fungi for colonization of heart wood tend not to be the best characteristics for successful acquisition of non-functional sapwood (see below) so fungi adopting other ecological strategies predominate.

Though functional sapwood is inimical to colonization by most decay fungi, it is made accessible by injury or rapid death of bark. Colonization following wounding has been extensively studied, especially in North American angiosperms (see references in Rayner and Boddy 1988, Blanchette 1992). Typically, zones of fungal colonization, discoloration and decay adopt a characteristic shape dictated by the nature and location of the wound (Fig. 2). If the wound penetrates through several or many annual rings a tapering column of stain and decay is often formed, which spreads preferentially axially towards the inner wood and is markedly restricted tangentially and at the interface with wood laid down by the cambium subsequent to injury. The CODIT (Compartmentalization Of Decay In Trees) theory attempted to explain the limitation of colonization within the vicinity of wounds by suggesting that functional sapwood tissues respond to injury and colonization by

walling themselves off from fungal invasion by the production of barriers (Shigo 1979, 1984). Certainly gums, tyloses, suberized layers and other allelopathic chemicals are formed, which can have inhibitory effects against fungi (e.g. Blanchette and Biggs 1992), but in fact, the localization of decay can be largely explained in terms of wood anatomy and maintenance of functional sapwood, which as already stated is inimical to growth (Boddy and Rayner 1983a, Boddy 1992a).

Wood in the vicinity of wounds invariably becomes discoloured before it becomes decayed. Non-basidiomycete fungi and bacteria are readily isolated from these regions, but decay-causing basidiomycetes tend to be isolated later. These observations led to the theory of succession which suggested that non-basidiomycete fungi and bacteria are necessary to precondition the wood by detoxification of phenolic substances etc. produced by the tree, allowing the wood decay basidiomycetes to follow (e.g. Shigo 1979). In fact, wood decay basidiomycetes have a powerful battery of enzymes that allows them to utilize lignocellulose and other recalcitrant compounds and to colonize wood that has not previously been colonized (Rayner and Boddy 1988). The reason that stain fungi are usually found before basidiomycetes is that they arrive first, rapid dispersal being among their R-selected (ruderal) ecological characteristics (see below). In CWD, fungi previously limited to the vicinity of a wound can grow into and decay surrounding previously uncolonized tissues, as the high water content/poor aeration stresses are removed upon drying.

Some decay fungi can gain access to intact sapwood by pathogenic mechanisms. This can include destruction of living cells and production of pectinolytic enzymes that destroy pit membranes, which allows colonization by preventing maintenance of hostile microenvironmental conditions by the tree. Establishment of a sufficient inoculum base is often critical for successful active pathogenesis, and can occur through heart rot and wound colonization. Three major types of active pathogenesis can be distinguished: ectotrophic root infection, wound infection and canker production (Rayner and Boddy 1988). Ectotrophic pathogens which decay wood produce extensive growth of superficial mycelium over the root surface prior to invading the root interior, and can proceed many centimetres or even over a metre in advance of internal infection of woody roots. Such growth provides an extensible inoculum base from which cambium and other outer host cells can be killed, subsequently leading to alleviation of the stressful microenvironment of the sapwood, and opening up a way for spread into the interior. *Heterobasidion annosum* (Fr.) Bref. (cause of "Fomes root rot" in conifers), *Armillaria* species ("honey" "bootlace" or "shoestring" fungi) in broad-leaves and conifers, *Phellinus weirii* (Murrill) R.L. Gilbertson (in conifers), *Inonotus tomentosus* (Fr.: Fr.) S. Teng (in spruce), and *Ganoderma* species are examples of those wood decay fungi that operate ectotrophic active pathogenic strategies worldwide (e.g. Rayner and Boddy 1988).

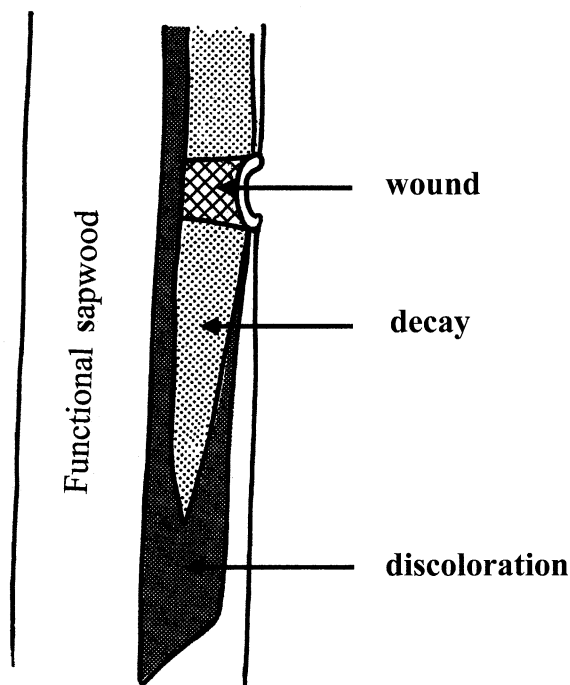


Fig. 2. Diagram illustrating localization of discoloration and decay in the vicinity of a sapwood wound in a standing tree.

Wounded tissue can act as a focus for infection of wood by active pathogenesis, by allowing a fungus (e.g. *Stereum sanguinolentum* (Alb. & Schw.) Fr. in conifers and *Chondrostereum purpureum* (Fr.) Pouz. in angiosperms) to establish an inoculum base from which to extend. Cankers – localized patches or strips of bark resulting from the growth of pathogenic microorganisms – can be an effective means for a decay fungus to establish itself in a living tree since they allow access to underlying xylem. However, many-canker forming fungi (e.g. *Nectria* spp.) are not generally regarded as wood decay fungi, and many decay fungi that do form cankers (e.g. *Inonotus obliquus* (Fr.) Pilát, *Phellinus pini* (Fr.) Ames and *Biscogniauxia nummularia* (Bull.) O. Kuntze) do so as a result of colonizing bark from the underlying wood (e.g. Rayner and Boddy 1988, Hendry et al. 1998). On the other hand, *Hypoxylon mammatum* (Wahlenb.) Mill. on *Populus tremuloides* does colonize wood from the overlying canker (see references in Manion and Griffin 1986).

Following tree death or felling, fungi that have become established via active pathogenesis continue to decay the wood. Eventually, however, they are replaced by more combative saprotrophic decay fungi (see below).

Sapwood decay originating from latent fungal propagules

Patterns of decay in sapwood of attached angiosperm branches and standing trunks showing no obvious sign of major damage are very different from those originating as unspecialized opportunist colonizers of wounds or as root or wound pathogens. Frequently, longitudinally extensive

(several or many metres) decay columns occupied by a single fungal individual develop rapidly – often in less than one growing season, as indicated by annual ring counts (Fig. 3). This has been described in detail for oak (*Quercus robur* and *Q. petraea*: basidiomycetes *Peniophora quercina* (Fr.) Cooke, *Phlebia rufa* (Fr.) M.P. Christ., *Stereum gausapatum* Fr. and *Vuilleminia comedens* (Nees: Fr.) Maire), ash (*Fraxinus excelsior*: ascomycetes *Daldinia concentrica* (Bolt.: Fr.) Ces. & De Not. and *Hypoxylon rubiginosum* Pers.: Fr.), hazel (*Corylus avellana*: ascomycete *Hypoxylon fuscum* (Pers.: Fr.) Fr. and basidiomycete *Stereum rugosum* (Pers.: Fr.) Fr.), birch (*Betula* spp.: basidiomycete *Piptoporus betulinus* (Bull.: Fr.) Karst.) and beech (*Fagus sylvatica*: basidiomycete *V. comedens* and ascomycetes *Biscogniauxia nummularia* and *Eutypa spinosa* (Pers.) Tul. & C. Tul.) (Boddy and Rayner 1983b, Boddy et al. 1985, 1987, Rayner and Boddy 1986, Boddy 1994, Hirst 1995, Hendry et al. 1998). Since linear extension rates, even under optimal conditions in the laboratory, are often insufficient to explain such rapid development it is unlikely that colonization is by mycelial spread from a single focus such as a wound. A more likely scenario is that propagules (e.g. yeasts, spores, mycelial fragments) of these fungi are already present in the sapwood of trunks and branches, but are prevented from developing when the xylem is functional, due to high water content (and/or an associated factor such as aeration) and low nutrient availability. These propagules are extensively but sparsely distributed along a column of wood. When drying begins mycelia start to develop from the propagules and if they encounter other mycelia of the same genotype they fuse to form large individuals. The latent presence of many of these pioneer decay fungi in sapwood has been demon-

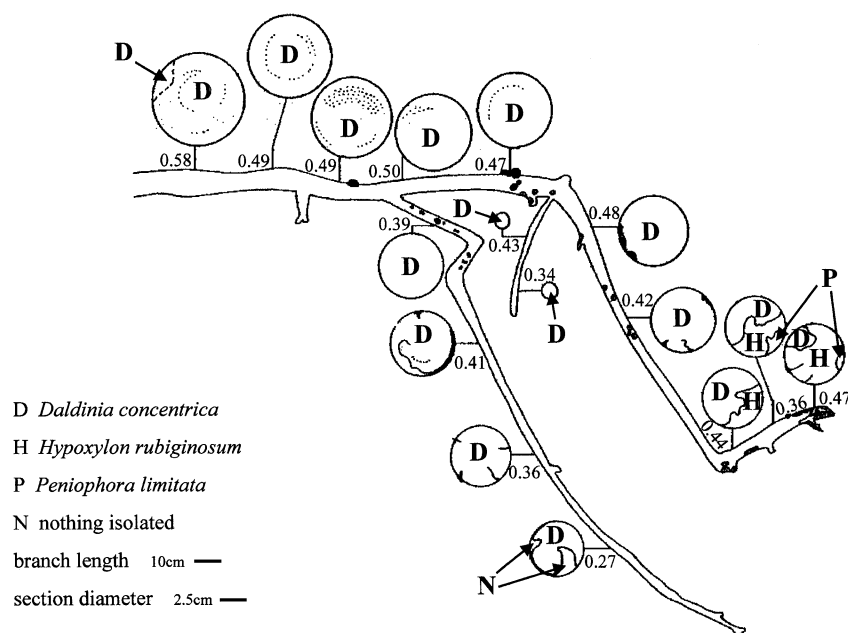


Fig. 3. Decay community structure in an attached ash *Fraxinus excelsior* branch. Figures indicate density (g cm⁻³). Within the wood there was a single individual each of *Daldinia concentrica*, *Hypoxylon rubiginosum*, and *Peniophora limitata*. *Exidia thurettiana* was fruiting on the middle section of the top fork, but was not isolated from within; it may have been killing the cambium. *Peniophora limitata* was fruiting at the distal end of the top fork, and *D. concentrica* was fruiting on the main branch and proximal ends of the forks.

strated in all of the aforementioned tree species (Chapela and Boddy 1988a, Griffith and Boddy 1990, Hendry 1993, Hirst 1995) and in trembling aspen *Populus tremuloides*, American beech *Fagus grandifolia* (Chapela 1989) and alder *Alnus* spp. (Fisher and Petrini 1990) by making isolations directly from freshly felled wood or, more commonly, after incubating lengths of wood cut from apparently healthy twigs, branches and trunks under conditions allowing gradual drying. Pockets of stain and decay are evident soon after drying begins, and interestingly in beech these are more prevalent in certain annual rings than in others. Pairings of isolates of the same species developing in widely separated wood lengths confirmed that, for many species, genetically identical propagules are longitudinally well dispersed before overt development (Hendry 1993, Hirst 1995). The ways by which these propagules gain entry to sapwood is still unknown, but is likely to vary between fungal species and/or fungal/host combinations, but probably includes entry through damaged roots, bud scars, stubs and branchlets, insect activity, and by crossing the cambium from small foci in the bark.

Specificity of pioneer fungi

Pathogens, heart rots and latent invaders

Selectivity for particular habitat types is widespread amongst fungi utilizing all sorts of organic substrata, not just wood, and the causes are complex (e.g. Rayner et al. 1985).

Heartrot fungi vary considerably in the extent to which they are selective for particular tree taxa, ranging from those that are virtually specific for tree genera, e.g. *Fistulina hepatica* (Fr.) Schaef. on *Quercus* (and occasionally *Castanea*) and *Phellinus pini* on *Pinus*, to those that can attack a wide range of species, e.g. *Armillaria gallica* Marxmüller & Romagn. on angiosperms and *Heterobasidion annosum* on conifers (e.g. Rayner and Boddy 1988). Between these extremes are fungi which are strongly selective for a particular tree genus but which do also occur, though relatively infrequently, on others, e.g. *Grifola frondosa* (Dicks.: Fr.) S.F. Gray and *Inonotus dryadeus* (Pers.: Fr.) Murr. on *Quercus*, and *Phellinus chrysoloma* (Fr.) Donk on *Picea*. Also, there are some fungi selective for several trees that are often unrelated, e.g. *Laetiporus sulphureus* (Bull.: Fr.) Murr. on *Quercus* (and *Castanea* which is in the same family), *Prunus*, *Salix* and *Taxus*. Differences in fruit body morphology, ecology, cultures and molecular biology suggest that there may be five taxa of *Laetiporus* in North America (Burdall et al. 1998), though in the subalpine zone of the Alps there were insufficient differences between ITS sequences of *L. sulphureus* from conifers and broad-leaved trees to warrant separation into separate species (Rogers et al. 1998). With *H. annosum* different species names have been proposed for the different intersterility groups (P, S and F) (Niemelä and Korhonen 1998). The intersterility groups show selec-

tivity for hosts, *Pinus* spp. being the main hosts of the P group, *Picea abies* for the S group, though the F group is found on *Abies* spp., other conifers and angiosperms (Korhonen et al. 1998). However, intersterility is not complete and there remains debate as to whether the intersterility groups should be designated as different species.

Selectivity of heart-rot fungi is probably related to microenvironmental conditions within the heart wood, non-selectivity or broad-range selectivity being seen in fungi that colonize trees where heartwood imposes less extreme conditions, and narrow selectivity occurring in species or populations adapted to the specific harsh conditions in heartwood of certain trees. Unfortunately, little research has been done on adaptation in heart-rot fungi, though since there appears to be no difference in tolerance of heart-rot and sap-rot fungi to elevated CO₂ and reduced O₂ (Highley et al. 1983), adaptation is likely to be related to other abiotic constraints, e.g. wood extractives, volatiles and pH. For example, *Fistulina hepatica* has a low optimum pH for growth and can utilize tannins as sole carbon source, which correlates with its selectivity for *Quercus* (see references in Rayner and Boddy 1988). As well as the ability to grow under apposite abiotic regimes, selection pressures are likely to be imposed on the establishment and even entry phase, where, for example, ability to germinate on exposed heartwood may be crucial. Selection pressures are most likely to apply when establishment involves active pathogenesis. Thus, with *Heterobasidion annosum* different intersterility groups have evolved with some selectivity for host tree species (see above).

With some of those fungi that develop in sapwood only after a period of latency, there may also be intimate interactions with the host that impose selectivity. There are recognition responses between *Hypoxylon fragiforme* (Pers.: Fr.) Kickx and living beech cells (Chapela et al. 1993), and several fungi found latently in beech respond to beech callus (Hendry et al. 1993). Major determinants of overt development, however, include rate of drying, gaseous regime and temperature. In beech, while *H. fragiforme*/*Biscogniauxia nummularia* developed under all drying regimes, *Coniophora puteana* (Schum.) Karst. only developed under moderate drying regimes (Chapela and Boddy 1988a). *Coniophora puteana* did not develop below 20°C, *Nectria coccinea* (Pers.: Fr.) Fr. (developing from bark) declined with increasing temperature, none developing above 30°C, and from 25°C to 30°C *B. nummularia* increased while *H. fragiforme* decreased (Hendry 1993). Some fungi may be latently present in a narrow range of trees, though insufficient work has yet been done to be categorical about this, while others are widely present latently within functional sapwood. For example, *Daldinia concentrica* (identified by morphology in culture) is a common latent species in *Quercus*, *Fraxinus excelsior*, *Fagus sylvatica* and *Betula* spp. (Griffith and Boddy 1990). In southern Britain sporocarps are exceptionally common on *F. excelsior* and occur occasionally on *F. sylvatica*; in northern Britain it is common on

Betula (Whalley and Watling 1980). However, while saying this, the *D. concentrica* complex does include species with habitat preferences: *D. loculata* (Lév) Sacc. commonly occurs on burnt *Betula* and *D. petriniae* Ju, J.D. Rogers & F.S.M. González on unburnt *Alnus* and *Betula* (Johannesson et al. 2000).

Other pioneers: R-selection

Pathogenic and heart-rot fungi, and those that invade with a latent strategy may be considered to have a lot of S-selected characteristics, in other words characters that fit them for colonization of the rigorous environment of the functional tree. Pioneers of sapwood of CWD and those colonizing wood in the vicinity of wounds face a very different environment. The harsh conditions of functional tissues with high water content and living cells have been removed. These disturbed environments, therefore, favour organisms with ruderal (R-selected) characteristics, including effective dispersal, early arrival and early exit as more stressful (e.g. due to desiccation or lowering of nutrients) and/or combative conditions intensify. They tend to be relatively non-selective for tree taxa.

Fungal community structure and development

Principles

Fungal communities in wood are continually changing both temporally and spatially (e.g. Rayner and Boddy 1988, Boddy 1992b). These changes are complex and multidimensional, following a diverse array of pathways rather than occurring in simple stages following an ordered pattern. Community development begins as soon as wood becomes dysfunctional, colonization starting with fungi latently present within the wood, pathogens or fungi on the surface or rapidly arriving at the surface. As wood begins to be colonized, even before the entire volume is occupied, changes begin with new arrivals trying to effect entry, domain of incumbents overlapping and changes in microenvironment shifting the balance between one individual/species and another. Community structure continually changes during wood decomposition until eventually the resource has completely decomposed, and consequently the idea of a climax community is inappropriate.

Arrival and establishment

Fungi may arrive at woody resources either as vegetative mycelium or as propagules – usually sexual or asexual spores. Not surprisingly, establishment processes are quite varied depending on the mode of arrival.

Propagules may be dormant awaiting the arrival of a new resource or may be dispersed to the resource by an

essentially passive (except for zoospores) means, including in air and water currents, rain splash, aerosols and via animal vectors. Distances dispersed vary considerably (Stenlid and Gustafsson 2001). Contact with an appropriate resource therefore occurs largely by chance. However, in some examples of animal vectoring, mutualistic relationships with certain animal vectors not only result in carriage to an appropriate environment but also, often, insertion within the wood avoiding the hostile surface environment. Spores generally contain limited endogenous nutrient supplies, so successful establishment is highly dependent on encountering locally favourable conditions. When arriving at closed communities entry is likely to be even more difficult if the fungi already present can operate aggressive defence mechanisms. Many of the pioneer fungi have a lot of ruderal characteristics (see above). Some of the later colonisers that arrive as spores colonize by replacing specific predecessor species (Niemelä et al. 1995). For example, *Lenzites betulina* (L.: Fr.) Fr. which is specifically mycoparasitic on *Coriolus* (= *Trametes*) species, and *Pseudotrametes* (= *Trametes*) *gibbosa* (Pers.: Pers.) Bond. & Sing. which is mycoparasitic on *Bjerkandera adusta* (Willd.: Fr.) Karst. (Rayner et al. 1987). If spores are genetically similar (which is more likely if asexually derived) there are possibilities of synergism. However, where there are genetic differences somatic incompatibility phenomena militate against synergism (Rayner et al. 1984).

Arrival by mycelium, on the other hand, allows synergism between hyphae, and provides the ability to translocate water, carbon and mineral nutrients obviating the necessity of obtaining these from the immediate environment during establishment (e.g. Boddy 1993, 1999, Rayner 1996). Many of the wood decay fungi that arrive as mycelium form linearly aggregated hyphal systems – cords and rhizomorphs, that are long-lived, cover many m² of forest floor, operate variable search patterns for new resources, reallocate biomass to successful search pathways and reallocate nutrients according to demand (Boddy 1993, 1999).

Following arrival, there must be a phase of resource capture during which the fungus gains command over territory, in the form of a volume of wood, and then has access to the carbon and mineral nutrient resources held within that territory. In the case of pioneers the wood is largely uncolonized and acquisition of territory can be termed primary resource capture. In contrast, later colonizers commonly have to employ combative mechanisms to wrest territory from previous occupants – termed secondary resource capture. Subsequently, there follows a phase of exploitation, where resources are utilized and converted into energy for growth, for consolidating (i.e. resisting adverse abiotic conditions or attack by competitors), and/or exiting the wood as propagules or mycelium.

Community development pathways – driving forces for change

When fungal communities begin to develop the conditions in wood can range between very high environmental stress imposed on the fungi at one extreme to low stress following disturbance at the other extreme (Cooke and Rayner 1984, Rayner and Webber 1984, Rayner and Boddy 1988, Boddy 1992b). An example of a situation where community development is initiated under high stress is in sapwood of standing tree trunks and branches, whereas felled or windblown wood and wood in the vicinity of wounds in standing trees is often relatively stress free. Fungi initiating community development in the former tend to have stress tolerant characteristics suiting them for the harsh environment of recently functional sapwood. In contrast, those initiating colonization in the latter situation have predominately ruderal characteristics, though pioneers that are latently present also have S-selected characteristics. Community composition then depends on which fungi arrive and which are already there, and the way that communities develop depends on four main driv-

ing forces: stress aggravation (increase), stress alleviation (decrease), disturbance and combat (Fig. 4). Disturbance pushes community composition towards fungi having more ruderal characteristics, whereas development from an open to a closed community results in intensification of combat and the presence of more combative species. Aggravation of stress leads to species tolerant of the particular stress, whereas stress alleviation allows fungi with a preponderance of ruderal or combative characteristics to dominate. Ultimately, as the resource becomes well decayed nutrients begin to become limited, disturbance increases as the wood fragments and soil animals invade, and the community changes to comprise species with ruderal/stress (low nutrients/invertebrate grazing) tolerant characteristics. Obviously, fungi do not usually display characteristics that are all R-selected, all S-selected or all C-selected, but combinations of these. Moreover, the characteristics of a particular fungus may vary at different times, and indeed even in different parts of the mycelium (Pugh and Boddy 1988).

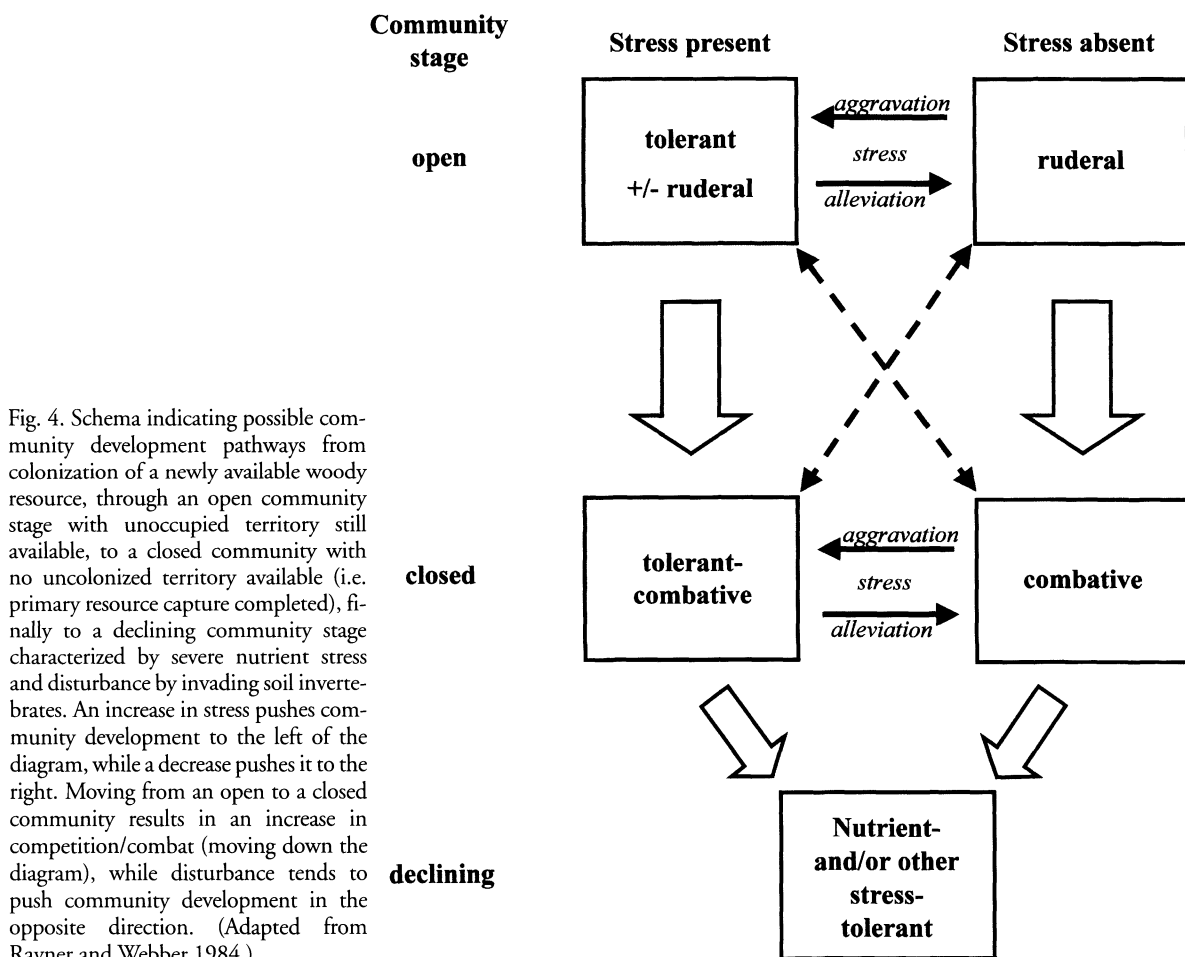


Fig. 4. Schema indicating possible community development pathways from colonization of a newly available woody resource, through an open community stage with unoccupied territory still available, to a closed community with no uncolonized territory available (i.e. primary resource capture completed), finally to a declining community stage characterized by severe nutrient stress and disturbance by invading soil invertebrates. An increase in stress pushes community development to the left of the diagram, while a decrease pushes it to the right. Moving from an open to a closed community results in an increase in competition/combat (moving down the diagram), while disturbance tends to push community development in the opposite direction. (Adapted from Rayner and Webber 1984.)

Community development and decay initiated in the canopy

The high water content and corresponding low O_2 content of functional sapwood produces a high stress environment for wood decay fungi. Community development in attached oak (*Quercus robur* and *Q. petraea*) branches has probably been studied in most detail, and is based on 3-dimensional sectioning and mapping, isolation, incubation in moist conditions to allow direct development of mycelium, incubation of functional branches under different drying regimes, and estimation of decay state (density; $g\ cm^{-3}$) of many branches at different stages of decay (Boddy and Rayner 1983b, Boddy 1992b).

In southern Britain, five basidiomycetes – *Peniophora quercina*, *Stereum gausapatum*, *Vuilleminia comedens*, *Pellinus ferreus* (Pers.) Bourd and *Phlebia rufa* – are commonly found as pioneers, all being frequently located close to functional sapwood, forming extensive individuals, and in the case of the first three being shown to be latently present in functional sapwood. *Exidia glandulosa* Fr. appears principally to cause cambial death and loosening of bark, but is also sometimes found extending into sapwood. *Coriolus versicolor* (L.: Fr.) Quel., *Phlebia radiata* Fr. and *Stereum hirsutum* (Willd.: Fr.) S.F. Gray are all found in decayed wood, are aggressive combatants against the other fungal colonizers and are considered secondary invaders. The three other main secondary colonizers are *Peniophora lycii* (Pers.) v. Höhn & Litsch, *Hyphoderma setigerum* (Fr.) Donk and *Schizopora paradoxa* (Fr.) Donk, the former being found in terminal regions and the latter two being associated with desiccation and insect activity.

The primary colonizers have S-selected characters that enable them to exist latently within the functional sapwood, and then to develop rapidly as the high water content/poor aeration stress begins to be alleviated. Which of the pioneers develops in any particular location depends on which species are present and also on the rate, extent and direction of stress alleviation (Hendry 1993). Combativeness also varies depending on the conditions obtaining (Boddy 2000). This is particularly evident in ash *Fraxinus excelsior* where the role of pioneers is taken by the ascomycetes *Daldinia concentrica* and *Hypoxyton rubiginosum* (Boddy et al. 1987, Fig. 3). Under ambient conditions *D. concentrica* replaces *H. rubiginosum*, but under conditions that sometimes obtain following loss of sapwood function the balance shifts in favour of the latter (Boddy et al. 1985) allowing it to become extensively established. As conditions change further following drying the balance between the primary colonizers can change.

When combative secondary colonizers arrive, whether or not they become established depends on whether the conditions have ameliorated sufficiently to allow them to grow, and whether they are the better combatant under the conditions obtaining. The primary colonizers differ in their relative combative abilities, e.g. *Phlebia rufa* tends to

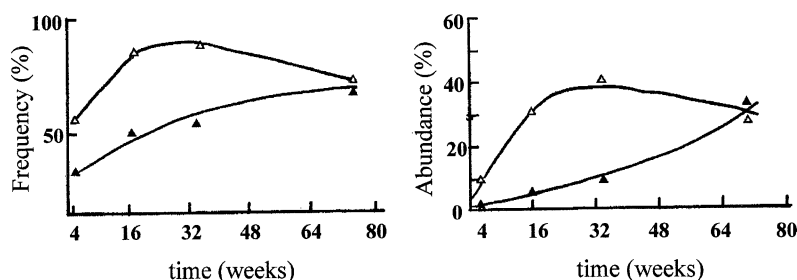
be more combative than *Vuilleminia comedens* (Boddy and Rayner 1983b), and hence which is present may determine whether or not a particular secondary colonizer becomes established. Both these combative secondary colonizers and the primary colonizers can be replaced by the relatively non-combative but desiccation and grazing-stress tolerant secondary colonizers *Hyphoderma setigerum* and *Schizopora paradoxa*. While neither of these are better able to grow at lower water potentials than the other primary and secondary colonizers (Boddy 1983), they are able to survive such adverse and fluctuating conditions (*S. paradoxa* produces chlamydospores), and presumably rapidly redevelop when conditions improve.

The extent of decay occurring in the canopy before fall is very variable (e.g. Boddy and Swift 1983, Harmon et al. 1986). Complete decay of sapwood can occur in the canopy but only if the branches are supported by central heartwood or wings of prematurely formed heartwood (Boddy and Rayner 1981). Otherwise, when wood becomes weakened by decay it falls to the floor, where decomposition continues. Unfortunately, there do not appear to have been any studies on communities developing following fall. Some insight can be obtained from the studies of fungal community development in felled wood, but the starting points are very different. The communities that have already developed in standing wood are likely to affect subsequent patterns of colonization on the forest floor.

Community development in felled wood on the forest floor

Felling represents a disturbance event that makes available wood for colonization under conditions that are relatively non-stressful. Possibly the best studied system is felled beech *Fagus sylvatica* logs (e.g. Ueyama 1966, Siepmann 1973, Coates and Rayner 1985a, b, c, Lange 1986, 1992, Chapela and Boddy 1988b, Chapela et al. 1988, Boddy et al. 1989). The general patterns of community structure and development were similar in the different studies, though species composition was not always the same. Primary colonizers can become established from cut ends, wounds etc. and via propagules latently present within the wood before felling. The latter, e.g. *Biscogniauxia nummularia*, *Cryptosporiopsis fasciculata* (Tode) Petrak, *H. fragiforme*, *Libertella faginea* Desm. and *Nectria coccinea*, develop rapidly as conditions are ameliorated, colonization from cut ends being slower because it depends on arrival of air- or soil-borne spores or of mycelia growing through soil (Fig. 5; Chapela and Boddy 1988b). When logs are placed vertically on soil the different source of colonizing fungi, i.e. from soil or air, is apparent (Coates and Rayner 1985a, b, c, Fig. 6). Penetration from an aerial cut surface was slower than from one in contact with soil, presumably due to the harsher microenvironment of the aerial cut surface. The overall recruitment of species and individuals follows

Fig. 5. Percentage frequency (proportion of logs colonized) and abundance (proportion of total number of chips from which fungi were isolated) of latently established fungi (open symbols) and non-latently colonizing basidiomycetes (closed symbols) in 20 cm length healthy beech *Fagus sylvatica* branches (2–6 cm diam.) on the forest floor, with time. (Redrawn from Chapela and Boddy 1988b).



a steadily increasing but decelerating course (Fig. 5), as might be expected on resources of limited size. Continuous recruitment of new species occurred for at least 70 weeks (Fig. 5), presumably as a result of new species arriving while others are declining, though to start with there is probably some element of “closer packing” in the limited volume of wood.

At early stages, in wood discoloured but not visibly decayed, various ascomycetes, e.g. *Ascocoryne sarcoides* (Jacq.: S.F. Gray) Groves & Wilson, and basidiomycetes, e.g. *Chondrostereum purpureum* were common (Coates and Rayner 1985a, b, c, Chapela and Boddy 1988b). After a couple of weeks, basidiomycetes, principally *Byerkandera adusta*, *Coriolus versicolor* and *Stereum hirsutum*, began to establish from aerially exposed surfaces, their decay columns becoming clearly resolved from 24 weeks, though they were usually truncated at ca 2 cm depth. The white-rot ascomycete, *Xylaria hypoxylon* (L.: Fr.) Greville, became increasingly evident (on some sites though not others) from 12 to 52 weeks, arriving both by aerial spores and via the soil. At this stage community structure contrasted

markedly with that in attached branches where, typically, extensive individuals developed. In the felled wood there was initially numerous small decay columns (Fig. 6) reflecting colonization by prolific numbers of spores (e.g. Rayner and Boddy 1988), though occasionally long columns of *Biscogniauxia nummularia* were evident, reflecting its origin from latent propagules (Fig. 6).

The rhizomorphic *Armillaria gallica* was present on some sites, and cord-forming saprotrophs, e.g. *Megacollybia platyphylla* (Pers.: Fr.) Kotl. & Pouz., *Phallus impudicus* Pers. and *Phanerochaete velutina* (DC: Pers.) Parmasto, were present on most. Time before arrival of these depended on proximity of logs to established systems, and while *A. gallica* could colonize peripheral regions (where it was usually restricted, causing little decay) immediately, there was a delay before the cord-forming basidiomycetes colonized, presumably due to the high water content stress still obtaining. Though colonization by the cord-formers was initially slow (Fig. 5), they eventually occupied very large volumes (Fig. 6) replacing previous incumbents during combative interactions.

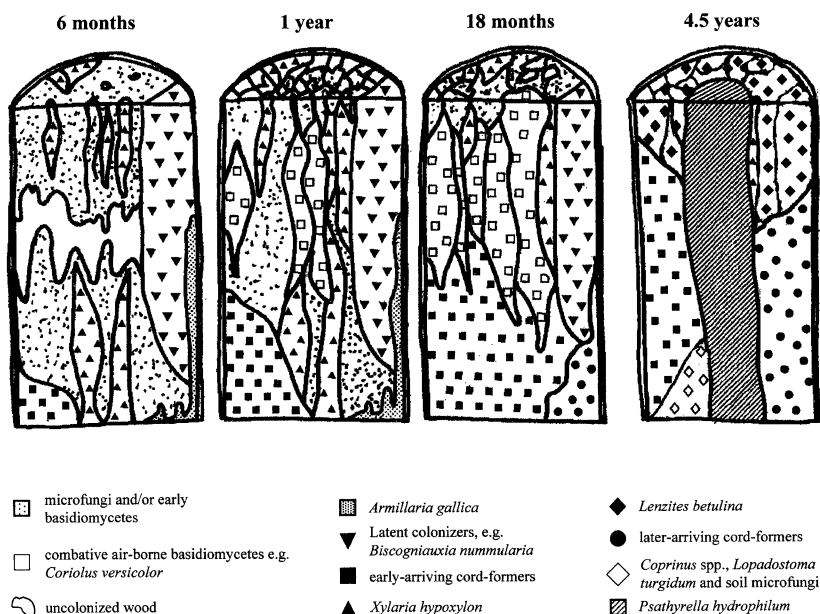


Fig. 6. Idealized diagram illustrating a “typical” pattern of natural decay community development in felled beech *Fagus sylvatica* logs placed upright with bases buried in soil and litter in a mixed temperate deciduous woodland. (6–18 months adapted from Coates and Rayner (1985c).)

After 1 yr *Chondrostereum purpureum* was infrequent, as were *Biscogniauxia nummularia* and *Hypoxylon fragiforme* after 1–1.5 yr. Similarly, *Bjerkandera adusta* declined after 1.5 yr, though *Stereum hirsutum* persisted, albeit in a small number of logs, and *Coriolus versicolor* and *Xylaria hypoxylon* were present respectively in 45 and 90% of logs after 4.5 yr. Though cord-forming basidiomycetes still dominated many logs after 4.5 yr, the basidiomycetes *Coprinus* spp., *Lenzites betulina*, *Psathyrella piluliformis* (Bull.: Fr.) P.D. Orton (= *P. hydrophilum*), the ascomycete *Lopadostoma turgidum* (Pers.) Traverso, and various soil Mucorales and deuteromycetes were also prevalent (Chapela et al. 1988).

To summarise in terms of ecological characteristics and driving forces for change, the first colonisers of the initially relatively stress free environment of felled sapwood were latently present or rapidly arrived as spores. The decline of the latent invaders may have largely resulted from increased stress to them as drying continued, reflecting results of laboratory experiments where secondary colonizers were absent (Chapela and Boddy 1988b). The decline of the other colonizers, however, was undoubtedly due to competitive exclusion by more combative fungi. There is a clear hierarchy of combative ability though this can be considerably modified by environmental regime (Boddy 2000). In agar culture, *Armillaria gallica*, *Xylaria hypoxylon* and *Lopadostoma turgidum* are least combative (Coates and Rayner 1985c, Chapela et al. 1988), though by virtue of the pseudosclerotial plates that they produce, the first two are more resistant to replacement. *Coriolus versicolor* and *Stereum hirsutum* are more combative than these three; *Megacollybia platyphylla*, *Phallus impudicus* and *Phanerochaete velutina* are more combative still; and yet more combative are *Hypholoma fasciculare* (not necessarily better than *P. velutina*), *Lenzites betulina*, *Psathyrella piluliformis* and *Sistotrema brinkmanii* (Bres.) J. Erikss. Hierarchies of combative ability have also been described in other tree species, e.g. Norway spruce *Picea abies*; (Holmer and Stenlid 1997). The arrival of Mucorales and deuteromycetes reflects a “backwards” shift in community development resulting from the disturbance activities of invading soil animals. Communion by soil invertebrates militates against the majority of wood decay basidiomycetes, but favours fungi with ruderal (plus some S-) characteristics (Swift and Boddy 1984).

There is evidence, from a gradient analysis of fruit bodies on large decaying beech trunks in Denmark, that basidiomycete community structure becomes increasingly unpredictable and diverse at late stages of decay (Heilmann-Clausen pers. comm.), perhaps reflecting the variety of microhabitats and different patterns of species occupation and decay during earlier stages of decay. Fruit body surveys have indicated a similar increase in species heterogeneity in conifer logs during late stages of decay (Renvall 1995, Høiland and Bendiksen 1996), though fruit body surveys should be interpreted cautiously (see following section).

Relevance of fruit body surveys

Sporocarps are “the tip of the ice berg”, the mycelium being the part of the fungus that effects decomposition of woody substrata. While the foregoing is based on mycelial distribution and activity (evidenced by isolation, direct incubation yielding mycelial outgrowth, and mycelial structures in wood – e.g. pseudosclerotial plates) the vast majority of studies have concentrated on the distribution and abundance of fruit bodies (e.g. Lange 1986, 1992, Renvall 1995, Niemelä et al. 1995, Sippola and Renvall 1999). Information on the latter should be interpreted with caution since distribution and abundance of fruit bodies may often not reflect presence, distribution and abundance of mycelium. Absence of a fruit body does not necessarily imply absence of the fungus; while presence of a fruit body indicates the presence of a fungus – at least in the recent past – the fungus may not be a wood-rotting species, but may have come from the soil or litter to fruit.

The presence of sporocarps of fungi that are definitely present in the wood cannot be regarded as giving precise information about the succession of fungi in wood. Rapid commitment of mycelial biomass into reproductive effort is a ruderal characteristic, whereas later/intermittent fruiting is an S- or C-selected character. Also, fungi require access to sufficient resources before fruiting occurs, and different species require different triggers for fruiting. The mycelia of species that fruit later may therefore sometimes even have been present before that of earlier fruiting species.

Fruit bodies do give some indication of ability to disperse, but lack of fruit bodies does not necessarily mean that species/individuals are not spreading, since some can achieve considerable vegetative spread by outgrowth as mycelia or mycelial aggregates (e.g. Boddy 1993, 1999), some produce asexual spores formed on/in the mycelium and/or are dispersed by insect vectors. Fruit bodies should not necessarily be taken as a sign of an active/fit mycelium as they may in fact be produced as a response to unfavourable conditions (abiotic or biotic). Production of a fruit body of one fungus on another should not necessarily be taken as evidence of parasitism or replacement of the latter by the former; the species may simply be following similar routes of egress. In view of the foregoing, apparent successor-predecessor relationships (see above; e.g. Niemelä et al. 1995) should also be viewed with caution, though there is laboratory evidence (Holmer et al. 1997) supporting at least some of these relationships.

On the positive side, fruit body surveys may detect a few species that might be easy to miss by culturing onto a general artificial medium such as malt agar. For example, some of the late stage basidiomycetes may have specific nutritional requirements, e.g. *Pluteus* species (Banerjee 1994). Also, for large scale survey work, determining the presence of mycelia in wood may often be unrealistic, though for species that do not readily fruit a combined approach may be essential.

Information on the relationships between fruit bodies and mycelia in wood, on any particular site, is clearly needed. While mycelial surveys are ideal, they may, however, often not be practical. In which case data should be interpreted bearing in mind all of the very many problems indicated above.

Overall decomposition processes

Major determinants of decay

The decomposer organisms themselves and a host of abiotic environmental factors determine decay rate. There is considerable variation in decay rate between species. For example, decay of pine (*Pinus* spp.) wood blocks after 12 months (25°C, 70% water content) ranged from < 5% for *Antrodia ramentacea* (Berk. & Br.) Donk to almost complete decomposition by *Hyphodontia spathulata* (Schrad.: Fr.) Parmasto (Blumenfeld 1984). Henningsson (1965) classified fungi into five groups based on their annual decay rate of birch (*Betula*) wood blocks in the laboratory: Group I (<10%), e.g. soft-rot fungi, *Ascocoryne sarcoides* and *Stemphylium* sp.; Group II (10–25%), e.g. *Chondrostereum purpureum*, *Daedaleopsis confragosa* (Bolt.: Fr.) Schroet. and *Hymenochaete tabacina* (Sow.) Lév.; Group III (25–50%), e.g. *Fomes fomentarius* (L.: Fr.) Kickx and *Stereum hirsutum*; Group IV (50–75%), e.g. *Bjerkandera adusta* and *Piptoporus betulinus*; Group V (>75%), e.g. *Coriolus versicolor*, *Ganoderma adspersum* (Schultz.) Donk. and *Lenzites betulina*. Variation in wood decay rate effected by different species lies in the relationship between metabolic rate and ecological strategy. For example, rapid extension rate is often inversely correlated with decay rate, e.g. the pioneer *C. purpureum*, while slow to moderate extension can be associated with rapid decay, e.g. the heart-rot fungus *G. adspersum* (Henningsson 1965). In contrast, *C. versicolor* combines a rapid growth rate with a rapid decay rate and a defensive, combative strategy. The ascomycetes *Daldinia concentrica* and *Xylaria hypoxylon* decay wood relatively slowly but hold territory for extended periods – *D. concentrica* has been found occupying large volumes of wood in ash trees over 25 yr after felling (unpubl.). *Xylaria hypoxylon* maintains the wood at a low water content by virtue of the pseudosclerotial plates (PSPs) formed around the decay columns that it occupies; if these PSPs are removed and water is added, wood decay rate is extremely rapid (Boddy et al. 1989). Decay rate can vary considerably between different strains and between homokaryotic and heterokaryotic mycelia (Da Costa and Kerruish 1965, Amburgey 1970, Abou-Heilah and Hutchinson 1977).

Extractives and volatiles, pH, temperature, water availability and gaseous regime are all major determinants of wood decay rate, as is size, which exerts its effect indirectly by influencing water relations, gaseous regime and temper-

ature, and the time taken for fungal colonization (see references in Boddy 1986, Rayner and Boddy 1988).

Heterogeneity of decay within wood

Clearly abiotic variables are major determinants of wood decay rate. However, there is often considerable variation in decay rate between woody resources that appear similar, in terms of size, state of decay etc. and the climatic conditions that they are experiencing. Further, decay rate models based on climatic factors alone leave considerable variation unaccounted for (e.g. see Boddy 1986). Since, as described above, wood decomposition is effected largely by a variety of different fungi, but also by various invertebrates, bacteria and actinomycetes, the rate and pattern of decomposition will depend on community composition and the functioning of individual component decomposer organisms under the prevailing microenvironmental conditions. Unfortunately, however, there have been few attempts to combine studies on synecology with studies on decomposition processes. Nonetheless, it is possible to highlight important issues.

The structure of fungal communities in decomposing wood can obviously influence overall decomposition rate, since different organisms are able to catabolise different molecules at different rates, and their abilities may vary depending on abiotic environmental regime, which can vary considerably over a small scale (Boddy 1984, 1986). This is well illustrated by the variation in water content, state of decay (quantified as density) and instantaneous decay rate (quantified as rate of CO₂ evolution from excised wood over ca 2 h) in different regions of beech logs one year after felling (Boddy et al. 1989, Fig. 7). Variation in decay rate between different regions reflected species present, water content and an interactive effect of water content with species. Moreover, there was evidence that interaction (deadlock or replacement) between species also affects decay rate. There was further evidence of inhibition of wood decomposition when high basidiospore loads of single species were applied to cut surfaces of beech logs (Coates and Rayner 1985a) and spruce *Picea sitchensis* stumps (Redfern et al. 1997). The intense intraspecific interactions that resulted even prevented formation of decay columns of individual species, and inhibited production of sporocarps.

That inter-specific interactions affect decay rate (as reflected by changes in CO₂ evolution) was confirmed in laboratory experiments in which pairings were made by securing two precolonized beech *Fagus sylvatica* wood cubes (8 cm³) together, with transversely cut vessels on adjacent surfaces (Owens 1989). Increases in CO₂ evolution were detected during, for example, replacement of *Stereum gausapatum* by *Bjerkandera adusta*, and of *Flammulina velutipes* (Curt.: Fr.) Karst. by *Phanerochaete velutina*, and deadlock between *Lenzites betulina* and *F. velutipes* in

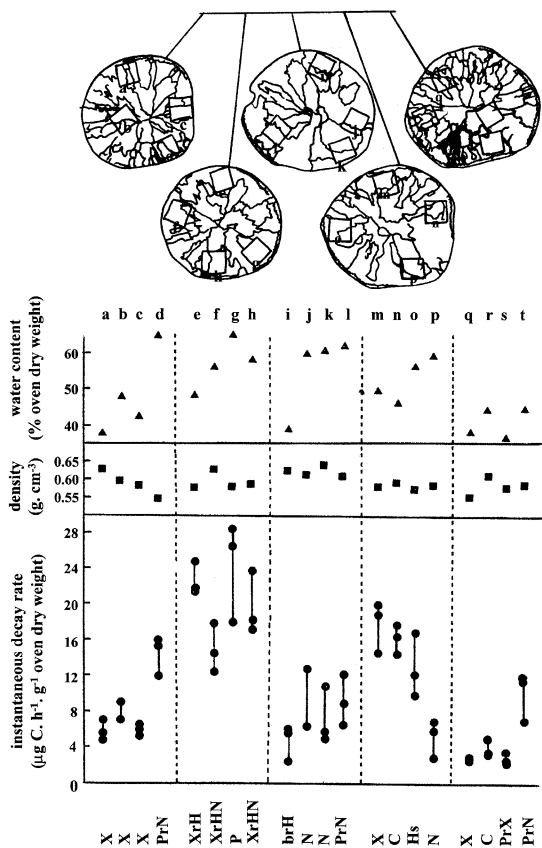


Fig. 7. Variation in fungal community composition, water content (% oven dry weight, triangles), state of decay (density – g cm^{-3} , ■) and instantaneous decay rate ($\mu\text{g C h}^{-1} \text{g}^{-1}$ oven dry weight, ●, three replicates) in 50 cm length beech *Fagus sylvatica* logs after 14 months on the forest floor. Discs were cut at 9.5 cm intervals and $2 \times 2 \times 2$ cm cubes were excised to estimate water content, density and decay rate. Black lines are “interaction zone lines” between different fungal individuals (of the same or different species) or, in the case of *Xylaria hypoxylon* and *Armillaria gallica*, pseudosclerotial plates formed within and around individual decay columns. Abbreviations: C, *Coriolus versicolor*; Hs, *Hypoxylon serpens*; H, *Hypoxylon fragiforme*; N, *Nectria* sp.; P, *Phanerochaete velutina*; X, *Xylaria hypoxylon*; b, basidiomycete; r, replacing. (Redrawn from Boddy et al. 1989.)

wood. Occasionally there were decreases during interactions, e.g. when *Stereum hirsutum* replaced *Chondrostereum purpureum*. Such changes in CO_2 evolution during combative interactions, are likely to reflect changes in metabolic activity of mycelia required to defend against or overcome an opponent. However, it should be noted that increased CO_2 evolution from woody resources, may not only result from increased instantaneous decay rate of the wood but also from use of compounds stored within mycelia. Decay rate also alters as colonization proceeds at early stages in the absence of competitors (Owens 1989).

Conclusions

A picture of the patterns and processes involved in the decomposition of CWD is emerging, especially for temperate angiosperms. The tree species examined needs to be widened and greater emphasis on direct indicators of fungal presence within wood (mycelium vs carpophores) would be beneficial. Many of the general principles are likely to be the same for boreal angiosperms and conifers, though fungal species involved and rates of community change and decomposition are likely to differ. One major difference between conifers and angiosperms may be that fungi latently present in sapwood play a key role as pio-

neers in the latter, but may not in the former, though this remains to be investigated. To completely understand variability in overall decay rate of CWD, knowledge of fungal community structure is required. Studies embracing both synecology and decomposition processes are therefore urgently required.

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