
Fungal succession or sequence of fruit bodies?

Sally C. Fryar

National Parks and Wildlife Service NSW, P.O. Box 1967, Hurstville, NSW 2220, Australia;
email: scfryar@bigpond.com

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Succession is one of the most widely known ecological concepts. It is intuitive and yet extremely complex. There have been many fungal succession studies on a wide diversity of substrates and yet we still know very little about the mechanisms that drive succession. Direct methods of observing fungal succession (change in occupation of space by thalli) use destructive techniques and therefore change in mycelia in a point in space over time cannot be observed. However, these direct destructive methods, with appropriate replication, are extremely useful for discovering general patterns of succession. Indirect methods often observe only the fruit body sequence on a substrate. These studies can also be extremely useful, but need to be interpreted with caution. In addition the underlying assumption that sporulation reflects changes in mycelial occupation of space in the substrate needs to be considered carefully.

Key words: ecological concepts, ecology, fungal succession.

Succession

“Succession is one of the oldest, most basic, yet still in some ways, most confounded of ecological concepts” (McIntosh, 1980). Ecological succession is the process of temporal change in community composition (Morin, 1999) with various mechanisms such as facilitation, tolerance and inhibition driving the compositional change (Connell and Slatyer, 1977). Broadly, there are two types of succession. Primary succession is the development of communities on exposed ground which has never borne vegetation (e.g. after volcanic eruption). Secondary succession is the development of communities on soils already developed, but which have been damaged or destroyed. Most succession studies to date deal with secondary succession.

The concept of ecological succession has been theorized for over a century, but it wasn't until the work of Clements and Cowles that the concept was developed in depth (Miles, 1987). Clements (1916) published a review of succession in which he presented a speculative theory of succession based on the idea of a climax community, whereby in a particular climatic region, vegetation changed in one direction towards a single community type (the

climax community). This concept has since been widely criticized and ecologists now analyse successional data in ways that can detect multiple directions of change (Miles, 1987).

Fungal succession or sequence of fruit bodies?

Rayner and Todd (1979) defined fungal succession “as the sequential occupation of the same site by thalli (usually mycelia) either of different fungi or of different associations of fungi”. Importance is placed on the occupation of sites by mycelium. A succession has occurred if one (or more) mycelium has replaced (not necessarily actively) another mycelium (or other mycelia). Fungi replace one another as their dynamic communities of mycelia alter in space and time (Frankland, 1998).

Fungal succession is often confused with a sequence of fungi sporulating on a substrate. Initially the “coprophilous fungal succession” was attributed to the nutritional hypothesis whereby the sequence of fruit bodies seen on dung after defecation was due to the Zygomycetes using the simple sugars, starches, and proteins first (and subsequently sporulating), then the Ascomycetes using the hemicelluloses and celluloses (and sporulating), followed by the basidiomycetes using the lignin and cellulose (then sporulating). Over 38 years ago Harper and Webster (1964) helped to clarify this matter by demonstrating that the time taken to fruit is independent of the nutritional status of the dung. On sterile dung, these fungi required the same number of days to produce mature ascocarps and basidiocarps, as did field collections incubated in the laboratory. They also found that the majority of coprophilous fungal spores germinate 6 hours after defecation. The mycelia then grow simultaneously in the substrate but take different lengths of time to produce fruit bodies. To avoid confusion, fungal succession may be better termed “mycelial succession” to emphasise the importance of observing changes in mycelial distribution. In addition, the term “sequence of fungal sporulation” should be used rather than the term “fruit body succession” to provide further clarification in describing these processes.

Types of fungal succession

Fungal successions can be studied at two different levels: that at the substratum level, and that at the whole community level (Grubb, 1987; Frankland, 1998). Most fungal succession studies focus on the substratum level such as terrestrial wood (Lange, 1992), dung (Nagy and Harrower, 1979; Kuthubutheen and Webster, 1986), hay (Breton and Zwaenepoel, 1991), aquatic wood (Fryar *et al.*, 2002), pine cones (Kasai *et al.*, 1995), wool (Ghawana *et al.*, 1997), sugar cane (Sandhu and Sidhu, 1980), straw (Harper

and Lynch, 1985) and living leaves (Wildman and Parkinson, 1979). Some of these studies could be more accurately described as “a sequence of fruit bodies” rather than “a fungal succession”. Community level fungal successions usually involve following the change in fungal species composition in relation to vegetational change (e.g. Crites and Dale, 1998; Senn-Irlet and Bieri, 1999).

Fungal successions can also be divided into primary and secondary successions. A number of studies have examined the mycorrhizal fungal communities (primary succession) developing on areas affected by volcanic eruption (e.g. Carpenter *et al.*, 1987; Titus and del Moral, 1998). Most substrate successions can be considered to be secondary successions. They are generally a result of a disturbance event (even if at a micro-scale) within an already existing community.

Direct and indirect methods for studying fungal succession

Ideally, to observe fungal succession we would be able to observe the hyphae occupying a particular volume of space in a substrate over time. Unfortunately, all of our current techniques are destructive which means that we cannot observe the mycelia in a given area of substrate over time. General patterns of succession however, can be deduced, using destructive techniques. For example, Ponge (1991) observed both sporulating structures and hyphae in Scots pine litter and was able to discern fungal succession patterns. Because the observation of fungal hyphae inside substrates results in the destruction of the sample, some inference must be made as to the fungal succession. However, with appropriate replication and experimental design, this problem can be overcome to some extent by generalising about the hyphae present at different stages of succession. A number of studies have used this technique to demonstrate fungal successions, particularly mycorrhizal fungal successions (e.g. de Mendonça Bellei *et al.*, 1992).

Molecular methods, although also destructive may become more important in investigating fungal succession as they directly detect the mycelium present in a substrate.

Indirect methods, usually observing fruit bodies on a substrate over time, have been used extensively for “observing” fungal succession (e.g. Bettucci and Silva, 1992; Lange, 1992). Results from these studies can be valid, but need to be viewed with caution and it must be remembered that we are not seeing the true fungal succession (i.e. mycelial succession). While it is reasonable to suppose that the fruit bodies are a reflection of changes in occupation of sites by hyphae of different species, it must be remembered that this is merely the most likely hypothesis. Fungal succession is not directly observed using this method and therefore it can never be assumed that fungal

succession is the cause of the sequence of fruit bodies. If the time taken for a species to produce a fruit body in a natural fruit body sequence is much greater than the time normally taken for that species to produce fruit bodies when grown alone, then it is likely that the observed pattern is due to the fungal succession, rather than simply differential time taken to sporulate.

Interestingly, some mycorrhizal fungal studies have found similar results using direct and indirect methods (Deacon *et al.*, 1983; Mason *et al.*, 1984), whereas others have found differing results (Meier *et al.*, 1990; Shaw *et al.*, 1992).

Another indirect method of observing fungal succession is to examine what is presumed to be different age classes of substrata (or communities). For example, fungal succession studies in leaf litter often use different layers of the leaf litter to infer a succession. The top layers are less decomposed and more recent, while lower layers are more decomposed and have been on the forest floor for longer periods. Investigators collect litter from the different layers to observe the succession of fungi (e.g. Ponge, 1991; Aoki *et al.*, 1992). Similarly, the succession of fungi along with the rest of a community can be studied by examining the fungi present in forests of different ages (e.g. Crites and Dale, 1998; Senn-Irlet and Bieri, 1999). However, care must be taken to ensure sufficient replication and in particular avoiding the problem of pseudoreplication (Hurlbert, 1984) or spatial autocorrelation (Legendre, 1993). Pseudoreplication can be a problem if only one forest site of each age is used. Replicates within those forests will not be true replicates (pseudoreplicates).

Other indirect methods involve the isolation of fungi from substrates using different media (e.g. Harper and Lynch, 1985; Aoki *et al.*, 1992; Kasai *et al.*, 1995). This method can also be very powerful, but has the problem that all isolation media are selective to some extent and that some fungi are not easily cultured.

Mechanisms of succession

While many studies have documented fungal successions, very few have determined the mechanisms for succession (Frankland, 1992). To understand succession, two general questions must be answered: (1) what determines when each species becomes established after a disturbance and; (2) what determines when each species disappears from the successional sequence? Species that are lost during the course of succession are often assumed to be victims of competitive exclusion by later successional species (Farrell, 1991). Unfortunately, this assumption has rarely been experimentally tested for fungi or any other organisms (Farrell, 1991). Holmer and Stenlid (1997) however, used laboratory competition experiments to find that species that usually

produce fruit bodies in the later stages of succession in the field were strong competitors in laboratory tests, while the species which often sporulate during the earlier stages of field succession were weaker competitors. This suggests that inhibition is an important mechanism in the observed succession.

While observational studies of fungal succession will still be important, it is essential that the processes underlying fungal succession be uncovered for a full understanding of fungal succession.

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