Fungal succession at different scales

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Fungal succession can be considered at the macro- or micro-scale levels. Macro-scale succession can be recognized as the integration of different kinds of seres of fungi associate with a plant community. On the other hand, micro-scale succession can be recognized as substratum succession or fungal succession associated with plant succession at the patch level. Succession of pyrophilous fungi following forest fire is categorized as macro-scale succession, but succession of pyrophilous fungi following bonfires and that of ammonia fungi following addition of ammonia are categorized as micro-scale succession. Nutrient cycling in the areas disturbed by local burning or the addition of ammonia is maintained the activities of existing microbes including fungi such as pyrophilous fungi and ammonia fungi (These fungi are present in small numbers in undisturbed areas, but quickly increase in biomass following the disturbances). This paper explores the concept of macro- and micro-scale succession in fungi.

Key words: ammonia fungi, fungal succession, pyrophilous fungi, secondary succession, substratum succession.

Introduction

Plant succession as traditionally understood by plant ecologists is quite different to fungal succession, which can occur at a macro-scale or micro-scale. Swift (1982) has outlined the differences between ecosystem succession (macro-scale) and decomposition succession (micro-scale). Fungi depend entirely on other organisms such as animals and plants for substrata for their growth. Fungal succession is therefore related to plant successions at various scales (see Prentice, 1992). The relationship between plant succession and fungal succession is therefore explored in this paper. The differences between micro-scale and macro-scale fungal succession is also discussed in order to clarify our understanding of fungal community dynamics.

Fungal succession and plant succession

Fungi are found in terrestrial and aquatic ecosystems and play an important role in nutrient cycling of organic matter. They can absorb inorganic matter such as ammonia and nitrates as well as small organic molecules such as amino acids and sugars, as a result of their activity (Garraway and Evans, 1984). Thus, fungi are entirely dependent on other organisms for their growth, namely a host or substratum comprising other organisms. Different fungal assemblages (= mycota) are present in each part of each substratum and each host. For example, phylloplane fungi, endophytes, wood-attacking fungi, litter decomposing fungi, plant parasitic fungi, root-inhabiting fungi, and mycorrhizal fungi, are found in the various niches of only one tree (Hyde, 1995). The fungal community at the macro-scale consists of many different fungal communities at the micro-scale. These fungal species have mutual interactions with the plant and animal species and these interactions change during succession processes.

The traditional view of succession is an orderly process of community change resulting from modification of the physical environment by organisms, and accumulation of organic matter by the fixation of CO_2 in the air and immobilization of inorganic material in the soil, into the system, until the system attains a steady state, known as the climax (Clements, 1936). This can be recognized in a more generalized view, as orderly irreversible changes of biocoenosis (Clements, 1963). Odum (1969) emphasized the importance of biological attributes in controlling succession, rather than physical factors, namely all organisms comprising the biota (fauna, flora, mycota, microbiota) which continuously react with each other and gradually change the environment. The succession of plant communities can be expressed as the changes in the fixation of carbon dioxide and organic material in the ecosystem, or expressed as the changes in the accumulation of energy in the ecosystem (Odum, 1969). Progress in the succession of the plant community is accompanied by an increase in species diversity and heterogeneity and that of the complexity of stratification (Odum, 1969). These changes comprise an increase in diversity of symbiosis among plant species and other organisms in the plant community and attainment of stability of biocoenosis (Odum, 1969).

Frankland (1992), however, noted that there was a decrease in diversity of mycorrhizal fungi during the final stage of forest development as indicated in decomposer succession by Swift (1982). Succession comprises autogenic (within system) processes and external (allogenic) processes and either process becomes superior to the other depending on circumstances during succession (Richards, 1987). These changes finally cause a kind of ecological homeostasis, and macroscopically the structure of the community attaining a steady state, the climax as described above. The climax is thus an important concept of the succession of a plant community (Clements, 1936).

Characteristics of substratum succession in fungi, however, cannot fit into the climax concept. The reduction in saprobic fungal numbers reaches a theoretical value of zero when the resource is exhausted (Frankland, 1992). However, fungal succession on decomposing organic matter rarely reaches this end-point (Frankland, 1992). When fungal succession is considered in the whole litter layer, it can be concluded that fungal succession depends on continuous input of new materials from the plant community and output of organic materials as the result of microbial activities in the soil layers. Each soil layer has different types of microbial communities at each stage of succession (see Swift, 1976). The litter components, however, gradually change with the succession of the plant community. This suggests that, over a long term, we cannot deny the presence of the climax condition when the changes in fungal communities are recognized at a macro-scale (the integrated fungus community composed of various fungal communities at a micro-scale). In contrast, the attribution of symbiosis, such as mycorrhiza, has been evaluated for some whole forest ecosystems. This means that each kind of fungal succession has been discussed at a different scale by mycologists (e.g. Chang and Hudson, 1967; Griffin, 1972; Sagara, 1975; Ogawa, 1980; Watling, 1981; Cooke and Rayner, 1984; Breton and Zwaenepoel, 1991; Hudson 1992; Lange, 1992; Kasai *et al.,* 1995)

Succession of fungal communities can be shown more clearly by a comparison of one classical example using xeric succession in a plant community (Clements, 1963). All vegetation and most organic matter are destroyed when there is a strong disturbance in a restricted area due to the eruption of a volcano. Firstly lichens that are most adapted to dry and oligtrophic environments invade the area covered by lava and volcanic ashes. In other words, the mycobionts of the lichens are the first fungal colonisers following the disturbance. Lichens continue to inhabit the area until the climax vegetation is reached, although there are gradual changes in the composition of lichen species in each process of the plant succession. From the standpoint of dominant species or size of biomass, lichens cannot be expressed as the main component of the process of any succession except in Tundra and Alpine zones (Hale, 1974).

From the viewpoint of dominant plant species, plant communities usually change in sequence from mosses, annual plants, perennial plants, scrubs and intolerant trees to shade trees (Odum, 1971). Succession of plant communities in terrestrial environments following volcanic eruptions, however, does not always follow these sequential changes (see van der Valk, 1992). Moreover, the plant community in each process of the succession comprises patchy distribution of plant species, recognized as different processes of the succession (Prentice, 1992).

This data indicates that the observation scale strongly affects the concept of succession even when considering plant succession (Prentice, 1992). We, however, can choose suitable scales when observing changes in vegetation (Prentice, 1992), which may be related to the size of humans, but have no relevance to the microbial communities. This may be the main reason why mycologists have used different concepts in examining different types of fungal succession. In this article, I conclude that we should consider fungal succession at two scales, macro-scale and micro-scale succession, but the division is somewhat arbitrary.

Primary fungal succession

Little data are available to allow a comparison of relationships between the succession of plant communities and those of microfungal communities. Possible exceptions are the seres of microfungi in soil communities that are associated with changes in vegetation across developing sand dune systems (Brown, 1958; Nicolson and Jonston, 1979; Frankland, 1981; Allen, 1991). Data for the succession of plant communities and associated macrofungal communities, on the other hand, are relatively well known. This is due to records from fungal taxonomists working on larger fungi, but data has not been generated for the fungal succession itself (e.g. Breitenbach and Kränzlin, 1981; 1986; 1991; 1995; 2000; Lincoff, 1981; Imazeki and Hongo 1987, 1989; Bougher and Syme, 1998). There is also an accumulation of data on fungi in plant communities by mycological ecologists (e.g. Ogawa, 1980; Fleming, 1984). Data for the succession of the plant community and that of plant parasitic fungi are also relatively well-known because of the work of plant pathologists (e.g. Kobayashi *et al.,* 1992). For example, saprobic and symbiotic fungi inhabiting forests in Japan, such as a *Fagus crenata* climax forest in a cool temperate area is well researched (e.g. Ogawa *et al.*, 1981). Other well researched examples include *Castanopsis cuspidata* climax forest (e.g. Murakami, 1989), and secondary forests such as *Pinus densiflora* in a warm temperate region (e.g. Ogawa, 1980). These reports clearly indicate that fungal communities in each niche comprising integrated fungal communities, which gradually change as a whole with the succession of the plant communities.

Secondary fungus succession

Fungal communities change with the alteration of the plant communities following different types of disturbances, such as the addition of animal wastes or animal disturbance, as well as forest fires, land slides and deforestation. These former events may disturb small areas of the understory but usually plant ecologists recognize disturbances as changes in the plant community at a larger scale, such as forest fire and deforestation (Clements, 1963). Secondary succession of plant communities occurs as a result of disturbances in a certain area of vegetation and is defined as the successive process following different degrees of disturbance in a certain area of vegetation. It commences under the condition of the presence of relatively medium water-content, which contains considerable organic matter and a large number of dominant migrants (propagules) such as buried seeds in soil (Clements, 1963).

Mycologists, therefore, focus on the changes in the fungal communities at quite small levels (as small as a 1 cm^3), as well as the changes in the plant community. This reflects the difference between the average sizes of plant bodies and those of fungal bodies. For example, 1 cm^3 observation area for a microfungal community is possibly equivalent to a 10 m^3 or more observation area for plant communities. Moreover most secondary succession in fungi are substratum succession, namely succession on each organic material that are naturally provided by the activities of other organisms and / or part or whole individual body of organisms. Therefore, most substratum succession starts on natural common organic materials and cannot be recognized as disturbance in the sense of plant ecologists.

Secondary fungal succession at macro-scale

Large scale disturbance such as a forest fire causes changes in the fungal community and those of the plant community. This is secondary fungal succession resulting from the secondary succession of the plant community. It takes several or more years to return to the same fungal community observed before the disturbance (Horikoshi, 1989). Even after a large forest fire, however, the influence of heat is usually restricted to the surface horizon(s) of soils and large amounts of organic matter remains in the soil. The pH values and the NH_4-N concentration of the burnt soil increases with the release of cations from the soil following the heat treatment (Horikoshi, 1989). Moreover, heat causes substances, such as furfural, which physiologically activate organisms (e.g. stimulation of basidiospore germination of the pyrophilus fungus, *Coprinus radiatus*; Mills and Eilers, 1973), to be produced from existing organic substances (see Cochrane, 1958). These conditions are suitable for the pyrophilous fungi to colonise the burnt areas for a short time after the large forest fire, even though a large forest fire induces the retrogressive succession of the plant community (Horikoshi *et al.,* 1986).

Secondary fungal succession at micro-scale

Small scale disturbances, such as a localized fire (e.g. bonfire) (Sagara, 1975, 1992), the application of the large amounts of ammonia (Sagara, 1975;

Suzuki *et al.,* 2002), and trenching of the forest floor (Laiho, 1970), cause changes in the fungal community, without changes in the whole plant community. The fungal community will return to its original state within 2 to 3 years (see Sagara, 1975). In other words, these fungal successions following various kinds of the disturbances are recognized as patchy fungal succession in the original plant community. For example, in nature, there may be many patches of ammonia rich areas derived from the urination of vertebrates, and decomposition of faeces or dead bodies of vertebrates, such as mammals and birds (see Sagara, 1995). In such areas, we can observe the successive occurrence of ammonia fungi, which are adapted to a high ammonia concentration under neutral to weak alkaline conditions (Suzuki, 1989; Sagara, 1992). This sequential occurrence of reproductive structures is sometimes called "succession" as has been observed in coprophilous fungi (Harper and Webster, 1964; Lodha, 1974). Ammonia fungi consist of saprobic and ectomycorrhizal fungi and the former usually occur at the early stage of the succession and mycorrhizal fungi occur at the late stage of the succession (Sagara, 1975, 1992). The saprobic and mycorrhizal ammonia fungal community may have almost an equivalent role in nutrient cycling to that occurring in the fungal communities before the disturbances (see Fukiharu *et al.,* 1997; Sato and Suzuki, 1997). Namely, ammonia fungi have similar roles in cycling of the inorganic and / or organic matter that also function in non-disturbed areas by natural fungi (fungi only grow vigorously in non-disturbed areas).

Multi latent microbes seres in ecosystem

Each vegetation type comprises many kinds of microbial communities. Such communities are composed of many sub-communities of latent microbes (microbes having very small biomasses in non-disturbed areas which quickly increase the biomasses after the disturbance). These include communities of ammonia fungi, pyrophilous fungi, and fungi occurring after trenching. The fungi that colonise areas following disturbances have roughly an equivalent function to the fungi operating in each process of succession when there are no disturbances. In any ecosystem, it is likely that the latent microbes including different kinds of latent fungi appearing after various kinds of disturbances and each sere of latent microbes have almost equivalent roles to the microbes previously inhabiting the disturbed sites. These latent fungi quickly colonise a disturbed area, then occur alongside the remerging original fungi and finally disappear to small numbers as the community returns to its original state. Nutrient cycling in disturbed areas occurs without interruption due to the activities of the latent microbes, which replace the activities of microbes in non-disturbed areas. This may be described as "compensatory effects on nutrient cycling" following disturbance.

Conclusions

Large-scale fungal succession as a concept is similar to that of ecosystem succession as categorized by Odum (1969) or successions at the landscape and regional scales (Prentice, 1992). It is not the same as the concept of succession at the global scale (Prentice, 1992). The concept of fungal succession at the micro-scale is partially similar to that of the succession at the patch scale (Prentice, 1992) and the concept of the decomposer succession (Swift, 1982). Most fungal successions are secondary succession with the exception of fungal succession over a very long time scale (e.g. decade and century). Fungi such as pyrophilous fungi and ammonia fungi, which flourish following disturbances are also thought to be part of the mycota which exists, albeit in low biomass in undisturbed areas. The nutrient cycling in the disturbed areas is maintained without severe interruption by the compensatory activities of these latent microbes which including fungi such as pyrophilous fungi and ammonia fungi. This situation can be termed "multi-compensation mechanism" for nutrient cycling in disturbed-ecosystems.

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