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REVIEW

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Propagation strategy of ammonia fungi

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Abstract Ammonia fungi invade forest floors immediately after a enrichment disturbance by a large input of ammonium-nitrogen. Latent form(s) of the ammonia fungi are spores and/or mycelium fragments. Ammonia fungi are characterized by their rapid germination stimulated by the presence of ammonium-nitrogen under neutral to weakly alkaline conditions. Each ammonia fungus establishes its territory during suppressed combative abilities of other microbes following ammonium-nitrogen disturbance. Early-phase ammonia fungi (EP fungi) quickly sporulate before nonammonia fungi colonize with the declining of ammonium-nitrogen concentration associated with descending pH. Ectomycorrhizal species of late-phase ammonia fungi (LP fungi) escape from the L-F horizon as a result of interactions between EP fungi and form mycorrhizae in the H-A horizon when other fungal activities are suppressed by the ammonium-nitrogen disturbance. Ectomycorrhizal ammonia fungi initially use ammonium-nitrogen when the pH rises because of the ammonium-nitrogen disturbance and then gradually utilize both ammonium- and nitrate-nitrogen when the effects of the ammonium-nitrogen disturbance weaken. Early-stage EP fungi are ruderal stress-tolerant strategists whereas late-stage EP fungi are combative ruderal strategists. LP fungi are combative strategists from the standpoint of the interactions between other ammonia fungi. This classification is based on differences in their respective propagation strategies.

Key words Ammonia fungi · Colonization · Ecological strategies · Physiological characteristics · Spore germination

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Introduction

Many ecological groups of fungi have been proposed, based on various ecological features, i.e., by substrates (substrata) associated with major decomposable compounds and fungal responses to stress and disturbance. For example, litter-decomposing fungi (Millar 1974; Hering 1982; Watling 1982), wood-attacking fungi (Käärik 1974; Lisiewska 1992; Dix and Webster 1995; Kirk et al. 2008), fungicolous fungi (Hirsch and Braun 1992; Kirk et al. 2008), coprophilous fungi (Lodha 1974; Hudson 1980; Cooke and Rayner 1984; Richards 1987; Lisiewska 1992; Dix and Webster 1995; Kirk et al. 2008), chitinolytic fungi (Hudson 1980), and keratinophilic fungi (Hudson 1980; Richards 1987; Gams 1992) are ecological groups of fungi that are defined based on the former categorization, whereas pyrophilous fungi (Hudson 1980; Lisiewska 1992; Dix and Webster 1995; Kirk et al. 2008) are defined based on the latter categorization.

In 1965, Sagara and Hamada reported on fungal species that occurred after urea treatment in the forest (Sagara and Hamada 1965). Thereafter, Sagara applied different kinds of chemical reagents both in the field and in the laboratory (litter packed in plant pots) and found a chemoecological group of fungi termed "ammonia fungi" (Sagara 1975). "Ammonia fungi" are one of the ecologically defined fungal groups that sequentially develop reproductive structures (exclusively or relatively luxuriantly) on the soil after the sudden addition of ammonia, or of some other nitrogenous material that reacts as a base, or of alkali (Sagara 1975). Many ammonia fungus species have also been recognized as member(s) of other ecological groups such as fungicolous fungi, coprophilous fungi, and pyrophilous fungi, as each fungus species can be categorized by different ecological criteria (Table 1; Sagara 1973, 1975, 1976a,b, 1992; Suzuki 2004). In 1992, Sagara proposed a natural ecological group of fungi, "postputrefaction fungi," which are recognized by their occurrence at animal waste-decomposing sites such as urine, feces, and dead bodies (Sagara 1975, 1992; cf. Sagara 1995; Sagara et al. 2008). Several fungi were collected only from deserted middens (latrines) of mammals, but not from

Table 1. Succession, belonging to overlapping ecological group, and nutritional mode of postputrefaction fungi

Fungus species belonging to postputrefaction fungi	Fungus species belonging to				Nutritional mode
	Ammonia fungi	Coprophilous fungi	Pyrophilous fungi	Fungicolous fungi	
Early Successional Phase					
Zygomycota					
Rhopalomyces strangulatus					Saprotrophy[d]
Anamorphic fungi					
Amblyosporium botrytis	–[a–d]	–[f]		–[f]	Saprotrophy[a–d]
Cladorrhinum foecundissimum	–[a,c]				Saprotrophy[a,c]
Doratomyces purpureofuscus	–[a]				Saprotrophy[a]
Ascomycota					
Ascobolus denudatus	–[a–c]	–[a]			Saprotrophy[a–c]
Chetomium globosum	–[a]	–[a]			Saprotrophy[a]
Pseudombrophila petrakii	–[b,d]				Saprotrophy[b,d]
Peziza moravecii	–[a,b]				Saprotrophy[a,b,d]
Humaria velonovskyi	–[a]		–[a]		Saprotrophy[a,d]
Basidiomycota					
Coprinopsis cinerea	–[a,c]	–[a]			Saprotrophy[a,c]
Coprinopsis echinospora	–[a,d]				Saprotrophy[a,d]
Coprinopsis neolagopus	–[a–c]				Saprotrophy[a–c]
Coprinopsis phlyctidospora	–[a–d]		–[g]		Saprotrophy[a–d]
Coprinopsis stercorea	–[a,b]	–[a]			Saprotrophy[a–c]
Crucispora rhombisperma	–[a–c]				Saprotrophy[a–c]
Lyophyllum tylicolor	–[a–d]				Saprotrophy[a–d]
Late Successional Phase					
Collybia cookei	–[a,b]			–[a]	Nectrotrophy[b]
Anamika lactariolens	–[c]				Biotrophy (EM)[b]
Calocybe leucocephala	–[a,b]				?Saprotrophy[b]
Hebeloma radicosum	–[c,e]				Biotrophy (EM)[c–e]
Hebeloma radicosoides					Biotrophy (EM)[c–e]
Hebeloma spoliatum	–[a–d]				Biotrophy (EM)[b]
Hebeloma vinosophyllum	–[a–d]				Biotrophy (EM)[b]
Laccaria bicolor	–[a,b,d]		–[a]		Biotrophy (EM)[b,d]

EM, ectomycorrhizal symbiosis
[a] Sagara (1975)
[b] Sagara (1995)
[c] Fukiharu and Horigome (1996)
[d] Sagara et al. (2008)
[e] Sagara et al. (2000)
[f] Pirozynski (1969)
[g] Suzuki et al. (2002a)

any other sites of ammonium-nitrogen enrichment (Sagara 1975, 1992, 1995; Sagara et al. 2008). Therefore, the category of "postputrefaction fungi" is a larger set including the category of ammonia fungi (Table 1; Carter and Tibbett 2003; Tibbett and Carter 2003; Sagara et al. 2008). Up to now, more than 70 fungal taxa have been recorded as "postputrefaction fungi" by the application of urea and/or other nitrogenous material(s) both in the field and in the laboratory and by the observation of fruit bodies occurring in the middens (latrines) of mammals (Laiho 1970; Lehman and Hudson 1977; Suzuki et al. 2002a; Carter and Tibbett 2003; Tibbett and Carter 2003; Sagara et al. 2008).

The mechanisms of colonization, establishment, and successive appearance of reproductive structures (= occurrence) of "ammonia fungi" have been examined in field and laboratory (Suzuki 2006; Sagara et al. 2008). Research on the physiological characteristics of ammonia fungi has helped to elucidate their propagation strategies.

In this review paper, therefore, I intend to analyze the propagation strategy of ammonia fungi in relationship to their ecological strategy in an ammonium-nitrogen-rich environment, especially focused on the physiological characteristics of different developmental stages in each ammonia fungus, because the physiological characteristics of fungus species of postputrefaction fungi such as *Hebeloma radicosum*, which colonizes only in mammalian latrines, but not in ammonia-nitrogen-treated soils, have not been examined (Sagara et al., 2000, 2008).

Sequential appearance of reproductive structures of ammonia fungi in the field

The reproductive structures of ammonia fungi appear sequentially after disturbance by a large amount of ammonium nitrogen associated with alkalinization of the soil. The sequential occurrence of ammonia fungi proceeds as follows: anamorphic fungi → cup fungi (Ascomycota) → agaric fungi with small basidiomata → agaric fungi with larger basidiomata (Sagara 1975, 1992, 1995; Suzuki et al. 2002b; Imamura and Yumoto 2004, 2008; Sagara et al. 2008). The

phase from anamorphic fungi to agarics with smaller basidiomata is described as the early phase, and the fungi are called early-phase fungi (EP fungi). The phase of agarics with larger basidiomata is described as the late phase, and the fungi are called late-phase fungi (LP fungi). The EP fungi are saprobic and most of the LP fungi are biotrophic, a few possibly being saprobic (see Table 1: Sagara 1995; Fukiharu and Horigome 1996; Yamanaka 1999, 2008; Imamura and Yumoto 2004, 2008; Suzuki 2006; Sagara et al. 2008).

Changes in soil conditions following a large input of ammonium-nitrogen

The pH, ammonium-nitrogen concentration, and water content of soils rapidly increase immediately after urea application and then gradually decrease during the occurrence of EP fungi. The pH returns to control level by the end of the first flush, usually within half a year after application of a large amount of ammonium-nitrogen. Ammonium-nitrogen concentration, nitrate-nitrogen concentration, and water content return to the control levels at the end of the second flush of LP fungi, namely, about 2 years after urea application (Yamanaka 1995a,c; Suzuki et al. 2002b). Ammonium-nitrogen is the major nitrogen form in the soil immediately after urea application, and then it gradually changes into nitrate-nitrogen. The nitrate-nitrogen concentration reaches a maximum at around the first flush of LP fungi (Yamanaka 1995a–c; Suzuki 2000a; Suzuki et al. 2002b; He and Suzuki 2004; Sagara et al. 2008).

Invasion of ammonia fungi in the field

Invasion sequence

The invasion sequence of EP fungi, i.e., saprobic ammonia fungi, in the field has been examined by cultivating soils collected from the forest floor at different days after urea application and packed into sterilized test tubes. The results suggested that the EP fungi *Amblyosporium* (*Am.*) *botrytis*, *Ascobolus* (*As.*) *denudatus*, *Peziza* (*Pe.*) *moravecii*, and *Coprinopsis* (*Co.*) *phlyctidospora* (syn.: *Coprinus phlyctidosporus*) invade almost simultaneously and another EP fungus, *Lyophyllum* (*Ly.*) *tylicolor* (syn.: *Tephrocybe tesquorum*), invades subsequently. The EP fungi invade soils that have 100–1000 times higher concentrations of ammonium-nitrogen associated with weakly alkaline to neutral conditions following urea application. The sequence of invasion by the five EP fungi does not equate exactly with the observed succession in the forest. These results suggest that the successive occurrence of EP fungi in the field partially results from the sequential colonization of each ammonia fungus accompanied by the time needed for formation of reproductive structures by each fungus in urea-treated soils (Suzuki 1989, 2006; Suzuki et al. 2002b). The invasion time of ectomycorrhizal ammonia fungi cannot be examined by soil incubation without host plant(s), but, at the latest, invasion may begin during the occurrence of EP fungi; this is estimated from the time required for fruiting on various media and the time for the first flush in the field, following an application of a large amount of ammonium-nitrogen. The invasion of LP fungi probably initiates in the soil that maintains higher pH, nitrogen concentration, and water content than the control soil.

Latent form(s) and spatial distribution

The spatial distributions of EP fungi *Am. botrytis*, *As. denudatus*, *Ly. tylicolor*, *Coprinopsis (Co.) neolagopus*, and *Co. phlyctidospora* have been studied by incubation of soil cores (5 cm × 5 cm × 5 cm) collected from 200 sections (5 cm × 5 cm) placed in a square (50 cm × 100 cm). In an experiment done in a broad-leaved tree forest, *Am. botrytis*, *As. denudatus*, *Ly. tylicolor*, *Co. neolagopus*, and *Co. phlyctidospora* appeared from the soils collected from the 200 sections at the frequencies of 77, 43, 25, 11, and 144, respectively (Suzuki 2006). Sagara suggests that plots wider than 50 cm × 100 cm are required for urea application in the field to survey the whole species assemblage of ammonia fungi that inhabit the area (Sagara 1976b). This condition means that more than one propagule of each EP fungus exist in the 50 cm × 100 cm area of forest floor (Suzuki et al. 2002b; Suzuki 2006).

EP fungi *Am. botrytis*, *As. denudatus*, and *Co. phlyctidospora* were trapped by sterilized urea-treated-soil (trapping soil) packed in a bottle that had been placed on the desk in the field (Suzuki 2006). This result suggests that air-borne spores and/or air-borne mycelial fragments as well as mycelia colonizing from areas adjacent to an ammonium-nitrogen-disturbed site can act as invasive forms of ammonia fungi in the ammonium-nitrogen-disturbed site, although we cannot completely exclude the possibility that those propagules were carried by animals and inoculated onto the trapping soil.

The results of the two experiments described above support the idea that spores and/or small pieces of mycelia are latent form(s) of EP fungi for their propagation in the ammonium-nitrogen-disturbed site. Direct isolation of LP fungi from the forest floor and identification by molecular techniques will give us more precise information about the spatial distribution of both EP and LP fungi.

Abiotic factors affecting the propagation of ammonia fungi

Spore germination

Conidium germination of the early-stage EP fungus *Am. botrytis*, which appears first in the succession, is stimulated with 0.3–600 mM NH_4Cl aqueous solution adjusted at pH 5.0–9.5. Optima of NH_4Cl concentration and pH for conidium germination of *Am. botrytis* are 300 mM and 8.0, respectively (cf. Table 2; Licyayo 2007). Ascospore germination of the early-stage EP fungus *As. denudatus*, which

Table 2. Maximum germination responses of spores observed in different ecological groups of fungi

Fungus species	Spore type	Ecological group				Phenol	Acetic acid	Furfral[e]	Furoic acid[e]	NH_4Cl			$(NH_4)_2HPO_4$	Control	H_2O	References
		AF[a]	CF[b]	FF[c]	PF[d]	1 mM	50 mM	1 mM	0.1 mM	10 mM[f]	100 mM[g]	300 mM[f]	100 mM	1% Ethanol		
Anamorphic fungi																
Amblosporium botrytis	Conidium	○	○	○								64			0	Licyayo 2007
Ascomycota																
Ascobolus denudatus	Ascospore	○	○							93						Suzuki and Iijima, unpublished data
Ascodesmis macrospora	Ascospore		○			0	97							0		Udagawa and Furuya 1979; Furuya 1990
Peziza moravedcii	Ascospore	○								17						Suzuki and Iijima, unpublished data
Podospora curvicolla	Ascospore		○			93	0							0		Udagawa and Furuya 1979; Furuya 1990
Podospora longicollis	Ascospore		○			52	0							0		Udagawa and Furuya 1979; Furuya 1990
Podospora paucisetta	Ascospore		○			9	0							0		Udagawa and Furuya 1979; Furuya 1990
Podospora setosa	Ascospore		○			21	0							0		Udagawa and Furuya 1979; Furuya 1990
Basidiomycota																
Coprinopsis cinerea	Basidiopore	○											90		0	Suzuki et al. 1982
Coprinopsis phlyctidospora	Basidiopore	○			○								67		0	Suzuki et al. 1982
Coprinopsis radiata	Basidiopore				○			88	30							Mills and Eilers 1973
Hebeloma spoliatum	Basidiopore	○									74				0	Suzuki, unpublished data
Hebeloma vinosophyllum	Basidiopore	○									83				0	Deng and Suzuki 2008

[a] Ammonia fungi
[b] Coprophilous fungi
[c] Fungicolous fungi
[d] Pyrophilous fungi
[e] Chemical treatment with a heat shock treatment (45°C for 4 h)
[f] Adjusted at pH 8
[g] Adjusted at pH 10 for *Ascobolus denudatus* and pH 9 for *Peziza moravecii*

appears as the second species in the succession, is remarkably stimulated with 10 mM NH_4Cl aqueous solution adjusted at pH 8–10 and 100 mM NH_4Cl aqueous solution adjusted at pH 7–8 (cf. Table 2; Suzuki and Iijima, unpublished data). Ascospore germination of the early-stage EP fungus *Pe. moravecii*, which appears as third in the succession, is remarkably stimulated by 10 mM NH_4Cl aqueous solution adjusted at pH 9–10 (Suzuki and Iijima, unpublished data). Basidiospore germination of late-stage EP fungi *Coprinopsis (Co.) cinerea* (syn.: *Coprinus cinereus*) and *Co. phlyctidospora* are stimulated by 1–100 mM $(NH_4)_2HPO_4$ aqueous solution (pH 8.3–7.5) (cf. Table 2; Suzuki et al. 1982). Basidiospore germination of ectomycorrhizal species of LP fungus *Hebeloma (He.) vinosophyllum* is stimulated by 10–500 mM NH_4Cl aqueous solution adjusted at pH 4.5–9.0. Optima for the spore germination of *He. vinosophyllum* are 100 mM NH_4Cl and a pH of 8.0 (Deng and Suzuki 2008a). Basidiospore germination of another ectomycorrhizal LP fungus, *Hebeloma (He.) spoliatum*, is stimulated by 100 mM NH_4Cl aqueous solution adjusted at pH 8.0 (cf. Fig. 1, Table 2; Suzuki, unpublished data). Spores of these seven species geminate only weakly or not at all in distilled water (Suzuki et al. 1982; Suzuki 2006; Deng and Suzuki 2008a; Suzuki and Iijima, unpublished data). These findings indicate that sexual and asexual spore germinations of ammonia fungi are stimulated by ammonium-nitrogen concentrations of 10 to 100 mM at neutral to weakly alkaline conditions (Suzuki 1989, 2004, 2006).

At 15°C, conidium germination of *Am. botrytis* is initiated within 12 h and germination percentage reaches above 64% after 4 days under optimum conditions (see Table 2; Licyayo 2007). At 15°C, the percentage germination of ascospores in *As. denudatu*s, which are treated with 10 mM NH_4Cl aqueous solution adjusted at pH 10, exceeds 70% within 1 day and reaches a maximum of 93% by day 3 (see Table 2; Iijima and Suzuki unpublished data). The percentage germination of ascospores in *Pe. moravecii* exceeds 17% for 1-day incubation at 15°C by treatment with 10 mM NH_4Cl aqueous solution adjusted at pH 9 (Table 2; Iijima and Suzuki, unpublished data), although the optimal conditions for the germination of this fungus have not yet been examined. Within 3 days, the germination percentage of *Co. cinerea* reaches a maximum of 77% (incubation at 25°C), and that of *Co. phlyctidospora* reaches a maximum of 67% (incubation at 20°C: Table 2; Suzuki et al. 1982). The germination percentage of *He. vinosophyllum* reaches 73% in 2 weeks when incubated at the optimum temperature of 25°C (Table 2; Deng and Suzuki 2008a). The basidiospore germination of *He. spoliatum* exceeds 70%, when incubated at 15°C (see Table 2; Suzuki, unpublished data). Percentage germinations of most saprobic and ectomycorrhizal ammonia fungi are generally higher than those of saprobic and ectomycorrhizal nonammonia fungi (Horikoshi and Suzuki 1990).

To examine whether ammonium-nitrogen is actually effective in the field, the stimulation of spore germinations of *Am. botrytis*, *As. denudatus*, *Co. phlyctidospora*, and *He. vinosophyllum* were examined in sterilized water extracts of soils collected at different times after urea application (Suzuki 2006). Further experiments involving a combination of cation-exchange residue and anion-exchange residue suggest that the major stimulatory component in ammonium-nitrogen-rich soils is the ammonium ion (Suzuki et al., unpublished data). This result shows that no strong inhibitory factors for spore germination are present in the forest soils, and that ammonium-nitrogen and pH are the principal factors for the stimulation of spore germination of ammonia fungi in the field as well as in the laboratory.

Ascopores of some coprophilous Discomycetes (which do not belong to ammonia fungi) show stimulation of germination by phenol and acetic acid and sometimes reach extremely higher germination percentages by various kinds of chemicals including phenolic compounds, but not by ammonium-nitrogen (see Table 2; Udagawa and Furuya 1979; Furuya 1990). Spore germination of most litter-inhabiting fungi and wood-attacking fungi is induced simply by the presence of water, although the percentage germination of these fungi usually not exceeds 50%. Spore germination of pyrophilous fungi is stimulated with heat shock or by the presence of furfural, which is formed from pentose exposed to fire. The maximum germination percentages of the pyrophilous fungi are less than 10% when they treated simply by chemicals, but become much higher by means of heat treatment with many chemicals such as furfural (see Table 2; Mills and Eilers 1973).

Clearly EP fungi (saprobic ammonia fungi) are characterized by rapid germination at high percentages under the presence of ammonium-nitrogen at neutral to weakly alkaline conditions and that the ectomycorrhizal ammonia fungi of LP fungi are characterized by higher percentages under the presence of ammonium-nitrogen at neutral to weakly alkaline conditions. Generally speaking, rapid germination with a higher germination percentage is an important feature of *r*-selected fungal species such as ammonia fungi, coprophilous fungi, and pyrophilous fungi. Probably, most ammonia fungi germinate almost simultaneously in the field after a sudden disturbance by a large amount of nitrogenous material(s), irrespective of the sequence of the succession.

Spore longevity

Spore longevity is one of major significance to the colonization strategy of fungi in the field. Germination percentages of basidiospores of the ectomycorrhizal ammonia fungi *He. vinosophyllum* and *He. spoliatum* (see Fig. 1) gradually decrease with storage period. The decline is greater and longevity less in dry conditions than in wet conditions (Fig. 1; Suzuki 2003; Deng and Suzuki 2008a). It is expected that basidiospores of *He. vinosophyllum* and *He. spoliatum* maintain their germination ability for at least 5 months and 2 years, respectively (cf. Fig. 1; Deng and Suzuki 2008a). The estimated longevity periods of LP fungi are not short compared to those of spores in nonammonia fungi (Horikosi and Suzuki 1990). These results support the assumption that the invasion and colonization of ammonia fungi can be initiated by spores as well as by mycelium fragments,

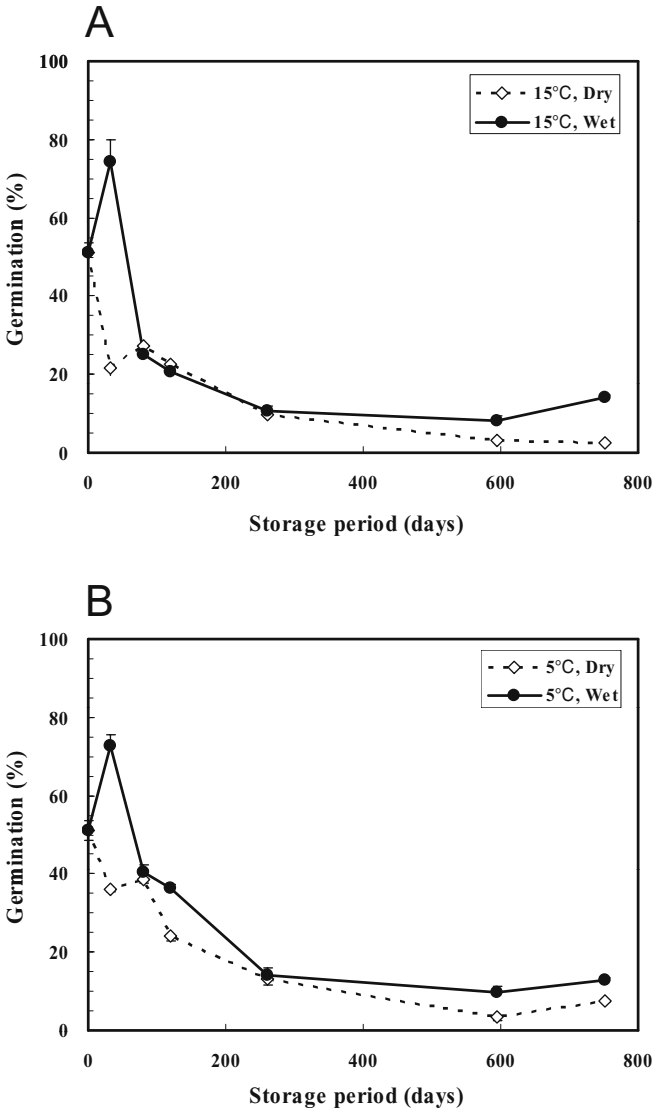

Fig. 1. Effects of storage conditions on longevity of basidiospores in *Hebeloma spoliatum*. Basidiospores stored at 15°C in dry condition or wet condition were incubated in 100 mM NH_4Cl aqueous solution adjusted to pH 8 by NaOH. Incubation of spore suspensions was done at 5ºC (**B**) and 15ºC (**A**) in darkness for 20 days. *Vertical bar* indicates standard error. (From Suzuki, unpublished data)

because the basidiospores of LP fungi would survive for extended periods on the forest floors, until ammonium-nitrogen enrichment occurs (cf. Sagara 1976b; Suzuki 2006; Sagara et al. 2008).

Vegetative growth

Early-stage EP fungi such as *Am. botrytis* and *Peziza (Pe.) urinophila* grow well at pH 7–9 and late-stage EP fungi such as *Coprinopsis* (*Co.) echinospora* and *Ly. tylicolor* at pH 6–8, whereas ectomycorrhizal ammonia fungi of the LP fungi such *He. vinosophyllum* and *Hebeloma (He.) radicosoides* grow vigorously at pH 5–7. Most EP fungi and LP fungi grow slightly even at pH 4 (Yamanaka 2003). The pH of most Japanese forest soils without urea application aligns at 3.5–6.5 (Sagara 1975, 1992; Yamanaka 1995a–c; Fukiharu et al. 1997; Sato and Suzuki 1997; Suzuki 2000a; Suzuki et al. 2002b; He and Suzuki 2004). These findings indicate that both EP and LP fungi adapt to the weakly alkaline and neutral conditions at the vegetative growth stage and initiate the colonization of the forest floor shortly after enrichment by a large amount of ammonium-nitrogen. However, ammonia fungi have the ability to colonize even under acidic conditions, and sporadic small mycelia probably remain even after colonization by nonammonia fungi when pH declines (Sagara et al. 2008).

The early-stage EP fungus *Am. botrytis* grows well in ammonium-nitrogen and organic nitrogen such as L-asparagine and urea but not in nitrate-nitrogen. Early-stage EP fungi in Discomycetes such as *Pseudombrophila (Ps.) petrakii* (syn.: *Pseudombrophila deerata*), and *Peziza* (*Pe.) urinophila* grow sparsely in synthetic media, even in those containing ammonium-nitrogen, L-asparagine, or urea. Late-stage EP fungi in Basidiomycota such as *Ly. tylicolor*, *Co. echinospora*, and *Co. phlyctidospora* grow well in both inorganic nitrogen such as ammonium-nitrogen and organic nitrogen such as L-asparagine and urea (Yamanaka 1999). Ectomycorrhizal ammonia fungi of LP fungi such as *He. vinosophyllum* and *He. radicosoides* also grow well in both inorganic nitrogen sources such as NH_4Cl, KNO_3, KNO_2, and organic nitrogen sources such as L-asparagine and urea. Another LP fungus, *Laccaria (La.) bicolor*, grows well in ammonium-nitrogen, L-asparagine, and urea, but only sparsely in nitrate-nitrogen and L-asparagine (Yamanaka 1999; Sagara et al. 2008). Late-stage EP fungus *Co. phlyctidospora* and LP fungi *He. vinosophyllum*, *He. radicosoides*, and *La. bicolor* assimilate nitrate-nitrogen as well as ammonium-nitrogen and other organic nitrogenous materials (Yamanaka 1999). Based on these results, Sagara et al. (2008) indicate that nitrogen use in ammonia fungi seems similar to that in nonammonia fungi, because saprobic species are generally known to grow better on ammonium-nitrogen or amino acids than on nitrate-nitrogen and the ectomycorrhizal species are known to grow better on nitrate-nitrogen than ammonium-nitrogen or amino acids. When comparing biomass of the vegetative growth of *He. vinosophyllum* for ammonium-nitrogen at 7–8 (pH optimum) and nitrate-nitrogen at 5–6 (pH optimum), that obtained from the former cultivation is larger than that obtained from the latter (Suzuki 2006). Assimilation of nitrite-nitrogen is also reported in the cultivation of *He. vinosophyllum* in a synthetic medium adjusted at pH 7–8. The biomass obtained from the cultivation by nitrite-nitrogen equates to that obtained the cultivation by nitrate-nitrogen but is smaller than biomass obtained from the cultivations by ammonium-nitrogen and urea (Suzuki 2006).

The early-stage EP fungi *Am. botrytis* and *Pe. moravecii* have vegetative growth maxima at 0.3–1.0 M and 0.01–0.1 M, respectively. The upper limit concentration of NH_4Cl for their vegetative growth is 1.3 M NH_4Cl. Early-stage EP fungi *As. denudatus* and late-stage EP fungi *Co. phlyctidospora* and a *Coprinopsis* sp. (an allied species of *Co. phlyctidospora* in Oceania) (Fig. 2: Suzuki et al. 2002a),

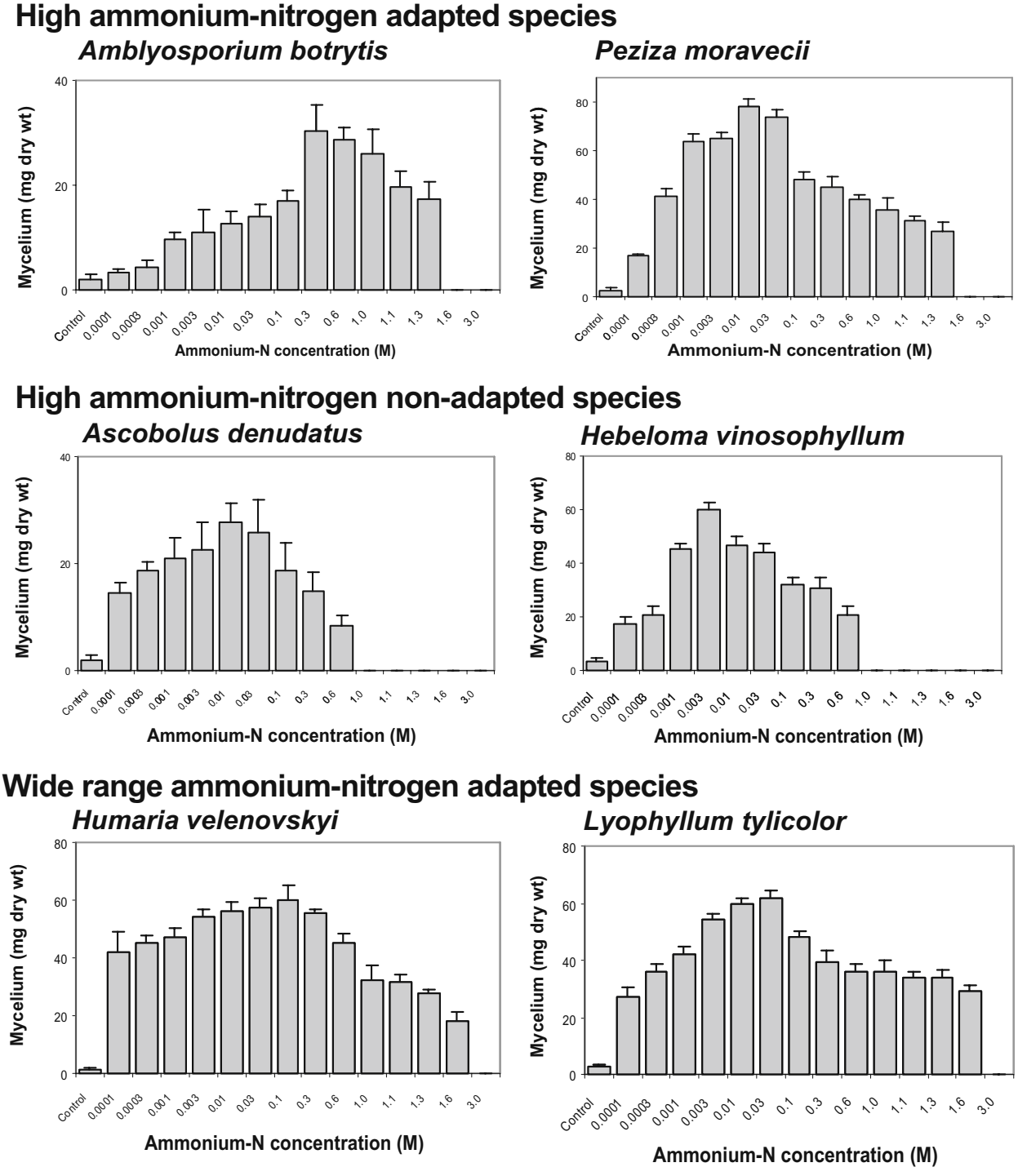

Fig. 2. Three types of responses of the vegetative growth of ammonia fungi to ammonium-nitrogen concentration. Isolates of various ammonia fungus species were cultured in a synthetic medium with different concentration of NH_4Cl adjusted to pH 7. Incubation was at 25ºC in darkness. Incubation of early-phase ammonia fungi (EP fungi) was conducted for 14 days and that of late-phase fungi (LP fungi) for 28 days. *Vertical bar* indicates standard error. (Modified from Licyayo and Suzuki 2006)

and LP fungi *He. vinosophyllum* and *Hebeloma aminophilum* have vegetative growth maxima at around 0.003–0.1 M NH_4Cl (Fig. 2; Licyayo and Suzuki 2006). The upper-limit concentration of NH_4Cl for their vegetative growth is 0.6 M NH_4Cl. The late-stage EP fungi *Humaria (Hu.) velenovskyi* (sometimes occurring at the late phase of the succession) and *Ly. tylicolor* have growth optima in a wider range of NH_4Cl concentrations. The upper-limit concentrations for their vegetative growth are 1.6 M. *Hu. velenovskyi* grows vigorously even at 0.0001 M NH_4Cl (Fig. 2; Licyayo and Suzuki 2006). These findings indicate that ammonia fungi can be divided into three groups in terms of adaptation to

ammonium ion concentration: (1) species adapted to a high concentration of ammonium ion, composed of some EP fungi (saprobic ammonia fungi), (2) species adapted to a wide range of ammonium ion concentrations, composed of some EP fungi (saprobic ammonia fungi), and (3) species nonadapted to a high concentration of ammonium ion, composed of some EP fungi and LP fungi (Fig. 2; Licyayo and Suzuki 2006).

These results suggest that the major nitrogen source for vegetative growth of ammonia fungi is ammonium-nitrogen at neutral to weakly alkaline conditions, irrespective of their nutritional modes, and that the nitrogen source utilized by the ectomycorrhizal ammonia fungi gradually switches from ammonium-nitrogen to nitrate-nitrogen associated with the decline of pH in the urea-treated soil.

Reproductive structure formation

The late-stage EP fungus *Co. cinerea* forms a basidioma primordium even in darkness when urea or ammonium-nitrogen is supplied as the sole nitrogen source in a potato dextrose-agar medium. On the other hand, the fungus does not fruit in aqueous solutions of nonbasic ammonium salts. The presence of ammonium-nitrogen (0.05–0.4 g NH_3/medium) for at least 24 h induces primordium formation (Morimoto et al. 1981). The late-stage EP fungus *Coprinopsis tuberosa* (syn.: *Coprinus stercorarius*, *Coprinus tuberosus*) fruits in light when urea (0.25–1.0 g urea/l) is applied to a potato dextrose-agar medium (Morimoto et al. 1982). Another late-stage EP fungus, *Co. phlyctidospora*, fruits both in light and in darkness when urea (0.2–1.7 g urea/l) is applied to liquid media (He and Suzuki 2003). These results suggest that urea and/or ammonium-nitrogen would stimulate fruiting of saprobic EP fungi, in vitro. Vegetative growth and basidioma formation of the late-stage EP fungus *Ly. tylicolor* is stimulated by γ-ray-sterilized forest soil having been collected from an Ao horizon and incubated for 5 days after application of urea, namely, when ammonium-nitrogen concentration in the soil increased (Yamanaka 2001). These results suggest that higher concentrations of ammonium-nitrogen affect the reproductive structure formation of ammonia fungi, mainly as a result of stimulation of their vegetative growth.

Most agarics form basidiomata after the vegetative growth has reached a stationary phase, whereas the EP fungus *Ly. tylicolor* initiates basidiomata during the linear growth phase on media (Suzuki 1989). *Ly. tylicolor* forms basidia and basidiospores directly on mycelia (mycelial basidium formation) (Yamanaka and Sagara 1990) and on the tops of young, undeveloped basidiomata as well as on mature ones. These short-circuits to basidiospore formation are observed not only in the laboratory but also in field experiments with urea (Sagara et al. 2008). Yamanaka and Sagara (1990) indicate that *Ly. tylicolor* may well reproduce sexually even when nitrogen is insufficient for the formation of normal basidiomata. They also speculate that such a nitrogen supply may be expected from decomposition of resources such as a dead worm or bird droppings (Yamanaka and Sagara 1990). The ectomycorrhizal ammonia fungus (LP fungus) *He. vinosophyllum* produces basidiospores on monokaryotic basidiomata as well as on dikaryotic ones, when growing on a nutrient-rich agar medium. The numbers of basidiospores produced by the former are 1/40 of those produced by the latter (Table 3; Deng and Suzuki 2008b). The maximum germination percentage of the basidiospores produced by the monokaryon reaches 14%–23%, although the maximum germination percentage of the basidiospores produced by the dikaryons reaches 72% (Table 3; Deng and Suzuki 2008b); this is another shortcut to basidiospore formation. Monokaryotic fruitings have been reported in several saprobic nonammonia fungi (Stahl and Esser 1976), but not in ectomycorrhizal nonammonia species. These results suggest that an ectomycorrhizal ammonia fungus, *He. vinosophyllum*, has the ability to disperse via spores derived from monokaryotic mycelia, whick would be an advantage for sustaining higher populations of the latent propagules.

The ectomycorrhizal ammonia fungi *He. spoliatum*, *He. vinosophyllum*, and *Anamika (An.) lactarioens* (syn.: *Alnicola lactarioens*) fruit on a nutrient-rich medium such as MY agar medium. Vegetative growth rates of the ectomycorrhizal ammonia fungi are higher than those of the ectomycorrhizal nonammonia fungi, which suggests that these *Hebeloma* spp. and *An. lactarioens* have the ability to colonize even without the mycorrhizal symbiosis. They are, therefore, facultative mycorrhizal fungi. The dikaryotic isolates of the *Hebeloma* spp. and *An. lactarioens* do not form mature basidiomata on nutrient-poor substrates such as litter (Suzuki, unpublished data). These findings suggest that symbioses with the host plants are indispensable for their successful basidioma formation in the field.

In monoculture on natural substratum, the vegetative growth rate of mycelium of each ammonia fungus increases when it is cultured in the soils collected around the period

Table 3. Basidiospore productivity and germination ability in *Hebeloma vinosophyllum*

Isolate	Basidioma type*	Spore numbers per pileus	Spore germination (%)
Dikaryon	Type I	$1.0 \times 10^7 \pm 2.7 \times 10^6$b**	72.1 ± 2.0c**
Monokaryon	Type II	$1.2 \times 10^5 \pm 6.4 \times 10^4$a	13.7 ± 2.4a
Monokaryon	Type III	$2.1 \times 10^5 \pm 1.2 \times 10^5$a	22.6 ± 1.3b

Different alphabetical letters in each column indicate significant difference at $P < 0.05$ according to the Tukey–Kramer test
*See Deng and Suzuki (2008b)
**Means and SE are calculated from six basidiomata for each type
Source: Modified from Deng and Suzuki (2008b)

of occurrence of each species in the field. Both the early-stage EP fungi *Am. botrytis* and *As. denudatus* and the late-stage EP fungi *Ly. tylicolor* and *Co. phlyctidospora* form reproductive structures on the urea-treated forest soils sterilized by γ-rays when they are cultured on soils collected around the occurrence period of each species in the field (Suzuki 2006). The ectomycorrhizal LP fungus *He. vinosophyllum* similarly forms basidiomata primordia on urea-treated forest soils sterilized by γ-rays when they are cultured on soils collected around the period of occurrence of each species in the field. However, they cannot grow into mature basidiomata (Suzuki 2006). The duration of the reproductive structure formation of these five species in monoculture is remarkably longer than that observed in the field (Suzuki, unpublished data). These observations suggest that the duration of the occurrence of each ammonia fungus is remarkably regulated by the changes in soil conditions resulting from the activities of soil organisms, including the ammonia fungi themselves and by the interactions among the ammonia fungi (Suzuki 1989).

Enzyme activities

Most early-stage EP fungi (saprobic ammonia fungi) show clear proteolytic and lipolytic activities. The early-stage EP fungi such as *Am. botrytis* and *As. denudatus* show clear cellulolytic activity but not ligninolytic activity. Other early-stage EP fungi such as *Pe. moravecii* and *Pe. urinophila* do not show clear ligninolytic activity in spite of their cellulolytic activity. Most late-stage EP fungi such as *Ly. tylicolor* and *Co. echinospora* show definite cellulolytic, ligninolytic, proteolyic, lipolytic, and chitinolytic activities. The LP fungi (ectomycorrhizal ammonia fungi) *He. vinosophyllum* and *He. radicosoides* show slight cellulolytic, ligninolytic, chitinolytic, proteolytic, and lipolytic activities. Another ectomycorrhizal LP fungus, *La. bicolor*, shows slight proteolytic and lipolytic activities, but not cellulolytic, ligninolytic, and chitinolytic activities (Enokibara et al. 1993; Yamanaka 1995c; Soponsathien 1998a,b; Ikehata et al. 2004; Sagara et al. 2008). pH optima for the cellulolytic enzymes of EP fungi are between 6.8 and 9.0, whereas those for the cellulolytic enzymes of LP fungi are between 5.5 and 6.8 (Enokibara et al. 1993). Ligninolytic enzymes of EP fungi and LP fungi have a wide optimum spectrum, from weakly acidic to weakly alkaline conditions (Soponsathien 1998a,b).

Weight losses of embedded leaves and wood pieces (completely burried in soil) are accelerated in the forest floor treated with urea until the termination of the occurrence of EP fungi. In the urea-treated forest floor of *Castanopsis-Quercus* dominating mixed forest, the weight loss of embedded wood pieces becomes larger than that of embedded leaves (Suzuki 2006). In *Pasania (Pa.) edulis* forest, the decomposition of embedded stem sticks of *Pa. edulis* is accelerated by urea application, whereas the decomposition of the embedded fallen leaves (leaf litter) is not (He and Suzuki 2004). These results and the foregoing results suggest that EP fungi, especially late-stage EP fungi, are principal members for decomposing the embedded samples composed of polycarbohydrates. The definite decomposition of lignin would not occur in the ammonium-nitrogen-disturbed sites until the colonization of late-stage EP fungi. The decomposition rates of lignin would gradually increase and reach the initial level (the level before the enrichment disturbance by a large input of ammonium-nitrogen) with the recolonization of preinhabiting nonammonia fungi by the decline of the ammonium-nitrogen concentration associating with the acidification of the ammonium-nitrogen-disturbed sites. The LP fungi (ectomycorrhizal fungus) *Hebeloma* spp. probably utilize plant materials by virtue of their slight decomposing activities as well as from soluble sugars derived from the decomposing activities of other microbes and slowly invade the territories of EP fungi. The *Hebeloma* spp., however, soon establish mycorrhizal symbiosis to evade the combative interaction with other microbes, especially with late-stage EP fungi (saprobic ammonia fungi). The habitat segregation would be established eventually between the EP fungi (saprobic ammonia fungi) mainly colonizing in L-F horizons and ectomycorrhizal fungi in LP fungi mostly colonizing in H-A horizons. In other words, both saprobic and ectomycorrhizal ammonia fungi would be expressed as pioneer fungi in each horizon.

Biotic factors affecting the propagation of ammonia fungi

Interactions among ammonia fungi in urea-treated soils (mixed cultures)

In the mixed culture of five species, reproductive structure formation of early-stage EP fungus *As. denudatus*, late-stage EP fungi *Ly. tylicolor* and *Co. phlyctidospora*, and LP fungus *He. vinosophyllum* are reduced, but not that of the early-stage EP fungus *Am. botrytis*. This tendency is most drastic in *Ly. tylicolor*, because its fruiting is completely inhibited in the five-species mixed cultures even by the cultivation of the five fungus species in the urea-treated soils collected at their fruiting periods in the field (Suzuki 2006). This finding suggests that the habitat segregation among saprobic ammonia fungi, which mostly inhabit in the L-F horizon and the surface area of H horizons, is established at the micro-scale as well as the habitat segregation between saprobic species and ectomycorrhizal species, as already described.

Interactions between ammonia fungi on agar media (coculture)

Cocultures on malt extract–yeast extract agar media with pH 5.5, 7.0, 8.0, and 9.0 among the early-stage EP fungi *Am. botrytis*, *As. denudatus*, *Ps. petrakii*, and *Pe. moravecii* generally do not inhibit or accelerate the reproductive structure formation of the opposed EP ammonia fungi. Among the early-stage EP fungi, *Am. botrytis*, *As. denudatus*, and *Pe. moravecii* intermingle with each other (Table 4). The

Table 4. Interaction among ammonia fungi on the MY agar medium under acidic and neutral to weak alkaline conditions

Fungus species	Amb[a]		Asd[b]		Lt[c]		Cp[d]	
	Ac[f]	N-AL[g]	Ac	N-AL	Ac	N-AL	Ac	N-AL
Asd	N (even)	N (superior)						
Lt	Dc (even)	Dc (even)	N (even)	N (even)				
Cp	Dc (even)	Dc (even)	Dc (even)	Dc (even)	Di (even)	Di (even)		
Hv[e]	Dc (even)	Dc (inferior)	Dc (even)	Dc (inferior)	Di (even)	Di (inferior)	Di (even)	Di (inferior)

Responses observed on the fungus species shown in the 1st row to that shown in the 2nd–5th row in the interactions between ammonia fungi
Responses between ammonia fungi were expressed as follows: Di, inhibition deadlock; Dc, competing deadlock; N, neutral intermingling
[a] *Amblyoporium botrytis*
[b] *Ascoboulus denudatus*
[c] *Lyophyllum tylicolor*
[d] *Coprinopsis phlyctidospora*
[e] *Hebeloma vinosophyllum*
[f] pH 4.0–5.5
[g] pH 7.0–9.0
Source: Modified from Suzuki (2006) and Licyayo et al. (2007)

late-stage EP fungus *Ly. tylicolor* inhibits the growth of other EP fungi. Another late-stage EP fungus, *Co. phlyctidospora*, invades other EP fungi but does not deeply invade into the territories of early-stage EP fungi (see Table 4). The LP fungus *He. vinosophyllum* tends to accelerate the basidiomata formation of *Co. phlyctidospora* at pH 5.5 and 9.0. *He. vinosophyllum* forms the highest numbers of basidiomata at pH 5.5 (Table 4; Suzuki 2006; Licyayo et al. 2007). These results indicate that the staggered appearance of ammonia fungi results partly from interspecific interactions as well as from abiotic effects.

Changes in the soil microbial population

In *Pinus (Pi.) densiflora* forests, the propagule number of total bacteria falls slightly about 1 week after urea treatment and then increases to a value about 1000 times greater than that of the control at the time of occurrence of EP fungi. For the following 2 years, the propagule number of total bacteria gradually declines, coinciding with the period of occurrence of LP fungi (Yamanaka 1995a). A similar pattern of changes in the populations of nematodes is also reported in the *Pi. densiflora* forest following urea application (Yamanaka 1995b). Yamanaka (1995b) assumed that the wastes and dead bodies of bacteria and nematodes were decomposed and utilized by the ammonia fungi. The ammonium oxidizers are not detected during the initial 60 days following the urea treatment; afterward, they increase to 2.6×10^7/g dry soil in the F horizon and to 4.1×10^8/g dry soil in the H horizon, 272 and 167 days after urea treatment, respectively (Yamanaka 1995a). The propagule number of nitrite oxidizers decreases and then increases to 3.9×10^7/g dry soil in the F horizon and to 3.4×10^7/g dry soil in the H horizon following urea treatment (Yamanaka 1995a). In *Pasania edulis* forest, the propagule number of cellulose-decomposing bacteria decreases 15 days after urea application, and then gradually increases, but does not return to the control level until 150 days after urea application (He and Suzuki 2004). In *Castanopsis*- and *Quercus*-dominated mixed forest, the propagule number of soil microfungi also suddenly decreases just after urea application and rapidly increases 10- to 100 fold above that of the control during the fruiting period of early-stage EP fungi. Thereafter, the propagule number of soil microfungi returns to the level in control soil during the fruiting period of late-stage EP fungi (Suzuki and Kikuchi, unpublished data).

These observations just discussed indicate that ammonia fungi begin to invade when the activities of other microbes are suppressed, because the population of cellulose-decomposing bacteria, which would compete with the saprobic ammonia fungi, decreases by the high concentration of ammonium-nitrogen at neutral to alkaline conditions. However, the causal relationship between the invasion and colonization abilities of ammonia fungi and the population impact of other microbes has not been confirmed.

Ecological strategies of ammonia fungi

In 1984, Cook and Rayner proposed a concept for ecological strategies of fungi based on the ecological and evolutionary theory proposed for plants (Grime 1977, 1979). It involves three primary ecological strategies of saprobic microbes, arising from ruderal selection (*R*-selection), stress-tolerant selection (*S*-selection), and combative selection (*C*-selection) (Cook and Rayner 1984). The *R*-selected specie are ephemeral and active only in habitats characterized by a low degree of combative competition and stress. Typically, the *R*-selected species are ephemeral and characterized by rapid spore germination and an abbreviated vegetative growth phase with high and rapid reproductive potential. The *S*-selected species are persistent so long as stress conditions prevail because of their high enzymatic competence. They are subject to replacement when stress is alleviated. The *C*-selected fungi are long lived as a consequence of their high enzymatic competence complemented by slow or intermittent reproduction. The *S*-selected fungi and *C*-selected fungi are not necessarily characterized by rapid spore germination and growth. It seems probable that many species combine characteristics of each in sec-

ondary or even tertiary strategies (Cook and Rayner 1984). Some *S*-selected fungi also have *R*-selected features such as rapid spore germination, high mycelial extension rates, and low enzymatic competence and may combine stress-tolerant ruderal (*S-R*) strategies. Fungal activity within a fully occupied resource may itself give rise to stress factors, for instance, by the removal of assimilable nutrients before refractory ones, or the accumulation of excretory products. Under such circumstances a stress-tolerant combative (*S-C*) strategy would confer an obvious advantage (Cook and Rayner 1984). A degree of combative ability is therefore essential for survival so that a combative ruderal (*C-R*) strategy can be envisaged as beneficial toward the end of the first stages of colonization of a wide range of habitats. The operation of *C-R* strategies has been demonstrated during colonization of burnt soil and feces (Singh and Webster 1973; Wicklow and Hirschfield 1979).

Based on the concept of Cooke and Rayner (1984), the physiological and ecological features of the ammonia fungi just described suggest that their ecological strategies can be expressed as follows. The early-stage EP fungi such as *Am. botrytis* and *As. denudatus* are *S-R* strategists whereas late-stage EP fungi such as *Co. phlyctidospora* and *Ly. tylicolor* are *C-R* strategists. Ectomycorrhizal species of LP fungi such as *He. vinosophyllum* and *He. spoliatum* colonize as *C-R* strategists from the standpoint of interactions with ectomycorrhizal nonammonia fungi and as *C* strategists from that of interactions between the ectomycorrhizal ammonia fungi and saprobic ammonia fungi. These differences occur because ectomycorrhizal ammonia fungi colonize with relatively higher growth rates and are defined as facultative ectomycorrhizal fungi that colonize as both saprotrophy and biotrophy. The typical *R*-selected species colonize substrata rich in soluble carbohydrates. The ammonia fungi would be regarded as *R*-selected fungal species, as they primarily utilize relatively easily available carbohydrates. On the whole, the chemoecological group of fungi, ammonia fungi, comprise ruderal species combined with different elements of secondary strategies: stress tolerant or combative.

Conclusions

Ammonia fungi are principally characterized by rapid spore germination in the presence of ammonium-nitrogen at a neutral and weakly alkaline condition and by their high germination percentage under their optimum conditions. Optimal ammonium-nitrogen concentration for the spore germination of the ammonia fungi is 10–100 mM ammonium-nitrogen at around pH 8, irrespective of fungus species of different successive occurrence following a sudden ammonium-nitrogen disturbance. Ammonia fungi do not germinate in the presence of nitrate-nitrogen. The vegetative growth of ammonia fungi is also characterized by their response to pH and concentration of ammonium-nitrogen. Ammonia fungi comprise three physiological types of species concerning their responses to the ammonium-nitrogen: fungi adapted to high concentrations of ammonium-nitrogen, fungi adapted to a wide range of ammonium-nitrogen concentration, and fungi nonadapted to a high concentration of ammonium-nitrogen but somewhat tolerant of a relatively high concentration of ammonium-nitrogen. Early-stage EP fungi grow well at pH 7–8 and late-stage EP fungi at pH 6–7, whereas the LP fungi show optimal growth at pH 5–6. Early-stage EP fungi and most late-stage EP fungi grow vigorously in ammonium-nitrogen but not in nitrate-nitrogen. Some late-stage EP fungi and LP fungi grow well in both ammonium-nitrogen and nitrate-nitrogen.

From the standpoint of physiological and ecological characteristics, the ammonia fungi can be categorized as follows: the early-stage EP fungi are stress-tolerant ruderal strategists and the late-stage EP fungi are *S-R* strategists and *C-R* strategists. Ectomycorrhizal species of LP fungi have two features, as *C-R* and as *C* strategists, based on the concepts of Cooke and Rayner (1984).

Not only the EP fungi but also the LP fungi can colonize litter immediately after an input of a high concentration of ammonium-nitrogen associated with neutral to weakly alkaline conditions. The ammonia fungi probably colonize from spores and/or mycelia that were inhibited or dormant before the disturbance by ammonium-nitrogen. Competition with other microbes would be suppressed by the high ammonium-nitrogen concentration accompanying weak alkaline to neutral conditions, because colonization of ammonia fungi is superior to that of other microbes under weakly alkaline to neutral conditions. The vigorous growth of ammonia fungi causes the decline of pH and ammonium-nitrogen concentration in their substratum as a result of the assimilation of ammonium-nitrogen. Large amounts of nitrogen are immobilized into the mycelia of ammonia fungi accompanying their vegetative growth. EP fungi, namely saprobic ammonia fungi, quickly form reproductive structures before nonammonia fungi initiate the colonization in the ammonium-nitrogen-disturbed soils associated with the declining ammonium-nitrogen concentration and pH. The major nitrogen form just after the soils are urea treated is ammonium-nitrogen, and the ammonium-nitrogen gradually changes into nitrate-nitrogen and reaches maximum concentration at around the period of the first flush of LP fungi. The ectomycorrhizal ammonia fungi of LP fungi would first utilize ammonium-nitrogen when soil pH rises in response to the ammonium-nitrogen disturbance, and then gradually utilize both ammonium- and nitrate-nitrogen associated with the declining of ammonium-nitrogen concentration and increasing nitrate-nitrogen concentration in the disturbed soil. Ectomycorrhizal ammonia fungi escape from the L-F horizon as a result of interactions between the saprobic ammonia fungi and form mycorrhizae with their host plant(s), where colonization of ectomycorrhizal nonammonia fungi is suppressed by the high ammonium-nitrogen concentration associated with a weakly alkaline condition resulting from the ammonium-nitrogen disturbance.

Each ammonia fungus also has an individual propagation strategy: e.g., the late-stage EP fungus *Ly. tylicolor*

forms mycelial basidia on dikaryotic hyphae and the ectomycorrhizal LP fungus *He. vinosophyllum* forms basidiospores on a monokaryotic basidioma. These are shortcuts to propagation, by basidiospores, without producing dikaryotic basidiomata.

Sagara (1995) proposed a cleaning symbiosis for the ecological role of ectomycorrhizal ammonia fungi that colonize mammalian middens, and this concept comprises nutrient cycles in animal waste-decomposing sites; namely, in ecosystems, both saprobic and ectomycorrhizal ammonia fungi have a role in the immobilization of nitrogen derived from animal wastes such as urine, feces, and dead bodies. In ammonium-nitrogen-disturbed habitats, ammonia fungi propagate to replace the previous fungal inhabitants and take over their ecological function. This replacement may be described as a "compensatory effects" in nutrient cycles (Suzuki 2000b, 2006).

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