Mycoscience (2004) 45:123–130
DOI 10.1007/s10267-003-0165-5

FULL PAPER

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The time of urea treatment and its effects on the succession of ammonia fungi in two warm temperate forests in Japan

Received: November 6, 2002 / Accepted: November 25, 2003

Abstract We studied the effects of the timing of urea treatment on the succession of ammonia fungi. In two evergreen *Castanopsis cuspidata* forests and in one deciduous *Quercus serrata* forest, we applied 343 g urea to 25 and 15 plots of 0.5 m^2, respectively, at three different times of the year. Ten of the early-phase (EP) species, considered to be saprotrophic, and 6 of the late-phase (LP) ones, considered ectomycorrhizal, fruited. In both phases, the commencement, peak, and cessation of fruiting took place simultaneously among all the plots treated at the same time. The fruiting occurred in summer and autumn. Quantity and size of the fruit bodies was larger in the LP than in the EP species. Fruiting of EP species was affected by the treatment time and that of LP species by interaction of the treatment time and vegetation type. EP was short and occurred as one period, whereas LP was long and occurred as two or more fruiting seasons. We found that species composition, dominant species, and degree of its dominance in fruiting of the ammonia fungi are predictable for different treatment times of the year and different vegetation types.

Key words Ammonia fungi · Ectomycorrhizal fungus · Fruiting season · Saprotrophic fungus · Urea treatment

Introduction

"Ammonia fungi" are "a chemoecological group of fungi which sequentially develop reproductive structures exclusively or relatively luxuriantly on the soil after a sudden addition of ammonia, some other nitrogenous materials which react as bases by themselves or on decomposition, or alkalis" (Sagara 1975, p. 270). This definition referred solely to the assemblage of fungal species reproducing on the soil surface. Sagara (1976, 1995) applied the concept of "succession" to the change of fruiting species of the ammonia fungi and of the abundance of their fruit bodies, and defined two successional phases: early phase (EP) and late phase (LP). These phases are especially marked in ectomycorrhizal (ECM) forests, and each phase has a unique species composition.

Sagara (1975, 1995) discussed nutritional modes of the ammonia fungi based on the literature and on the results from his laboratory and field experiments. The fungi classified as EP species consist of such genera as *Peziza*, *Lyophyllum*, and *Coprinus*, and have the ability to fruit on forest soil treated with urea in the laboratory in the absence of living plants (Sagara 1975). The fungi classified as LP species did not fruit in the laboratory experiment mentioned above (Sagara 1975) or in the root exclusion experiment in the field (Sagara 1995). The latter group consists mainly of species of *Hebeloma* and *Laccaria*, which are well known as ECM genera (Kropp and Mueller 1999; Mermeisse et al. 1999). Therefore, Sagara (1995) considered that the EP species are saprotrophic (SAP) and most LP species ECM. This view has been consistently supported by the studies on chemical characteristics of the urea-treated soil and on physiology of the ammonia fungi (Enokibara et al. 1993; Morimoto et al. 1981, 1982; Suzuki 1978, 1989; Suzuki et al. 1982; Yamanaka 1995a–c, 1999, 2001).

If EP species are SAP and LP species ECM, these two are considered to form different functional groups. Different functional groups may exhibit different characteristics in their fruiting. First, the quantity and size of fruit bodies are known to be generally larger in ECM species than in SAP ones (Fukiharu 1991; Fukiharu and Kato 1997; Murakami 1987; Vogt et al. 1992). Second, the existence of host specificity or host preference as mentioned by Imazeki and Hongo (1987), Otani and Hongo (1988), Kranabetter et al. (1999), Massicotte et al. (1999), and Molina and Trappe

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(1982) may affect the species composition of ECM communities. Because these two characteristics are quite widespread, they may also be observed in fruiting of the ammonia fungi. Furthermore, the treatment time of the year would affect the species composition of the ammonia fungi, as was pointed out by Sagara (1975, 1989).

On the other hand, the fruit body production in fungi is generally affected by climatic conditions irrespective of their nutritional modes. Murakami (1989) and Fukiharu (1991) recognized three major fruiting seasons for macromycetes, i.e., early summer, late summer to early autumn, and late autumn, in evergreen *Castanopsis* forests in Japan. This phenology may also be observed in the fruiting of ammonia fungi.

However, the preceding studies on the succession of the ammonia fungi (Fukiharu 1991; Sagara 1975, 1995; Suzuki et al. 2002; Yamanaka 1995a–c) were not sufficient in replication of plots or in providing quantitative data (e.g., dry weight) to explain the temporal change of fruit body production. Therefore, in this study, we investigated (1) the phenology of fruit body production under different conditions such as time of urea treatment of the year and type of vegetation; and (2) the effects of treatment conditions on the species composition of ammonia fungi and on the amount of fruit body production by each ammonia fungus. We conducted urea treatment experiments at three different times of the year in two types of vegetation in warm temperate Japan; one was a climax forest and the other a secondary forest in the seral stage.

Materials and methods

Study sites

Three experimental study sites were located in two types of vegetation: two evergreen broad-leaved forests dominated by *Castanopsis cuspidata* (Thunberg) Schottky (sites C1 and C2) and one deciduous broad-leaved forest dominated by *Quercus serrata* Murray (site Q). Sites C1 and Q were located at Yoshida-kaguraoka-cho (35°1′30″ N, 135°47′ E, 100 m alt), and site C2 at Kamitakano-saimyoujiyama (35°4′ N, 135°48′ E, 150 m alt). The sites were selected on the conditions that most of the canopy trees were about 20–50 cm in diameter at breast height (30 cm on average) and that the soil pH value was about 5 (A. Imamura, unpublished data).

The understories of forests at the three sites consisted mostly of the same plant species. They were *Q. glauca* Thunberg, *Ilex pedunculosa* Miq., *I. chinensis* Sims, *Cleyera japonica* Sieb. Et Zucc., *Eurya japonica* Thunberg, and *Camellia japonica* L. In sites C1 and C2, some artificially planted trees of *Cryptomeria japonica* (L.f) D. Don and *Chamaecyparis obtusa* (Sieb. et Zucc.) Endlicher joined the dominant trees in the canopy layer. In site Q, *Lyonia ovalifolia* (Wall.) Drude subsp. *neziki* Hara was growing in the subcanopy layer. Besides the dominant species (*C. cuspidata* and *Q. serrata*), only *Q. glauca* is known to be ectomycorrhizal (Maeda 1954). As *Q. glauca* was common to all the experimental sites, we established urea plots at places lacking the species in the canopy. Nomenclature of the plants follows Kitamura and Murata (1979a, b).

Treatments and observations

To induce fruiting of the ammonia fungi, fertilizer urea in granular form (N 46%; Kumiai-Nyouso, National Federation of Agricultural Co-operative Associations, Japan) was scattered by hand onto the plots. The amount of urea applied to each plot was 343 g (160 g N). The urea treatment was conducted at three different times of the year as experiments (Exp.) 1–3: Exp. 1 was established on May 25, 1999 (late spring), Exp. 2 on August 22, 1999 (late summer), and Exp. 3 on January 31, 2000 (midwinter). Five urea plots were set up for each study site in each experiment. Site C2 was used only for Exps. 2 and 3. In each experiment, urea plots were placed in new ground where such experiments had never been conducted. The total number of plots was 40. The plots were marked out 0.5 m wide horizontally and 1 m long along the slope.

The plots were visited every 3–7 days for about 1 month after the treatment and every 7–14 days thereafter. The fungal fruit bodies developing inside the plots were counted for each species and then harvested. Dry weight of the fruit bodies for each species was measured by drying at 55°C for 1 week. Data collection was continued until August 25, 2001.

Data analysis

The fungi found on the plots were classified into two groups according to Sagara (1995): EP and LP species. ANOVA was used to test the significance of difference in total fruit body production between the EP and LP species in each experiment. Two-way ANOVA was used to examine the significance of effects of the treatment time of the year, as exemplified as Exps. 1, 2, and 3, and of the vegetation types as exemplified by the *Castanopsis* forest (sites C1 and C2) and the *Quercus* forest (site Q), on fruit body production of each fungus.

"Time to fruiting" means the number of days between treatment and production of fruit bodies of the ammonia fungi. Difference in the time to fruiting between the two or among the three sites in each experiment were compared using two categories of index: the number of days passed after treatment until the first production of fruit bodies by any ammonia fungus (DFO) and the number of days passed after treatment until the first peak (in dry weight) of fruit body production (DFP). DFP was shown by the peak of fruit body production totaled for all the EP species and that totaled for all the LP species. It was assessed with the moving average using data from three observation occasions (the present, the previous, and the following). Differences in DFO and DFP were examined by Mann–Whitney *U* test for Exp. 1 and by Kruskal–Wallis test for Exps. 2 and 3.

Table 1. List of the ammonia fungi found fruiting in this study

Abbreviation	Scientific name	Reference for the nomenclature
EP (the early phase)		
Deuteromycetes (anamorphic fungi)		
Ab	*Amblyosporium botrytis* Fres.	Sagara (1975)
Ascomycota		
Ah	*Ascobolus hansenii* Paulsen et Dissing	Sagara (1992)
Ad	*A. denudatus* Fries	Sagara (1992)
Pu	*Peziza urinophila* Y.-Z. Wang et Sagara	Wang and Sagara (1997)
Pm	*P. moravecii* (Svrcek) Donadini	Sagara (1992)
Pp	*Pseudombrophila petrakii* (Sacc.) Brumm.	Brummelen (1995)
Basidiomycota		
Lt	*Lyophyllum tylicolor* (Fr.: Fr.) M. Lange et Sivertsen	Imazeki and Hongo (1987)
Cn	*Coprinus neolagopus* Hongo et Sagara	Imazeki and Hongo (1987)
Cp	*C. phlyctidosporus* Romagn.	Imazeki and Hongo (1987)
Ps	*Panaeolina sagarae* Hongo	Imazeki and Hongo (1987)
LP (the late phase)		
Basidiomycota		
Al	*Alnicola lactariolens* Clémençon et Hongo	Clémençon and Hongo (1994)
Hv	*Hebeloma vinosophyllum* Hongo	Fukiharu (1991)
Hs	*H. spoliatum* (Fr.) Karst.	Fukiharu (1991)
Hr	*H. radicosoides* Sagara, Hongo et Y. Murak.	Sagara et al. (2000)
Lb	*Laccaria bicolor* (Maire) P.D. Orton	Mueller (1992)
La	*L. amethyistina* Cooke	Mueller (1992)

Table 2. Fruit body production by EP and LP species

	EP species			LP species		
	No. of fruit bodies	Total dry weight (mg)	Mean dry weight (mg)	No. of fruit bodies	Total dry weight (mg)	Mean dry weight (mg)
Exp. 1	795	11 039	13.88	685	86 873**	126.8***
Exp. 2	3871	51 428	13.28	1365	213 400***	156.3***
Exp. 3	1371	22 042	16.07	2321	361 820***	155.8***

Significance of difference between EP and LP species in the total and mean dry weight of fruit bodies for each experiment was tested by ANOVA
** Significant effect at $P < 0.01$
*** Significant effect at $P < 0.001$

StatView J-5.0 (SAS Institute, Cary, NC, USA) was used in all the statistical analyses.

Results

Fruit body production

Ten of the known EP species and six of the known LP species were observed in EP and LP, respectively, in the form of either conidia, ascocarps, or basdiocarps (Table 1). *Laccaria amethystina* has been recently confirmed as a LP ammonia fungus (Imamura 2001) and was therefore included here. We did not consider *Amblyosporium botrytis*, which belongs to Deuteromycetes (anamorphic fungi sensu Kirk et al. 2001) and does not develop macroscopic sporophores. Also, we did not count the numbers of fruit bodies of *Ascobolus hansenii* and *A. denudatus* because they were too small and too abundant for field observation.

Quantity of fruit bodies

The total dry weight of fruit bodies of all the LP species was significantly larger than that of all the EP species in each experiment. The mean dry weight of fruit bodies for each phase was also significantly larger in LP than in EP for each experiment (Table 2).

Effect of treatment time of the year and vegetation type on EP species

As shown in Table 3a, seven EP species fruited in Exp. 1, eight in Exp. 2, and six in Exp. 3. *Lyophyllum tylicolor* and *Coprinus phlyctidosporus* fruited in almost all the plots in all the experiments. *Ascobolus denudatus*, *Peziza urinophila*, *P. moravecii*, and *C. neolagopus* also fruited in more than half the plots. *A. denudatus* fruited less frequently in Exp. 1, *P. urinophila* did not fruit in Exp. 3, *P. moravecii* fruited more frequently in Exp. 3, and *C. neolagopus* did not fruit in Exp. 1. *Pseudombrophila (Ps.) petrakii* and *Panaeolina (Pa.) sagarae* fruited in nine, three,

Table 3a,b. Mean dry weight (±SD; mg) of fruit bodies and frequency of occurrence (in bold) as for each species of the ammonia fungi fruiting after the urea treatment at different times of the year in two types of vegetation

a. EP (the early phase)

		Fungal species[1]								
Exp.	Site[2]	Ah	Ad	Pu	Pm	Lt	Pp	Cn	Cp	Ps
1	C1	133[c]** ± 117	69.8 ± 81.4	218 ± 233	61.4 ± 36.7	906 ± 678	61.4[b] ± 84.4	0	80.2 ± 132	0
		4	**2**	**4**	**1**	**5**	**2**	**0**	**4**	**0**
	Q	35.7[c] ± 23.7	0	466 ± 455	0 ± 0	361 ± 164	27.4[b] ± 61.3	0	71.0 ± 131	0
		4	**0**	**5**	**1**	**5**	**1**	**0**	**2**	**0**
2	C1	0	323.2[b] ± 256	2247.4[c] ± 1512	0 ± 0	566 ± 327	0	703.6[c]*** ± 252	381.56[b] ± 181	282 ± 268
		0	**5**	**5**	**1**	**5**	**0**	**5**	**5**	**3**
	Q	3.74 ± 8.36	361[b] ± 178	3693.2[c]** ± 1367	0	366 ± 117	0	59.2[c] ± 69.5	279[b] ± 225	0
		1	**5**	**5**	**0**	**5**	**0**	**3**	**5**	**0**
	C2	0	138.2[b] ± 125	422[c] ± 286	0	68 ± 134	0	707.4[c]*** ± 377	495[b] ± 227	6.4 ± 14.3
		0	**4**	**4**	**0**	**2**	**0**	**5**	**5**	**1**
3	C1	0	329.2[b] ± 296	0	17.2[c] ± 24.2	2007 ± 651	0	0 ± 0	74.8 ± 78.9	0
		0	**5**	**0**	**3**	**5**	**0**	**1**	**5**	**0**
	Q	0	149[b] ± 121	0	318.8[c] ± 213	529 ± 228	0	0.20 ± 0.44	205 ± 169	0
		0	**5**	**0**	**5**	**5**	**0**	**1**	**5**	**0**
	C2	0	346[b] ± 327	0	841.6[c] ± 189	184 ± 406	0	0	230 ± 174	0
		0	**5**	**0**	**5**	**1**	**0**	**0**	**5**	**0**

b. LP (the late phase)

		Fungal species[1]					
Exp.	Site[2]	Al	Hv	Hs	Hr	Lb	La
1	C1	12812[c] ± 6824	383.0 ± 786.6	219.6 ± 178.4	0	0	0
		5	**3**	**5**	**0**	**0**	**0**
	Q	3218[c] ± 1426	5.0 ± 11.1	322.4 ± 520.2	0	388.4 ± 538.6	25.0 ± 55.9
		5	**1**	**5**	**0**	**2**	**2**
2	C1	16576[c] ± 9683	2210 ± 3009	23.0 ± 51.4	0	329.4[a] ± 736.5	0
		5	**3**	**1**	**0**	**1**	**0**
	Q	10623[c] ± 2481	1497 ± 2323	685.4 ± 1496	485.8 ± 976.2	5080[a]* ± 4191	0
		5	**4**	**4**	**2**	**4**	**0**
	C2	2845[c] ± 3031	2222 ± 2440	100.0 ± 51	0	0	0
		5	**5**	**1**	**0**	**0**	**0**
3	C1	2062 ± 1473	9138[a]* ± 6709	3875[c] ± 4214	630.2 ± 1120	0	0
		4	**5**	**5**	**2**	**0**	**0**
	Q	294.2 ± 976	534.8[a] ± 976	25641[c]* ± 24177	386.4 ± 405.9	9236[a]* ± 9018	0
		3	**4**	**5**	**2**	**5**	**0**
	C2	108.4 ± 207	7535[a]* ± 4997	7477[c] ± 8213	0	0	0
		2	**5**	**5**	**0**	**0**	**0**

Five plots were established in each site for each experiment.
Significance of the effects of the treatment time of the year and of the vegetation type on the amount of the fruit body production was tested by two-way ANOVA
[1] For abbreviations of species names, see Table 1
[2] C1, C2, *Castanopsis cuspidata* forests; Q, *Quercus serrata* forest
[a] Significant effect by treatment time of the year at $P < 0.05$
[b] Same at $P < 0.01$
[c] Same at $P < 0.001$
** Significant effect by treatment time of the year and vegetation type at $P < 0.01$
*** Same at $P < 0.001$

and four plots, respectively. Almost all the fruit bodies of *A. hansenii* were recorded from Exp. 1, and none from Exp. 3. *Ps. petrakii* fruited only in Exp. 1, and *Pa. sagarae* fruited only in the plots of *Castanopsis* forests in Exp. 2.

When viewed as the mean dry weight of fruit bodies of each EP species obtained at each site and in each experiment (Table 3a), many of the EP species tended to be affected by the treatment time of the year but not by the vegetation type. *Pa. sagarae* and *L. tylicolor* were not affected by these factors. Seven species were significantly affected by the treatment time: *A. hansenii* was more abundant in Exp. 1; *A. denudatus* in Exps. 2 and 3; *P. urinophila* in Exp. 2; *P. moravecii* in Exp. 3; *Ps. petrakii* in Exp. 1; *C. neolagopus* in Exp. 2; and *C. phlyctidosporus* in Exp. 2. Only three species, i.e., *A. hansenii*, *P. urinophila*, and *C. neolagopus*, were affected by the vegetation type and moreover by interaction of the treatment time and the vegetation type. Namely, *A. hansenii* was more abundant in the *Castanopsis* forest by Exp. 1, *P. urinophila* in the *Quercus* forest by Exp. 2, and *C. neolagopus* in the *Castanopsis* forests by Exp. 2.

Effect of treatment time of the year and vegetation type on LP species

As shown in Table 3b, five LP species were found in Exp. 1, five in Exp. 2, and five in Exp. 3. *Alnicola lactariolens*, *Hebeloma vinosophyllum*, and *H. spoliatum* fruited in almost all the plots. *H. radicosoides*, *Laccaria bicolor*, and *L. amethystina* fruited less frequently, i.e., in 6, 12, and 2 plots, respectively, among the 40 plots in total.

Viewed as the mean dry weight of fruit bodies of each LP species obtained at each site and in each experiment, fruit body production tended to be affected by interaction of the treatment time and the vegetation type (Table 3b). However, for *H. radicosoides* and *L. amethystina*, any significant effects of these factors were not detected. *A. lactariolens*, *H. vinosophyllum*, *H. spoliatum*, and *L. bicolor* were significantly affected by the treatment time; namely, the first was more abundant in Exps. 1 and 2, the second in Exp. 3, the third in Exp. 3, and the fourth in Exp. 3. *H. vinosophyllum*, *H. spoliatum*, and *L. bicolor* were significantly affected by the vegetation type and moreover by interaction of the treatment time and the vegetation type; namely, the first was more abundant in the *Castanopsis* forests by Exp. 3, the second in the *Quercus* forest by Exp. 3, and the third in the *Quercus* forest by Exps. 2 and 3. *A. lactariolens* fruited most abundantly among all the LP species, being affected only by the treatment time, although its fruit body production was remarkably large in the *Castanopsis* forests. This species was always dominant, especially in the *Castanopsis* forests, except for Exp. 3 in which *H. vinosophyllum* and *H. spoliatum* were dominant in the *Castanopsis* forests and in the *Quercus* forest, respectively (Table 3b).

Time to fruiting

EP species began to fruit about 20, 15, and 60 days after the treatment in Exp. 1, Exp. 2, and Exp. 3, respectively, and LP species about 90, 300, and 150 days after the treatment in Exp. 1, Exp. 2, and Exp. 3, respectively. The EP lasted for about 1.5 month (June 1999–July 1999) in Exp. 1, 3 months (August 1999–October 1999) in Exp. 2, and 3 months (March 2000–May 2000) in Exp. 3. The LP lasted intermittently for about 15–16 months (August 1999–November 2001) in Exp. 1, 13 months (June 2000–July 2001) in Exp. 2, and 11 months (September 2000–July 2001) in Exp. 3 (Fig. 1).

The peak of fruiting in EP viewed as the total fruit bodies produced by all the species occurred only once in all the

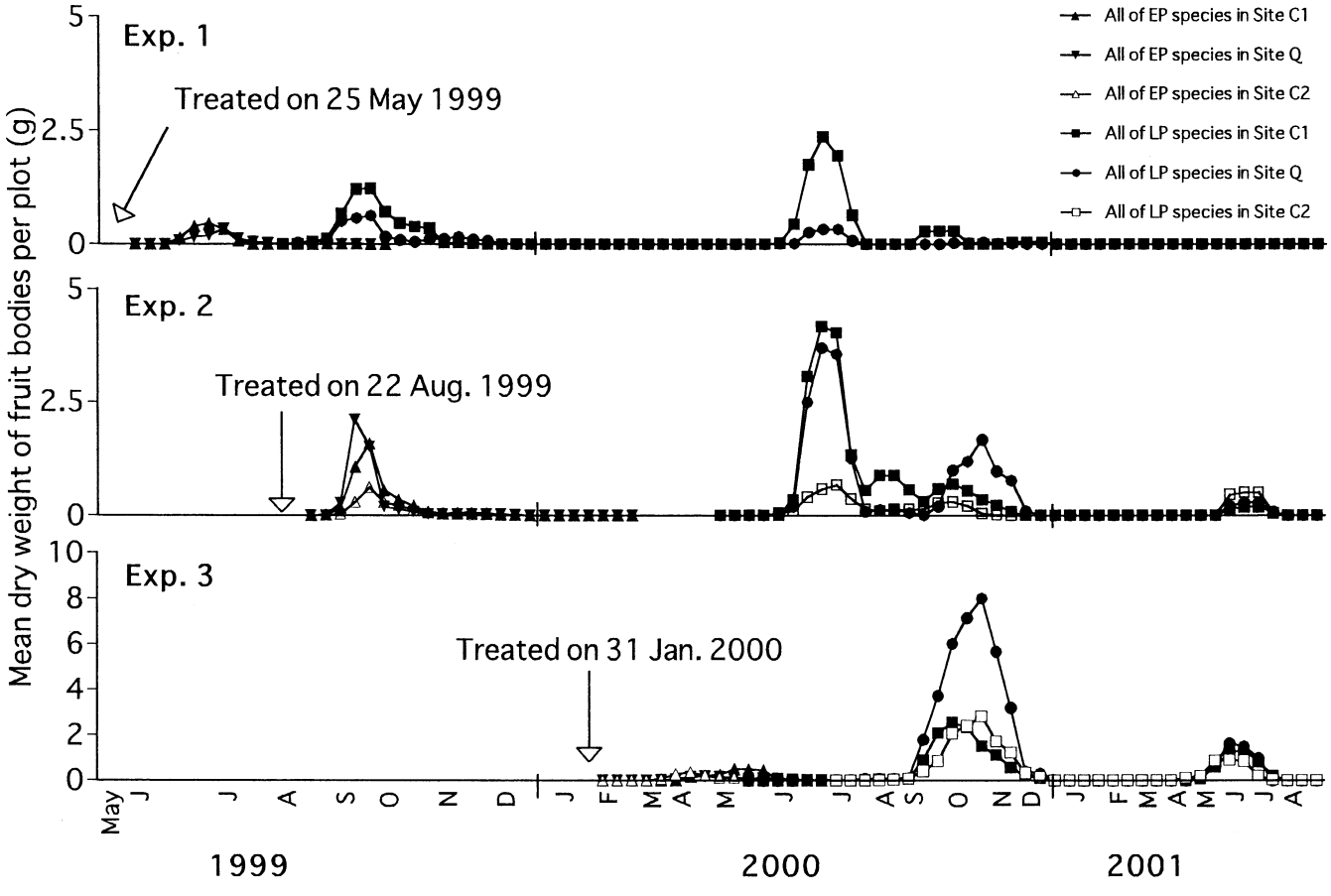

Fig. 1. Temporal changes of fruitbody production by the ammonia fungi after treatment of soil with urea at different times of the year in different types of vegetation. Each dot denotes the total dry weight of fruit bodies of all the species for EP and LP. Notice the difference in y-axis. Site C1 and C2: *Castanopsis cuspidata* forests; Site Q: *Quercus serrata* forest

three experiments: about 40 days after the treatment by Exp. 1 (June 1999), 30 days by Exp. 2 (September 1999) and 80–100 days by Exp. 3 (May 2000) (Fig. 1). That in LP occurred twice or more as flushes of fruiting, in which the same species fruited repeatedly: about 120 (September 1999), 400 (July 2000), and 500 days (October 2000) after the treatment by Exp. 1; about 310 (July 2000), 410 (October 2000), and 680 days (June 2001) after the treatment by Exp. 2; and 260 (October 2000) and 500 days (June 2001) after the treatment by Exp. 3 (Fig. 1). Thus, the LP were longer than the EP.

The fruiting took place almost simultaneously among the plots, even of different forests, within each experiment. For the EP, no significant difference for both DFO (days passed after treatment until the first occurrence of fruit bodies) and DFP (days passed after treatment until the first peak of fruit body production) was found among all the sites (C1, Q, and C2), except for DFP at site C1 by Exp. 3 ($P = 0.02$) where fruiting was delayed for about 10 days (Table 4). For LP, no significant difference for either DFO or DFP was found among the sites (Table 4).

Discussion

Fruiting phenology

In this study, the ammonia fungi generally fruited abundantly on all the plots at all the sites in all the experiments. As the analysis on DFO and DFP indicated, the succession of the ammonia fungi proceeded almost simultaneously among different plots and sites within each experiment. Although the EP species in site C2 of Exp. 3 started to fruit in late spring in this study, as Fukiharu and Hongo (1995) reported that the time of fruit body production of the ammonia fungi sometimes precedes the general mushroom season or extends longer, the peaks of fruit body production in the present study were either in early summer, late summer to autumn, or late autumn. These times of the year are generally recognized as the major fruiting seasons of macromycetes, especially in the evergreen *Castanopsis* forest of Japan (Murakami 1989; Fukiharu 1991). Fukiharu and Hongo (1995) discussed the reason why some of the EP and LP ammonia fungi, induced by urea treatment in their study site of southern Rhyukyus, fruited even in January to April and inferred that it might be related to the greater precipitation and higher temperature in that place than in the main islands of Japan. Under natural conditions in the vicinities of sites C1 and Q, *A. lactariolens* and *H. vinosophyllum* among the LP species fruited also in September and October 2000 (autumn) and June 2001 (early summer), along the strolling path of pet dogs (Oda et al. 2002). Thus, it can be said that, even when induced at different times of the year in different types of vegetation as the present method, the fruiting phenology of the ammonia fungi is consistent with that of naturally fruiting macromycetes and that this phenology is predictable.

Table 4. Results of the analysis of difference in the time to fruiting of EP and LP species for each experiment among the sites treated at the same time

Exp.[a]	EP		LP	
	DFO	DFP	DFO	DFP
Exp. 1*	0.60 $U = 10.0$	0.29 $U = 7.5$	0.10 $U = 5.5$	0.75 $U = 11.0$
Exp. 2**	0.33	0.18	0.85	0.47
Exp. 3**	0.053	0.020[b]	0.50	0.43

DFO, days passed after treatment until the first occurrence of fruit bodies; DFP, days passed after treatment until the first peak (in dry weight) of fruiting

[a] Urea treatment was conducted on May 25, 1999, in Exp. 1, on Aug. 22, 1999, in Exp. 2, and on Jan. 31, 2000, in Exp. 3

[b] Significant effect at $P < 0.05$

* Tested by Mann–Whitney U test

** Tested by Kruskal–Wallis test

Characteristics of fruiting by the urea treatment

The characteristics of fruiting in the EP and LP ammonia fungi observed in the present study are summarized in Table 5. The total quantity of fruit bodies produced was larger in LP than in EP in all three experiments. The EP species developed smaller but many fruit bodies whereas the LP showed larger and many fruit bodies. Murakami (1987) and Fukiharu and Kato (1997) reported that fruit body production by ECM species under natural conditions tended to be larger than that by SAP species in *Castanopsis* forests.

The period of EP was generally shorter than that of LP, and this may be related to the fact that favorable conditions for spore germination, mycelial growth, and fruit body production of the EP species, i.e., a high level of ammonium-N (10–50 mg/g dry soil) and high pH value of soil (7–8) (Morimoto et al. 1981; Suzuki 1978; Suzuki et al. 1982, 2002; Yamanaka 2001), do not persist long in the soil (Suzuki et al. 2002; Yamanaka 1995a,c, 1999). It may also be rele-

Table 5. Characteristics of fruiting in the early phase (EP) species and in the late phase (LP) species of the ammonia fungi as concluded by the present study

Fungi	No. and amount of fruit bodies	Source of significant effect on fruiting	No. and duration of fruiting periods
EP species	Many but small	Treatment time	Only one and short
LP species	Many and larger	Treatment time and vegetation type	Two to three and long

vant to the loss of ammonium-N by nitrification in soil (Yamanaka 1995a) and by consumption in growth and reproduction by the ammonia fungi themselves (Yamanaka 1999). On the other hand, favorable conditions for LP species, i.e., a higher level of nitrate-N (0.1–1 mg/g dry soil), a lower level of ammonium-N (10 μg/g dry soil), and lower pH value (around 5) (Yamanaka 2001) are considered to be more longlasting (Suzuki et al. 2002; Yamanaka 1995a,c, 1999).

Fruiting of each EP species was shown to be affected by treatment time of the year and that of LP species by interaction of the treatment time and the vegetation type, with some exceptions. Exceptions are seen either in those species that fruited less frequently, i.e., *Pa. sagarae*, *H. radicosoides*, and *L. amethystina*, or in those which fruited most frequently and abundantly, i.e., *L. tylicolor* and *A. lactariolens*. *L. tylicolor* was not affected at all, and *A. lactariolens* was affected only by the treatment time. On the whole, the difference of the vegetation type was more effective on fruiting and species composition of LP than on those of EP. This result suggests that, in LP species, there exists a sort of "host preference" in the sense of Imazeki and Hongo (1987) and Otani and Hongo (1988), who based their reports on fruit body collecting experiences in various types of forests, rather than "host specificity" in the sense of Molina and Trappe (1982), Kranabetter et al. (1999), and Massicotte et al. (1999), who based their reports on observation of ECM connection between fungi and their host plants.

By replicated plot setting at different times of the year in different types of vegetation, we found that the vegetation type clearly affected the fruiting of LP species, belonging to closely related genera, *Hebeloma* and *Alnicola* of Cortinariaceae, under dominant plants belonging to closely related genera, *Castanopsis* and *Quercus*, of Fagaceae. This fact may indicate that LP species are the symbionts of plants.

From these investigations, it is indicated that the species composition, the dominant species, and the degree of its dominance in fruiting of the ammonia fungi can be predicted for different conditions of treatment such as treatment time and vegetation type. This finding should be a great advantage from the study of the ammonia fungi, which may be applied for investigation of ectomycorrhizas, because the species diversity of fungal communities under natural conditions, even on the local scale in soil, could be a great obstacle, as suggested by Bruns (1995).

Acknowledgments We thank Emeritus Prof. N. Sagara, Kyoto University, for kindly helping us to complete this study. We thank Prof. S. Taguchi, Graduate School of Human and Environmental Studies, Kyoto University, for enabling us to work under his guidance. The senior author (A.I.) thanks Mr. H. Kobayashi, a student at the time at the same school, for suggestions and assistance.

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