

Seasonal occurrence and spatial distribution of fruitbodies of ectomycorrhizal fungi on the border of a man-made and a naturally regenerated forest

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Abstract

The seasonal occurrence and spatial distribution of fruitbodies of ectomycorrhizal fungi, which are produced on the ground, was assessed in a mixed stand which consists mainly of naturally regenerated trees of *Abies firma*, *Carpinus laxiflora* and *Quercus serrata* and planted trees of *Cryptomeria japonica* and *Chamaecyparis obtusa*. Five surveys from early October to early November at the study site indicated that *A. firma*, *C. laxiflora* and *Q. serrata* had ectomycorrhizal associations. Nineteen species of ectomycorrhizal fungi were recorded throughout the study period. The fruitbodies of *Russula* sp. 1, presumably associated with the roots of *C. laxiflora* and *Q. serrata* were the most abundant. The fruitbodies emerged sporadically and were located more frequently outside of the estimated root system areas (RSAs) of *C. laxiflora*. The numbers of species and fruitbodies of ectomycorrhizal fungi presumably associated with *A. firma* were very few, although *A. firma* was dominant in the stand. The fruitbodies of ectomycorrhizal fungi rarely occurred where non-ectomycorrhizal plants such as *Cryptomeria japonica* and *Chamaecyparis obtusa* were abundant. These results suggest that the spatial distribution of the fruitbodies reflects not only the growth pattern of ectomycorrhizal mycelia but also the location and density of trees in each species.

Key words: ectomycorrhiza, fruitbody, mixed stand, root area system, spatiotemporal pattern

I. Introduction

Mycorrhizal symbiosis has been considered to be one of the mutualistic interactions between plants and fungi, where plant roots and fungal mycelia together form a biological complex, known as mycorrhiza. It is known that the majority of terrestrial plants form mycorrhiza (HARLEY, 1989). In fact, 76% of all the plants examined in a European survey were shown to have mycorrhizal association (HARLEY and HARLEY, 1987).

Most fungal species of the major taxonomic groups, Zygomycotina, Ascomycotina, Basidiomycotina and Deuteromycotina, establish mycorrhizal associations (ISAAC, 1992). Mycorrhizas can roughly be classified into two groups according to their morphology: endomycorrhiza and ectomycorrhiza. In general, most of the fungi which form the ectomycorrhizas belong to Basidiomycetes although some fungi belonging to As-

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(Accepted : Nov. 7, 1994)

comycetes have also been observed to do so. In Japan, these fungi are known to produce their fruitbodies on the ground every year mainly from the rainy season to the autumn. The host plants of the ectomycorrhizal fungi are mostly from Pinaceae, Fagaceae, Betulaceae and Myrtaceae which are distributed mainly in the Northern Hemisphere, especially north of the temperate zone.

A number of studies have suggested that those host plants are likely to have some benefit from the ectomycorrhizal symbiosis (REID *et al.*, 1983; SLANKIS, 1974; MARX *et al.*, 1989; CHALOT *et al.*, 1988; HARLEY and SMITH, 1983). In Japan, OGAWA (1975, 1977a, b) has undertaken intensive studies on *Tricholoma matsutake*, an edible ectomycorrhizal fungus. The relationships between ectomycorrhizal fungi and host trees have hitherto been discussed on the basis of the observations of fruitbodies on the ground and/or on the ectomycorrhizal analysis according to their morphology or the amount of mycorrhizal root tips under the ground (MASON *et al.*, 1982; FLEMING, 1983; DEACON *et al.*, 1983). Moreover, these studies undertaken on small trees and seedlings have shown that a certain fungal species might have a specific relationship with the host. However, little is known about the mechanism of mycorrhizal symbiosis and the adaptive significance of mycorrhizal formation in mature woody plants.

The primary objective of this study is to obtain basic information in order to clarify the interactions between trees and ectomycorrhizal fungi: the spatiotemporal pattern of fruitbodies and the effect of surrounding flora on the spatial distribution of the fruitbodies.

II. Study site

The study site was located in the town of Inabu, Aichi, Japan (680m a.s.l.; 35° 11' N, 137° 33' E). The site faced the south-west descent in the region of 2°~37° and was separated into two areas by a ridge; one area is on the west side of the ridge with steep inclinations, while the other is on the east side of the ridge and has a less steep slope. The soil type was mixed B- or B1-type with a thick A layer. The annual precipitation and mean air temperature are about 2,300 mm and 8.3°C, respectively.

The site was situated in a mixed stand which consists mainly of naturally regenerated trees of fir, *Abies firma* Sieb. et Zucc., and planted trees of sugi, *Cryptomeria japonica* D. Don, and hinoki, *Chamaecyparis obtusa* Endl.. Only a few fir and a maple trees, *Acer palmatum* Thunb., occupied the middle height class. Species of young woody plants and seedlings, which formed the forest floor, at this site included *Callicarpa japonica* Thunb., *Vaccinium hirtum* Thunb., *Acanthopanax sciadophylloides* Fr. et Sav., *Elaeagnus umbellata* Thunb., *Ilex macropoda* Miq., *I. crenata* Thunb., *Acer crataegifolium* Sieb. et Zucc., *Rhus trichocarpa* Miq., *Phellodendron amurense* Ruprecht, *Pourthiaea villosa* Decaisne var., *Hydrangea hirta* Sieb. et Zucc., *Akebia trifoliata* Koidzumi, *Magnolia obovata* Thunb. and *Lindera triloba* Blume.

III. Field survey

In the study site, five plots, 10×10 m in area were located adjacently, and then each

was divided into four subplots each with an area of 5×5 m (Fig. 1). The site was surveyed five times at intervals of about a week from early October to early November in 1993. The species and seasonal fluctuations of ectomycorrhizal fungi were determined in terms of fruitbodies which occurred on the forest floor. All fruitbodies in each subplot were mapped, identified and counted at every survey. To avoid a double count, recorded fruitbodies were clipped in the subplots. For woody plants higher than 1.3 m, species, locations and girth at breast heights (GBH) were recorded. The projection area of the crown was also measured, but only for the trees which had formed ectomycorrhizas.

IV. Results

1. Species composition and spatial distribution of plants

The tree layer at the study site was occupied by five species: *A. firma*, *Carpinus laxiflora* Blume, *Quercus serrata* Thunb., *Cryptomeria japonica* and *Chamaecyparis obtusa*. Most trees of the former three species occurred on the steep slopes, whereas the latter two were distributed mainly on the less steep slopes. Table 1 shows the composition of these five species in each plot.

A. firma, *C. laxiflora* and *Q. serrata* which invariably form ectomycorrhizas (abbreviated as ECM plant) accounted for 43% of all woody plants in the plots. On the other hand, *Cryptomeria japonica*, *Chamaecyparis obtusa* and *Acer palmatum* showed no association with ectomycorrhizal fungi (abbreviated as NECM plant). Among ECM plants, *A. firma* was the most dominant species in number, occupying about 85%, of the study site and with a tree density of 580 trees ha⁻¹. The GBHs ranged from 4.0 to 244.5 cm, which suggests that there was a large difference in growth between suppressed and non-suppressed trees. Moreover, there was a large difference in density between ECM and NECM plants depending on the position of the subplot (Table 1).

2. Seasonal occurrence of fruitbodies and species composition

The ECM plants observed in the plots were *A. firma*, *C. laxiflora*, *Q. serrata*. Nineteen species of ectomycorrhizal fungi belonging to seven genera were recorded while number of fruitbodies totalled 327 throughout the study period (Table 2). The fruitbodies of *Russula* sp. 1, which are quite similar in morphology to those of *Russula cyanoxantha* (per. com., Mr. H. Yamada) accounted for about 80% of the total number, followed by those of *R. ochroleuca* occupying about 14%. The number of fruitbodies occurring on the ground reached a peak on Oct. 9, 1993 but decreased after that (Table 2).

In the vicinity of the plots, fruitbodies of mycorrhizal fungi, *Lactarius laeticolorus* and *R. ochroleuca* were observed. Sixteen species of saprophytic fungi were observed in the plots during this study (Table 3).

3. Spatial patterns of fruitbodies of *Russula* sp. 1 and its host tree, *C. laxiflora*

Russula sp. 1 produced no fruitbodies in the subplots (e.g. P1-2, P1-3, P4-2 and P5-3) where *Cryptomeria japonica* and *Chamaecyparis obtusa* were abundant (Fig. 1, Table 1). The fruitbodies of *Russula* sp. 1 and those of *Russula cyanoxantha* are very similar to each other and the latter are known to be found on the forest floor where trees of Fagaceae

Table 1. Status of major woody plants and total number of fruitbodies in each subplot.

Subplot No.	P1-1	P1-2	P1-3	P1-4	P2-1	P2-2	P2-3	P2-4	P3-1	P3-2	P3-3	P3-4	P4-1	P4-2	P4-3	P4-4	P5-1	P5-2	P5-3	P5-4
<i>Quercus serrata</i>																				
	1							1	1	1		1								
<i>Carpinus laxiflora</i>																				
	1				1	3	1	4	6	2	2	6	1							
<i>Abies firma</i>																				
No. of species	2	1	1	1	1	3	2	2	2	2	1	2								2
No. of trees	2	1	3	1	4	8	3	3	6	2										1
mean GBH* (cm)	49.6	235	39.9	16.4	28.2	71.7	40.6	102	47.9	31.2										198
<i>Acer palmatum</i>																				
	1	6	6	2	4								1	2	2	2				1
<i>Chamaecyparis obtusa</i>																				
	1												4	4						5
<i>Cryptomeria japonica</i>																				
No. of trees	2	6	6	2	4								1	1	6	6	2			5
mean GBH(cm)	19.6	37.8	33.8	23.5	34.7								8.3	29.4	39.4	56.7	56.2			32.6
Tree density (No./ha)	1600	2400	2400	1200	2000	1600	3200	1200	2400	1200	2400	1200	400	2400	2400	800	800	2000	1600	400
ECM No./total No. of trees (%)	50		33.3	100	20	100	100	100	100	100	100	66.7								
NECM No./total No. of trees (%)	50	100	100	66.7	80							33.3	100	100	100	100	100	100	100	100
No. of fruitbodies emerged	15	1	7	48	3	32	25	20	22	18	6	9	20	1	5	19	46	7	1	22

* : Girth at breast height.

Spatial distribution of ectomycorrhizal fungi

Table 2. List of ectomycorrhizal fungi which produced fruitbodies and their numbers of occurrence in the study site at Inabu from Oct. 9 to Nov. 4, 1993.

Species	Date					Total No.
	Oct. 9	Oct. 15	Oct. 21	Oct. 29	Nov. 4	
<i>Amanita vaginata</i>	2					2
<i>Cortinarius</i> sp.	3	1				4
<i>Inocybe lacera</i>			1			1
<i>Inocybe lanuginella</i>			1			1
<i>Laccaria bicolor</i>	1					1
<i>Laccaria laccata</i>			1			1
<i>Rhodophyllus crassipes</i>	1					1
<i>Rhodophyllus rhodopolius</i>	3	4				7
<i>Russula alboareolata</i>			1			1
<i>Russula amoena</i>	1					1
<i>Russula compacta</i>	1					1
<i>Russula ochroleuca</i>	32	11				43
<i>Russula rubescens</i>			1			1
<i>Russula vesca</i>			2			2
<i>Russula virescens</i>	1					1
<i>Russula</i> sp. 1	159	66	19	1	5	250
<i>Russula</i> sp. 2			1		1	2
<i>Tricholoma portentosum</i>					2	2
<i>Tricholoma saponaceum</i>	4	1				5
Total No.	208	83	27	1	8	327

Table 3. List of saprofitic fungi which produced fruitbodies in the study site at Inabu from Oct. 9 to Nov. 4, 1993.

Species	Date				
	Oct. 9	Oct. 15	Oct. 21	Oct. 29	Nov. 4
<i>Camarophyllus pratensis</i>		○			
<i>Clavulinopsis pulchra</i>		○	○	○	○
<i>Conocybe</i> sp.			○		
<i>Hygrocybe psittacina</i>		○			
<i>Mycena alcalina</i>	○				
<i>Mycena galericulata</i>		○			
<i>Mycena haematopoda</i>			○		
<i>Mycena pura</i>			○		
<i>Omphalina epichysium</i>			○		
<i>Psathyrella candolliana</i>			○	○	
<i>Psathyrella piluliformis</i>	○	○	○	○	○
<i>Psathyrella spintrigera</i>			○		
<i>Rhodophyllus murrainii</i>	○				
<i>Strobilurus ohshimae</i>			○		
<i>Tricholoma</i> sp.		○			
Unknown sp.		○			

Open circles indicate fungal species whose fruitbodies were confirmed in the plot.

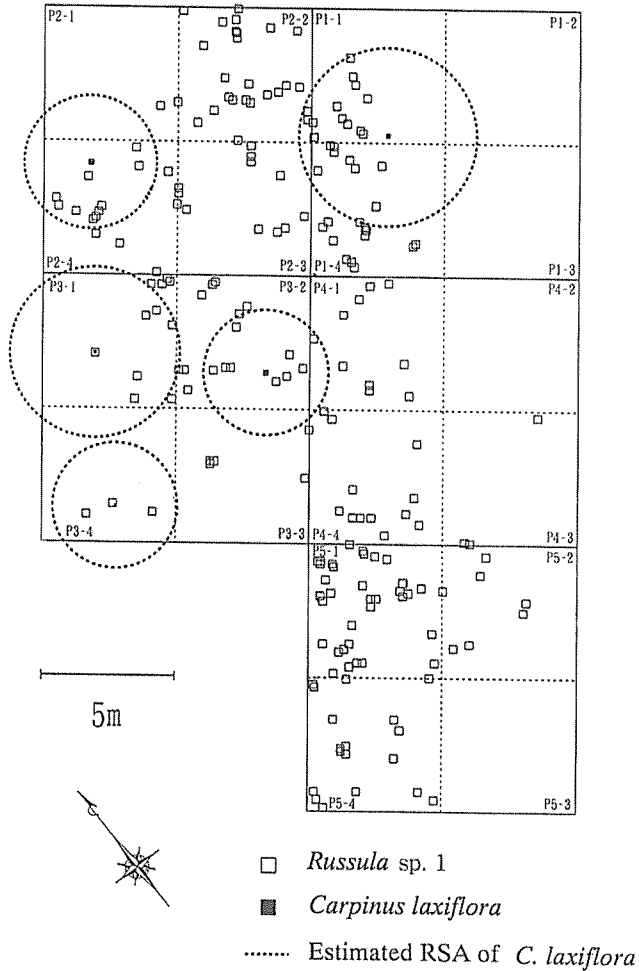


Fig. 1. The relationship between the positions of fruitbodies of *Russula* sp. 1 and the estimated RSA of *Carpinus laxiflora* (□, *Russula* sp. 1; ■, *C. laxiflora*;, Estimated RSA of *C. laxiflora*).

and Betulaceae are abundant (IMAZEKI and HONGO, 1989).

In the present study the relationship between the spatial patterns of fruitbodies of *Russula* sp. 1, which are the most abundant, and its speculative host tree *C. laxiflora* could be analyzed based on the concept of a root system area (RSA) (KARIZUMI, 1979). The RSA is defined as the horizontal distribution area of root systems, where fine and thin roots grow densely (Fig. 2). According to the classification by KARIZUMI (1979), the root system of *C. laxiflora* belongs to the beech type. In a 70 years old beech, the root system area was estimated to be about 0.4 times as large as the crown projection area (HILF, 1927). The ratio of RSA to the crown projection area could thus be applied to that of *C. laxiflora* in this study (Fig. 2). The relationship between estimated RSAs of *C. laxiflora* and the positions of fruitbodies shows that the fruitbodies had a tendency to occur more frequently outside the estimated RSAs of *C. laxiflora* rather than inside (Fig. 1).

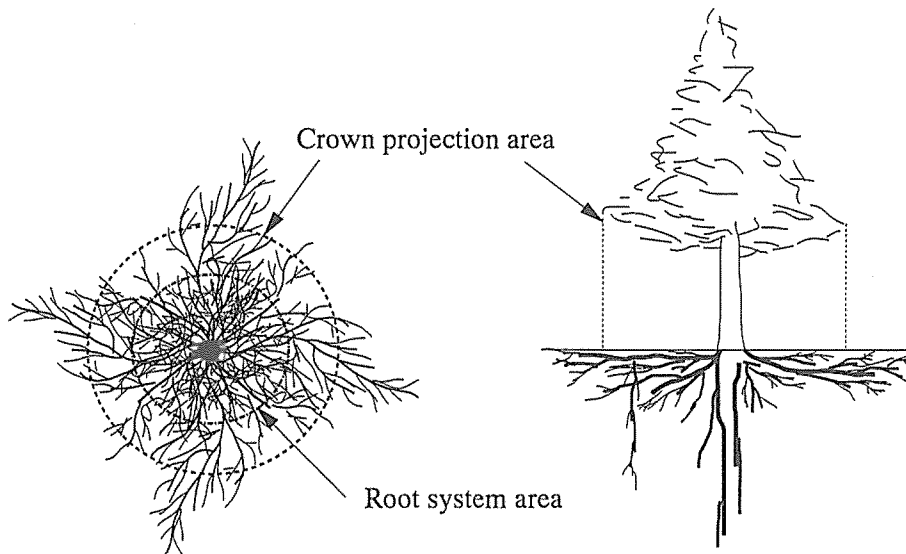


Fig. 2. The concept of root system area (RSA).

V. Discussion

Fruitbodies were produced by nineteen species of the ectomycorrhizal fungi, three of which *Tricholoma sapanaceum*, *T. portentosum* and *R. rubescens* were suspected of forming the mycorrhiza with *A. firma* (IMAZEKI and HONGO, 1987, 1989). The total number of fruitbodies produced by three species in the plots were no more than 3% of the whole fruitbody production, although *A. firma* was about five times the number of *C. laxiflora* and *Q. serrata* trees. The variation in fungal species composition might be affected by the succession of ectomycorrhizal fungi associated with the age of stands (DEACON and FLEMING, 1992).

The number of species of ectomycorrhizal fungi and the number of their fruitbodies recorded in the present study differed greatly from those of another plantation of *A. firma* (NARA *et al.*, 1992). In their study, six species were observed during a 6 month observation period, and *Lactarius laeticolorus*, which rarely emerged in the present study site, was the most abundant. The difference in the number of fruitbodies could have been due to the difference in environmental conditions such as topography, water and nutrient contents of the soil or by the combination of *A. firma* with other ECM plants and/or NECM plants. By contrast, the fruitbodies of *Russula* sp. 1, which are most likely to be associated with the roots of *C. laxiflora* and *Q. serrata*, were most abundant in the plots. However, the author could not clarify the relationship between the temporal pattern of fruitbody abundance and the presence of the above two ECM plants.

In the present study, fruitbodies of *Russula* sp. 1 occurred more frequently outside the RSAs of *C. laxiflora* (Fig. 1). The growth patterns of ectomycorrhizal mycelia related to the spatial patterns of fruitbody occurrence could be classified into three types (OGAWA,

1980): a fairy-ring type, where fruitbodies occur in the shape of a ring, a mycelial-strand type, where fruitbodies are distributed gregariously, and a rhizomorph type, where fruitbodies appear sporadically. On the basis of the above, the growth pattern of *Russula* sp. 1 was classified as a rhizomorph type. The present results support earlier information that most species of *Russula* are likely to form rhizomorphs (OGAWA, 1980). The relationship between the spatial pattern of fruitbodies and the RSA might be a crucial clue to clarify the nature and function of ectomycorrhizal fungi.

Considering the characteristics of a rhizomorph-type fungus such as *Russula* sp. 1, the mycelia could have extended and fruited in plots predominated by NECM plants, as well as in plots of ECM plants. However, the present results showed that few fruitbodies of ectomycorrhizal fungi were produced in each subplot where the NECM plants were dominant (Table 1). Litters of the NECM plants might suppress fruitbody production as pointed out by OKABE (1979), who has reported that *Cryptomeria japonica* could greatly influence the flora of fungi. The fruitbody production of ectomycorrhizal fungi might be affected by the alteration of nutritive conditions in the soil due to accumulation of litters and antagonistic interactions between ectomycorrhizal fungi and vesicular-arbuscular (VA) mycorrhizal fungi (*Cryptomeria japonica* and *Chamaecyparis obtusa* form VA mycorrhizas).

In the present study, the spatial distribution of ectomycorrhizal fungi in terms of their fruitbodies suggests a specific relationship between ECM plants and the fungal species. However, more field observations are needed to reveal the fungal flora and to clarify the nature, the succession and the functional role of ectomycorrhizas. This can be undertaken by studying both below the ground, mycorrhizas, and the aboveground, fruitbodies.

Acknowledgments

The author would like to thank Mr. H. YAMADA for identification of the fruitbodies and Mr. T. MIZOGUCHI, For. and Forest Prod. Res. Inst., for his invaluable suggestions. Thanks are also extended to Dr. N. HIJII, Nagoya University, for his critical review of the manuscript and to the members of the Forest Protection Laboratory and the Nagoya University Forest for their helpful assistance.

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人工林と二次林の境界部付近における外生菌根菌の子実体発生とその分布

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モミを優占種とする二次林とスギ・ヒノキの人工林との混交林内において、樹木と外生菌根菌との相互関係を明らかにするために、地上部に形成される外生菌根菌の子実体とその分布を調査した。調査地内において、モミ、アカシデ、コナラの3種が外生菌根を保持していた。調査期間中に発生した外生菌根菌の子実体は全部で19種類であった。子実体の発生本数が最も多かったのは、アカシデとコナラに外生菌根を形成していると推測されるカワリハツに類似するベニタケ属の1種であった。この子実体は調査地内に散在しており、その発生位置はアカシデの推定根系圏の外側で多く認められた。一方、モミは優占種であるが、全体としてこれに外生菌根を形成していると考えられる菌の子実体は、種数、本数ともに少なかった。また、外生菌根菌の子実体は、外生菌根非形成樹種であるスギ、ヒノキの立木密度が高いプロットではほとんど発生しなかった。以上のことから、地上部に形成される外生菌根菌の子実体発生とその分布は、菌糸体の成長様式のほか、樹種ごとの立木位置を反映したものであることが示唆された。