Mycoscience 38: 37–44, 1997

An analysis on the spatial distribution patterns of basidiocarps of Agaricales in a *Castanopsis*-dominated forest in Kyoto

Toshimitsu Fukiharu [1] and Makoto Kato [2]

[1] Natural History Museum and Institute, Chiba, Aoba-cho 955–2, Chuo-ku, Chiba-shi, Chiba 260, Japan
[2] Biological Laboratory, Yoshida College, Kyoto University, Sakyo-ku, Kyoto 606, Japan

Accepted for publication 9 January 1997

Spatial distribution patterns of basidiocarps of Agaricales were studied in a *Castanopsis*-dominated forest in Kyoto. Sixty-seven species were recorded, of which 45 species and 99% of total dry weight were ectomycorrhizal fungi belonging to Amanitaceae, Cortinariaceae, Russulaceae, Boletaceae and Strobilomycetaceae. The data were analyzed statistically by using the $\hat{m}$-m regression method. Three distribution patterns were recognized: aggregated, random and uniform. Although total basidiocarps were distributed randomly, basidiocarps of most species showed aggregated distributions, suggesting mycelium of ectomycorrhizal and saprotrophic fungi extend in a limited area in the soil. The degree of aggregation was different among species and this difference was suggested to reflect the difference of niche among the species.

Key Words——basidiocarp; *Castanopsis*-dominated forest; ectomycorrhizal fungi; mean crowding; spatial distribution pattern.

The surface layers of forest soil are inhabited by many species of fungi. Saprotrophic fungi compete and share the niche of the organic horizon, and ectomycorrhizal fungi also compete and share the niche of ectomycorrhizal plant-root surface. The strategy of dispersal and survival of each species is represented by the shape and size of its mycelial mat and colony. Study of mycelial mats and colonies by direct observation is almost impossible, however, because they are dispersed under the ground. In addition it is very difficult to identify them to the species level by the appearance of mycelia in the soil. Consequently, many researchers have tried to estimate the shape and size of underground mycelial mats and colonies from the distribution patterns of basidiocarps.

The simplest method to study the distribution patterns of basidiocarps is the visual "mapping method", that is to record the appearance of basidiocarps of each species on a map (Augstin, 1974; Ford et al., 1980; Mason et al., 1982; Fujita et al., 1983; Dahlberg and Stenlid, 1990). Another is the "grid method", which shows the frequency or quantity of occurrence observed visually on each small grid of the study area (Cotter and Bills, 1985; Murakami, 1987, 1989). In addition to visual comparison by this grid method, mathematical analysis of basidiocarp distribution enables us to discuss the results objectively. Mathematical studies of distribution patterns of basidiocarps, however, are rare (Okabe, 1981; Jansen, 1984).

In this study, spatial distribution patterns of basidiocarps of Agaricales were analyzed using the index of mean crowding and the regression method of mean crowding (Iwao, 1968; Iwao and Kuno, 1971). Then the application of the indices to the spatial distribution of basidiocarps was discussed.

Materials and Methods

Studies were carried out in a forest located on Higashiyama hills, Kyoto city, Japan (35.00′N, 135.48′E). The maximum and minimum averages of air temperature and precipitation in 1985 and 1986 at Kyoto Univ., ca. 4 km distance from this site, were 23.6°C, 7.2°C, 1,689 mm, and 22.8°C, 6.2°C, 1368 mm respectively. The forest was dominated by a fagaceous evergreen tree, *Castanopsis cuspidata* (Thunb.) Schottky (Fig. 1). Two 15 m × 15 m quadrats, C1 and C2, were placed in the study area. C1 was placed on a gentle slope facing west at an altitude of 160 m and C2 was placed on a flat at an altitude of 175 m. Ectomycorrhizal trees in these quadrats were *Castanopsis cuspidata*, *Quercus glauca* Thunb., *Pinus densiflora* Sieb. et Zucc. The quadrats were surveyed every 1 or 2 wk from 25 July to 17 December in 1985 (12 times) and 5 April to 17 December in 1986 (26 times). All mature basidiocarps of Agaricales with the diameter of cap wider than 1 cm were collected after mapping. The basidiocarp specimens were dried for 48 h at 60°C and then weighed for further analysis.

Spatial distribution of the basidiocarps of each species was analyzed by using $\hat{m}$-m regression method (Iwao, 1968; Iwao and Kuno, 1971). Mean crowding

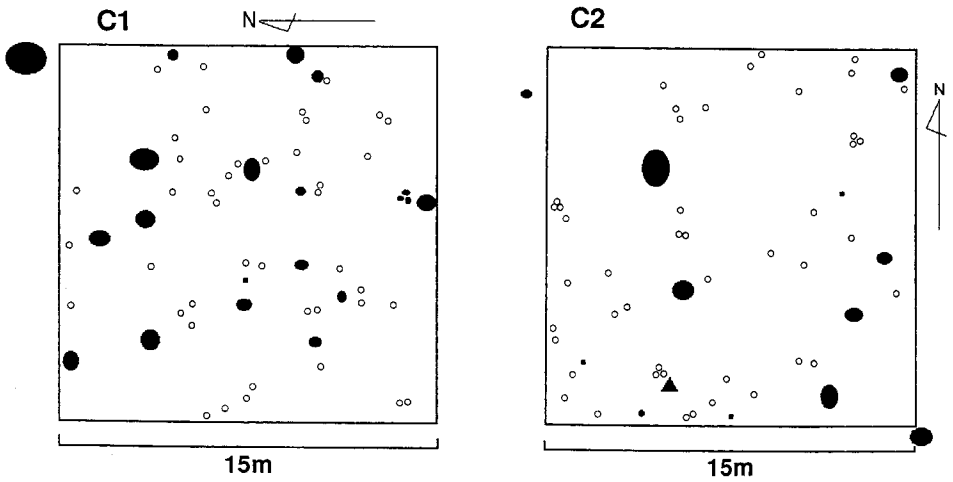

Fig. 1. Map of the study site showing distribution of trees.
●, *Castanopsis cuspidata*; ■, *Quercus glauca*; ▲, *Pinus densiflora*; ○, (C1) *Camellia japonica, Aucuba japonica, Ilex pedunculosa, Chamaecyparis obtusa, Cleyera japonica, Photinia glabra.*; ○, (C2) *Pieris japonica, Evodiopanax innovans, Rhododendron reticulatum, Myrica rubra, Acanthopanax sciadophylloides, Eurya japonica, Ilex pedunculosa, Vaccinium bracteatum*. Solid symbols (●, ■, ▲) indicate ectomycorrhizal trees (Maeda, 1954) and the symbol size shows above the extent of the major and minor axis of the trunk measured about 5 cm above the soil surface. Open circles (○) indicate endomycorrhizal trees (Maeda, 1954).

($\overset{*}{m}$), the average number of individuals per individual per quadrat is calculated as follows,

$$\overset{*}{m}_x = \frac{\sum_{i=1}^{N} X_i(X_i-1)}{\sum_{i=1}^{N} X_i}$$

where N is the total number of subquadrats, and X_i is the number of the individuals in i-th subquadrat. In this study the quadrats were divided into three size-classed units: Unit 1, Unit 4 and Unit 16 as shown in Fig. 2, and each basidiocarp was regarded as an individual.

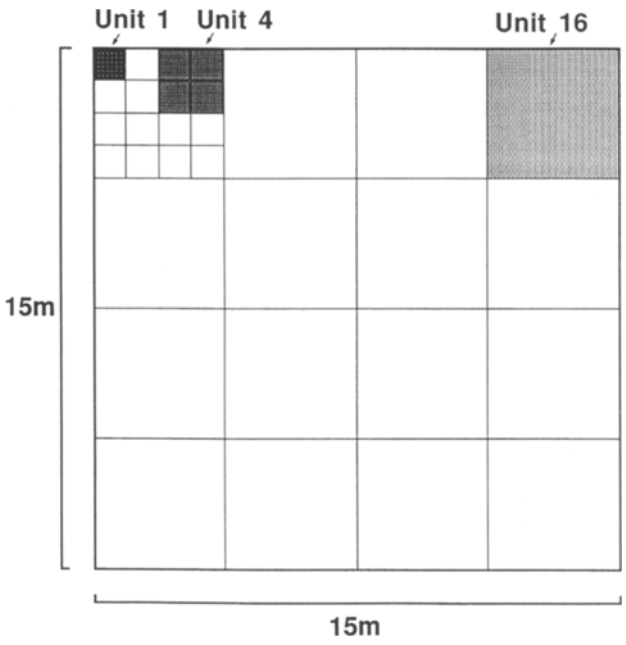

Fig. 2. Size of subplot for distribution analysis.
Quadrats were divided in three size classes: Units 16, 4 and 1.

Mean crowding is linealy related with the mean density (m) as shown by $\overset{*}{m}=B+Am$ (Iwao, 1968). In this regression, the intercept on $\overset{*}{m}$ axis B, named "index of basic contagion", indicates the basic component of distribution. In the original concept, the basic component shows whether each species is distributed as single individuals or groups of individuals. The slope A, named density-contagiousness coefficient, indicates how the basic components are distributed over space. When $A=1$, basic components are randomly distributed (the line $\overset{*}{m}=m$ is called the "random line", hereafter). When $A>1$, basic components are aggregately distributed. When $A<1$, basic components are uniformly distributed.

Results

Species names and abbreviations, numbers and dry weights of basidiocarps that appeared in quadrats C1 and C2 in 1985–86 are shown in Tables 1 and 2. Total number of basidiocarps was 2,811, and 67 species were recorded in the research area. Among them, 45 species, 93% of total number of basidiocaps (2,613 in 2,811) and 99% of the total dry weight, were ectomycorrhizal species such as Amanitaceae, Cortinariaceae, Russulaceae, Boletaceae and Strobilomycetaceae.

Three typical spatial distribution patterns were recognized in 1986 in quadrat C2 (Fig. 3). *Russula japonica* (Rus12) showed aggregated distribution, and the values of indices A and B were 7.58 and 2.36. The large value of index A indicated a highly aggregated distribution. The value of index B showed that the basic component of this species was about 3, suggesting that basidiocarps were highly aggregated in groups of three. *Cortinarius galeroides* (Cor 6) was almost randomly distributed. Indices A and B were 1.49 and 5.03, suggest-

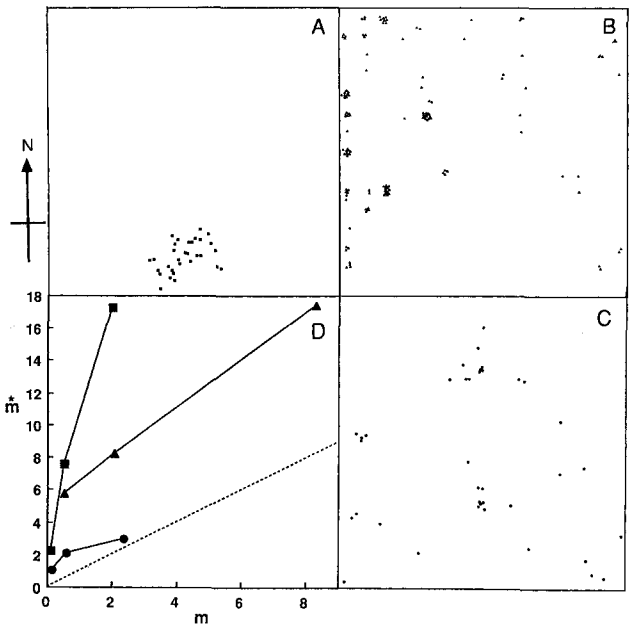

Fig. 3. Three typical spatial distribution patterns in a 15 × 15 m quadrat C2 (A–C) and their $\hat{m}$-m relations (D).
A, ■ *Russula japonica*; B, ▲ *Cortinarius galeroides*; C, ● *Russula omiensis*. The broken line in D indicates the regression for a random distribution.

ing that a group of six basidiocarps were weakly aggregated and distributed almost randomly. *Russula omiensis* (Rus16) showed moderately uniform distribution. Indices A and B were 0.77 and 1.20, suggesting that the basic component was about 2, and the moderately uniform distribution was indicated by the slope $A<1$.

Parameters A and B of $\hat{m}$-m regressions for each species in C1 and C2 in 1985 and 1986 are shown in Tables 1 and 2. Correlations between the parameters A and B of each species are shown in Fig. 4. Most species are situated to the right side of the $A=1$ line, which indicates that most species are distributed aggregately. But some genera and families showed characteristic distribution patterns, e.g., the genus *Russula* (Rus7–16) had wide range of A values, from highly aggregated species (Rus12) to weakly aggregated species (Rus14) and also moderately uniformly distributed species (Rus16). Distribution patterns of total basidiocarps appearing in quadrat C1 and C2 in 1986 (Figs. 5, 6) were analyzed by the same method. Indices A and B were 1.02, 2.66 in C1 and 1.24, 7.77 in C2. This shows that the distribution patterns of total basidiocarps in each quadrat were almost random. This indicates that there was almost an even distribution of the resources saprotrophically and ectomycorrhizally in the study sites. Concerning the ectomycorrhizal species, negative correlation was observed between the logarithmic value of dried basidiocarp weight and index B ($P<0.05$) (Fig. 7), but not between index A ($P<0.05$).

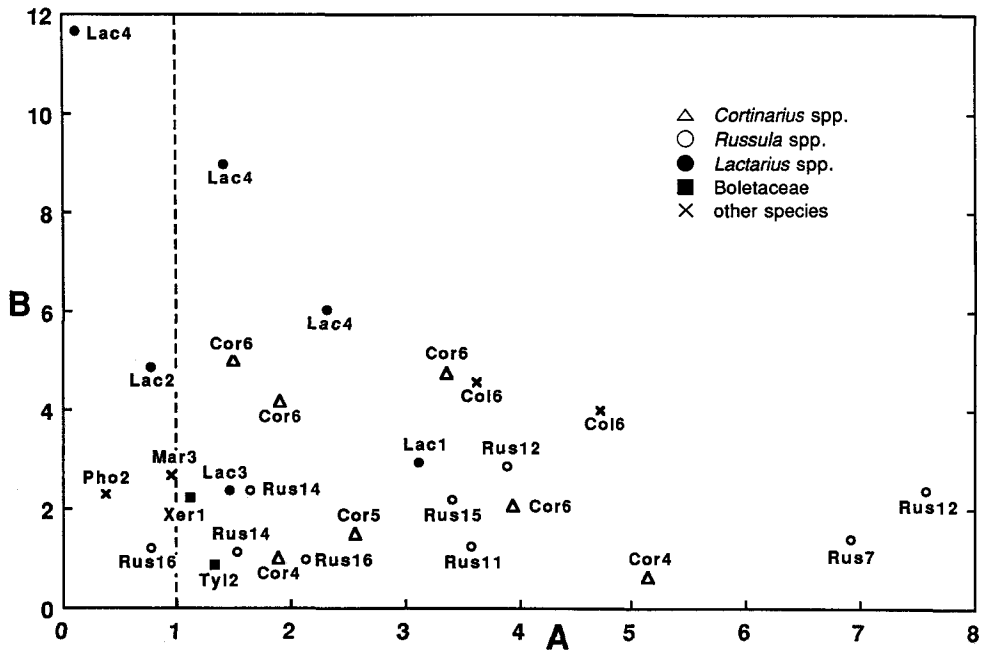

Fig. 4. Relationship between density-contagiousness coefficient (A) and index of basic contagion (B) in $\hat{m}$-m regression in quadrats C1 and C2 in 1985-86.
The broken line ($A=1$) indicates the regression for the random distribution, the right side of the line ($A>1$) shows the aggregated distribution and left side of the line ($A<1$) shows the tendency to uniform distribution. Only species with >10 basidiocarps were shown. Symbols X and others denote saprotrophic and ectomycorrhizal fungi, respectively. Abbreviations of species names are shown in Tables 1, 2.

Table 1. Total number and dry weights (g) of fungal basidiocarps in quadrat C1 in 1985–86.

Family and species	Species code	Nutrition	1985				1986			
			Number of basidiocarps	Total dry wt. of basidiocarps	$\overset{*}{m}$-m analysis		Number of basidiocarps	Total dry wt. of basidiocarps	$\overset{*}{m}$-m analysis[a]	
					A	B			A	B
Tricholomataceae										
Tricholoma sp.	Tri1	S[b]	1	0.200			0	0.000		
Collybia sp. 1	Col1	S	4	0.500			0	0.000		
Collybia sp. 2	Col2	S	0	0.000			1	0.045		
Oudemansiella pudens	Oud1	S	0	0.000			1	0.150		
Marasmius sp. 1	Mar1	S	0	0.000			5	0.035	0.00	4.00
Marasmius sp. 2	Mar2	S	1	0.005			0	0.000		
Marasmius sp. 3	Mar3	S	92	0.153	0.96	2.69	0	0.000		
Mycena haematopoda	Myc4	S	10	0.130			0	0.000		
Amanitaceae										
Amanita spreta	Ama3	M[c]	1	0.300			0	0.000		
Amanita fuliginea	Ama4	M	0	0.000			1	0.450		
Amanita pseudoporphiria	Ama5	M	1	0.500			3	1.950	0.00	0.67
Amanita citrina var. *grisea*	Ama8	M	0	0.000			1	0.277		
Agaricaceae										
Lepiota sp.	Lep1	S	0	0.000			2	0.004		
Strophariaceae										
Naematoloma sp.	Nae1	S	2	0.200			0	0.000		
Pholiota sp. 1	Pho1	S	1	0.100			0	0.000		
Cortinariaceae										
Inocybe lutea	Ino1	M	0	0.000			1	0.305		
Cortinarius sp. 1	Cor1	M	0	0.000			2	0.060		
Cortinarius sp. 2	Cor2	M	0	0.000			3	0.345	8.13	0.44
Cortinarius sp. 3	Cor3	M	0	0.000			3	0.046	0.00	2.00
Cortinarius subalboviolaceus	Cor4	M	0	0.000			22	5.500	1.89	1.02
Cortinarius anomalus	Cor5	M	3	0.500			5	0.850	0.00	0.40
Cortinarius galeroides	Cor6	M	16	0.220	3.95	2.06	30	0.360	3.36	4.75
Rhodophyllaceae										
Rhodophyllus sp. 1	Rho1	S	0	0.000			1	0.010		
Rhodophyllus sp. 2	Rho2	S	0	0.000			1	0.200		
Russulaceae										
Russula sp. 1	Rus1	M	0	0.000			5	3.862	0.00	0.80
Russula sp. 2	Rus2	M	1	0.400			1	1.040		
Russula sp. 3	Rus3	M	2	4.000			0	0.000		
Russula sp. 4	Rus4	M	0	0.000			3	1.790	0.00	0.00
Russula sp. 5	Rus5	M	1	0.600			0	0.000		
Russula sp. 6	Rus6	M	3	1.100			0	0.000		
Russula sp. 7	Rus7	M	0	0.000			13	5.900	6.92	1.38
Russula sp. 8	Rus8	M	0	0.000			2	0.450		
Russula sp. 9	Rus9	M	0	0.000			1	0.110		
Russula sp. 10	Rus10	M	0	0.000			2	0.002		
Russula densifolia	Rus13	M	0	0.000			1	2.780		
Russula castanopsidis	Rus14	M	34	17.200	1.52	1.12	116	73.080	1.64	2.38
Russula omiensis	Rus16	M	0	0.000			19	7.410	2.14	0.98
Russula kansaiensis	Rus17	M	0	0.000			2	0.170		
Lactarius sp. 2	Lac2	M	0	0.000			63	0.398	0.78	4.86
Lactarius gracilis	Lac3	M	7	0.500			82	4.697	1.47	2.36
Lactarius camphoratus	Lac4	M	0	0.000			60	4.620	2.32	6.02
Boletaceae										
Xerocomus sp.	Xer1	M	266	196.800	1.11	2.22	3	2.220	0.00	−0.11
Aureoboletus thibetanus	Aur1	M	2	2.200			1	1.190		
Boletus sp.	Bol1	M	0	0.000			1	0.220		
Tylopilus ruglosoreticulatus	Tyl3	M	2	0.200			0	0.000		
Tylopilus sp. 1	Tyl1	M	0	0.000			1	0.300		
Tylopilus sp. 2	Tyl2	M	0	0.000			82	40.020	1.33	0.86
Strobilomycetaceae										
Boletellus emodensis	Bol1	M	0	0.000			1	0.830		

a) Blank: the values could not be calculated, b) Saprotrophic, c) Ectomycorrhizal.

Discussion

By a mapping method, Ogawa (1977) and Endo (1972) showed that many agaric species in the forest are distributed in aggregations. This means that many agaric species occupy limited areas in the forest. A mathematical analysis in this study also showed that most agaric species are distributed in aggregations. But the degree of aggregation, shown by index A, was different among the species and among the genera.

As shown in the results, it is suggested that the distribution of resources in the study sites was relatively even (Figs. 5, 6). But given this uniform distribution of resources, what was the main cause of the difference in the degree of aggregation as indicated by A? For example, *Russula* spp. showed wide range of values of index A from 0.77 to 7.58. And the identified *Russula* species that appeared in theses study sites may be divided into three groups according to index A. The first group has large A values and is represented by *Russula japonica*

Table 2. Total number and dry weights (g) of fungal basidiocarps in quadrat C2 in 1985–86.

Family and species	Species code	Nutrition	1985				1986			
			Number of basidiocarps	Total dry wt. of basidiocarps	$\overset{*}{m}$-m analysis A	$\overset{*}{m}$-m analysis B	Number of basidiocarps	Total dry wt. of Basidiocarps	$\overset{*}{m}$-m analysis[a] A	$\overset{*}{m}$-m analysis[a] B
Tricholomataceae										
Collybia sp. 3	Col3	S[b]	12	1.066	0.00	1.56	0	0.000		
Collybia sp. 4	Col4	S	0	0.000			3	0.238	0.00	2.00
Collybia sp. 5	Col5	S	0	0.000			1	0.038		
Collybia sp. 6	Col6	S	25	0.855	4.72	4.01	11	0.477	3.63	4.55
Mycena sp. 1	Myc1	S	1	0.012			0	0.000		
Mycena sp. 2	Myc2	S	0	0.000			1	0.004		
Mycena galericulata	Myc3	S	0	0.000			5	1.178	0.00	0.00
Amanitaceae										
Amanita sp. 1	Ama1	M[c]	1	0.030			0	0.000		
Amanita sp. 2	Ama2	M	0	0.000			3	7.500	0.00	2.00
Amanita fuliginea	Ama4	M	5	3.315	7.62	1.33	0	0.000		
Amanita pseudoporphiria	Ama5	M	4	2.600	0.00	1.50	0	0.000		
Amanita citrina var. *citrina*	Ama6	M	9	3.330	4.06	1.81	0	0.000		
Amanita citrina var. *alba*	Ama7	M	0	0.000			3	1.110	2.71	0.22
Amanita volvata	Ama9	M	6	16.906	1.35	0.89	2	5.636		
Strophariaceae										
Pholiota sp. 2	Pho2	S	14	1.096	0.37	2.29	0	0.000		
Cortinariaceae										
Inocybe lutea	Ino1	M	0	0.000			3	0.915	5.42	1.11
Cortinarius subalboviolaceus	Cor4	M	0	0.000			11	2.750	5.14	0.64
Cortinarius anomalus	Cor5	M	21	1.289	2.57	1.52	0	0.000		
Cortinarius galeroides	Cor6	M	220	3.080	1.91	4.18	123	1.722	1.49	5.03
Gymnopilus sp.	Gym1	S	3	0.224	0.00	0.00	0	0.000		
Russulaceae										
Russula sp. 4	Rus4	M	0	0.000			1	0.906		
Russula sp. 11	Rus11	M	3	1.663	4.06	−0.11	16	6.731	3.58	1.24
Russula japonica	Rus12	M	32	100.470	3.89	2.86	31	97.340	7.58	2.36
Russula castanopsidis	Rus14	M	2	1.300			9	5.850	1.81	0.74
Russula lilacea	Rus15	M	14	6.661	3.42	2.17	0	0.000		
Russula omiensis	Rus16	M	0	0.000			38	4.750	0.77	1.20
Lactarius sp. 1	Lac1	M	11	2.368	3.12	2.94	0	0.000		
Lactarius sp. 2	Lac2	M	3	0.057	5.42	1.11	4	0.019	0.00	0.00
Lactarius gracilis	Lac3	M	0	0.000			2	0.093		
Lactarius camphoratus	Lac4	M	17	1.110	0.11	11.65	1149	74.685	1.41	8.99
Boletaceae										
Xerocomus nigromaculatus	Xer2	M	1	0.773			0	0.000		

a) Blank: the values could not be calculated, b) Saprotrophic, c) Ectomycorrhizal.

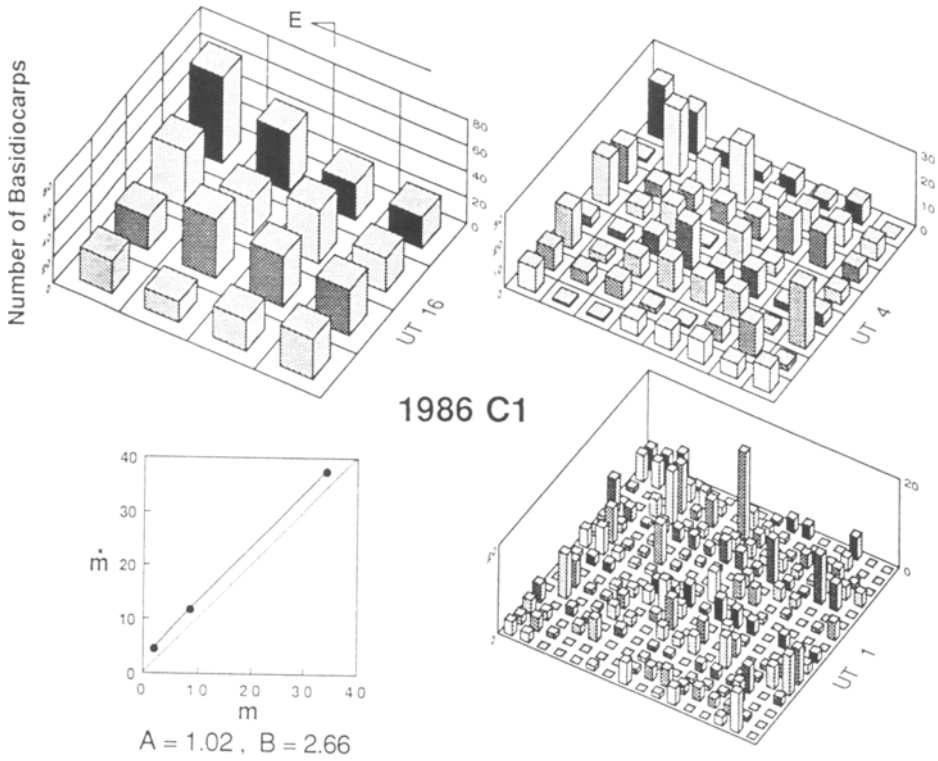

Fig. 5. Distribution pattern of basidiocarps which appeared in a quadrat C1 in 1986.
Histograms show total numbers of basidiocarps in subquadrats. The lower left graph shows $\hat{m}$-m relations of total number of basidiocarps. The broken line indicates the regression for a random distribution.

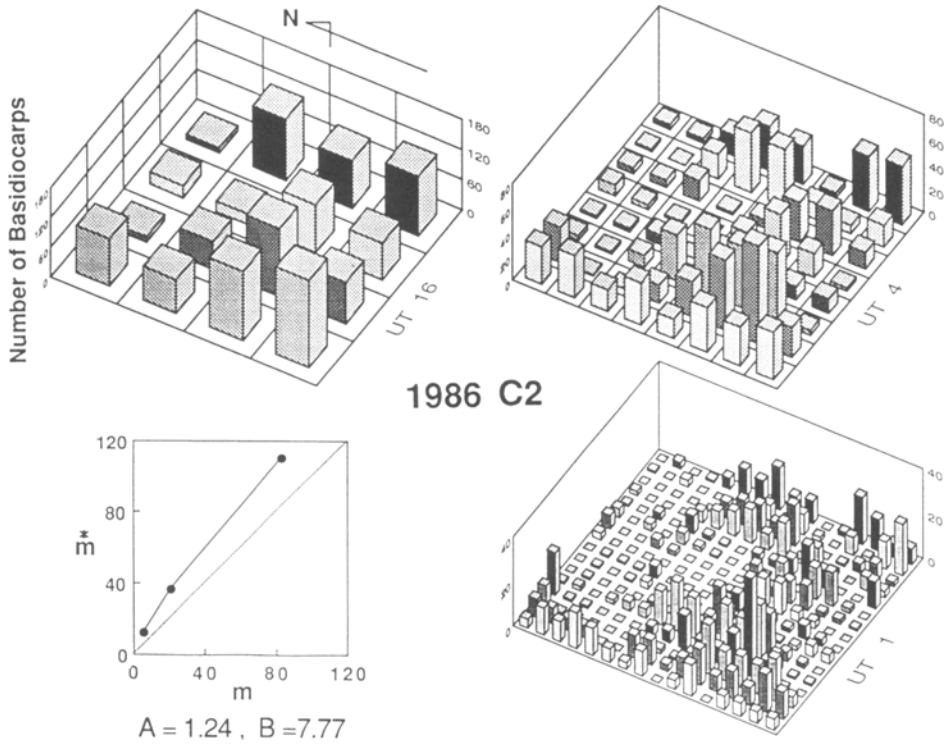

Fig. 6. Distribution pattern of basidiocarps which appeared in a quadrat C2 in 1986.
Histograms show total numbers of basidiocarps in subquadrats. The lower left graph shows $\hat{m}$-m relations of total number of basidiocarps. The broken line indicates the regression for a random distribution.

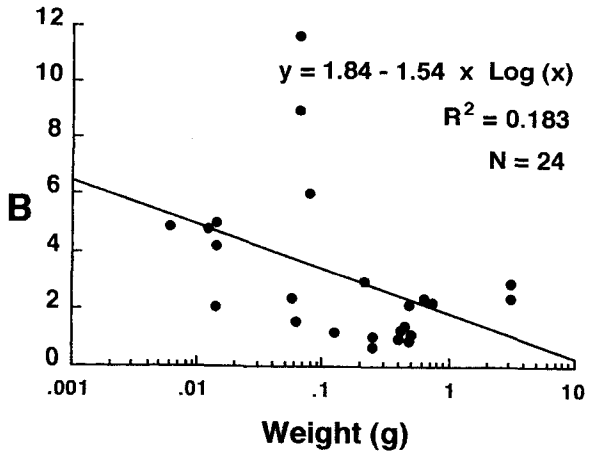

Fig. 7. Negative correlation between the index of basic contagion (B) and logarithmic dry weight of basidiocarp of ectomycorrhizal fungal species ($P<0.05$).

(Rus12, A=3.89, 7.58); the second has medium A values and is composed of *R. castanopsidis* (Rus14, A=1.52, 1.81) and *R. lilacea* (Rus15, A=3.42); and the last group has small A values and is represented by *R. omiensis* (A=0.77, 2.14). The field observations showed that the basidiocarps of the large A group species, *R. japonica*, originated from the mineral soil and the basidiocarps of the middle A group species, *R. castanopsidis* and *R. lilacea*, grew from the organic horizon. Thus, the basidiocarps of two groups originated from different soil layers. This suggests that these two different *Russula* groups extend their mycelia in and inhabit quite different soil layers.

The field observations also showed that most of the agaric species appeared at the end of July, but *R. omiensis*, a small A group species, appeared in April and November, when there were few other agaric species in the field. In this case, the difference in index A degree might be attributed to the difference of fruiting season of basidiocarps. Thus, the difference in the size of index A between these three *Russula* groups was suggested to originate from the difference of their spatial and seasonal niches. Differences in the size of index A in other species, genera and families might be attributable to the same reason.

The parameter of mean crowding ($\overset{*}{m}$) (Lloyd, 1967), used in this study, was originally developed to indicate the possible effect of mutual interference or competition among individuals. This parameter can be applied properly only to freely moving animals that live in a continuous, apparently uniform habitat. However, Iwao (1968) and Iwao and Kuno (1971) pointed out that the concept of mean crowding and the regression method of mean crowding can generally be applied to any kind of animal or plant including sessile, terrestrial or gregarious organisms and to any size of quadrat. However, it is true that the mean crowding is a parameter describing only the spatial relationship of each individual among individuals. In this study, individuals were basidiocarps and these indices show only how many other basidiocarps are situated near each basidiocarp, not the directions of neighboring basidiocarps. Consequently, these indices do not describe the shape of the fungal colony.

Quadrat size for study is another important point when we apply this method to fungal colonies. Quadrat size should be large enough to cover a fungal colony, and subquadrat size small enough to detect a fungal colony. The shape and size of mycorrhizal fungal colony are variable. For example, a colony of *Tricholoma matsutake* was round one about 5 m in diam (Ogawa, 1975), one of *Tricholoma bakamatsutake* was a semicircle of about 2 m in diam (Ogawa and Ohara, 1978; Terashima and Mizoguchi, 1995), and those of *Tricholoma fulvocastaneum* and *Lyophyllum semitale* were linear colonies of about 8 m in length (Murata, 1971). A colony of *Lyophyllum shimeji* was semicircular, about 14 m in diam (Fujita et al., 1982), while *Russula densifolia*, *Lactarius volemus* and *Boletus griseus* made round colonies of about 4, 0.3 and 4.5 m in diam, respectively (Endo, 1972). Therefore, the size of the subquadrat should meet the requirement of allowing analysis of fungal colonies of variable size (1–10–? m) and form (round, straight or irregular). Consequently, the size of the minimum subquadrat should be selected for detecting the smallest colony size. Jansen (1984) analyzed the distribution patterns of the basidiocarps using 17 quadrats (20–30 m × 35–50 m), and the minimum subquadrat size was 5 m square. She analyzed 680 colony examples (140 species) and recognized 537 random distributions (109 species), and 143 clustered distributions (35 species). In her study, significant uniform patterns were not found at all and significant clustering did not occur often. In this study, however, most species were distributed aggregated (clustered) and a few species distributed randomly or uniformly. This difference might have resulted from the minimum subquadrat size adopted. Jansen's minimum size was 5 m square, but the minimum size in this study was 0.96 m square. Her minimum size may be rather large to detect smaller size colonies. Maximum size is also important. In this study the maximum quadrat size was 15 m square, which may not be enough if there are colonies larger than this size in the study area.

Spatial distribution of the basidiocarps has long attracted mycologist's concern, and we have used the words such as sporadic, solitary, scattered and gregarious to describe the habit of basidiocarp distribution in each species. If indices A increase, as in the case of *R. japonica* (Rus12), we call this distribution gregarious, and also if index B increases, as in the case of *L. camphoratus* (Lac4), we call this distribution gregarious but not sporadic or solitary. And if indices A or B take a small value, as in *R. castanopsidis* (Rus16), we call this distribution scattered. The traditional words for describing basidiocarps distribution patterns may thus have some correlation with these indices and also with each species niche. But we should not forget that these indices are also affected by the dry weight of basidiocarps of each species, as in the case of index B in this study.

Acknowledgements——The authors thank to Prof. Akira Suzuki, Chiba University for critical reading of the manuscript and making helpful suggestions, and Dr. Tsuguo Hongo for identifying most of the specimens. We thank the College of Agriculture of Kyoto University for allowing us to cite the meteorological data.

Literature cited

Augstin A., von 1974. Über die Verteilung einiger Täublingsarten auf kleinstem Raum. Zeitschr. Pilzkunde **40**: 215–220.

Cotter, V. T. and Bills, G. F. 1985. Comparison of spatial patterns of sexual and vegetative states of *Boletinus merulioides*. Trans. Br. Mycol. Soc. **85**: 520–524.

Dahlberg, A. and Stenlid, J. 1990. Population structure and dynamics in *Suillus bovinus* as indicated by spatial distribution of fungal clones. New Phytol. **115**: 487–493.

Endo, M. 1972. Plant sociological observation on the terrestrial larger fungi in an evergreen broad-leaved forest. Jpn J. Ecol. **22**: 51–61.

Ford, E. D., Mason, P. A. and Pelham, J. 1980. Spatial patterns of sporophore distribution around a young birch tree in three successive years. Trans. Br. Mycol. Soc. **75**: 287–296.

Fujita, H., Ito, T., Kobayashi, F. and Ogawa, M. 1982. Ecological studies of *Lyophyllum shimeji* in *Pinus densiflora* forest. Trans. Mycol. Soc. Japan **23**: 391–403.

Fujita, H., Kobayashi, F. and Takeoka, M. 1983. Investigations (1976–1977) on the occurring and the environmental factor of MATSUTAKE (*Tricholoma matsutake* Singer) —Larger fungi occurring in the natural stand of *Pinus densiflora* Sieb. et Zucc. at Tanba, Kyoto—. Bull. Kyoto Pref. Univ. Forests **27**: 25–37.

Iwao, S. 1968. A new regression method for analyzing the aggregation pattern in animal population. Res. Popul. Ecol. **10**: 1–20.

Iwao, S. and Kuno, E. 1971. An approach to the analysis of aggregation pattern in biological populations. In: Statistical ecology, vol. 1. Spatial patterns and statistical distributions, (ed. by Patil G. P., Pielou, E. C. and Waters, W. E.), pp. 461–513. Penn. State Univ. Press University Park, Penn.

Jansen, A. E. 1984. Vegetation and macrofungi of acid oak woods in the north-east of the Netherlands. Agric. Res. Rep. **923**: 1–162.

Lloyd, M. 1967. Mean crowding. J. Anim. Ecol. **36**: 1–30.

Maeda, M. 1954. The meaning of mycorrhiza in regard to systematic botany. Kumamoto J. Sci. Ser. B. **3**: 57–84.

Mason, P. A., Last, F. T., Pelham, J. and Ingleby, K. 1982. Ecology of some fungi associated with an aging stand of birches (*Betula pendula* and *B. pubescens*). For. Ecol. Manage. **4**: 19–39.

Murakami, Y. 1987. Spatial distribution of *Russula* species in *Castanopsis cuspidata* forest. Trans. Br. Mycol. Soc. **89**: 187–193.

Murakami, Y. 1989. Spatial changes of species composition and seasonal fruiting of the Agaricales in *Castanopsis cuspidata* forest. Trans. Mycol. Soc. Japan **30**: 89–103.

Murata, Y. 1971. Ecological studies on the larger fungi occurring around the shiro of *Tricholoma fulvocastaneum* Hongo in oak wood. Trans. Mycol. Soc. Japan **12**: 117–125.

Okabe, H. 1981. Studies on the myco-sociological methods (II). Distribution pattern of autochthonous and zymogenous saprobic fungi. Bull. Kyoto Univ. Forests **53**: 8–23.

Ogawa, M. 1975. Microbial ecology of mycorrhizal fungus, *Tricholoma matsutake* (Ito et Imai) Sing. in pine forest I. Fungal colony ('Shiro') of *Tricholoma matsutake*. Bull. Gov. For. Exp. Sta. **272**: 79–121.

Ogawa, M. 1977. Ecology of higher fungi in *Tsuga diversifolia* and *Betula ermani-Abies mariesii* forest of subalpine zone. Trans. Mycol. Soc. Japan **18**: 1–19.

Ogawa, M. and Ohara, H. 1978. Microbial ecology of "Shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species VIII. *Tricholoma bakamatsutake* Hongo in *Quercus mongolica* var. *grosseserrata* forest and *Q. serrata* forest. Trans. Mycol. Soc. Japan **19**: 391–405.

Terashima, Y. and Mizoguchi, T. 1995. Nutritional environment of soil and roots in and around mycelial blocks of an ectomycorrhizal fungus *Tricholoma bakamatsutake* in an evergreen Fagaceae forest. Mycoscience **36**: 167–172.