Analysis of mushroom diversity in successional young forests and equilibrium evergreen broad-leaved forests

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Eight examination stations were constructed in young red pine forests and mature evergreen broad-leaved woods. A total of 32 quadrats of 10 × 10 m each were examined for vegetation and mushroom distribution and diversity once a week for one year. A total of 9707 individual mushrooms, amounting to 1470.23 g in dry weight, were analyzed for fungal communities. The results were arranged in a sequence of succession. The mushroom diversities, expressed as Shannon's $\bar{H}$, increased constantly to the equilibrium at around 3.0 in the climax forests. The distribution of the proportion of saprophytic fungi depicted a similar curve and reached equilibrium at around 0.3. The seasonal segregation in mushroom fruiting also developed and reached equilibrium. Ecological distances between the forests were estimated from the mushroom results and were compared with those estimated from the woody plant diversities. Fungal succession took place more rapidly or was more exaggerated than that of woody plants. From these results, the fungal succession and diversity in the climax forest was discussed.

Key Words——ecological distance; habitat segregation; mushroom diversity; succession.

Introduction

Fungi, as one of the main decomposers, play an important role in the material cycle of forest ecosystems. They usually reside underground or under tree barks, and therefore their recognition or identification is possible only in terms of the fruiting mushroom. Fungi are heterotrophic, and their energy is supplied from various parts of forest plants, animals, and even other fungi. The biomass of fungi is linearly proportional to that of woody plants. Thus, standing crops and diversity of woody plants and forest succession have a strong effect on fungal flora and its quantity through development of a variety of niches (e.g. Rayner and Boddy, 1988).

In the lowlands of western Japan, present-day forests are composed mainly of red pine (*Pinus densiflora* Sieb. et Zucc.) and deciduous oak (*Quercus serrata* Thunb. ex Murray). Most of them contain substitutional vegetation due to human activities. However, the potential vegetation is evergreen broad-leaved dominated by evergreen oaks (*Castanopsis sieboldii* [Makino] Hat. ex Yamaz. et Mashi. or *C. cuspidata* [Thunb. ex Murray] Schotty) (Miyawaki et al., 1978; Nakanishi et al., 1983). The substitutional red pines and others are expected to be gradually replaced by members of the climax vegetation. Fungal flora follows this plant succession and manifests its own successional patterns.

A local vegetation (V) is usually determined by a formula such as V=f (cl, p, r, o, t), in which cl, p, r, o, and t mean climate factor, characteristics of soil, geographical factor, biotic factor, and successional age, respectively (Major, 1951). An experiment was designed to trace fungal succession *inter se* by exclusion of the former three factors. Thirty-two observation sites were chosen within a circle of 3 km in diameter. Mushroom variability was analyzed in terms of dry weight. Successional changes were described in terms of development of habitat segregation and seasonal fruiting segregation. The fungal community in the ecological equilibrium state is discussed.

Materials and Methods

Study sites Eight examination stations were chosen in Yashiro Town, Kato-gun, Hyogo Prefecture, and designated as ST1 to ST8. They are all located within a circle of 3 km in diam centered on the campus of Hyogo University of Teacher Education. All are located at an elevation of around 90 m above sea level, and none are on an extreme slope. ST7 and ST8 are in the woods attached to shrines established more than 280 years age. Each station is composed of four adjacent quadrats each measuring 10 × 10 m. They are named ST1NE to ST8SW, where N, E, S, and W represent the cardinal directions. A total of 32 quadrats was thus established. The average annual precipitation is 1385 mm, and the average temperature is 15.6°C (Kobe Marine Meteorological Observatory). Kira's warmth index is 127.
Examination of forest stands All the forest trees with height of more than 0.5 meters were scored after iden-

tification in 1990. The mean height and diameter at breast height (DBH) of canopy trees were also measured directly or by the trigonometric method. The vegetation was examined by the Braun-Blanquet method (Nakanishi et al., 1983). Absorption of sunlight was measured with a lux meter (ANA500S, Tokyo Photo Electric Co.) at four points on the soil surface for each quadrat during each of the four seasons. At the same time, the humus soil "A layer" (containing sublayers A_0, A_1, and A_2, according to Odum, 1971) was measured directly.

Examination of mushrooms All the visible mushrooms were collected in each quadrat once a week for one year from December 1989 to November 1990. After identification of species, they were kept overnight in an oven at 80°C under continuous air circulation. The dry weight was recorded for each specimen.

Analysis Diversities in woody plants and mushrooms were expressed by a quantity known as the species diversity index, $\bar{H}$ (Shannon and Weaver, 1962). $\bar{H} = -\Sigma (n_i /N)\log_e(n_i/N)$, where n_i is the individual number (or dry weight) of species i, and N is the sum of n_i. Ecological distance based on the diversities between pairs of examination stations was shown by the index of Euclid distance, ED_r (Whittaker, 1975). $ED_r = \sqrt{\Sigma(p_a-p_b)^2/2}$, where p_a and p_b are the frequencies of a certain species at stations a and b, respectively. The similarity index, SI, was defined as follows: $SI = 2C/(A+B)$, where A and B are the number of species observed at stations A and B, respectively. C is the number of species observed in common. The dissimilarity index, DI, was defined as 1-SI (Odum, 1971).

Results

1. Ecological characteristics of immature and mature forests

Stations ST1 to ST6 are distributed within a forest, called satoyama, dominated by red pines and deciduous oaks. Stations ST7 and ST8 are located in the woods of separate shrines, where the high canopy was formed by evergreen oaks, mainly *Quercus myrsinaefolia* Blume in ST7 and *Castanopsis cuspidata* in ST8. The station numbers were arranged in a sequence of successional ages. The ecological characteristics of all the stations are summarized in Table 1. In ST4, *Juniperus rigida* Sieb. et Zucc. was dominant over red pine. The vegetation is also shown in Fig. 1. All the values for the absorption of sunlight, thickness of the A layer, height of canopy trees, and diameter at breast height (DBH) of canopy trees were proportional to the successional ages there. The species diversity of woody plants ($\bar{H}$) also increased lineally with age. However, the maximum value of 2.69 was observed at ST6. The ages were estimated by the numbers of stairs of verticillated branches of red pines (Uehara, 1961). Those of ST7 and ST8 were from the historical records of the shrines. The character leaf type is defined as the proportion of evergreen broad-leaved species among the total number of species. This quantity increased toward the equilibrium value of around 0.9. The ecological distances between the examination stations are shown in Table 2 in terms of the Euclid distance (ED_r) and the dissimilarity index (DI). The average substitution rate was 0.0025 per year for ED_r, and 0.004 for DI.

Table 1. Summary of ecological characters associated with succession.

Dominating woody plant	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7	Station 8
	Pinus densiflora	*P. densiflora*	*P. densiflora*	*Juniperus rigida*	*P. densiflora*	*P. densiflora*	*Quercus myrsinaefolia*	*Castonopsis cuspidata*
Age (year)	3.9*	6.4	14.6	22.3	23.7	30.5	280<	280<
Absorption of sunlight (%)	44	77	89	69	96	82	99	98
Thickness of A layer (cm)	0.0	2.5	3.2	3.3	6.3	5.7	8.0	7.5
Height of canopy trees (m)	2.67	5.42	5.65	5.58	10.15	9.63	13.19	13.41
DBH of canopy trees (cm)	2.8	6.7	8.7	10.4	13.0	14.1	28.2	28.4
Diversity in woody plant ($\bar{H}$)	1.46	1.84	2.42	2.31	2.54	2.69	2.14	2.42
Leaf type**	0.03	0.10	0.18	0.21	0.39	0.35	0.94	0.87
Mushroom diversity in number ($\bar{H}$)	1.15	2.08	0.80	1.69	2.22	2.48	2.39	3.09
Mushroom diversity in weight ($\bar{H}$)	0.36	1.51	1.71	2.04	1.82	2.53	2.92	3.31
S/T ratio*** in mushroom number	0.31	0.19	0.04	0.71	0.53	0.73	0.77	0.68
S/T ratio*** in mushroom weight	0.00	0.02	0.10	0.41	0.11	0.28	0.28	0.35
Temporal segregation in number ($\bar{H}$)	2.06	2.64	2.06	2.15	2.38	2.44	2.83	2.54
Temporal segregation in weight ($\bar{H}$)	2.01	2.36	2.32	2.15	1.93	2.16	2.54	2.58
Mushroom type (weight/no.)	0.43	1.37	1.88	0.19	0.59	0.40	0.61	0.62

* Estimated from mean age of *P. densiflora*.
** Proportion of evergreen broad-leaved trees.
*** Proportion of saprophytic fungi.

No.	Species name
1	Ilex rotunda Thunb.
2	Alnus japonica (Thunb.) Steud.
3	Rosa multiflora Thunb.
4	Pinus thunbergii Parlatore
5	Robinia pseudoacacia L.
6	Ilex macropoda Miq.
7	Clethra barvinervis Sieb. et Zucc.
8	Lespedeza bicolor Turcz.
9	Vaccinium hirtum Thunb. var. pubescens (Koidz.) Yamazaki
10	Sorbus japonica (Decne.) Hedlund
11	Viburnum dilatatum Thunb.
12	Millettia japonica (Sieb. et Zucc.) A. Gray
13	Prunus jamasakura Sieb. ex Koidz.
14	Quercus serrata Thunb. ex Murray
15	Quercus variabilis Blume
16	Castanea crenata Sieb. et Zucc.
17	Pourthiaea villosa (Thunb.) Decne. var. laevis (Thunb.) Stapf.
18	Diplomorpha sikokiana (Franch. et Savat.) Honda
19	Vaccinium smallii A. Gray var. glabrum Koidz.
20	Rhododendron macrosepalum Maxim.
21	Rhamnus crenata Sieb. et Zucc.
22	Lyonia ovalifolia (Wall.) Drude var. elliptica (Sieb. et Zucc.) Hand. - Mazz
23	Pinus densiflora Sieb. et Zucc.
24	Rhododendron obtusum (Lindl.) Planchon var. Kaempferi (P.) W.
25	Vaccinium oldhammii Miq.
26	Juniperus rigida Sieb. et Zucc.
27	Rhododendron reticulatum D. Don
28	Eurya japonica Thunb.
29	Pieris japonica (Thunb.) D. Don
30	Smilax china L.
31	Ilex pedunculosa Miq.
32	Trachelospermum asiaticum (Sieb. et Zucc.) Nakai
33	Rhus trichocarpa Miq.
34	Cleyera japonica Thunb.
35	Vaccinium bracteatum Thunb.
36	Ilex crenata Thunb.
37	Photinia glabra (Thunb.) Maxim.
38	Viburnum wrightii Miq.
39	Sorbus alnifolia (Sieb. & Zucc.) C. Koch
40	Quercus glauca Thunb. ex Murray
41	Evodiopanax innovans (Sieb. et Zucc.) Nakai
42	Acanthopanax sciadophylloides Franch. et Savat.
43	Symplocos coreana (Lev.) Ohwi
44	Chamaecyparis obtusa (Sieb. et Zucc.) Endl.
45	Wisteria floribunda (Willd.) DC.
46	Viburnum erosum Thunb. var. punctatum Franch. et Savat.
47	Abelia serrata Sieb. et Zucc.
48	Illicium anisatum L.
49	Quercus myrsinaefolia Blume
50	Carpinus laxiflora (Sieb. et Zucc.) Bl.
51	Quercus sessilifolia Blume
52	Osmanthus heterophyllus (G. Don) P. S. Green
53	Abies firma Sieb. et Zucc
54	Camellia sinensis (L.) O. Kuntze
55	Ilex chinensis Sims
56	Camellia japonica L.
57	Ternstroemia gymnanthera (Wright et Arn.) Beddome
58	Ardisia crenata Sims
59	Cinnamomum japonicum Sieb. ex Nakai
60	Podocarpus macrophyllus (Thunb.) D. Don
61	Ligustrum japonicum Thunb.
62	Symplocos prunifolia Sieb. et Zucc.
63	Callicarpa mollis Sieb. et Zucc.
64	Cinnamomum camphora (L.) Presl
65	Cryptomeria japonica (L. fil.) D. Don
66	Castanopsis cuspidata (Thunb. ex Murray) Schottky

Fig. 1. Floral distribution in 32 quadrats, each measuring 10×10 m. The vegetation patterns were grouped by dashed lines into the eight examination stations, which are arranged in order of successional age. The figures indicate the individual numbers. The vertical line covers species observed commonly in all the stations.

No.	Function	Species name	1	2	3	4	5	6	7	8	9	10	11	12
1	M	Hygrophorus hypothejus (Fr. : Fr.) Fr.	0.32											
2	S	Collybia sp. 1	0.03	0.04										
3	M	Hygrophorus sp. 1	0.05	0.06										
4	M	Pisolithus tinctorius (Pers.) Coker et Couch	24.68											
5		Clitocybe sp. 1	0.24	0.78										
6	S	Omphalina sp. 1	0.10											
7	M	Cortinarius sp. 1	0.31	0.49										
8	S	Psathyrella sp. 1	0.09	0.14										
9		Rhodophyllus sericellus (Bull. : Fr.) Quel. sp. 1	0.01											
10			0.05											
11	S	Geronema fibula (Bull. : Fr.) Sing.	0.09	0.02	0.01	0.04								
12	M	Tricholoma ustale (Fr. : Fr.) Kummer	1.43	1.67	7.27	9.50	6.21							
13	M	Dermocybe sp. 1	0.22	0.52										
14		Rhodophyllus sp. 1	0.19											
15	M	Tricholoma japonicum Kawamura	7.03											
16	M	Hygrophorus pudorinus (Fr.) Fr.	0.88											
17	M	Rhizopogon nigrescens Coker & Couch	1.41											
18	M	Suillus granulatus (L. : Fr.) O. Kuntze	0.28											
19	M	Cortinarius sp. 2	2.20											
20	S	Agaricus arvensis Schaeff. : Fr.	6.31											
21	S	Ischnoderma sp. 1	3.02											
22	M	Cortinarius shigaensis Hongo	11.67											
23	M	Gomphidius roseus (Fr.) Karst.	0.49											
24	M	Suillus luteus (L. : Fr.) S. F. Gray	1.09	9.04	48.59	19.57	1.68	0.31	1.01					
25	M	Suillus bovinus (L. : Fr.) O. Kuntze	2.31	0.11	1.20	2.48	3.29	0.21	0.52	7.94	1.28			
26	M	Chroogomphus rutilus (Schaeff. : Fr.) O. K. Miller	0.11	0.18	0.81									
27	M	Hydnellum concrescens (Pers. ex Schw.) Banker	51.21	13.36	65.44	1.06	6.79	1.51						
28	M	Phellodon niger (Fr.) Karst.	0.31	0.49										
29	M	Cortinarius sp. 3	0.65	0.37	0.59									
30	M	Cortinarius sp. 4	0.15											
31	S	Stereopsis burtianum (Peck) Reid	0.08	0.09	0.01	6.12								
32	M	Cortinarius sp. 5	0.08											
33	M	Tricholomopsis rutilans (Schaeff. : Fr.) Sing.	0.32	0.32										
34	S	Mycena sp. 1	0.01											
35	M	Amanita neoovoidea Hongo	0.64											
36	M	Amanita squarrosa Nagasawa & Hongo	0.61	1.32	2.26									
37	S	Marasmius sp. 1	0.08											
38		sp. 2	1.31											
39	M	Lactarius subzonarius Hongo	0.03											
40	S	Hymenochaetaceae sp. 1	2.81											
41	M	Leccinum extremiorientale (L. Vass.) Sing.	10.12											
42	M	Rozites caperata (Pers. : Fr.) Karst.	0.53											
43	M	Inocybe asterospora Quel.	0.11											
44	M	Inocybe sp. 1	0.01											
45	M	Russula rubescens Beardslee	0.31											
46		Trichoromataceae sp. 1	0.06											
47	S	Clavaria vermicularis Swartz : Fr.	0.29	1.14										
48	S	Marasmius crinisequi F. Muell.	0.02	0.01	0.02									
49	M	Laccaria tortilis (Bolt.) S. F. Gray	0.02											
50	M	Boletellus russellii (Frost) Gilb.	3.35	7.17	3.62	2.02								
51	S	Gloeophyllum saepiarium (Wulf : Fr.) Karst.	1.18											
52	S	Psilocybe sp. 1	0.04											
53	M	Rhodophyllus rhodopolius (Fr.) Quel.	2.38											
54	M	Amanita gymnopus Corner & Bas	0.52											
55	M	Inocybe sp. 2	0.12											
56	S	Collybia sp. 2	1.41											
57	S	Dermocybe sp. 2	0.18											
58	S	Marasmiellus chamaecyparidis (Hongo) Hongo	0.08											
59	M	Pycnoporus coccineus (Fr.) Bond. et Sing.	1.50											
60	S	Dermocybe clinamomea (L. : Fr.) Wunsche	0.23	6.10	6.56	2.18	0.11	1.66	0.18					
61	M	Rhodophyllus sp. 2	0.06	0.03										
62	M	Tricholoma auratum (Fr.) Gill.	6.90	1.31	5.28	0.21								
63	M	Lactarius hatsudake Tanaka	1.41	2.88	1.21	0.29	0.62	0.52						
64	M	Cantharellus luteocomus Bigelow	0.18	0.61	0.11	0.21	1.62	0.95	1.24	0.12				
65	M	Cortinarius galeroides Hongo	0.22	0.03			1.24							
66	M	Lactarius akahatsu Tanaka	0.78	1.29										

No.	M/S	Species
67	M	Hydnum repandum L. : Fr. var. album Quel.
68	M	Neolecta vitellina (Berk.) Korf et Rogers
69	S	Russula emetica (Schaeff. : Fr.) S. F. Gray
70	S	Rhodophyllus sp. 3
71	M	Lycoperdon perlatum Pers.
72	S	Collricia cinnamomea (Pers.) Murr.
73	M	Agaricus praeclaresquamosus Freeman
74	M	Lactarius gracilis Hongo
75	S	Collybia dryophila (Bull. : Fr.) Kummer
76	S	Mycena vulgaris (Pers. : Fr.) Quel.
77	M	Lactarius chrysorrheus Fr.
78	M	Laccaria laccata (Scop. : Fr.) Berk. & Br.
79	S	Rhodophyllus cyanoniger (Hongo) Hongo
80	S	Rhodophyllus staurosporus (Bres.) J. Lange
81	S	Schizophyllum commune Fr. : Fr.
82	S	Thelephora palmata Scop. : Fr.
83	M	Russula neoemetica Hongo
84	M	Amanita pantherina (DC. : Fr.) Krombh.
85	S	Oudemansiella platyphylla (Pers. : Fr.) Moser in Gams
86	M	Cortinarius anomalus (Fr. : Fr.) Fr.
87	S	Naematoloma fasciculare (Hudson : Fr.) Karst.
88	S	Collricia dependens (Berk. et Curt.) Imazeki
89	S	Oligoporus tephroleucus (Fr.) Gilbn. et Ryv.
90	M	Amanita porphyria (Alb. & Schw. : Fr.) Secr.
91	M	Amanita rubescens Pers. : Fr.
92	M	Laccaria bicolor (Maire) P. D. Orton
93	M	Daedaleopsis tricolor (Bull. : Fr.) Bond. et Sing.
94	M	Russula liliacea Quel.
95	M	Lepiota cygnea J. Lge.
96	S	Mycena galericulata (Scop. : Fr.) S. F. Gray
97	M	Phylloporus bellus (Mass.) Corner
98	S	Exidia uvapassa Lloyd
99	M	Cortinarius sp. 6
100	M	Russula cyanoxantha (Schaeff.) Fr.
101	M	Stroblomyces confusus Sing.
102	M	Russula japonica Hongo
103	M	Russula castanopsidis Hongo
104	M	Amanita pseudoporphyria Hongo
105	M	Cortinarius tenuipes (Hongo) Hongo
106	S	Bisporella citrina (Batsch. : Fr.) Korf et Carpenter
107	S	Gymnopilus liquiritiae (Pers. : Fr.) Karst.
108	S	Exidia glandulosa Fr.
109	S	Marasmius cohaerens (Alb. & Schw. : Fr.) Cooke & Quel.
110	S	Coriolus versicolor (L. : Fr.) Quel.
111	S	Marasmius levelleanus (Berk.) Pat.
112	S	Pluteus atricapillus (Batsch) Fayod
113	M	Amanita cecillae (Berk. & Br.) Bas
114	M	Marasmius sp. 2
115	M	Amanita spissacea Imai
116	M	Cortinarius pseudosalor J. Lange
117		sp. 3
118		sp. 4
119	M	Laccaria amethystea (Bull.) Murr.
120	M	Lactarius sp. 1
121	M	Lactarius sp. 2
122	S	Mycena sp. 2
123	M	Russula aeruginea Lindbl. apud Fr.
124	M	Cortinarius salor Fr.
125	M	Elaphomyces granulatus Fr.
126	M	Cordyceps ophioglossoides (Ehrh.) Fr.
127	S	Inocybe nodulosospora Kobayasi
128	S	Marasmiellus sp. 1
129	M	Xerocomus nigromaculatus Hongo
130	M	Russula vesca Fr.
131	M	Xanthoconium affine (Peck) Sing.
132	M	Inocybe sp. 3
133	S	Crinipellis stipitaria (Fr.) Pat.
134	S	Daedaleopsis purpurea (Cke.) Imaz. et Aoshi.

No.		Species						
135	S	Heodictyon gracile Berk.		2	7			11.09
136	S	Naematoloma sublateritium (Fr.) Karst.				1		1.02
137	M	Russula sanguinea (Bull.) Fr.						1.73
138	S	Agaricus abruptibulbus Peck		8				1.48
139	S	Collybia sp. 3		1				0.42
140	S	Collybia sp. 4						0.15
141	M	Cortinarius sp. 7			2			0.29
142	S	Agaricus subrutilescens (Kauffm.) Hotson & Stuntz	2					2.31
143	M	Boletaceae sp. 1		1				1.61
144	S	Clavulinopsis fusiformis (Sow. : Fr.) Corner	12					0.23
145	S	Clavulinopsis miyabeana (S. Ito) S. Ito	16					0.13
146	M	Amanita volvata (Peck) Martin	1					1.11
147	M	Russula sp. 1		1				1.52
148	M	Russula sp. 2		1				0.03
149	M	Russula sp. 3						1.10
150	M	Russula sp. 4						0.18
151	M	Russula sp. 5	2					1.75
152	S	Crepidotus badiofloccosus Imai		9				1.58
153	M	Amanita virosa (Fr.) Bertillon	1	2	1			0.23 0.68 0.34 0.18
154	S	Crepidotus mollis (Schaeff. : Fr.) Kummer	32 60 50 120	8				0.47 1.32 1.54 0.03 0.03
155	S	Oudemansiella pudens (Pers.) Pegler	1	3	1			0.01 0.60 0.06
156	S	Oudemansiella radicata (Relhan : Fr.) Sing.	1					0.67 0.48
157	S	Roseofomes subflexibilis (Berk. et Curt.) Aoshi.	2 13	2	6			0.31 14.60 0.42 0.44
158	S	Collybia peronata (Bolt. : Fr.) Kummer		1	2			0.61 0.11
159	S	Mycena amygdalina (Pers.) Sing.	6		357			0.34 4.45
160	M	Boletellus emodensis (Berk.) Sing.	1					6.23 2.05
161	M	Dermocybe sp. 3	1		1			0.18 0.59
162	S	Psathyrella sp. 2	2		5			0.11 0.39
163	M	Russula sp. 6		2	4			0.03 0.10 0.13
164	S	Inocybe geophylla (Sow. : Fr.) Kummer	1	17 1 24				0.34 0.31 0.74 0.10 3.63
165	M	Russula omiensis Hongo	1 4	8 20				0.25 1.12 0.12 2.99 5.66 4.68
166	S	Marasmius siccus (Schw.) Fr.		3				0.01 0.01 0.01
167	M	Lactarius camphoratus (Bull. Fr.) Fr.	6	2	3			1.59 0.71 0.23
168	M	Lepista nuda (Bull. : Fr.) Cooke	9		5			6.58 9.59
169	M	Cortinarius sp. 8		2				0.91 0.29
170	S	Coriolus hirsutus (Wulf. : Fr.) Quel.			5			10.45
171	S	Lentinus edodes (Berk.) Sing.						27.32
172	M	Marasmiellus candidus (Bolt.) Sing.			2			0.01
173	M	Oudemansiella sp. 1						0.43
174	S	Sparassis crispa Wulf. : Fr.		1				2.79
175	S	Clavulina sp. 1						0.08
176	M	Tylopilus neofelleus Hongo			2			4.56
177	M	Tylopilus nigerrimus (Heim) Hongo & Endo	1					2.91
178	M	Austroboletus gracilis (Peck) Wolfe	1					1.09
179	M	Boletus ornatipes Peck						0.31
180	M	Tricholoma saponaceum (Fr.) Kummer		3				0.36
181	S	Collybia sp. 5	1					0.11
182	M	Russula sp. 7	1		2			1.71
183	M	Russula sp. 8						1.48
184	M	Russula sp. 9	1		3			0.31
185	M	Russula sp. 10						2.05
186	M	Cortinarius subalboviolaceus Hongo	6		6			1.16
187	M	Russula kansaiensis Hongo			4			0.11
188	M	Cortinarius sp. 9			1			4.08
189	M	Inocybe sp. 4			1			0.12
190		sp. 5	1					0.52
191		sp. 6	20		20			0.18
192		sp. 7						0.09
193		sp. 8	3		3			0.48
194		sp. 9			81			7.82

Fig. 2. Fungal flora in 32 quadrats, each measuring 10 × 10 m. The figures in the left half are the total number of individual mushrooms collected in a year. The figures in the right half indicate their dry weights. The vertical thin line covers the species commonly found in red pine forests. The vertical bold line covers the species commonly found in all the stations.

2. Mushroom diversity in successional and climax forests

All visible mushrooms were collected at weekly intervals for one year. The results are summarized in Fig. 2, and are expressed in terms of individual numbers (the left half in the figure) and dry weight (the right half). The species diversities ($\bar{H}$) in terms of both aspects are also shown in Table 1. For both cases, the values of $\bar{H}$ increased as the successional age progressed. It is notewothy that the maximum $\bar{H}$ values, 3.01 for individual numbers and 3.31 for dry weight, were observed at ST8. ST7 has similar values. Therefore, the values for ST8 seem to represent an ecological equilibrium. Some species of the genus *Boletus* were frequently observed in the young red pine forests, while some species of the genus *Russula* were noted in the evergreen broad-leaved forests. Rare mushrooms such as *Elaphomyces granulatus* Fr., *Cordyceps ophioglossoides* (Ehrh.) Fr. and *Ileodictyon gracile* Berk. were found in ST7. Some other species were commonly found in both immature and mature forests, and

Table 2. Ecological distances expressed as ED_r (bold figures) and DI (small figures) between the examination stations estimated from woody plant diversities.

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7	Station 8
Station 1	*	0.315 0.33	0.295 0.44	0.424 0.33	0.313 0.57	0.396 0.47	0.509 0.87	0.488 0.77
Station 2	*	*	0.336 0.40	0.400 0.30	0.320 0.65	0.365 0.49	0.447 0.81	0.427 0.72
Station 3	*	*	*	0.195 0.22	0.164 0.25	0.186 0.21	0.387 0.67	0.353 0.59
Station 4	*	*	*	*	0.259 0.37	0.216 0.32	0.400 0.81	0.368 0.69
Station 5	*	*	*	*	*	0.123 0.12	0.371 0.66	0.315 0.51
Station 6	*	*	*	*	*	*	0.357 0.51	0.310 0.52
Station 7	*	*	*	*	*	*	*	0.362 0.33
Station 8	*	*	*	*	*	*	*	*

See the text for the explanation of ED_r and DI.

Table 3. Ecological distances expressed as ED_r and DI between the examination stations.

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7	Station 8
Station 1	*	0.559 0.762 0.73	0.763 0.785 0.85	0.613 0.711 0.79	0.550 0.790 1.00	0.545 0.710 0.88	0.587 0.711 1.00	0.516 0.679 1.00
Station 2	*	*	0.678 0.593 0.85	0.503 0.510 0.86	0.418 0.595 0.85	0.408 0.480 0.88	0.470 0.484 0.91	0.378 0.438 0.94
Station 3	*	*	*	0.677 0.422 0.56	0.667 0.617 0.77	0.663 0.510 0.87	0.699 0.510 0.91	0.639 0.467 0.92
Station 4	*	*	*	*	0.489 0.531 0.77	0.482 0.406 0.66	0.534 0.413 0.92	0.447 0.357 0.86
Station 5	*	*	*	*	*	0.222 0.309 0.75	0.453 0.514 0.78	0.301 0.447 0.69
Station 6	*	*	*	*	*	*	0.415 0.375 0.73	0.255 0.293 0.69
Station 7	*	*	*	*	*	*	*	0.377 0.285 0.58
Station 8	*	*	*	*	*	*	*	*

The upper bold figures are from diversities measured in mushroom indinidual numbers. The middle bold figures are from those in mushroom dry weights. The bottom small figures are from the dissimilarities (DI).

represented the majority of all the specimens. From the point of view of mushroom diversities, the ecological distances between the forests were calculated and are summarized in Table 3, which contains the indices ED_r and DI. The average substitution rate was 0.0035 per year for ED_r, and 0.005 for DI. The fungal succession was thus more exaggerated than that of woody plants.

3. Development of segregation in energy source and seasonal fruiting

As ecological succession proceeds, forest stands develop their own seasonal flowering or fruiting segregational patterns as well as stratification into canopy, understory, shrub, and herb layers (e.g. Nakanishi et al., 1983). Heterotrophic fungi are also expected to develop similar segregation both spatially and temporally.

In the stations with younger forests, from ST1 to ST6, mycorrhizal fungi were dominant over saprophytic ones, as shown in Fig. 2, because the A layer was absent or thin. In contrast, the ratio of these two nutrient types was balanced in the aged forests of ST7 and ST8, owing to the accumulation of humus. This is in accordance with the results already reported (Shimono, 1988; Fujita, 1989; Murakami, 1989). The S/T ratio means the proportion of saprophytic fungi in total and is shown in Table 1. Classification into either mycorrhizal or saprophytic was done according to Imazeki and Hongo (1987, 1989) and Hongo (1990). The results are also represented graphically in Fig. 3. Equilibrium appears to be reached at around 0.7 in the individual number analy-

sis and at 0.3 in the dry weight analysis. A further analysis was tried employing the sum of dry weights divided by the sum of individual numbers. This quotient is tentatively named mushroom type and is shown in Table 1. The maximum value of mushroom type was 1.88 at ST3. The equilibrium seems to be at around 0.6 in the mature forests.

Segregation was also analyzed in terms of seasonal fruiting. The weekly collections were arranged in chronological order. The degree of diversity was expressed as H and termed temporal segregation. The results are shown in Table 1 and graphically represented in Fig. 4. The distribution curves for both individual number and dry weight rose gradually toward the equilibrium in the mature forests.

4. Correlation of mushroom diversities with other ecologigcal characters associated with succession

Mushroom diversity increased linearly up to the equilibrium. The distributions of other ecological characters represented similar pictures. So, some kinds of relationships would be expected between them. All the possible combinations were analyzed for correlation and regression between the mushroom diversities and the other successional characters listed in Table 1. The results are shown in Table 4 and Fig. 5. There were significant posititive correlations in all the combinations except those associated with the species diversity in woody plants and the mushroom type. Successional stages, therefore, can be recognized to some extent
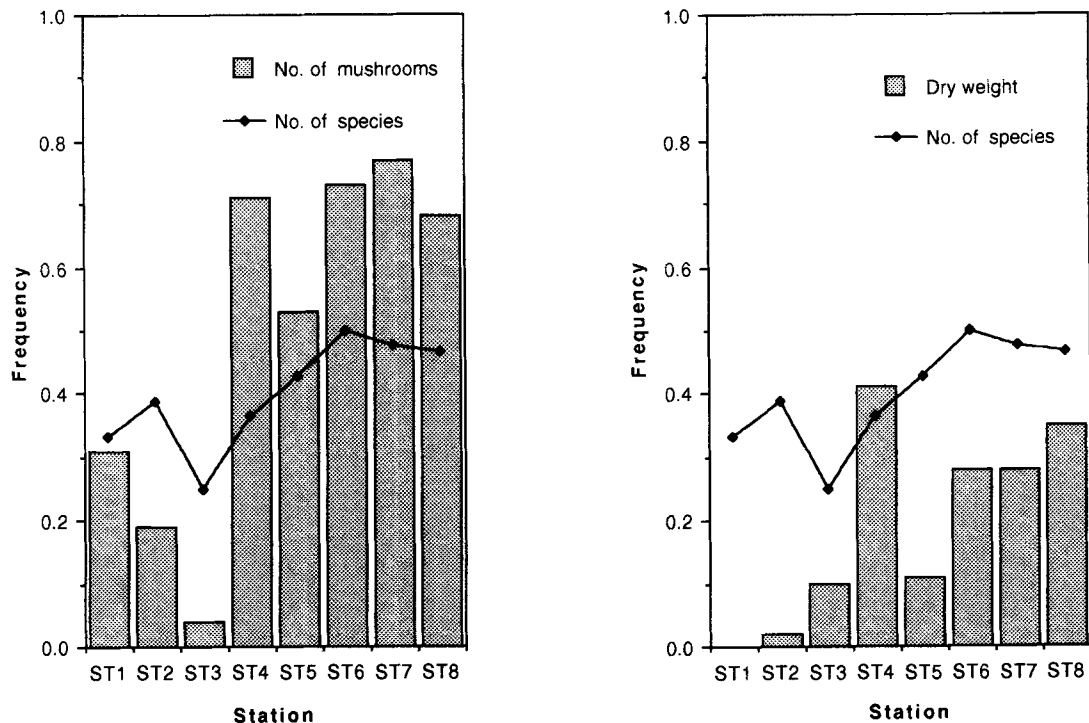

Fig. 3. Proportion of saprophytic fungi in the examination stations. The distribution in the left half was estimated from the data on individual mushroom number, and that in the right half from the data on dry weight.
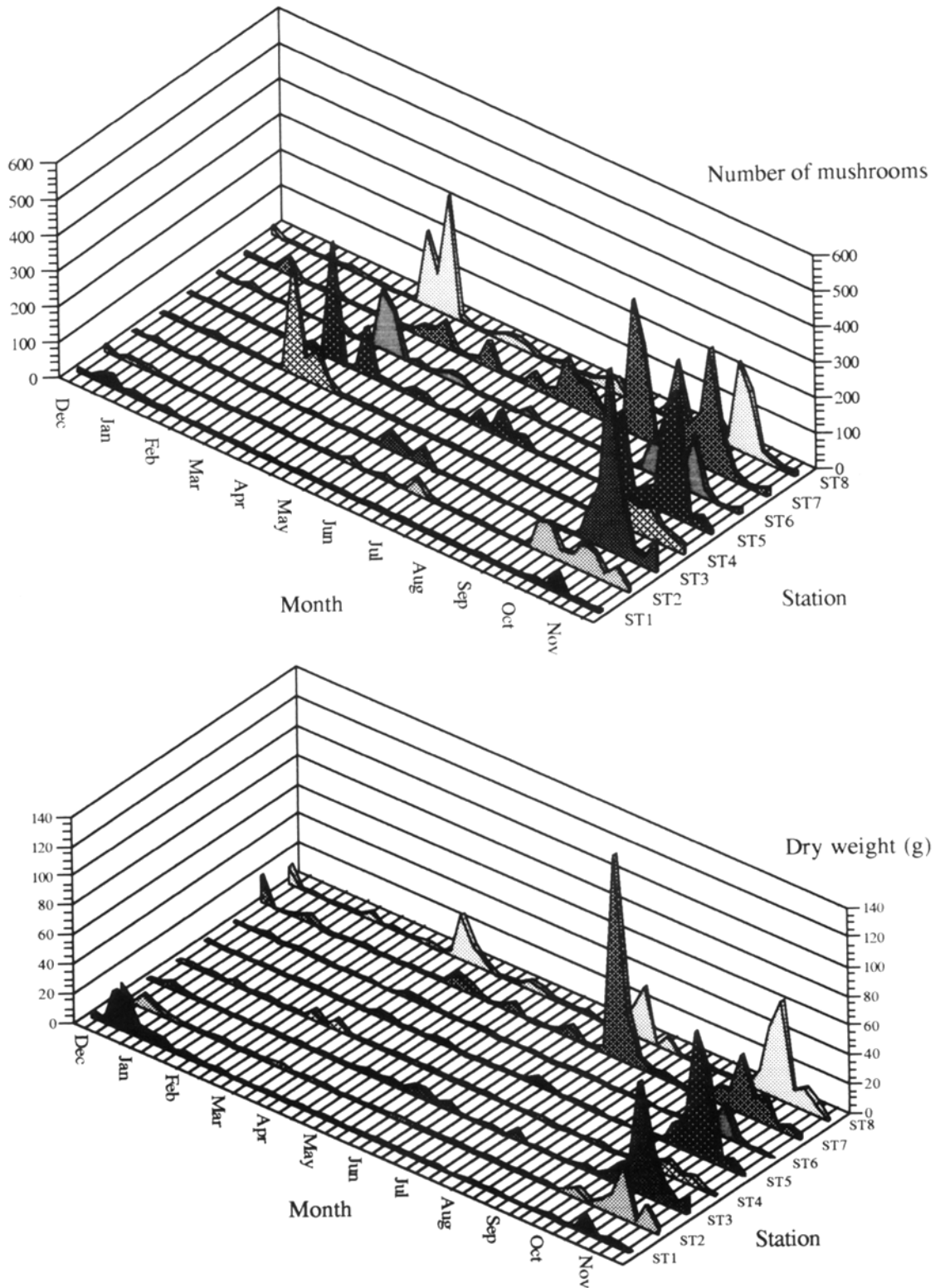
Fig. 4. Seasonal mushroom fruiting in the examination stations.
The upper half shows the number of mushrooms, and the lower half dry weight.

Table 4. Correlation coefficients between the ecological characters associated with succession. See the text for further explanation.

	Thickness of A layer	Height of woody plant	DBH of woody plant	Diversity in woody plant	Leaf type	Div. mush. in number	Div. mush. in weight	S/T ratio in mush. no.	S/T ratio in mush. weight	Temp. seg. in number	Temp. seg. in weight	Mushroom type
Absorption of sunlight	0.85***	0.81***	0.61**	0.59**	0.70***	0.57**	0.72***	0.22	0.36	0.56**	0.48*	0.10
Thickness of A layer		0.95***	0.72***	0.56**	0.89***	0.72***	0.84***	0.56**	0.51**	0.56**	0.45*	−0.04
Height of woody plant			0.84***	0.49*	0.94***	0.69***	0.77***	0.58**	0.50**	0.56**	0.43*	−0.03
DBH of woody plant				0.31	0.84***	0.60**	0.67***	0.50**	0.55**	0.44*	0.38*	0.00
Diversity in woody plant					0.27	0.28	0.47*	0.24	0.47*	0.14	0.20	−0.08
Leaf type						0.65**	0.76***	0.57**	0.50**	0.53**	0.44*	0.05
Div. mush. in number							0.80***	0.50**	0.37*	0.61**	0.39*	0.12
Div. mush. in weight								0.58**	0.61**	0.46*	0.54**	0.05
S/T ratio in mush. no.									0.66***	0.31	0.36	−0.12
S/T ratio in mush. weight										0.26	0.53**	0.00
Temp. seg. in number											0.72***	0.26
Temp. seg. in weight												0.09
Mushroom type												

* Significant at 5% level
** Significant at 1% level
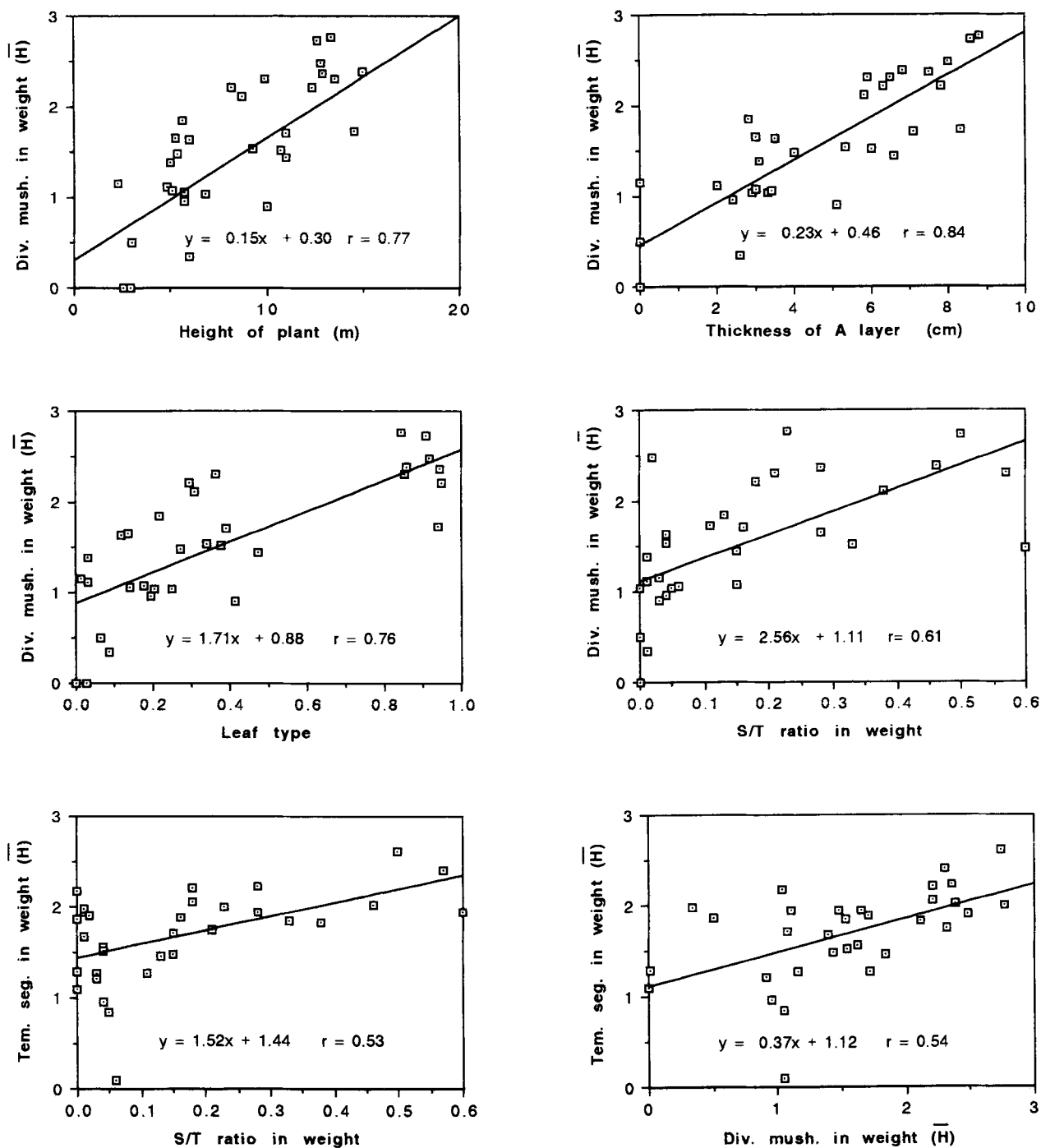*** Significant at 0.1% level

Fig. 5. Correlation and linear regression between the ecological characters associated with succession.

when mushroom diversity is obtained.

There was no significant correlation between ecological distances (ED$_r$ values) measured by woody plant diversities and by mushroom diversities (r=0.235, t=1.233, df=26, P>0.05). However, a significant positive correlation was seen between ecological distances expressed in DI values (r=0.637, t=4.213, df=26, P<0.001). Fungal succession takes place more rapidly than that of plants, especially in young forest ecosystems (Fig. 2 and

Table 3).

Discussion

1. Ecological characteristics of middle-aged red pine forests

In this study, mushroom diversity was analyzed for a year. It is well known that the biomass of mushrooms changes from year to year even in the same forest, and

long-term observation would be more ideal for analysis of species diversity. However, an outline of fungal succession and diversity seems to be recognisable from this observation.

From the foregoing results, we can speculate the ecological conditions in some transient forests approaching climax. They must be intermediate between those present in ST6 and ST7. Actually, middle-aged or well-developed pine forests or deciduous oak forests are at this stage. So far, mushroom surveys have been extensively done on this kind of forest (e.g. Hamada and Ohara, 1970; Fujita, 1989). The diversities (H) in woody plant and in mushroom are expected to be around 2.6 (Table 1). The fungal biomass is expected to be at the maximum since the net primary production is at the maximum in this successional stage (Kira and Shidei, 1967).

On the other hand, fungal succession is reviewed in its nutrient type and average shape in Fig. 6. Large mycorrhizal mushrooms are dominant in young forests. However, species are restricted, as seen in Fig. 2. The species diversity of mycorrhizal mushrooms increases gradually toward middle-aged forests, and thus the average size of mycorrhyzal mushrooms decreases. Saprophytic mushrooms appear in middle-aged forests. Habitat segregation is initiated. After undergoing some types of natural selection, the average size and standard deviation of mushrooms again increases and reaches equilibrium in mature forests. Large mushrooms again become dominant.

Some middle-aged red pine forests are expected to

be at nearly equilibrium, especially they are on steep or rocky slopes. Another examination station was chosen in Tannan Town, Hyogo Prefecture, 20 km east of the main examination station. Two quadrats (ST9N and ST9S) were examined for vegetation and terricolous mushrooms on 15 October 1989. The woody plant vegetation was almost the same as that of ST6. The ecological distances (ED$_r$) to ST6 and ST7 were 0.191 and 0.408, respectively. The canopy was formed by 47-year-old red pine trees with a mean height of 11.1 m and DBH of 24.8 cm, and the species diversity index was 2.06. The light absorption averaged 84.5%. The thickness of the A layer was 4.0 cm. The fungal flora was dominated by mycorrhizal mushrooms such as *Tricholoma matsutake* (S. Ito & Imai) Sing., *Phellodon niger* (Fr.) Karst., and *Rozites caperata* (Pers.: Fr.) Karst. at that time. Five and 13 mushrooms of *T. matsutake* were found in ST9N and ST9S, respectively. The woody plant diversity and the thickness of the A layer were slightly lower than the expected values (2.6 for H and 6 cm for the thickness). This difference may have been caused by the steep slope of this site. The ground inclination was 52° and 44° at ST9N and ST9S, respectively. On such slopes, leaf litter and humus hardly accumulate, and consequently the soil moisture is never very high. Red pines are favoured by these conditions (Nakanishi et al., 1983), which may account for the low H value. Well-developed red pines produce the maximum level of primary production, and large mycorrhizal mushrooms are favoured in this situation.
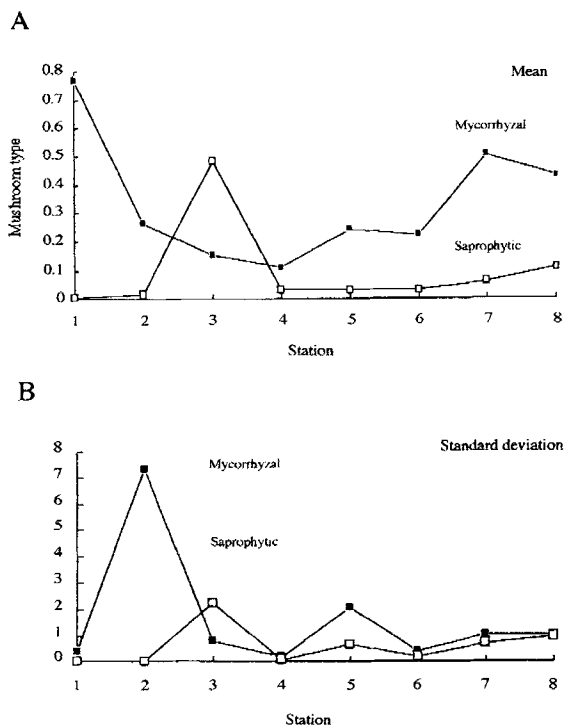
A

B

Fig. 6. Changes of mushroom type in the examination stations. Mushroom type is defined as the sum of dry weights divided by number of mushrooms, and it represents the average size of mushrooms. A: Mean, and B: Standard deviation.
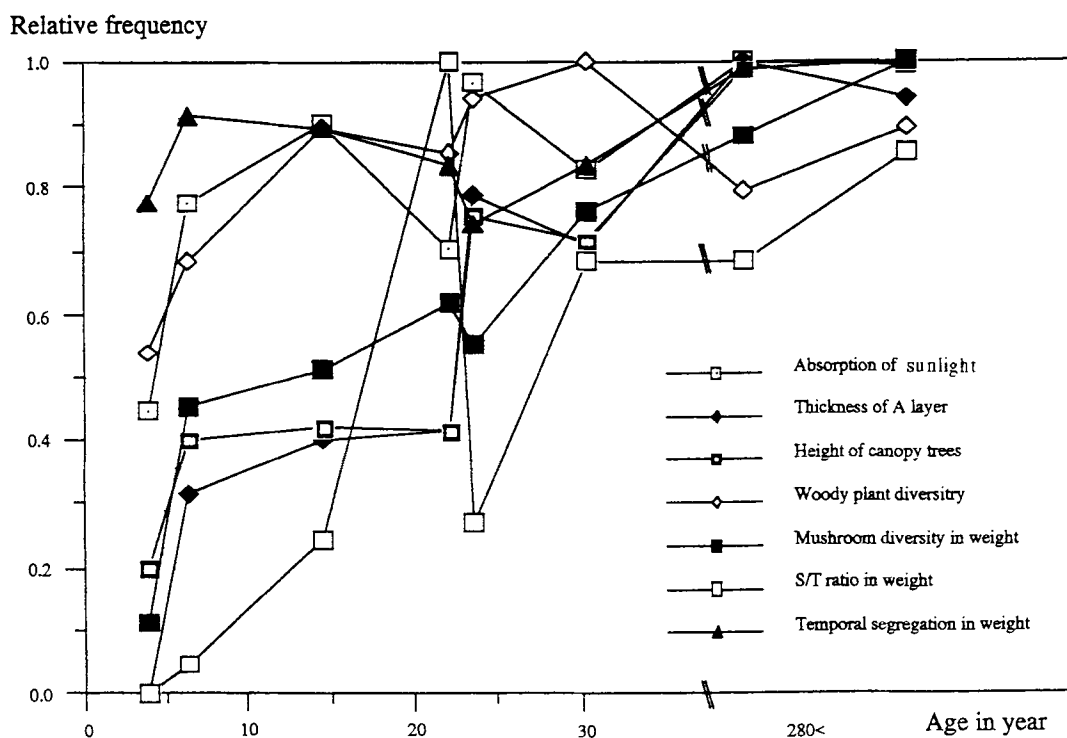
Relative frequency

Fig. 7. Changes of the ecological characters associated with succession.
They are expressed relative to the highest value.

2. Changes in mushroom diversities associated with woody plant succession

It is well known that fungal flora depends on forest vegetation. Therefore, it is affected by woody plant succession as well. The following characters were linearly proportional to the successional ages and reached equilibrium at the climax: absorption of sunlight, thickness of the A layer, height of canopy, and DBH of canopy trees. The mushroom diversities correspond to and follow these increments by developing spatial and temporal niche segregation. These changes are graphically shown in Fig. 7. Canopy development allows efficient utilization of energy from sunlight, and the amount of photosynthesis affects the subsequent volume of dead leaves and branches. A thick humus layer is able to keep a comfortable temperature and moisture level to induce fungal growth and fruiting, especially for saprophytic fungi. The diversity in mushroom species and construction of defined population structures leads to development of a stable population structure of predators. These predators may in turn help to distribute the spores into the ecosystem. They establishe a fine network of a sort of symbiosis in the climax ecosystem.

The greater the amount of gain of sun energy is, the larger are the volume and quantity of mycorrhizal mushrooms that may be produced. This tendency is expected in the early stage of succession, and is called the first successional stage. In line with the accumulation of humus, the rapid appearance of saprophytic fungi is expected; i.e., the S/T ratio should increase. Saprophytic fungi growing in the humus layer coexist with mycor-

rhizal fungi growing in the B soil layer. The average size of mycorrhyzal mushrooms decreases (Fig. 6). This corresponds to the second successional stage. After replacement of evergreen broad-leaved trees, the forest ground is never open to the sky, and dead leaves are supplied more constantly in all seasons. The thick humus layer develops new members of mycorrhizal fungi growing in the A layer in addition to those in the B layer. This is called the third successional stage and represents the climax. At this time, spatial and temporal segregation is complete (Murakami, 1987 and 1989). Such a balanced segregation is reported in subalpine climax forests as well (Ogawa, 1977). At the first successional stage, one of the typical mycorrhizal fungi is a species belonging to the genus Boletus, and that of the third stage is a species of the genus Russula (Fig. 2). The forests from ST1 to ST3 may represent the first successional stage. Those from ST4 to ST6 correspond to the second successional stage, which also includes ST9. The fungal communities examined in ST7 and ST8 thus suggest any ecological implications about stable and balanced diversity.

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