

FULL PAPER

Riyou Tsujino · Hirotohi Sato · Akio Imamura
Takakazu Yumoto

Topography-specific emergence of fungal fruiting bodies in warm temperate evergreen broad-leaved forests on Yakushima Island, Japan

Received: August 25, 2008 / Accepted: May 7, 2009

Abstract We conducted line route censuses of fungal fruiting bodies from August to September in 2005 and 2006 along ridges and valleys and compared the differences in the encounter rates of fungal fruiting bodies (= fruiting bodies seen per census kilometer) between types of topography and between fungal functional groups (i.e., ectomycorrhizal and saprobic fungi) in warm temperate evergreen broad-leaved forests on Yakushima Island, Japan. We found 251 fungal fruiting bodies (26 families, 50 genera, and 65 species) in total, including 51 bodies from Tricholomataceae, 41 from Russulaceae, 25 from Boletaceae, and 19 from Amanitaceae. The encounter rate of ectomycorrhizal fungi was greater at the ridge route (26.7 unit/km) than at the valley route (8.7 unit/km) and that of saprobic fungi was greater at the valley route (25.0 unit/km) than at the ridge route (12.5 unit/km). In addition, we conducted 7-year intermittent sampling and identified 40 families, 96 genera, and 142 species. The topography-specific emergence pattern of the intermittent sampling method was similar to that of the line census method. The fungal species composition in this study was possibly affected by a topographic gradient for both fungal functional groups through soil moisture, nutrient availability, and host tree distribution.

Key words Ectomycorrhizal fungi · Encounter rate · Route census · Tree distribution

Introduction

Fungi play important ecological roles in forest ecosystems as decomposers, mycorrhizal symbionts, and pathogens (Dix and Webster 1995). Many studies have found that the fungal species composition differs between forests depending on various characteristics of the forests, such as dominant tree species (Bills et al. 1986; Dighton et al. 1986; Yamashita and Hijii 2006) and forest management (Fujita 1989; Straatsma and Krisai-Greilhuber 2003; Bonet et al. 2004; Stokland and Kauserud 2004; Kranabetter et al. 2005). It is also known that the fungal spatial distribution patterns differ within a forest (Fukiharu and Kato 1997; Matsuda and Hijii 1998; Yamashita and Hijii 2006).

One of the reasons for this difference in the fungal spatial distribution patterns within a forest must be the heterogeneous environment in a small spatial scale. Previous studies about spatial distribution patterns of fungal fruiting bodies have considered litter distribution (Yamashita and Hijii 2006), vegetation (i.e., tree density, vegetation layer, and canopy gap) (Richard et al. 2004), and spatial autocorrelation within a few to tens of meters (Murakami 1989; Fukiharu and Kato 1997). On the other hand, local topographic variations (i.e., slope inclination, convexity and aspect of the ground, and elevation) create diverse microhabitat heterogeneity (Moody and Meentemeyer 2001; Takyu et al. 2002), such as soil surface wetness (Ashton et al. 1995; Daws et al. 2005) and nutrient availability (Tokuchi et al. 1999). Topography has been seen as a chief factor in ecological specialization (Bazzaz 1991; Harms et al. 2001), tree distribution patterns (Nagamatsu and Miura 1997; Harms et al. 2001; Tsujino et al. 2006), and ranging patterns of mammals (Dickson and Beier 2007; Tsujino and Yumoto 2009). Abiotic environmental factors created by topography were thought to be significant factors for fungi (Trudell and Edmonds 2004). Topography can be also a biotic environmental factor for ectomycorrhizal (ECM) fungi in relationship to topography-specific host tree distribution because they have mutualistic correlations with specific trees. Biotic and abiotic effects of topographic positions probably differ

R. Tsujino (✉) · T. Yumoto
Research Institute for Humanity and Nature, 457-4 Motoyama,
Kamigamo, Kita-ku, Kyoto 603-8047, Japan
Tel. +81-75-707-2478; Fax +81-75-707-2507
e-mail: turi@chikyu.ac.jp

H. Sato
Graduate School of Science, Kyoto University, Kyoto, Japan

A. Imamura
Department of Bioenvironmental Design, Faculty of
Bioenvironmental Science, Kyotogakuen University, Kyoto, Japan

among fungal functional groups. In this way, the topographic position was potentially an important factor in determining spatial distribution patterns of fungi, but the relationship between fungal distribution patterns and topographic position has not been much studied.

Thus, in this study, we aimed to clarify the relationship among the fungal functional groups (i.e., ectomycorrhizal fungi and saprobic fungi) and emergence patterns of fungal fruiting bodies in relationship to topography in warm temperate evergreen broad-leaved forests in Yakushima Island, Japan. Further, we discuss possible explanations of the relationship among fungi, tree distribution, and topography. We conducted a tree census in a 50 × 50 m quadrat and line route censuses of fungal fruiting bodies in late August to early September at two different topographic positions, a ridge route and a valley route.

Materials and methods

Study sites

Five study sites, Hanyama (180–260 m a.s.l.), Kawahara (180–370 m a.s.l.), Motida (140–220 m a.s.l.), Nakasegawa (170–240 m a.s.l.), and Nakano (190–290 m a.s.l.), were located in warm temperate forests on the western, northwestern, and southeastern part of Yakushima Island (30°20' N, 131°30' E), which lies about 70 km south of Kyushu, Japan. The study forests are warm temperate evergreen broad-leaved forests that consist mainly of broad-leaved evergreen Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae (Tsuji no and Yumoto 2004; Tsuji no et al. 2006), with no single dominant species.

Topographic positions

Geomorphic processes, which refer to interactions among translocation and redeposition of soil materials by overland flow, stream flow, and mass movements, differ in each of the micro-landforms (Nagamatsu and Miura 1997). We characterized the topography of the study areas as ridge area, upper side-slope, lower side-slope, foot slope, and valley area, according to the land surface, soil, and slope inclination (Hara et al. 1996; Nagamatsu and Miura 1997; Tsuji no and Yumoto 2007, 2008). The ridge area is a gentle convex slope that runs along a ridge. The upper side-slope below the ridge area is steeper than the ridge area. The valley area is a gentle concave slope that runs along a valley. The foot slope above the valley area is steeper and often consists of softer and deeper soil than that in the valley. The lower side-slope is a transitional topographic unit between the upper side-slope and foot slope. We condensed the two former slope types as the “upper slope area” and the latter three as the “lower slope area” for the following topographic analysis.

Line census of fungal fruiting bodies

We established one line census route on the ridge line in the upper slope area and one along the valley line in the lower slope area for each of the five study sites: in total, ten line census routes. Each census route was 210–350 m in length (Table 1).

It is well known that fungal fruiting is a seasonal event that depends on meteorological factors, especially temperature and rainfall (Endo 1972; Murakami 1989; Laganà et al. 2002). Previous research showed that late August to September season was one of mass emergence of fungal fruiting bodies in evergreen broad-leaved forests in Kyushu (Endo 1972; Murakami 1989). Thus, a census of fungi was conducted between 15 August and 15 September in 2005 and 2006 (Table 1).

We walked at a speed of about 1 km/h in daytime along the line census route and searched for fungal fruiting bodies of macrofungi around the line above the ground up to 2 m in height, including the trunks of living and dead trees. When we found fungal fruiting bodies directly, we harvested them to identify the fungi. In this census, one unit of fungal fruiting bodies was identified when fruiting bodies were close to other ones within 50 cm. We conducted route censuses repeatedly: once for Nakano, twice for Kawahara, and three times for Nakasegawa, Motida, and Hanyama, at intervals of 4–10 days (see Table 1). Fungi were classified into three functional groups: ectomycorrhizal (ECM) fungi, saprobic fungi, and other fungi, mostly unidentified fungi, according to Imazeki and Hongo (1987, 1989), Molina et al. (1992), and Hibbett et al. (2000). Fungi nomenclature followed Imazeki and Hongo (1987, 1989).

We calculated mean encounter rates (unit/km) of fungal fruiting bodies for each functional group and topography as the number of fungal fruiting body units seen per line census route kilometer. To clarify the relationship between topography and emergence of fungal fruiting bodies, a generalized linear mixed model (GLMM) was used to assess the factors affecting the encounter rates of each line census. Three fixed factors represented the encounter rates: (1) functional groups (ECM or saprobic fungi groups), (2) topographic positions (ridge or valley routes), and (3) the interaction of these two factors. The study sites and each census were input as random factors to avoid the influence of pseudo-replications. In this analysis, we omitted “other” types of fungi group because all these fungi were unidentified. We used the lmer function in lme4 package of R for

Table 1. Census route length and number of census times in 2005 and 2006

Sites	Route length (m)		No. census times	
	Ridge	Valley	2005	2006
Hanyama	300	230	2	1
Kawahara	210	300	1	1
Motida	310	230	2	1
Nakano	250	350	0	1
Nakasegawa	300	300	2	1

windows ver. 2.6.1 (R Development Core Team 2005). We used Akaike's information criterion (AIC) for model selection, with the minimum AIC as the best-fit estimator.

Intermittent sampling efforts of fungal fruit bodies

To reveal the fungal flora of evergreen broad-leaved forests in Yakushima Island and to compare seasonal variations of topographic locations and functional groups, we added more information of fungal fruiting bodies intermittently sampled. We stayed at Yakushima Island for 27 days in January, 56 days in February, 70 days in March, 39 days in April, 111 days in May, 98 days in June, 86 days in July, 111 days in August, 102 days in September, 112 days in October, 84 days in November, and 91 days in December, from May 2001 to November 2007; most of these days, except for rainy days, we went to evergreen broad-leaved forests at altitude 0–400 m, including the forests around the intensive fungal line census routes and other forests, mainly in Hanyama forest, to conduct field research of the relationship between topography and tree distribution pattern, such as published in Tsujino et al. (2006) and Tsujino and Yumoto (2007, 2008, 2009). In these field studies, we walked various topographic positions throughout whole seasons, and we found fungal fruiting bodies, some of which were recorded and/or harvested. In most of these sampling efforts, we assessed topographic position, such as the upper slope or lower slope area.

Because we did not intend to harvest fungal fruiting bodies from the specific topography and/or specific fungal species, we compared seasonal variation of fungal functional group composition (i.e., ECM vs. saprobic functional groups) in the intermittent sampling method for each month with the chi-square test and also compared seasonal variation of topographic locations for ECM and saprobic fungal functional groups in the intermittent sampling method for each month with the chi-square test. In these tests, we excluded data from unidentified functional groups or topography not detected. Also, we omitted testing the data of January to April and October to December because there were few data ($n < 5$).

Collection samples were dried and preserved as voucher specimens. All specimens were deposited in the herbarium of the Department of Botany, Graduate School of Science, Kyoto University (KYO).

Tree census

To investigate the relationship between topography and tree distribution, a 50 × 50 m study quadrat that included a typical slope from the ridge top to the valley bottom was established at 130 m from the Hanyama lines and at approximately 270 m a.s.l. in the Hanyama area in April 2001 (cf. Tsujino and Yumoto 2007). The mean annual temperature is approximately 21°C, and the annual rainfall is about 2600 mm (Tagawa 1980). The parent rock of the entire study quadrat was granite.

All living trees in the 50 × 50 m study quadrat with diameter at breast height (DBH; i.e., 1.3 m above ground) ≥ 10 cm were identified, mapped, tagged, and their DBH measured in September 2003. We calculated tree stem densities and basal area (BA; $DBH^2 \pi/4$) densities in the quadrat at two topographic positions, upper slope area and lower slope area. A binominal test was conducted to investigate the differences in tree stem density distribution between the upper slope and the lower slope. In this test, the expected number of trees on the upper slope and on the lower slope was calculated for each species as a product of the total tree number and the relative proportion of each topographic area of the total area of the study quadrat. Tree nomenclature followed Mitsuta and Nagamasu (1984).

Results

Fungal functional groups and topography

In the line censuses, we found 251 fungal fruiting bodies and identified 26 families, 50 genera, and 65 species, including 51 fruiting bodies from Tricholomataceae, 41 from Russulaceae, 27 from Polyporaceae, 25 from Boletaceae, and 19 from Amanitaceae (Table 2). In the ridge route census, we found 31 species and 92 units of ECM fungal fruiting bodies and 14 species and 43 units of saprobic fruiting bodies, whereas we found 9 species and 30 units of ECM fungal fruiting bodies and 22 species and 80 units of saprobic fruiting bodies in the valley route census (Table 2). Major families of the ridge routes were Russulaceae (32 units of fungal fruiting bodies), Amanitaceae (18 units), Boletaceae (17 units), Tricholomataceae (17 units), and Polyporaceae (12 units); those of the valley routes were Tricholomataceae (34 units), Polyporaceae (15 units), Russulaceae (9 units), Hygrophoraceae (8 units), and Boletaceae (8 units). However, no dominant fungal species was observed. We found 34 and 20 species only in the ridge routes or the valley routes, respectively; a total of 11 species occurred in both topographic routes (Fig. 1). Most ECM fungi (75%) species showed a ridge-specific emergence pattern whereas half the saprobic fungi (59%) showed a valley-specific emergence pattern (Fig. 1).

Statistic analysis of the encounter rates of fungi showed that the full model was selected with minimum AIC value (AIC = 394.1). Mean encounter rates of fruiting bodies of ECM fungi were greater on the ridge route (mean ± 1 SE = 26.7 ± 6.6 unit/km, $n = 12$) than on the valley route (8.7 ± 3.5 unit/km, $n = 12$); those of the saprobic fungi group were smaller on the ridge route (12.5 ± 3.5 unit/km, $n = 12$) than on the valley routes (25.0 ± 4.5 unit/km, $n = 12$); and those of the other fungi were not as different on the ridge route (1.1 ± 0.6 unit/km, $n = 12$) and on the valley route (0.6 ± 0.4 unit/km, $n = 12$) (Fig. 2).

In intermittent sampling efforts, we found 538 fungi fruiting bodies and identified 40 families, 96 genera, and 142 species, including 18 species from Russulaceae, 22 species from Boletaceae, 20 species from Amanitaceae, 13 species from Tricholomataceae, and 12 species from Polyporaceae

Table 2. Numbers of fungal fruiting bodies found from May 2001 to November 2007 at different topographic position in the intermittent sampling and the line census methods. US, LS, and ND of intermittent sampling method are the upper slope areas, lower slope areas, and not detected, respectively. Ridge and Valley in the route censuses indicate the ridge and valley routes, respectively

Function	Family		Line census		Intermittent sampling			Total
	Order	Species	Ridge	Valley	US	LS	ND	
ECM fungi			92	30	151	49	97	419
GASTEROMYCETIDAE							1	1
SCLERODERMATALES							1	1
Sclerodermataceae							1	1
<i>Scleroderma</i> sp.							1	1
HYMENOMYCETIDAE			92	30	151	49	96	418
AGARICALES			79	30	141	47	94	391
Amanitaceae			18	1	50	9	20	98
<i>Amanita castanopsidis</i>			1		2			3
<i>Amanita ceciliae</i>						1	1	2
<i>Amanita excelsa</i>					1			1
<i>Amanita farinosa</i>							1	1
<i>Amanita fuliginosa</i>					8		1	9
<i>Amanita fulva</i>			1	1	1	1		4
<i>Amanita hemibapha</i> subsp. <i>javanica</i>						1		1
<i>Amanita imazekii</i>					3			3
<i>Amanita japonica</i>			1					1
<i>Amanita lutescens</i>							1	1
<i>Amanita pseudoporphyria</i>			1		12	2	6	21
<i>Amanita rufoferruginea</i>			1		1			2
<i>Amanita sculpta</i>			1		1		1	3
<i>Amanita</i> spp.			5		9	3	3	20
<i>Amanita spissacea</i>					4		2	6
<i>Amanita sychnopyraxis</i> f. <i>subannulata</i>			1			1	1	3
<i>Amanita vaginata</i> var. <i>alba</i>					1			1
<i>Amanita vaginata</i> var. <i>punctata</i>							2	2
<i>Amanita vaginata</i> var. <i>vaginata</i>					2		1	3
<i>Amanita verna</i>			1		3			4
<i>Amanita virgineoides</i>			4					4
<i>Amanita virosa</i>			1		1			2
<i>Amanita volvata</i>					1			1
Boletaceae			17	8	43	12	23	103
Boletaceae spp.			1		14	1	7	23
<i>Boletus aokii</i>							1	1
<i>Boletus obscureumbrinus</i>					1			1
<i>Boletus ornatipes</i>			1		3			4
<i>Boletus quercinus</i>							1	1
<i>Boletus reticulatus</i>							1	1
<i>Boletus speciosus</i>							1	1
<i>Boletus</i> spp.					4			4
<i>Boletus umbriniporus</i>					1			1
<i>Boletus violaceofuscus</i>					1			1
<i>Gyrodon meruliodes</i>							1	1
<i>Gyroporus cyanescens</i>							1	1
<i>Gyroporus</i> spp.			1				1	2
<i>Leccinum hortonii</i>					3	1		4
<i>Phylloporus bellus</i>			3		4	1	1	9
<i>Phylloporus bellus</i> var. <i>cyanescens</i>				1		1		2
<i>Pulveroboletus auriflammeus</i>			1		3	1		5
<i>Pulveroboletus ravenelii</i>			1				1	2
<i>Tylopilus ballouii</i>			1		1	1	1	4
<i>Tylopilus nigerrimus</i>					2			2
<i>Tylopilus nigropurpureus</i>						1		1
<i>Tylopilus</i> spp.			5	2	2			9
<i>Tylopilus virens</i>			1		1	1	1	4
<i>Xanthoconium affine</i>			2					2
<i>Xerocomus chrysenteron</i>				5		1		6
<i>Xerocomus nigromaculatus</i>					1		1	2
<i>Xerocomus</i> spp.					1	1	4	6
<i>Xerocomus subtomentosus</i>					1	2		3
Cortinariaceae			5		4	4	8	21
<i>Cortinarius</i> spp.			2		2			4
<i>Cortinarius violaceus</i>						1	1	2
<i>Dermocybe phoenicea</i>					1			1
<i>Dermocybe</i> sp.						1		1

Table 2. Continued

Function	Family		Line census		Intermittent sampling			Total
	Order	Species	Ridge	Valley	US	LS	ND	
		<i>Gymnopilus</i> spp.					3	3
		<i>Hebeloma</i> sp.					1	1
		<i>Inocybe lutea</i>			1		1	2
		<i>Inocybe</i> spp.	2			2	2	6
		<i>Inocybe sphaerospora</i>	1					1
		Hygrophoraceae		8	1	2		11
		<i>Hygrocybe coccinea</i>		8	1	1		10
		<i>Hygrocybe</i> sp.				1		1
		Rhodophyllaceae		3	1	2	5	11
		<i>Rhodophyllus chamaecypris</i>		2				2
		<i>Rhodophyllus coelestinus</i> var. <i>violaceus</i>					1	1
		<i>Rhodophyllus murraini</i> f. <i>albus</i>					1	1
		<i>Rhodophyllus omiensis</i>				1		1
		<i>Rhodophyllus</i> spp.		1	1	1	3	6
		Russulaceae	32	9	29	14	32	116
		<i>Lactarius gerardii</i>				1		1
		<i>Lactarius piperatus</i>			1			1
		<i>Lactarius quietus</i>			1			1
		<i>Lactarius</i> spp.	4	3		1		8
		<i>Lactarius subzonarius</i>					1	1
		<i>Lactarius vellereus</i>				1		1
		<i>Lactarius volemus</i>			1			1
		<i>Russula alboareolata</i>			3	1	2	6
		<i>Russula casatanopsidis</i>	5		3			8
		<i>Russula compacta</i>			1	1		2
		<i>Russula cyanoxantha</i>			1		1	2
		<i>Russula densifolia</i>	1		1			2
		<i>Russula eburneoareolata</i>			1			1
		<i>Russula emetica</i>		1				1
		<i>Russula flavida</i>	1					1
		<i>Russula kansaiensis</i>					2	2
		<i>Russula lepida</i>	1				3	4
		<i>Russula mariae</i>			1		4	5
		<i>Russula nigricans</i>					2	2
		<i>Russula senecis</i>			1	1	3	5
		<i>Russula sororia</i>		2		1		3
		<i>Russula</i> spp.	18	3	14	7	14	56
		<i>Russula veterinosa</i>	2					2
		Strobilomycetaceae	7	1	11	4	5	28
		<i>Austroboletus fusisporus</i>	1					1
		<i>Austroboletus subvirens</i>	1			1		2
		<i>Boletellus elatus</i>	3		1			4
		<i>Boletellus emodensis</i>	1	1	6	1	1	10
		<i>Boletellus longicolis</i>	1					1
		<i>Boletellus obscurecoccineus</i>			2	1	3	6
		<i>Boletellus</i> spp.			2	1		3
		<i>Heimiella japonica</i>					1	1
		Tricholomataceae			2		1	3
		<i>Laccaria</i> sp.					1	1
		<i>Lyophyllum</i> sp.			1			1
		<i>Tricholoma</i> sp.			1			1
		APHYLLOPHORALES	13		10	2	2	27
		Cantharellaceae	4		6			10
		<i>Cantharellus luteocomus</i>	1					1
		<i>Cantharellus minor</i>			1			1
		<i>Cantharellus</i> spp.	3		5			8
		Thelephoraceae	9		4	2	2	17
		<i>Sarcodon</i> sp.			1			1
		<i>Thelephora aurantiotincta</i>	8		2			10
		<i>Thelephora palmata</i>				1		1
		<i>Thelephora</i> sp.	1		1	1	1	4
		<i>Thelephora vialis</i>					1	1
		Saprobic fungi	43	80	48	60	91	322
		DISCOMYCETES			2	3	3	8
		HELOTIALES			2			2
		Geoglossaceae			1			1
		<i>Cudonia japonica</i>			1			1

Table 2. Continued

Function	Family		Line census		Intermittent sampling			Total
	Order	Species	Ridge	Valley	US	LS	ND	
	Leotiaceae				1			1
	<i>Leotia lubrica</i> f. <i>lubrica</i>				1			1
	PEZIZALES					3	3	6
	Helvellaceae					1		1
	<i>Helvella ephippium</i>					1		1
	Morchallaceae						1	1
	<i>Morchella esculenta</i> var. <i>esculenta</i>						1	1
	Sarcosomataceae					2	2	4
	<i>Boedijnopeziza institia</i>						1	1
	<i>Phillipsia domingensis</i>					2	1	3
	PLECTOMYCETES		1	3		1		5
	EUROTIALES		1	3		1		5
	Dendrosphaeraceae					1		1
	<i>Dendrosphaera eberhardtii</i>					1		1
	Trichocomaceae		1	3				4
	<i>Trichocoma paradoxa</i>		1	3				4
	HETEROBASIDIOMYCETES		1			1	2	4
	AURICULARIALES		1			1	2	4
	Auriculariaceae					1		1
	Auriculariaceae sp.					1		1
	Tremellaceae		1				2	3
	<i>Holtermannia corniformis</i>						1	1
	<i>Tremella foliacea</i>						1	1
	<i>Tremella mesenterica</i>		1					1
	GASTEROMYCETIDAE		1		6	1	8	16
	TULOSTOMATALES						1	1
	Calostomataceae						1	1
	<i>Calostoma japonicum</i>						1	1
	PHALLALES					1	2	3
	Clathraceae					1	1	2
	<i>Pseudocolus schellenbergiae</i>					1	1	2
	Protophallaceae						1	1
	<i>Kobayasia nipponica</i>						1	1
	SCLERODERMATALES						1	1
	Astraeaceae						1	1
	<i>Astraeus hygrometricus</i>						1	1
	LYCOPERDALES		1		6		4	11
	Geastraceae				1			1
	<i>Geastrum mirabile</i>				1			1
	Lycoperdaceae		1		5		4	10
	<i>Calvatia craniiformis</i>		1		1		1	3
	<i>Calvatia</i> sp.						1	1
	<i>Lycoperdon perlatum</i>				4		2	6
	HYMENOMYCETIDAE		40	77	40	54	78	289
	AGARICALES		23	50	17	36	44	170
	Agaricaceae		3	3	4	10	8	28
	<i>Agaricus abruptibullbus</i>					2		2
	<i>Agaricus praeclaresquamosus</i>		1			1	2	4
	<i>Agaricus</i> spp.		1	1		1	2	5
	<i>Agaricus subrutilescens</i>				1	2	1	4
	<i>Lepiota cristata</i>					2		2
	<i>Lepiota praetervisa</i>			1				1
	<i>Lepiota</i> spp.			1	3	1	2	7
	<i>Leucocoprinus birnbaumii</i>		1					1
	<i>Leucocoprinus fragilissimus</i>					1		1
	<i>Macrolepiota</i> sp.						1	1
	Bolbitiaceae		2	1	1		1	5
	<i>Agrocybe cylindracea</i>		2	1	1		1	5
	Coprinaceae		1	2		1	5	9
	Coprinaceae sp.						1	1
	<i>Coprinus comatus</i>		1					1
	<i>Panaeolus sphinctrinus</i>						1	1
	<i>Psathyrella</i> spp.			2		1	2	5
	<i>Psathyrella velutina</i>						1	1
	Cortinariaceae						1	1
	<i>Galerina</i> sp.						1	1
	Crepidotaceae			5		1	2	8
	<i>Crepidotus mollis</i>			4		1	1	6

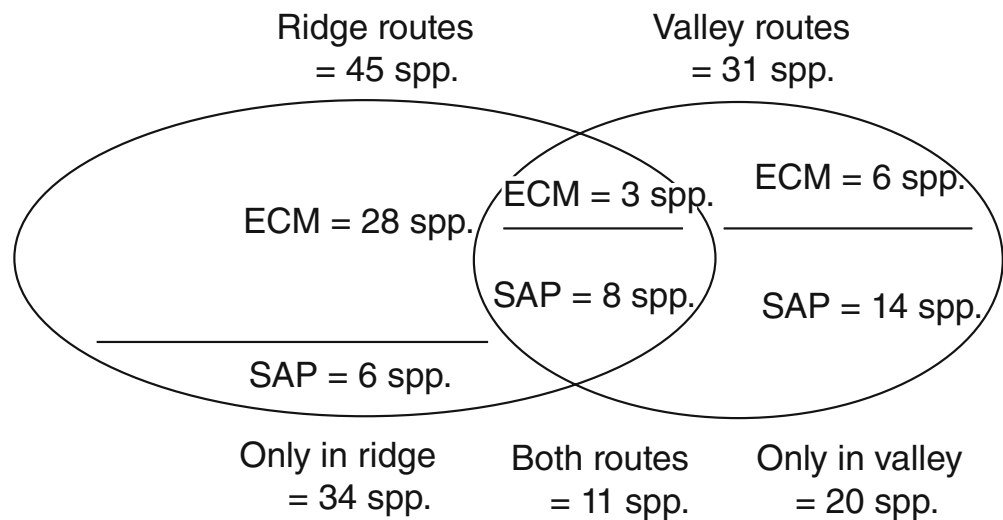
Table 2. Continued

Function	Family		Line census		Intermittent sampling			Total
	Order	Species	Ridge	Valley	US	LS	ND	
		<i>Schizophyllum commune</i>		1			1	2
	Pleurotaceae			1	1	2		4
		<i>Lentinus sajorcaju</i>			1			1
		<i>Panus</i> sp.		1				1
		<i>Panus tigrinus</i>				1		1
		<i>Pleurotus pulmonarius</i>				1		1
	Pluteaceae			1		1		2
		<i>Pluteus atricapillus</i>				1		1
		<i>Pluteus leoninus</i>		1				1
	Strophariaceae			2	3	2	1	8
		<i>Naematoloma fasciculare</i>		2	2	1	1	6
		<i>Phaeomarasmium erinaceella</i>				1		1
		<i>Pholiota</i> sp.			1			1
	Tricholomataceae		17	34	6	18	26	101
		<i>Armillariella</i> sp.				1		1
		<i>Collybia peronata</i>					1	1
		<i>Collybia</i> spp.				1	4	5
		<i>Cyptotrama asprata</i>		2		2	2	6
		<i>Dictyopanus gloeocystidiatus</i>					1	1
		<i>Filoboletus manipularis</i>	2	7		1	3	13
		<i>Hohenbuehelia reniformis</i>				1		1
		<i>Leucopaxillus septentrionalis</i>			1			1
		<i>Marasmiellus candidus</i>	1	12			1	14
		<i>Marasmiellus</i> spp.	4					4
		<i>Marasmius aurantioferrugineus</i>	6					6
		<i>Marasmius</i> spp.	4	5	2	1	1	13
		<i>Micromphale</i> sp.		2	1			3
		<i>Mycena</i> spp.		2	1	1	1	5
		<i>Oudemansiella canarii</i>		2		4	1	7
		<i>Oudemansiella mucida</i>		1		2		3
		<i>Oudemansiella radicata</i>			1	1	6	8
		<i>Oudemansiella</i> spp.				1	4	5
		<i>Panellus stypticus</i>				1		1
		<i>Pleurocybella porrigens</i>		1				1
		<i>Xeromphalina curtipes</i>					1	1
		<i>Xeromphalina</i> spp.				1		1
	Unidentified			1	2	1		4
	Agaricales spp.			1	2	1		4
	APHYLLOPHORALES		17	27	23	18	34	119
	Corticaceae		1			1		2
		Corticaceae spp.	1			1		2
	Ganodermataceae		1		8		5	14
		<i>Amauroderma rugosum</i>			6		5	11
		<i>Ganoderma neojaponicum</i>			1			1
		<i>Ganoderma</i> spp.	1		1			2
	Hymenochaetaceae					1	1	2
		<i>Phellinus igniarius</i>				1	1	2
	Podoscyphaceae			1			4	5
		<i>Cymatoderma lamellatum</i>		1			4	5
	Polyporaceae		12	15	13	11	16	67
		<i>Coltricia cinnamomea</i>			1		1	2
		<i>Coriolus hirsutus</i>					1	1
		<i>Laetiporus sulphureus</i>				1		1
		<i>Lenzites vespereus</i>			2	1	1	4
		<i>Microporus affinis</i>					1	1
		<i>Microporus vernicipes</i>	10	5	4	3	2	24
		<i>Oligoporus</i> spp.		1			2	3
		Polyporaceae spp.		4	2	2	4	12
		<i>Polyporellus brumalis</i>					1	1
		<i>Polyporus alveolarius</i>		1	1			2
		<i>Polyporus arcularius</i>					2	2
		<i>Polyporus</i> spp.	1	2	1	3		7
		<i>Polyporus varius</i>				1		1
		<i>Pycnoporus coccineus</i>			2			2
		<i>Trametes orientalis</i>					1	1
		<i>Trametes versicolor</i>	1	1				2
		<i>Trichaptum biforme</i>		1				1
	Ramariaceae				1			1

Table 2. Continued

Function	Family		Line census		Intermittent sampling			Total
	Order	Species	Ridge	Valley	US	LS	ND	
		<i>Ramaria</i> sp.			1			1
		Sclerotiniaceae	1	2	1	1	3	8
		<i>Dicephalospora rufocornea</i>	1	2	1	1	3	8
		Stereaceae	2	7		3	5	17
		<i>Stereum gausapatum</i>		2			1	3
		<i>Stereum ostrea</i>	2	3			1	6
		<i>Stereum</i> spp.		2		2		4
		<i>Xylobolus princeps</i>				1	1	2
		<i>Xylobolus spectabilis</i>					2	2
		Unidentified		2		1		3
		Aphylophorales spp.		2		1		3
Other		Unidentified spp.	4	2	6	5	31	48
Total			139	112	205	114	219	789

Fig. 1. Classification of species occurring in the line route census. A total of 65 species were found across two topographic routes. The number of species occurring only in ridge routes or valley routes were 34 and 20, respectively. A total of 11 species occurred in both topographic routes. *ECM* and *SAP* indicate ectomycorrhizal and saprobic fungal groups, respectively



(Table 2). In the upper slope area, we found 44 species and 151 units of ECM fungal fruiting bodies and 20 species and 48 units of saprobic fruiting bodies; we found 27 species and 49 units of ECM fungal fruiting bodies and 30 species and 60 units of saprobic fungal fruiting bodies in the lower slope area (Table 2).

The seasonal variation of fungal functional group composition in the intermittent sampling method was significantly different between May and September (χ^2 test, $\chi^2 = 20.61$, $P = 0.0004$). The numbers of ECM fungal fruiting bodies sampled were almost same as those of saprobic fungi in May (22 ECM units vs. 24 saprobic units), June (83 vs. 81), and August (30 vs. 23), whereas those were rather greater than those of saprobic fungi in July (83 vs. 30) and September (78 vs. 37) (Fig. 3a). The seasonal variation of topographic locations in the intermittent sampling method was not significantly different between May to September for ECM fungi (χ^2 test, $\chi^2 = 3.70$, $P = 0.4483$; Fig. 3b), but was significantly different for saprobic fungi ($\chi^2 = 13.23$, $P = 0.0102$; Fig. 3b). The numbers of ECM fungal fruiting bodies sampled on the upper slope area were greater than those on the lower slope area in May (8 units on the upper slope area vs. 2 units on the lower slope area), June (33 vs.

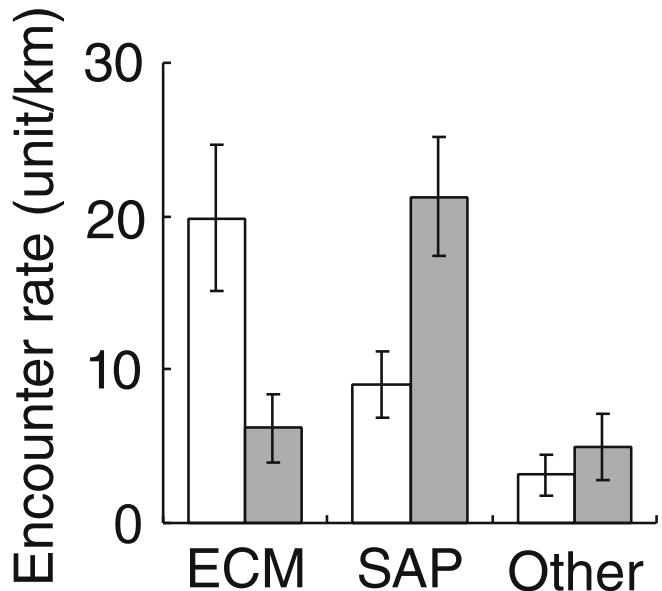


Fig. 2. Encounter rates of three functional groups on ridge (white bars) and valley (gray bars) routes (mean \pm 1 SE, $n = 12$). *ECM*, *SAP*, and *Other* indicate ectomycorrhizal, saprobic, and other fungal groups, respectively

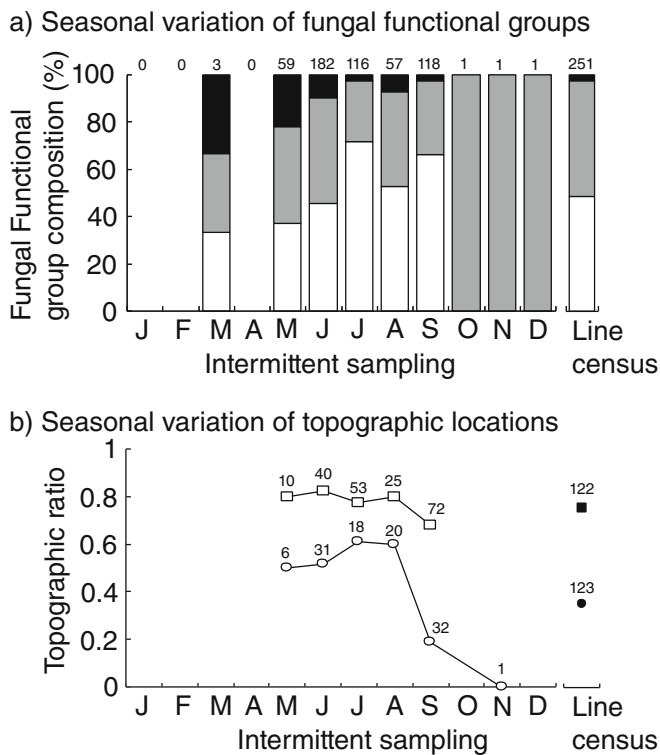


Fig. 3. **a** Functional group composition of fungal fruiting body samples of intermittent sampling from March to December and of the line censuses. Data of 7 years were pooled for the intermittent sampling method. *White, gray, and black bars* indicate ECM, saprobic, and other fungi, respectively. *Small numbers* above the bars indicate sample numbers. **b** Topographic ratios of fungal fruiting body samples (= the number of samples found on the upper slope area/summation of the numbers of samples found on the upper and lower slope areas) from May to November. *White squares and circles* indicate topographic ratios of ECM and saprobic fungi of the intermittent sampling, respectively; *black squares and circles* indicate topographic ratios of ECM and saprobic fungi of the line route census, respectively. *Small numbers* above the symbols indicate sample numbers

7), July (41 vs. 12), August (20 vs. 5), and September (49 vs. 23) (Fig. 3b). The numbers of saprobic fungal fruiting bodies sampled on the upper slope area were same or rather greater in May (3 units on the upper slope area vs. 3 units on the lower slope area), June (16 vs. 15), July (11 vs. 7), and August (12 vs. 8), but smaller in September (6 vs. 26) (Fig. 3b).

Tree distribution along topography

In the whole quadrat in the Hanyama area, Fagaceae, Hamamelidaceae, and Lauraceae were the top three dominant families and had 26.9 m²/ha (40.9%), 12.4 m²/ha (28.8%), and 4.3 m²/ha (6.5%) in BA, respectively. In the upper slope area of the quadrat, Fagaceae, Hamamelidaceae, and Ericaceae were the top three dominant families with 44.9 m²/ha (50.2%), 17.3 m²/ha (19.3%), and 4.6 m²/ha (5.1%) in BA, respectively. In the lower slope area in the quadrat, Fagaceae, Hamamelidaceae, and Lauraceae were the top three dominant families with 13.7 m²/ha

(28.3%), 8.8 m²/ha (18.1%), and 7.2 m²/ha (14.8%) in BA, respectively.

Tree densities were significantly greater on the upper slope for ten species: *Castanopsis cuspidata* var. *sieboldii*, *Distylium racemosum*, *Pasania edulis*, *Quercus salicina*, *Myrsine seguinii*, *Rhododendron tashiroi*, *Symplocos prunifolia*, *Vaccinium bracteatum*, *Syzygium buxifolium*, and *Myrica rubra* (binominal test, $P < 0.05$; Table 3), and on the lower slope for three species, *Ardisia sieboldii*, *Schefflera octophylla*, and *Litsea acuminata* (binominal test, $P < 0.05$; Table 3).

Discussion

Fungal community

Fungal fruiting body composition differed greatly between the two topographic positions in the line census method. The ECM fungal functional group dominated in the ridge route while not in the valley route, and the saprobic functional group dominated in the valley route but not in the ridge route. These findings indicated fungal communities differ between the two topographic positions, at least in the late summer mass emergence season (Table 2, Fig. 1).

To evaluate fungal diversity, temporal and spatial variation and their interaction should be taken into account (Braga-Neto et al. 2008), because fungal composition changed seasonally and spatially. Short-term observation was one of the weak points of this study, whereas the line route census in this study had advantages in systematic, simple, and convenient methodology and in covering a spatially heterogeneous environment within a forest and among forests. If the study period of these line censuses covered entire emergence seasons, the results of this study could be different. In fact, from the results of the seasonal variation of functional group composition, the ratio of ECM fungi to saprobic fungi changes seasonally from May to September, as a previous study showed in a warm temperate forest in Fukuoka, Japan (Murakami 1989). However, during rainy and post-rainy seasons, topographic locations in intermittent sampling for ECM fungi did not change much from May to September (Fig. 3b), similar to the results of the line census method. These results suggested that communities of fungal fruiting bodies on the upper slope area were dominated by ECM fungal species, whereas those on the lower slope area were not, and that the topography-specific ECM fungal fruiting body emergence pattern in this short-term study at one mass emergence season was probably a robust phenomenon throughout whole seasons.

Fungal functional groups and topography

We found, in these line censuses, that encounter rates of ECM fungi were greater on the ridge route than the valley route whereas those of saprobic fungi were greater on the valley route than the ridge route (see Fig. 1). Habitat partitioning of the fungal fruiting bodies emergence pattern

Table 3. Tree stem densities and basal area (BA) densities of stems ≥ 10 cm in DBH in a 50×50 m quadrat in Hanyama area. US and LS indicate the upper slope and lower slope area, respectively

Family	Species	Stem density (1/ha)				BA density (m ² /ha)		
		US	LS	Total	P	US	LS	Total
Aquifoliaceae	<i>Ilex goshiensis</i>	9.46	6.93	8	0.4881	0.12	0.09	0.10
Araliaceae	<i>Schefflera octophylla</i>	18.92	69.30	48	0.0484	1.00	2.43	1.82
Daphniphyllaceae	<i>Daphniphyllum teijsmannii</i>	18.92	0.00	8	0.1788	0.61	0.00	0.26
Ebenaceae	<i>Diospyros morrisiana</i>	18.92	0.00	8	0.1788	0.20	0.00	0.09
Ericaceae	<i>Rhododendron tashiroi</i>	141.91	76.23	104	0.0451	1.79	1.04	1.36
Ericaceae	<i>Vaccinium bracteatum</i>	94.61	6.93	44	0.0012	2.81	0.07	1.23
Euphorbiaceae	<i>Aleurites cordata</i>	0.00	20.79	12	0.1923	0.00	0.19	0.11
Fagaceae	<i>Castanopsis cuspidata</i>	37.84	0.00	16	0.0320	5.41	0.00	2.29
Fagaceae	<i>Pasania edulis</i>	435.19	76.23	228	<0.0001	11.44	1.66	5.79
Fagaceae	<i>Quercus phillyraeoides</i>	28.38	0.00	12	0.0756	10.90	0.00	4.61
Fagaceae	<i>Quercus salicina</i>	198.68	97.02	140	0.0149	17.13	12.06	14.20
Hamamelidaceae	<i>Distylium racemosum</i>	387.89	180.18	268	0.0008	17.26	8.79	12.37
Lauraceae	<i>Litsea acuminata</i>	0.00	55.44	32	0.0123	0.00	3.65	2.11
Lauraceae	<i>Neolitsea aciculata</i>	18.92	69.30	48	0.0484	0.32	3.15	1.96
Lauraceae	<i>Neolitsea sericea</i>	0.00	13.86	8	0.3332	0.00	0.35	0.20
Lythraceae	<i>Lagerstroemia subcostata</i>	0.00	6.93	4	0.5772	0.00	0.75	0.43
Myricaceae	<i>Myrica rubra</i>	47.30	0.00	20	0.0135	1.72	0.00	0.73
Myrsinaceae	<i>Ardisia sieboldii</i>	0.00	138.60	80	<0.0001	0.00	3.60	2.08
Myrsinaceae	<i>Myrsine seguinii</i>	198.68	76.23	128	0.0043	3.05	1.09	1.92
Myrtaceae	<i>Syzygium buxifolium</i>	66.23	0.00	28	0.0024	1.29	0.00	0.55
Symplocaceae	<i>Symplocos prunifolia</i>	170.29	83.16	120	0.0220	6.07	3.73	4.72
Theaceae	<i>Camellia japonica</i>	66.23	41.58	52	0.1533	1.20	0.70	0.91
Theaceae	<i>Camellia sasanqua</i>	0.00	6.93	4	0.5772	0.00	0.12	0.07
Theaceae	<i>Cleyera japonica</i>	151.37	180.18	168	0.1082	2.02	3.94	3.13
Theaceae	<i>Eurya japonica</i>	47.30	62.37	56	0.1923	0.54	0.77	0.67
Theaceae	<i>Ternstroemia gymnanthera</i>	56.76	20.79	36	0.0923	4.55	0.30	2.10
	Total	2213.81	1288.98	1680	<0.0001	89.43	48.47	65.79
	Survey area (m ²)	1057	1443	2500				

along a topographic gradient may be largely controlled by moisture and nutrients in the soil (Ogawa 1977; O'Dell et al. 1999; Trudell and Edmonds 2004). Trudell and Edmonds (2004) suggested that fungal fruiting body community differences were largely related to differences in ecosystem moisture and nitrogen abundance, and that within the ECM fungi, possible causal mechanisms involve mycelial morphology and carbon allocation within symbioses. In general, soils on ridges are thought to be drier and poorer in nutrients than those on slopes (Tokuchi et al. 1999). Thus, the fact that the ECM fungi are affected by nitrogen to a much greater degree than saprobic fungi results in lower ECM and higher saprobic proportions of total taxa at sites with higher nitrogen (i.e., the lower slope area) than at those with lower nitrogen (i.e., the upper slope area) (Fellner 1993; Wallenda and Kottke 1998; Trudell and Edmonds 2004).

Litter fungal fruiting body production in a tropical forest varied predictably in space and time, suggesting that litter fungi species are not randomly distributed at mesoscales (Braga-Neto et al. 2008). Saprobian fungal fruiting body abundance and/or diversity tended to be correlated with the amount of resource substrate, such as litter and dead wood (Yamashita and Hijii 2006; Yamashita et al. 2008). In general, the amount of litterfall varied with topography and was greatest at the valley bottom and decreased toward the ridges in the forests (Kusumoto and Enoki 2008). In contrast, the litter found at the top slope position decomposed slower than that at either the bottom or middle topographic

positions (Sariyildiz et al. 2005). However, there was much litter to some extent as a resource for saprobic fungi in both topographic positions. On the other hand, the topographic proportion of sapling fungi found in the intermittent sampling method changed less from May to August but much more from August to September (Fig. 3b). Because litter fungi were likely to be responding to water potential in the litter rather than rainfall per se (Braga-Neto et al. 2008), this may be because the saprobic fungal fruiting body emergence pattern was largely affected by some temporal environmental factor, such as moisture. Thus, we suggested that saprobic fungal fruiting body emergence in this study forest was affected by topographic position through the amount of litter abundance and temporal moisture condition.

Fungi, tree distribution, and topography

In this evergreen broad-leaved forest in Yakushima Island, Fagaceae, Hamamelidaceae, Lauraceae, and Ericaceae dominated (see Table 3). Especially Fagaceae, which have a mutualistic correlation with ectomycorrhizal fungi, dominated half of total BA in the upper slope area because four of the Fagaceae tree species distributed mainly on the upper slope area in these forests (see Table 2) (Aiba et al. 2001; Tsujino et al. 2006; Tsujino and Yumoto 2007). ECM is an important factor for the survival and growth of trees supported by ECM fungi as it stimulates their water and nutri-

ent uptake (Smith and Read 1997). Because the spatial distributions of fruiting bodies of ECM fungi are affected by the distribution of roots (Matsuda and Hijii 1998), topographic fungal fruiting body emergence in this study probably occurred because ECM fungi have a mutualistic partnership with these trees, and thus they have also a spatial correlation with these trees.

Furthermore, mycorrhizal-supported families of trees such as Fagaceae and Ericaceae were distributed mainly on the upper slope area and dominated 55.3% of BA in the upper slope area of the study quadrat compared to 30.6% in the lower slope area (see Table 3). In fact, Fagaceae tree species such as *Pasania edulis*, *Castanopsis cuspidate*, and *Quercus acuta* and Ericaceae tree species such as *Rhododendron tashiroi* and *Vaccinium bracteatum* distributed mainly on the ridge area in evergreen broad-leaved forests in Amami Ohshima Island, Okinawa Island, and other study plots in Yakushima Island (Hara et al. 1996; Aiba et al. 2001; Enoki 2003; Tsujino et al. 2006). Thus, we suggest that the symbiosis of mycorrhizal fungi with trees was one of the key factors affecting topography-specific tree distribution patterns as a kind of extended function of the plant roots in a stressful environment such as a ridge.

Acknowledgments We thank our friends and colleagues in Yakushima for their hospitality and help during the fieldwork. We are also grateful to Yakushima Forest Environment Conservation Center for permission to undertake the research. Sarugoya-committee and Field Research Center of Primate Research Institute of Kyoto University offered us excellent facilities. We thank two anonymous reviewers for their helpful suggestions and comments on the manuscript. This research was partly supported by the Grant for the Biodiversity Research of the 21st Century COE (A14), Research Project “Sustainability and biodiversity assessment on forest utilization option” and “A new cultural and historical exploration into human-nature relationships in the Japanese archipelago” of the Research Institute for Humanity and Nature, and a Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists for R.T.

References

- Aiba S, Hill DA, Agetsuma N (2001) Comparison between old-growth stands and secondary stands regenerating after clear-felling in warm-temperate forests of Yakushima, southern Japan. *For Ecol Manag* 140:163–175
- Ashton PMS, Gunatilleke CVS, Gunatilleke IAUN (1995) Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *J Trop Ecol* 11:263–279
- Bazzaz FA (1991) Habitat selection in plants. *Am Nat* 137:S116–S130
- Bills GF, Holtzman GI, Miller OK Jr (1986) Comparison of ectomycorrhizal-basidiomycete communities in red spruce versus northern hardwood forests of West Virginia. *Can J Bot* 64:760–768
- Bonet JA, Fischer CR, Colinas C (2004) The relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi in *Pinus sylvestris* forests of the central Pyrenees. *For Ecol Manag* 203:157–175
- Braga-Neto R, Luizão RCC, Magnusson WE, Zuquim G, Castilho CV (2008) Leaf litter fungi in a Central Amazonian forest: the influence of rainfall and topography on the distribution of fruiting bodies. *Biodivers Conserv* 17:2701–2712
- Daws M, Person RH, Burslem DFRP, Mullins CE, Dalling JW (2005) Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panamá. *Plant Ecol* 179:93–105
- Dickson BG, Beier P (2007) Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. *J Zool* 271:270–277
- Dighton J, Poskitt JM, Howard DM (1986) Changes in occurrence of basidiomycete fruit bodies fruiting forest stand development: with specific reference to mycorrhizal species. *Trans Br Mycol Soc* 87:163–171
- Dix NJ, Webster J (1995) *Fungal ecology*. Chapman & Hall, London
- Endo M (1972) Plant sociological observations on the terrestrial larger fungi in an evergreen broad-leaved forest (in Japanese with English synopsis). *Jpn J Ecol* 22:51–61
- Enoki T (2003) Microtopography and distribution of canopy trees in a subtropical evergreen broad-leaved forest in the northern part of Okinawa Island, Japan. *Ecol Res* 18:103–113
- Fellner R (1993) Air pollution and mycorrhizal fungi in central Europe. In: Pegler DN, Boddy L, Ing B, Kirk PM (eds) *Fungi of Europe: investigation, recording, and conservation*. Royal Botanic Gardens, Kew, pp 239–250
- Fujita H (1989) Succession of higher fungi in a forest of *Pinus densiflora* (in Japanese with English summary). *Trans Mycol Soc Jpn* 30:125–147
- Fukiharu T, Kato M (1997) An analysis on the spatial distribution patterns of basidiocarps of Agaricales in a *Castanopsis*-dominated forest in Kyoto. *Mycoscience* 38:37–44
- Hara M, Hirata K, Fujihara M, Oono K (1996) Vegetation structure in relation to micro-landform in an evergreen broad-leaved forest on Amami Ohshima Island, south-west Japan. *Ecol Res* 11:325–337
- Harms KE, Condit R, Hubbell SP, Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* 89:947–959
- Hibbett DS, Gilbert LB, Donoghue MJ (2000) Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. *Nature (Lond)* 407:506–508
- Imazeki R, Hongo T (1987) Coloured illustrations of mushrooms of Japan, vol I (in Japanese). Hoikusha, Osaka
- Imazeki R, Hongo T (1989) Coloured illustrations of mushrooms of Japan, vol II (in Japanese). Hoikusha, Osaka
- Kranabetter JM, Friesen J, Gamiet S, Koeger P (2005) Ectomycorrhizal mushroom distribution by stand age in western hemlock–lodgepole pine forests of northwestern British Columbia. *Can J For Res* 35:1527–1539
- Kusumoto B, Enoki T (2008) Contribution of a liana species, *Mucuna macrocarpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest. *J For Res* 13:35–42
- Laganà A, Angiolini C, Loppi S, Salerni E, Perini C, Barluzzi C (2002) Periodicity, fluctuations and successions of macrofungi in fir forests (*Abies alba* Miller) in Tuscany, Italy. *For Ecol Manag* 169:187–202
- Matsuda Y, Hijii N (1998) Spatiotemporal distribution of fruitbodies of ectomycorrhizal fungi in an *Abies firma* forest. *Mycorrhiza* 8:131–138
- Mitsuta S, Nagamasu H (1984) Flora of vascular plants (ferns, fern allies and phanerogams) of the Yaku-shima Wilderness area. In: Nature Conservation Bureau, Environment Agency of Japan (ed) *Conservation reports of the Yaku-shima wilderness area*, Kyushu, Japan. The Nature Conservation Society of Japan, Tokyo, pp 103–286
- Molina R, Massicotte HB, Trappe JM (1992) Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen MF (ed) *Mycorrhizal functioning*. Chapman & Hall, London, pp 357–423
- Moody M, Meentemeyer RK (2001) Environmental factors influencing spatial patterns of shrub diversity in chaparral, Santa Ynez Mountains, California. *J Veg Sci* 12:41–52
- Murakami Y (1989) Spatial changes of species composition and seasonal fruiting of the Agaricales in *Castanopsis cuspidata* forest. *Trans Mycol Soc Jpn* 30:89–103
- Nagamatsu D, Miura O (1997) Soil disturbance regime in relation to micro-scale landforms and its effects on vegetation structure in a hilly area in Japan. *Plant Ecol* 133:191–200
- O'Dell TE, Ammirati JF, Schreiner EG (1999) Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone. *Can J Bot* 77:1699–1711

- Ogawa M (1977) Ecology of higher fungi in *Tsuga diversifolia* and *Betula ermani*-*Abies mariesii* forests of subalpine zone. *Trans Mycol Soc Jpn* 18:1-19
- R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Richard F, Moreau P-A, Selosse M-A, Gardes M (2004) Diversity and fruiting patterns of ectomycorrhizal and saprobic fungi in an old-growth Mediterranean forest dominated by *Quercus ilex* L. *Can J Bot* 82:1711-1729
- Sariyildiz T, Anderson JM, Kucuk M (2005) Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biol Biochem* 37:1695-1706
- Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic Press, London
- Stokland J, Kauserud H (2004) *Phellinus nigrolimitatus*: a wood-decomposing fungus highly influenced by forestry. *For Ecol Manag* 187:333-343
- Straatsma G, Krisai-Greilhuber I (2003) Assemblage structure, species richness, abundance, and distribution of fungal fruit bodies in a seven year plot-based survey near Vienna. *Mycol Res* 107:632-640
- Tagawa H (1980) Vegetation on the western slope of Mt. Kuniwaridake, Yakushima Island (in Japanese). *Sci Rep Kagoshima Univ* 29:121-137
- Takyu M, Aiba S, Kitayama K (2002) Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecol* 159:35-49
- Tokuchi N, Takeda H, Yoshida K, Iwatsubo G (1999) Topographical variations in a plant-soil system along a slope on Mt. Ryuo, Japan. *Ecol Res* 14:361-369
- Trudell SA, Edmonds RL (2004) Macrofungus communities correlate with moisture and nitrogen abundance in two old-growth conifer forests, Olympic National Park, Washington, USA. *Can J Bot* 82: 781-800
- Tsujino R, Yumoto T (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. *Ecol Res* 19: 291-300
- Tsujino R, Yumoto T (2007) Spatial distribution patterns of trees at different life stages in a warm temperate forest. *J Plant Res* 120: 687-695
- Tsujino R, Yumoto T (2008) Seedling establishment of five evergreen tree species in relation to topography, sika deer (*Cervus nippon yakushimae*) and soil surface environments. *J Plant Res* 121: 537-546
- Tsujino R, Yumoto T (2009) Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. *J Anim Ecol* 78:119-125
- Tsujino R, Takafumi H, Agetsuma N, Yumoto T (2006) Variation in tree growth, mortality and recruitment among topographic positions in a warm-temperate forest. *J Veg Sci* 17:281-290
- Wallenda T, Kottke I (1998) Nitrogen deposition and ectomycorrhizas. *New Phytol* 139:169-187
- Yamashita S, Hijii N (2006) Spatial distribution of the fruiting bodies of Agaricales in a Japanese red pine (*Pinus densiflora*) forest. *J For Res* 11:181-189
- Yamashita S, Hattori T, Momose K, Nakagawa M, Aiba M, Nakashizuka T (2008) Effects of forest use on aphyllophoraceous fungal community structure in Sarawak, Malaysia. *Biotropica* 40: 354-362