Bleached Leaf Litter of Forest Trees and Associated Fruiting Bodies of Fungi in Tropical Asia and Australia

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Fungi play crucial roles in the decomposition of lignin in leaf litter, and fungal decomposition of lignin often leads to whitening, or bleaching, of leaf litter. The area of bleached portions on leaf surfaces was quantified along a climatic gradient at 15 sites in tropical, subtropical, and temperate evergreen forests in Asia and Australia. Bleached portions accounted for 3.5% to 30.8% on average of total leaf area and were significantly and positively correlated with mean annual temperature of the study sites. Another analysis showed that the number of tree species and stems whose leaf litter was bleached was higher in a subtropical forest than in a cool temperate or a subalpine forest. Fruiting bodies of eight fungal genera (*Coccomyces*, *Lophodermium*, and *Xylaria* in Ascomycota and *Crinipellis, Gymnopus, Marasmiellus, Marasmius*, and *Mycena* in Basidiomycota) were observed on the surface of bleached portions of leaf litter from a total of 78 tree species in 29 plant families collected in tropical and subtropical forests.

Key words: bleaching, fungal diversity, host tree specificity, lignin decomposition, ligninolytic fungi

1. Introduction

Fungi play crucial roles in the decomposition of lignin in leaf litter[1]. Lignin is a major structural component of leaf litter, and is resistant to decomposition[2]. Fungal decomposition of lignin often leads to whitening, or "bleaching", of leaf litter[1]. Previous studies have shown the emergence of fruiting bodies of macrofungi in Ascomycota and Basidiomycota on the surface of bleached portions of leaf litter, and demonstrated that their mycelia were responsible for lignin decomposition there[3].

A wide array of evidence has suggested a climatic gradient in the occurrence of bleached portions of leaf litter and associated fungi. For example, Osono in 2006[4] demonstrated that the extent of bleached area on leaf litter was greater in tropical than in temperate forests. Similarly, Osono in 2011[5] found a tendency for leaf litter of broad-leaved trees from tropical forests to harbor more ligninolytic fungal species than that from forests of cooler regions. Recently, Osono in 2015[6] reported that ligninolytic macrofungi in Basidiomycota were richer in a subtropical region than in a temperate or a subalpine region in Japan. However, the nature of the climatic controls of the extent of bleached portions and the association of bleaching fungi with host trees still remain unclear.

The purpose of the present study was to quantify the area of bleached portions on leaf surfaces and the number of tree species and stems whose leaf litter was bleached along a climatic gradient in tropical, subtropical, and temperate evergreen forests in Asia and Australia to explore possible climatic and geographic effects on the occurrence of bleached leaf litter.

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Macrofungal genera of fruiting bodies associated with the bleached portions of leaf litter were examined at four sites to examine the association of bleaching fungi with host tree species.

2. Materials and Methods

Bleached leaf litter of tree species was examined at 15 sites in tropical, subtropical, and temperate evergreen forests in Asia and Australia (Table 1). The latitude of the sites ranged from 35°10'N to 33°39'S, longitude ranged from 98°54'E to 153°06'E, elevation ranged from 61 to 774 m, mean annual temperature (MAT) ranged from 14.9°C to 29.0°C, and mean annual precipitation (MAP) ranged from 1220 to 3600 mm (Table 1). At each site, 10 quadrats (15 cm × 15 cm) were set on the forest floor along a 9-m transect at 1-meter intervals. Partly decomposed leaves that had undergone decomposition but retained more than half of their original leaf area were collected from beneath the surface leaf litter. The areas of these leaf materials were measured and used for calculation of the proportion of bleached area with respect to the total leaf area, and calculation of leaf mass per area (LMA) of bleached and surrounding unbleached portions of bleached leaf litter, and for estimation of the content of acid-unhydrolyzed residue (AUR) for bleached and unbleached portions, according to the method described previously[7].

By combining data of a forest census in a subtropical forest at Yanbaru in Japan[8] with the results of the present study, I calculated the number of tree species and stems whose leaf litter was bleached. Similar analyses were performed using data from a reported forest censuses plus bleached leaf litter in a cool temperate forest[9,10] and a subalpine forest[7,11] (Table 2).

Bleached leaf litter was further examined for the tree species and the genera of fungal fruiting bodies associated with the bleached portions at three study sites. Fieldwork was conducted seven times from March 2007 to January 2008 in a subtropical evergreen forest in Yanbaru, Okinawa, Japan, twice in February and June 2009 in a lowland tropical rainforest in Lambir Hill National Park, Sarawak, Malaysia, and twice in December 2008 and August 2009 in a lowland tropical rainforest in Daintree National Park, Queensland, Australia. Tree species of leaves were identified morphologically using binoculars (20× and 40×). Identification of fungal genera of fruiting bodies was primarily made macroscopically, and tissues of some small fruiting bodies were further analyzed for the DNA sequence of amplicions of the rDNA ITS region according to the method described previously[6]. Additional samples were preliminarily examined at Kirstenbosch National Botanical Garden in Cape Town, South Africa in October 2009.

3. Results and Discussion

Bleached portions accounted on average for 3.5% to 30.8% of total leaf area at the 15 sites investigated in the present study (Table 1). The bleached area (%) with respect to the total leaf area was significantly and positively correlated with MAT (Pearson's R=0.55, n=15, Probability<0.05) but was not significantly correlated with the latitude, longitude, elevation, or MAP (Pearson's R=-0.36 to 0.32, Probability>0.05). Leaf mass per area (LMA) and AUR content of bleached portions were consistently lower than those of unbleached portions (Table 1).

A forest census performed in a subtropical forest at Yanbaru in Japan[8] reported 1374 tree stems of 57 tree species within a 1-ha permanent plot located in the same area as that in the present study. Applying the results shown in Table 3 to these census data revealed that bleaching was noticeable for leaf litter of 29 (51%) of the 57 tree species, corresponding to 1204 (88%) of the 1374 stems (Table 2). Similar analyses using the data of forest census plus bleached leaf litter in a cool temperate forest[9,10] and a subalpine forest[7,11] provided further

Table 1. Bleached area (% total leaf area) on dead leaves of tree species and leaf mass per area (LMA) and content of acid unhydrolyzable residues (AUR) of bleached (BL) and unbleached portions (UB) on the leaves.

Site	Country	Forest type	Latitude	Longitude	Elevation (m)	MAT (°C)	MAP (mm)	Sampling	Bleached area (%)	LMA (mg/cm^2) BL	LMA (mg/cm^2) UB	AUR (mg/g) BL	AUR (mg/g) UB	Reference
Kamogawa	Chiba, Japan	Temperate evergreen forest	35°10'N	140°07'E	195	15.9	1790	Aug 2011	8.4 ± 1.7	9.8 ± 0.6	12.0 ± 0.6	284	370	This study
Otsu	Shiga, Japan	Temperate evergreen forest	35°00'N	135°51'E	130	14.9	1530	Jul 2010	5.4 ± 1.2	7.5 ± 0.7	9.6 ± 0.6	294	353	This study
Ashizuri	Kochi, Japan	Temperate evergreen forest	32°44'N	132°59'E	271	18.2	2479	Jul 2010	17.5 ± 1.9	8.3 ± 0.3	9.5 ± 0.5	304	367	This study
Aya	Miyazaki, Japan	Temperate evergreen forest	32°01'N	131°11'E	241	16.2	2757	Sept 2009	15.6 ± 1.0	10.2 ± 0.7	11.6 ± 0.6	301	384	This study
Yanbaru	Okinawa, Japan	Subtropical evergreen forest	26°44'N	128°14'E	275	22.9	2197	Dec 2004	22.4 ± 1.9	8.1 ± 0.5	10.0 ± 0.5	281	378	19
Ishigaki	Okinawa, Japan	Subtropical evergreen forest	24°25'N	124°10'E	72	24.3	2107	Sept 2007	30.8 ± 2.1	8.5 ± 0.5	10.7 ± 0.5	290	396	This study
Doi Suthep	Chiang Mai, Thailand	Tropical hill evergreen forest	18°48'N	98°54'E	774	20.6	2016	Feb 2003	7.9 ± 7.5	7.9 ± 1.2	11.0 ± 0.8	293	348	4
Sakaerat	Nakhon Ratchasima, Thailand	Tropical dry evergreen forest	14°29'N	101°54'E	576	26.0	1210	Feb 2003	16.6 ± 5.6	6.0 ± 0.2	9.8 ± 0.7	299	487	4
Penang Hill	Penang, Malaysia	Tropical rainforest	5°23'N	100°15'E	441	26.0	2000	Dec 2007	18.1 ± 2.9	7.5 ± 0.5	9.6 ± 0.7	336	505	This study
Lambir Hill	Sawarak, Malaysia	Lowland tropical rainforest	4°11'N	114°02'E	61	27.0	2740	Feb 2009	26.2 ± 4.2	9.3 ± 0.8	13.0 ± 0.7	358	472	This study
Sodong	South Sumatra, Indonesia	Tropical secondary forest	3°51'S	103°58'E	144	29.0	2610	Sept 2007	10.7 ± 0.8	5.2 ± 0.2	7.9 ± 0.4	335	466	12
Melbau	South Sumatra, Indonesia	Tropical secondary forest	3°51'S	103°58'E	144	29.0	2610	Sept 2007	27.1 ± 2.8	4.6 ± 0.2	7.9 ± 0.3	325	493	12
Daintree	QLD, Australia	Lowland tropical rainforest	16°06'S	145°26'E	102	25.6	3600	Dec 2008	11.1 ± 1.3	6.5 ± 0.2	7.8 ± 0.2	365	437	This study
Lamington	QLD, Australia	Subtropical rainforest	28°08'S	153°06'E	691	21.1	1341	Aug 2009	13.9 ± 2.1	12.3 ± 1.6	14.4 ± 1.7	374	456	This study
Ku-ring-gai Chase	NSW, Australia	Temperate rainforest	33°39'S	151°12'E	146	18.3	1220	Dec 2008	3.5 ± 0.8	11.5 ± 1.3	13.4 ± 1.6	314	451	This study

Table 2. Relative abundance of tree species of which bleached portions were observed on dead leaves.

Site	Climate	MAT	Number of tree species	Number of tree stems	Reference
Mt. Ontake	Subalpine	2°C	2/ 9 (22%)	125/1381 (9%)	7, 11
Ashiu	Cool temperate	9°C	10/40 (25%)	597/1572 (38%)	9, 10
Yanbaru	Subtropical	23°C	29/57 (51%)	1204/1374 (88%)	This study, 8

Data of vegetation survey within a one hectare permanent plot was used to calculate the respective relative abundances.

support for a climatic gradient in the bleached leaf litter in terms of the numbers of tree species and of stems, which were more abundant at warmer climates (Table 2).

The positive correlation between the bleached area and MAT suggest a temperature control on the abundance and activity of bleaching fungi. This is consistent with previous observations that ligninolytic fungi were more abundant in forests with warmer climates[4-6]. Care must be taken, however, as the extent of bleached portions can also be affected by factors other than temperature, including such factors as forest age, nutrient status, or stages of leaf litter decomposition[12-14]. Nonetheless, a few pure culture studies indicated that the fungal decomposition of lignin was sensitive to temperature[15-17], supporting my finding that temperature is a major factor affecting the occurrence of bleached leaf litter along the climatic gradient.

Fruiting bodies of eight fungal genera (three in Ascomycota and five in Basidiomycota) were observed on the surface of bleached portions of leaf litter for a total of 78 tree species in 29 plant families collected at four sites (Table 3).

A total of 32, 24, 20, and 2 tree species were found to be associated with fungal fruiting bodies on bleached portions of their leaf litter at Yanbaru, Lambir Hills, Daintree, and Kirstenbosch, respectively (Table 3, Fig. 1). Tree species in Dipterocarpaceae at Lambir Hills, Lauraceae at Yanbaru, Lambir Hills, and Daintree, Myrtaceae at four sites, and Theaceae at Yanbaru were frequently associated with fungal fruiting bodies on their bleached portions.

Fruiting bodies of *Coccomyces, Lophodermium*, and *Xylaria* were encountered on leaf litter of 42, 41, and 3 tree species, respectively, and those of *Crinipellis, Gymnopus, Marasmiellus, Marasmius*, and *Mycena* were encountered on leaf litter of 12, 5, 2, 10, and 26 tree species, respectively (Table 3, Fig. 2). One to six fungal genera were associated with each tree species.

Species in the eight fungal genera have been shown to have ligninolytic activity[3]. Of these, rhytismataceous genera in Ascomycota are known to include endophytic and pathogenic species, and can be more host-specific than litter-inhabiting basidiomycetes[18]. Future studies are needed to examine the species identity of these ligninolytic fungal genera and to verify the host range and geographic patterns of individual fungal species.

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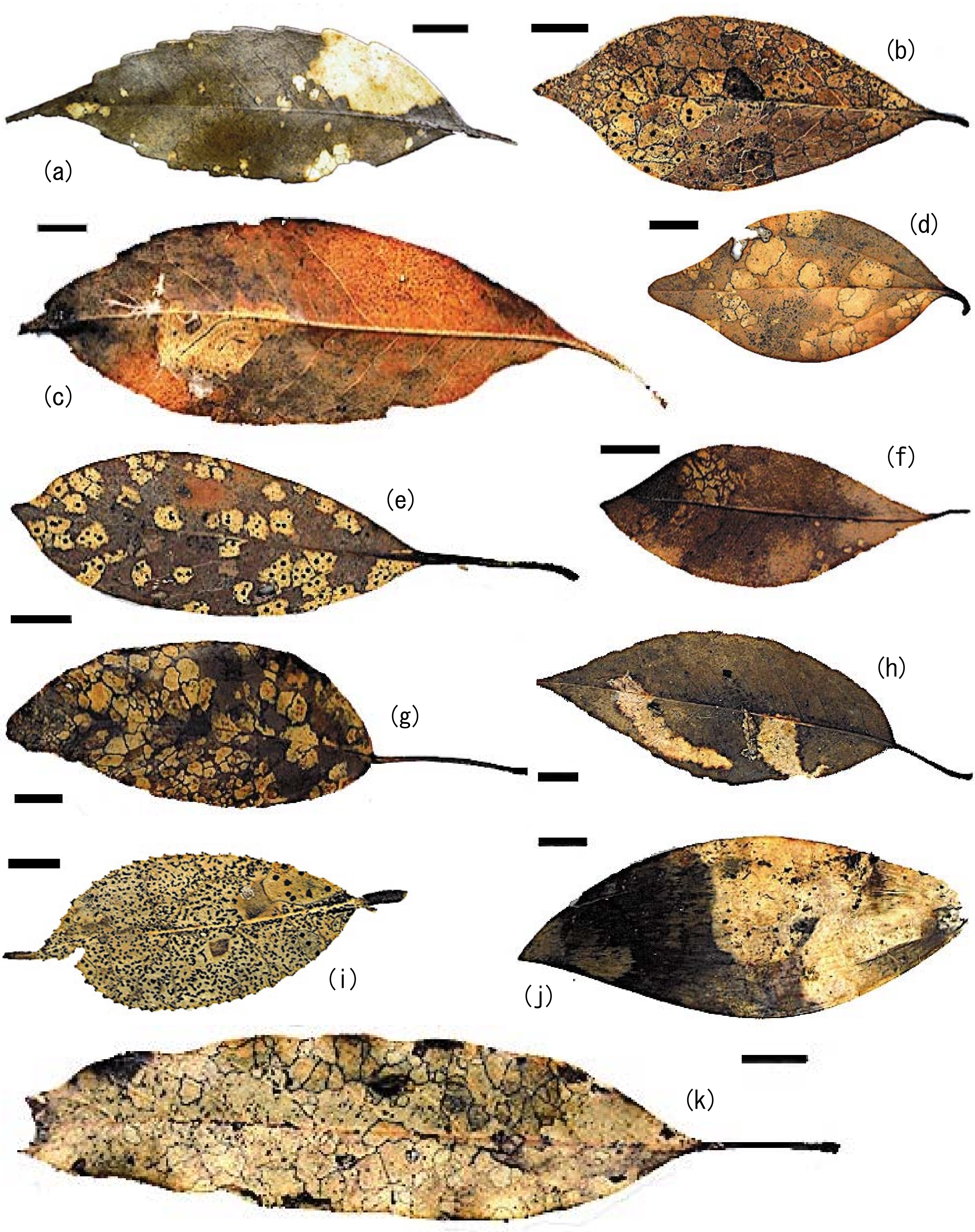

Fig. 1. Bleached leaf litter collected in a subtropical forest at Yanbaru, Japan. (a) *Castanopsis sieboldii*, (b) *Distylium racemosum*, (c) *Schima wallichii*, (d) *Cinnamomum doederleinii*, (e) *Persea thunbergii*, (f) *Syzygium buxifolium*, (g) *Elaeocarpus japonicus*, (h) *Tricalysia dubia*, (i) *Camellia japonica*, (j) *Podocarpus nagi*, (k) *Quercus miyagii*. Bars are 1 cm.

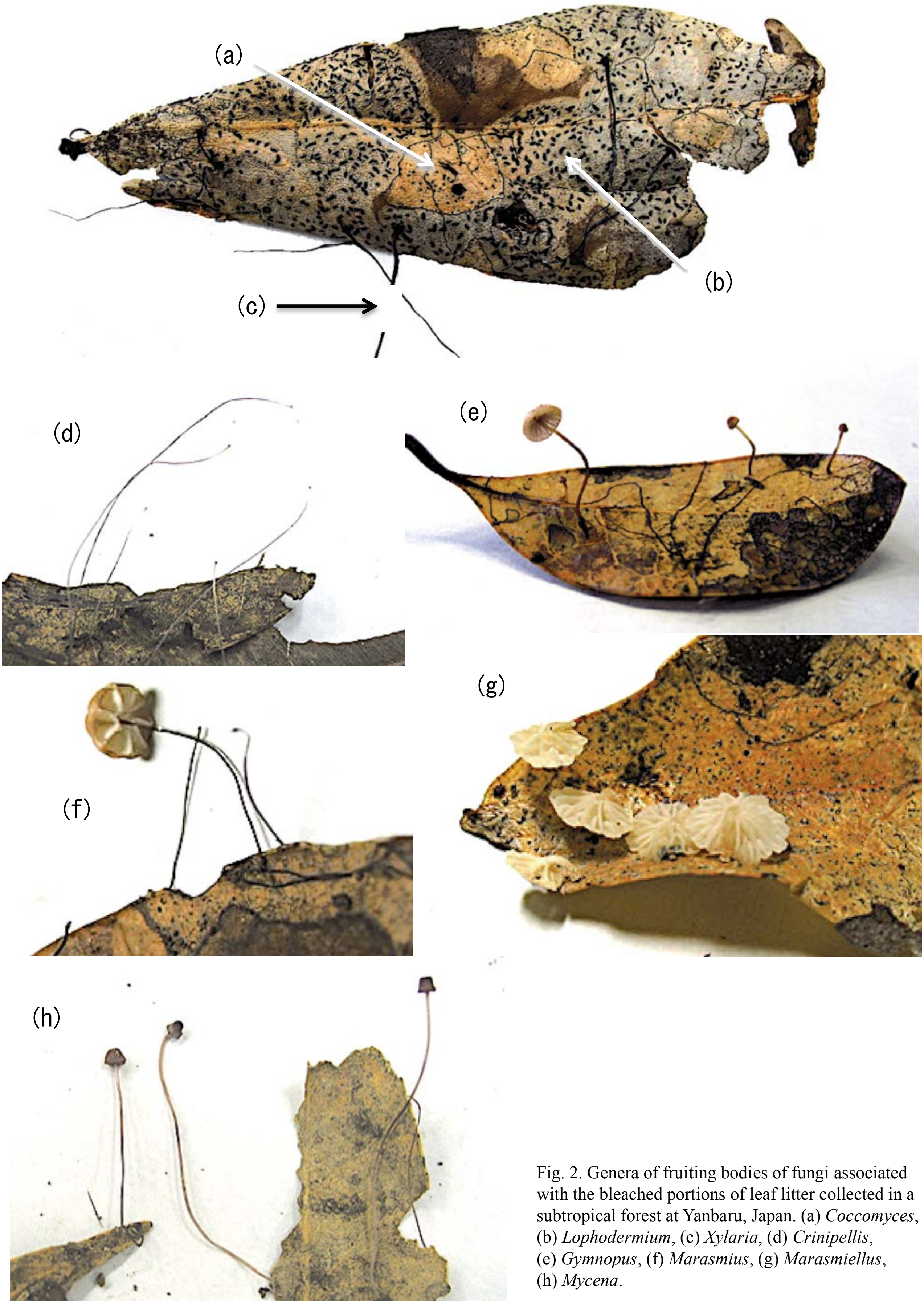

Fig. 2. Genera of fruiting bodies of fungi associated with the bleached portions of leaf litter collected in a subtropical forest at Yanbaru, Japan. (a) *Coccomyces*, (b) *Lophodermium*, (c) *Xylaria*, (d) *Crinipellis*, (e) *Gymnopus*, (f) *Marasmius*, (g) *Marasmiellus*, (h) *Mycena*.

Table 3. Presence of fruiting bodies of eight fungal genera on bleached portions of dead leaves of tree species.

Tree species	Plant family[a]	*Cocco-myces*	*Lopho-dermium*	*Xylaria*	*Crini-pellis*	*Gymno-pus*	*Maras-miellus*	*Maras-mius*	*Mycena*	Number of fungal genera
(1) Yanbaru (Okinawa, Japan), Mar, May, Jun, Jul, Sept, Nov 2007 and Jan 2008[b]										
Ilex goshiensis	Aq		+					+	+	3
Ilex maximowicziana var. *kanehirae*	Aq		+		+			+	+	4
Dendropanax trifidus	Aa		+						+	2
Schefflera octophylla	Aa								+	1
Daphniphyllum teijismannii	Da					+		+	+	3
Elaeocarpus japonicus	El	+			+					2
Elaeocarpus sylvestris	El		+							1
Rhododendron tashiroi	Er		+							1
Vaccinium wrightii	Er	+	+							2
Antidesma rigida	Eu				+				+	2
Castanopsis sieboldii	Fa		+		+	+	+	+	+	6
Quercus miyagii	Fa		+						+	2
Distylium racemosum	Ha	+			+			+	+	4
Cinnamomum doederleinii	La	+							+	2
Neolitsea sericea	La	+	+					+		3
Persea thunbergii	La	+			+				+	3
Myrica rubra	Mc	+	+		+				+	4
Ardisia quinquegona	Ms				+				+	2
Myrsine seguinii	Ms		+	+	+				+	4
Syzygium buxifolium	Mt		+						+	2
Pinus luchuensis	Pi		+							1
Lasinathus sp.	Rb								+	1
Psychotria rubra	Rb								+	1
Randia canthioides	Rb		+						+	2
Meliosma squamulata	Sa		+		+			+	+	4
Heterosmilax japonica	Sm		+		+	+			+	4
Camellia japonica	Th	+	+	+					+	4
Camellia lutchuensis	Th	+	+							2
Camellia sasanqua	Th	+	+						+	3
Schima wallichii	Th				+	+	+		+	4
Ternstroemia gymnanthera	Th	+	+	+					+	4
Tutcheria virgata	Th								+	1
Number of tree species		11	20	3	12	4	2	7	25	32
(2) Lambir Hill (Sarawak, Malaysia), Feb and Jun 2009										
Anisophyllea corneri	An	+								1
Santiria sp.	Bu	+								1
Dacryodes rostrata f. *cuspidata*	Bu	+								1
Santiria megaphylla	Bu	+	+							2
Dipterocarpus globosus	Di		+							1
Dryobalanopsis aromatica	Di	+								1
Shorea beccariana	Di	+	+							2
Shorea macroptera	Di	+	+							2
Shorea parvifolia	Di	+	+							2
Shorea kunstleri	Di	+								1
Shorea acuta	Di	+								1
Shorea macroptera subsp. *baillonii*	Di	+								1
Shorea sp.1	Di		+							1
Shorea sp.3	Di		+							1
Shorea sp.4	Di	+								1
Shorea sp.5	Di	+								1
Lithocarpus luteus	Fa		+							1

Table 3. Continued.

Tree species	Family[a]	*Cocco-myces*	*Lopho-dermium*	*Xylaria*	*Crini-pellis*	*Gymno-pus*	*Maras-miellus*	*Maras-mius*	*Mycena*	Number of fungal genera
Alseodaphne insignis	La	+								1
Endiandra clavigera	La	+								1
Pternandra coerulescens	Me	+								1
Ficus sp.	Mr	+								1
Eugenia megalophylla	Mt		+							1
Syzygium longiflorum	Mt	+								1
Pentace borneensis	Ti	+								1
Number of tree species		19	9	0	0	0	0	0	0	24
(3) Daintree (QLD, Australia), Dec 2008 and Aug 2009										
Normanbya normanbyi	Ae		+							1
Erycibe coccinea	Co		+							1
Elaeocarpus grandis	El	+								1
Beilschmiedia bancroftii	La	+								1
Cryptocarya grandis	La	+	+						+	3
Cryptocarya mackinnoniana	La	+								1
Cryptocarya murrayi	La	+								1
Endiandra leptodendron	La		+							1
Endiandra microneura	La	+								1
Litsea leefeana	La	+								1
Palmeria scandens	Mn					+				1
Acmena graveolens	Mt	+	+							2
Syzygium corniflorum	Mt	+						+		2
Syzygium erythrocalyx	Mt	+	+							2
Syzygium gustavioides	Mt		+							1
Syzygium kuranda	Mt	+	+							2
Syzygium sayeri	Mt		+							1
Musgravea heterophylla	Pr	+						+		2
Brombya platynema	Rt							+		1
Smilax australis	Sm		+							1
Number of tree species		12	10	0	0	1	0	3	1	20
(4) Kirstenbosch (Cape Town, South Africa), Oct 2009										
Cunonia capensis	Cu		+							1
Syzygium pondonense	Mt		+							1
Number of tree species		0	2	0	0	0	0	0	0	2
Total number of tree species		42	41	3	12	5	2	10	26	78

[a]Plant family: Aa, Araliaceae; Ae, Arecaceae; An, Anisophylleaceae; Aq, Aquifoliaceae; Bu, Burceraceae; Co, Convolvulaceae; Cu, Cunoniaceae; Da, Daphniphyllaceae; Di, Dipterocarpaceae; El, Elaeocarpaceae; Er, Ericaceae; Eu, Euphorbiaceae; Fa, Fagaceae; Ha, Hamamelidaceae; La, Lauraceae;Mc, Myricaceae; Me, Melastomataceae; Mn, Monimiaceae; Mr, Moraceae; Ms, Myrsinaceae; Mt, Myrtaceae; Pi, Pinaceae; Pr, Proteaceae; Rb, Rubiaceae; Rt, Rutaceae; Sa, Sabiaceae; Sm, Smilacaceae; Th, Theaceae; Ti, Tiliaceae.

[b]Bleached portions were noted on leaf litter, but no fruiting bodies of fungi were observed for additional seven tree species: *Podocarpus nagi* (Podocarpaceae), *Neolitsea aciculata* (Lauraceae), *Persea japonica* (Lauraceae), *Symplocos okinawaensis* (Symplocaceae), *Mucuna macrocarpa* (Leguminosae), *Sapium japonicum* (Euphorbiaceae), and *Tricalysia dubia* (Rubiaceae).

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