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ECOLOGICAL DISTRIBUTION OF HOMOBARIC AND HETEROBARIC LEAVES IN TREE SPECIES OF MALAYSIAN LOWLAND TROPICAL RAINFOREST[1]

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Tree species can generally be classified into two groups, heterobaric and homobaric leafed species, according to whether bundle-sheath extensions (BSEs) are found in the leaf (heterobaric leaf) or not (homobaric leaf). In this study, we study whether the leaf type is related to the growth environment and/or life form type, even in a tropical rain forest, where most trees have evergreen leaves that are generally homobaric. Accordingly, we investigated the distribution of leaf morphological differences across different life forms of 250 tree species in 45 families in a tropical rainforest. In total, 151 species (60%) in 36 families had homobaric leaves, and 99 species (40%) in 21 families had heterobaric leaves. We found that the proportion of heterobaric and homobaric leaf species differed clearly across taxonomic groups and life form types, which were divided into five life form types by their mature tree heights (understory, subcanopy, canopy, and emergent species) and as canopy gap species. Most understory (94%) and subcanopy (83%) species such as Annonaceae had homobaric leaves. In contrast, heterobaric leaf trees appeared more frequently in the canopy species (43%), the emergent species (96%) (such as Dipterocarpaceae), and the canopy gap species (62%). Our results suggest that tree species in the tropical rainforest adapt to spatial differences in the environmental conditions experienced at the mature height of each tree species, such as light intensity and vapor pressure difference, by having differing leaf types (heterobaric or homobaric) because these types potentially have different physiological and/or mechanical functions.

Key words: bundle-sheath extension; heterobaric leaf; homobaric leaf; life form type; morphology; tropical forest.

The morphological characteristics of plant organs are important in adaptation to growth environments because they are central to functions such as photosynthesis, movement of water, and absorption by root (Esau, 1960; Larcher, 2003). Plant leaves display diverse morphological characteristics across species, including their shape, size, and structure (Gifford and Foster, 1989; Thomas and Ickes, 1995; Dominy et al., 2003; Kenzo et al., 2004). Tree species can be classified into two groups, heterobaric and homobaric leaf species, according to the occurrence of bundle-sheath extensions (BSEs) in the leaf (Neger, 1918; Wylie, 1951; Terashima, 1992). BSEs are formed by parenchyma or sclerenchyma cells of the vascular bundle sheath, which extend to the epidermis on both sides of the leaf in heterobaric leaf trees (Wylie, 1943, 1952). As a result, the mesophyll of heterobaric leaves is separated into many small "bundle-sheath extension compartments" by BSEs (Terashima, 1992). In contrast, homobaric leaves lack BSEs and the internal structure of the leaf is relatively homogenous.

These leaf types differ not only in structural traits but also in mechanical and functional characteristics. For example, BSEs in heterobaric leaves may give mechanical support to the leaf blade (Wylie, 1952; Esau, 1960), act as a water conduit (Wylie, 1943), or cause non-uniform photosynthesis (Siebke and Weis, 1995; Mott and Buckley, 2000; West et al., 2005). Homobaric leaves, in contrast, have larger lateral movements of gases in the leaf than heterobaric leaves (Parkhurst, 1994; Rhizopoulou and Psaras, 2003; Pieruschka et al., 2005, 2006; but see Morison et al., 2005).

These morphological and functional differences between the two leaf types may relate to their growth environments and/or life form type (such as emergent, canopy, subcanopy, understory, and canopy gap species). Recent studies documented the strong ecological linkage among growth environments and/or life form (or adult tree size) with respect to tree growth and leaf physiological and morphological characteristics (e.g., Thomas and Bazzaz, 1999; Reich, 2000; Thomas, 2003; Sack et al., 2005; King et al., 2006; Sack and Frole, 2006). Some authors have suggested that heterobaric leaf trees will preferentially be found in deciduous forests, which have dry and/or cold seasons (Wylie, 1952; Terashima, 1992). In contrast, the proportion of homobaric leaf trees may increase in wet and warm regions, which are usually dominated by evergreen tree species. Many more evergreen tree species have homobaric leaves than deciduous tree species (Wylie, 1952; McClendon, 1992; Kashimura et al., 2000; Boeger et al., 2004). Consequently, in the tropical rainforest, most tree species may have homobaric leaves because the forest condition is humid all year round and consists mainly of evergreen trees, compared with other forest biomes.

In this study, we suppose that leaf type is correlated with growth environment and/or life form type rather than with forest biome, even in a tropical rainforest in which most trees have evergreen leaves. The spatial distribution of microenvi-

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ronmental factors such as light intensity, temperature, and humidity varies significantly even in a humid tropical rainforest (Whitmore, 1984, 1998). In particular, the upper canopy of the forest undergoes significant desiccating conditions because of the high light intensities, high temperature, and low humidity, whereas the interior of tropical rainforest is light-deficient and humid (Aoki et al., 1978; Yoda, 1978; Kumagai et al., 2001). Canopy gaps are also dry and are exposed to high irradiance compared with the forest floor under the closed canopy (Whitmore, 1998). As a result of the frequent water stress conditions in the canopy and in canopy gaps, most tree species may display heterobaric leaves even in tropical rainforests. On the other hand, homobaric leaf trees should be better represented in forest understory species because of the humid environment. If the proportion of species of each leaf type varies with location in the forest, this may also influence stand-level photosynthesis and transpiration traits, which may differ between leaf types (Terashima, 1992). However, only limited information is available on the distribution pattern and/or environmental response to different growth conditions of heterobaric and homobaric leaf trees.

In the present work, we investigated the distribution of leaf morphological differences across ecological types, distinguishing between heterobaric and homobaric leaf species, in different life forms of 250 tree species in 45 families in a tropical rainforest, which has high species richness, many life forms and complex microenvironments. In particular, we focused on the relation between each leaf type and their life form types, such as emergent, canopy, subcanopy, understory, and canopy gap species.

MATERIALS AND METHODS

Study site—The study was carried out in the Canopy Biology Plot (8 ha, 200 × 400 m; Inoue et al., 1994) and in the Canopy Crane Plot (4 ha, 200 × 200 m; Sakai et al., 2002) in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°12′ N, 113°50′ E, 150–250 m a.s.l.), in 2005. The mean height of the canopy in the stand was about 30–40 m; some emergent trees reached 50–70 m. The area has a humid tropical climate, with weak seasonal changes in rainfall and temperature (Kato et al., 1995). The annual precipitation at the Canopy Crane Plot (there is one weather station) averaged 2540 mm from 2000 to 2004. The average annual temperature from 2000 to 2003 was 26.3°C, with monthly means that varied from 25.6°C in February to 27.0°C in May.

Plant material—We collected the leaves of 434 individuals of 250 tree species in 127 genera in 45 families, from forest understory to emergent tree class and at a canopy gap in the plots (see Appendix). We used fully expanded and apparently nonsenescing leaves taken from the top of the crown. To collect leaf samples, we used a canopy observation system, including tree towers and aerial walkways at the Canopy Biology Plot (Inoue et al., 1994) and an 85 m canopy crane at the Crane Plot (Sakai et al., 2002). The canopy crane system provides three-dimensional access to the forest (Ozanne et al., 2003). Between two and five leaves of each species in the plots were sampled for microscopic observations. Nomenclature was checked in the Angiosperm Phylogeny Website, version 6 (http://www.mobot.org/MOBOT/Research/APweb) and in flora records of the study area (Anderson, 1980; Soepadmo and Wong, 1995; Soepadmo et al., 1996, 2002, 2004; Nagamasu and Momose, 1997; Soepadmo and Saw, 2000).

Sampling at growth stages between seedling and mature tree—To analyze the occurrence of BSEs in different growth stages and individuals, we selected 42 species in 22 genera in 14 families, such as Burseraceae, Dipterocarpaceae, Euphorbiaceae, and Moraceae, from the 250 species (see Appendix). The species selected are mainly typical canopy and emergent trees in the forest. In the survey, we mainly compared leaf type between seedlings (DBH < 3 cm) grown under dark forest understory and mature canopy individuals that had reached the bright canopy layer. Canopy openness on the sampled seedlings, which was calculated from a hemisphere photograph (Kenzo et al., 2006), was less than 10%. In total, samples from 226 individuals were collected for this study (see Appendix).

Leaf collection and occurrence of BSEs—Collected fresh leaves were observed in transmitted light and then fixed in FAA (40% formaldehyde : acetic acid : 70% ethanol; 2 : 1 : 17, v/v). Transverse slices were also prepared and observed with a light microscope (AFX-IIA, Nikon, Tokyo, Japan) equipped with a camera (DS-5M-L1, Nikon, Tokyo, Japan). Some samples were observed using a low-vacuum scanning electron microscope (JSM-5310LV; JEOL) at an accelerating voltage of 15 kV (Fig. 2).

We also performed a pressure-infiltration experiment (Fry and Walker, 1967; Beyschlag and Pfanz, 1990; Beyschlag et al., 1992, 1994; Hiromi et al., 1999) to separate the leaf types of 24 species in 14 families (see Appendix). Immediately after detachment from the tree, the leaf sample was immersed in either 30 mL or 100 mL 1% fuchsin acid solution, in a 50 mL or 200 mL syringe, respectively. Air bubbles in the syringe were removed through the syringe outlet. The water column in the syringe was pushed inward by the piston, so that water penetrated into the leaf via the stomatal pores. The infiltrated leaves were removed from the syringe and dried on blotting paper. If the leaf is heterobaric, then the compartments become visible, especially in the afternoon (Hiromi et al., 1999; Küppers et al., 1999; Fig. 3a). In homobaric leaves, liquid dyes diffuse, and the dye spots gradually expand into the whole leaf (Hiromi et al., 1999; Fig. 3b, c).

Based on these observations, all tree species collected were classified into heterobaric and homobaric leaf types (Fig. 1a, b). However, some species, such as *Magnolia gigantefolia* in Magnoliaceae and *Macaranga conifera* in Euphorbiaceae, displayed intermediate morphology. These leaves had BSEs only around the large veins, and the bundle sheath extension compartments were consequently very large compared with heterobaric leaves (Fig. 1c). In this study, these species were categorized as having homobaric leaves.

Categories of each tree species—All tree species studied fell into five categories based on mature tree height (understory, subcanopy, canopy, and emergent species) and whether they are canopy gap species. The height of mature trees of each species was determined by observation and literature survey (Anderson, 1980; Soepadmo and Wong, 1995; Soepadmo et al., 1996, 2002, 2004; Nagamasu and Momose, 1997; Sakai et al., 1999; Soepadmo and Saw, 2000; Lee et al., 2002). Thereafter, the tree species were classified into four categories by mature height (Sakai et al., 1999): forest understory (<12.5 m), subcanopy (12.5–27.5 m), canopy (>27.5–42.5 m), and emergent (>42.5 m) species. We collected 49, 78, 53, and 49 tree species from the forest understory, subcanopy, canopy, and emergent species, respectively (Table 1). Tree species that grow mainly in canopy gaps were classified independently (canopy gap species; 21 species), regardless of their height.

RESULTS

The leaf types, heterobaric or homobaric, from seedling to mature tree in 226 individuals in 42 species in 14 families did not vary between growth stages and individuals. However, the interval of BSEs on 36 studied species was usually denser in leaves of canopy individuals than in leaves of understory seedlings (Fig. 4).

In total, 99 species (40%) in 21 families displayed heterobaric leaves, and 151 species (60%) in 36 families of species studied had homobaric leaves (Table 1). The proportion of species with each leaf type differed significantly among categories (χ^2 test, $P < 0.0001$, df = 4, $N = 250$ species; SPSS version 11.5, SPSS, Inc., Chicago, Illinois, USA). The proportion of heterobaric leaf trees was only 6% for forest understory species and 17% for subcanopy species. The proportion increased to 43% for canopy species and reached 96% for emergent species. The proportion in the canopy gap species was also quite high (62%).

We also found a significant relation between taxonomic

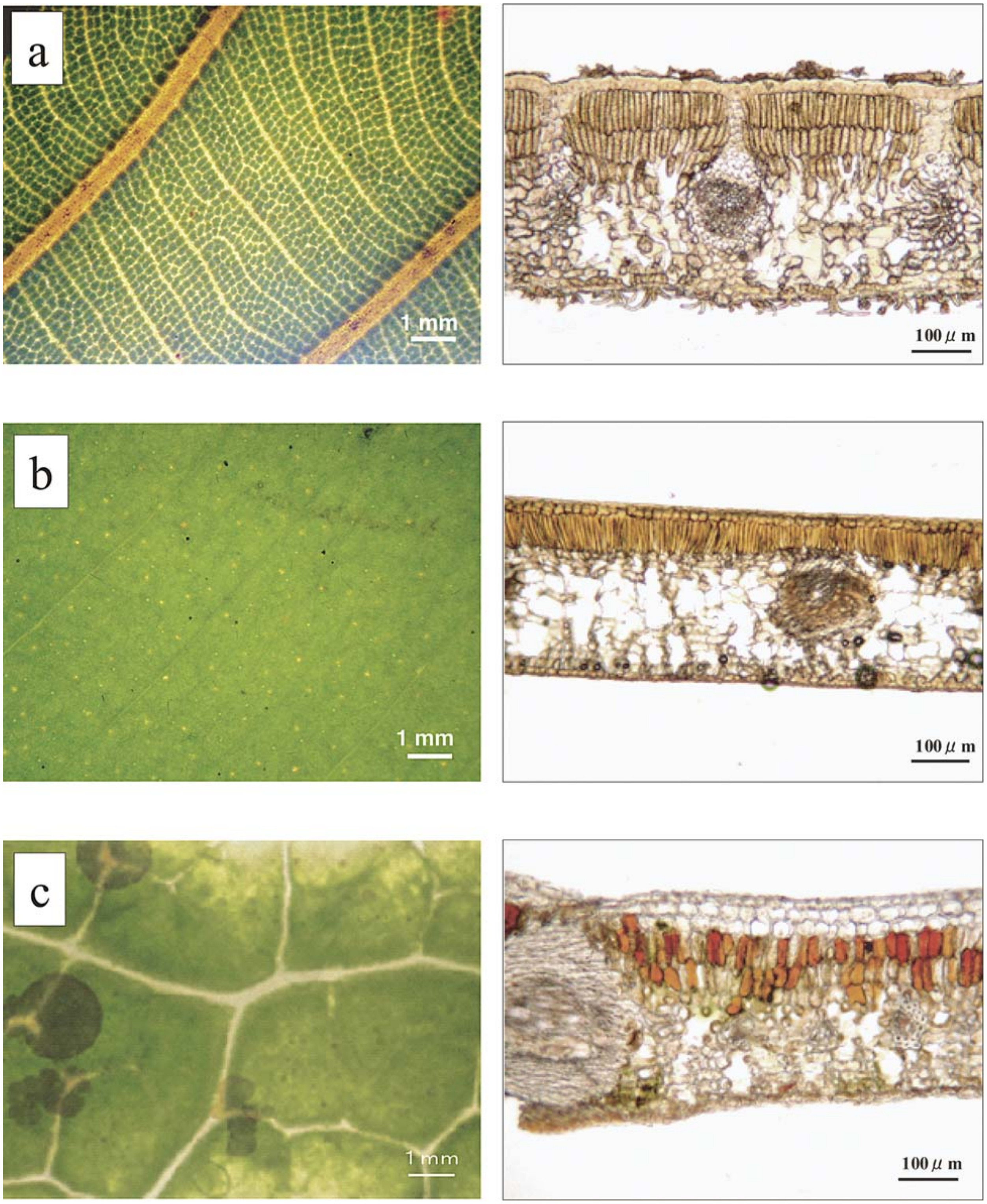

Fig. 1. Photographs of leaf surfaces (left panels) and transverse sections (right panels) of leaves from rainforest trees in Malaysia. (a) Heterobaric leaf from canopy (*Lithocarpus luteus*), (b) homobaric leaf from subcanopy (*Eugenia subrufa*), and (c) homobaric leaf from understory (*Magnolia gigantefolia*).

group (family) and leaf type (χ^2 test, $P < 0.0001$, df = 13, N = 184 species, in 14 families with >five species sampled for each family in this study; SPSS version 11.5; Table 2). All species of Dipterocarpaceae, consisting mainly of canopy and emergent tree, were classified as heterobaric leaf trees. In contrast, Annonaceae, Rubiaceae and Melastomataceae, which appeared mainly in the forest understory, had only homobaric leaves (Table 2). However, seven families, such as Euphorbia-

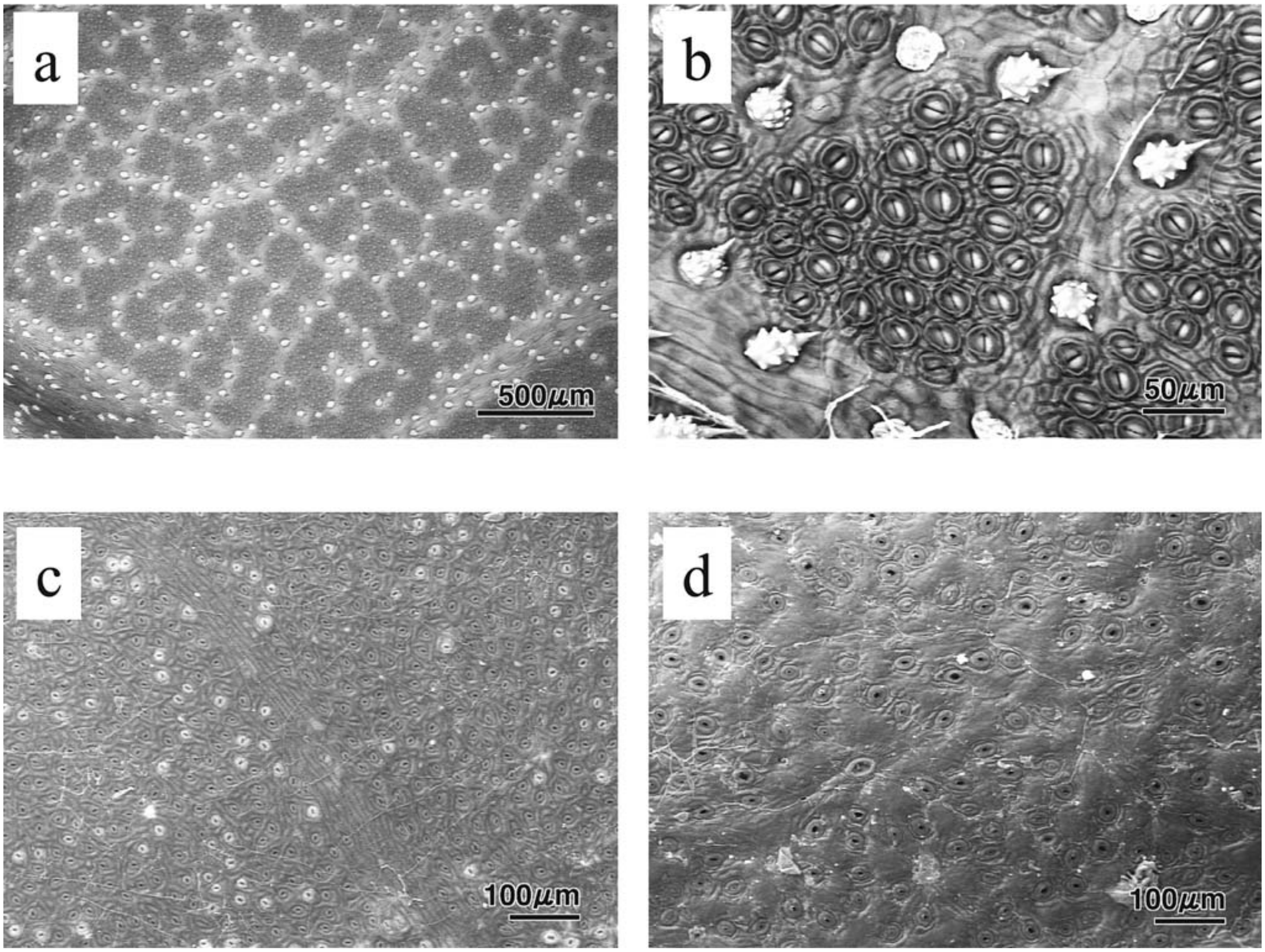

Fig. 2. SEM micrograph of abaxial side of the leaves from tree species in the rainforest of Malaysia. (a, b) Heterobaric leaf from canopy (*Artocarpus anisophyllus*), (c) homobaric leaf from subcanopy (*Ctenolophon parvifolius*), and (d) homobaric leaf from canopy (*Diospyros pseudomalabarica*).

ceae, Lauraceae, Burseraceae, and Sapotaceae, included trees of both leaf types. Tree species of both leaf types were even found in the same genus within these families: for example, genus *Macaranga* in Euphorbiaceae and *Santiria* in Burseraceae included both leaf types (see Appendix).

DISCUSSION

The leaf type of tree species, either heterobaric or homobaric leaf, may depend on life form types in the tropical rainforest. In general, evergreen tree species tend to have homobaric leaves compared with deciduous tree species (Wylie, 1952). Nevertheless, upper canopy and gap species, especially the most emergent species in the tropical rainforest, displayed heterobaric leaves even from the small seedling stage (Fig. 4, Table 1).

The difference in the distribution of leaf types along with mature tree height may be related to the steep microenvironment gradient with forest height. In canopy conditions in a tropical rainforest, tree leaves suffer strong desiccating conditions from the higher vapor pressure difference (VPD), temperature, and stronger winds than leaves in the understory (Aoki et al., 1978; Yoda, 1978; Chazdon et al., 1996). The presence of BSEs might confer an advantage on heterobaric leaves over homobaric leaves in the high-stress canopy environment. BSEs may be responsible for rapid stomatal response to drought signals, such as reduction of water potential in the mesophyll or a higher concentration of abscisic acid (ABA) by rapid transportation of these signals via the transpiration stream in BSEs (Terashima, 1992). BSEs may also contribute to the support and protection of the leaf blade against collapse after severe dehydration or other stress (Wylie, 1943, 1951, 1952; Lucas et al., 1991; Choong et al., 1992; Terashima, 1992), may protect against evaporation following injury to the leaf blade (Aldea et al., 2005), and may guide sunlight to thicker sun leaves (Karabourniotis et al., 2000; Nikolopoulos et al., 2002). The higher proportion of heterobaric leaf trees in the gap species may also be related to their dry and sunny growth environment, just as in the upper canopy conditions.

Conversely, the understory of a tropical rainforest is more suited to homobaric leaves, which may tend to have greater leaf performance in shade condition than heterobaric leaves. Light environments in the tropical rainforest change significantly with decreasing forest height, usually with only a low

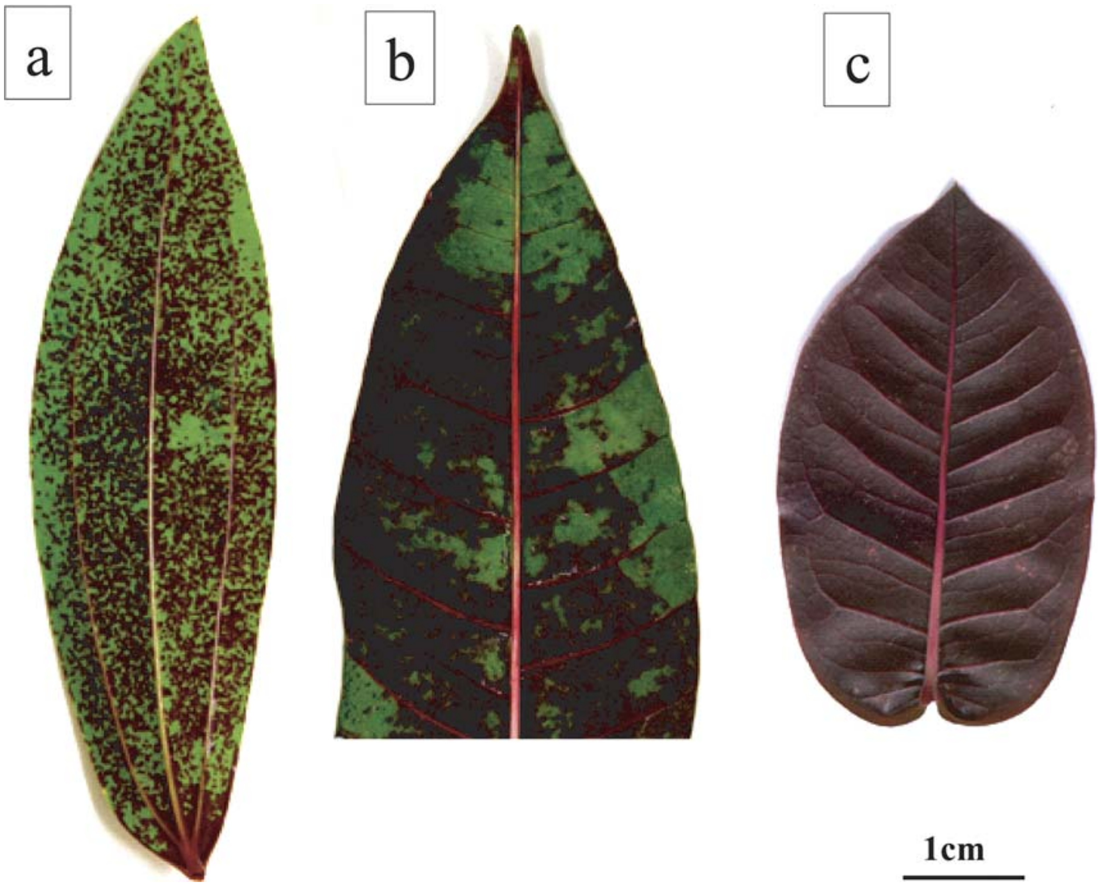

Fig. 3. Photographs of leaves infiltrated with fuchsin acid solution. (a) Heterobaric leaf from subcanopy (*Cinamonium javanicum*), (b) homobaric leaf from subcanopy (*Dyera costulata*), and (c) homobaric leaf from understory (*Ixola* sp.).

percentage of the sunlight reaching the forest floor (Yoda, 1978; Chazdon, 1988; Chazdon et al., 1996). Under such conditions, most growing plants that reproduce in the understory have greater leaf performance in the shade (Whitmore, 1998). The lack of BSEs may improve the ability to use available sunflecks, because lateral CO_2 diffusion from shaded to illuminated areas of the homobaric leaf will enhance photosynthesis (Lawson and Morison, 2006; Pieruschka et al., 2006). Homobaric leaves also increase their proportion of photosynthetically active leaf areas (Terashima, 1992). In a study of BSEs in 31 temperate heterobaric leaf tree species, Nikolopoulos et al. (2002) reported that the photosynthetically active leaf area ranged from 91% to 48% according to an increasing density of BSEs. These characteristics could contribute to the photosynthetic efficiency under limited light. Even heterobaric leaves growing under shaded conditions, as in the seedling stage under the understory and the mature stage in the inner crown, generally have larger BSE compartments than heterobaric leaves growing under sunny conditions in the same species (Fig. 4; Crocker, 1919; Wylie, 1951; Roth, 1984; Koike et al., 1997; Nikolopoulos et al., 2002). Some authors have also found that species of temperate deciduous trees with thicker leaves tend to have denser BSEs (Wylie, 1952; Nikolopoulos et al., 2002). However, some understory trees such as the genus *Goniothalamus* in this study, had very thick leaves (more than 400 μm), but they were homobaric. Future study may be still needed on the relation between leaf thickness and BSE occurrence in the leaves.

TABLE 1. Number of sampled tree species in the five habitats in a lowland tropical rainforest in Malaysia and proportion of trees with heterobaric leaves among the five life forms.

Life form	No. tree spp. with heterobaric leaf	No. tree spp. with homobaric leaf	Total	Tree spp. with heterobaric leaf (%)
Understory	3	46	49	6.1
Subcanopy	13	65	78	16.7
Canopy	23	30	53	43.4
Emergent	47	2	49	95.9
Canopy gap	13	8	21	61.9
Total	99	151	250	39.6

The tree leaf type, whether heterobaric or homobaric, is also related to the taxonomic group (family and/or genus), which is usually reflected by life form type and/or growth habitat at around the mature stage. Families mainly appearing in the canopy layer, such as Dipterocarpaceae, tend to have heterobaric leaves. In contrast, families mainly appearing in the forest understory, such as Annonaceae, Rubiaceae, and Melastomataceae, tend to have homobaric leaves (Table 2, Appendix). However, families such as Euphorbiaceae, Lauraceae, Burseraceae, and Sapotaceae, which include tree

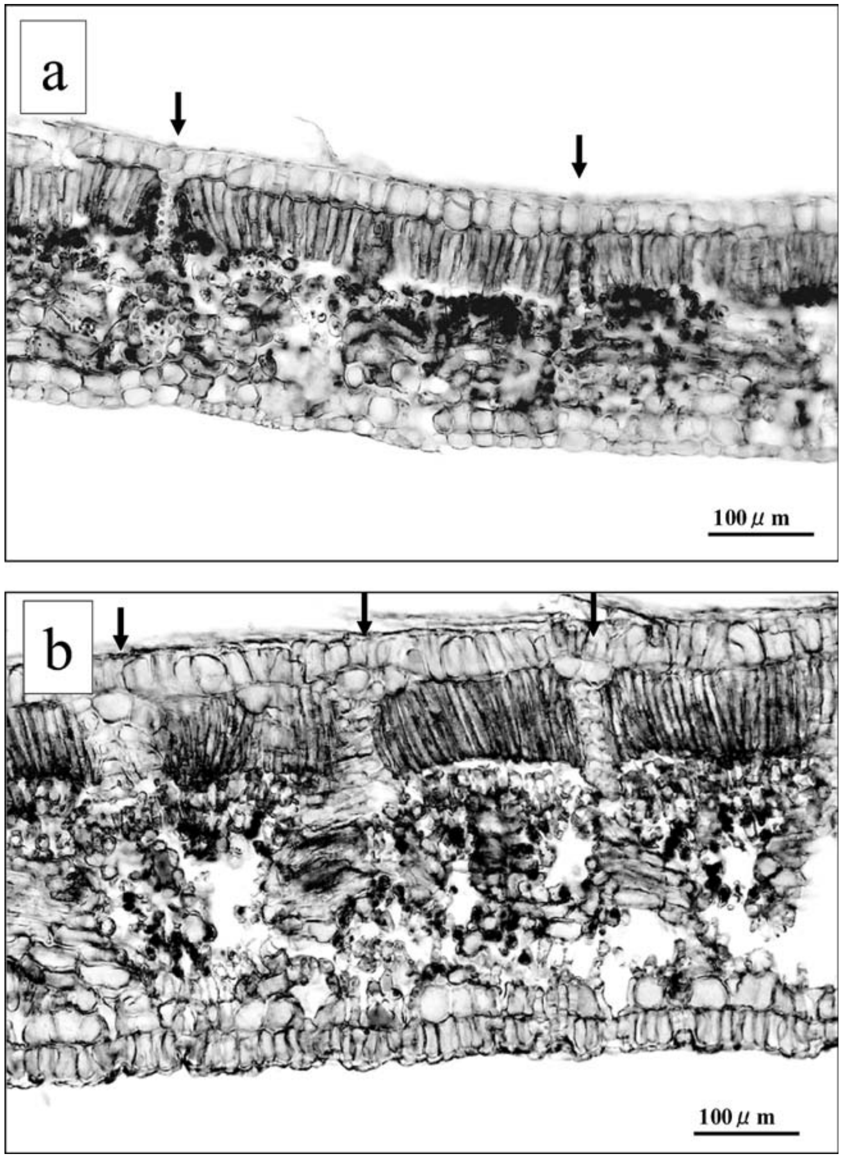

Fig. 4. Light micrographs of transverse sections of leaves (*Shorea acuta*). (a) Leaf of seedling on the dark forest floor, (b) leaf of mature tree in the bright canopy. Intervals of the bundle-sheath extensions were denser in the mature tree leaf. Arrows indicate bundle-sheath extensions.

species of various life form types, from understory to emergent, included both heterobaric and homobaric leaf trees (Table 2, Appendix). Furthermore, some genera in these families, such as *Macaranga* (Euphorbiaceae) and *Santiria* (Burseraceae), included trees of both leaf types (see Appendix). The leaf type in a single species does not change through its growth stages or between individuals. These results suggest that the leaf type in each species depends on the growth habitats and/or life form types at the mature height of each tree species, which are in turn commonly related to the forest microenvironments at the adult tree stage. In addition, it is reported that in tropical rainforest species, the interspecific leaf physiological properties of seedlings, such as the photosynthetic rate, are significantly related to the adult tree habitat, even if the seedlings themselves were grown in the same environment (Thomas and Bazzaz, 1999; Cai et al., 2005; Martínez-Garza and Howe, 2005). Our results, showing that the leaf type is fixed throughout the stages, from seedlings to mature individuals, of the same species, may reflect these interspecific differences in leaf physiological traits at the seedling stage.

In conclusion, we found a clear distribution pattern for the leaf type, categorized as either heterobaric or homobaric leaves, in the growth environment and/or life form types and in the taxonomic groups, in this tropical rain forest. Our results suggest that tropical tree species might adapt to the spatial gradient of the physical variables, such as light intensity and VPD, at the mature height of each tree species by having different leaf types—heterobaric or homobaric—which may have different physiological and mechanical functions. To study this phenomenon further, the functional roles of each leaf in the various environments must be determined.

TABLE 2. Leaf types for various plant species listed by taxonomic classification.

Superorder	Order	Family	No. heterobaric leaf species	No. homobaric leaf species	Total no. species	Heterobaric tree ratio (%)
Magnolides	Laurales	Lauraceae*	4	6	10	40.0
	Magnoliales	Annonaceae*	0	9	9	0.0
		Magnoliaceae	1	2	3	33.3
		Myristicaceae*	0	17	17	0.0
Core eudicots	Dilleniaceae	Dilleniaceae	2	0	2	100.0
	Santalales	Olacaceae	1	3	4	25.0
Rosids	Myrtales	Crypteroniaceae	0	1	1	0.0
		Melastomataceae*	0	5	5	0.0
		Myrtaceae*	0	7	7	0.0
Eurosids I	Cucurbitales	Anisophylleaceae	0	2	2	0.0
		Datiscaceae	1	0	1	100.0
	Fabales	Fabaceae	1	3	4	25.0
		Polygalaceae*	1	4	5	20.0
	Fagales	Fagaceae	3	0	3	100.0
	Malpighiales	Clusiaceae	3	1	4	75.0
		Euphorbiaceae*	4	27	31	12.9
		Ixonanthaceae	1	0	1	100.0
		Linaceae	0	1	1	0.0
		Rhizophoraceae	0	1	1	0.0
		Salicaceae	0	4	4	0.0
		Violaceae	0	1	1	0.0
	Oxalidales	Elaeocarpaceae	1	0	1	100.0
	Rosales	Moraceae*	7	2	9	77.8
		Ulmaceae	2	0	2	100.0
Eurosids II	Malvales	Dipterocarpaceae*	47	0	47	100.0
		Malvaceae*	3	5	8	37.5
		Thymelaeaceae	0	3	3	0.0
	Sapindales	Anacardiaceae*	0	6	6	0.0
		Burseraceae*	8	5	13	61.5
		Meliaceae	0	4	4	0.0
		Rutaceae	0	1	1	0.0
		Sapindaceae	0	3	3	0.0
		Simaroubaceae	0	2	2	0.0
Asterids	Cornales	Cornaceae	0	2	2	0.0
	Ericales	Actinidiaceae	0	1	1	0.0
		Ebenaceae	2	1	3	66.7
		Lecythidaceae	0	1	1	0.0
		Sapotaceae*	3	5	8	37.5
		Theaceae	0	1	1	0.0
Euasterids I	Gentianales	Apocynaceae	0	2	2	0.0
		Loganiaceae	0	3	3	0.0
		Rubiaceae*	0	9	9	0.0
	Icacinaceae	Icacinaceae	0	1	1	100.0
	Lamiales	Lamiaceae	2	0	2	100.0
		Verbenaceae	2	0	2	100.0
Total	18	45	99	151	250	39.6

* These 14 families were used for statistical analysis. Phylogenetic relationships followed APG II (2003).

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APPENDIX. List of tree species of a Malaysian lowland tropical rainforest with leaf type, life form, and total sampling number of individuals and leaves.

Family	Species	Leaf type[a]	Life form[b]	Sapling[c]	Large size[d]	Leaf no.[e]	P-i[f]
Actinidiaceae	*Saurauia ridleyi*	Homo	1	1		3	
Anacardiaceae	*Gluta macrocarpa*	Homo	2	1		3	
	Mangifera havilandii	Homo	2	1		3	
	Semecarpus glaucus	Homo	2	1		3	
	Semecarpus sp.	Homo	2	1		3	
	Swintonia acuta	Homo	3		1	3	
	S. foxworthyi	Inter	3	2	3	15	
Anisophylleaceae	*Anisophyllea disticha*	Homo	1	1		3	
	A. nitida	Homo	2	1		4	
Annonaceae	*Goniothalamus parallelovenius*	Homo	1	1		3	
	G. sinclairianus	Homo	1	1		3	
	G. velutinus	Homo	1	1		3	
	Goniothalamus sp1	Homo	1	1		3	
	G. sp2	Homo	1	1		3	
	Mezzettia macrocarpa	Homo	2	1		3	
	Polyalthia motleyana	Homo	1	1		3	
	Popowia pisocarpa	Homo	1	1		3	1
	Xylopia malayana	Homo	1	1		3	
Apocynaceae	*Alstonia pneumatophora*	Homo	4	1	2	9	2
	Dyera costulata	Inter	4	3	1	12	2
Burseraceae	*Canarium apertum*	Hetero	3		1	3	
	C. littorale	Hetero	3		1	3	
	C. aff. *pilosum*	Inter	2	1		3	
	C. sp. C by Kochuman	Hetero	2		1	3	
	Dacryodes incurvata	Hetero	3	2	2	12	
	D. rugosa	Hetero	3		1	3	
	Santiria apiculata	Hetero	3	2	3	15	
	S. grandiflora	Inter	3		1	5	
	S. griffithii	Homo	3	1		4	
	S. laevigata	Inter	3		1	4	
	S. mollis	Inter	2	2	3	15	1
	S. aff. *rubiginosa*	Hetero	2	1		3	
	Triomma malaccensis	Hetero	4		1	3	
Clusiaceae	*Calophyllum* cf. *macrocarpum*	Hetero	3		1	3	
	C. aff. *soulattri*	Hetero	3	1	1	6	
	Garcinia parvifolia	Homo	2		1	3	
	Kayea elmeri	Hetero	2		1	3	
Cornaceae	*Alangium* aff. *javanicum*	Homo	1	1		3	
	Mastixia aff. *pentandra*	Homo	3		1	3	
Crypteroniaceae	*Crypteronia griffithii*	Inter	2	1		3	
Datiscaceae	*Octomeles sumatrana*	Hetero	G		1	3	
Dilleniaceae	*Dillenia suffruticosa*	Hetero	G		1	3	3
	D. sumatrana	Hetero	G		1	3	
Dipterocarpaceae	*Cotylelobium melanoxylon*	Hetero	4		1	6	
	Dipterocarpus acutangulus	Hetero	4		1	3	
	D. geniculatus	Hetero	4		1	3	
	D. globosus	Hetero	4	5	10	45	
	D. pachyphyllus	Hetero	4	3	1	12	2

APPENDIX. Continued.

Family	Species	Leaf type[a]	Life form[b]	Sapling[c]	Large size[d]	Leaf no.[e]	P-i[f]
	D. palembanicus	Hetero	3		1	3	
	D. stellatus	Hetero	4		1	3	
	Dipterocarpus tempehes	Hetero	4	2	1	14	
	Dryobalanops aromatica	Hetero	4	6	11	46	3
	D. beccarii	Hetero	4	1		5	
	D. lanceolata	Hetero	4	5	5	30	2
	Hopea dryobalanoides	Hetero	4	2	1	9	
	H. griffithii	Hetero	2		1	3	1
	H. sphaerocarpa	Hetero	1		1	3	
	Parashorea macrophylla	Hetero	4	5	1	18	
	P. smythiesii	Hetero	4		1	3	
	Shorea acuta	Hetero	4	6	11	51	
	S. argentifolia	Hetero	4	1	1	6	
	S. beccariana	Hetero	4	6	7	40	
	S. biawak	Hetero	3	3	3	18	
	S. bullata	Hetero	4	1	2	9	
	S. crassa	Hetero	4		1	3	
	S. curtisii	Hetero	4		1	3	
	S. exelliptica	Hetero	4	5	1	18	
	S. falciferoides	Hetero	4		1	5	
	S. fallax	Hetero	4	1	2	9	1
	S. ferruginea	Hetero	4	1	1	6	
	S. geniculata	Hetero	4		1	3	
	S. isoptera	Hetero	4	3	2	15	
	S. laxa	Hetero	4	2	1	9	
	S. leprosula	Hetero	4	1		3	
	S. macrophylla	Hetero	4	2	1	9	
	S. macroptera	Hetero	4	9	6	45	
	S. ovalis	Hetero	4		1	3	
	S. ovata	Hetero	4	6	2	24	
	S. parvifolia	Hetero	4	2	3	15	2
	S. pauciflora	Hetero	4		1	3	
	S. pilosa	Hetero	4	1	1	6	2
	S. pinanga	Hetero	4		1	3	
	S. quadrinervis	Hetero	4		1	3	
	S. scaberrima	Hetero	4		1	3	
	S. seminis	Hetero	4	2	1	12	
	S. slootenii	Hetero	4	2	1	9	
	S. smithiana	Hetero	4	1	1	6	1
	S. virescens	Hetero	4	1		3	
	Vatica micrantha	Hetero	3	1	2	9	
	V. oblongifolia	Hetero	3		1	3	
Ebenaceae	*Diospyros mindanaensis*	Homo	2		1	3	
	D. pendula	Hetero	2		1	3	
	D. pseudomalabarica	Hetero	3	2	1	9	
Elaeocarpaceae	*Sloanea javanica*	Hetero	2		1	3	1
Euphorbiaceae	*Agrostistachys longifolia*	Homo	1	1		3	
	Antidesma neurocarpum	Homo	1	1		3	
	Aporosa chalarocarpa	Homo	2	1		3	
	A. granularis	Homo	1	1		3	
	A. sarawakensis	Homo	1	1		6	
	A. aff. *subcaudata*	Inter	1	1		3	
Euphorbiaceae	*Baccaurea kunstleri*	Inter	2		1	3	
	B. sarawakensis	Homo	2		1	5	
	Blumeodendron kurzii	Homo	3		1	3	
	Chaetocarpus castanocarpus	Homo	2		1	3	
	Cleistanthus baramicus	Homo	2		1	3	
	C. glaber	Homo	1	1		3	
	C. pseudopodocarpus	Hetero	1	1		3	
	Dimorphocalyx denticulatus	Homo	1	1		3	
	Drypetes longifolia	Homo	1	1		3	
	Endospermum diadenum	Inter	G		1	3	
	Galearia fulva	Hetero	G		1	3	
	Homalanthus populneus	Homo	G	1		3	1
	Koilodepas laevigatum	Homo	2	1		3	
	Macaranga brevipetiolata	Homo	2	1		3	
	M. conifera	Inter	2		1	3	1
	M. gigantea	Hetero	G		1	3	
	M. kingii	Homo	1	1		3	

APPENDIX. Continued.

Family	Species	Leaf type[a]	Life form[b]	Sapling[c]	Large size[d]	Leaf no.[e]	P-i[f]
	M. praestans	Homo	1	1		3	
	M. trachyphylla	Hetero	G	1		3	1
	M. winkleri	Homo	G	1		4	
	Mallotus sp.	Homo	1	1		6	
	Pimelodendron griffithianum	Homo	2	1		3	
	Ptychopyxis glochidiifolia	Homo	2	1		3	
	Tapoides villamilii	Homo	2	1		3	
	Trigonostemon aff. *ionthocarpus*	Homo	1	1		3	
Fabaceae	*Dialium kunstleri*	Homo	3		1	6	
	Fordia brachybotrys	Inter	1	1		3	
	Koompassia malaccensis	Hetero	4	2	4	18	
	Parkia singularis	Homo	2	1		3	
Fagaceae	*Castanopsis* sp.	Hetero	3		1	3	
	Lithocarpus luteus	Hetero	G		1	6	
	Quercus merrillii	Hetero	2		1	3	1
Icacinaceae	*Gomphandra cumingiana*	Homo	1	1		3	
Ixonanthaceae	*Allantospermum borneense*	Hetero	4	1	2	20	
Lamiaceae	*Callicarpa* sp.	Hetero	G		1	3	
	Vitex pinnata	Hetero	G		1	4	1
Lauraceae	*Actinodaphne* aff. *myriantha*	Hetero	3		1	3	
	Actinodaphne sp.	Hetero	3		1	3	
	Beilschmiedia cf. *perakensis*	Hetero	1	1		3	
	Cinnamomum javanicum	Hetero	2	2	1	9	2
	Cryptocarya ferrea	Homo	2	1		3	
	Dehaasia firma	Inter	2	1		3	
	Endiandra clavigera	Inter	2	1		3	
	Eusideroxylon zwageri	Homo	3	3	2	15	
	Litsea machilifolia	Homo	3		1	3	
	L. aff. *rubicunda*	Homo	1	1		3	
Lecythidaceae	*Barringtonia* sp.	Homo	1	1		3	
Linaceae	*Ctenolophon parvifolius*	Homo	2	1		3	
Loganiaceae	*Fagraea caudata*	Homo	1	1		3	
	F. cuspidata	Homo	2		1	3	
Loganiaceae	*Fagraea racemosa*	Homo	G	1		3	
Magnoliaceae	*Magnolia ashtonii*	Hetero	4		1	3	
	M. candollii	Homo	2	1		3	
	M. gigantefolia	Inter	1		1	3	1
Malvaceae	*Durio acutifolius*	Homo	2	3	2	15	2
	Durio sp.	Homo	2	1		3	
	Microcos gracilis	Hetero	2	1		3	
	Pentace laxiflora	Homo	3		1	3	
	Scaphium longipetiolatum	Hetero	4		1	3	
	S. macropodum	Hetero	4	1	2	9	
	Sterculia megistophylla	Homo	2	1		3	
	S. rubiginosa	Homo	2	1		3	
Melastomataceae	*Melastoma beccarianum*	Homo	G	1		4	
	M. malabathricum	Homo	G	1		4	1
	Memecylon paniculatum	Homo	2	1		3	
	M. scolopacinum	Homo	1	1		3	
	Memecylon sp.	Homo	1	1		3	
Meliaceae	*Aglaia rufinervis*	Homo	1	1		3	
	A. tomentosa	Homo	1	1		3	
	Chisocheton sarawakanus	Homo	2		1	3	
	Dysoxylum rugulosum	Homo	2		1	3	
Moraceae	*Artocarpus anisophyllus*	Hetero	3		1	3	
	A. dadah	Hetero	3		1	3	
	A. elasticus	Hetero	3		1	3	
	A. integar	Hetero	3	2	2	12	
	A. odoratissimus	Hetero	G		1	3	
	Artocarpus sp.	Homo	2	1		3	
	Ficus uncinata	Hetero	G		1	3	
	Ficus	Hetero	G		1	3	
	Parartocarpus venenosus	Homo	3		1	3	
Myristicaceae	*Gymnacranthera bancana*	Homo	3		1	6	
	G. contracta	Homo	3		1	3	
	G. farquhariana	Homo	3		1	3	
	Horsfieldia borneensis	Homo	3		1	3	
	H. fragillima	Homo	3		1	3	
	H. grandis	Homo	2		1	3	

APPENDIX. Continued.

Family	Species	Leaf type[a]	Life form[b]	Sapling[c]	Large size[d]	Leaf no.[e]	P-i[f]
	H. pallidicaula	Homo	2		1	3	
	H. polyspherula	Homo	2		1	3	
	H. tenuifolia	Homo	2		1	3	
	Knema latericia	Homo	2		1	3	
	K. latifolia	Homo	2		1	5	
	K. pallens	Inter	3		1	3	
	K. stenophylla	Homo	2		1	3	
	Myristica borneensis	Homo	2		1	3	
	M. gigantea	Homo	3		1	3	
	M. smythiesii	Homo	2		1	3	
	Myristica sp.	Homo	2		1	3	
Myrtaceae	*Eugenia subrufa*	Homo	3		1	3	
	E. cf. *rosulenta*	Homo	3		1	3	
	Eugenia sp.1	Homo	2		1	3	
Myrtaceae	*Eugenia* sp.2	Homo	2		1	3	
	Eugenia sp.3	Homo	2		1	3	
	Eugenia sp.4	Inter	2		1	3	
	Whiteodendron moultonianum	Homo	3		1	3	
Olacaceae	*Anacolosa frutescens*	Homo	3	1		3	
	Scorodocarpus borneensis	Homo	3		1	3	
	Strombosia ceylanica	Hetero	3		1	3	
	Strombosia sp.	Homo	2	1		3	
Polygalaceae	*Xanthophyllum affine*	Homo	3		1	3	
	X. beccarianum	Inter	2		1	3	
	X. clovis	Inter	2		1	3	
	X. pauciflorum	Inter	2		1	3	
	Xanthophyllum sp.	Hetero	2		1	3	
Rhizophoraceae	*Carallia brachiata*	Homo	2		1	3	
Rubiaceae	*Anthocephalus cadamba*	Homo	G		1	3	
	Chasalia curviflora	Homo	1	1		3	
	C. stipulacea	Homo	1	1		3	
	Ixora stenophylla	Homo	1	1		3	
	I. woodii	Homo	1	1		3	
	Ixora sp.	Homo	1	1		3	2
	Pavetta axillaris	Homo	1	1		5	
	Tarenna sp	Homo	G	1		3	
	Urophyllum hirsutum	Homo	1	1		4	
Rutaceae	*Glycosmis superba*	Homo	1	1		3	
Salicaceae	*Casearia elliptifolia*	Homo	1	1		3	
	Hydnocarpus pinguis	Homo	2	1		3	
	H. woodii	Homo	3		1	3	
	Ryparosa hullettii	Homo	2	1		3	
Sapindaceae	*Lepisanthes fruticosa*	Homo	1	1		3	
	Xerospermum laevigatum	Homo	2	1		3	
	X. noronhianum	Inter	2	1		3	
Sapotaceae	*Madhuca crassipes*	Hetero	3		1	5	
	M. kingiana	Homo	2		1	3	
	M. kuchingensis	Hetero	2		1	3	
	M. sessilis	Homo	2		1	5	
	Palaquium sp.	Hetero	3		1	5	
	Payena endertii	Homo	3		1	3	
	Pouteria malaccensis	Homo	3		1	5	
	Pouteria sp.	Homo	3		1	3	
Simaroubaceae	*Eurycoma longifolia*	Homo	1	1		3	
	Simaba borneensis	Homo	3		1	3	
Theaceae	*Adinandra* sp.	Homo	1	1		3	
Thymelaeaceae	*Amyxa pluricornis*	Homo	2	1		3	
	Aquilaria microcarpa	Homo	2	1		3	
	Gonystylus stenosepalus	Homo	2		1	3	
Ulmaceae	*Gironniera nervosa*	Hetero	3	1	1	3	
	Trema orientalis	Hetero	G	1		3	
Verbenaceae	*Teijsmanniodendron coriaceum*	Hetero	2		1	3	
	T. simplicifolium	Hetero	2	1	2	9	
Violaceae	*Rinorea anguifera*	Homo	1	1		3	

[a] Hetero, heterobaric leaf tree; Homo, homobaric leaf tree; Inter, intermediate leaf type tree. [b] 1, understory (<12.5 m); 2, subcanopy (12.5–27.5 m); 3, canopy (27.5–42.5 m); 4, emergent (>42.5 m); G, canopy gap species. [c] The total number of individuals of sampled saplings (DBH < 3 cm). [d] The total number of large sized individual (DBH > 3 cm, almost all individuals reached 20 m at height). [e] The total number of sampled leaves for the study. [f] The number of individuals to assay pressure-infiltration experiment. Three leaves were used for the experiment.