Tree guild composition of a hill dipterocarp forest in West Sumatra, Indonesia

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ABSTRACT The guild composition of a hill dipterocarp forest was examined using growth traits of 1566 trees comprising 422 species through field observation at a 6-ha plot for 6 years in Sumatra. Three parameters, intrinsic growth rate, attainable maximum stem diameter, and stem hardness, were used for guild determination. The intrinsic growth rate showed a significant correlation with stem hardness, which suggested a trade-off between volume growth and architectural strength under the restraint of photosynthetic products. Four major guilds were determined, characterized as Soft wood-Small size-Fast growth, Soft-Big-Fast, Hard-Big-Slow, and Hard-Small-Slow traits. Ecological niches of these guilds were related to the large variance of resources in time and space of a tropical rain forest. A secondary forest part in the 6-ha plot retained high species diversity, but species composition was largely different from that of the mature stand. Human activities biased guild composition to reinforce the Soft-Small-Fast guild, with a reduction in the Hard-Big-Slow guild that included many marketable timber trees. Logging impacts on dipterocarp and fagaceous trees were assessed with reference to their spatial distribution and attributes of guilds.

Key words: attainable maximum tree size, climax species, guild composition, intrinsic growth rates, logging impacts, pioneer species, species diversity, stem hardness, Sumatra, tropical rain forest

Abbreviation

DBH : stem diameter at breast height

R^2 : coefficient of determination

RGR: relative growth rate of DBH

P: significant probability

INTRODUCTION

The high species richness of tropical trees could be sustained through their diverse growth features throughout their life history (Richard, 1996; Whitmore, 1998). Understanding coexistence mechanisms allows trees to be arranged as diverse resources within a tropical forest. Classification of tree growth features, such as pioneer versus non-pioneer (Swain and Whitmore, 1988), could provide a paradigm to understand not only their life strategy but also functional characteristics of the forest as an assemblage. Turner (2001) reviewed tree growth characteristics and coordinated them on two axes of successional stage and tree size. However, classifications based on quantitative data are few (Condit et al. 1996; Gitay et al. 1999; Baker et al. 2003; Laurance et al. 2004; Nascimento et al. 2005).

A tropical rain forest continually decreases in original structural features and area under impacts such as logging and land-use conversion (Brown and Lugo, 1990; FAO, 2005), forest fires (Toma et al. 2000), and drought (Yoneda et al. 2006a; Engelbrecht et al. 2007; Neptad et al. 2007). Building a quantitative evaluation of these impacts is necessary for sustainable forest management and protection. This study aimed to classify diverse species of a hill dipterocarp forest into guilds together with their growth traits, elucidate the life strategies of guilds in relation to diverse resources in time and space, and evaluate human impacts on guild composition.

Various attributes of a tree life cycle have been studied, e.g., seed size (Davies and Ashton, 1999), growth rate (Condit et al. 2004), shade tolerance (Baker et al. 2003), wood density (Yoneda et al. 1999; King et al. 2006), reproduction age (Thomas, 1996), maximum size

(Kohyama et al. 2003), and longevity (Lieberman et al. 1985). Nascimento et al. (2005) coordinated these various demographic traits and life-history attributes on two axes corresponding to light requirement and successional status, and tree sizes, as did Turner (2001). A reciprocal relationship between the intrinsic growth rate and maximum tree size can be considered as a spectrum of growth traits with successional status (Yamakura, 1996). Stem hardness could be a parameter related not only to physical architectural features but also physiological features such as the growth rate (Yoneda et al. 1999; Chairul and Yoneda, 2006) and wood density of stems (Thomas, 1996; King et al. 2006). Herein, we focus on three parameters for quantitative analysis of guild composition: the intrinsic growth rate, attainable maximum size, and stem hardness.

The growth rate and stem hardness of tropical trees were obtained from field observation in a hill dipterocarp forest over 6 years. An attainable maximum size of each taxon comprising several species of one genus was estimated from the size dependency of the growth rate on stem diameter. Eight guilds were determined using 2×2 classifications of the three parameters, and life strategies were examined through the distribution of diverse resources in time and space of a tropical forest. Human impacts on guild composition were assessed to compare them among forest stands experiencing different extents of disturbance.

MATERIALS AND METHODS

Study site

The study was conducted in a hill dipterocarp forest in Ulu Gadut, West Sumatra. The 6-ha site is on a sloping ridge with a maximum width of 200 m and an altitude of 546–654 m (Fig. 1). The vegetation is characterized by high species diversity, with 465 tree species over 10 cm

DBH and a dominance of Fagaceae over Dipterocarpaceae (Nishimura et al. 2006; Appendix 2). The climate is super-humid, with large annual variance in rainfall. Severe dry weather in 1997 reduced tree growth rates and led to some mortality (Yoneda et al. 2006a). Local inhabitants collect various forest products, creating a heterogeneous stand structure within a mature stand.

We assessed the intensity of human disturbances in a 6-ha plot by measuring the tree density of large hardwood trees with a DBH over 30 cm and stem hardness over 60 kg f cm^{-1} , which is one component of an intact stand because of the tree sizes and low growth rates (cf. Table 3) in this forest. Based on horizontal distribution, we divided this 6-ha plot into three blocks: PIN, BL-1, and BL-2 (Table 1). The PIN block was a mature stand containing many large hardwood trees (Yoneda et al. 1994), BL-1 was a selectively logged stand with many large hardwood trees remaining, and BL-2 was a stand with few large trees and included a secondary forest stand developed after clear-cutting (Yoneda et al.

Fig. 1. Horizontal distribution of hardwood trees in terms of stem hardness ($H_d \geq 60 \text{ kg f cm}^{-1}$). Closed circles and dots show big and small trees, respectively, with a boundary value of 30 cm DBH. Based on horizontal distribution patterns, the 6-ha plot was divided into three blocks: PIN, BL-1, and BL-2 (Table 1). Dark-shaded areas are sites without observations. The outer frame shows the 6.55-ha Pinang-pinang baru plot (Nishimura et al. 2006).

Table 1. General stand features of the three blocks in the 6-ha plot (Fig. 1). Block PIN is a mature stand, BL-2 experienced the highest impacts of logging, and BL-1 suffered an intermediate impact. *BA* and *DN* are the basal area and stem density, respectively, of total trees > 15 cm DBH at the first observation in 1996. *NA* and *NB* are ratios (percentages) of the number available trees to total trees available for observation of stem hardness and boundary conditions of guilds, respectively. *a* and *H'* are Fisher and Shannon indices of species diversity, respectively. *H'* has a base logarithm = 2.

Block	Area (ha)	<i>BA</i> ($\text{m}^2 \text{ ha}^{-1}$)	<i>DN</i> (ha^{-1})	<i>NA</i> (%)	<i>NB</i> (%)	Species number	<i>a</i>	<i>H'</i>
PIN	1	37	368	91	34	130	79	6.3
BL-1	2.38	30	323	87	43	276	160	7.4
BL-2	2.54	28	311	71	33	285	169	7.4
Total	5.92	30	326	81	37	461	200	7.9

Table 2. Structural dimensions of common species among blocks. Figures in the upper three rows show ratios of common species between the corresponding two blocks to the total values of each block (column), and one in the "Common" row is the ratio of common species among the three blocks.

Block	Species number			Stem number			Basal Area		
	PIN	BL-1	BL-2	PIN	BL-1	BL-2	PIN	BL-1	BL-2
PIN	0.54	0.03	0.02	0.14	0.02	0.03	0.11	0.03	0.02
BL-1	0.06	0.36	0.44	0.04	0.10	0.48	0.05	0.10	0.42
BL-2	0.05	0.45	0.38	0.06	0.49	0.10	0.04	0.43	0.12
Common	0.35	0.16	0.16	0.76	0.39	0.38	0.79	0.44	0.43
Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

1999).

PIN had 35% of its total species number in common with the other two blocks, and these species had higher dominance in basal area and stem number as much as 80% (Table 2). In BL-1 and -2, these common species decreased to 16% in species number and 40% in basal area and stem number both, while common species between these two blocks except PIN constituted as much as 45% in every dimension of each block.

Tree census

A census of all trees with a DBH > 10 cm was repeated five times over 6 years from May 1996 to October 2002. Recruited trees were recorded at every observation. The stem hardness (H_d) of all trees over 15 cm DBH was determined in 1996. This was defined as the maximum power (kg f cm^{-1}) required to pull out a nail (JISA 5508, 68 mm long, 3.05 mm diameter) driven to a depth of 60 mm (Yoneda, 1997). Data on H_d were gained for 81% of the total trees over 15 cm DBH (Table 1).

Definition of the relative growth rate

The relative growth rate of the DBH (RGR) was defined as $RGR = \ln (DBH_2/DBH_1)/(t_2 - t_1)$, where DBH_1 and DBH_2 are the DBH at times t_1 and t_2 , respectively. The RGR of each individual was estimated by the least-squares method, with data from the entire 6-year period. A data set of both H_d and RGR showed high correlations with time ($R^2 > 0.9$) for 37% (716 trees) of the total number of trees (Table 1). This data set was used for the following definition of growth parameters and tree guilds.

Definition of the intrinsic growth rate and attainable maximum DBH of a taxon

A linear model using multiple regression showed that the RGR of the 716 trees was significantly negatively correlated ($P = 1.6 \times 10^{-16}$, $R^2 = 0.097$) with both DBH and H_d , with standardized partial regression coefficients of

-0.220 for DBH and -0.193 for H_d . This showed that H_d was as important a parameter of RGR as the DBH. Growth analysis at species level was, however, technically difficult because of the small number of trees per species, and we defined a group of species with similar H_d belonging to the same genus as a taxon having similar ecological behavior (ter Steege and Harmond, 2001; Laurance et al. 2004). The RGR-DBH relationship of each taxon was approximated by a straight line with a negative slope, where

$$RGR = -a \text{ DBH} + b. \quad (1)$$

The two intercepts of the straight line from Eq. (1) on the RGR and DBH axes were defined as the intrinsic growth rate (R_0) and attainable maximum size of the DBH (D_{max}) of a taxon, respectively. These were obtained from $R_0 = b$ and $D_{max} = b/a$, respectively. For the following definition of a tree guild, we determined these two parameters in 34 taxa comprising 354 trees, with a high correlation of $R^2 > 0.09$ from Eq. (1) (Table 3).

Definition of a tree guild

A tree guild was defined as a group of taxa having similar growth traits for R_0 , D_{max} , and H_d . Eight guilds were defined by dichotomy employing average values for 34 taxa of $H_d = 47 \pm 11 \text{ kg f cm}^{-1}$, $D_{max} = 69 \pm 34 \text{ cm}$, and $R_0 = 0.051 \pm 0.024 \text{ cm cm}^{-1} \text{ yr}^{-1}$. Each parameter was divided into two categories, with the average as a border value, as *Soft* and *Hard* categories for H_d , *Small* and *Big* categories for D_{max} , and *Slow* and *Fast* categories for R_0 . The eight guilds were determined by a 2×2 classification of these categories ($8 = 2^3$). Symbols of guilds were derived from the initial letters of the above categories, e.g., *SBF* denoting the *Soft-Big-Fast* guild (Table 3).

Estimation of guild composition in a plot

The guild composition of the 6-ha plot was examined using 1566 trees having an observed H_d and 81% of total trees being over 15 cm DBH (Table 1). These trees were

Table 3. Growth features of eight guilds and 34 taxa obtained from 354 trees in the 6-ha plot. R_o , D_{max} , and r are the intrinsic growth rate, attainable maximum DBH, and correlation coefficient from the regression of Eq. (1), respectively. H_d is the average stem hardness of each taxon.

Guild	Taxon		No. of Species	No. of trees	D_{max} (cm)	R_o (yr ⁻¹)	r	H_d (kg f cm ⁻¹)
	Family	Genus or Species						
soft & small & slow (SSS)	Cornaceae	<i>Mastixia trichotoma</i>	1	12	43	0.049	-0.69	38 ± 15
	Icacinaeae	<i>Gomphandra</i> spp.	2	9	35	0.041	-0.55	28 ± 3
	Lecythidaceae	<i>Barringtonia</i> spp.	3	6	54	0.026	-0.72	47 ± 9
	Sapotaceae	<i>Ganua</i> spp.	2	6	56	0.045	-0.81	40 ± 14
	Styracaceae	<i>Styrax serrulatum</i>	1	17	45	0.050	-0.34	43 ± 5
soft & small & fast (SSF)	Apocynaceae	<i>Voacanga</i> spp.	2	6	32	0.079	-0.66	30 ± 3
	Lauraceae	<i>Beilschmiedia</i> spp.	2	5	28	0.098	-0.80	38 ± 8
	Lauraceae	<i>Endiandra</i> spp.	2	7	59	0.055	-0.87	42 ± 4
	Sapotaceae	<i>Payena</i> spp.	2	5	37	0.110	-0.97	42 ± 5
	Tiliaceae	<i>Grewia florida</i>	1	8	26	0.129	-0.77	39 ± 5
	Tiliaceae	<i>Grewia cf. florida</i>	1	10	40	0.054	-0.69	40 ± 7
	Verbenaceae	<i>Geunsia hexandra</i>	1	10	46	0.082	-0.50	30 ± 7
soft & big & slow (SBS)	Burseraceae	<i>Santiria</i> spp.	5	8	80	0.036	-0.43	43 ± 9
	Dipterocarpaceae	<i>Parashorea lucida</i>	1	5	148	0.047	-0.60	43 ± 2
	Elaeocarpaceae	<i>Elaeocarpus</i> spp.	6	8	77	0.038	-0.81	45 ± 4
	Moraceae	<i>Artocarpus</i> spp.	10	24	104	0.036	-0.62	38 ± 10
SBF	Moraceae	<i>Ficus</i> spp.	4	7	104	0.053	-0.41	32 ± 8
	Fagaceae	<i>Quercus oidocarpa</i>	1	6	104	0.052	-0.79	42 ± 5
hard & small & slow (HSS)	Dipterocarpaceae	<i>Vatica</i> spp.	3	4	59	0.050	-0.65	50 ± 3
	Ebenaceae	<i>Diospyros</i> spp.	2	5	50	0.030	-0.64	51 ± 5
	Euphorbiaceae	<i>Aporosa</i> spp.	6	10	43	0.033	-0.63	60 ± 16
	Euphorbiaceae	<i>Cephalomappa</i> spp.	2	16	62	0.034	-0.65	52 ± 6
	Euphorbiaceae	<i>Cleistanthus glandulosus</i>	1	16	34	0.041	-0.70	66 ± 15
	Sapindaceae	<i>Xerospermum noronhianum</i>	1	8	69	0.037	-0.59	54 ± 12
HSF	Bombacaceae	<i>Durio</i> spp.	2	9	43	0.051	-0.78	52 ± 9
	Theaceae	<i>Eurya</i> spp.	2	5	33	0.072	-0.72	50 ± 5
hard & big & slow (HBS)	Dipterocarpaceae	<i>Hopea dryobalanoides</i>	1	9	126	0.025	-0.51	70 ± 13
	Fagaceae	<i>Castanopsis rhamnifolia</i>	1	8	81	0.039	-0.32	51 ± 6
	Fagaceae	<i>Lithocarpus meijerii</i>	1	5	125	0.033	-0.72	66 ± 18
	Fagaceae	<i>Lithocarpus</i> spp.	15	34	120	0.036	-0.45	58 ± 13
	Fagaceae	<i>Quercus gemelliflora</i>	1	5	113	0.046	-0.73	56 ± 10
	Myrtaceae	<i>Eugenia</i> spp.	16	23	84	0.032	-0.49	60 ± 12
	Sapindaceae	<i>Nephelium</i> spp.	6	34	98	0.034	-0.62	61 ± 15
HBF	Fagaceae	<i>Quercus argentata</i>	1	4	89	0.072	-0.70	52 ± 3

first classified into taxa with the observed H_d using the same procedure mentioned previously. Trees belonging to the above-mentioned 34 taxa accounted for 46% of the 1566 target trees and were *a priori* classified into their determined guilds (Table 3). The R_o and D_{max} of other taxa

comprising the remaining 54% of trees were determined from the following regression obtained from the 34 taxa:

$$R_o = -0.001 H_d + 0.102 \quad [\text{cm cm}^{-1} \text{ yr}^{-1}, \text{ kg f cm}^{-1}] \quad (2)$$

The details of this regression are shown in the results, and

$D_{max} = 1.17 D_m + 8.50$, [cm, cm] (3)
 where D_m is the maximum observed DBH of a taxon ($R^2 = 0.720$), even though the maximum observed tree size was biased by sample sizes for estimating the attainable maximum size (Kohyama et al. 2003). Guilds of other taxa except the 34 taxa were determined from observed H_d and estimates of R_0 and D_{max} .

RESULTS

Growth traits of taxa

Growth properties of the 34 taxa were examined in terms of the intrinsic growth rate (R_0), attainable maximum DBH (D_{max}), and stem hardness (H_d). A significant correlation was observed among properties ($P < 0.05$; Table 4), but a negative correlation was seen between R_0 and D_{max} caused by artificial analytic effects because a species group from random sampling produced a similar correlation. R_0 tended to decrease with increasing H_d , having a large variance at lower H_d (Fig. 2). We approximated this relationship with a straight line [Eq. (2);

Table 4. Correlation among three parameters of the growth traits for 34 taxa in the 6-ha plot: intrinsic growth rate (R_0), attainable maximum DBH (D_{max}), and stem hardness (H_d). Figures show the correlation coefficients (bold) and significance (italics).

parameter	R_0	D_{max}	H_d
R_0	—	0.005	0.004
D_{max}	-0.467	—	0.026
H_d	-0.476	0.381	—

Fig. 2. Relationship between R_0 and H_d of the 34 taxa. A straight line with a negative slope was obtained from Eq. (2). Vertical and horizontal broken lines show the average values: $R_0 = 0.051 \text{ cm cm}^{-1} \text{ yr}^{-1}$ and $H_d = 47 \text{ kg f cm}^{-1}$.

$P = 0.004$, $R^2 = 0.227$] within the range of observed H_d , although a reciprocal relationship would be more appropriate biologically. D_{max} was positively correlated with H_d , but the significance ($P = 0.026$, $R^2 = 0.145$) was lower than for the two other relationships ($P < 0.005$; Table 4).

Species composition of a guild

Four hundred and twenty-two identified species were used for guild determination in the 6-ha plot. SSF (Soft-Small-Fast) had the highest species diversity (142 species; Appendix 1). *Grewia* (Tiliaceae), *Geunsia* (Verbenaceae), *Knema* (Myristicaceae), *Mallotus* (Euphorbiaceae), *Palaquium* (Sapotaceae), *Villebrunea* (Urticaceae), and *Litsea* (Lauraceae) were dominant in this guild. Three guilds, HBS (Hard-Big-Slow), HSS (Hard-Small-Slow), and SBF (Soft-Big-Fast), had 80, 71, and 60 species, respectively, with dominant species of *Lithocarpus* (Fagaceae), *Eugenia* (Myrtaceae), *Nephelium* (Sapindaceae), *Swintonia* (Anacardiaceae), *Aglaia* (Meliaceae), *Castanopsis* (Fagaceae), *Hopea*

Fig. 3. Guild composition of three structural dimensions of the three blocks, PIN (●), BL-1 (○), and BL-2 (▲), in the 6-ha plot. Symbols on the x-axis show two categories of tree size (Small or Big) and growth rates (Slow or Fast) of the guilds.

(Dipterocarpaceae), *Pometia* (Sapindaceae), and *Quercus* (Fagaceae) for *HBS*, and *Cleistanthus*, *Cephalomappa* and *Aoprosa* (Euphorbiaceae), and *Diospyros* (Ebenaceae) for *HSS*. In *SBF*, the dominant species belonged in *Macaranga* (Euphorbiaceae), *Ficus* (Moraceae), *Litsea*, *Palaquium*, and *Sterculia* (Sterculiaceae), *Maduca* (Sapotaceae), *Shorea* (Dipterocarpaceae), *Canarium* (Burseraceae), and *Quercus* (Fagaceae). The remaining four guilds [*SSS* (Soft-Small-Slow), *SBS* (Soft-Big-Slow), *HSF* (Hard-Small-Fast) and *HBF* (Hard-Big-Fast)] had low species diversity, containing 14, 25, 17, and 13 species, respectively.

Guild composition of a plot

Figure 3 shows the guild composition of the three blocks. In PIN, *SSF* (Soft-Small-Fast) and *HBS* (Hard-Big-Slow) were the major guilds, with nearly the same dominance in species number and stem density, followed by *SBF* (Soft-Big-Fast) and *HSS* (Hard-Small-Slow). Outstanding dominance of *HBS* in terms of basal area was characteristic of the PIN block. BL-2 was characterized by a high dominance of *SSF* in every structural feature. BL-1 had intermediate structural features between the other two blocks. The other four guilds (*SSS*, *SBS*, *HSF*, and *HBF*) were minor components in all blocks.

DISCUSSION

Growth traits of a tree taxon

A linear relationship between the RGR and DBH of each taxon [Eq. (1)] shows that the time trend of DBH could be approximated by a simple logistic equation (Shinozaki, 1961). Two parameters of Eq. (1), R_0 and D_{max} , correspond to the intrinsic growth rate (r) and maximum size (K) of the logistic growth curve, respectively. A negative correlation between R_0 and H_d might suggest a trade-off between the initial volume growth rate and architectural strength under a restraint of photosynthetic products (Yoneda et al. 1999; King et al. 2006). A similar negative correlation between R_0 and D_{max} , could have resulted from artificial effects of the analysis method used. However, Yamakura (1996) found the same correlation for tropical tree species using long-term monitoring data from Malaysia (Ng and Tang, 1974), and major species of a subtropical forest in Japan also showed the same correlation (Yoneda, unpublished data). These results suggest that a tree taxon used in this study likely realized the negative correlation between R_0 and D_{max} through constraints on available resources, although Kohyama et al. (2003) found no correlation between the initial growth

rate in height and attainable maximum height in a tropical rain forest. Yamakura (1996) considered the negative correlation as the result of a spectrum of growth traits of tropical tree species under an r - K life strategy model (MacArthur and Wilson, 1967; Pianka, 1972). Condit et al. (2004) and Nascimento et al. (2005) also found a significant correlation among several demographic parameters, including the growth rate, maximum diameter, and wood density in Amazonian trees. These findings support the theory whereby pioneer and climax species show opposite growth traits (Swain and Whitmore, 1988; Baker et al. 2003).

The simple logistic equation shows that the time ($T_{D_{max}/2}$) to satisfy $DBH = D_{max}/2$ on the growth curve is $\ln(D_{max}/D_0 - 1)/R_0$, where D_0 is the initial DBH at $t = 0$. When we examined the relationships between D_{max} and $T_{D_{max}/2}$, about 83 major taxa (Appendix 1) showed dispersed distribution on these coordinates (Fig. 4). This reveals habitat segregation in time and space, when $T_{D_{max}/2}$ is regarded as not only a chronological parameter but also a spatial parameter because of the mosaic stand structure in a mature forest consisting of different phases. The diversity of intrinsic growth rates is considered a common evolutionary product of plants and animals that adapt to given resources in a biome (Arendi, 1997). In the present study, the wide range and continuum of intrinsic growth rates of the 83 taxa was related to a large space-time variance of resource availability in a mature tropical rain forest, with wide variations in the attainable maximum size and stem hardness.

Life strategies of guilds

Four major guilds were created using a mechanical process of classification. A higher correlation was observed between R_0 and D_{max} than between R_0 and H_d , which produced two prominent guilds, *SSF* (Soft-Small-Fast) and *HBS* (Hard-Big-Slow), together with two other major guilds, *SBF* (Soft-Big-Fast) and *HSS* (Hard-Small-Slow).

SSF contains not only typical pioneer species, but also highly diverse species (Appendix 1, 2). Kohyama and Suzuki (1994) found that *Grewia florida* (*SSF*) and *Mastixia tricotoma* (*SSS*) were shade-intolerant and that two species in the *HSS* guild, *Cleistanthus glandulosus* and *Gonystylus foerbesii*, were shade-tolerant based on horizontal distribution patterns in the PIN block. These results suggest opposite responses to light between *SSF* and *HSS*, particularly at the seedling stage. *HSS* was characterized by long tree longevity with slow growth rates under shade conditions, in comparison to *SSF*. *SSF*

Fig. 4. Bottom: Relationship between an attainable maximum DBH (D_{max}) and time required for $D_{max}/2$ growth of 83 major taxa in the 6-ha plot where $D_0 = 1$ cm (Appendix 1). SSF = ○, SSS = ●, SBF = ▽, SBS = ▼, HSF = △, HSS = ▲, HBF = □, and HBS = ■. Top: Schematic diagram of growth curves for the major four guilds based on simple logistic growth.

showed a clear positive correlation between the maximum tree size and longevity among taxa within the guild, when $T_{D_{max}/2}$ was taken as a parameter of longevity (Fig. 4). This might be a gradient of adaptive growth traits closely associated with reproductive traits under a disturbance regime (Thomas, 1996; Chairul and Yoneda, 2006). Some genera of Dipterocarpaceae were also classified into HSS (Appendix 1), although their biased population structure, which lacks mature-sized trees due to logging, means that this result should be interpreted with caution (Nishimura et al. 2006).

The SBF (Soft-Big-Fast) guild has some advantages under intermediate disturbance conditions (Connell, 1978). It included many dominant secondary forest genera such as *Litsea*, *Ficus*, *Palaquium*, and *Sterculia*, as well as some typical pioneer trees with large D_{max} (Yoneda, 2000; Yoneda et al. 2006b). The average D_{max} of SBF was

significantly smaller than that of HBS ($P < 0.001$), but this guild included some species with $D_{max} > 100$ cm such as *Shorea lepidota* and *Canarium vulgare*. Their growth traits might judge them as being "heliotrophic climax species" (Yamakura, 1996), like *Shorea leprosula* in Malaysia. These species would be useful in silviculture together with some species of HBF such as *Dysoxylum excelsum*.

HBS was composed of major species in emergent and dominant layers in the PIN block. Hard wood could be a useful architectural property for very tall emergent trees and canopy trees with a large crown in dominant layers such as fagaceous trees. This guild had large variance in D_{max} without a clear correlation between D_{max} and $T_{D_{max}/2}$. Soil resources, such as water and nutrients, and not light resources, might be the major factors for this variance.

Figure 4 coordinates the four guilds on two axes of time and space. That is, the dominance of canopy trees would successively change from SSF to HBS through SBF under stable environmental conditions because of their different D_{max} , and HSS could complete their long life span as understory species because of their high shade tolerance (Baker et al. 2003).

Turner (2001) reviewed the growth traits of tropical trees and classified them into four guilds along two major axes expressing successional status (Pioneer vs. Climax) and tree size (Small vs. Big). Our four major guilds, SSF, HBS, SBF, and HSS, correspond well to Turner's four guilds, *Small Pioneer*, *Climax*, *Large Pioneer*, and *Understory*, respectively. Nascimento et al. (2005) successfully classified tree species of the Amazonian rain forest into four similar experimental guilds.

Four other minor guilds, SSS, SBS, HSF, and HBF, were related by a large variance in R_0 - D_{max} and R_0 - H_d relationships, and could be evaluated as ecological interfaces among the four major guilds. These guilds had low species diversity, although they included some taxa with high dominance (Appendix 1). We assessed their traits in relation to the four major guilds based on their D_{max} and $T_{D_{max}/2}$ coordinates (Fig. 4). Two taxa of SSS (Soft-Small-Slow), *Mastixia* and *Styrax*, were close to SSF; four taxa of SBS (Soft-Big-Slow) were close to HBS; one taxon of HSF (Hard-Small-Fast), *Durio*, was close to SSF; and two taxa of HBF (Hard-Big-Fast), *Quercus* and *Dysoxylum*, were close to SBF. These four minor guilds might play important roles as a major guild under certain environmental conditions in a new disturbance regime in the future.

Human impacts on guild composition

Human impacts were examined through a comparison of guild composition among the three blocks, based on the assumption that PIN < BL-1 < BL-2 showed a gradient of human disturbance, although the complex topographic conditions would also be an important parameter of the habitat (Ito et al. 2003; Nishimura et al. 2008). Blocks 1 and 2 were characterized by a higher dominance of *SSF* (Soft-Small-Fast) over *HBS* (Hard-Big-Slow) in species number in comparison with the PIN block (Fig. 3). Common species between BL-1 and BL-2 accounted for about 45% of total species number (Table 2), and *SSF* was a dominant guild in both. Higher species richness of *SSF* could be related to higher diversity of habitat for these pioneer trees following logging activity (Yoneda et al. 1999). *Geunsia pentandra* (Verbenaceae) is the most representative in secondary vegetation (FDMPIM, 1978), including fallow fields after slash-and-burn practices (Hashimoto et al. 2007), *Symplocos fasciculata* (Symplocaceae) is found in primary and secondary forests (Nooteboom, 1977), and *Grewia florida* (Tiliaceae) is a common species in gaps in primary stands in this plot (Kohyama and Suzuki, 1994). These two blocks share the diverse habitats of *SSF*. A similar guild composition in species number between BL-1 and BL-2 could result from similar habitat composition at the guild level with high diversity at the species level, and different intensities of logging impact between them were related to different guild compositions in the dimensional features of stem number and basal area (Fig. 3).

Low species richness in *HBS* (Hard-Big-Slow) over *SBF* (Soft-Big-Fast) and *HSS* (Hard-Small-Slow) was another property at BL-1 and -2, and was probably related to selective logging of dipterocarps as the major target species (Nishimura et al. 2006). Three of the four remaining major dipterocarps showed a biased distribution to the PIN and BL-1 blocks (Nishimura et al. 2008) belonging to *HBS*, and another dipterocarp of the *SBS* guild, *Parashorea lucida*, had major habitats in BL-1 and BL-2. The different distributional patterns in *HBS* and *SBS* in the present dipterocarps suggest different impacts of logging among the three blocks rather than an influence of topographic conditions.

High dominance and high species diversity of Fagaceae is a floristic feature of this forest (Fujii et al. 2006; Nishimura et al. 2006). Five of the ten major fagaceous species had a random distribution, presumably caused by biotic interactions such as the high dispersal ability of seeds, while another five species were aggregated (Nishimura et al. 2008). All five spatially

aggregated species belonged to *HBS* and had biased distributions to the PIN and BL-1 blocks. Four (*Lithocarpus hystrix*, *L. lucidus*, *L. macphailii*, and *Quercus oideocarpa*) of the five randomly distributed species were mainly found in BL-1 and BL-2, and three of these four (except *L. macphailii*) belonged to softwood guilds. This habitat segregation between soft- and hardwood guilds of these fagaceous trees might be caused by the same factors as for the dipterocarps.

Canopy trees of a mature rain forest in this area have suffered high mortality since the latter half of 1990s because of dry weather and logging (Yoneda et al. 2006). This has led to rapid reduction and extinction of species of *HBS* in the fragmented hill dipterocarp forest. Luan et al. (2004) also found recent dynamic and large-scale changes in guild composition in undisturbed Amazonian forests. Thus, building a quantitative evaluation of changes in these rain forests is critical for sound management and protection, although clarifying the mechanisms quantitatively is difficult because of the complex impacts of both human and natural disturbances.

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Appendix 1. Guild composition of the 6-ha plot and major taxa with high relative dominance of over 0.5% as the sum of the relative values of basal area (BA) and tree number (TN).

Guild (total sp. number)	Family	Genus	Taxon Major species	No. of Species	BA (%)	TN (%)
SSS (14spp)	Clusiaceae	<i>Garcinia</i>	<i>G. celebica</i>	2	0.3	0.4
	Cornaceae	<i>Mastixia</i>	<i>M. trichotoma</i>	1	0.6	1.2
	Icacinaeae	<i>Gomphandra</i>	<i>G. pseudojavanica</i>	3	0.2	0.6
	Lecythidaceae	<i>Barringtonia</i>	<i>B. macrostachya</i>	4	0.3	0.6
	Sapotaceae	<i>Ganua</i>	<i>G. palembanica</i>	2	0.6	0.6
	Styracaceae	<i>Styrax</i>	<i>S. serrulatum</i> , <i>S. paralleluneurum</i>	2	1.3	2.7
SSF (142spp)	Actinidaceae	<i>Sauraria</i>	<i>S. nudiflora</i>	1	0.3	0.3
	Annonaceae	<i>Polyalthia</i>	<i>P. lateriflora</i>	3	0.3	0.5
	Apocynaceae	<i>Voacanga</i>	<i>V. foetida</i>	2	0.7	0.9
	Euphorbiaceae	<i>Endospermum</i>	<i>E. moluccanum</i>	1	0.2	0.4
	Euphorbiaceae	<i>Macaranga</i>	<i>M. pruinosa</i>	4	0.3	0.5
	Euphorbiaceae	<i>Mallotus</i>	<i>M. paniculatus</i> , <i>M. retinoides</i>	5	0.7	1.6
	Flacourtiaceae	<i>Hydnocarpus</i>	<i>H. kunstleri</i>	3	0.2	0.4
	Icacinaeae	<i>Platea</i>	<i>P. excelsa</i>	1	0.4	0.5
	Lauraceae	<i>Beilschmiedia</i>	<i>B. bangkai</i>	2	0.4	0.6
	Lauraceae	<i>Cryptocarya</i>	<i>C. nitens</i>	6	0.1	0.4
	Lauraceae	<i>Endiandra</i>	<i>E. rubescens</i>	1	0.8	0.6
	Lauraceae	<i>Litsea</i>	<i>L. mappacea</i> , <i>L. resinosa</i>	4	0.6	1.1
	Melastomaceae	<i>Pternandra</i>	<i>P. carulescens</i> , <i>P. cordata</i>	3	0.2	0.5
	Myristicaceae	<i>Knema</i>	<i>K. hookeriana</i>	9	0.5	0.9
	Olacaceae	<i>Strombosia</i>	<i>S. javanica</i>	1	0.2	0.4
	Rubiaceae	<i>Pleiocarpidia</i>	<i>P. enneandra</i>	1	0.2	0.6
	Sapotaceae	<i>Palaquium</i>	<i>P. hexandrum</i> , <i>P. rostratum</i>	5	0.7	1.3
	Sapotaceae	<i>Payena</i>	<i>P. acuminata</i>	2	0.7	0.7
	Symplocaceae	<i>Symplocos</i>	<i>S. faciculata</i>	2	0.6	1.4
	Thymelaeaceae	<i>Aquilaria</i>	<i>A. malaccensis</i>	1	0.4	0.4
	Tiliaceae	<i>Grewia</i>	<i>G. florida</i>	1	0.4	1.1
	Tiliaceae	<i>Grewia</i>	<i>G. cf. florida</i>	1	1.4	2.1
	Urticaceae	<i>Pipturus</i>	<i>P. argenteus</i>	2	0.3	0.6
	Urticaceae	<i>Villebrunea</i>	<i>V. rubescens</i>	2	0.5	1.7
	Verbenaceae	<i>Geunsia</i>	<i>G. hexandra</i>	1	1.5	2.0
SBS (25spp)	Burseraceae	<i>Santiria</i>	<i>S. laevigata</i> , <i>S. apiculata</i>	5	1.3	1.0
	Dipterocarpaceae	<i>Parashorea</i>	<i>P. lucida</i>	1	2.4	0.8
	Elaeocarpaceae	<i>Elaeocarpus</i>	<i>E. glaber</i> , <i>E. littoralis</i>	9	1.0	1.2
	Moraceae	<i>Artocarpus</i>	<i>A. lancifolius</i> , <i>A. rigidus</i>	9	6.1	2.9
SBF (60spp)	Anacardiaceae	<i>Buchanania</i>	<i>B. arborescens</i>	1	0.7	0.1
	Asteraceae	<i>Vernonia</i>	<i>V. arborea</i>	1	0.6	0.3
	Burseraceae	<i>Canarium</i>	<i>C. vulgare</i>	3	1.3	0.4
	Dipterocarpaceae	<i>Shorea</i>	<i>S. lepidota</i>	4	1.0	0.6
	Euphorbiaceae	<i>Macaranga</i>	<i>M. gigantea</i> , <i>M. hypoleuca</i> , <i>M. triloba</i>	3	2.6	3.2
	Euphorbiaceae	<i>Mallotus</i>	<i>M. laevigata</i>	1	0.2	0.6
	Fagaceae	<i>Quercus</i>	<i>Q. oideocarpa</i>	2	1.2	0.6
	Lauraceae	<i>Litsea</i>	<i>L. cubeba</i> , <i>L. robusta</i>	10	1.1	1.2
	Lauraceae	<i>Phoebe</i>	<i>P. elliptica</i>	3	0.4	0.3
	Magnoliaceae	<i>Magnolia</i>	<i>M. gigantifolia</i>	1	0.3	0.3
	Moraceae	<i>Ficus</i>	<i>F. ribes</i>	9	1.2	1.7
	Sapindaceae	<i>Lepisanthes</i>	<i>L. tetraphylla</i>	1	0.3	0.3
	Sapotaceae	<i>Madhuca</i>	<i>M. sericea</i>	4	0.9	1.3
	Sapotaceae	<i>Palaquium</i>	<i>P. obovatum</i>	2	1.8	2.1
HSS (71spp)	Sterculiaceae	<i>Sterculia</i>	<i>S. rubiginosa</i>	7	0.8	1.1
	Dipterocarpaceae	<i>Hopea</i>	<i>Hopea</i> sp.	2	0.2	0.4
	Dipterocarpaceae	<i>Shorea</i>	<i>S. atrinervosa</i> , <i>S. maxiwelliana</i>	2	0.4	0.6
	Dipterocarpaceae	<i>Vatica</i>	<i>V. cf. ridleyana</i>	4	0.4	0.3
	Ebenaceae	<i>Diospyros</i>	<i>D. sumatrana</i>	4	0.3	0.9
	Euphorbiaceae	<i>Aporosa</i>	<i>A. antenifera</i>	7	0.5	0.9
	Euphorbiaceae	<i>Cephalomappa</i>	<i>C. malloticarpa</i>	2	1.5	1.5
	Euphorbiaceae	<i>Cleistanthus</i>	<i>C. glandulosus</i>	2	2.0	3.8
	Meliaceae	<i>Dysoxylum</i>	<i>D. caulostachyum</i>	3	0.2	0.4
	Rubiaceae	<i>Nauclea</i>	<i>N. crytopoda</i> , <i>purpurascens</i>	2	0.2	0.4
HSF (17spp)	Sapindaceae	<i>Xerospermum</i>	<i>X. noronhianum</i>	1	0.4	0.6
	Alangiaceae	<i>Alangium</i>	<i>A. javanicum</i> (Bl.) King.	3	0.5	1.1
	Bombacaceae	<i>Durio</i>	<i>D. griffithii</i> , <i>D. zibethinus</i>	3	0.7	1.5
	Euphorbiaceae	<i>Mallotus</i>	<i>M. penangensis</i>	3	0.3	0.4
	Theaceae	<i>Eurya</i>	<i>E. acuminata</i>	2	0.2	0.7
	Anacardiaceae	<i>Swintonia</i>	<i>S. schwenkii</i>	2	5.6	1.0
	Clusiaceae	<i>Calophyllum</i>	<i>C. soulatri</i>	1	0.8	0.3
	Dipterocarpaceae	<i>Hopea</i>	<i>H. dryobalanoides</i>	1	1.0	0.9
	Euphorbiaceae	<i>Drypetes</i>	<i>D. negecta</i>	2	0.3	0.4
	Fagaceae	<i>Castanopsis</i>	<i>C. rhamnifolia</i>	2	1.4	1.0
HBS (80spp)	Fagaceae	<i>Lithocarpus</i>	<i>L. javensis</i> , <i>L. meijerii</i>	19	9.8	4.1
	Fagaceae	<i>Quercus</i>	<i>Q. gemelliflora</i>	1	1.2	0.4
	Flacourtiaceae	<i>Ryparosa</i>	<i>R. kunstleri</i>	2	0.5	0.4
	Lecythidaceae	<i>Planchonia</i>	<i>P. valida</i>	1	0.9	0.1
	Meliaceae	<i>Aglaiia</i>	<i>A. ganggo</i>	13	0.8	1.4
	Myrtaceae	<i>Eugenia</i>	<i>E. lineata</i> , <i>E. clavimyrus</i>	22	3.2	4.0
	Sapindaceae	<i>Nephelium</i>	<i>N. juglandifolium</i> , <i>N. mutabile</i>	7	4.7	3.1
	Sapindaceae	<i>Pometia</i>	<i>P. alnifolia</i>	3	0.7	0.6
HBF (13spp)	Euphorbiaceae	<i>Blumeodendron</i>	<i>B. tokbrai</i>	1	0.6	0.3
	Euphorbiaceae	<i>Ptychopyxis</i>	<i>P. bacciformis</i>	1	0.5	0.3
	Fagaceae	<i>Quercus</i>	<i>Q. argentata</i>	1	1.2	0.4
	Lythraceae	<i>Lagerstroemia</i>	<i>L. ovalifolia</i>	1	0.8	0.1
	Meliaceae	<i>Dysoxylum</i>	<i>D. excelsum</i>	8	2.2	1.7
	Sapotaceae	<i>Palaquium</i>	<i>P. gutta</i>	1	0.7	0.8

Appendix 2. Guild of the top 30 dominant species for all trees with DBH > 10 cm in a 6.55-ha plot, Pinang-pinang baru, including this study site (cf. Fig. 2).
(Modified Table 2 from Nishimura et al.(2006))

Rank	Abundance			Basal area			Family	Species	Guild	Proportion	Family	Guild	Proportion
	Species												
1	<i>Cleistanthus glandulosus</i> Jabl.						Euphorbiaceae	HSS	3.3%		Anacardiaceae	HBS	4.0%
2	<i>Villebrunea rubescens</i> (Bl.) Bl.						Urticaceae	SSF	3.2%		Fagaceae	HBS	2.7%
3	<i>Grewia florida</i> Miq.						Tiliaceae	SSF	2.2%		Moraceae	SBS	1.9%
4	<i>Styrax serrulatum</i> Roxb.						Styracaceae	SSS	1.7%		Euphorbiaceae	HSS	1.9%
5	<i>Macaranga triloba</i> (Bl.) Muell. Arg.						Euphorbiaceae	SSS	1.7%		Dipterocarpaceae	SBS	1.8%
6	<i>Symplocos faciculata</i> Zoll.						Symplocaceae	SSF	1.5%		Tiliaceae	SSF	1.6%
7	<i>Palaquium obovatum</i> Engl. var. <i>occidentale</i>						Sapotaceae	SBF	1.5%		Verbenaceae	SSF	1.4%
8	<i>Geunsia hexandra</i> (T. et B.) Kds.						Verbenaceae	SSF	1.4%		Fagaceae	HBS	1.3%
9	<i>Nephelium lappaceum</i> Linn.						Sapindaceae	HBS	1.0%		Sapindaceae	HBS	1.3%
10	<i>Mallotus laevigata</i> (M.A.) Airy Shaw						Euphorbiaceae	SBF	0.9%		Euphorbiaceae	SBF	1.2%
11	<i>Macaranga hypoleuca</i> Muell-Arg.						Euphorbiaceae	SBF	0.9%		Sapindaceae	HBS	1.2%
12	<i>Voacanga foetida</i> (Bl.) Rolfe.						Apocynaceae	SSF	0.9%		Fagaceae	HBS	1.1%
13	<i>Diospyros sumatrana</i> Miq. var. <i>decifens</i>						Ebenaceae	HSS	0.9%		Dipterocarpaceae	HBS	1.1%
14	<i>Shorea maxwelliana</i> King						Dipterocarpaceae	HSS	0.8%		Fagaceae	HBS	1.1%
15	<i>Mastixia trichotoma</i> Bl.						Cornaceae	SSS	0.8%		Styracaceae	SSS	1.1%
16	<i>Hopea dryobalanoides</i> Miq.						Dipterocarpaceae	HBS	0.7%		Fagaceae	HBf	1.1%
17	<i>Cephalomappa malloica</i> J.J. Smith						Euphorbiaceae	HSS	0.7%		Urticaceae	SSF	1.0%
18	<i>Eurya acuminata</i> DC.						Theaceae	HSF	0.7%		Moraceae	SBS	1.0%
19	<i>Pternandra coerulescens</i> Jack						Melastomataceae	SSF	0.7%		Meliaceae	HBf	1.0%
20	<i>Ficus ribes</i> Reinw. ex Bl.						Moraceae	SBF	0.7%		Euphorbiaceae	HSS	1.0%
21	<i>Pleiocarpidia enneandra</i> (Walk.) Sch.						Rubiaceae	SSF	0.7%		Sapotaceae	SBF	0.9%
22	<i>Madhuca sericea</i> (Miq.) H.J.L						Sapotaceae	SBF	0.7%		Fagaceae	HBS	0.9%
23	<i>Durio griffithii</i> (Mast.) Bakh.						Bombacaceae	HSF	0.6%		Bursaceae	SBS	0.9%
24	<i>Palaquium hexandrum</i> Engl.						Sapotaceae	SSF	0.6%		Sapindaceae	HBS	0.9%
25	<i>Durio zibethinus</i> Murr.						Bombacaceae	HSF	0.6%		Fagaceae	HBS	0.8%
26	<i>Vitex gamosepala</i> Griff.						Verbenaceae	-	0.6%		Symplocaceae	SSF	0.8%
27	<i>Swintonia schwenkii</i> (T. & B.) T. & B.						Anacardiaceae	HBS	0.6%		Fagaceae	SBF	0.8%
28	<i>Payena acuminata</i> (Bl.) Pierre						Sapotaceae	SSF	0.6%		Dipterocarpaceae	-	0.8%
29	<i>Platea excelsa</i> Bl. var. <i>borneensis</i>						Icacinaceae	SSF	0.6%		Asteraceae	SBF	0.7%
30	<i>Laportea stimulans</i>						Urticaceae	SSF	0.6%		Moraceae	SBS	0.7%