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Leaf longevity of tropical shrub species in an open forest in Sumatra

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ABSTRACT Leaf longevity of tropical shrub species was examined with reference to the intensity of disturbance. Species with lower stem hardness likely prioritize a higher volume of growth at early growth stages over the physical strength of the stem. This trait is thought to be advantageous for species suffering frequent disturbance, thus it is believed that stem hardness could be used as a measure of adaptability to disturbance. The weight ratio of leaves to stalks on a twig is an important parameter to assess the leaf longevity satisfying the minimum maintenance costs of a twig. In this study, the leaf longevity of shrubs was shown to be reciprocally related to the weight ratio. Based on this relationship, it was revealed that these species gain suitable leaf longevity by regulating this weight ratio under conditions of the minimum maintenance. A positive correlation between leaf longevity and stem hardness was also observed among shrub species. Assessment of the niche of these species in a secondary sere according to stem hardness verified that leaf longevity increases with progressing succession as a result of regulation of the weight ratio.

Key words: disturbance, leaf longevity, secondary succession, tropical shrub species, twig structure

INTRODUCTION

High seed production from early growth stages, as well as a strong vegetative propagation ability, is an important regeneration strategy for shrub species that experience frequent disturbance. Recently, Yoneda (2006) showed that the tropical shrub *Piper aduncum* has gained a vigorous reproductive trait through effective carbon gain and nutrients acquisition as a result of its high turnover rate of leaves, and proposed a model in which species adapting to high disturbance shorten their leaf longevity by regulating the weight ratio of leaves to stalks on a twig. The model expects hyperbolic relationships between leaf longevity and the weight ratio among species along the secondary sere of vegetation. This study aims to verify this model with several tropical shrub species suffering different frequency of human disturbance such as slashing.

In competing among shoots for light resources, fast growth to reproduction size would be a preferential trait for regeneration in unstable sites without severe water or nutrient stress. However, under a given cost investment there is a trade-off between the volume growth rate of a stem and its hardness in terms of physical strength (Yoneda, 1997: Yoneda *et al.*, 1999). Frequent disturbance decreases the minimum shoot size at reproductive stages of the shrub species, which is thus expected to prefer higher growth rates to physical strength from the point of view of cost-performance. Based on these relationships, we try to verify stem hardness as a measure indicating the extent of adaptability of shrub species to disturbance.

Leaf longevity of shrub species can be directly observed by long-term demographic observations. If the observed leaf longevity shows a proportional relationship with the values estimated from twig structure by the hyperbolic relation of the model satisfying the minimum maintenance cost, we can confirm that leaf longevity is gained by regulating the weight ratio of leaves to stalks under these conditions.

Based on the verification of stem hardness as a measure of adaptability to disturbance, we can then confirm whether leaf longevity decreases with increasing disturbance from observations of the correlation between leaf longevity and stem hardness. We also try to verify the applicability of the proposed model with successive changes in leaf longevity in a secondary sere according to the above three verification steps. To determine how these relationships apply to climax species in a mature forest, we compare their characteristics of leaf longevity with those of shrub species.

MATERIALS AND METHODS

Study site and plant materials

This study was carried out from July 2000 to December 2002 in the school forest of Andalas University (HPPB: 00° 55' S, 100° 28' E; Yoneda *et al.*, 2000), 17 km east of Padang City, West Sumatra, Indonesia. Major observations were conducted in an area of open forest on a gentle slope situated around 300 m above sea level (a.s.l.). This open forest was artificially established to represent a young secondary forest for educational purposes. Supplementary data was collected from a neighboring closed forest consisting of small stands at various regeneration stages on steep slopes ranging from 300 to 450 m a.s.l., in which some big trees above 50 cm in stem diameter at breast height (*dbh*) were distributed sporadically. Monthly rainfall during the study period was 361 ± 183 mm with no month receiving less than 100 mm according to the nearest Meteorological Station in Padang.

The total number of tree species observed in the open forest was 42. Most were secondary species but a few climax and cultivated species were also observed, such as *Aleurites moluccana, Archidendron jiringa* and *Hevea brasiliensis* (Appendix). The number of species observed in the closed forest was 20, including some species also observed in the open forest.

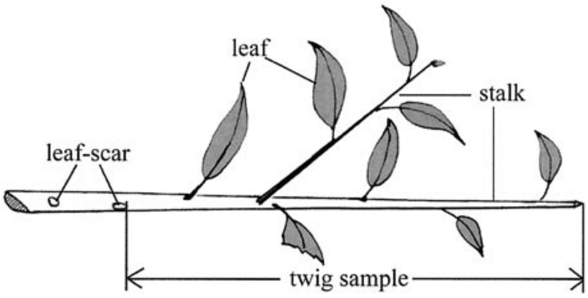

Fig. 1. Schematic diagram of the twig unit used for observations of the weight ratio of leaves to stalks.

Table 1. Sample sizes used for four observations conducted in HPPB, Sumatra. Numbers in parentheses represent numbers of twigs. *RGRD* represents observations of the relative growth rates of stem diameter.

Numbers of species/shoots sampled		Leaf longevity	Twig form	*RGRD*	Stem hardness
Open forest					
	species	21	25	28	35
	shoots	23(66)	28(35)	35	45
Closed forest					
	species	–	–	20	20
	shoots	–	–	26	26

Demographical observation of leaves

Leaf longevity of 21 species was observed in the open forest using a demographic method. Changes in the number of leaves on a twig with defoliation and recruitment were observed at monthly intervals for 1.9 years from October 2000 to July 2001. In total, we monitored 66 twigs on 23 shoots defined as an assemblage of one stem and its branches (Table 1 & Appendix). The census was conducted continuously until death, and the demographic data under nearly dynamic equilibrium conditions of standing leaf number was applied to the analysis. The actual observation period of these twigs was 1.4 ± 0.43 years on average. Leaf longevity was defined as the ratio of the average standing leaf number to the average annual number of defoliated leaves during the observation period.

Analysis of twig structures

The weight ratio of leaves to stalks on a twig is a useful parameter for determining leaf longevity (Yoneda, 2005), while ratios of foliage to non-photosynthetic organs are also important parameters to assess the productive structure of a community (Monsi & Saeki, 1953; Kira & Shidei, 1967) and an individual tree (Shinozaki *et al.*,1964; Oohata & Shinozaki, 1979; Yoneda, 1993). In October 2000, we observed this ratio in 25 species in the open forest. Two or three twigs were collected from a non-shaded main branch of each shoot then oven dry weights of leaves and stalks were measured including the part of each twig holding the present leaves (Fig. 1). A total of 35 twigs from 28 shoots were observed (Table 1 & Appendix). The average size of these twigs was 27 ± 14 cm (range: 4.4 – 66 cm) in length by 0.91 ± 0.65 cm (0.33 – 3.2 cm) in diameter at the end of the major stalk. The length and maximum width of the lamina of 10 leaves from each species were measured and the surface area of a single leaf was calculated as the product of the length and width.

Based on a mathematical model, Yoneda (2006) showed that the weight ratio of leaves (*L*) to stalks (*I*) on a twig is expected to have a reciprocal relationship with leaf longevity when a mature twig, as a regeneration unit, minimizes its maintenance cost by minimizing its weight. It showed that leaf longevity (*Sopt*) was expressed by the following equation for a twig with a life cycle of *n* years:

$$Sopt = n \,/\, (L/I + 1) \qquad (1)$$

We calculated leaf longevity of all collected twig samples by this equation, assuming that the weight ratio of leaves to stalks of a sample was equivalent to the L/I ratio and $n = 1$ irrespective of species.

Relative growth rates of stem diameter and hardness

Dbh growth rates of non-shaded shrubs and trees in HPPB were observed using an aluminum band-type dendrometer at bimonthly intervals for 2.4 years from July 2000. The maximum *dbh* range was 10 – 50 cm (most were less than 30 cm) in the open forest and 19 – 69 cm in the closed forest at the first observation in 2000. Observations were conducted using 61 shoots from 48 species (Table 1 & Appendix).

Stem hardness was assessed as the maximum power required to remove a standard sized nail from the stem (Yoneda, 1997). Observations were carried out in August 2000 using 71 shoots (Table 1 & Appendix), and heights of these shoots were observed in October 2000.

RESULTS AND DISCUSSION

Relationship between stem hardness and the observed growth traits

Heights of each species at the maximum *dbh* showed a positive correlation with *dbh* without any clear differences between the open and closed forests, and the range of these two dimensions tended to increase with increasing stem hardness (Fig. 2). Almost all shrubs in the open forest tended to show lower stem hardness (Appendix). Analysis of covariance with all data showed that stem hardness has no significant direct correlation with tree height ($P = 0.225$) but significantly influences it indirectly through its positive correlation with *dbh* ($P < 0.05$).

In the open forest, the stem hardness of shrubs with a *dbh* of 10 – 15 cm had a negative correlation with the average relative growth rate of *dbh* (*RGRD*) during the study period of 2.4 years (Fig 3). This relationship was not significant for trees with a *dbh* above 15 cm, but trees in the closed forest showed a significant relationship at a wider *dbh* range ($P < 0.05$).

Stem hardness is a physical property concerned with the structural strength of a tree and positively correlated with bulk density (Yoneda, 1997). This shows that trees have a trade-off relationship between volume growth and physical strength under a given cost investment. Shrubs in the open forest with a *dbh* of less than 15 cm satisfied this relationship, but this correlation was lost with increasing *dbh* because of larger decrease of growth rates of trees with lower hardness (Fig. 3). This shows that these trees with softer wood reach their mature stages at around *dbh* = 15 cm. Thomas (1996) showed that smaller tree species displayed smaller reproductive size thresholds on both an absolute and a relative basis in tree height for tropical rain forest trees. These suggest that trees with lower bulk density, being smaller tree sizes (Fig. 2), turn their major investment from vegetative (stem growth) to reproductive organs (fruit production) at the *dbh* under the conditions without large reduction of their production, because stem hardness tends to remain constant within species irrespective of stem size (Yoneda *et al.*, 1999). This would be the reason for cancellation of the correlation at the size. If we assume this *dbh* to be the minimum size of these trees of reproductive stage, it can be suggested that shrubs with lower stem hardness reach reproductive age earlier. This trait would be advantageous for species suffering repeated disturbance. These findings suggest that stem hardness could be used as a measure to assess the extent of species adaptability to vegetation disturbance.

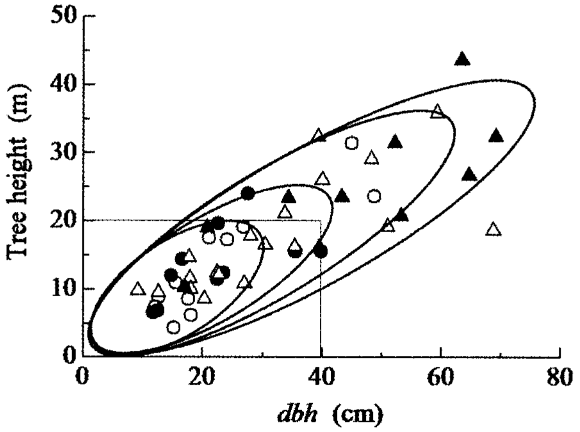

Fig. 2. Allometric relationship between the maximum tree height and stem diameter at breast height (*dbh*) of each species in HPPB, Sumatra. Stem hardness was divided into four classes as follows: 5–10 kg f cm^{-1} (open circles), 10–15 kg f cm^{-1} (closed circles), 15–20 kg f cm^{-1} (open triangles) and above 20 kg f cm^{-1} (closed triangles), respectively. The four ellipses roughly show the maximum range of these two dimensions for each class.

The trade-off relationship between volume growth

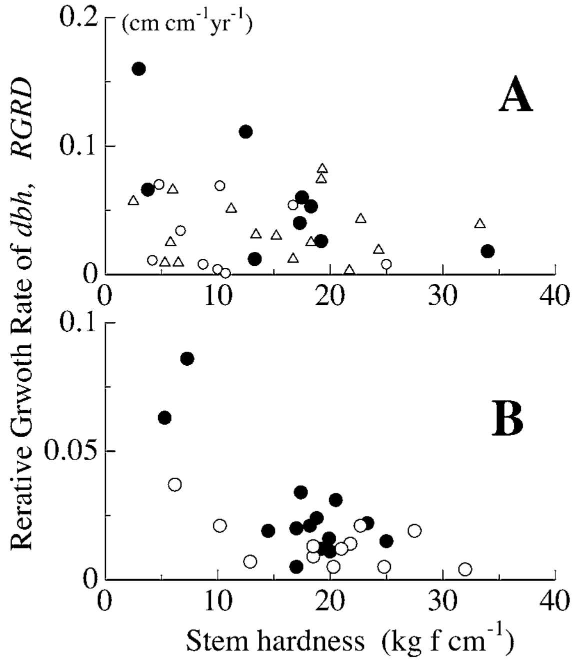

Fig. 3. Relationship between relative growth rates of *dbh*, *RGRD*, and stem hardness of shrubs in an open forest area (A) and a closed forest (B). Stem diameter was divided into three and two classes as follows. A: 10–15 cm (closed circles), 15–20 cm (open circles), above 20 cm (open triangles), and B: 20–40 cm (closed circles), above 40 cm, respectively.

Table 2. Correlation between leaf longevity and morphological traits (hardness and leaf area, respectively) of shurubs in an open forest in HPPB, Sumatra. Values show coefficients of correlation (bold) and significant levels.

	Longevity	*Sopt*	Hardness	Leaf area
Longevity	–	0.001	0.05	NS
Sopt	**0.920**	–	0.01	0.05
Hardness	**0.572**	**0.572**	–	NS
Leaf area	**-0.568**	**-0.487***	**-0.425***	–

*Correlation among species with a leaf area of less than 500 cm^2. *Spot* represents the leaf longevity estimated from twig structure using Eq. (1) (see text for details).

and physical strength was also observed in the closed forest throughout a wider *dbh* range (Fig. 3). It was also observed in a secondary forest in this area among trees up to 20 cm in *dbh* (Yoneda *et al.*, 2006). In these two forests, which suffer a lower frequency of disturbance than the open forest, competition for light resources should prioritize fast growth to canopy height. This suggests that, in each forest, the trade-off relationship occurs among trees within the range of the minimum *dbh* corresponding to canopy height.

Leaf longevity and stem hardness

Demographic observations of shrubs in the open site revealed a leaf longevity of 0.23 to 1.20 years (Appendix). The lowest value was observed for the small scrub *Melastoma malabathricum* followed by many typical pioneer shrubs such as *Ficus, Trema, Macaranga* and *Mallotus*. Species with higher stem hardness tended to have longer leaf longevity ($P < 0.05$; Table 2).

In the open forest, the optimum leaf longevity, *Sopt*, were estimated with dimensional data of the collected twig samples. Calculated *Sopt* values showed a nearly proportional relationship with the leaf longevity values obtained from demographic observations ($P < 0.001$; Fig. 4). This shows that *Sopt* can be used as a measure for evaluating the relative values of leaf longevity, even though, because of the apriori assumption that $n = 1$, the absolute values were largely different from the observed values.

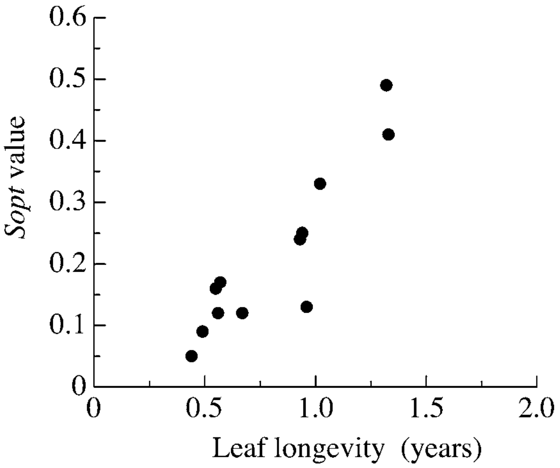

Fig. 4. Relationship between leaf longevity obtained from demographic observations and *Sopt* values calculated from observations of the twig structure of shrubs in an open forest, Sumatra.

Sopt values of 25 species in the open forest had a positive correlation with stem hardness ($P < 0.01$; Table 2). As with the results from the demographic observations, these findings show that shrubs with higher stem hardness tend to have longer leaf longevity.

The strong positive correlation between the *Sopt* values and observed leaf longevity shows the applicability of the model in Eq. (1) to these shrubs (Table 2). A similar positive correlation between the *Sopt* values and relative leaf longevity, which is estimated by the ratio of present to total leaves on a stalk 2 years old, was observed for canopy trees in the Japanese warm-temperate evergreen oak forest ($P < 0.001$: unpublished data of Kanazawa, 2001). Based on the basic assumption of the mathematical model expressed in Eq. (1), these results show that leaf longevity is regulated under conditions minimizing the maintenance cost of a mature twig. The *Sopt* values were negatively correlated with the average leaf area of twig samples from HPPB ($P < 0.05$; Tables 2). It is likely that this is the result of the physical relationship between the *L/I* ratio and leaf area of twigs restrained by space, though leaf area is also influenced by the specific leaf area.

It was previously shown that short leaf longevity allows continuous high fruit production from early growth stages through effective utilization of energy and nutrients (Yoneda, 2006). As a reproductive strategy, this trait is advantageous for species growing in habitats suffering frequent disturbance. The negative correlation between stem hardness and *RGRD* supports the suggestion that these species lower their stem hardness for higher volume growth of the shoot until maturity. A positive correlation between leaf longevity and stem hardness was also observed. However, leaf longevity as a physiological property does not directly affect stem hardness, though a short leaf life span could save construction costs of stems and branches with low stem hardness because of lowered leaf biomass as a result of effective leaf production (Yoneda, 2006). This positive correlation would result from independent adaptation of reproductive and vegetative growth traits to habitats with frequent disturbance. For species in a mature forest diverse in time and space, adaptability to resources such as light, water and nutrients is a major factor affecting leaf longevity (Chabot & Hicks, 1982: Ackerly and Bazzaz, 1995). Assessment of the niche of shrub species in a secondary sere according to stem hardness, showing the extent of species adaptability to disturbance, revealed a positive correlation with leaf longevity. This shows that leaf longevity tends to increase with progressing succession. Moreover, the high correlation between leaf longevity and *Sopt* values revealed that shrub species in the sere have gained an adaptive leaf longevity trait through regulation of the weight ratio of leaves and stalks on a twig. These findings therefore support the applicability of the proposed model for the gradient of leaf longevity in a secondary sere (Yoneda, 2005).

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Appendix 1. List of the species included in the four observations conducted in this study. Upper column in "Open forest" shows 21 species for demographical observation. "Form" means those included in observations of twig structure. Numbers show numbers of shoots and twigs (in parentheses), respectively.

Family name	Species name	Leaf longevity		Form number	*RGRD* number	Hardness	
		(years)	number			(kg f cm^{-1})	number
Open forest							
Melastomataceae	*Melastoma malabathricum* Linn.	**0.23 ± 0.02**	2(5)	–	–	–	–
Ulumaceae	*Trema orientalis* Bl.	**0.34 ± 0.05**	1(3)	–	–	–	–
Moraceae	*Ficus pandana* Burm. f.	**0.40 ± 0.01**	1(3)	1(2)	1	7	1
Moraceae	*Ficus grossularioides* Burm. f.	**0.42 ± 0.12**	1(4)	–	–	–	–
Moraceae	*Ficus fulva* Reinuw. ex Bl.	**0.42 ± 0.01**	1(2)	1	1	13	1
Moraceae	*Ficus* sp.	**0.52 ± 0.07**	1(3)	–	–	–	–
Theaceae	*Schima wallichii* (DC.) Korth.	**0.54 ± 0.02**	1(3)	1	2	17 ± 0.5	2
Verbenaceae	*Vitex pubscens* Vahl.	**0.55 ± 0.16**	1(4)	1(2)	1	30 ± 5	2
Euphorbiaceae	*Macaranga triloba* (Bl.) Muell. Arg.	**0.56 ± 0.02**	1(2)	2(3)	1	10	1
Euphorbiaceae	*Mallotus paniculatus* (Lam.) Muell. Arg.	**0.59 ± 0.08**	1(2)	–	–	–	–
Euphorbiaceae	*Macaranga javanica* (Bl.) Muell. Arg.	**0.61 ± 0.04**	1(3)	1	2	15 ± 3	2
Piperaceae	*Piper aduncum* Linn..	**0.68 ± 0.07**	1(3)	–	–	–	–
Euphorbiaceae	*Mallotus* sp.	**0.77 ± 0.14**	1(3)	–	–	–	–
Ixonanthaceae	*Ixonantes petiolaris* Bl.	**0.81 ± 0.06**	1(2)	1	2	24 ± 2	2
Moraceae	*Ficus variegata* Bl.	**0.82 ± 0.06**	1(3)	1	3	5 ± 2	3
Euphorbiaceae	*Hevea brasiliensis* Muell. Arg.	**0.99 ± 0.05**	1(4)	1	–	19	1
Symplocaceae	*Symplocos cochinchinensis* (Lour.) Moore	**1.02 ± 0.21**	2(4)	1(2)	1	13	1
Moraceae	*Artocarpus kemando* Miq.	**1.06 ± 0.06**	1(4)	–	1	11	1
Theaceae	*Eurya acuminata* DC.	**1.14 ± 0.14**	1(3)	1	1	18	1
Clusiaceae	*Cratoxylon* cf *formosum* (Jack) Dyer	**1.14 ± 0.11**	1(3)	–	–	34	1
Myrtaceae	*Rhodamia cinerea* Jack.	**1.20 ± 0.19**	1(3)	1	–	41	1
Euphorbiaceae	*Aleurites moluccana* (L) Willd	–	–	1	1	**4**	1
Sterculiaceae	*Sterculia rubiginosa* Vent.	–	–	–	1	**4**	1
Tilliaceae	*Trichespermum javanicum* Bl.	–	–	–	2	**4 ± 2**	2
Apocynaceae	*Alstonia angustiloba* Miq.	–	–	1	1	**5**	1
Araliaceae	*Arthrophyllum diversifolium* Bl.	–	–	1	1	**7**	1
Euphorbiaceae	*Macaranga gigantea* (Reichb. f. & Zoll.) Muell. Arg.	–	–	1	2	**8 ± 3**	2
Lauraceae	*Litsea diversifolia* Bl.	–	–	1	1	**10**	1
Sterculiaceae	*Commersonia batramia* Merr.	–	–	1	1	**15**	1
Fabaceae	*Archidendron jiringa* (Jack) Nielsen	–	–	1	–	**16**	1
Euphorbiaceae	*Baccaurea macrophylla* Muell. Arg.	–	–	1	–	**16**	1
Aquifoliaceae	*Ilex cymosa* Bl.	–	–	2(4)	–	**16 ± 7**	2
Euphorbiaceae	*Macaranga tanarius* (L.)Muell. Arg.	–	–	1	1	**17**	1
Euphorbiaceae	*Glochidion rubrum* Bl.	–	–	1	–	**17**	1
Fagaceae	*Lithocarpus hystrics* (Korth.) Soepadmo	–	–	2(3)	1	**17**	1
Lecythidaceae	*Baringtonia gigantostachya* Koord. Val.	–	–	–	1	**19**	1
Clusiaceae	*Garcinia lucens* Pierre	–	–	–	1	**19**	1
Elaeocarpaceae	*Elaeocarpus glaber* (NL.)	–	–	–	1	**19**	1
Moraceae	*Arthocarpus dadah* Miq.	–	–	–	2	**20 ± 2**	2
Clusiaceae	*Garcinia parvifolia* Miq.	–	–	–	1	**24**	1
Fagaceae	*Quercus argentata* Korth.	–	–	1	–	**32**	1
Fabaceae	*Milletia atropurpurea* Benth.	–	–	–	1	**33**	1
Closed forest							
Euphorbiaceae	*Macaranga gigantea* (Reichb. f. & Zoll.) Muell. Arg.	–	–	–	2	**6 ± 0.6**	2
Euphorbiaceae	Macaranga hypoleuca (Reichb. f. & Zoll.) Muell. Arg.	–	–	–	1	**7**	1
Lauraceae	*Litsea elliptica* (Bl.) Boerl.	–	–	–	1	**10**	1
Fagaceae	*Quercus oidocarpa* Korth.	–	–	–	1	**13**	1
unidentified	unidentified	–	–	–	1	**15**	1
Euphorbiaceae	*Baccaurea macrophlla* Muell. Arg.	–	–	–	1	**17**	1
Euphorbiaceae	*Croton laevifolius* Bl.	–	–	–	1	**17**	1
Sapotaceae	*Palaquium rostratum* (Miq.) Burck	–	–	–	1	**17**	1
Fabaceae	*Archidendron jiringa* (Jack) Nielsen	–	–	–	1	**18**	1
Dipterocarpaceae	*Dipterocarpus grandiflorus* Blanco	–	–	–	1	**19**	1
Dipterocarpaceae	*Shorea multifora* (Bucrk) Sym.	–	–	–	1	**19**	1
Myristicaceae	*Knema furfuracea* (Hk. et. Th.)	–	–	–	1	**19**	1
Fagaceae	*Lithocarpus elegans* (Bl.) Hatus. Ex Soepadmo	–	–	–	1	**20**	1
Anacardiaceae	*Swintonia schwenchii* (T. & B.) T. & B.	–	–	–	1	**21**	1
Burseraceae	*Santeria tomentosa* Bl.	–	–	–	1	**21**	1
Celastraceae	*Bhesa paniculata* Arn.	–	–	–	1	**22**	1
Fagaceae	*Quercus argentata* Korth.	–	–	–	6	**22 ± 3**	6
Anacardiaceae	*Melanochya* cf *caesia* (BL) Ding Hou	–	–	–	1	**23**	1
Sapindaceae	*Nephelium* sp.	–	–	–	1	**28**	1
Fabaceae	*Koompassia* sp.	–	–	–	1	**32**	1