FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Why are young leaves red?

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According to one general estimate, approximately one-third of plant species in tropical forests delay the greening of their leaves until full expansion (Coley and Kursar 1996). This may result from either delayed chlorophyll synthesis or delayed development of the chloroplasts themselves (Whatley 1992, Kursar and Coley 1992a, Juniper 1993, Coley and Kursar 1996). A 'delayed greening' strategy is thought to provide newly flushing leaves, particularly those that are shade tolerant, with some protection against damage by potentially invasive organisms (Kursar and Coley 1992a, b, c). This protection derives, not from expensive investment in potent physicochemical defences, but from keeping young leaves virtually devoid of nutritive value until they reach full size. Because young leaves suffer the greatest predation from invertebrate herbivores (Coley 1983), this strategy could have high selective value for shade-tolerant tree species possessing long leaf lifespans, particularly if these grow on poor soils.

Since there is little colour in the cell wall, it might be assumed that flushing leaves of such species would simply be pale. However, a substantial proportion of forest species that delay leaf greening also have a considerable quantity of anthocyanin pigment in their new leaves, giving them a reddish or, very rarely, a bluish tint (Coley and Kursar 1996, Lee 2001). These pigments are generally chemically inactive and are commonly used as colouring agents in the food industry (Strack and Wray 1994). Several reasons have been advanced to explain the presence of these anthocyanins:

- they may be *fungicidal* (Coley and Aide 1989).
- they may *photoprotect* leaves against UV damage, or prevent *photoinhibition* (Gould et al. 1995).
- their colour could make them *cryptic* to those herbivores blind to the red part of the spectrum (Stone 1979, Juniper 1993).

The suggestions that anthocyanins increase leaf temperature (Smith 1909), or protect against ultraviolet radiation have largely been discounted (Lee et al. 1987). A more recent hypothesis is that plants may attract herbivores by reddening young leaves in order to protect mature ones (Lüttge 1997). This has never apparently been followed up, but appears improbable. We therefore focus on the three hypotheses above, of which the likelihood of each could be partly evaluated by a habitat survey of anthocyanin frequency in young tropical forest leaves. This has, however, never been attempted on a quantitative basis. Here, we survey the literature, attempt to define delayed greening (with and without anthocyanin presence) and demonstrate the use of a simple colourimeter to assess its incidence. We then discuss what these results imply for the three hypotheses given above and the potential role of a large-scale survey.

Data

Data based on subjective observations are already available for Barro Colorado Island, Panama (Coley and Kursar 1996) and dry and wet sites in Costa Rica (Opler et al. 1980). These are given in Table 1, along with quantified estimates from Kibale Forest, Uganda (Dominy 2002). Here, we add data from Bukit Timah Nature Reserve, Singapore, Chamela-Cuixmala Biosphere Reserve, Mexico, and Marenco Wildlife Refuge, Costa Rica. Bukit Timah Nature Reserve (103° 47′ E, 1° 21′ N) is a small 225 ha reserve of mature lowland dipterocarp and secondary forest in Central Singapore (Corlett 1990). The Chamela-Cuixmala Biosphere Reserve is located along the Pacific coast of Jalisco state, central México, and covers an area of approximately 13 000 ha (104° 56′–105° 10′ W, 19° 22′–19° 39′ N). At least 1120 vascular plants have been identified in this tropical dry forest region (Lott 1993). Marenco Wildlife Refuge (83° 44′ W, 8° 39′ N) is on the Osa Peninsula in southwestern Costa Rica and located approximately 5 km north of the San Pedrillo Park Ranger Station in Corcovado National Park. The reserve encompasses an area of 700 ha including 300 ha of mature forest, 200 ha of forest in advanced regeneration or mature forest that has only experienced selective logging, with the rest being open area or pasture. More than 700 species of vascular plants have been identified from the Osa Peninsula, most of which are likely found in Marenco (Quesada et al. 1997).

Quantified colour measurement

We measured the upper surface colour of mature and youngest leaves with a portable spectrocolourimeter (Miniscan, Hunter, Reston, VA, USA). This was configured to provide output in terms of the 1976 Commission Internationale d'Eclairage (CIE) L* a* b* colour space. The device provides a D65 (artificial daylight) xenon flash illuminant to measure the reflectance spectrum from diffused light (avoiding any influence of shininess, which could be evaluated independently) over wavelengths between 400 and 700 nm. Leaves were placed on a white tile for viewing via an 8 mm diameter aperture. When the youngest leaves were very small, several leaves had to be arranged side by side. The evaluations are thus sometimes approximate, particularly for L*, which defines lightness (scale: 0 for black; 100 for perfect white). Colour information is contained in the a* and b* axes, where a* denotes a green-red value (with green being negative and red positive) and b* the blue-yellow value (blue negative and yellow positive).

Such measurements quantify subjective colour determinations by trichromatic human observers under daytime viewing conditions typifying that in large forest gaps. While falling short of providing a full reflectance spectrum, it provides a quick and convenient method to register colour. Lee et al. (1994) and Lucas et al. (1998) describe previous use of this colour scale in ecological studies.

Species classification

The neutral points are $a^* = 0$ and $b^* = 0$ and thus the presence of anthocyanins in detectable quantities should be signalled by $a^* > 0$ for red and $b^* < 0$ for blue. The category of "delayed greening without anthocyanins" is more arbitrarily defined. Since paleness is partly defined by lightness, we decided on $L^* > 60.0$ with $a^* < 0$ but > -3.1 since no mature (green) leaf has a value of a* so high. Life form was assigned to a class of tree, shrub or climber. Shade-tolerant or light-demanding habits were recorded according to the criteria described by Metcalfe and Grubb (1995). Shade-tolerant species were further divided into either understorey plants, defined as those species never growing > 10 m in Chamela, > 15 in Marenco and not > 20 m in Bukit Timah (depending on canopy height) or overstorey (the remainder). The understorey category included shrubs. The data from these surveys are listed in the Appendix.

Table 1. Data for the percentage of species that flush red leaves at seven tropical forest sites. Latitudes are rounded to the nearest degree, rainfall to the nearest 100 mm.

Site	Latitude	Annual rainfall (mm)	Approx. size of vascular flora	No. of species observed	% of spp. with youngest leaves that are red	Sources
Central America:						
Chamela	19° N	700	1100	95	7	Lott (1993), this study
Comelco	10° N	1500	105*	95*	18	Opler et al. (1980)
Barro Colorado Island	9° N	2700	1400	175	36	Croat (1978), Coley and Kursar (1996)
La Selva	10° N	4000	170*	154*	16	Opler et al. (1980)
Marenco	8° N	3400	700	63	24	Quesada et al. (1997), this study
Asia:						
Bukit Timah	1° N	2600	900	114	60	Corlett (1990), this study
Africa:						
Kibale	0° N	1700	350*	121	51	Dominy (2002)

* trees, treelets and shrubs only

Table 2. Colour distributions of young leaves as a function of forest strata and light-demanding vs shade-tolerant habits. The categories 'red' and 'pale' represent delayed greening with and without anthocyanins respectively. The number of pale leaves in Kibale was not recorded.

	Light demanding	Shade tolerant	Understorey	Overstorey
Chamela				
Red	4	3	2	5
Pale	1	1	2	0
Green	40	44	50	34
Bukit Timah				
Red	10	58	34	24
Pale	2	4	3	0
Green	9	22	11	11
Marenco				
Red	5	12	7	9
Pale	0	1	0	1
Green	10	36	14	33
Kibale[1]				
Red	21	28	10	25
Green	11	28	14	15

[1] From Dominy (2002)

Colour distributions of young leaves

The data in Table 1 show that the number of species with young anthocyanin-containing leaves seems to be very variable, ranging from 7 to 62%, with Chamela at 7% and Bukit Timah at 62%. There is no apparent correlation with rainfall. Blue variants seem extremely rare: only three species from Bukit Timah (*Aporusa benthamiana*, *Drypetes pendula* and *Lasianthus maingayi*) had negative b* values (see Appendix). These leaves appeared subjectively to be burgundy in colour. The rest ranged from pale pink to deep red. Secondly, at Chamela, Marenco, and Bukit Timah, pale young leaves were very rare (Table 2). Delayed greening without anthocyanins may be the exception rather than the rule. Thirdly, variation in the presence of anthocyanins is common even within genera. It is extremely doubtful that there is much phylogenetic inertia to the development of this trait, which, Coley and Kursar (1996) contend, may have evolved convergently many times. Chi-square tests comparing the distribution of young red leaves in the understorey and overstorey, and between light-demanding and shade-tolerant habits, revealed a significant difference only at Bukit Timah, where young red leaves were significantly more likely to be found in shade-tolerant plants ($\chi^2 = 33.9$; d.f. 1; $p < 0.001$). Similar to Kibale (Dominy 2002), data from Chamela and Marenco do not show significant differences for these comparisons.

What hypotheses are worth pursuing?

The results clearly indicate that general statements in the literature do not accurately reflect either the prevalence or distribution of young red leaves in tropical forests, which is variable between sites. Only in Bukit Timah does delayed greening as a whole ('red' plus 'blue' plus 'pale') predominate in shade-tolerant plants. With regard to the three general hypotheses given above, this brief survey helps to establish which is the most likely explanation for them being red.

Although a drip-tip may significantly reduce the likelihood of fungal growth (Ivey and DeSilva 2001), the essential antifungal defence of mature leaves appears to be the cuticle, a hydrophobic wax-laden epithelial secretion that is often microroughened. Water does not wet such surfaces, with potential pathogens being collected and removed by virtually spherical water droplets that easily roll off the leaf (Barthlott and Neinhuis 1997). Young leaves are left vulnerable, however, because cuticle development takes time (Coley and Kursar 1996). The hypothesis that leaf anthocyanins resist fungal infection (Coley and Aide 1989) led Coley and Kursar (1996) to suggest that red leaves might be more prevalent in the wetter understorey than in the drier canopy. This prediction, however, is not supported by the data given here.

The data in the sites listed here suggest that delayed greening is most often associated with anthocyanins (i.e. very few young leaves are pale) and that these are nearly always red rather than blue (meaning that anthocyanins are generally being maintained at an acidic pH). This skewed colour distribution suggests that the optical properties of anthocyanins may be of greatest importance.

Trees whose young leaves are exposed to strong sunlight could suffer damage from exposure to UV radiation (e.g. UV-B wavelengths of 280–315 nm). Compounds with an absorption peak in the UV range, such as flavonoids, would seem the logical choice for such protection as seen, for example, in alpine plants (Veit et al. 1996). If anthocyanins were primarily photoprotective, we presume that young canopy leaves would be particularly at risk as they grow in much brighter conditions than those in the understorey. This is not supported by the data given here, where the overstorey had no greater tendency to flush red than did the understorey.

Prevention of photoinhibition is a similarly unconvincing explanation for anthocyanin presence. Xanthophyll pigments, rather than anthocyanins, are known to protect against photoinhibition in young green leaves in tropical forests (Krause et al. 1995). However, Gould et al. (1995) claim that the leaves of deeply-shaded understorey trees have a delicate photosynthetic apparatus adapted to low light levels. They contend that, were it not for the presence of anthocyanins, photosynthesis might be inhibited by exposure to sunflecks penetrating the canopy in the middle of the day. Generalising from this, it might be expected that the understorey, rather than overstorey, flushes red. The data given here, however, do not support any significant difference between understorey and overstorey. If chlorophyll levels are very low in leaves with delayed greening (Whatley 1992), anthocyanin presence seems irrelevant to prevention of photoinhibition, as little light would be absorbed. Finally, we note that a common location for most of the anthocyanin is just above the lower epidermis and well away from photosynthetic tissue (Lee et al. 1987). This would appear to offer little benefit for either photoprotection or photoinhibition. If this is so, the last possibility (crypsis) is worth exploring further.

Virtually all invertebrate herbivores have good vision in the blue region, but most lack a red receptor. The peak reflectance from leaf anthocyanins often lies at ~ 630 nm (Lee et al. 1987), or beyond the perception of most invertebrates, which typically lack long-wavelength receptors absorbing above 532 nm. However, some Lepidoptera, e.g. *Papilio* spp., have a long-wavelength receptor tuned to 610 nm (Menzel and Backhaus 1991, Arikawa and Uchiyama 1996). In a survey, only 17 out of 232 visual receptors, housed in > 50 species, had peak light absorption at or above 580 nm (Menzel and Backhaus 1991). These receptors may not always be intended to facilitate feeding or oviposition – Kelber (1999) has argued that one butterfly species, *Papilio aegeus*, uses its red (610 nm) receptor to avoid red leaves.

The common ancestor of insects and crustaceans probably lacked a long-wavelength pigment (Briscoe 2000). In contrast, the ancestral vertebrate almost certainly possessed it (Robinson 1994), being retained in most living groups except the mammals, where it (twice) re-evolved in anthropoid primates (to a tuning of around 565 nm – Bowmaker 1998). Folivory on red flushing leaves has been claimed as a major influence on this since higher primates tend to depend on leaves as an important fallback food (Dominy and Lucas 2001). A few non-mammalian vertebrates have this receptor tuned to ~ 620 nm (Bowmaker 1998), but these are not important folivores. We can conclude that leaves saturated with red anthocyanins are inevitably going to be perceived by most potential leaf predators as somewhat dark (Lucas et al. 1998) or possibly dead (Stone 1979). Indeed, although Aide (1988) argued that plants may time leaf flush to avoid periods of invertebrate abundance, it may very well be the case that invertebrates time their abundance to avoid periods when young leaves are perceived as unpalatable (but see Wright and van Schaik 1994) on the importance of solar irradiation.

A more complete understanding of where herbivore densities are greatest in a forest may help resolve the question of why young leaves are red. At present, however, this is far from clear. While invertebrate diversity and density may be higher in the canopy (Stork 1988), it is curious that herbivory is typically higher in the understorey (Lowman and Moffett 1993). Statements in general reviews by Coley and Kursar (1996) and Coley and Barone (1996) are in conflict over this and Lowman (1995) has established that herbivory rates in the canopy can be very high. Murphy (1973) found very high densities of herbivores in the understorey at Bukit Timah, but there have been no canopy studies to match this at the other sites. It is likely that, although particular families and genera of invertebrates may have obvious adaptations to either canopy, understorey or ground level, overall densities would relate to the quantity of edible foliage (Malcolm 1997) and, thus, be equally frequent in both overstorey and understorey. Regardless, it appears that crypsis (Juniper 1993) is the most plausible current suggestion to explain the incidence of red leaves: it is possible that the case for this is stronger than might appear (sic).

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Appendix. The pattern of diversity in leaf colour at Bukit Timah, Chamela, and Marenco.

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
BUKIT TIMAH									
Alangiaceae									
Alangium nobile (C. B. Clarke) Harms	T	U	ST	38.0	6.4	8.4	31.8	−4.4	3.3
Anacardiaceae									
Buchanania arborea (Blume) Blume	T	U	ST	44.3	25.5	12.9	33.1	−5.2	5.2
Campnosperma auriculatum (Blume) Hook.f.	T		LD	51.0	−9.6	28.4	36.8	−5.9	10.0
Gluta wallichii (Hook.f.) Ding Hou	T	O	ST	43.0	0.8	27.0	31.6	−5.9	10.3
M. quadrifida Jack	T	O	ST	34.3	15.7	7.5	32.4	−3.3	2.6
Anisophylleaceae									
Anisophyllea disticha (Jack) Baill.	ST	U	ST	49.8	14.6	10.0	35.2	−6.3	8.9
Annonaceae									
Artobotrys suaveolens (Blume) Blume	C	O	ST	43.1	−0.6	16.0	43.9	−6.7	13.2
Cyathocalyx ramuliflorus (Maingay ex Hook.f. & Thomson) Scheff.	T	O	ST	40.3	−1.7	19.4	31.6	−5.0	6.3
Fissistigma rubiginosum (A. DC.) Merr.	C	O	ST	33.9	1.8	5.8	33.8	−6.0	7.5
Popowia fusca King	T	U	ST	38.5	10.4	9.9	35.8	−7.0	9.8
Xylopia malayana Hook.f. & Thomson	T	U	ST	40.8	7.0	13.9	33.9	−6.1	6.0
Apocynaceae									
Alstonia angustiloba Miq.	T		LD	45.7	4.0	28.2	36.5	−7.9	11.5
Dyera costulata (Miq.) Hook.f.	T		LD	42.0	9.8	15.7	33.0	−5.2	7.4
Arecaceae									
Caryota mitis Lour.	P	U	ST	61.8	−13.5	39.7	35.0	−5.8	6.1
Burseraceae									
Canarium pilosum Benn.	T	U	ST	31.7	7.7	4.0	35.1	−6.4	9.6
Dacryodes rostrata (Blume) H. J. Lam	T	O	ST	46.6	15.9	10.7	36.8	−9.5	13.0
Santiria apiculata Benn.	T	O	ST	55.8	−5.0	34.0	37.7	−9.9	12.7
Connaraceae									
Connarus semidecandrus Jack	C	O	ST	58.8	8.8	25.7	34.2	−6.6	8.5
Compositae									
Vernonia arborea Buch.-Ham.	T		LD	41.8	−4.0	18.0	39.2	−6.9	13.3
Dilleniaceae									
Dillenia suffruticosa (Griff.) Mart.	S		LD	41.2	6.3	15.7	34.2	−8.7	10.7
Dipterocarpaceae									
Dipterocarpus caudatus Foxw. ssp. *penangianus* (Foxw.) P. S. Ashton	T	O	ST	47.8	3.0	22.8	43.7	−12.0	21.1
Hopea mengarawan Miq.	T	O	ST	40.9	0.9	12.8	46.3	−10.5	24.9
Shorea curtisii Dyer ex King	T	O	ST	38.7	12.4	8.2	31.8	−6.4	7.1
S. leprosula Miq.	T	O	ST	64.8	1.1	38.8	36.1	−8.2	13.7
Ebenaceae									
Diospyros buxifolia (Blume) Hiern.	ST	U	ST	37.0	4.9	9.4	33.3	−4.0	5.6
Elaeocarpaceae									
Elaeocarpus ferrugineus (Jack) Steud.	T	U	ST	28.3	19.9	11.4	36.1	−8.8	11.6
E. petiolatus (Jack) Wall.	T	U	ST	40.7	15.7	13.5	38.8	−8.8	14.7
Euphorbiaceae									
Aporusa benthamiana Hook.f.	T	U	ST	31.1	3.5	−1.7	36.4	−8.8	11.4
A. prainiana King ex Gage	T	U	ST	38.8	0.9	3.7	35.7	−6.6	12.4
A. michrostachya (Tul.) Müll. Arg.	ST	U	ST	42.5	2.6	5.2	35.7	−7.2	8.7
Baccaurea parviflora (Müll. Arg.) Müll. Arg.	ST	U	ST	48.4	17.2	19.3	34.1	−5.2	5.2

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Drypetes pendula Ridl.	T	U	ST	26.8	10.8	−1.3	31.9	−4.3	3.7
Endospermum diadenum (Miq.) Airy Shaw	T		LD	76.9	−3.1	10.2	34.5	−7.7	10.7
Macaranga conifera (Zoll.) Müll. Arg.	ST		LD	34.0	6.4	4.3	33.0	−6.7	7.8
M. gigantea (Rchb.f. & Zoll.) Müll. Arg.	ST		LD	51.1	−6.3	26.1	34.4	−7.5	10.1
M. heynei I.M. Johnston	ST		LD	49.0	8.2	16.7	33.1	−6.6	7.6
M. hypoleuca (Rchb.f. & Zoll.) Müll. Arg.	ST		LD	61.7	−2.8	14.0	37.9	−8.22	10.4
M. trichocarpa (Rchb.f. & Zoll.) Müll. Arg.	C	U	ST	36.0	8.6	11.3	36.7	−9.0	13.4
M. triloba (Blume) Müll. Arg.	ST		LD	34.5	8.9	11.2	29.6	−6.7	8.4
Mallotus paniculatus (Lam.) Müll. Arg.	ST		LD	52.6	10.5	26.4	32.5	−5.5	6.1
M. penangensis Müll. Arg.	ST	U	ST	68.3	−0.3	27.4	34.1	−3.3	4.6
Fagaceae									
Castanopsis lucida (Nees) Soepadmo	T	O	ST	40.8	−7.6	13.6	35.4	−6.4	9.1
C. wallichii King ex Hook.f.	T	O	ST	53.9	−9.7	36.6	37.1	−7.4	11.2
Lithocarpus conocarpus (Oudem.) Rehder	T	O	ST	42.7	11.7	10.6	33.1	−4.6	4.3
Guttiferae									
Calophyllum pulcherrimum Wall. ex Choisy	T	O	ST	54.0	11.9	20.2	39.4	−9.9	15.3
Cratoxylum formosum (Jack) Dyer	T	U	ST	36.7	11.4	9.5	35.2	−6.9	9.6
Garcinia eugeniifolia Wall. ex T. Anderson	T	U	ST	35.0	14.4	9.1	34.6	−5.6	9.4
G. nigrolineata Planch. ex T. Anderson	T	U	ST	64.7	−2.9	24.0	33.6	−5.1	5.3
Icacinaceae									
Gomphandra quadrifida (Blume) Sleumer	ST	U	ST	41.2	−8.4	19.5	34.1	−6.4	6.6
Lauraceae									
Actinodaphne glomerata (Blume) Nees	T	U	ST	43.6	0.9	8.0	34.3	−6.9	7.7
Beilschmiedia madang Blume	T	U	ST	39.0	17.4	14.2	32.6	−6.3	7.3
Litsea accedens (Blume) Boerl.	T	U	ST	42.6	30.2	10.8	34.1	−6.7	8.5
Leguminosae									
Albizia splendens Miq.	T	O	ST	51.8	−11.0	29.4	33.4	−4.9	5.5
Bauhinia semibifida Roxb.	C	O	ST	38.4	13.1	11.3	27.6	−3.6	1.9
Derris amoena Benth.	C	O	ST	37.2	16.5	15.4	37.5	−10.4	13.1
Dialium platysepalum Baker	T	O	ST	44.3	−8.3	22.1	34.4	−5.5	6.8
Parkia speciosa Hassk.	T	O	ST	54.2	−2.4	14.7	34.2	−8.2	9.1
Sindora wallichiana Grah. ex Benth.	T	O	ST	40.7	5.3	18.8	34.3	−6.4	7.4
Loganaceae									
Fagrea fragrans Roxb.	T		LD	62.4	−9.7	45.6	38.9	−8.1	14.3
Strychnos axillaris Colebr.	C	U	ST	37.5	10.8	5.03	35.5	−5.3	7.7
Melastomataceae									
Melastoma malabathricum L.	S		LD	44.2	−11.2	22.4	36.3	−6.9	8.2
Pternandra echinata Jack	T	U	ST	31.3	1.4	3.5	36.0	−7.0	9.3
Meliaceae									
Sandoricum koetjape (Burm.f.) Merr.	T		ST	55.6	−2.0	28.9	35.4	−6.3	8.6
Moraceae									
Artocarpus integer (Thunb.) Merr.	T	O	ST	50.5	−13.0	31.1	32.0	−3.8	4.2
A. lanceifolius Roxb.	T		LD	47.0	−8.9	27.8	37.5	−8.1	14.4
Ficus fistulosa Reinw. ex Blume	ST		LD	41.1	15.5	13.2	36.4	−9.7	14.2
F. grossularioides Burm.f.	ST		LD	48.9	5.8	25.9	36.9	−8.3	13.1
F. sagittata Vahl	C	O	ST	38.3	5.9	6.3	34.4	−6.3	9.61
Streblus elongatus (Miq.) Corner	ST	O	ST	33.4	4.5	3.9	34.4	−5.8	7.5

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Myristaceae									
Knema intermedia (Blume) Warb.	T	U	ST	41.8	11.6	29.6	34.7	−6.0	9.1
K. latericia Elmer	T	U	ST	63.6	−5.0	38.0	33.2	−5.94	6.7
K. laurina (Blume) Warb.	ST	U	ST	49.3	4.6	21.2	40.6	−9.9	17.2
K. malayana Warb.	ST	U	ST	56.7	−2.3	16.9	31.1	−3.3	2.7
Myristica elliptica Wall. ex Hook.f. & Thomson	T	O	ST	62.4	−0.1	12.6	38.9	−9.5	14.4
Myrsinaceae									
Ardisia sanguinolenta Blume	ST	U	ST	36.5	1.4	10.3	34.4	−4.3	6.5
Myrtaceae									
Syzygium chloranthum (Duthie) Merr. & L.. Perry	T	U	ST	32.9	8.5	3.2	33.6	−5.7	7.3
S. glaucum (King) P. Chantaranothai & J. Parn.	T	U	ST	55.4	−12.6	33.6	36.4	−8.1	8.7
S. grande (Wight) Walp.	T	U	ST	62.0	−6.3	21.5	35.7	−6.7	8.8
S. inophyllum DC.	T	U	ST	37.4	3.8	9.4	33.0	−5.0	5.3
S. nigricans (King) Merr. & L. M. Perry	T	U	ST	33.5	2.2	3.5	35.1	−6.1	9.3
S. pustulatum (Duthie) Merr.	T	U	ST	45.2	6.5	15.4	37.2	−7.8	11.8
S. sp. 1	T	U	ST	32.1	2.0	3.4	32.3	−4.4	5.0
S. sp. 2	T	U	ST	34.2	5.1	2.9	35.4	−6.7	10.0
S. sp. 3	T	U	ST	57.2	−11.1	31.0	30.7	−3.1	2.3
Rhodamnia cinerea Jack	ST		LD	56.6	−8.4	25.7	36.3	−5.2	9.3
Ochnaceae									
Brackenridgea hookeri (Planch.) A. Gray	T	?	ST	32.2	16.5	1.7	38.0	−10.3	16.5
Olacaceae									
Ochanostachys amentacea Mast.	T	O	ST	36.6	−7.8	12.1	36.9	−7.7	9.5
Scorodocarpus borneensis (Baill.) Becc.	T	U	ST	32.6	12.2	2.6	30.1	−3.9	4.6
Strombosia javanica Blume	T	U	ST	38.8	−8.7	13.4	32.5	−4.7	5.1
Polygalaceae									
Xanthophyllum eurhynchum Miq. ssp. *maingayi* (Hook. ex A. W. Benn.) Meijden	T	U	ST	54.4	−13.5	43.0	29.4	−4.5	6.8
Rhamnaceae									
Ziziphus calophylla Wall. ex Hook.f.	C	O	ST	50.8	15.3	12.1	34.6	−7.7	9.9
Z. elegans Wall.	C	O	ST	43.5	10.5	14.3	35.7	−7.1	8.1
Rhizophoraceae									
Gynotroches axillaris Blume	T	U	ST	41.2	−0.03	14.9	34.1	−4.8	4.4
Pellacalyx saccardianus Scort.	T	U	ST	45.6	−2.0	20.8	36.0	−6.5	9.4
Rosaceae									
Prunus polystachya (Hook.f.) Kalkman	T		LD	46.5	−11.1	26.8	31.0	−6.24	7.8
Rubiaceae									
Lasianthus maingayi Hk.f.	S	U	ST	32.2	3.5	−1.6	32.3	−4.7	4.3
Nauclea officinalis (Pierre ex Pit.) Merr. & Chun	T	U	ST	33.0	3.7	2.1	33.2	−6.2	6.5
Porterandia anisophyllea (Jack ex Roxb.) Ridl.	ST		LD	56.7	−10.0	30.1	31.8	−4.9	5.6
Timonius wallichianus (Korth.) Valeton	ST		LD	32.9	8.7	3.5	36.2	−8.5	10.4
Uncaria sp.	C	O	ST	45.3	−13.3	27.8	43.5	−11.6	22.0
Unidentified sp.	?		?	43.6	16.5	14.9	34.8	−7.1	7.7
Sapindaceae									
Nephelium lappaceum L.	T	O	ST	33.0	14.4	3.2	31.3	−4.3	3.3
Pometia pinnata J. R. Forst. & G. Forst.	T	O	ST	42.8	−11.7	24.2	32.9	−5.5	6.2

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Sapotaceae									
Madhuca kingiana (Brace) H. J. Lam	T	O	ST	32.5	10.2	6.4	32.4	−4.5	4.0
Palaquium gutta (Hook.f.) Baill.	T	O	ST	44.2	3.8	17.5	35.4	−4.3	6.9
P. microphyllum King & Gamble	T	O	ST	39.0	11.2	4.8	32.4	−5.1	6.2
Pouteria maingayi (C. B. Clarke) Baehni	T	O	ST	45.1	18.5	16.6	37.8	−6.8	11.3
Symplocaceae									
Symplocos fasciculata Zoll.	ST		LD	55.7	−13.4	40.7	31.8	−7.9	12.2
Theaceae									
Adinandra dumosa Jack	ST		LD	45.5	8.2	23.7	35.3	−8.0	10.1
Tiliaceae									
Grewia sp. 1	?	O	ST	49.4	−8.4	26.1	38.7	−7.7	13.9
Pentace triptera Mast.	T	O	ST	46.3	10.2	17.4	32.5	−4.8	5.1
Ulmaceae									
Gironniera parvifolia Planch.	T	U	ST	50.0	5.0	16.3	38.2	−9.2	13.3
Trema cannabina Lour.	S		LD	50.5	−13.4	31.7	36.6	−8.4	10.2
Verbenaceae									
Clerodendrum villosum Bl.	ST		LD	45.4	−8.6	20.6	33.1	−6.6	6.4
CHAMELA									
Achatocarpaceae									
Achatocarpus gracilis H. Walt.	ST	U	ST	46.5	−8.6	14.2	45.0	−7.8	12.1
Anacardiaceae									
Comocladia engleriana Loes.	ST	U	ST	44.5	8.0	16.1	43.8	−9.2	18.3
Spondias purpurea L.	T	O	LD	58.3	−13.3	32.1	47.0	−10.8	18.5
Apocynaceae									
Plumeria rubra L.	T	O	LD	50.9	−6.9	13.9	41.9	−8.4	12.1
Thevetia ovata (Cav.) A. DC.	S	U	ST	49.4	−13.2	25.2	47.8	−11.7	19.2
Bignoniaceae									
Clytostoma binatum (Thunb.) Sandw.	C	U	ST	48.6	−10.7	20.8	49.5	−12.1	22.8
Crescentia alata HBK.	T	O	LD	53.7	−13.1	28.5	48.2	−11.1	21.2
Tabebuia donnel-smithii Rose	T	O	LD	49.0	−10.7	20.0	46.5	−10.6	16.4
T. impetiginosa (Mart.) Standl.	T	O	LD	48.7	−12.5	22.6	48.8	−12.0	20.7
T. rosea (Bertol.) DC.	T	O	LD	52.8	−9.3	26.2	44.8	−10.0	14.6
Bombacaceae									
Ceiba aesculifolia (HBK.) Britt. & Rose	T	O	LD	57.1	−11.0	31.2	40.6	−7.4	9.5
C. grandiflora Rose	ST	O	LD	41.5	−6.9	8.6	43.6	−8.3	12.2
C. pentandra (L.) Gaertn.	T	O	LD	64.2	−6.1	38.2	40.7	−4.5	9.3
Pseudobombax ellipticum (HBR.) Dugand	ST	O	ST	47.0	16.9	12.0	41.0	−6.5	7.4
Boraginaceae									
Cordia alliodora (Ruiz & Pav.) Oken.	T	O	LD	45.1	−9.6	16.4	44.9	−9.7	16.4
C. elaeagnoides DC.	T	O	LD	52.3	−6.3	17.1	45.8	−11.1	18.3
Burseraceae									
Bursera arborea (Rose) Riley	T	O	LD	49.4	−12.4	21.8	46.6	−11.8	19.4
B. excelsa (HBK.) Engl.	ST	U	ST	47.6	−10.2	20.8	45.1	11.0	17.9
B. heteresthes Bullock	T	O	LD	52.6	−14.0	26.0	42.6	−9.1	12.2
B. instabilis McVaugh & Rzed.	T	U	LD	42.2	−10.2	14.1	46.1	−12.2	19.0

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Capparidaceae									
Capparis indica (L.) Fawc. & Rendle.	S	U	ST	52.0	−5.1	17.3	42.8	−7.7	13.7
C. verrucosa Jacq.	ST	U	ST	47.7	−8.9	18.0	45.6	−9.5	15.7
Crataeva tapia L.	ST	U	ST	44.5	−9.1	15.3	41.7	−7.4	10.5
Forchhammeria pallida Liebm.	T	U	LD	50.7	−7.2	20.0	49.4	−7.9	23.1
Caricaceae									
Jacaratia mexicana A. DC.	T	O	LD	50.7	−11.9	24.6	43.3	−10.0	14.6
Cochlospermaceae									
Cochlospermum vitifolium (Willd.) Spreng.	T	O	LD	39.0	−7.8	10.1	41.6	−785.0	7.4
Compositae									
Liabum caducifolium Robins. & Bartlett	C	O	LD	59.7	−11.4	33.6	38.5	−8.4	8.7
Milleria quinqueflora L.	S	U	ST	43.8	−9.5	12.6	40.4	−9.0	11.8
Convolvulaceae									
Ipomoea wolcottiana Rose	T	O	LD	54.9	−12.3	30.0	43.0	−10.7	15.5
Erythroxylaceae									
Erythroxylum havanense Jacq.	S	U	ST	57.7	−12.4	34.3	49.0	−11.7	21.7
Euphorbiaceae									
Celaenodendron mexicanum Standl.	T	O	LD	50.5	−12.3	24.8	38.3	−8.5	8.9
Cnidosculus spinosus Lundell	ST	U	ST	49.4	−11.2	22.4	38.1	−7.6	7.0
Croton alamosanus Rose	S	U	ST	53.8	−11.6	30.9	40.8	−7.8	10.3
C. chamelensis Lott	S	U	ST	44.9	−13.3	21.2	42.3	−11.2	14.4
C. pseudoniveus Lundell	ST	U	ST	52.0	−10.7	23.9	47.3	−9.8	17.3
C. suberosus HBK.	S	U	ST	41.5	−7.0	7.9	41.4	−8.1	8.0
Jatropha bullockii Lott	S	U	ST	35.4	5.8	3.6	43.6	−4.4	11.4
J. chamelensis Perez-Jimenez	T	O	LD	34.1	8.1	0.8	37.1	0.2	5.2
J. malacophylla Standl.	T	U	LD	47.3	−2.1	17.8	48.6	−8.0	21.3
J. cf. *standleyi* Steyerm.	ST	U	ST	69.1	−4.9	8.9	44.1	−9.4	12.8
Manihot chlorosticta Standl. & Goldman	C	U	ST	43.8	−6.3	10.2	40.0	−6.8	8.1
Phyllanthus botryanthus Müll.Arg.	S	U	ST	58.8	−13.4	35.1	46.8	−11.2	17.2
P. mocinianus Baill.	ST	U	ST	59.3	−13.4	31.0	50.0	−13.3	25.9
Flacourtiaceae									
Casearia corymbosa HBK.	S	U	ST	58.4	−0.8	29.6	54.0	−11.6	28.9
C. tremula (Griseb.) Wright	ST	U	ST	53.6	−9.4	23.9	47.8	−8.8	14.5
Hernandiaceae									
Gyrocarpus jatrophifolius Domin	ST	U	ST	41.5	−6.0	8.6	36.9	−4.7	2.7
Julianaceae									
Amphipterygium adstringens (Schlect.) Schiede.	T	O	LD	47.8	−10.4	20.7	42.1	−10.4	14.1
Leguminosae									
Acacia hindsii Benth.	T	O	LD	46.6	−10.4	20.5	49.5	−9.0	17.0
Apoplanesia paniculata Presl.	ST	U	ST	53.3	−12.4	32.2	43.8	−11.0	16.3
Bauhinia ungulata L.	S	U	LD	53.6	−13.7	31.9	47.6	−12.0	19.6
Caesalpinia coriaria (Jacq.) Willd.	T	O	LD	38.1	−9.6	12.8	36.1	−8.4	8.4
C. eriostachys Benth.	T	O	LD	50.8	−12.2	26.9	48.4	−12.5	25.0
C. platyloba S. Wats.	ST	U	ST	51.5	−12.5	29.3	47.1	−11.7	20.1
C. pulcherrima (L.) Sw.	ST	U	ST	43.3	−7.4	15.3	64.6	−7.8	12.1
C. sclerocarpa Standl.	T	O	LD	60.3	−4.0	21.5	48.4	−10.4	20.4

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Enterolobium cyclocarpum (Jacq.) Griseb.	T	O	LD	50.7	−12.2	29.3	40.5	−8.6	10.8
Erythrina lanata Rose var. *occidentalis* (Standl.) Krukoff & Barneby	ST	U	ST	58.4	−11.6	36.1	45.2	−10.3	18.8
Haematoxylum brasiletto Karst.	T	O	LD	49.6	−12.8	24.4	49.1	−13.8	24.8
Hymenaeae courbaril L.	T	O	LD	45.0	5.7	17.5	36.6	−5.8	5.7
Lonchocarpus eriocarinalis Micheli	T	O	LD	50.6	−10.2	24.2	46.9	−10.7	18.5
L. magallanesii Sousa	ST	U	ST	58.6	−5.8	11.7	40.9	−7.3	8.7
L. sp.	ST	U	ST	53.9	−11.8	31.0	40.2	−7.3	8.4
Lysiloma microphyllum Benth.	T	O	LD	45.1	−11.7	19.8	37.9	−9.0	10.2
Pithecellobium dulce (Roth.) Benth.	T	U	LD	50.1	−4.6	23.3	53.8	−13.0	28.2
Malpighiaceae									
Malpighia emiliae W. R. Anderson	S	U	ST	50.6	−11.9	23.4	44.9	−10.4	14.9
Malvaceae									
Hibiscus citrinus Fryxell	S	U	LD	50.1	−12.9	26.0	41.3	−11.0	15.0
Meliaceae									
Swietenia humilis Zucc.	T	O	LD	47.8	5.7	17.4	41.5	−7.7	10.1
Trichilia trifolia L. ssp. *palmeri* (C. DC.) Pennington	ST	U	ST	46.3	−9.4	18.2	38.4	−5.9	5.5
Moraceae									
Ficus cotinifolia HBX.	T	O	LD	56.6	−12.1	32.2	55.7	−13.8	30.4
F. goldmanii Standl.	T	O	LD	36.1	−8.4	8.3	46.6	−11.4	19.0
F. pertusa L. f.	T	O	LD	46.0	−11.0	19.7	35.5	−2.9	3.3
Myrtaceae									
Eugenia capuli (Schlect. & Cham.) Berg.	S	U	ST	55.4	−7.6	24.9	43.9	−3.8	12.3
Psidium guajava L.	T	O	LD	50.1	−6.8	20.8	42.6	−8.3	12.3
P. sartorianum (Berg.) Ndzu.				60.1	−10.9	35.0	41.6	−8.5	11.3
Nyctaginaceae									
Guapira cf. *macrocarpa* Miranda	T	O	LD	59.6	−11.2	29.6	45.6	−9.2	13.6
Phytolaccaceae									
Rivinia humilis L.				54.7	−13.0	30.5	47.7	−11.1	20.0
Piperaceae									
Piper abalienatum Trel.	S	U	ST	57.4	−13.1	31.8	52.7	−12.8	26.1
P. stipulaceum C. DC.	S	U	ST	56.3	−12.1	36.5	40.5	−8.1	7.8
Polygonaceae									
Coccoloba barbadensis Jacq.	T	O	LD	47.0	26.0	15.0	49.8	−9.9	24.2
Ruprechtia fusca Fern.	ST	U	ST	46.4	−10.9	18.8	51.4	−8.7	18.0
Rhizophoraceae									
Rhizophora mangle L.	ST	U	LD	50.4	−9.8	23.8	34.7	−5.6	5.9
Rubiaceae									
Guettarda elliptica Sw.	ST	U	ST	57.0	−11.1	28.7	54.6	−12.7	26.6
Hintonia latiflora (Sesse & Moc. ex DC.) Bullock	ST	U	ST	54.8	−11.2	25.9	46.8	−11.9	19.6
Randia aculeata L.	S	U	ST	56.5	−13.0	33.3	44.9	−10.7	17.6
R. malacocarpa Standl.	S	U	ST	46.8	−11.9	22.6	46.0	−11.6	18.4
Sapindaceae									
Cupania dentata DC.	ST	U	ST	60.2	−12.7	37.0	47.4	−11.3	18.4
Paullinia cururu L.	S	U	ST	44.9	−11.3	16.4	44.1	−10.9	16.1
P. fuscescens BBR.	C	U	ST	66.3	−9.7	27.9	52.2	−14.1	30.1
P. sessiliflora Radlk. in Rose	C	U	ST	51.4	−10.7	23.8	50.0	−11.7	24.2

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Thouina paucidentata Radlk.	ST	U	ST	55.7	−13.6	30.6	52.2	−13.2	26.1
Thouinidium decandrum (Humb. & Bonpl.) Radlk.	T	O	LD	42.2	−8.3	10.9	41.1	−6.9	8.0
Simaroubaceae									
Recchia mexicana Moc. & Sesse	T	U	ST	54.7	−13.1	29.9	49.3	−12.1	22.0
Sterculiaceae									
Guazuma ulmifolia Lam.	ST	U	ST	57.2	−10.2	32.8	52.1	−11.8	26.4
Helicteres baruensis Jacq.	S	U	ST	48.0	−11.3	22.9	43.4	−10.4	15.9
Tiliaceae									
Heliocarpus pallidus Rose	T	O	LD	59.7	−10.7	33.0	41.2	−10.4	12.6
MARENCO									
Acanthaceae									
Bravaisia integerrima (Spreng.) Standl.	ST	U	ST	74.4	−6.4	15.1	38.0	−7.4	11.1
Anacardiaceae									
Anacardium occidentalis L.	ST	U	LD	34.6	16.9	3.3			
Spondias mombin L.	T	O	LD	48.5	−9.6	25.6	40.4	−10.5	17.2
Annonaceae									
Anaxagorea crassipetala Hemsl.	ST	U	ST	48.7	1.1	16.9	35.9	−7.1	3.1
Guatteria amplifolia Triana & Planch.	T	U	ST	46.1	−9.1	20.4	40.4	−10.6	17.3
Apocynaceae									
Aspidosperma spruceanum Benth. ex Müll. Arg.	T	O	ST	56.5	−14.2	36.9	42.5	−9.5	18.5
Lacmellea panamensis (Woodson) Markgr.	T	O	ST	41.5	−7.9	9.2	31.8	−4.1	2.1
Araliaceae									
Dendropanax arboreus (L.) Decne. & Planch.	T	O	ST	46.2	−11.3	25.8	34.1	−5.0	6.5
Bombacopsis sessilis (Benth.) Pittier	T	O	LD	31.6	4.4	0.9	39.9	−7.9	14.7
Ochroma pyramidale (Cav. ex Lam.) Urb.	T	O	LD	48.2	3.3	19.3	39.3	−10.3	18.0
Pachira aquatica Aubl.	T	O	ST	63.6	6.3	3.7	35.9	−6.4	10.1
Burseraceae									
Protium pittieri (Rose) Engl.	T	O	ST	51.5	−13.0	29.4	36.7	−7.4	9.3
Tetragastris panamensis (Engl.) Kuntze	T	O	ST	53.0	4.5	21.2	35.8	−7.2	8.2
Caryocaraceae									
Caryocar costaricense Donn. Sm.	T	O	ST	40.2	5.3	14.3	39.2	−10.6	13.7
Cecropiaceae									
Cecropia sp.	T	O	LD	44.2	4.1	18.6	42.4	−8.1	19.1
Coussapoa sp.	C	O	ST	33.4	6.5	7.2	37.7	−7.2	11.9
Pourouma bicolor Mart.	T	O	ST	51.3	−12.6	29.7	32.2	−5.7	4.8
Combretaceae									
Terminalia amazonia (Gmel.) Exell	T	O	ST	45.1	−2.4	21.9	44.6	−8.9	21.4
Euphorbiaceae									
Croton smithianus Croizat	T	O	LD	55.8	−10.2	35.1	39.3	−10.3	15.9
Hyeronima oblonga (Tul.) Müll. Arg.	T	O	ST	57.8	−4.0	14.9	39.2	−9.6	14.6
Sapium laurifolium (A. Rich.) Griseb.	T	O	ST	41.1	−0.7	12.4	37.7	−8.4	10.4
Flacourtiaceae									
Laetia procera (Poepp.) Eichler	T	O	ST	55.9	−3.7	35.8	37.2	−7.6	11.3
Tetrathylacium macrophyllum Poepp.	ST	U	ST	42.0	8.8	13.0	42.5	−10.8	18.6

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Clusiaceae									
Calophyllum longifolium Willd.	T	O	ST	60.7	−12.2	41.7	36.1	−6.7	8.7
Clusia rosea Jacq.	C	O	ST	49.9	7.8	24.9	41.7	−7.3	14.7
Garcinia madruno (Kunth) Hammel	ST	U	ST	42.0	5.9	13.1	34.7	−7.1	7.7
Symphonia globulifera L.f.	T	O	ST	63.0	−6.2	38.0	33.2	−5.5	4.4
Vismia ferruginea Kunth	ST	O	LD	48.8	−2.2	24.8	35.6	−6.9	7.7
Lauraceae									
Licaria sp.	ST	U	ST	42. 5	7.6	16.7	35.0	−7.1	8.1
Nectandra hihua (Ruiz & Pav.) Rohwer	T	O	ST	61.5	−12.8	37.1	36.0	−6.3	8.4
Lecythidaceae									
Couratari scottmorii Prance	T	O	ST	55.6	−13.4	31.5	38.4	−9.0	9.5
Leguminosae									
Inga goldmanii Pittier	ST	U	ST	46.8	−12.3	24.3	38.5	−9.2	11.6
I. multijuga Benth.	ST	U	LD	45.0	−11.1	22.1			
I. spectabilis (Vahl) Willd.	ST	U	ST	45.3	−6.0	14.0	38.8	−7.8	12.5
Lonchocarpus macrophyllus Kunth	T	O	ST	39.1	−5.9	10.5	41.9	−5.7	17.1
Magnoliaceae									
Magnolia gloriensis (Pittier) Govaerts	T	O	ST	54.0	−14.7	28.6	36.1	−6.6	9.0
Malphigiaceae									
Byrsonima crassifolia (L.) Kunth	T	O	LD	61.0	−9.7	34.9	33.1	−4.3	3.6
Marcgraviaceae									
Magraviastrum sp.	C	O	ST	53.1	−12.3	31.1	35.9	−7.4	8.5
Melastomataceae									
Bellucia pentamera Naudin	ST	U	ST	53.6	−0.9	18.4	40.3	−10.1	19.8
Miconia argentea (Sw.) DC.	ST	U	LD	51.9	6.9	16.1	32.3	−4.9	3.8
Meliaceae									
Carapa guianensis Aubl.	T	O	ST	53.6	3.4	16.7	34.6	−6.4	7.8
Guarea pterorhachis Harms	ST	U	ST	34.9	2.3	6.4	35.5	−6.8	7.6
Trichilia septentrionalis C. DC.	T	O	ST	42.0	−12.0	18.5	32.5	−4.5	4.4
Moraceae									
Brosimum utile (Kunth) Pittier	T	O	ST	39.3	19.9	13.8	35.7	−5.9	8.4
Ficus bullenei I. M. Johnst.	T	O	ST	55.7	−2.6	31.6			
F. obtusifolia Kunth	T	O	ST	41.9	−10.0	18.6	36.8	−7.8	11.2
F. tonduzii Standl.	ST	U	ST	52.9	−2.8	32.7	38.4	−9.0	13.2
Myristicaceae									
Compsoneura sprucei (A. DC.) Warb.	ST	U	ST	64.8	−11.9	43.4	36.6	−6.5	9.4
Otoba novogranatensis Mold.	T	O	ST	49.3	−8.7	25.8	38.2	−6.9	11.7
Virola guatemalensis Warb.	T	O	ST	57.7	−12.0	38.4	33.8	−4.7	6.2
V. koschnyi Warb.	T	O	ST	53.6	−10.9	39.7	36.4	−8.1	11.3
V. sebifera Aubl.	T	O	ST	52.3	−9.0	33.2	37.8	−9.6	13.4
Myrsinaceae									
Parathesis aeruginosa Standl.	ST	U	ST	52.3	−9.3	26.7	46.4	−10.8	21.6
Rubiaceae									
Pentagonia tinajita Seem.	S	U	ST	63.5	−9.4	42.0	46.4	−11.3	25.3
Posoqueria latifolia (Rudge) Roem. & Schult.	ST	U	LD	38.0	−8.2	11.9	29.4	−5.1	3.0

Appendix (Continued).

Family and species	Life form[a]	Height classification[b]	Shade tolerance[c]	Youngest leaf			Mature leaf		
				L	a	b	L	a	b
Simaroubaceae									
Simaba cedron Planch.	ST	U	LD	33.8	−4.9	3.7	31.0	3.4	−0.4
Smilacaceae									
Smilax sp.	C	U	ST	54.4	−11.9	29.9	36.9	−7.8	11.7
Sterculiaceae									
Guazuma ulmifolia Lam.	ST	U	LD	51.9	−10.8	29.7	40.6	−10.4	18.7
Tiliaceae									
Luehea seemannii *Triana & Planch.*	T	O	LD	46.2	−8.7	21.3	35.2	−5.1	7.3
Mortoniodendron anisophyllum (Standl.) Standl. & Steyerm.	T	O	ST	47.3	−10.0	20.9	42.7	−8.6	17.8
Trichospermun galeottii (Turcz.) Kosterm.	T	O	LD	55.1	−12.0	33.7	35.8	−5.9	8.4
Vochysiaceae									
Qualea paraensis Ducke	T	O	ST	45.2	−0.3	18.8	35.8	−9.7	13.4
Vochysia ferruginea Mart.	T	O	ST	50.5	−2.5	24.9	44.0	−10.2	18.8
V. guatemalensis Donn. Sm.	T	O	ST	46.3	−12.8	27.2	41.1	−9.0	14.3

[a] C, woody climber; P, palm; S, shrub (1–2 m); ST, small tree (5–15 m); T, tall tree (>15 m)
[b] U, understorey, O overstorey
[cb] ST, shade tolerant; LD, light demanding