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The Variation in leaf structure of seedlings in the families Dipterocarpaceae, Clusiaceae and Myrtaceae under different light environments

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Abstract

Light has been characterized as the most important environmental factor that affects the leaf structure of tree seedlings in tropical rain forests in South and Southeast Asia. Many studies have been carried out on leaf structure of early-successional and late-successional species and also among the species within the same successional status. These studies provide a clearer understanding of the ecological distribution of each species. The present study examined the leaf structure of six canopy tree species that are considered to be relatively shade tolerant in lowland rain forests in Sri Lanka.

Seedlings of *Dipterocarpus zeylanicus, D. hispidus* (Dipterocarpaceae), *Mesua ferrea, M. nagassarium* (Clusiaceae), *Syzygium firmum* and *S. rubicundum* (Myrtaceae) were grown in different controlled environmental shelters that simulated a range of light environments found in the groundstorey of the rain forests. Two treatments exposed seedlings to different duration of full sunlight. These simulated the groundstorey Photosynthetic Photon Flux Density (PFD) that were comparable to the canopy openings of about 200 m^2 and 400m^2. Three other shelters exposed seedlings to uniform diffuse light conditions that simulated amounts and qualities of radiation like that of the forest understorey (PFD 50, R:FR ratio 0.23; PFD 350, R:FR ratio 0.97; PFD 800, R:FR ratio 1.05). A control light treatment provided full sun light quality (PFD 2000, R:FR ratio 1.27) for seedling growth.

The attributes measured were thicknesses of leaf blade, upper and lower epidermis, palisade mesophyll and number of layers, and stomatal frequency. Results show that *Syzygium* species have the highest leaf blade, and palisade cell thickness and stomatal frequency followed in order by *Mesua* > *Dipterocarpus*. This suggests that *Syzygium* species are more light tolerant but less drought tolerant. The thickest upper and lower epidermis in Dipterocarps reveal that they are more efficient in water use. *Syzygium* and *Dipterocarpus* exhibited double rows of cells in palisade mesophyll when exposed to full sun. These findings elucidate some of the relationships between leaf anatomy and the species ecology across the forest topography.

1. Introduction

Light intensity during the development of a leaf can modify its anatomy and morphology including the number and dimensions of mesophyll cells (Wilson and Copper, 1969). These anatomical modifications of leaves differ dramatically between tree species. Differences in stomatal density, leaf thickness, epidermal thickness and palisade mesophyll thickness of tree species have been related to their successional status, their age and crown position in the canopy (Ashton and Berlyn, 1994; Carpenter and Smith, 1975; Jackson, 1967; Wylie, 1951). Sun leaves often have similar anatomical adaptations as drought avoiding plants while shade leaves often resemble those of drought intolerant species (Ashton and Berlyn, 1992; Lee *et al.,* 1990).

The degree of within-species adaptation and plasticity of leaves more closely associated with the shade-tolerance and successional status of the species. Leaf adaptation of generalist species, that can have seedlings growing in a range of light conditions within a forest have a larger morphological plasticity than specialist species. Species considered to be shade-intolerant have larger morphological plasticity than shade-tolerant ones (Ashton and Berlyn, 1992).

Many studies have shown that leaf anatomy and morphology differ between tree species categorized as early-and late-successional species (Carpenter and Smith, 1975; Fetcher *et al.,* 1983; Loach, 1967). Little work has been done that examines these relationships between selected tree species within the same successiona status (Gamage *et al.,* 1996; Ashton and Berlyn, 1992). This study examined the variation in leaf structure among seedlings of six canopy tree species that have been characterized as late-successional. The study tested the hypothesis that species of the same regeneration guild have distinct anatomical response at the leaf level.

2. Materials and methods

Study site description

This study was done at the field station of the Sinharaja World Heritage Site, a forest located in the southwest of Sri Lanka. This forest is an everwet mixed-dipterocarp type comprising a canopy dominated by the genera *Shorea* section Doona (Dipterocarpaceae) and *Mesua* (Clusiaceae) (De Rosayro, 1942; Gunatilleke and Ashton, 1987).

The region receives 4,000-6000mm of rain per year. Most rain falls during the southwest monsoons (May-July) and the northeast monsoons (October-January). Seasonal temperatures range between 25^0 and 27^0 C (Ashton, 1992). The topography is undulating between valley and ridge with a mean elevation above sea level of about 600m. The differences between valley and ridge are generally less than 100m. Soils are classified as podzols following the USDA (1975) terminology, or red yellow latosols using the classification system of the Food and Agriculture Organization (Moorman and Panabokke, 1961). They vary from weakly defined humults with a thick organic pad (2cm) on the ridges to udults with little or no organic accumulation but high in weathered clays and low in coarser sands (Ashton *et al.,* 1995). The soils are derived in situ from underlying metamorphic charnokitic and knondalitic gneiss (Cooray, 1967).

The six species in the study are *Dipterocarpus zeylanicus* Thw., *D. hispidus* Thw. (Dipterocarpaceae), *Mesua ferrea* L., and *M. nagassarium* (Burm.f) Kosterm. (Clusiaceae), *Syzygium firmum Thw.*, and S. *rubicundum* Wight and Arn. (Myrtaceae). *Dipterocarpus zeylanicus, D. hispidus, Mesua ferrea and Syzygium firmum* are endemic to southwest Sri Lanka. All species are often dominant in the canopy stratum of the late-successional forest. Both *D. zeylanicus* and *D. hispidus* are widespread in the lower elevations that are below 300 m altitude (Dassanayake and Fosberg, 1980; FAO, 1985). *Mesua ferrea* occurs in or near streams, but not on low lying poorly drained land. *Mesua nagassarium* is generally restricted to ridgetops. *Syzygium* species are very common in the Wet and Intermediate zones of Sri Lanka. *Syzygium firmum* occupies deep soils of valleys to mid slopes. *Syzygium rubicundum* occurs on midslopes (Ashton, 1981).

Experimental Design

Design of the controlled environmental shelters

Twenty- four well ventilated environmental shelters were constructed in a fully open clearing at the Sinharaja field station in January, 1996 to examine the seedling leaf physiology, morphology and anatomy of the study species. They were designed to create light treatments that represented a range of photosynthetic photon flux densities (PFD) and red: far red ratios (R:FR) found within the Sinharaja forest (Ashton, 1992).

Six combinations of irradiance and spectral quality were created across the twenty-four shelters as shown in Table 1. Different combinations of irradiance amount and spectral quality were coded as: full sun (FS); large opening (LO); small opening (SO); open edge (OE); forest edge (FE); and forest understorey (FU). Light treatments altering the duration of direct PFD (small opening, large opening), were created by constructing a series of parallel vertical slats aligned north-south, horizontally placed 2 m above the ground and across the complete interior of a shelter. As the sun rose and set the duration and number of sunlight periods of direct PFD was controlled by slat orientation (N-S), slat height, and the proximity of slats to one another. For shelters altering the quality and intensity of PFD (open edge, forest edge, forest understorey) a mix of pigments (1 part Hostaperm Violet RL; 0.25 part Solvaperm yellow G dye; 0.40 part carbon black; obtained from Hoechst-Celanese, Inc., Coventry, RI 02816, USA) was sprayed onto UV durable plastic film in a concentration of 10% with clear varnish. The amount sprayed regulated the R: FR ratio and the intensity of PFD. A photo spectro-radiometer (LI-COR 1800) verified the treatment. All shelters allowed for adequate ventilation without the using electrical power.

Leaf anatomy experiment

To study internal leaf structures, permanent slides were prepared. Sample leaves were taken from seedlings approximately 2 years old of each species in each light treatment. Undamaged leaves that were fully expanded were selected. Six seedlings were selected for each species in each light treatment.

From each seedling one leaf was selected and one leaf strip (0.5 x 1.0cm) was taken from the middle portion of the lamina across the mid-rib. The leaf strips were immediately fixed in FAA (Formalin: Acetic acid: Ethanol) and transported to the laboratory for anatomical measurements. Fixed leaf strips were thoroughly washed with running water, dehydrated in an ethanol series, immersed in xylene, and embedded in wax. Cross sections

Table 1. Irradiance quality and quantity that seedlings were exposed.

Light Treatment (Assigned Abbreviation)	Maximum Measured Photosynthetic Photon Flux Density (PFD) ($\mu mol\ m^{-2}\ s^{-1}$)	Maximum Daily PFD ($mol\ m^{-2}$)	Duration of Direct Light (h)	Red:Far Red Ratio
i. Full sun (FS)	1600	38.1	-	1.27
ii. Direct light at center of a large (300-400 m2) canopy opening (LO)	1600	13.3	6	1.27
iii. Same as ii above, but a small (150-200 m2) canopy opening (SO)	1600	7.4	2	1.27
iv. 60% shade with light quality similar to that at the sunny edge of a large canopy opening (OE)	800	16.3	-	1.05
v. 82% shade with light quality similar to that at a the shaded edge of a large canopy opening (FE)	350	6	-	0.97
vi. 99% shade with light quality similar to the forest understorey (FU)	50	1.2	-	0.23

of 10 μm thickness were taken using a rotary microtome, mounted on slides, stained with safranine and fast green following a modified procedure of Berlyn and Miksche (1976), and mounted in canadabalsam. One slide from each leaf strip was prepared and measured for thicknesses of leaf, cuticle, palisade mesophyll, upper epidermis and lower epidermis at 10 separate poins, taking care to avoid the region around the midrib. Measurements were made with a light microscope using 5 x 10-mm micrometer eye-piece and 0.01 x 100mm objective. Cell dimensions were done at 400 x magnification and leaf thickness at 100x magnification.

Data analysis

Data were analyzed by ANOVA using Statistica version 5. All data were log transformed prior to analysis. Analyses tested for differences between species, light treatments and interactions between species and treatments.

3. Results

Leaf blade thickness

There were significant differences and interactions among species. All species produced thicker leaves when grown in full sun. Additionally there were differences among species within a light treatment.

Leaf thickness appeared to be related to the water conservation efficency of the species and it increased with the increase in the amount of light. The shade-tolerant and more conservative *S. firmum* had the thickest leaves in the full sun light treatment followed in order by *M. ferrea* > *M. nagassarium* > *S. rubicundum* > *D.zeylanicus* > *D.hispidus* (Table 2, Fig1) Results showed that Mesua species have a higher blade thickness than Dipterocarpus species.

Table 2. Means of seedling leaf blade thickness (μm) for Syzygium, Dipterocarpus and Mesua species grown for 24 months in different light (FU-forest understorey, FE-forest edge, OF-outside edge, FS-full sun, SO-small opening, LO-large opening) treatments. Standard errors are in parentheses.

	FU	FE	OE	FS	SO	LO
SF	189.17 (3.53)	295.17 (2.13)	363.17 (4.87)	404.50 (5.98)	371.00 (3.81)	384.67 (2.64)
SR	191.50 (1.67)	125.67 (1.39)	159.50 (1.95)	186.83 (1.75)	158.83 (1.75)	164.17 (2.89)
DZ	126.07 (3.39)	133.50 (0.86)	150.73 (1.54)	161.13 (2.46)	141.94 (4.69)	150.47 (4.89)
DH	85.60 (1.64)	96.07 (1.16)	102.67 (2.68)	112.07 (4.78)	112.47 (3.93)	103.93 (1.47)
MF	173.90 (3.85)	189.20 (2.02)	210.33 (2.01)	224.56 (2.06)	218.20 (6.38)	229.07 (1.35)
MN	179.40 (0.68)	189.27 (3.97)	205.80 (2.25)	209.94 (1.56)	184.45 (2.60)	185 22 (4 18)

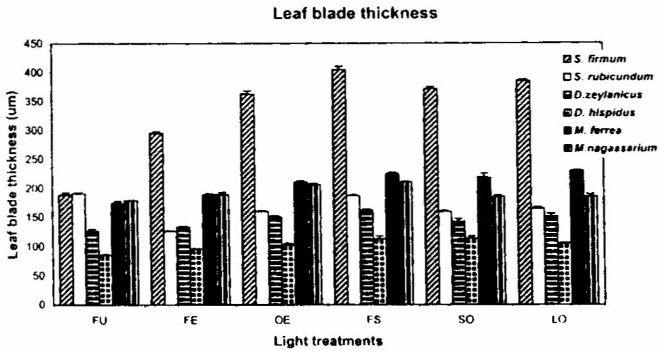

Fig 1. Leaf blade thickness (μm) for *Syzygium*, *Dipterocarpus* and *Mesua* species in different light treatments (FU- forest understorey, FE-forest edge, OE-outside edge, FS-full sun, SO-small opening, LO-large opening.) Bars indicate one standard error of mean.

Component dimensions

The species exhibit significant differences in epidermal cell thickness. These differences followed similar trends among species for each light treatment for both upper and lower epidermal cells. All species had their thickest upper epidermal cell dimensions in the full sun. Over all the light treatments the upper epidermis was thickest in *D. zeylanicus* and was thinnest in the *Mesua* species. *Syzygium* spp. showed intermediate thickness (Table 3, Fig. 2) The lower epidermis was also thickest in *D. zeylanicus* and thinnest in . *M. nagassarium* in all light treatments (Table 3, Fig. 3). Between the *Syzygium* species *S. firmum* had the thicker lower epidermis. Unlike *Mesua* and *Syzygium,* both *Dipterocarpus* species exhibited double rows of lower epidermal cells, which were most visible in leaves of seedlings that were grown under in high light treatments.

Table 3. Summary of upper and lower epidermal cell thickness (μm) for *Syzygium, Dipterocarpus* and *Mesua* species grown for 24 months in different light (FU-forest understorey, FE- forest edge, OE-outside edge, FS-full sun, SO- small opening, LO large opening) treatments. Standard errors are in parentheses.

	FU	FE	OE	FS	SO	LO
Upper epidermal cell thickness (μm)						
SF	11.98 (0.275)	15.76 (0.212)	19.36 (0.332)	19.88 (0.307)	17.72 (0.302)	4 (0.241)
SR	11.82 (0.176)	13.52 (0.286)	18.20 (0.324)	21.44 (0.284)	17.60 (0.321)	16.44 (0.367)
DZ	25.30 (0.402)	26.93 (0.392)	29.61 (1.180)	32.20 (0.937)	29.42 (0.332)	26.70 (0.325)
DH	14.63 (0.693)	16.02 (0.450)	16.64 (0.270)	17.86 (0.499)	16.67 (0.617)	18.26 (0.505)
MF	7.53 (0.067)	7.19 (0.106)	7.64 (0.286)	8.20 (0.115)	7.30 (0.205)	8.06 (0.173)
MN	6.83 (0.114)	7.83 (0.196)	7.73 (0.084)	8.36 (0.053)	7.00 (0.412)	8.06 (0.199)
Lower epidermal cell thickness (μm)						
SF	8.64 (0.184)	10.42 (0.181)	12.00 (0.278)	10.84 (0.166)	10.00 (0.182)	10.14 (0.232)
SR	8.34 (0.282)	9.42 (0.197)	9.28 (0.224)	10.32 (0.200)	10.40 (0.218)	8.92 (0.214)
DZ	13.39 (0.264)	13.36 (0.148)	12.83 (0.287)	15.58 (0.551)	13.57 (0.342)	15.36 (0.231)
DH	10.70 (0.274)	10.80 (0.252)	11.83 (0.517)	11.83 (0.517)	11.46 (0.684)	12.60 (0.199)
MF	9.10 (0.071)	9.95 (0.301)	10.74 (0.254)	11.86 (0.340)	10.93 (0.575)	11.30 (0.415)
MN	5.26 (0.137)	5.56 (0.302)	5.40 (0.106)	6.29 (0.081)	5.36 (0.167)	6.10 (0.256)

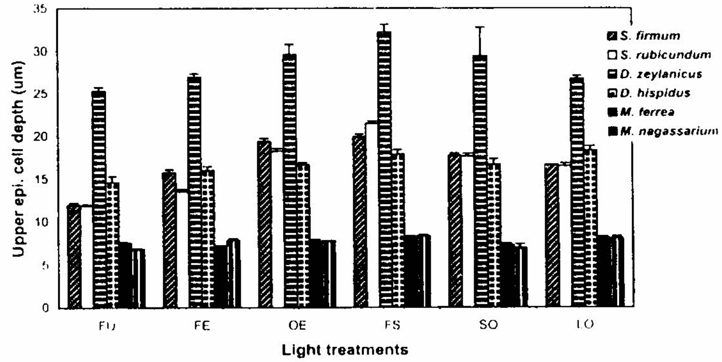

Fig. 2 Upper epidermal cell thickness (μm) for *Syzygium*, *Dipterocarpus* and *Mesua* species in different light treatments (FU-forest understorey, FE-forest edge, OE-outside edge, FS-full sun, SO small opening, LO-large opening). Bars indicate one standard error of mean.

Changes in palisade mesophyll thickness to different light treatments were significant for all species. This may be caused either by cellular elongation or the differentiation of multiple palisade layers in response to increased light. In general full sun leaves had thicker palisade cells compared to that of shade leaves. This was most noticeable for *S. firmum*>*S. rubicundum* >*M. ferrea*>*M. nagassarium*>*D. zeylanicus*>*D. hispidus* (Table 4, Fig. 4) Unlike *Mesua, Dipterocarpus* and *S. firmum* had several palisade cells stacked upon each other.

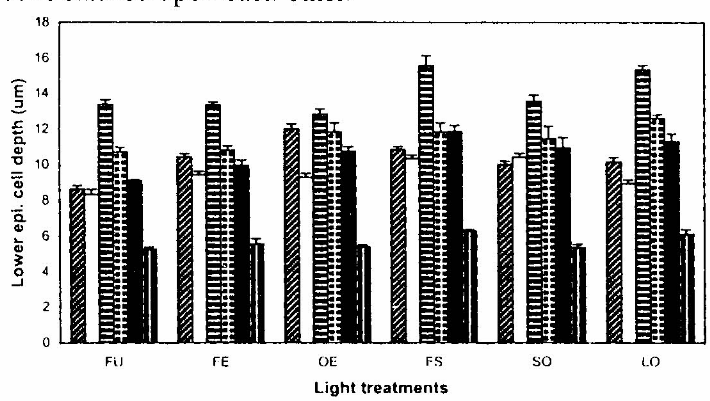

Fig. 3 Lower epidermal cell thickness (μm) for *Syzygium*, *Dipterocarpus* and *Mesua* species in different light treatments (FU- forest understorey, FE-forest edge, OE-outside edge, FS-full sun, So small opening, LO-large opening). Bars indicate one standard error of mean.

Table 4. Summary of palisade cell depth (μm) for *Syzygium, Dipterocarpus* and *Mesua* species grown for 24 months in different light (FU- forest understorey, FE-forest edge, OE- outside edge, FS-full sun, SO-small opening, LO-large opening) teatments. Standard errors are in parentheses.

	FU	FE	OE	FS	SO	LO
SF	46.30 (1.050)	63.72 (0.913)	80.80 (1.302)	81.64 (1.193)	67.72 (0.861)	79.64 (2.291)
SR	48.48 (0.540)	37.32 (0.344)	45.16 (0.577)	42.56 (0.642)	45.24 (0.528)	45.56 (0.987)
DZ	31.14 (0.948)	33.83 (0.342)	39.25 (1.250)	42.73 (1.050)	32.53 (1.530)	38.30 (1.100)
DH	28.63 (0.554)	31.43 (0.187)	33.26 (1.140)	38.36 (2.430)	32.66 (0.274)	33.93 (0.641)
MF	34.86 (1.290)	37.33 (0.798)	39.88 (1.280)	46.23 (1.770)	38.12 (0.376)	39.56 (0.381)
MN	31.80 (0.657)	36.16 (0.456)	44.86 (1.330)	43.20 (0.046)	34.25 (0.074)	38.20 (0.459)

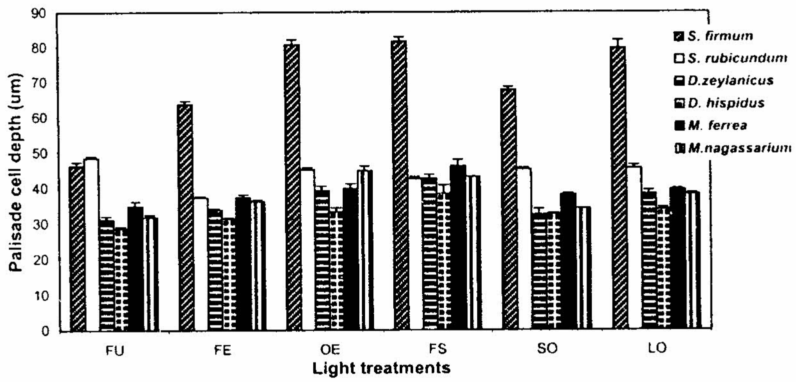

Fig. 4 Palisade cell depth (μm) for *Syzygium*, *Dipterocarpus* and *Mesua* species in different light treatments (FU-forest understorey, FE-forest edge, OE-outside edge, FS-full sun, SO-small opening, LO-large opening). Bars indicate one standard error of mean.

Stomatal frequency

In all six species stomata were found only on the abaxial surface and this corroborates many other studies of tree species (Metcalf and Chalk, 1965). All species had significantly higher numbers of stomata per unit area in leaves that were exposed to full sun (Table, 5 Fig. 5). Differences beween species were also apparent. These differences followed similar trends between the species for both shade and full sun. *Syzygium* had significantly higher stomatal frequencey than other specis both in sun and shade. Between *Syzygium, S. firmum* was the highest, while between *Dipterocrpus, D. hispidus* was the highest. In *Mesua,* both species were similar in stomatal frequency in some light treatments. Overall, *M. ferrea* had higher stomatal frequency than *M. nagassarium.*

Table 5. Summary of stomatal frequency (no. mm^{-2}) for *Syzygium*, *Dipterocarpus* and *Mesua* species grown for 24 months in different light (FU- forest understorey, FE-forest edge, OE-outside edge, FS-full sun, SO-small opening, LO-large opening) treatments. Standard errors are in parentheses.

	FU	FE	OE	FS	SO	LO
SF	279 (8.55)	350 (4.79)	474 (10.40)	483 (9.23)	472 (10.36)	456 (15.39)
SR	249 (17.20)	282 (4.13)	353 (5.52)	387 (11.71)	348 (6.98)	342 (10.04)
DZ	140 (7.81)	191 (6.42)	207 (7.84)	216 (16.80)	190 (12.10)	191 (8.98)
DH	247 (12.70)	224 (8.01)	328 (5.79)	332 (22.10)	274 (20.80)	333 (7.30)
MF	272 (9.01)	272 (4.51)	304 (5.59)	314 (7.07)	275 (10.70)	298 (10.20)
MN	226 (13.00)	279 (9.49)	267 (14.79)	284 (5.79)	236 (13.50)	264 (7.15)

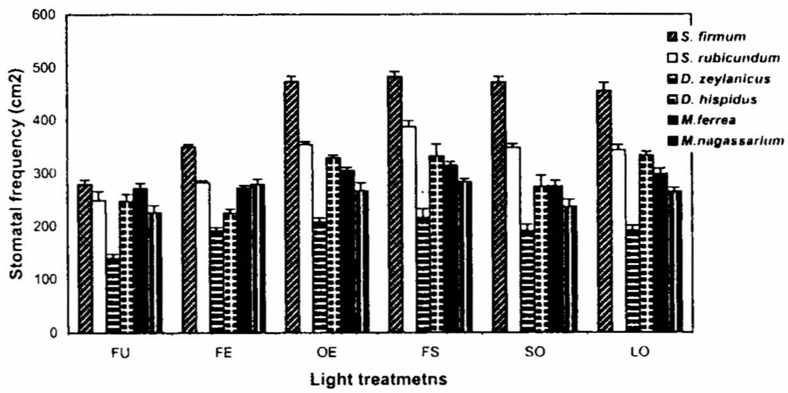

Fig. 5 Stomatal frequency (mm-^{2}) for *Syzygium*, *Dipterocarpus* and *Mesua* species in different lighat treatments (FU-forest understorey, FE-forest edge, OE-outside edge, FS-full sun, SO-small opening LO-large opening). Bars indicate one standard error of mean.

4. Discussion

Differences in anatomical characteristics taken in combination can partly determine the physiological shade-and drought-tolerance of a species (Ashton and Berly, 1992).

Leaf blades were thicker for *Syzygium* species than *Mesua* and *Dipterocarpus*. However, *S. rubicundum* had thinner leaf blades than *Mesua species*. *S. firmum* that is considered shade-tolerant had the thickest leaf blade. Hence it is more resistant to heat loading compared to *Dipterocarpus* and *Mesua*. Clear differences in epidermal cell dimensions also occurred between genera. Both upper and lower epidermal cells were thicker for *D. zeylanicus*, suggesting that they are more efficient in water use.

Anatomical differences are also apparent in palisade cell thickness. *Syzygium* spp. had thicker palisade cells than *Dipterocarpus,* and *Mesua.* Therefore *Syzygium* spp. are able to capture more light than other species since thicker palisade cells enable an increase in chloroplasts and greater efficiency in light capture (Lee et al., 1990). Between the *Syzygium* species the more shade intolerant, *S. rubicundum* had lower palisade cell depth compared to the more shade-tolerant, *Syzygium firmum* in both sun and shade. *Syzygium rubicundum* also having a thinner leaf blade seems to be more exploitive.

Absolute differences reveal that *Syzygium* has a higher stomatal frequency than *Dipterocarpus* and *Mesua.* This suggests that they are relatively less drought-tolerant, than *Dipterocarpus* and *Mesua,* since species with higher stomata are less drought - tolerant, while species having lower stomatal frequency are moderate in drought-tolerance (Ashton and Berlyn, 1992).

The stomatal frequency for all genera increased with the increase of light intensity. These differences in stomatal frequencies could be a result of environmental influence on stomatal differentiation as well as due to cell expansion (Volkenburgh and Davies, 1977). Stomatal frequency varies due to a change in leaf size under differing light and water stressed conditions. Low light can cause a decrease in stomatal frequency due to an increased leaf area but dose not affect stomatal mother cell differentiation. Similarly under water stress, restricted leaf expansion can cause an increase in stomata (Chia and Brun, 1975). However these conditions do not seem to be related to *Syzygium* since these species increased leaf area with increasing light as well as in stomatal frequency (Gamage *et al.* , 1998). In other tropical species *(Shorea)* there was little change in leaf size under varying light environments (Ashton and Berlyn, 1992). Stomatal frequency was affected by prevailing environmental conditions (Levickaja, 1961; Cutler, 1978; Simon *et al.,* 1990) and reactions of auxins in stomatal cells (Cameron, 1969). Therefore the increase in stomatal frequency with the increasing light intensity could be related to the effect of prevailing environmental conditions on the initiation of stomata or to the reaction of auxins in *Syzygium* species.

In conclusion, this study demonstrated that species classified as late-successional canopy trees have leaf anatomical characteristics that change with light availability. Comparing the genera the thicker leaf blades, palisade cell thickness and greater number of stomata in *Syzygium* species suggest that they are more shade-intolerant but less drought tolerant than *Mesua* and *Dipterocarpus.* Even though *Dipterocarpus* spp. are considered more shade-intolerant than *Mesua spp.,* both had similar responsiveness of leaf structure to change across light treatments.

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