

EFFECT OF LIGHT INTENSITY ON GROWTH, LEAF PRODUCTION, LEAF LIFESPAN AND LEAF NUTRIENT BUDGETS OF *ACACIA MANGIUM*, *CINNAMOMUM INERS*, *DYERA COSTULATA*, *EUSIDEROXYLON ZWAGERI* AND *SHOREA ROXBURGHII*

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Received September 2007

TONG, P. S. & NG, F. S. P. 2008. Effect of light intensity on growth, leaf production, leaf lifespan and leaf nutrient budgets of *Acacia mangium*, *Cinnamomum iners*, *Dyera costulata*, *Eusideroxylon zwageri* and *Shorea roxburghii*. Saplings of *Acacia mangium*, *Cinnamomum iners*, *Dyera costulata*, *Eusideroxylon zwageri* and *Shorea roxburghii* were grown side by side at 4, 7, 25, 50 and 100% relative light intensities (RLIs) to facilitate comparison under identical soil and climate conditions. The comparisons cover height increment, diameter increment, rate of production of new leaves, leaf lifespan and leaf nutrient content. The study was carried out in just under two years and the best plants grew from 30 cm to over 300 cm tall. *Acacia mangium* and *S. roxburghii* grew fastest at 100% RLI. The other three species grew fastest at 25% RLI. In height, *A. mangium* at 100% RLI grew four times faster than the second best species, *S. roxburghii*, and 21 times faster than the slowest species, *E. zwageri*. Leaf lifespan, found to be maximum at 4% RLI, was shortened by a constant amount by each doubling of light intensity. For example, each doubling of light intensity shortened the leaf lifespan of *S. roxburghii* by 70 days, and that of *A. mangium* by 40 days. Photo-senescence of leaves is proposed as a mechanism driving phenological events in the non-seasonal humid tropics. Old leaves at the point of shedding had lower NPK contents than newly expanded leaves. The difference is a measure of internal nutrient recycling of NPK. Mg was sometimes internally recycled, sometimes not, while Ca was usually accumulated. In the two fastest-growing species, *A. mangium* and *S. roxburghii*, the NPK content in new leaves tended to peak at about 25% RLI while the growth rate reached its maximum at 100%. Leaf nutrient content did not mirror the rate of growth. *Acacia mangium* had the highest rate of nutrient uptake per growing shoot—10 to 16 times that of *S. roxburghii*. At 100% RLI it grew fastest, had the shortest leaf lifespan and the highest leaf turnover rate.

Keywords: Nutrient cycling, nutrient uptake, senescence, phenology, growth modelling

TONG, P. S. & NG, F. S. P. 2008. Kesan keamatan cahaya terhadap pertumbuhan, penghasilan daun, usia daun dan bajet nutrien daun *Acacia mangium*, *Cinnamomum iners*, *Dyera costulata*, *Eusideroxylon zwageri* dan *Shorea roxburghii*. Anak pokok *Acacia mangium*, *Cinnamomum iners*, *Dyera costulata*, *Eusideroxylon zwageri* dan *Shorea roxburghii* ditanam sebelah-menyebelah pada keamatan cahaya relatif (RLI) 4%, 7%, 25%, 50% dan 100% untuk memudahkan perbandingan di bawah keadaan tanah dan cuaca yang serupa. Perbandingan meliputi pertambahan ketinggian, pertambahan diameter, kadar pertumbuhan daun baru, usia daun dan kandungan nutrien daun. Kajian dijalankan selama hampir dua tahun. Anak pokok terbaik tumbuh dari 30 cm hingga lebih daripada 300 cm. *Acacia mangium* dan *S. roxburghii* tumbuh paling cepat pada 100% RLI. Ketiga-tiga spesies yang lain tumbuh paling cepat pada 25% RLI. *Acacia mangium* pada 100% RLI tumbuh empat kali lebih tinggi daripada *S. roxburghii*, iaitu spesies kedua tinggi dan 21 kali lebih tinggi daripada *E. zwageri*, iaitu spesies yang paling lambat pertumbuhannya. Usia daun adalah maksimum pada 4% RLI. Usia daun dipendekkan pada kadar yang tetap dengan setiap penggandaan keamatan cahaya. Misalnya, dengan setiap penggandaan keamatan cahaya, usia daun dipendekkan 70 hari bagi *S. roxburghii* dan 40 hari untuk *A. mangium*. Foto-senesen daun dicadangkan sebagai mekanisme yang mengawal kejadian fenologi di kawasan tropika yang tidak bermusim dan lembap. Daun tua pada masa gugur mempunyai kandungan NPK yang lebih rendah daripada daun baru yang matang. Perbezaannya ialah sukatan kitar semula dalaman untuk NPK. Mg kadang-kadang dikitar semula secara dalaman. Ca biasanya dikumpulkan. Untuk *A. mangium* dan *S. roxburghii* yang mempunyai pertumbuhan paling cepat, kandungan NPK dalam daun baru adalah maksimum pada 25% RLI sementara kadar pertumbuhan menjadi maksimum pada 100% RLI. Kandungan nutrien daun tidak mencerminkan kadar pertumbuhan. *Acacia mangium* mempunyai kadar pengambilan nutrien bagi setiap pucuk yang paling tinggi, iaitu 10 hingga 16 kali berbanding dengan *S. roxburghii*. Pada 100% RLI, *A. mangium* tumbuh paling cepat, mempunyai usia daun yang paling pendek dan kadar pertumbuhan daun baru yang paling tinggi.

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INTRODUCTION

In the humid tropics close to the equator, where there is no winter or periodic dry season to limit growth, it is possible for trees to produce new leaves and shed old ones continuously, throughout the year. However, in his pioneering studies on tropical tree phenology, Holttum (1931, 1940) found that most trees in the humid tropics undergo periodic leaf renewal—shedding all old leaves at one go and producing new ones at the same time. However, the periods are not uniform, and the degree of synchronization is normally very low. For example, the period for a tree may vary between five and seven months and if monitored over many years, it will be found that its leaf renewal event can occur in any calendar month. Another tree of the same species, even growing close by, may have a slightly different periodicity, perhaps six to eight months, and its leaf renewal event will also not be tied to any calendar month. In any forest in the humid tropics, one can find some trees in leaf renewal activity at any time of the year. However, now and then, the individuality of trees appears to be over-ridden, so that a higher proportion of trees than normal are observed renewing their leaves in synchrony. Flowering is associated with leaf renewal, and when the degree of synchrony is exceptionally high, covering a large geographical area and involving different families, genera and species, we have what is commonly called a gregarious flowering event (Ng 1977). After that, the trees become unsynchronized again.

It is during their seedling and sapling stages that trees of the humid tropics take advantage of the favourable climate to grow continuously

through the year (Ng 1979). Some produce new leaves one at a time at an even rate. Others produce leaves in flushes of several leaves at a time, but the flushes themselves occur at an even rate and at frequent intervals of time. The shedding of leaves in juveniles is also continuous, but lags behind the production of new leaves, as a result of which shoots of juvenile trees accumulate leaves. In the case of trees that produce leaves in flushes, two to nine consecutive flush generations of leaves may accumulate on a juvenile shoot before the oldest leaves are shed.

Ng's (1992) study on leaf production and leaf lifespan in seedlings of *Dryobalanops aromatica* under 4, 38 and 100% relative light intensities (RLIs) was the first attempt in Malaysia to quantify leaf production rate and leaf lifespan of juvenile trees. He found that *D. aromatica* had the highest leaf production rate at 38% RLI and longest leaf lifespan at 4% RLI.

This study investigates growth, leaf production, leaf life span and leaf nutrient contents of saplings of *Acacia mangium*, *Cinnamomum iners*, *Dyera costulata*, *Eusideroxylon zwageri* and *Shorea roxburghii*, under relative light intensities of 4, 7, 25, 50 and 100%. The study began with plants 30–60 cm tall and ended with the tallest plants exceeding 300 cm tall. The study was carried out in slightly under two years.

The species were selected to represent a wide range of examples or models in taxonomy, growth, architecture, timber, ecology and utilization (Table 1). The definitions of tree architectural models follow the system of Hallé, *et al.* (1978). Four of the species are important in the timber trade, while the fifth is a popular tree for roadside planting.

Table 1 Characteristics of the five studied species

Species and family	Timber class	Tree model	Utilization
<i>Acacia mangium</i> (Leguminosae)	Light hardwood (mangium)	Roux	Plantation pulpwood
<i>Cinnamomum iners</i> (Lauraceae)	Light hardwood (medang)	Massart	Ornamental roadside planting
<i>Dyera costulata</i> (Apocynaceae)	Light hardwood (jelutong)	Petit	White wood for light uses (toys, pencils, etc.)
<i>Eusideroxylon zwageri</i> (Lauraceae)	Heavy hardwood (Bornean ironwood)	Roux	Heavy construction timber
<i>Shorea roxburghii</i> (Dipterocarpaceae)	Light to medium hardwood (white meranti)	Roux	General construction timber

MATERIALS AND METHOD

The research facility (Figure 1) was situated in an open field at Bandar Utama, just outside Kuala Lumpur, at 3° 08' 48" N, 101° 36' 21" E; at elevation 89 m above sea level. A rectangular metal frame 3 m tall, 6 m wide and 23 m long was erected, with its long axis running in NS direction. The structure was divided along its long axis into sections. Each section was roofed over with commercially available shade netting. The nets were fixed so as to cover the top, and to drape over the upper portions of the eastern and the western sides. In Kuala Lumpur, where the angle of the sun varies only slightly through the year, this design effectively shielded the plants from unfiltered sunlight throughout the day. The north and south sides were left open to ensure adequate air circulation. An adjacent area outside the plant house served as the full-sun (100% RLI) plot.

The air temperature, as measured on the roof of a building nearby, varied between 35 °C at about midday and 22 °C just before dawn, without seasonal variation.

The mean annual rainfall in Kuala Lumpur is about 93 inches (237 cm), distributed so that no month is without at least several days of rain. The study site itself was never under water stress because the ground slopes gently from east to west, and on the eastern side is a large lake. On the western side is a stream. Water seeps continuously from the lake to the stream. There

was no need to water the plants at all except for a few days after establishing the plot.

The shade nets were rated by the percentage of light they allowed to pass through. The percentage of light passing through, as a proportion of the full light, was calculated by comparing simultaneous measurements made under the shade net and under open sky. This measure is the relative light intensity or RLI (Sasaki 1983). It is relatively independent of time of day and cloud condition.

To ensure homogeneity in soil conditions, the soil used in the study was an artificial mixture of subsoil loam, cocopeat and charcoal particles, in equal proportions. Cocopeat is what remains of coconut husks after the long fibres have been extracted for industrial use. It is totally organic. The charcoal particles are a by-product of the briquette industry in which briquettes are made from compressed sawdust fired in kilns. The briquettes are broken into small pieces for horticultural use. The upper layer of soil in the experimental area was stripped away to a depth of 0.5 m by machine and replaced with this prepared mixture.

Each species in the study was represented by 30 seedlings of the same age and approximately equal height (30–60 cm tall depending on species) selected from the nursery of the Forest Research Institute Malaysia. At the study site the seedlings were transferred individually to large perforated polybags of 30 × 30 cm size, containing the prepared soil mixture. The filled polybags



Figure 1 The experimental plot

were then arranged in rows, 50 cm apart, and planted three-quarters into the ground. Soil moisture was able to seep into the bags through the perforations, and roots growing out would encounter the same prepared soil as what was inside the polybags. It was intended that the rims of the bags would help keep fertilizers in place for each plant, but fertilization was found to be unnecessary.

Under each RLI, each species was represented by six seedlings in a row, and the rows were aligned in east–west direction in order of *D. costulata*, *A. mangium*, *C. iners*, *S. roxburghii* and *E. zwageri*, so each species always had the same neighbouring species.

Each plant had a single dominant leader shoot. Height and diameter measurements of the leader shoot were taken at the start and end of the study for each plant. Height was measured from ground level to the tip of the leader shoot. Diameter was measured at 14 cm above the ground.

The rate of leaf production and leaf lifespan were monitored on the leader shoot and one selected branch shoot of each plant. The selected branches began as the uppermost branches at the start of the study but became the lower branches as new branches were produced above them. The plants were monitored every two or three days. This involved monitoring 150 plants and their leaves, for which a tagging system using coloured wires was established. As plants grow, they change in shape and size, and the observer can get easily disorientated. A systematic arrangement provides good visual orientation whereas a randomized arrangement for 150 plants would have made the monitoring of such parameters very difficult if not impossible.

Leaf nutrient contents were determined for each species under each RLI at two stages: (a) new leaves as soon as they were fully expanded, and old leaves at the point of shedding. The leaves were dried at room temperature using silica gel. Leaves were accumulated to make up at least 20 g of dry matter for laboratory analysis. The analyses were carried out by a local laboratory providing this service for the plantation industries. The samples were analyzed for N, P, K, Mg and Ca.

The planned study period for growth was 65 weeks, from June 2004 till September 2007, but the study of growth for a species was effectively ended when the tallest plants of that species reached the height (3 m) of the overhead shade net and had no more room for upward

extension. In the case of the fastest growing species, *A. mangium*, this happened in 16 weeks. For species with long leaf lifespans (such species fortunately did not reach the roof during the period of study), the study was extended to 92 weeks, which was the maximum time available for the study.

The compact area of this experiment, the fixed arrangement of neighbouring plants and the homogenization of the soil ensured that except for the light regime, all plants would experience comparable environmental conditions throughout the study.

The leaf nutrient data were provided as percentages of leaf dry matter (dry weight). We converted them to mg per leaf by the formula $A / 100 \times B / C$ where A is the nutrient content as a percentage of leaf dry weight, B is the dry weight of the leaf sample and C is the number of leaves making up the sample. The difference in nutrient content between the old and new leaves gives a measure of nutrient withdrawal or accumulation. The nutrient content in mg per leaf multiplied by the rate of leaf production gives a measure of the rate of nutrient uptake per growing shoot.

Nutrient content as percentage of dry matter cannot be used directly for tracking nutrient movements in leaves. Take for example, a species in which the dry matter content of old leaves is twice that of new leaves. If the percentage of nutrient Z as a percentage of dry matter is the same in new and old leaves, the percentage figures would show no change, but the actual amount of nutrient Z would have doubled.

The sample sizes of leaves used in nutrient determination were 25–37 for *C. iners*, 22–50 for *A. mangium*, 14–50 for *S. roxburghii*, 11–35 for *E. zwageri* and 7–18 for *D. costulata*. The sample sizes could not be standardized because the availability of leaves at the required stages was dependent on the rate of production and ageing of leaves, which varied greatly between species.

RESULTS

The means and standard errors of the mean, for height increment, diameter increment, and number of leaves produced are based on six plants per species per RLI, reduced to five, four or rarely three plants where there were mortalities. For leaf life span, the means and standard errors of the mean are based on the

number of tagged leaves that were shed during the study period. 'New' leaves are always new leaves that have just fully expanded. 'Old' leaves are senescent leaves at the point of shedding.

The results are tabulated in Tables 2 to 11 and graphed in Figures 2 to 10.

Acacia mangium

In *A. mangium*, the leaves are in alternate arrangement, i.e. one leaf per node. Throughout the study period of 16 weeks, the shoots produced new leaves continuously and evenly, with no sign of seasonality. Old leaves were shed continuously.

The rate of growth as indicated by height increment (Figure 2), diameter increment (Figure 3) and rate of leaf production (Figure 4) increased with increasing light intensity and reached its maximum under open sky (100% RLI). Leaf lifespan declined with increasing light intensity (Figure 5).

The rate of leaf production was lower on branches than on leaders at 50–100% RLI, but about the same at lower light intensities (Table 2). There was no consistent difference in leaf lifespans between leaders and branches.

Cinnamomum iners

The leaves are in opposite arrangement, i.e. two per node, and produced in flushes. A flush begins from a rested terminal bud and consists

of usually two pairs of scale leaves followed by two pairs of foliage leaves. The axillary buds of the first pair of scale leaves concurrently expand and bear a pair of scale leaves followed by a pair of foliage leaves. Each flush of growth therefore results in eight leaves. The flushes occurred regularly, with no trace of seasonality.

Height increment (Figure 2) and leaf production rate (Figure 4) peaked at about 25% RLI but diameter increment (Figure 3) continued to improve up to 100% RLI. Leaf lifespans could not be determined because none of the labelled leaves were shed even when the study was extended to 92 weeks. Successive generations of leaf flushes were accumulated, making a densely-leafed crown.

On branches, growth was also in flushes but at a distinctly lower rate (Table 4). The leaf lifespans of the labelled leaves all exceeded the extended study period of 92 weeks, at all RLIs.

Dyera costulata

In *D. costulata*, leaves are produced in whorls of six to eight leaves per node, each whorl being equivalent to a flush with an average of seven leaves. The shoots grow one node (one flush) at a time, with a distinct bud-resting period between flushes. The rate of flushing was regular at all RLIs.

Height and diameter increment, and leaf production (Figures 2–4) all peaked at about 25% RLI. Although the leaves belonging to the

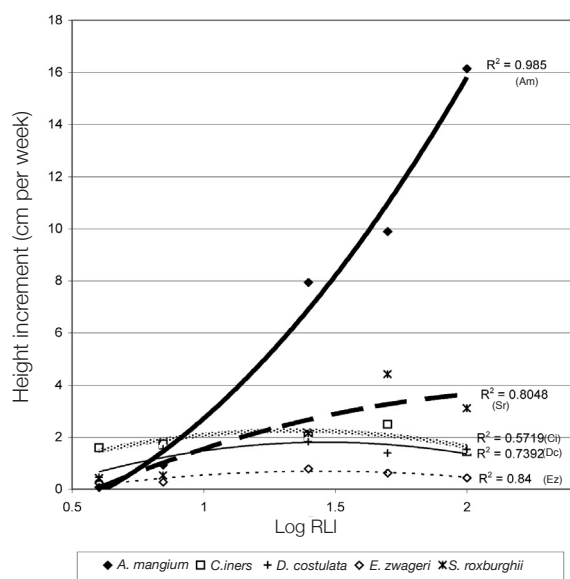


Figure 2 Height growth in relation to relative light intensity

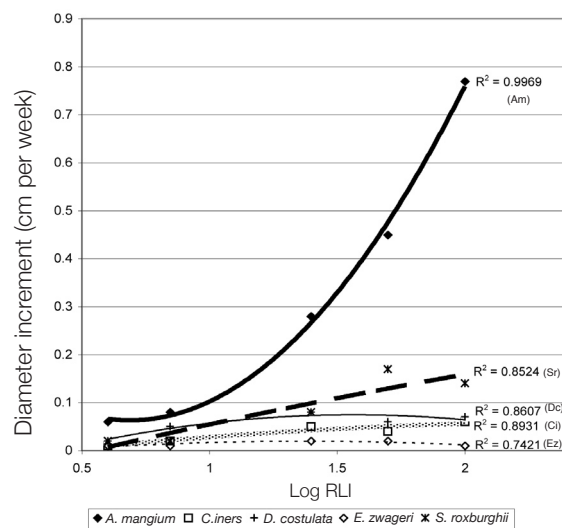


Figure 3 Diameter growth in relation to relative light intensity

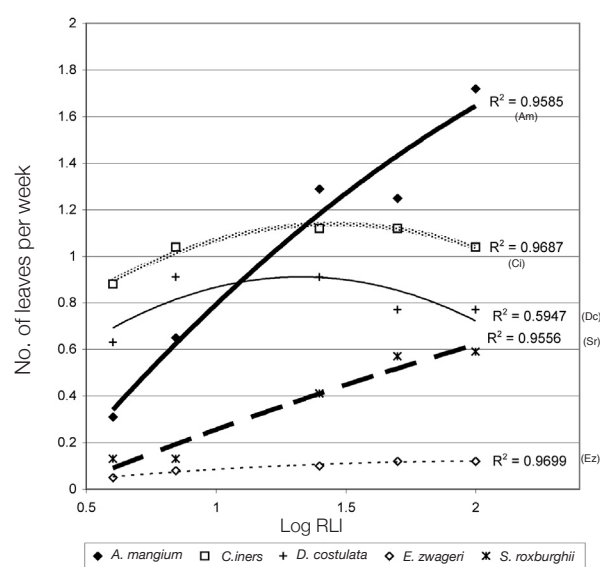


Figure 4 Leaf production in relation to relative light intensity

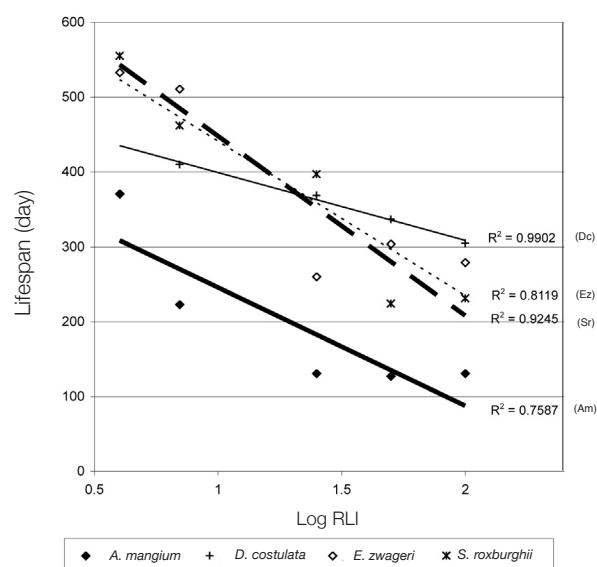


Figure 5 Leaf lifespan in relation to relative light intensity

Table 2 Growth of leader and branch shoots of *Acacia mangium* under various RLIs

Shoot	RLI				
	4%	7%	25%	50%	100%
Leader					
No. of leader shoots monitored	5	6	6	6	6
Ht. increment (cm) in 16 weeks	1.1 ± 0.78	14.8 ± 5.35	127.0 ± 25.45	158.2 ± 10.10	258.3 ± 10.09
Ht. increment per week	0.07	0.93	7.94	9.89	16.15
Diam. increment in 16 weeks	0.9 ± 0.26	1.4 ± 0.32	4.4 ± 0.41	7.2 ± 1.49	12.3 ± 0.44
Diam. increment per week	0.06	0.08	0.28	0.45	0.77
No. of leaves in 16 weeks	5.0 ± 0.10	10.3 ± 0.11	20.7 ± 0.10	20.0 ± 0.14	27.5 ± 0.12
No. of leaves per week	0.31	0.65	1.29	1.25	1.72
Lifespan of leaves (days)	371 ± 22.54	223 ± 10.52	131 ± 2.24	127 ± 2.78	131 ± 1.85
No. of leaves shed in 16 weeks	7	50	86	86	86
Branch					
No. of branches monitored	5	6	6	6	6
No. of leaves in 16 weeks	4.83 ± 0.05	10.5 ± 0.08	20.4 ± 0.10	18.8 ± 0.10	25.3 ± 0.09
No. of leaves per week	0.30	0.66	1.28	1.18	1.58
Lifespan of leaves (days)	229 ± 11.81	214 ± 6.91	136 ± 3.86	134 ± 3.74	127 ± 3.07
No. of leaves shed in 16 weeks	16	47	52	44	50

same whorl were all of the same age, they were not all shed on the same day. To determine the average leaf lifespan, the average lifespan of each whorl was calculated first; then the overall average was calculated from all the whorls produced under each RLI. The lifespan of

leaves (Figure 5) declined with increase in RLI. The study was extended to the 92nd week in the hope of obtaining a larger sample size of leaves reaching the end of their lives. Nevertheless at 4% only one whorl was shed, giving an unreliable estimate of the leaf lifespan at 4%.

Table 3 Nutrient flux in leaves of *Acacia mangium*

Nutrient			RLI				
			4%	7%	25%	50%	100%
N	New leaves	% dry wt	2.97	3.24	3.13	3.00	2.89
		mg per leaf	7.2	14.6	52.0	53.4	31.5
	Old leaves	% dry wt	2.74	2.57	2.15	2.20	2.05
		mg per leaf	4.0	7.9	27.9	36.7	15.9
		% N withdrawn	7.7	20.7	31.3	26.7	29.1
P	New leaves	% dry wt	0.14	0.13	0.16	0.15	0.19
		mg per leaf	0.3	0.6	2.6	2.7	2.1
	Old leaves	% dry wt	0.13	0.11	0.1	0.11	0.16
		mg per leaf	0.2	0.3	1.3	1.8	1.3
		% P withdrawn	33.3	50.0	50.0	33.3	38.1
K	New leaves	% dry wt	2.19	2.03	1.96	1.83	1.50
		mg per leaf	5.3	9.2	32.4	30.4	16.3
	Old leaves	% dry wt	1.62	1.83	1.5	1.46	1.01
		mg per leaf	2.4	5.6	19.4	24.4	7.8
		% K withdrawn	54.7	39.1	40.1	19.7	52.1
Mg	New leaves	% dry wt	0.19	0.18	0.18	0.18	(0.6)
		mg per leaf	0.5	0.8	2.9	3.1	
	Old leaves	% dry wt	0.2	0.18	0.14	0.16	(1.47)
		mg per leaf	0.3	0.6	1.8	2.7	
		% Mg withdrawn	40	25	37.9	12.9	
Ca	New leaves	% dry wt	0.77	0.81	0.77	0.74	(0.14)
		mg per leaf	1.9	3.7	12.8	13.2	
	Old leaves	% dry wt	1.03	1.04	0.95	0.92	(0.16)
		mg per leaf	1.6	3.2	12.3	15.4	
		Ca change	-	-	-	+	
New leaf dry matter content as % fresh wt		17.95	20.10	51.80	45.13	25.13	
Old leaf dry matter content as % fresh wt		16.22	19.16	56.76	47.40	27.33	

Outliers (data within parentheses) are assumed erroneous and ignored in analysis.

Table 4 Growth of leader and branch shoots of *Cinnamomum iners* under various RLIs

Shoot	RLI				
	4%	7%	25%	50%	100%
Leader					
No. of leader shoots monitored	5	6	6	6	6
Ht. increment (cm) in 61 weeks	96.7 ± 17.36	106.1 ± 13.32	124.6 ± 21.61	151.6 ± 19.89	87.8 ± 15.26
Ht. increment per week	1.59	1.74	2.04	2.49	1.44
Diam. increment in 61 weeks	0.7 ± 0.19	1.5 ± 0.38	2.8 ± 0.38	2.6 ± 0.44	3.4 ± 0.45
Diam. increment per week	0.01	0.02	0.05	0.04	0.06
No. of flushes in 61 weeks	6.6 ± 0.02	7.8 ± 0.02	8.7 ± 0.02	8.7 ± 0.02	7.7 ± 0.02
No. of flushes per week	0.11	0.13	0.14	0.14	0.13
No. of leaves per week (8 per flush)	0.88	1.04	1.12	1.12	1.04
Branch					
No. of branches monitored	5	6	6	6	6
No. of flushes in 64 weeks	3.0 ± 0.02	3.0 ± 0.02	4.0 ± 0.02	4.5 ± 0.02	7.2 ± 0.17
No. of flushes per week	0.05	0.05	0.06	0.07	0.11
No. of leaves per week (8 per flush)	0.4	0.4	0.48	0.56	0.88

Table 5 Nutrient flux in leaves of *Cinnamomum iners*

Nutrient			RLI				
			4%	7%	25%	50%	100%
N	New leaves	% dry wt	1.74	1.62	1.64	1.47	1.48
		mg per leaf	12.7	9.7	11.8	8.7	7.9
	Old leaves	% dry wt	1.44	1.30	1.23	1.08	1.36
		mg per leaf	6.6	7.0	9.9	6.5	7.2
		% withdrawn	48	27.8	16.1	25.3	8.9
P	New leaves	% dry wt	0.14	0.13	0.16	0.14	0.12
		mg per leaf	1.0	0.7	1.1	0.8	0.6
	Old leaves	% dry wt	0.10	0.10	0.11	0.10	0.08
		mg per leaf	0.5	0.6	0.9	0.6	0.4
		% withdrawn	50.0	14.3	18.2	25	33.3
K	New leaves	% dry wt	1.55	1.35	1.14	1.12	0.90
		mg per leaf	11.3	8.1	8.2	6.6	4.8
	Old leaves	% dry wt	0.74	0.51	0.45	0.41	0.43
		mg per leaf	3.4	2.7	3.6	2.5	2.3
		% withdrawn	69.9	66.7	56.1	62.1	52.1
Mg	New leaves	% dry wt	0.13	0.11	0.11	0.10	0.10
		mg per leaf	0.9	0.7	0.8	0.6	0.5
	Old leaves	% dry wt	0.11	0.12	0.11	0.07	0.07
		mg per leaf	0.5	0.6	0.9	0.4	0.4
		% Mg withdrawn	44.4	14.3	?	33.3	20
Ca	New leaves	% dry wt	0.35	0.35	0.40	0.33	0.39
		mg per leaf	2.5	2.1	2.9	2	2.1
	Old leaves	% dry wt	1.14	1.36	1.18	1.39	1.10
		mg per leaf	5.2	7.3	9.5	8.3	5.8
		Ca change	+	+	+	+	+
New leaf dry matter content as % fresh wt		36.98	34.97	34.21	39.75	40.76	
Old leaf dry matter content as % fresh wt		45.87	48.88	58.99	48.00	53.36	

? indicates outlier

Dyera costulata is usually unbranched until the leader shoot is 1–3 m tall. In this study, plants at 4 and 7% RLIs produced no branches during the period of study (Table 6). Branching occurred in five plants at 25%, two at 50% and four at 100% RLI. The rate of whorl production was slower on branches than on leaders.

Eusideroxylon zwageri

Leaves are produced one per node, i.e. in alternate arrangement, and there is usually a sylleptic branch developed at each node.

Growth was slow compared to the other species, with height and diameter increment (Figures 2 and 3) peaking at 25% RLI. Unexpectedly, the leaf production rate reached its maximum at 100% RLI (Figure 4). The study on leaf lifespan was carried

forward to the 92nd week, but even so, only 13 leaves were shed at 100% RLI (Table 8) and this was the maximum. At 4 and 7% RLI, only two and four leaves were shed respectively. Leaf lifespan dropped with increase in RLI (Figure 5).

The rate of leaf production was distinctly higher on branches than on leaders (Table 8).

Shorea roxburghii

The leaves are produced in alternate arrangement, i.e. one leaf per node, and there is usually a sylleptic branch at each node.

From the trend lines in Figures 2, 3 and 4, the rates of height and diameter increment and rate of leaf production all reached their maximum at 100% RLI. The leaf lifespan declined with increase in light intensity (Figure 5).

Table 6 Growth of leader and branch shoots of *Dyera costulata* under various RLIs

Shoot	RLI				
	4%	7%	25%	50%	100%
Leader					
No. of leader shoots monitored	6	6	5	6	5
Ht. increment (cm) in 64 weeks	29.0 ± 6.99	98.8 ± 16.62	116.7 ± 11.71	88.9 ± 10.82	97.9 ± 9.15
Ht. increment per week	0.45	1.54	1.82	1.39	1.53
Diam. increment 64 weeks	1.2 ± 0.37	3.0 ± 0.48	5.4 ± 0.26	3.7 ± 0.32	4.6 ± 0.55
Diam. increment per week	0.02	0.05	0.08	0.06	0.07
No. of whorls in 64 weeks	6.0 ± 0.02	8.5 ± 0.02	8.4 ± 0.02	7.2 ± 0.02	6.8 ± 0.02
No. of whorls per week	0.09	0.13	0.13	0.11	0.11
No. of leaves per week (7 per whorl)	0.63	0.91	0.91	0.77	0.77
Lifespan (days) of whorls	347?	410 ± 22.21	369 ± 43.90	337 ± 27.69	305 ± 10.90
No. of whorls shed in 92 weeks	1	7	8	15	22
Branch					
No. of branches monitored	0	0	5	2	4
No. of whorls in 64 weeks			5.0 ± 0.02	5.0 ± 0.03	3.25 ± 0.02
No. of whorls per week			0.08	0.08	0.05
No. of leaves per week (7 leaves per whorl)			0.56	0.56	0.35
Lifespan (days) of whorls			465 ± 12.73	326 ± 42.54	310 ± 26.92
No of whorls shed in 92 weeks			2	4	5

Table 7 Nutrient flux in leaves of *Dyera costulata*

Nutrient	RLI						
	4%	7%	25%	50%	100%		
N	New leaves	% dry wt	2.12	2.49	2.38	2.84	1.39
		N mg per leaf	56.4	70.0	36.6	71.3	36.4
	Old leaves	% dry wt		1.83	1.43	1.67	1.31
		mg per leaf		15.8	20.7	22.2	15.1
		% N withdrawn		77.4	43.4	68.6	58.5
P	New leaves	% dry wt	0.16	0.12	0.14	0.19	0.09
		P mg per leaf	4.2	3.5	2.2	4.7	1.7
	Old leaves	% dry wt		0.08	0.05	0.05	0.04
		mg per leaf		0.7	0.7	0.6	0.5
		% P withdrawn		80.0	68.2	87.2	70.6
K	New leaves	% dry wt	1.35	1.04	0.71	1.10	0.61
		K mg per leaf	35.9	29.2	10.9	27.6	11.7
	Old leaves	% dry wt		0.93	0.37	0.49	0.47
		mg per leaf		0.8	5.4	6.5	5.4
		% K withdrawn		97.3	50.5	76.4	53.8
Mg	New leaves	% dry wt	0.20	0.20	0.28	0.24	0.25
		Mg mg per leaf	5.3	5.6	4.3	6.0	4.8
	Old leaves	% dry wt		0.25	0.29	0.36	0.33
		mg per leaf		2.2	4.2	4.8	3.8
		% Mg withdrawn		60.7	7.0	20.0	20.8
Ca	New leaves	% dry wt	0.45	0.70	1.47	0.64	1.10
		Ca mg per leaf	12.0	19.7	22.6	16.1	21.2
	Old leaves	% dry wt		1.65	1.81	1.50	1.83
		mg per leaf		14.2	26.2	20	21.1
		Ca change		-	+	+	-
New leaf dry matter content as % fresh wt			31.40	30.15	30.80	29.00	35.52
Old leaf dry matter content as % fresh wt				41.56	76.30	51.67	47.11

At 4% RLI, one plant did not produce branches (Table 10). The leaf production rate was distinctly lower on branches than on leaders at all RLIs. The leaves on the branches had longer lifespans than the leaves on leader shoots at comparable RLIs.

DISCUSSION

Rates of height and diameter increment

In the comparison of rates of height and diameter increment in Figures 2 and 3, it can be seen that the rate of growth for all species is closely correlated with the RLI. The rate of growth was close to zero at 4%, but improved noticeably at 7%. The rates peaked at about 25% for *D. costulata* and *E. zwageri*, but continued to improve up to 100% for *A. mangium* and *S. roxburghii*. In *C. iners*, height increment peaked at 25% but diameter increment reached maximum at 100%.

Acacia mangium outgrew all the other species at 25–100% RLI. At 100%, it grew at about four times the maximum rate of the second best performer, *S. roxburghii*.

Trees are often reputed to be ‘fast-growing’, ‘light-demanding’, ‘slow-growing’ or ‘shade-tolerant’ (Swaine & Whitmore 1988). *Acacia*

mangium is a typical ‘fast-growing’ and ‘light-demanding’ species but the present experiment shows that even for *A. mangium*, there can be a zero state, at about 4% RLI, at which the plants merely stay alive with no growth. Presumably, a zero state occurs whenever any vital factor in a site becomes limiting. At 7% *A. mangium* grew a little. At 25%, it already outgrew all the other species, registering 8 cm height increment per week (Table 2). At 100% RLI, its growth rate doubles to 16 cm per week. Hence no species can be said to be ‘fast-growing’ or ‘slow-growing’ without reference to site conditions. The minimum is always zero, and the maximum is the best observed and recorded. In between, any rate is possible. The great virtue of *A. mangium* is that it is fast-growing over such a wide range of conditions that the label ‘fast-growing’ can be applied to it almost anywhere in the humid tropics.

Of the site factors that affect growth rate, the one that has received most attention is light. For example, Nicholson (1960) found five dipterocarp species, *Parashorea malaanonan*, *Shorea leptoclados*, *Shorea leprosula*, *Dryobalanops aromatica* and *Dipterocarpus stellatus* to grow optimally at 87.5% RLI. Mori (1980) found *Calamus manan* (a liana) to grow optimally at 50% RLI; Sasaki and Mori (1981) found *Vatica*

Table 8 Growth of leader and branch shoots of *Eusideroxylon zwageri* under various RLIs

Shoot	RLI				
	4%	7%	25%	50%	100%
Leader					
No. of leader shoots monitored	4	5	5	3	3
Ht. increment (cm) in 65 weeks	15.1 ± 2.1	18.0 ± 4.89	50.7 ± 14.66	40.3 ± 6.2	28.8 ± 10.08
Ht. increment per week	0.23	0.28	0.78	0.62	0.44
Diam. increment in 65 weeks	0.6 ± 0.16	0.6 ± 0.26	1.5 ± 0.36	1.3 ± 0.38	0.8 ± 0.35
Diam. increment per week	0.01	0.01	0.02	0.02	0.01
No. of leaves in 65 weeks	3.5 ± 0.02	5.0 ± 0.02	6.8 ± 0.02	7.7 ± 0.03	8.0 ± 0.04
No. of leaves per week	0.05	0.08	0.10	0.12	0.12
Lifespan of leaves(days)	533 ± 53.00	511 ± 24.50	260 ± 24.64	304 ± 13.47	279 ± 31.78
No. of leaves shed	2	4	9	11	13
Branch					
No. of branches monitored	4	5	4	3	3
No. of leaves in 64 weeks	5.0 ± 0.02	10.2 ± 0.02	13.5 ± 0.04	14.0 ± 0.04	14.0 ± 0.04
No. of leaves per week	0.08	0.16	0.21	0.22	0.22
Lifespan of leaves (days)	440 ± 30.95	336 ± 39.66	356 ± 18.91	244 ± 12.65	250 ± 21.01
No. of leaves shed	13	11	21	32	30

Table 9 Nutrient flux in leaves of *Eusideroxylon zwageri*

Nutrient			RLI				
			4%	7%	25%	50%	100%
N	New leaves	% dry wt	1.94	1.86	1.92	1.83	1.6
		N mg per leaf	8.1	6.4	12.7	12.1	7.4
	Old leaves	% dry wt	1.08		1.01	0.93	1.1
		mg per leaf	4.7		7.6	5.9	5.5
		% withdrawn	42.0		40.2	51.2	25.7
P	New leaves	% dry wt	0.14	0.14	0.17	0.17	0.13
		P mg per leaf	0.6	0.5	1.1	1.1	0.6
	Old leaves	% dry wt	0.05		0.12	0.08	0.05
		mg per leaf	0.2		0.9	0.5	0.3
		% withdrawn	66.7		18.2	54.5	50.0
K	New leaves	% dry wt	1.92	1.67	1.59	1.04	1.25
		K mg per leaf	8.0	5.8	10.5	6.9	5.8
	Old leaves	% dry wt	1.02		0.43	0.39	0.55
		mg per leaf	4.4		3.2	2.5	2.8
		% withdrawn	45.0		69.5	63.8	51.7
Mg	New leaves	% dry wt	0.25	0.26	0.22	0.18	0.17
		Mg mg per leaf	1.0	0.9	1.5	1.2	0.8
	Old leaves	% dry wt	0.36		0.33	0.26	0.23
		mg per leaf	1.6		2.5	1.6	1.2
		Mg change	+		+	+	+
Ca	New leaves	% dry wt	0.77	0.81	0.69	0.69	0.68
		Ca mg per leaf	3.2	2.8	4.6	4.6	3.1
	Old leaves	% dry wt	1.29		1.21	1.06	0.89
		mg per leaf	5.6		9.1	6.7	4.5
		Ca change	+		+	+	+
New leaf dry matter content as % fresh wt		26.14	27.03	29.82	32.32	31.67	
Old leaf dry matter content as % fresh wt		48.90		40.82	37.11	39.33	

Due to an oversight, old leaves at 7% RLI were not analyzed.

Table 10 Growth of leader and branch shoots of *Shorea roxburghii* under various RLIs

Shoot	RLI				
	4%	7%	25%	50%	100%
Leader					
No. of leader shoots monitored	5	6	5	4	4
Ht. increment (cm) in 38 weeks	15.8 ± 9.12	20.2 ± 10.63	81.3 ± 18.02	167.8 ± 17.68	117.9 ± 8.71
Ht. increment per week	0.42	0.53	2.14	4.42	3.10
Diam. increment in 38 weeks	0.9 ± 0.24	0.9 ± 0.12	3.0 ± 0.33	6.4 ± 0.86	5.3 ± 0.40
Diam. increment per week	0.02	0.02	0.08	0.17	0.14
No. of leaves in 38 weeks	4.8 ± 0.03	4.8 ± 0.04	15.6 ± 0.05	21.8 ± 0.06	22.3 ± 0.08
No. of leaves per week	0.13	0.13	0.41	0.57	0.59
Lifespan of leaves (days)	555 ± 36.97	462 ± 81.16	397 ± 13.74	224 ± 13.01	231 ± 7.57
No. of leaves shed	4	6	26	31	33
Branch					
No. of branches monitored	4	6	5	4	4
No. of leaves in 58 weeks	2.4 ± 0.01	6.0 ± 0.03	8.3 ± 0.03	15.5 ± 0.06	26.8 ± 0.08
No. of leaves per week	0.04	0.10	0.14	0.27	0.46
Lifespan of leaves (days)	> 663	537 ± 27.03	448 ± 41.84	453 ± 13.39	333 ± 18.88
No. of leaves shed	0	9	8	26	30

Table 11 Nutrient flux in leaves of *Shorea roxburghii*

Nutrient			RLI				
			4%	7%	25%	50%	100%
N	New leaves	% dry wt	2.15	2.17	2.40	2.99	1.92
		N mg per leaf	4.0	7.8	23.3	8.7	6.0
	Old leaves	% dry wt	0.94	1.01	1.03	1.21	1.12
		mg per leaf	2.9	5.8	8.5	6.6	8.3
		% withdrawn	27.5	25.6	63.5	24.1	?
P	New leaves	% dry wt	0.12	0.16	0.23	0.23	0.19
		P mg per leaf	0.2	0.6	2.3	0.9	0.6
	Old leaves	% dry wt	0.06	0.07	0.07	0.08	0.00
		mg per leaf	0.2	0.4	0.5	0.4	0.0
		% withdrawn	0.0	33.3	78.3	55.6	?
K	New leaves	% dry wt	1.24	1.24	1.22	1.03	0.93
		K mg per leaf	2.3	4.5	11.9	4.1	2.9
	Old leaves	% dry wt	0.57	0.55	0.49	0.43	0.53
		mg per leaf	1.8	3.2	4.0	2.4	3.9
		% withdrawn	21.7	28.9	66.4	41.5	?
Mg	New leaves	% dry wt	0.22	0.22	0.22	0.15	0.13
		Mg mg per leaf	0.4	0.8	2.1	0.6	0.4
	Old leaves	% dry wt	0.22	0.23	0.22	0.17	0.17
		mg per leaf	0.7	1.3	1.8	0.9	1.3
		Mg change	+	+	-	+	+
Ca	New leaves	% dry wt	0.72	0.75	0.48	0.34	0.56
		Ca mg per leaf	1.4	2.7	4.7	1.4	1.8
	Old leaves	% dry wt	1.43	1.76	1.62	1.59	1.80
		mg per leaf	4.4	10.11	13.3	8.7	13.4
		Ca change	+	+	+	+	+
New leaf dry matter content as % fresh wt			33.81	40.71	45.43	27.01	33.27
Old leaf dry matter content as % fresh wt			70.68	64.06	77.47	60.47	73.92

? indicates outlier

odorata, *Dipterocarpus oblongifolia*, *Shorea assamica* and *Hopea helferi* to grow optimally at 32–53% RLIs; Ashton and de Zoysa (1989) found *Shorea trapezifolia* to grow optimally in ‘partial sun’; and Zipperlen and Press (1996) found *S. leprosula* and *Drybalanops lanceolata* to grow optimally in ‘medium light’. This range of examples confirm what is rather obvious, that for non-pioneer species (species not known to colonize open ground), 100% RLI is too high for optimal growth.

Leaf production rates on leader shoots

Shoot extension is the result of new nodes (and internodes) added at the shoot apex. Since nodes are the positions where leaves arise, the leaf production rate can be used as a measure

of growth where leaves are produced one leaf per node, as in *A. mangium*, *E. zwageri* and *S. roxburghii*. In *D. costulata*, which bears six to eight leaves per node, the ‘leaf production rate’ is six to eight times the node production rate. Here we standardize at seven times to simplify calculation. For *C. iners*, where the unit of shoot extension is a flush consisting of closely-spaced scale leaves followed by foliage leaves, the average number of foliage leaves per flush is eight.

For all species, the minimum rate of leaf production was observed at 4%. The graphs are more or less convex in all species (Figure 4). In the case of *C. iners* and *D. costulata*, the rate of leaf production actually declined at RLIs above 25%. *Acacia mangium*, producing 1.2–1.7 leaves per week, outperformed all the other species at 25–100% RLI.

Other studies on tropical saplings that may be cited for comparison include that of Ng (1979) who monitored the rates of node (leaf) development in leader shoots in open situations for 11 tropical juvenile trees. For species that develop one leaf per node, he found the rates to be constant through time. He called this 'continuous' growth. The rates he obtained were 3.43–3.88 leaves per week in *Carica papaya* ('Solo' variety); 1.85–2.00 leaves per week in *Macaranga tanarius*; 0.58–0.78 leaves per week in *Dillenia grandifolia*; 0.45 leaves per week in *Dipterocarpus chartaceus*, 0.43 leaves per week in *Oroxylum indicum*; 0.25–0.35 leaves per week in *Shorea platyclados* and *Shorea ovalis*; 0.18 leaves per week in *Symingtonia populnea*. The highest rate of leaf production, at 3.43–3.88 per week in *C. papaya*, is possibly the highest leaf production rate ever recorded, and is remarkable considering the relatively large size of the papaya leaf and that each leaf axil is the site of an inflorescence and a fruit. For *A. mangium*, there is a record by Lim (1993) of about 0.5–1 leaves per week on an active growing shoot.

For two species with flushing growth, Ng found the rates of flushing to be constant through the year, at 0.10 flushes per week in *Harpullia confusa* and 0.11 flushes per week in *Dacryodes rostrata*. For the oil palm *Elaeis guineensis*, there has been much attention because each leaf axil is the site of an inflorescence and potentially a fruit bunch. Oil palm has been found to produce 0.81 leaves per week from germination until 21 months (Wormer 1958), while a 10-year-old oil palm had a leaf production rate of 0.42 leaves per week (Hartley 1967). Considering the huge size and biomass of the oil palm leaf, its habit of flowering at every axil, and its massive fruit bunch, this is a remarkably high rate of production.

Leaf production on branches relative to leaders

In *A. mangium*, the leaf production rate in branches was found to be slightly lower than in the leaders. In *S. roxburghii*, *C. iners* and *D. costulata*, the leaf production rates in branches were distinctly lower. The most obvious result of a lower leaf production rate in branches compared with leaders is to produce juvenile crowns that are taller than broad and this explains why juvenile

trees of these species have vertically elongated crowns. In *E. zwageri*, the branches produced leaves at a faster rate than the leaders, resulting in juvenile trees with short broad crowns.

Leaf lifespans

For all the species, leaf lifespan was longest at 4% RLI. We opted for straight lines as lines of best fit for the scatter diagram in Figure 5 and found that the R^2 values of all the lines exceeded 0.7, indicating good fits, and providing support for a simple model of photo-senescence. The model is that leaf life span is reduced by equal amounts for each doubling of light intensity. The steepest drop was in *S. roxburghii*, from about 550 days at 4% RLI to about 200 days at 100% RLI, each doubling of light intensity cutting about 70 days from its leaf lifespan. *Dyera costulata* was the most resistant, losing about 30 days for each doubling of light intensity.

The fastest-growing species, *A. mangium*, had the shortest leaf lifespan of all, at 124–371 days, giving it the highest leaf turnover rate. It lost about 40 days of leaf lifespan for each doubling of light intensity.

The leaf lifespan was longest for *C. iners*, which shed none of the monitored leaves in 644 days of observation, even under full sunlight.

Elsewhere, leaf lifespans have been found to vary from a few weeks in ephemerals, to as much as 25 years in *Araucaria*, a tropical conifer (Chabot & Hicks 1982). Coley (1983) and Williams *et al.* (1989) have found that in evergreen tropical forests, the leaf lifespan of pioneer species in high light environments is generally less than a year, and often as low as two months, while the leaf lifespan of understorey plants may be five years or more. In general, shade species have been found to have long leaf lifespans (King 1994, Lusk & Contretras 1999, Valladares *et al.* 2000).

Short leaf lifespans have been associated with fast rates of growth (Reich *et al.* 1992, Ackerly & Bazzaz 1995, Ryser & Urbas 2000, Navas *et al.* 2003). Ng (1992) found that short leaf lifespan was compensated by higher leaf production until 38% RLI but not beyond 38% RLI in *D. aromatica*. Ackerly and Bazzaz (1995) found self-shading to be an important factor in extending leaf lifespan.

Significance of photo-senescence in tropical phenology

Holtum (1931) had the idea that leaves have a fixed life span according to their species, and this would explain the occurrence of the periodic cycles of leaf renewal observed in a climate that has no seasons. However, Holtum could not explain why, when he monitored the same trees year after year, that successive cycles were never exactly of the same length of time. Although the present study is on juvenile trees, and juveniles do not undergo leaf renewal in a total periodic manner, it proves that leaves do indeed have a lifespan—but it is not a calendar lifespan. It is a service lifespan, affected by the intensity and duration of light experienced by the leaves. This provides a possible explanation for Holtum's observations. Cloudy days would have a weaker ageing effect and sunny days a stronger effect. No two calendar periods would ever experience exactly the same weather pattern; hence and no two leaf cycles will take exactly the same length of time.

The service lifespan model also provides a model to explain synchronization, including the exceptionally high synchronization event known as gregarious flowering. A period of cloudy weather would slow down senescence for all trees. If this is followed by a sequence of sunny days, such trees would be pushed over their limits all within a short period of time. The percentage of trees brought into synchrony in this way would depend on the particular combination of cloudy and sunny days triggering the event. A weak combination would trigger a weak degree of synchronization. A strong combination would trigger a strong degree of synchronization. A model of synchronization based on photo-senescence would match the observed behaviour better than other models for the humid tropics where daylength and water availability vary little from month to month.

Since leaf ageing is linked to new leaf production, and new leaf production is linked with flowering, it may be possible to test this model using artificial light to see if leaf renewal and flowering can be induced by forced photo-senescence of leaves. This could be a possibility in seed orchards, where trees are kept small.

Leaf dry matter content and internal recycling of nutrients

In *A. mangium* the leaf dry matter content was more or less the same in old and new leaves, but

this is exceptional (Table 3). In all the other species, the dry matter content in old leaves was 1.1 to 2.5 times that in new leaves (Tables 5, 7, 9, 11).

The leaf dry matter content was relatively unaffected by light in *C. iners* and *E. zwageri*. However, it was much affected by light in *A. mangium* and *S. roxburghii*, peaking at 25% RLI in both new and old leaves. In *D. costulata*, new leaves were relatively unaffected but old leaves peaked at 25% RLI.

In all species, the amount of NPK in old leaves was less than in new leaves, indicating that these nutrients are always withdrawn to some extent before leaf fall. Taking all five species together, the amount withdrawn was 7.7–77.4% of N, 14.3–80% of P and 19.7–97.3% of K.

The fate of Mg was variable. It was withdrawn in *A. mangium*, *C. iners* and *D. costulata* to the extent of 7–60.7%, but it was accumulated in *E. zwageri*. In *S. roxburghii*, the evidence was unclear, ranging from slight accumulation to slight withdrawal.

Ca was accumulated as the leaf aged in *C. iners*, *E. zwageri* and *S. roxburghii*. It fluctuated between slight accumulation and slight withdrawal in *A. mangium* and *D. costulata*.

Nutrient content in new leaves

In every species the leaf nutrient content varied with RLI. In *A. mangium*, peak NPK content occurred at about 25% RLI (Figure 6) but the growth rate reached its maximum at 100% RLI. A similar pattern was obtained in *S. roxburghii* (Figure 7) and to some extent in *E. zwageri*. In all cases the trends in nutrient content were independent of trends in growth rate. The conclusion of this study is that the leaf nutrient content does not reflect the rate of growth, and cannot be used to predict growth.

Rate of nutrient uptake

The nutrient content per leaf multiplied by the number of leaves produced on a shoot per week gives the rate of nutrient uptake in mg per shoot per week. For leader shoots the comparative data for N, P and K are given in Table 12 and illustrated in Figures 8 to 10. The values corresponding to peak growth rate (at 100% RLI for *A. mangium* and *S. roxburghii* and 25% RLI for the other three species) are indicated

in bold in Table 12. From this comparison the rate of nutrient uptake under conditions of peak growth was highest in *A. mangium* followed by *D. costulata*, *C. iners*, *S. roxburghii* and *E. zwageri* in descending order.

The most interesting comparison is between the two fastest growing species, *A. mangium* and *S. roxburghii*. *Acacia mangium*, growing four times faster than *S. roxburghii* at 100%RLI, took up 15 times as much N, 10 times as much P and 16 times as much K (Table 12). *Dyera costulata* and

C. iners both exceeded *S. roxburghii* in nutrient uptake but gave much poorer growth rates. *Eusideroxylon zwageri* was most nutrient-thrifty but also most slow-growing.

Acacia mangium was planted on a large scale in Peninsula Malaysia from about 1985 till 1995 for timber production, on the expectation that it would grow to 45 cm diameter in 15 years (Ng 1996). Growth was impressive for 8–10 years, after which it declined and the trees never reached the expected diameter. Our present

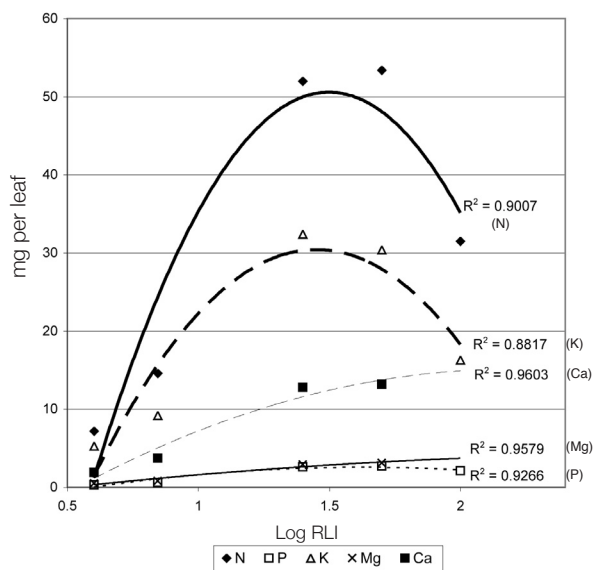


Figure 6 Nutrient content of new leaves of *Acacia mangium* in relation to relative light intensity

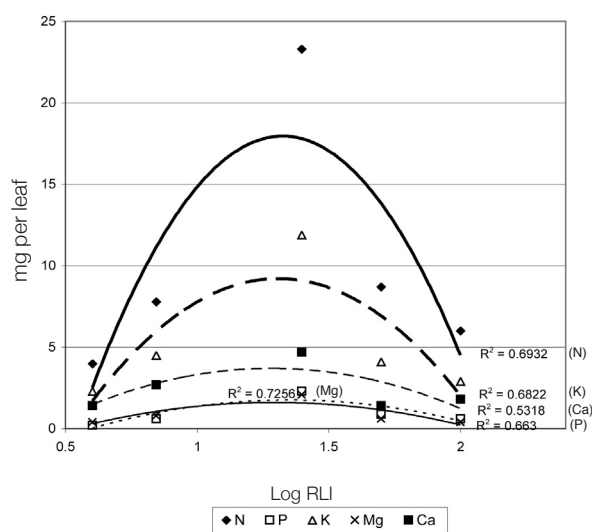


Figure 7 Nutrient content of new leaves of *Shorea roxburghii* in relation to relative light intensity

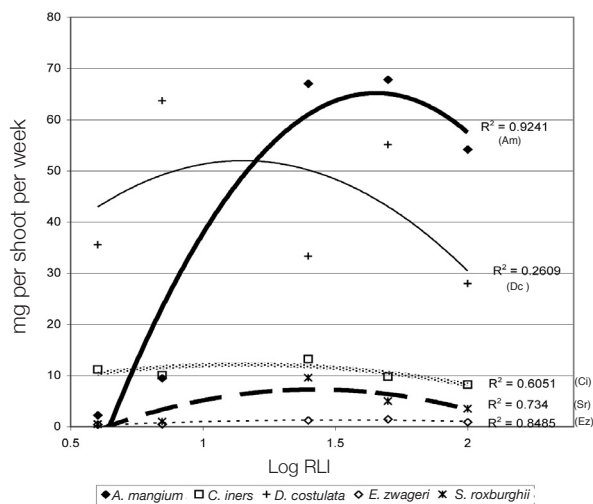


Figure 8 N uptake by leader shoots in relation to relative light intensity

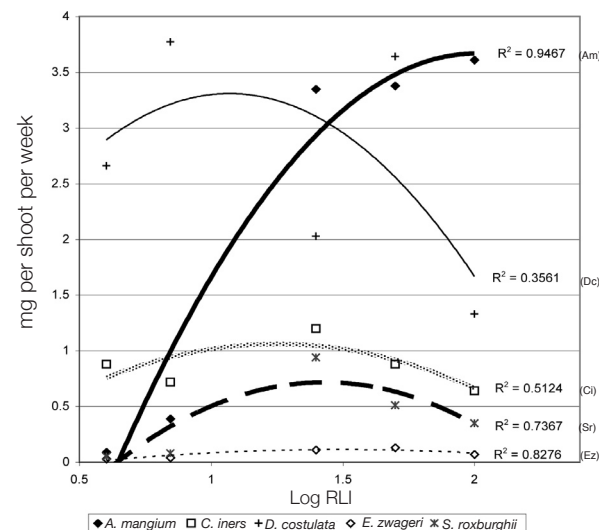


Figure 9 P uptake by leader shoots in relation to relative light intensity

Table 12 Leader shoot nutrient uptake per week

Nutrient	Species	RLI				
		4%	7%	25%	50%	100%
N	<i>Acacia mangium</i>	2.23	9.49	67.08	67.87	54.18
	<i>Cinnamomum iners</i>	11.2	10.08	13.20	9.76	8.24
	<i>Dyera costulata</i>	35.56	63.7	33.32	55.09	28.0
	<i>Eusideroxylon zwageri</i>	0.41	0.51	1.27	1.45	0.89
	<i>Shorea roxburghii</i>	0.52	1.01	9.55	4.96	3.54
P	<i>Acacia mangium</i>	0.09	0.39	3.35	3.38	3.61
	<i>Cinnamomum iners</i>	0.88	0.72	1.20	0.88	0.64
	<i>Dyera costulata</i>	2.66	3.77	2.03	3.64	1.33
	<i>Eusideroxylon zwageri</i>	0.03	0.04	0.11	0.13	0.07
	<i>Shorea roxburghii</i>	0.05	0.08	0.94	0.51	0.35
K	<i>Acacia mangium</i>	1.64	5.98	41.80	38.00	28.00
	<i>Cinnamomum iners</i>	9.92	8.4	9.20	7.36	4.96
	<i>Dyera costulata</i>	22.61	26.6	9.94	21.28	9.03
	<i>Eusideroxylon. zwageri</i>	0.40	0.46	1.05	0.83	0.70
	<i>Shorea roxburghii</i>	0.30	0.59	4.88	2.34	1.71

Values in boldface correspond with peak growth.

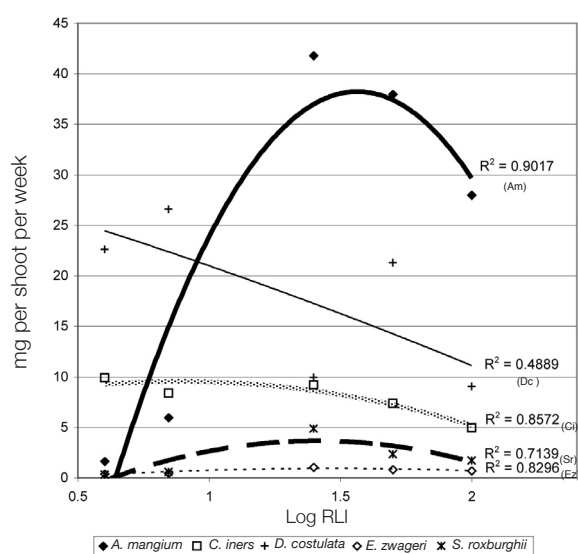


Figure 10 K uptake by leader shoots in relation to relative light intensity

results suggest the possibility of soil nutrient exhaustion. The other four species are known to grow into big trees of 60 cm diameter or more in natural forests. *Shorea roxburghii*, with its relatively high growth rate and low nutrient uptake, recommends itself for attention as a species for forest regeneration.

CONCLUSIONS

This is possibly the first attempt to develop a model of forest tree behaviour in the humid tropics, linking growth with light and nutrition across a range of contrasting species.

The test of a model is how well it explains or predicts reality. This model suggests a few things about reality that may have escaped notice before. One is that the distinction between light-demanding and shade-tolerant trees is not symmetrical. The drop from 100 to 50% represents only one halving of light, compared to the drop from 50 to 4%, which covers more than three halvings. The response of plants to a change from 4 to 8% may be as large as the response to a change from 50 to 100%. This comes out clearly in the effect of light on leaf lifespans.

In this study, except for differences in the soil in which the seedlings were initially raised, nutrient availability was the same for all the plants. Yet growth rates, nutrient content and nutrient uptake rates were remarkably different between species. This suggests that fertilization may boost the growth of some species but will probably do nothing for most others.

ACKNOWLEDGEMENTS

The site, shade house, machinery and labour for establishing the experiment was provided by Bandar Utama City Corp. The first author was supported by a cash award from Rotary Club (Kajang) and a partial scholarship from the Forest Research Institute Malaysia. This paper is based on her thesis submitted to Universiti Putra Malaysia for the degree of Master of Science.

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