Annals of Botany **97**: 245–255, 2006
doi:10.1093/aob/mcj023, available online at www.aob.oxfordjournals.org

Leaf Life Span Plasticity in Tropical Seedlings Grown under Contrasting Light Regimes

GREGOIRE VINCENT*

Institut de Recherche pour le Développement (IRD) UMR AMAP, TA40/PS2, 34398 Montpellier Cedex 5, France

Received: 7 July 2005 Returned for revision: 15 September 2005 Accepted: 12 October 2005 Published electronically: 18 November 2005

- *Background and Aims* The phenotypic plasticity of leaf life span in response to low resource conditions has a potentially large impact on the plant carbon budget, notably in evergreen species not subject to seasonal leaf shedding, but has rarely been well documented. This study evaluates the plasticity of leaf longevity, in terms of its quantitative importance to the plant carbon balance under limiting light.
- *Methods* Seedlings of four tropical tree species with contrasting light requirements (*Alstonia scholaris*, *Hevea brasiliensis*, *Durio zibethinus* and *Lansium domesticum*) were grown under three light regimes (full sunlight, 45 % sunlight and 12 % sunlight). Their leaf dynamics were monitored over 18 months.
- *Results* All species showed a considerable level of plasticity with regard to leaf life span: over the range of light levels explored, the ratio of the range to the mean value of life span varied from 29 %, for the least plastic species, to 84 %, for the most. The common trend was for leaf life span to increase with decreasing light intensity. The plasticity apparent in leaf life span was similar in magnitude to the plasticity observed in specific leaf area and photosynthetic rate, implying that it has a significant impact on carbon gain efficiency when plants acclimate to different light regimes. In all species, median survival time was negatively correlated with leaf photosynthetic capacity (or its proxy, the nitrogen content per unit area) and leaf emergence rate.
- *Conclusions* Longer leaf life spans under low light are likely to be a consequence of slower ageing as a result of a slower photosynthetic metabolism.

Key words: *Alstonia scholaris*, carbon balance, *Durio zibethinus*, *Hevea brasiliensis*, *Lansium domesticum*, leaf life span, light, plasticity.

INTRODUCTION

The ecological significance of leaf life span in relation to plant distribution and growth performance has been reviewed by Chabot and Hicks (1982) and Körner (1991). A number of hypotheses have been put forward to explain observed patterns of leaf life span; on the basis of strong current evidence, the carbon balance hypothesis is regarded as being the most important: leaf life span has a direct multiplying effect on leaf photosynthetic rate, which permits species with inherently low or environmentally limited physiological capacities to obtain higher carbon yields from each individual leaf (Chabot and Hicks, 1982; Kikuzawa, 1995; Givnish, 2002; Hikosaka, 2005). In addition, long-lived leaves use the nutrients invested in them more efficiently than do shorter-lived leaves (there is a longer amortization period), though remobilization of nutrients within a plant may reduce this nutrient-use-efficiency advantage (Chabot and Hicks, 1982; Escudero *et al.*, 1992; Escudero and Mediavilla, 2003).

A recently published worldwide analysis of leaf economics, which compared 2548 species, stresses the commonality of the trends governing correlations between key features of leaf economics (Wright *et al.*, 2004). Strikingly, climatic variables only explain a small portion of the overall variation and the same economic principles apply across biomes. This meta-analysis notably pinpoints the strong trade-off that exists between leaf photosynthetic capacity and leaf life span.

Negative relationships between photosynthetic rates of young leaves and leaf life span have been reported within natural assemblages of species from various functional groups and biomes—deciduous forest herbs, arctic, desert and Mediterranean-climate plant species (Chabot and Hicks, 1982), neotropical trees (Reich *et al.*, 1991) and tropical saplings (King, 1994).

Relatively less attention appears to have been paid, however, to the phenotypic plasticity of leaf life span and its relationship with photosynthetic rate. A number of recent observations point towards a general pattern which occurs in response to low resource conditions: shortages of nutrients, light or water appear to result both in a reduction in leaf-level photosynthetic potential and an increase in leaf life span. Cordell *et al.* (2001) found a significant negative correlation between leaf life span and photosynthetic capacity in *Metrosideros polymorpha*; in that particular case, variation in these leaf traits was interpreted as a reflection of different nutrient availabilities along a soil chronosequence. Another example of co-variation of both the above traits was given by Gratani *et al.* (2000), where a decrease in leaf life span and a correlative increase in photosynthetic activity were observed in *Quercus ilex* in Rome. This was interpreted as an adaptive strategy of the species in response to pollution. Casper *et al.* (2001) also observed an increase in leaf life span and a concomitant reduction in photosynthetic rate in a herbaceous desert perennial in response to drought. Other, more casual, observations seem to support the idea that such co-variation between leaf photosynthetic capacity and leaf life span may be of widespread

---

* For correspondence. E-mail: G.Vincent@cgiar.org

occurrence. For example, leaf life span was found to decrease with height (and with the associated increase in PPFD) within the canopy of several shade-tolerant tree species in a Malaysian rainforest stand (Osada *et al*., 2001). Those authors also reported that the leaf production rate in the upper part of the crown was faster than that in the lower part, and cited other studies that point to a higher turnover rate in sun leaves than in shade leaves (Schoettle *et al*., 1991; Lowman, 1992).

Taken together the reports cited above suggest that a reduced metabolic activity under limiting resource availability—and notably light—may delay leaf senescence and consequently extend leaf life span.

Leaf life span and leaf carbon budget

The net carbon gain per unit leaf mass over a leaf's lifetime can be expressed as the product of three terms: the leaf life span; the time-averaged net photosynthetic rate per unit area; and the specific leaf area (SLA).

Maximum photosynthetic rate under non-limiting light conditions ($P_{\max}$), an important determinant of the photosynthetic capacity and hence of the time-averaged net photosynthesis rate, and SLA, have been repeatedly shown to adjust to the prevailing light regime in which a plant is growing (Bazzaz and Carlson, 1982; Walters and Field, 1987; Popma and Bongers, 1991; Straus-Debenedetti and Bazzaz, 1991; Chazdon and Kaufmann, 1993; Lei and Lechowicz, 1997; Kursar and Coley, 1999; Evans and Poorter, 2001; Vincent, 2001; King, 2003). Leaf photosynthetic capacity has also been reported to decline with leaf age (Kikuzawa, 1995; Kitajima *et al*., 1997; Ackerly, 1999; Kitajima *et al*., 2002; Escudero and Mediavilla, 2003; Senevirathna *et al*., 2003). However, despite its multiplicative effect on carbon gain, the potential effect of light regime on leaf life span and its implication in terms of the plant carbon budget seems to have received relatively less scrutiny.

If reduced photosynthetic/metabolic activity in leaves delays senescence, then experimental manipulation of photosynthetic activity by artificial shading should reveal a parallel adaptation of leaf life span. Such acclimation is more likely to be observed in the absence of strong seasonality, which may impose a limit upon a leaf's life span independent of its physiological age.

The primary objective of the present experiment was therefore to test whether the above hypothesis held true for a set of tropical tree species with contrasting light requirements grown in contrasting light environments under a tropical moist climate.

The second objective of this experiment was to evaluate the plasticity of leaf longevity, in terms of its quantitative importance to the carbon balance of the plant, relative to other important carbon-acquisition parameters, at the level of the leaf, which are also known to be affected by the light regime to which the leaves are exposed.

MATERIALS AND METHODS

The four species studied occur naturally in tropical moist forest. All four species are of economic importance and are common in rubber agroforests in Indonesia. Rubber agroforests are extensively managed mixed rubber plantations in which many forest species spontaneously regenerate after the initial slash-and-burn episode (Gouyon *et al*., 1993).

Species descriptions

Lansium domesticum Corr. Serr. (Meliaceae) is a small to medium-sized tree. An understorey specialist, under natural conditions the species completes its entire life cycle in the understorey and is adapted to shade. Its seedlings do not, physiologically, adapt readily to very open conditions (Vincent, 2001) and are sensitive to water stress (author's personal observation).

Durio zibethinus Murray (Bombacaceae) is a medium-sized to large tree, native to south-east Asia (Ashton, 1988). Under natural conditions, its early development occurs in the shade, while the adult tree reaches the top canopy.

Hevea brasiliensis (A. Juss.) Muell.-Arg. (Euphorbiaceae) is a large tree native to the forests of Amazonia, but cultivated widely throughout the humid tropics as a source of latex for commercial rubber production The species can be classified as a 'non-pioneer light demander' species, *sensu* Hawthorne (1995), as it can readily germinate and establish itself in the shade; however, the growth of its seedlings is significantly limited by light levels below approx. 50 % sunlight (pers. obs.). In the present experiment, seedling stocks were used. Both the branches and the main axis of rubber exhibit rhythmic growth. Rhythmic growth is endogenously controlled, although its rate may be influenced exogenously by light level or drought (Hallé, 1968).

Alstonia scholaris (L.) R. Br. (Apocynaceae) is a medium-sized to large tree, which can grow up to 35 m in height. *Alstonia* species produce a latex which contains alkaloids and can be tapped from the bark; however, they are principally grown for timber production (commercial name 'Pulai'). *Alstonia* species grow in both primary and secondary lowland evergreen to deciduous rain forest (Ashton, 1988). Natural regeneration of *Alstonia* spp. occurs preferentially in open areas at forest edges and in secondary forest, and is considered to be a light-demanding species (Ashton, 1988; Laumonier, 1996). Its architecture is modular, conforming to PREVOST's model (Mueller 1985), with a sympodial trunk and tiers of sub-horizontal branches.

Branch modules originate in a restricted subapical region of their parent module. The apical meristem in each module gives rise to two to four leaf whorls and one whorl of four scale leaves before parenchymatization occurs. Under favourable growth conditions, all four subterminal axillary buds grow out; but, usually only the one or two lower modules will, in turn, produce renewal modules. Through repetition of this pattern, horizontal sympodial branch complexes are formed ('plagiotropy by substitution'; Hallé *et al*., 1978).

Trunk modules are vertically oriented. After a rest period of a few months, a renewal axis originates from an axillary bud just below the uppermost branch tier. Trunk modules are longer than branch modules: up to ten leaf whorls are developed before parenchymatization occurs. Normally, only the last whorl (which is made up of scalar leaves) will give rise to a branch tier; this tier is usually composed of four branch complexes.

Experimental design and implementation

The experiment was located at the experimental site of the Biological Management of Soil Fertility Project in Lampung, Sumatra (4°31′S, 104°55′E). Long-term mean annual rainfall is approx. 2500 mm, with a moderate dry season occurring during the period June to September (Holmes, 1998). Soils in the area are classified as Ultisols following the USDA soil classification (van der Heide *et al.*, 1992). They are typically acidic, with low cation exchange capacities, and low levels of exchangeable K.

The experiment was arranged as a randomized complete block design with two blocks: each block contained three light-level treatments (full sunlight, 45 % sunlight and 12 % sunlight). Within each block, a split-plot design was used, with light environment as the main plot, and tree species as sub-plots. Thus, each block contained each of the 12 possible light–species combinations. Potted seedlings approx. 30–60 cm in height, between 3 and 6 months old, were obtained from local farmers' nurseries and were planted at a spacing of 1 × 1·5 m in April 1999. Neutral shading nets, which were positioned 2·5 m above the ground (and which were allowed to hang down at the sides to a height of 1 m above the ground), were used to obtain the two shade levels: 45 % sunlight and 12 % sunlight. Actual differences in the shading levels achieved between treatments were checked in November 1999 by means of a set of QSO-SUN Apogée quantum sensors positioned across the experimental plot. The ratio of daily integrated photosynthetically active radiation over a 15-d measurement period, averaged over the two blocks, was found to be 56 % of the unshaded subplot for the medium shading intensity and 92 % for the highest shading intensity, i.e. in reasonable agreement with the targeted shading intensities.

After 15 months of growth (in the case of *Hevea* and *Alstonia*) or after 21 months of growth (in the case of *Durio* and *Lansium*), five or six individuals from each species × treatment × block combination were randomly selected and harvested in order to estimate total biomass accumulation and organ biomass fractions. Plants were oven dried (at 70 °C for 72 h) and leaves, stems, coarse roots and fine roots were weighed separately. In the case of *Hevea* and *Alstonia*, total root biomass could not be determined at the final harvest, due to the large size of these plants, and so was assessed by taking core samples. Only overall above-ground biomass accumulation and organ fractions are reported here.

In addition, specific leaf area was estimated for each individual plant, by weighing punched-out samples of leaf laminae (between 300 and 500 cm^2 per plant). Leaf nitrogen content was also assessed (via the Kjeldahl method) using one composite sample (*Alstonia* and *Hevea*) or three composite samples (*Lansium* and *Durio*) per species × treatment × block combination. The leaves sampled for nitrogen content were drawn randomly and independently from those used for specific leaf mass estimates. More samples were taken for *Lansium* and *Durio* than for *Alstonia* and *Hevea* as equipment failure meant that photosynthetic rates could not be measured for the former species. Leaf nitrogen per unit area is used as a proxy for photosynthetic capacity for those species. Nitrogen content per unit leaf area is a useful proxy for photosynthetic capacity (Field and Mooney, 1986; Evans, 1989; Vincent, 2001), especially when used for intraspecific plant comparisons, as species may differ significantly in terms of the leaf nitrogen fraction allocated to the photosynthetic system (Vincent, 2001).

Nitrogen content per unit leaf area was calculated as the product of specific leaf mass and nitrogen content per unit mass. The standard error of leaf nitrogen content per unit area was estimated following Goodman (1960), by combining least square mean and associated standard error ANOVA estimates of specific leaf mass and nitrogen content per unit mass for each species.

During the monitoring period, plots were regularly clean-weeded to minimize competition; but, no fertilizer was applied to correct the soil's low chemical fertility. The main stems of the *Alstonia* and *Hevea* seedlings reached the shading net before the end of the monitoring period. Therefore, plants greater than 1·5 m in height were systematically pruned in February 2000 to a height of 1·5 m. In June 2000, the plants spared for the leaf demography census were pruned a second time to a height of 1·5 m. Rainfall on the site was recorded daily throughout the duration of the experiment.

Leaf demography

From May 1999 to November 2000, three seedlings per species per treatment per block were monitored every 2 weeks. Leaf demography analyses were conducted separately for each species.

Leaf survival. Leaf emergence rate (LER), and the subsequent senescence of the leaves produced, was monitored on the main stem of all seedlings and on one first-order branch once branching had occurred. Leaves present at planting were not included in the leaf survival analysis as they had developed in a different light environment and may not have acclimated fully to their new light environment (Kamaluddin, 1993). In the case of the sympodial growth of the horizontal axes of *Alstonia*, and when more than one module originated from the previously formed module, a single module was arbitrarily selected from the lowermost modules; leaf production on this module was monitored. *Lansium*'s leaves are compound; therefore, leaflets were monitored individually, because non-synchronous leaflet abscission on the same leaf was common. Hereafter, the term 'leaves' refers to leaflets in the case of *Lansium*.

Leaf 'birth date' and 'death date' were taken to be the date of the first record of a fully expanded leaf and the date of the first record of a missing leaf, respectively. The death dates of those leaves still alive at the end of the monitoring period are unknown; such incomplete observations are said to be 'censored' (Lee, 1992). Similarly, leaves that died as a result of herbivory (<1·5 % of the total leaf population monitored), or that died because their bearing axis was pruned, were also considered to be censored. Data were processed using the Systat v 9·0 survival-analysis module. Non-parametric methods were used (Kaplan–Meier estimator and Tarone and Ware tests) to make treatment and axis-type comparisons and to analyse block effects.

Leaf emergence rate. The LER was defined as the number of terminal leaves produced per unit time per terminal meristem. LERs were computed for each monitoring date and expressed on a standard basis (per 14-d period). Hence, for each date × species × shade-level × block × axis-type combination, LER was computed as the average of three observations. All horizontal axes of *Alstonia* considered for the LER belonged to the first horizontal set of branches developed by all plants in all treatments. In the special case of *Alstonia* main stems, in which prolonged rest periods alternate with periods of rapid shoot elongation, only the active period of growth of the first renewal module of the main stem was considered when calculating the LER of the main stem. The period over which the first renewal axis developed varied among individual trees, in terms of both its start date and its duration.

Pearson correlation coefficients of LER (and leaf mortality rates) time series among the different shade treatments were computed to test for the existence of an overall pattern in leaf dynamics which may override or at least blur the expected pattern in leaf longevity.

Except in the case of *Alstonia* main stems, data were analysed using the Friedman ANOVA procedure in Systat v 9·0, to test for treatment and blocking effect. In the former case, the Kruskal–Wallis test was used to compare treatments, because the periods of axis growth in individual plants did not match. Statistical analyses of data from *Hevea* and from the horizontal branches of *Alstonia* were conducted both for the entire period of monitoring (39 intervals of 2 weeks) and for the first 20 intervals before the main shoot was pruned. Results for the two periods were similar; therefore, the full data sets (39 intervals) are presented and discussed here. For the other two species, the whole growing period was also used (39 intervals). Data are shown per species per treatment, and also per axis type when differences in axis type proved statistically significant.

Leaf photosynthetic capacity

In addition to nitrogen content per unit leaf area, which was assessed for all species in all treatments, gas exchange measurements were conducted on *Alstonia* and *Hevea* seedlings. Light saturated net photosynthetic assimilation rate (i.e. the photosynthetic capacity, $A_{\max}$) and dark respiration rate (R_{d}) were measured for these two species at the end of the experiment, on a limited number of young fully expanded leaves per treatment, using a CIRAS 1 portable infrared gas analyser (PPSystem, Hitchin, Herts., UK). An external lamp unit fitted to the leaf chamber provided white light with a photosynthetic photon flux density (PPFD) of approx. 1800 μmol m^{-2} s^{-1}. The maximum assimilation rate was measured in the morning at a saturating light level (which varied according to shading level). Relative humidity was set so that the air exiting the leaf chamber would be close to the ambient air value (between 70 % and 80 %). CO_2 concentrations were adjusted so that the CO_2 concentration of the air exiting the chamber was 340 ± 10 ppm. The maximum assimilation rate was considered to have been reached when the assimilation rate did not increase any further after 5 min. No distinction was made between leaves borne on horizontal and vertical axes.

TABLE 1. *Above-ground biomass per plant, total leaf area per plant and above-ground leaf area ratios of tropical seedlings grown under contrasting light levels*

	Full sunlight	45 % sunlight	12 % sunlight	*P*
(A) Above-ground dry weight biomass (g)				
Lansium	–	26·7 (2·3)	14·0 (2·6)	<0·001
Durio	–	91·8 (11·7)	66·6 (11·4)	n.s.
Hevea	447 (43)	519 (41)	194 (45)	<0·001
Alstonia	881 (125)	1064 (125)	300 (114)	<0·001
(B) Total leaf area (m^2 per plant)				
Lansium	–	0·18 (0·02)	0·12 (0·02)	n.s.
Durio	–	0·41 (0·07)	0·42 (0·07)	n.s.
Hevea	1·47 (0·23)	2·07 (0·22)	1·29 (0·24)	n.s.
Alstonia	2·51 (0·48)	3·24 (0·48)	2·03 (0·44)	n.s.
(C) Above-ground leaf area ratio (cm^2 of leaf area per gram of above-ground dry weight biomass)				
Lansium	–	79·4 (4·9)	104·1 (5·8)	<0·01
Durio	–	37·3 (1·5)	44·6 (1·3)	<0·001
Hevea	32·2 (3·0)	40·3 (2·8)	61·9 (3·1)	<0·001
Alstonia	28·2 (3·5)	32·1 (3·5)	77·8 (3·2)	<0·001

Data presented are ANOVA least square means (standard error in parentheses); at least ten plants were sampled per treatment per species.

To compare the level of plasticity of the various morphological and physiological parameters monitored, the relative range of variation of the parameter, later referred to as the degree of plasticity, was used. For any parameter, it is simply defined as the range of observed values (over the entire range of light conditions explored) divided by the mean value over the same range.

Note that the limited number of light environments explored in the present experiment does not adequately sample the entire range of suitable conditions for the different species. As a consequence, any species ranking in terms of their plasticity for a particular parameter should be taken as conditional to the experimental design used here and may not reflect the overall species plasticity.

RESULTS

Overall growth

Plant mortality was low in all treatments, except under full sunlight, in that treatment mortality reached 100 % in *Lansium* seedlings and 91 % in *Durio* seedlings. In the latter species, mortality rates were low initially, but increased with time. Both species clearly appeared to be intolerant of full sunlight at the seedling stage. Therefore, the incomplete data for *Lansium* and *Durio* grown under full sunlight are not presented here. The lightest shading (45 % sunlight) allowed maximum above-ground biomass accumulation for all species (Table 1, A). Plants grown with 45 % sunlight also tended to have the highest leaf area per plant though this was not statistically significant (Table 1, B). In all

TABLE 2. *Correlations among different shade treatments (three light levels), in terms of leaf emergence rate (A) and leaf mortality rate (B) in four tropical tree species*

	LER full sunlight		LER 45 % light			
Variable	*Hevea*	*Alstonia* (horizontal axes)	*Lansium*	*Durio*	*Hevea*	*Alstonia* (horizontal axes)
(A) Leaf emergence rate (LER): correlation coefficients						
LER 45 % light	0·52**	0·80**	–	–	–	–
LER 12 % light	0·36*	0·72**	0·81**	0·76**	0·54**	0·64**
(B) Leaf mortality rate (LMR): correlation coefficients						
LMR 45 % light	0·48**	0·43**	–	–	–	–
LMR 12 % light	0·42**	0·18	0·77**	0·61**	0·83**	0·12

Each Pearson correlation coefficient calculated from 39 pairs of observations. Significance symbols: **$P < 0·01$; *$P < 0·05$.

TABLE 3. *Mean LERs (number of leaves produced per terminal meristem per period of 14 d) of seedlings of four tropical tree species grown under different shading intensities (standard errors are given in parentheses)*

	Full sunlight[‡]	45 % sunlight	12 % sunlight	*P* value (Friedman ANOVA)	Plasticity (%)
Lansium	–	1·57 (1·53)	1·09 (1·12)	<0·02	36
Durio	–	0·85 (0·74)	0·32 (0·38)	<0·001	97
Hevea	4·17 (2·65)	5·68 (4·03)	3·29 (3·19)	<0·001	55
Alstonia – branch*	2·38 (1·54)	2·24 (1·54)	2·24 (1·40)	<0·59	6
Alstonia – trunk[†]	13·02 (1·26)	10·64 (1·12)	9·38 (1·40)	<0·245[§]	33

Note: Plasticity is defined as the range of variation of LER observed across light treatments relative to the mean LER over all light treatments.
* First tier of horizontal branches.
[†] First renewal axis of main shoot, before any pruning occurred (dates of growth periods differ for different plants).
[‡] No data presented for *Lansium* and *Durio*, due to high mortality.
[§] Kruskal–Wallis test.

species, above-ground leaf area ratio (leaf area per unit weight above-ground biomass) increased as shading increased (Table 1, C).

Leaf dynamics

Except in the case of *Alstonia*, data on leaf dynamics on the main stem and first-order branches were pooled for all species, as no difference was detected between the main axis and branches in terms of either the LER or leaf life span.

No correlation between rainfall and LER was found for any species (data not shown). However, for all species, and for all treatment pair combinations, the LER in one treatment was significantly correlated with the LER in the other (Table 2A); for three out of four species, leaf mortality rates were also correlated in all treatment pairs (Table 2B). When data from the various treatments were pooled to compute the mean leaf mortality rates per species, a significant negative rank correlation was found for three out of four species between rainfall and mortality rates per period (data not shown). Thus temporal variation of the climatic environment (probably in relation to the water regime) likely affected overall leaf dynamics in the present study.

The mean LER over the entire monitoring period was significantly affected by shading intensity in *Lansium*, *Durio* and *Hevea* seedlings (Table 3), in which the maximum LER was achieved under 55 % shade, and the minimum under 88 % shade. The difference in LER between the two light environments was 3-fold for *Durio*, which was the most sensitive species in this respect.

TABLE 4. *Number of leaves per whorl (ANOVA least square means estimates, standard error in parentheses) in* Alstonia *seedlings, and number of leaves per cluster in* Hevea *seedlings, as affected by shading intensity*

Fraction of sunlight	*Hevea:* main shoot*	*Alstonia*: main shoot (first renewal axis)	*Alstonia*: horizontal branch (first horizontal tier)
100 %	14·1 (0·4)	6·2 (0·2)	4·5 (0·1)
45 %	15·9 (0·4)	5·3 (0·2)	4·5 (0·1)
12 %	12·0 (0·5)	5·0 (0·2)	4·0 (0·1)
P-value	<0·001	<0·001	<0·001

* Rank of leaf cluster on main axis is used as a covariate in the case of rubber, to control for the observed increase in the number of leaves with rank of growth unit on stem. Only growth units produced on the main axis, during the first 8 months of growth (prior to pruning) are considered here.

In *Alstonia*, the LER was much higher on the main shoot (single module) than on the horizontal branch (consisting of a series of modules); but growth was restricted to a few months per main shoot axis. The average number of leaves per whorl was also higher on the main shoot than on the branch. Although the effect of shading was not statistically significant, the mean LER of *Alstonia* appeared to reach a maximum under full sunlight and to decrease with increasing shading intensity. For both axis types, a weak (though

TABLE 5. *Median leaf life span (in days) of seedlings of four tropical tree species grown under three shading intensities*

	No. of observations					
Species/axis type	Uncensored	Censored	Full sunlight*	45 % sunlight	12 % sunlight	Plasticity (%)
Lansium	134	347	–	266	416	44
Durio	149	175	–	215	>413 (63 %)	>66
Hevea	835	1511	227	230	300	29
Alstonia – all axes	639	1254	199	242	446	84
Alstonia – trunk	173	720	135	>255 (52 %)	321	78
Alstonia – branches	466	534	200	228	>455 (53 %)	>87

Treatment effects were highly significant for all species and axis types for *Alstonia* species (Tarone–Ware log rank test).

Note: In cases where more than half of the leaves had survived at the end of the experiment, the median life span could not be estimated. A lower bound estimate of the leaf median survival time is given instead (denoted by '>xxx') and the final observed survival percentage added in parentheses.

'Plasticity' is defined as the range of variation in the median survival time across light treatments relative to the mean value over all light treatments.

* No data presented for *Lansium* and *Durio*, due to high mortality.

highly statistically significant) negative association was found between leaf number per whorl and shade level (Table 4), indicating that the production of individual meristems was also affected by shading intensity in *Alstonia*. In *Hevea*, the increased LER observed under moderate shading resulted from the compound effect of a faster growth unit emergence rate (data not shown) and a greater number of leaves produced per cluster (Table 4).

Leaf survival analysis

Shading intensity affected the median leaf survival time of all species. The general trend observed was an increase in leaf life span with increasing shade (Table 5 and Fig. 1). In *Alstonia,* leaves produced by the faster elongating main shoot had life spans that were significantly shorter than those of leaves produced by the branches. Of the four species studied, the maximum level of plasticity in leaf life span was found in the *Alstonia* seedlings (Table 5).

Specific leaf area, leaf nitrogen content and leaf photosynthetic capacity

In all four species, the following general trends were found with increasing shade: an increase in specific leaf area (Table 6); an increase in leaf nitrogen per unit mass—except for *Durio*—(Table 7); a decrease in leaf nitrogen per unit area (Fig. 2); and decreases in photosynthetic capacity and dark respiration (*Hevea* and *Alstonia*, Fig. 3).

DISCUSSION

All four species studied exhibited a high degree of plasticity in terms of leaf life span; the degree of plasticity observed (expressed as the ratio of range to mean value) ranged from 29 % to 84 % in median leaf life span over the range of light levels explored. The common trend shared by all species was increased leaf longevity under low light, which was paralleled by a decrease in leaf photosynthetic (or its proxy leaf nitrogen content per area) as hypothesized. This pattern was obvious despite the fact that temporal variation of the climatic environment tended to synchronize overall leaf dynamics (Table 2).

Leaf life span refers to the period lasting from leaf emergence and subsequent leaf expansion to leaf shedding (leaf initiation and early development before emergence are, arbitrarily, not considered as part of leaf life span). Leaf shedding is preceded by leaf senescence, the final stage of leaf development, which marks the transition from net carbon and nitrogen assimilation to a period of catabolism, followed by nutrient diversion to the developing sinks. Leaf senescence requires *de novo* gene expression and protein synthesis, and is controlled in a highly co-ordinated manner (Nooden *et al*., 1997; Weaver and Amasino, 2001; Lim *et al*., 2003; Yoshida, 2003). In the botanical literature, however, confusion seems to exist with regard to leaf ageing (i.e. the increase in leaf age and the associated changes in leaf physiology) and leaf senescence (the ultimate developmental phase). For instance, it has been suggested (Chabot and Hicks, 1982; Ono *et al*., 2001) that the onset of senescence coincides with a decrease in $P_{\max}$ (photosynthetic rate under saturating PPFD) and that the 'removal of nitrogen and other materials seems [to be] responsible for the decline in photosynthetic capacity' (Chabot and Hicks, 1982). However, recent reports contradict this statement. For example Kitajima *et al*. (2002) report constant leaf nitrogen content per unit leaf mass over the entire life span of the leaves of the tropical tree *Cecropia longipes,* despite a steady decrease in $P_{\max}$ with leaf age. Similarly Escudero and Mediavilla (2003) showed that leaf ageing had significant negative effects on photosynthetic rates per unit leaf area but found no evidence of N reallocation within the canopy during most of the leaf lifetime of the nine woody evergreen Mediterranean species examined.

Senescence, defined as an active degenerative process, is known to respond to a wide range of external and internal signals (Nooden *et al*., 1997; Biswal and Biswal, 1999), possibly in an age-related way (Weaver and Amasino, 2001). The interplay between light and senescence, with which this paper is concerned, appears to be complex and to depend on whether light restriction affects the whole plant or only parts of the plant.

A first set of observations made on the *Arabidopsis thaliana* model plant indicates that (whole-plant) reduced photosynthetic activity delays the induction of leaf senescence. This was the conclusion of a review of experiments

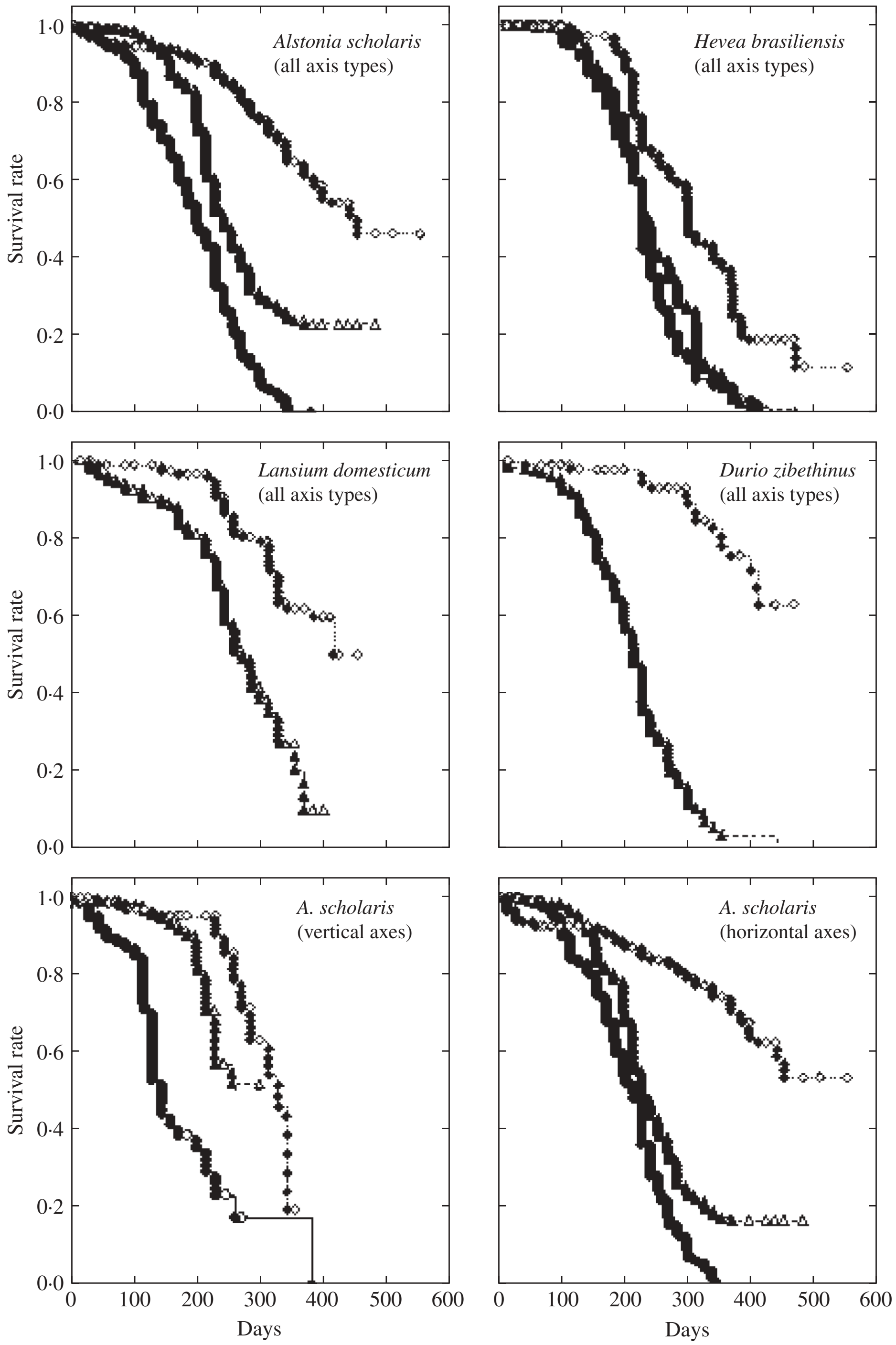

FIG. 1. Survival functions of leaves of tropical seedlings grown under three light levels; no data is presented for *Lansium* and *Durio* in full light, due to high levels of mortality. Symbols: circle + continuous line, 100 % sunlight; triangle + dashed line, 45 % sunlight; diamond + dotted line, 12 % sunlight; cross, censored observation.

conducted using arabidopsis delayed-leaf-senescence mutant oresara4 (Yoshida, 2003). Similarly, after manipulating the whole-plant light environment, Nooden *et al*. (1996) concluded that light dosage rather than photoperiod plays a role in promoting/delaying senescence. Weaver and Amasino (2001) showed that the leaves of arabidopsis plants placed temporarily in the dark showed delayed senescence. The mechanisms involved in this process of retarded ageing under low light are as yet unclear, due to the complex signalling pathways that appear to be involved in senescence induction. Reduced metabolic rate in chloroplasts in particular could lead to less oxidative stress, which might be a crucial factor in senescence in plants (Munne-Bosch and Alegre, 2002).

TABLE 6. *Specific leaf area (cm^2 g^{-1}) as affected by shading level (one-way ANOVA least square means, standard error in parentheses; at least ten plants sampled per treatment per species)*

	Full sunlight*	45 % sunlight	12 % sunlight	Plasticity (%)	*P*
Lansium	–	133 (14)	197 (16)	39	<0·01
Durio	–	98 (2)	115 (2)	16	<0·001
Hevea	140 (5)	171 (5)	229 (7)	49	<0·01
Alstonia	90 (6)	112 (6)	224 (6)	94	<0·001

Note: 'Plasticity' is defined as the range of variation in the SLA across light treatments relative to the mean over all light treatments.

* No data presented for *Lansium* and *Durio*, due to high mortality.

TABLE 7. *Least square mean values (standard error in parenthesis) of leaf nitrogen content per unit mass (%) of seedlings grown under different light intensities*

	Full sunlight*	45 % sunlight	12 % sunlight
Treatment mean (significance test $P < 0·014$)	1·59 (0·25)	1·75 (0·09)	2·11 (0·09)
Lansium	–	1·43 (0·13)	1·72 (0·13)
Durio	–	1·23 (0·13)	1·11 (0·13)
Hevea	2·62 (0·21)	2·71 (0·21)	3·21 (0·21)
Alstonia	1·30 (0·21)	1·62 (0·21)	2·40 (0·21)

Overall *F*-test of two-way ANOVA highly significant ($P < 0·001$), species × treatment interaction not significant ($P = 0·09$).

* No data presented for *Lansium* and *Durio*, due to high mortality.

Accelerated physiological ageing under high light is also consistent with a recent report of an accelerated decline in photosynthetic rate with leaf age in more exposed faster-growing shoots than in leaves borne on slower-growing, less-exposed shoots (Kitajima *et al*., 2002). Similarly Pearcy and Sims (1994) report that the shade leaves of *Allocasia macrorrhiza* live more than twice as long as sun leaves, and that the latter sustain a higher photosynthetic capacity than shade leaves only for about half their lifetime.

On the other hand, Weaver and Amasino (2001) showed that senescence was hastened in the leaves of arabidopsis when they were deprived of light individually, but that this was not the case when the whole plant was deprived of light, so demonstrating that the senescence of an individual leaf is controlled by the light status of the rest of the plant. Experiments to determine the effect of selective shading on the branches of young trees also indicate that the fate of a branch and, notably, whether it is shed or not, depends more on shading-induced asymmetric competition among branches than on the level of shading itself (Henriksson, 2001; Sprugel, 2002).

Self-shading has been argued to be an important determinant of leaf life span in the rapidly growing erect shoots of pioneer species, a view which is supported by preliminary observations (Ackerly, 1999). Similarly, the optimal nitrogen allocation theory (Hikosaka, 2003) predicts leaf dynamics on the basis of carbon economy principles, i.e. that lower and older leaves are dropped as they become shaded because it increases the overall canopy productivity—or some other measure of plant fitness related to carbon acquisition. The optimal nitrogen allocation theory specifically incorporates the positive correlation between leaf nitrogen content and leaf photosynthetic rate, assumes optimal vertical distribution of nitrogen in the canopy, and considers nitrogen partial resorption from senescing leaves. The model of canopy dynamics proposed by Hikosaka (2003) reproduces a number of observed patterns including the reduction of leaf life span under high light, as a consequence of the slower canopy development and retarded self-shading.

The degree of self-shading (or shading by neighbours) is, however, difficult to assess precisely as it is subject to change over time as the plant and its neighbours develop and will affect differently the different leaves of the various cohorts monitored. A 3-D reconstruction of seedlings' architecture and growth could help researchers ascertain the spatio-temporal pattern of self-shading (Pearcy and Yang, 1996).

It is doubtful that self-shading played a significant role in shaping the pattern of increased leaf longevity under low light observed in the present experiment for the following two reasons:

(1) Within a species, self-shading intensity should be strongly correlated with individual plant leaf area index (and hence leaf area per plant). However, mean leaf area per plant was similar in the most extreme light regimes (Table 1, B) and was not significantly higher in the 45 % light treatment. For all species, the highest leaf area per plant and an intermediate leaf life span was found to occur in the latter treatment. Note that a similar leaf area per plant was achieved despite significant differences in above-ground biomass accumulation. This was because all species exhibited a marked increase in above-ground leaf area ratio with increasing shading (Table 1, C).

(2) In the present experiment, absolute levels of self-shading or shading by neighbours were probably moderate (in comparison with the level of imposed artificial shading), either as a result of slow growth (*Lansium* and *Durio*) or repeated pruning at 1·5 m, which prevented significant self-shading of the sampled axes in the fast-growing species (*Alstonia* and *Hevea*).

It is rather difficult to demonstrate clearly, through experiments, that self-shading does regulate leaf life span. This was attempted in an ingenious experiment by Ackerly and Bazzaz (1995), who used artificial light gradients to mimic

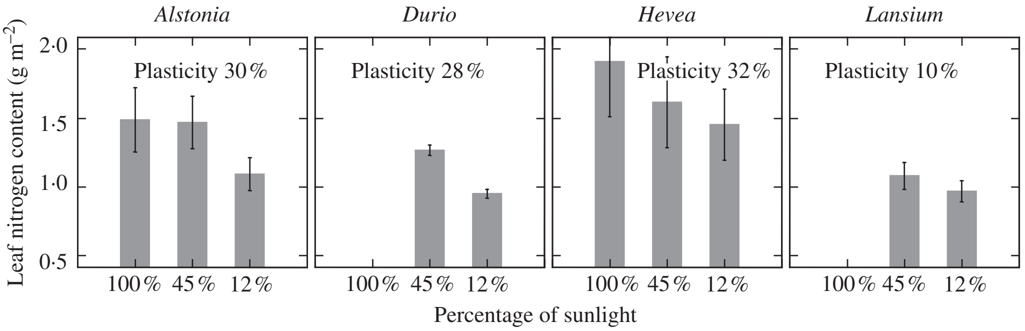

FIG. 2. Leaf N content per unit area (a proxy for photosynthetic potential) of tropical tree seedlings growing under three light levels. Error bars represent standard error of the mean. 'Plasticity' is defined as the range of variation of the parameter monitored across light treatments relative to the mean; no data is presented for *Lansium* and *Durio* in full light, due to high levels of mortality.

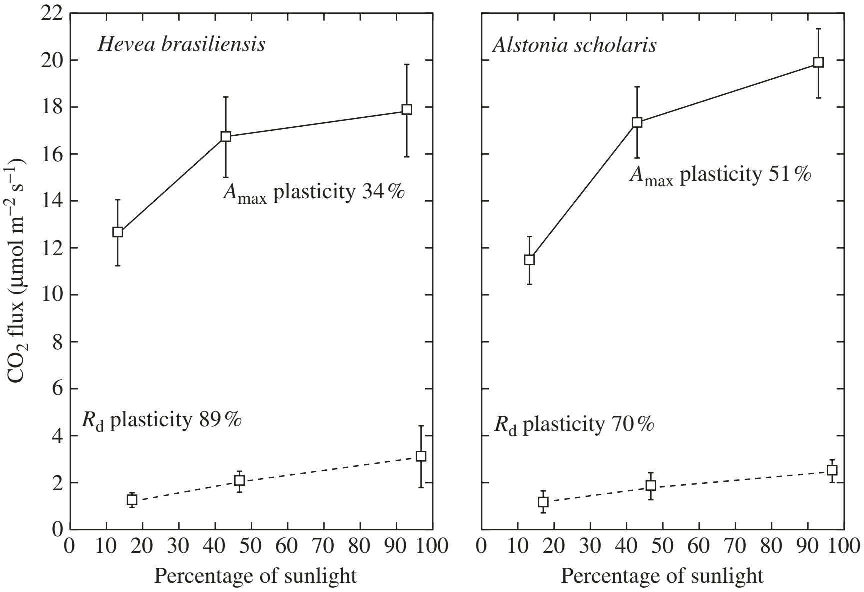

FIG. 3. Maximum photosynthetic rate (A_{max}, continuous line) and dark respiration (R_d, dashed line) of *Hevea brasiliensis* (left) and *Alstonia angustiloba* (right) seedlings growing under three light levels. Plasticity is defined as the range of variation of the parameter monitored across light treatments relative to the mean value over all light treatments. Error bars represent 95 % confidence interval of the mean.

the effect of self-shading. In their experiment, seedlings of *Heliocarpus appendiculatus,* a fast-growing pioneer tropical species, were grown under controlled conditions. This involved manipulating both ambient light (two levels) and light gradient (two levels) independently, by growing seedlings in cylinders of black cardboard (half-lined with aluminium foil in order to reflect light onto the lower leaves and create a less steep light gradient). The authors themselves pointed out that the vertical light gradients achieved in this way were, however, 'somewhat steeper' (*sic*) than those measured on field-grown seedlings (six times steeper in the case of the steep light gradient) (Ackerly and Bazzaz, 1995). A reduction in leaf longevity in the steep self-shading gradient only occurred in the shaded treatment, possibly as a result of dark-triggered senescence due to the extremely low light values achieved in that treatment in the lowermost parts of the plants (the author's interpretation). By contrast, under high light levels (≥850 µmol m^{-2} s^{-1} between 0600 and 1800 h), increasing the steepness of the light gradient had no measurable effect on leaf longevity. Hence, based upon the latter experiment, it cannot be firmly concluded that self-shading regulates leaf longevity in *Heliocarpus appendiculatus*.

This phenotypic plasticity of leaf life span to irradiance has been previously recorded in a number of cases. The life span of saplings of the shade-tolerant tropical species *Elateriospermum tapos* (Euphorbiaceae) was found to be prolonged in the shaded understorey in comparison to that of saplings growing in gaps (Osada *et al*., 2003). Similar observations have been reported for *Dendrocnide moroides* and *Dendrocnide cordifolia*, two Australian Urticaceae species (Hurley, 2000). Seedlings of the fast-growing pioneer *Heliocarpus appendiculatus* exhibited increased leaf longevity under 35 % light intensity (Ackerly and Bazzaz, 1995). An increase in the leaf life expectancy of the annual *Linum usitatissimum* has been reported when it was grown with 50 % shade (Bazzaz and Harper, 1977). Incidentally, increased density (and shading gradient) did not translate into a reduction in longevity in that experiment (table 1, p. 199 in Bazzaz and Harper 1977). Lusk (2002), studying the acclimation of evergreen seedlings in temperate rainforest, found a similar overall trend of decreasing leaf turnover rate under increasing shade.

It seems that such phenotypic plasticity is widespread; notably, it does not appear to be limited to a specific successional position or life form or to non-seasonal climate. Such generality lends further support to the interpretation that extended leaf life span under low light may be a mere consequence of the slowed ageing associated with lower metabolic rates.

Most importantly, the degree of phenotypic plasticity observed in leaf life span was of a similar order of magnitude to the degree of plasticity observed in both specific leaf area and photosynthetic capacity. This implies that leaf life span plasticity contributes significantly to carbon gain efficiency under low light. Within species, the relationship between specific leaf area and leaf life span was positive. This result appears to contradict the trend that has generally been reported in across-species comparisons (Reich *et al.*, 1991, 1999). However, although a paradox appears to exist, this is not actually the case. In a forest environment under low light conditions, the long-term survival of seedlings that exhibit a low growth rate will depend strongly on their capacity to retain their leaves over long periods of time (Lusk, 2002). Hence, the longer-lived leaves of shade-tolerant species are likely to show other associated morphological characteristics that decrease their vulnerability to physical damage and herbivory. Increased mechanical resistance of leaf tissues to herbivory or to other forms of physical damage (such as the production of a waxy cuticle, specialized hairs, trichomes, silica particles, etc.), is often associated with a reduction in specific leaf area. Nevertheless, irrespective of their optimal light regime, plants commonly adjust the anatomical and physiological properties of their leaves to their current light environment: a 'tactical' response to shading. Leaf blade thickness is usually increased under high light levels, mainly as a result of an increase in the thickness of the palisade layer (Bongers and Popma, 1988; Ashton and Berlyn, 1992; Wiebel *et al.*, 1994). Hence, different mechanisms may explain the contradictory trends in co-variability found in specific leaf area and leaf longevity in inter- and intra-specific comparisons. The extent of the variation may also differ significantly in each case. Although the order of magnitude of the variation in SLA between species within a biome—encompassing various life forms including forbs, broadleaved trees and shrubs, and needle-leaved conifers—can reach a factor of 10 (Reich *et al.*, 1999), the order of magnitude of the variation in SLA and leaf longevity recorded here is only 2.

For each of the four species, the relationship between leaf life span and leaf nitrogen per unit leaf area was found to be negative, as was the relationship between $A_{\max}$ and R_d for the two species for which gas exchange measurements were conducted. These findings are consistent with the view that reduced photosynthetic activity delays leaf senescence. One consequence is that the total carbon fixed per leaf may be fairly stable across light levels since the increased photosynthetic rates in high light would be compensated for by a reduced period of photosynthetic activity due to hastened senescence. Testing this assumption would require comparing the age-associated decline in photosynthetic rate under contrasted light regimes. Clarification of the physiological mechanisms at play in the slowing down of leaf ageing under shade is clearly beyond the scope of the present study. However, the negative relationship found between leaf emission rate and leaf life span supports the idea that plant acclimation to shading is a highly integrated physiological response (Givnish, 1988). Hence the findings of this study strongly call for researchers, when exploring leaf-level carbon budgets under a range of light conditions, to take into account the plasticity of leaf life span in addition to the other parameters more routinely examined, such as photosynthetic rate (and its rate of decline with leaf ageing) and leaf construction costs.

ACKNOWLEDGEMENTS

This work was conducted while the author was visiting scientist at the World Agroforestry Center in Indonesia. The author gratefully acknowledges the help received from Saiful, Ni'matul and Agus Ruhiyana in conducting the fieldwork. Thanks are also due to Hubert de Foresta, Brenda Casper and an anonymous reviewer for the valuable suggestions made on an earlier version of this paper, and to SCRIPTORIA Academic English Editing Services for editing this manuscript.

LITERATURE CITED

Ackerly D. 1999. Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* **119**: 300–310.

Ackerly DD, Bazzaz FA. 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* **101**: 289–298.

Ashton PS. 1988. *Manual of the non-dipterocarp trees of Sarawak.* Kuching, Malaysia: Forest Department Sarawak.

Ashton PMS, Berlyn GP. 1992. Leaf adaptations of some *Shorea* species to sun and shade. *New Phytologist* **121**: 587–596.

Bazzaz FA, Carlson RW. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* **54**: 313–316.

Bazzaz FA, Harper JL. 1977. Demographic analysis of the growth of *Linum usitatissimum. New Phytologist* **78**: 193–208.

Biswal UC, Biswal B. 1999. Leaf senescence: physiology and molecular biology. *Current Science* **77**: 775–782.

Bongers F, Popma J. 1988. *Trees and gaps in a Mexican tropical rain forest: species differentiation in relation to gap associated environmental heterogeneity.* Utrecht, The Netherlands: Utrecht University.

Casper BB, Forseth IN, Kempenich H, Seltzer S, Xavier K. 2001. Drought prolongs leaf life span in the herbaceous desert perennial *Cryptantha flava. Functional Ecology* **15**: 740–747.

Chabot BF, Hicks DJ. 1982. The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**: 229–259.

Chazdon RL, Kaufmann S. 1993. Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. *Functional Ecology* **7**: 385–394.

Cordell S, Goldstein G, Meinzer FC, Vitousek PM. 2001. Regulation of leaf life-span and nutrient-use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. *Oecologia* **127**: 198–206.

Escudero A, Mediavilla S. 2003. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. *Journal of Ecology* **91**: 880–889.

Escudero A, Arco JMd, Sanz IC, Ayala J. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* **90**: 80–87.

Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* **78**: 8–19.

Evans JR, Poorter H. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell and Environment* **24**: 755–767.

Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the economy of plant form and function.* Cambridge: Cambridge University Press.

Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* **15**: 63–92.

Givnish TJ. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* **36**: 703–743.

Goodman LA. 1960. On the exact variance of products. *Journal of the American Statistical Association* **55**: 708–713.

Gouyon A, de Foresta H, Levang P. 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. *Agroforestry Systems* **22**: 181–206.

Gratani L, Crescente MF, Petruzzi M. 2000. Relationship between leaf life-span and photosynthetic activity of *Quercus ilex* in polluted urban areas (Rome). *Environmental Pollution* **110**: 19–28.

Hallé F, Martin R. 1968. Etude de la croissance rythmique chez l'*Hevea (Hevea brasiliensis* Mull. Arg. Euphorbiacees-Crotonidees). *Adansonia* **8**: 475–503.

Hallé F, Oldeman RAA, Tomlinson PB. 1978. *Tropical trees and forests. an architectural analysis*. Berlin: Springer-Verlag.

Hawthorne WD. 1995. *Ecological profiles of Ghanaian forest trees*. Oxford: Oxford Forestry Institute.

van der Heide J, Setijono S, Syekhfani, Flach EN, Hairiah K, Ismunandar S, *et al*. 1992. Can low external input cropping systems on acid upland soils in the humid tropics be sustainable? Background of the UniBraw/IB nitrogen management project in Bunga Mayang (Sungkai Selatan, Kotabumi, N. Lampung, S. Sumatra, Indonesia). *Agrivita* **15**: 1–10.

Henriksson J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. *Oecologia* **126**: 482–486.

Hikosaka K. 2003. A model of dynamics of leaves and nitrogen in a plant canopy: an integration of canopy photosynthesis, leaf life span, and nitrogen use efficiency. *American Naturalist* **162**: 149–164.

Hikosaka K. 2005. Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. *Annals of Botany* **95**: 521–533.

Holmes DA. 1998. *Rainfall and Droughts in Indonesia, a Study for the World Bank. Vol. 3A. Sumatra*. Washington DC: World Bank, 81 pp.

Hurley M. 2000. Growth dynamics and leaf quality of the stinging trees *Dendrocnide moroides* and *Dendrocnide cordifolia* (family Urticaceae) in Australian tropical rainforest: implications for herbivores. *Australian Journal of Botany* **48**: 191–201.

Kamaluddin M, Grace J. 1993. Growth and photosynthesis of tropical forest tree seedlings (*Bischofia javanica* Blume) as influenced by a change in light availability. *Tree Physiology* **13**: 189–201.

Kikuzawa K. 1995. Leaf phenology as an optimal strategy for carbon gain in plants. *Canadian Journal of Botany* **73**: 158–163.

King D. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**: 948–957.

King DA. 2003. Allocation of above-ground growth is related to light in temperate deciduous saplings. *Functional Ecology* **17**: 482–488.

Kitajima K, Mulkey SS, Wright SJ. 1997. Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *American Journal of Botany* **84**: 702–708.

Kitajima K, Mulkey SS, Samaniego M, Wright SJ. 2002. Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. *American Journal of Botany* **89**: 1925–1932.

Körner C. 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology* **5**: 162–173.

Kursar TA, Coley PD. 1999. Contrasting modes of light acclimation in two species of the rainforest understory. *Oecologia* **121**: 489–498.

Laumonier Y. 1996. *The vegetation and physiography of Sumatra*. Kluwer Academic Publishers.

Lee ET. 1992. *Statistical methods for survival data analysis. 2nd edn*. New York: John Wiley & Sons, Inc.

Lei TT, Lechowicz MJ. 1997. Functional responses of *Acer* species to two simulated forest gap environments: leaf-level properties and photosynthesis. *Photosynthetica* **33**: 277–289.

Lim PO, Woo HR, Nam HG. 2003. Molecular genetics of leaf senescence in Arabidopsis. *Trends in Plant Science* **8**: 272–278.

Lowman MD. 1992. Leaf growth dynamics and herbivory in five species of Australian rain-forest canopy trees. *Journal of Ecology* **80**: 433–447.

Lusk CH. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. *Oecologia* **132**: 188–196.

Munne-Bosch S, Alegre L. 2002. Plant aging increases oxidative stress in chloroplasts. *Planta* **214**: 608–615.

Nooden LD, Hillsberg JW, Schneider MJ. 1996. Induction of leaf senescence in *Arabidopsis thaliana* by long days through a light-dosage effect. *Physiologia Plantarum* **96**: 491–495.

Nooden LD, Guiamet JJ, John I. 1997. Senescence mechanisms. *Physiologia Plantarum* **101**: 746–753.

Ono K, Nishi Y, Watanabe A, Terashima I. 2001. Possible mechanisms of adaptive leaf senescence. *Plant Biology* **3**: 234–243.

Osada N, Takeda H, Furukawa A, Awang M. 2001. Leaf dynamics and maintenance of tree crowns in a Malaysian rain forest stand. *Journal of Ecology* **89**: 774–782.

Osada N, Takeda H, Kitajima K, Pearcy RW. 2003. Functional correlates of leaf demographic response to gap release in saplings of a shade-tolerant tree, *Elateriospermum tapos. Oecologia* **137**: 181–187.

Pearcy RW, Sims DA. 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. In: Caldwell MM, Pearcy RW, eds. *Exploitation of environmental heterogeneity by plants*. San Diego, CA: Academic Press.

Pearcy RW, Yang W. 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia* **108**: 1–12.

Popma J, Bongers F. 1991. Acclimation of seedlings of 3 Mexican tropical rain-forest tree species to a change in light availability. *Journal of Tropical Ecology* **7**: 85–97.

Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf life span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* **86**: 16–24.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, *et al*. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**: 1955–1969.

Schoettle AW, Smith WK, Kaufmann MR, Landsberg JJ. 1991. Interrelation between shoot characteristics and solar irradiance in the crown of *Pinus contorta* ssp. *latifolia*. *Tree Physiology* **9**: 245–254.

Senevirathna AMWK, Stirling CM, Rodrigo VHL. 2003. Growth, photosynthetic performance and shade adaptation of rubber (*Hevea brasiliensis*) grown in natural shade. *Tree Physiology* **23**: 705–712.

Sprugel DG. 2002. When branch autonomy fails: Milton's Law of resource availability and allocation. *Tree Physiology* **22**: 1119–1124.

Straus-Debenedetti S, Bazzaz FA. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* **87**: 377–387.

Vincent G. 2001. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedlings. *Journal of Tropical Ecology* **17**: 495–509.

Walters MB, Field CB. 1987. Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. *Oecologia* **72**: 449–456.

Weaver LM, Amasino RM. 2001. Senescence is induced in individually darkened Arabidopsis leaves, but inhibited in whole darkened plants. *Plant Physiology* **127**: 876–886.

Wiebel J, Chacko EK, Downton WJS, Lüdders P. 1994. Influence of irradiance of photosynthesis, morphology and growth of mangoosteen (*Garcinia mangostana* L.) seedlings. *Tree Physiology* **14**: 263–274.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, *et al*. 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Yoshida S. 2003. Molecular regulation of leaf senescence. *Current Opinion in Plant Biology* **6**: 79–84.