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Leaf dynamics of seedlings of rain forest species in relation to canopy gaps

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Summary. Leaf dynamics of eight tropical rain forest species seedlings was studied in three environments: the shaded forest understorey, a small gap of $\pm 50\ \mathrm{m}^2$, and a large gap of $\pm 500\ \mathrm{m}^2$. Leaf production rate and leaf loss rate were enhanced in gaps, and a large gap resulted in larger increases than a small gap. For most species net leaf gain rate was larger in gaps, although this rate was not always largest in the large gap. Leaf loss decreased, and leaf survival percentages increased with increasing shade tolerance of species, indicating a slower leaf turnover for more shade tolerant species. Leaf area growth rate was only partly determined by net leaf gain rate. Ontogenetic effects on leaf size were also important, especially in the large gap. Species which possessed leaves with high specific leaf weight (SLW) showed lower leaf loss rates and higher leaf survival percentages than species with low SLW leaves. Leaf life span seemed to be related to leafcost per unit area. The relation of specific patterns in leaf production and leaf loss to the regeneration mode of the species is briefly discussed.

Key words: Canopy gaps – Leaf dynamics – Seedling growth – Shade tolerance – Tropical rain forest

Recently, much emphasis has been given to the importance of canopy gaps for the regeneration of tropical rain forest species (Bazzaz and Pickett 1980; Denslow 1980; Hartshorn 1980; Whitmore 1982, 1984; Pickett 1983; Bazzaz 1984; Brokaw 1985; Martínez-Ramos 1985). Species are thought to be differentiated in their response to the environmental conditions related to gaps of different sizes. Photosynthetically active radiation (PAR) is a limiting resource in the forest understorey, while in gaps PAR rapidly increases with gap size (Chazdon and Fetcher 1984). Detailed knowledge on the growth response of species to gap-associated micro-environmental heterogeneity should lead to an understanding of the degree of differentiation among species in the way they exploit this resource (Bazzaz and Pickett 1980). This differentiation between species will probably be most pronounced during early stages in their life cycle.

A comparison of the growth of seedlings of ten rain forest species in three different environments (Popma and Bongers 1988) showed a range in growth responses from species unable to grow in the shade but with strong growth in the sun, to species with relatively high growth rates in both shade and sun environments. The growth of all species was enhanced in gaps. Plants grown in a large gap had a sun-plant morphology, while plants grown in a small gap, or below a closed canopy, showed a shade-plant morphology. Differences in growth rate and plant morphology (between environments as well as between species) may be partly determined by differences in leaf dynamics. Through regulation of leaf production and abscission several aspects of a plant's growth and morphology may be modulated, notably: total leaf area, leaf area ratio (LAR), unit leaf rate (E), biomass growth rate ($\mathrm{RGR_w}$) and leaf characteristics. A high leaf turnover rate leads to a greater proportion of younger leaves on the plant, which are known to have higher rates of photosynthesis (cf. Chabot and Hicks 1982). This might result in higher unit leaf rates. On the other hand, a high leaf turnover rate would imply a relatively large loss in biomass and thus a lower E, as E is based on the net biomass increase. Biomass growth rate is the product of the unit leaf rate and the leaf area ratio (provided that values are instantaneous estimates; Evans 1972). Most changes in leaf characteristics can only be achieved by the production of new leaves and the abscission of old ones.

Based on these considerations two hypotheses can be put forward concerning the effects gaps may have on the leaf dynamics of the seedlings:

1. Leaf turnover of all species is related to light availability and will increase with increasing gap size. When more light is available net photosynthesis is higher and more leaves can be produced (Langenheim et al. 1984). Leaf life spans may be shorter under high light conditions because of an increased probability of damage (photo-destruction of pigments, dessication, over-heating).

2. Shade tolerant species should have lower leaf turnover rates than shade intolerant species. Species which are able to grow and survive at low light levels may be designated as shade tolerant. They should conserve assimilated carbon as much as possible. Shade intolerant (pioneer) species usually occur in gaps, where competition for light is strong. For these species a high leaf turnover may enable a rapid and flexible deployment of leaf area ('foraging') in search of high light levels (Bazzaz and Pickett 1980).

The purpose of this paper is to test both hypotheses for tropical rain forest tree seedlings. Furthermore, the rela-

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Present address and address for offprint requests: Department of Forestry, Agricultural University, P.O. Box 342, 6700 AH Wageningen, The Netherlands tionship between leaf dynamics and plant growth, morphology and architecture in gaps of different sizes will be evaluated.

Site and species

This study was carried out at the tropical biological station "Los Tuxtlas" in the state of Veracruz, Mexico (18°35′ N, 95°07′ W). Mean annual rainfall is 4639 mm and mean annual temperature is 24.6° C (climatological station of Coyame, at a distance of 35 km from the reserve). A description of the structure, floristic composition and dynamics of the forest can be found in Bongers et al. (1988a) and Popma et al. (1988).

The eight species studied vary ecologically from the pioneer tree species *Cecropia obtusifolia* Bertol. which is found only in large gaps, to the small understorey trees *Amphitecna tuxtlensis* A. Gentry and *Psychotria simiarum* Standl. *Myriocarpa longipes* Liebm. is a pioneer shrub growing mainly in gaps, but mature individuals can also be found in the shaded forest understorey. *Pseudolmedia oxyphyllaria* Donn. Sm. is a subcanopy tree, and *Brosimum alicastrum* Sw., *Cordia megalantha* Blake and *Omphalea oleifera* Hemsl. are upper canopy trees. The two pioneer species have small seeds with induced germination. The other species have relatively large seeds, which mostly germinate rapidly after seed fall, whereafter a seedling bank is formed (Popma and Bongers 1988). Information on nomenclature is given by Ibarra-Manríquez (1985). Species will be referred to using their generic names only.

Methods

Per species seedlings were raised from seeds from one parent tree to minimize genetic differences between plants. Only in the case of *Cordia*, recently emerged shade-born seedlings were collected in the field below one parent tree. The seedlings of most species were grown in a moderately shaded greenhouse until they were large enough (at least two leaves above the cotyledones) to start the experiment, and the remains of attached seeds had fallen off. *Cecropia* and *Myriocarpa* were raised in a sunny greenhouse. All species were grown in black plastic bags filled with 2×10^{-3} m^3 homogenized forest soil. After the start of the experiment, seedlings were randomly divided over three mosquito cloth greenhouses in different field conditions: mature forest with a closed canopy (FU treatment), a small (50 m^2) canopy gap which received approx. one hour of direct insolation daily (SG treatment), and a large gap which received nearly 7 h of direct insolation daily (LG treatment). The large gap was actually a roadside clearing similar to a gap of approximately 500 m^2. The FU plants received between 0.9 and 2.3% of the daily photosynthetic photon flux (DPPF) above the canopy of the forest, the SG plants received between 2.1 and 6.1%, and the LG plants received between 38.6 and 53.4% (Bongers et al. 1988b). During the dry season (March–May) plants were watered every other day. No extra nutrients were added. The mosquito cloth efficiently excluded most insect herbivores. Occasionally however insecticide had to be sprayed. Damaged plants (due to either herbivore action, pathogens or manipulations) were excluded from further analyses.

Because of differences in seed and/or seedling availability and lack of space in the greenhouses not all species were studied at the same time. The experiment started (T = 0, when individuals of a species were randomly divided over the three greenhouses) 5 December 1983 (*Cordia, Omphalea*), 6 April 1984 (*Psychotria*), 14 May 1984 (*Pseudolmedia*), 7 July 1984 (*Brosimum, Myriocarpa, Amphitecna*) and 26 October 1984 (*Cecropia*). The length of time species were studied (see Table 3) was different due to space limitations in the greenhouses, to size of the individuals, and to the time available for the whole experiment. All measurements were done between 5 December 1983 and 5 February 1985. An experimental group consisted on average of 9 (range 5–10) individuals. The plants were relocated regularly to randomize possible effects of location within the greenhouses.

Table 1. Relative growth rates of dry weight and leaf area of seedlings of tropical rain forest species grown in three environmental conditions[a]

Species[b]	RGR_w			RGR_a		
	FU	SG	LG	FU	SG	LG
Cecropia obtusifolia	−0.67	3.67	18.80	−4.80	2.33	9.13
Myriocarpa longipes	0.53	7.27	10.67	5.20	12.20	9.30
Cordia megalantha	2.77	6.83	10.83	3.27	6.37	4.77
Omphalea oleifera	2.90	4.77	8.77	5.63	7.60	11.17
Psychotria simiarum	2.97	8.63	13.00	2.10	6.77	8.90
Brosimum alicastrum	3.40	5.93	11.43	1.90	2.87	4.60
Amphitecna tuxtlensis	6.40	7.80	14.87	5.83	7.30	8.50
Pseudolmedia oxyphyllaria	7.67	9.10	13.83	6.53	8.90	9.47

[a] RGR_w in 10^{-3} g·g^{-1}·day^{-1} (Popma and Bongers 1988), RGR_a in 10^{-3} m^2·m^{-2}·day^{-1}

[b] Species in order of increasing shade tolerance

At the start of the experiment (T = 0) a color-coded plastic ring was placed around the petiole of all leaves (in *Omphalea* the study of leaf demography started at T = 72 days). Regularly plants were checked for abscised and for newly produced leaves. These new leaves were given a color-coded ring. Leaves were considered as being produced when the leaf blade was at least 1 cm long. At the end of the experiment plants were harvested according to the methods described in Bongers et al. (1988b). Relative biomass growth rate (RGR_w), relative leaf area growth rate (RGR_a), unit leaf rate (E), leaf-area ratio (LAR), root-shoot ratio (R/S), specific leaf weight (SLW) and specific leaf water content (SLWC) were calculated as described in Popma and Bongers (1988). Relative growth rates of these species in FU, SG and LG are summarized in Table 1.

Results

Leaf dynamics

The leaf production rate of all species was highest in LG and lowest in FU (Fig. 1A). The SG values were intermediate. Differences between environments were less pronounced as far as leaf loss rates are concerned, although these were mostly highest in LG as well (five species). Only two species had different leaf loss rates in FU and SG (*Omphalea, Psychotria*). Three species (*Cecropia, Brosimum, Amphitecna*, Fig. 1B) did not show differences between environments in leaf loss rate. For *Cecropia* leaf loss rate was constantly high in all environments studied. For *Am-*

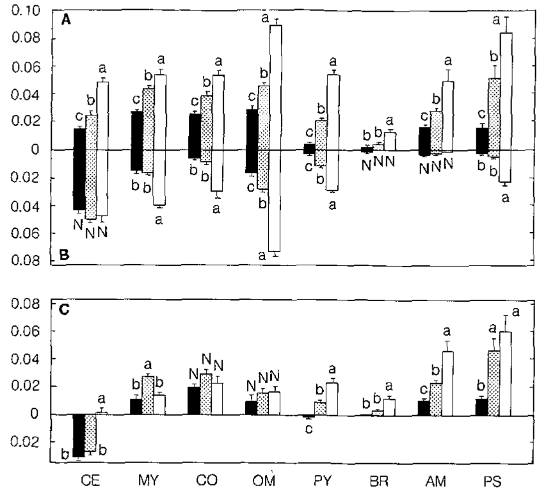

Fig. 1 A–C. Leaf production rate (**A**), leaf loss rate (**B**) and net leaf gain rate (**C**) of seedlings of tropical rain forest species. Black bars represent the forest understorey (FU treatment), shaded bars represent the small gap (SG treatment) and open bars represent the large gap (LG treatment). Values are mean number of leaves per day (±SE). Values with different letters (within a species) are significantly different at the 5% level, an N indicates not significant. (F-test and Duncan's multiple range test.) Species are indicated at the abscissa: CE = *Cecropia*, MY = *Myriocarpa*, CO = *Cordia*, OM = *Omphalea*, PY = *Psychotria*, BR = *Brosimum*, AM = *Amphitecna*, PS = *Pseudolmedia*

phitecna and *Brosimum* on the other hand leaf loss was very low in all environments. Differences in leaf loss rates may have existed between environments in the latter species, but the period of observation (270 days) was too short to draw conclusions on this matter. Five species had the highest net leaf gain rate in LG, two species in SG (Fig. 1C). *Omphalea* did not show differences in net leaf gain rate between environments. While 7 species had significant differences between all three environments in leaf production rates, only two species had such differences in leaf loss rates and net leaf gain rates.

A comparison between species (Fig. 1) shows that *Omphalea* and *Pseudolmedia* had the highest leaf production rate in LG and SG. *Myriocarpa* had among the highest leaf production rates in SG and the highest one in FU. The leaf production rate of *Brosimum* was exceptionally low in all three environments. Leaf loss rates were relatively high in *Cecropia* and *Omphalea*, and very low in *Brosimum*, *Amphitecna* and also *Pseudolmedia*. The net leaf gain rate was relatively high for *Pseudolmedia* (LG and SG) and *Amphitecna* (LG). In FU *Cordia* had the highest value but the difference with other species was small. The net leaf gain rate of *Cecropia* was low in all three environments: in FU and SG even clearly negative, which probably indicates that plants were slowly dying.

Within any one species the response to different environments was similar. The rates of leaf production and loss increased when light availability (gap size) increased. Species compared in the same environment showed many different types of production/loss patterns. Responses varied from high production/high loss (*Omphalea*), to high production/low loss (*Amphitecna*), low production/low loss (*Brosimum*), and intermediate production/high loss (*Cecropia*).

The difference in leaf loss rate between environments suggests that leaves lived longer in FU and SG than in LG. Figure 2 shows leaf survival percentages for different cohorts of leaves of *Psychotria*, as an example of the five species which had similar survival curves (i.e. *Myriocarpa*, *Cordia*, *Omphalea*, *Psychotria*, *Pseudolmedia*). Leaf survival percentages were lowest in LG, and mostly highest in FU, while differences between FU and SG were small. Survival percentages of early cohorts were lower than those of later ones, indicating that mostly the oldest leaves were shed first. Leaf survival percentages of the other three species (*Cecropia*, *Brosimum* and *Amphitecna*) were not different between environments. In *Cecropia* these percentages were around 25% for the first cohort and around 95% for the second cohort, at the end of the experiment in all treatments. Leaves of the other two species nearly did not fall: after 210 days leaf survival percentages were higher than 90%.

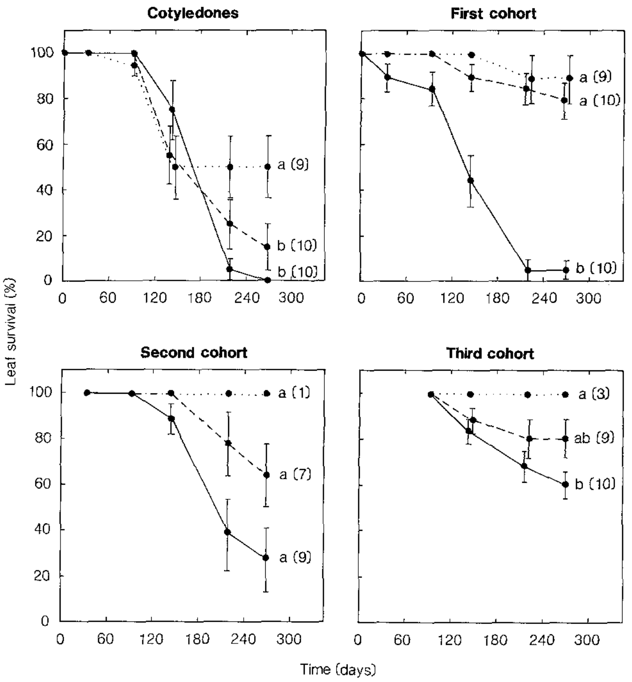

Fig. 2. Leaf survival percentages (±SE) of the cotyledones and of different cohorts of leaves of *Psychotria simiarum*. (.......) = FU, (----) = SG, (——) = LG. Values in parenthesis show the number of plants with leaves in a specific cohort. Different letters indicate that values at T = 270 days are significantly different between environments at the 5% level (F-test and Duncan's multiple range test)

Leaf dynamics and growth response

Within any one environment no correlation existed between RGR_w and leaf production rate. In FU and SG, RGR_w was negatively correlated to leaf loss rate and in SG positively to net leaf gain rate (Table 2). RGR_a was positively correlated to net leaf gain rate in FU and SG, while it was negatively correlated to leaf loss rate in FU and positively to leaf production rate in SG and in LG. Species with a high E had a low leaf loss rate in SG and LG, but not in FU. LAR was positively correlated with leaf loss rate in LG. Species with a high leaf loss rate tended to have a low SLW and a high SLWC (significant only in LG). Species with a high SLW in LG had high net leaf gain rates.

Table 2. Pearson correlations between leaf dynamics and growth characteristics in three environmental conditions for seedlings of 8 tropical rain forest tree species*

	RGR_w	RGR_a	E	LAR	R/S	SLW	SLWC	Leaf size
FU								
leaf production rate	−0.16	0.36	−0.15	0.56	0.21	−0.67	0.58	0.34
leaf loss rate	**−0.71**	**−0.71**	−0.61	0.30	0.68	−0.51	0.67	0.15
net leaf gain rate	0.55	***0.90***	0.46	0.11	0.38	0.02	−0.23	0.07
SG								
leaf production rate	0.23	**0.74**	−0.21	0.46	**−0.77**	−0.43	0.35	0.27
leaf loss rate	**−0.75**	−0.27	**−0.71**	0.46	−0.02	−0.69	0.33	0.35
net leaf gain rate	**0.75**	**0.76**	0.40	−0.02	−0.56	0.22	0.01	−0.07
LG								
leaf production rate	−0.11	**0.75**	−0.26	0.41	−0.47	−0.17	0.32	0.56
leaf loss rate	−0.13	0.63	**−0.80**	***0.86***	−0.55	**−0.77**	**0.81**	**0.73**
net leaf gain rate	0.02	0.15	0.67	−0.55	0.09	**0.74**	−0.60	−0.21

* Significant correlations are indicated in **bold** ($P<0.05$) or in ***bold-italic*** ($P<0.001$)

Table 3. Total leaf area, mean leaf size, net leaf gain and leaf production of seedlings

Species (*n*)	Treatment[a]	Total leaf area (10^{-2} m^2)			Leaf size (10^{-2} m^2)			Total net leaf gain (no. of leaves)			Total leaf production (no of leaves)			ΔT[b]
		mean	SE		mean	SE		mean	SE		mean	SE		
Cecropia	ST	0.52	0.054		0.09	0.009								99
9[c]	FU	0.32	0.058	b*	0.13	0.014	n	−2.9	0.50	b	1.4	0.18	c	
9	SG	0.66	0.184	b	0.17	0.030	n	−2.5	0.39	b	2.4	0.34	b	
10	LG	1.29	0.154	a	0.20	0.015	n	0.09	0.418	a	4.8	0.29	a	
Myriocarpa	ST	0.20	0.039		0.04	0.007								210
9	FU	0.60	0.130	c	0.08	0.012	b	2.3	0.76	b	5.6	0.34	c	
10	SG	2.57	0.397	a	0.27	0.035	a	5.8	0.47	a	9.2	0.47	b	
10	LG	1.40	0.182	b	0.20	0.018	a	2.9	0.50	b	11.3	0.84	a	
Cordia	ST	0.39	0.044		0.05	0.005								246
8	FU	0.84	0.130	b	0.08	0.009	n	4.8	0.59	n	6.3	0.31	c	
9	SG	1.76	0.180	a	0.11	0.011	n	7.1	0.92	n	9.3	0.73	b	
7	LG	1.20	0.201	b	0.11	0.014	n	5.4	1.49	n	12.9	0.83	a	
Omphalea	ST	1.29	0.152		0.25	0.037								174
9	FU	4.92	0.482	b	0.78	0.104	b	1.8	0.80	c	4.8	0.40	c	
9	SG	7.80	1.015	b	0.92	0.076	b	2.7	0.47	b	7.7	0.41	b	
9	LG	18.20	1.132	a	1.85	0.202	a	2.9	0.75	a	15.6	0.85	a	
Psychotria	ST	0.15	0.024		0.05	0.004								270
9	FU	0.26	0.019	c	0.07	0.004	n	−0.33	0.289	c	0.89	0.351	c	
10	SG	0.91	0.070	b	0.15	0.012	n	2.4	0.40	b	5.6	0.40	b	
10	LG	1.63	0.115	a	0.16	0.011	n	6.2	0.88	a	14.2	0.99	a	
Brosimum	ST	0.32	0.028		0.15	0.012								210
9	FU	0.48	0.036	b	0.22	0.021	n	0.0	0.0	b	0.11	0.111	b	
9	SG	0.59	0.049	b	0.22	0.021	n	0.67	0.166	b	0.67	0.166	b	
10	LG	0.85	0.095	a	0.19	0.012	n	2.5	0.45	a	2.5	0.45	a	
Amphitecna	ST	0.27	0.028		0.04	0.003								210
10	FU	0.91	0.063	b	0.10	0.005	n	2.2	0.33	c	3.2	0.29	c	
10	SG	1.23	0.110	ab	0.10	0.006	n	4.9	0.46	b	5.7	0.37	b	
5	LG	1.58	0.265	a	0.10	0.005	n	9.6	1.89	a	10.0	2.00	a	
Pseudolmedia	ST	0.22	0.031		0.04	0.007								264
10	FU	1.25	0.227	b	0.09	0.006	n	3.1	0.53	b	4.0	0.58	c	
8	SG	2.32	0.521	ab	0.10	0.009	n	12.1	2.36	a	13.5	2.35	b	
10	LG	2.71	0.394	a	0.11	0.009	n	16.0	3.27	a	22.1	3.13	a	

[a] ST = start value, FU = forest understorey, SG = small gap, LG = large gap, species ordered from least to most shade tolerant

[b] ΔT = time (days) of leaf demography study

[c] number of individuals for leaf demography study

* means with the same letter are not significantly different between treatments within a species (ANOVA and Duncan's multiple range test, $P<0.05$)

Plants with a high net leaf gain rate may be expected to have a high RGR_a. However, a low, or even negative, net leaf gain rate does not necessarily imply a low or negative RGR_a. Plants can have a low net leaf gain rate due to a combination of a high leaf production rate and a high leaf loss rate. If newly produced leaves are larger than older ones this can result in a positive RGR_a. This effect occurred in several species (Table 3). *Cecropia* had a nearly zero net leaf gain in LG, but a considerable increase in leaf area. In SG this species had a clearly negative net leaf gain but an increase in total leaf area. For *Myriocarpa* the net leaf gain in FU and LG were not different, but the total leaf area in LG was nearly twice that in FU. *Psychotria* had a negative net leaf gain in FU while total leaf area increased. *Omphalea* showed the same net leaf gain in SG and LG but large differences in leaf production and total leaf area. In all these cases the deviation was due to the fact that the newly produced leaves were larger than the older ones, resulting in larger mean leaf areas when the leaf production rate was equal to or higher than the leaf loss rate. The fact that no correlation was found among species between net leaf gain rate and RGR_a in LG (where leaf production was highest), while the same parameters were correlated in FU and SG, indicates that ontogenetic effects on leaf size may be important determinants of RGR_a. Furthermore, differences in the relationship between net leaf gain and RGR_a were also due to overall differences in leaf size among species. *Omphalea* and *Myriocarpa* had the same net leaf gain in LG, but differences in total leaf area were very large due to the large difference in mean leaf size. *Myriocarpa* and *Amphitecna* had approximately the same increase in total leaf area in LG, although the net leaf gain rate of the last species was more than three times that of the former species in that environment (Table 3).

Discussion

The effect of gap conditions on leaf dynamics

Is leaf turnover enhanced in gaps? In all species the production rate of leaves was higher in environmental conditions related to gaps than in the forest understorey, and a large gap had stronger effects than a small one. Leaf loss rates were also enhanced in gaps. Differences in leaf loss rates between treatments were sometimes small, however, and three species showed no differences. The increased leaf production and leaf loss rates in gaps result in a higher leaf turnover. However, the net result for the plant differed between species. Only four species had the highest net leaf gain rate in the large gap environment, and only three species had the lowest one in the forest. In some species net leaf gain decreases at high light intensities.

These results are in agreement with those of Langenheim et al. (1984) who showed that seedlings of three Amazonian and two Australian tropical rain forest tree species had higher leaf production in the sun than in the shade. The same was found for adult individuals of understorey species in Costa Rica (Bentley 1979) and for adult individuals of some rain forest species in Mexico (Tinoco-Oranjuren and Vazquez-Yanes 1983; Meave del Castillo 1987). They all found that leaf turnover was highest under high light conditions.

Exact leaf life spans could not be calculated because only in very few cases (always LG) all leaves of a cohort had fallen off. The differences in leaf survival percentages however clearly indicate that mean leaf life spans are shortest in the large gap and longest in the forest environment.

Leaf dynamics and shade tolerance

The second hypothesis states that shade tolerant species should have lower leaf turnover rates than shade intolerant ones. In a previous paper (Popma ånd Bongers 1988) we arranged the species in order of increasing shade tolerance, where shade tolerance was defined as the relative biomass growth rate (RGR_w) in the forest understorey (Table 1). The results of the present study do not support this hypothesis as far as leaf production rate is concerned. No significant correlations existed between shade tolerance and leaf production rates. As far as leaf abscission is concerned the hypothesis is supported. A significant negative correlation between leaf loss rate and shade tolerance was found in FU and SG (Pearson correlation coefficient $R = -0.71$ and -0.70, respectively, $P<0.05$). Net leaf gain tended to increase with shade tolerance, although the correlation was only significant in LG ($R=0.94$, $P<0.05$). Taking production and loss into account leaf turnover tended to decrease with increasing shade tolerance.

This is in accordance with Shukla and Ramakrishnan (1984) who found that early successional tree species in a tropical humid forest in India had higher turnover rates of leaves than late successional species. Meave del Castillo (1987) found the same for three woody species (among which *Pseudolmedia* and *Myriocarpa*) in Mexican rain forest. Both studies concerned adult individuals however.

In a large gap, shade intolerant species grow faster (Augspurger 1984; Brokaw 1985; Popma and Bongers 1988) and consequently may have a higher net leaf gain than shade tolerant ones. The latter is not the case in the species studied here however. Net leaf gain rate in the large gap even had a strong positive correlation with shade tolerance (Pearson correlation coefficient of 0.94, $P<0.001$). Low or high net leaf gains did not imply low or high values for total plant leaf area (Table 3), due to a complex interaction between leaf dynamics, and environmental and ontogenetic effects on leaf size.

The relatively low abscission rates and long leaf life spans of the shade tolerant species might be related to a strategy of conservation of carbon. These species in general grow under conditions where light is limiting and assimilates are therefore scarce.

Leaf dynamics and growth response

Within species leaf production rate increased with RGR_w, whereas between species in any one environment this relationship did not exist (Table 2). Species with a high leaf loss rate tended to have a high LAR (significant in LG only), and also tended to have low unit leaf rates (significant in SG and LG). RGR_a is a function of net leaf gain rate and mean leaf size. In the shade (FU and also SG), the leaf production rate was low (Fig. 1), which means that differences in total leaf area over time due to ontogenetic effects on mean leaf size will be minimal. Net leaf gain will be the most important determinant of RGR_a in this case, irrespective of the way it is achieved (by lower loss as in FU, or by higher production as in SG, Table 2). In the sun (LG), leaf production was high, and ontogenetic effects on leaf size might be considerable. This may explain why net leaf gain rate in FU and SG was correlated to RGR_a, while in LG this was not the case (Table 2).

Within any of the three light environments leaf loss rate and SLW tended to be negatively correlated, although this was only significant in LG. This can be understood by assuming that in a single environment leaf life span is related to the investments made to produce that leaf (cf. Chabot and Hicks 1982). However, within all species the high SLW leaves produced in LG were shed earlier than the low SLW leaves produced in FU and SG. Due to higher photosynthetic rates the high light leaves might pay for themselves more quickly (cf. Jurik and Chabot 1986). As younger leaves have a higher photosynthetic capacity than older ones (cf. Chabot and Hicks 1982) it might be advantageous to replace a leaf relatively quickly since the new leaf will pay for ifself rapidly and then produce greater profit than an old leaf (cf. Jurik and Chabot 1986).

Shade intolerant species need to position their leaves in the sun for optimal functioning (Bazzaz and Pickett 1980). The ability to rapidly change the position of their leaf area by means of a fast turnover might therefore be more important for these species than for shade tolerant ones. *Cecropia,* a heliophytic pioneer species, had a high leaf loss rate and a low leaf survival percentage, irrespective of environment. Probably the mean leaf life span of this species is not very flexible. In the field this species always grows under high light conditions, and thus with sufficient assimilates to produce new leaves. The shade tolerant species *Brosimum* and *Amphitecna* (and to a lesser extent also *Pseudolmedia*) hardly dropped any leaves in the period studied. Leaf life spans of these species were thus relatively long in all conditions studied here. Morphological changes are therefore probably slower than in the case of shade intolerant species with fast leaf turnover. However, it has been shown that shade tolerant rain forest species have a high physiological efficiency (indicated by their high unit leaf rates; Popma and Bongers 1988), and that their physiological flexibility (the ability to change E rapidly with a change in environment) is high as well (Fetcher et al. 1983; Oberbauer and Strain 1985; Bongers and Popma 1988). Under continuously varying environmental conditions physiological flexibility is probably more important than morphological flexibility for shade tolerant species. This may be reflected in a wider range of light availability in which an existing leaf can function properly.

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