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The photosynthetic characteristics of saplings of eight canopy tree species in a disturbed neotropical rain forest

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Abstract

Foliar gas exchange characteristics, understorey microclimate, and crown irradiation were assessed for saplings of eight canopy tree species in two plots of neotropical rain forest with different degrees of canopy opening. Species studied belonged to different putative guilds: shade intolerants (both short-lived—pioneers—and long-lived), intermediates, and shade-tolerants. A considerable overlap was recorded between species in values of the photosynthetic rate per unit leaf area (P_N). The highest median P_N (1.26 μmol m^{-2} s^{-1}) was recorded in the pioneer *Croton killipianus*, while slightly lower median values were recorded in *Simarouba amara* and *Pentaclethra macroloba*, and markedly lower values in two species of *Vochysiaceae* (*Qualea paraense* and *Vochysia ferruginea*), both putative intolerants. Highest median stomatal conductance (g_s) was also shown by *C. killipianus*, while *S. amara*, *P. macroloba*, and *L. procera* exhibited intermediate values, and the lowest g_s was shown by *V. ferruginea* and *Q. paraense*. Overall irradiance and crown irradiation, P_N, and g_s of saplings were higher in the plot which had previously received a silvicultural treatment. Most values of photosynthetic photon flux density (PPFD) were <100 μmol m^{-2} s^{-1} in both plots, with shortlived peaks of up to 2000 μmol m^{-2} s^{-1} in the treated plot. When the relationship between P_N and irradiance (I) was examined by fitting P_N/I curves, the degree of fit varied markedly between

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species, values of the regression coefficient r^2 were between 0.09 and 0.51. No significant differences between species were recorded in P_{max} and species also demonstrated little variation in the predicted values of dark respiration (R_D), values varying between -0.51 and -1.46 µmol m^{-2} s^{-1} in *Q. paraense* and *Minquartia guianensis*, respectively. Fitted values of apparent quantum efficiency were also fairly uniform, generally falling within the range 0.02-0.03 mol(CO_2) mol^{-1}(photon).

Additional key words: Costa Rica; guilds; hemispherical photograph; logging; modelling; silviculture; sustainable management.

Introduction

Classifications of tree species of tropical forests into functional groups or guilds showing similar patterns of dispersal ability, radiant energy requirements for successional regeneration, growth rate, and other characteristics have often been products of subjective experience rather than of detailed quantitative studies. While such subjective classifications are useful for practical forest management (Hutchinson 1988), recent research has focused on defining guilds on the basis of quantitative studies of the growth, demography, and ecophysiology of representative tree species (*e.g.*, Welden *et al.* 1991, Brown and Whitmore 1992, Clark and Clark 1992, Brown 1993, Clark *et al.* 1993, Whitmore and Brown 1996). At the physiological level, variation in photosynthetic characteristics is one of the principal factors associated with the separation of guilds of tree species. Early indications that pioneer tree species have higher maximum photosynthetic rates (P_{max}) and greater photosynthetic plasticity than the long lived species which dominate old growth forests have been verified recently (Chazdon *et al.* 1996, Strauss-Debenedetti and Bazzaz 1996). Although recent research has focused on the behaviour of seedlings in canopy gaps (Brown and Jennings 1998) it is clear that in old-growth tropical forests the low PPFD which predominates in the forest understorey represents a significant challenge to the growth and survival of saplings of all tree species (Chazdon *et al.* 1996).

The majority of ecophysiological studies on tropical trees have been undertaken in controlled environment. Relatively few data are available on ecophysiological responses in the field, and the relevance of laboratory or nursery-based investigations to the understanding of regeneration patterns in the field has been questioned (Clark and Clark 1987). The scarce information available from field studies indicates that the expectation of decreasing crown irradiation, rates of gas exchange, and growth with increasing species shade tolerance is too simplistic. Saplings of canopy tree species of putatively light-demanding and shade-tolerant guilds, for example, occupied similar light environments and had similar growth rates in a Costa Rican rain forest, although their gas exchange characteristics differed (Oberbauer *et al.* 1993). Woody species of subjectively delimited guilds in secondary successional environments of Amazonian Venezuela, on the other hand, showed variations in P_{max} which generally fitted expectations regarding differences between guilds, with highest values of P_{max} and g_s in pioneer species and lowest in "late successional trees" (Reich *et al.* 1995). However, in such studies, differences between species and guilds are confounded with differences between successional environments—

pioneers in young vegetation, and late-successional species in older forests—so that the extent to which the ecophysiological characteristics exhibited are intrinsic or environmentally determined remains unclear (Reich *et al.* 1995).

In the present study we describe the photosynthetic characteristics of naturally occurring saplings of eight canopy tree species in a disturbed neotropical rain forest, and try to relate the variation observed to microclimatic conditions close to ground level. We also wished to determine whether species of different subjectively-delimited guilds show, in the field, different photosynthetic characteristics.

Materials and methods

Site and species studied: The investigation was carried out at La Tirimbina Farm (now Tirimbina Rain Forest Center) located in the district of La Virgen, Sarapiquí Canton, Heredia Province, Costa Rica (10°24'N, 84°06'W) at an altitude of 180-200 m above sea level. The site is 7 km west of the La Selva Biological Station (McDade *et al.* 1994) and at a slightly higher altitude. The life zone is tropical wet forest (Holdridge's system; Tosi 1969), with mean annual precipitation of 3 864 mm and mean annual temperature of 24.5 °C. La Tirimbina lies on highly weathered old lava flows (see Sollins *et al.* 1994, their Fig. 4.1) with a topography of low hills and acid (pH 3.9-4.5), infertile clay soils.

The forest in which the study was carried out was undisturbed old-growth until around 1960, after which it was lightly logged at irregular intervals until 1989 (J.R. Hunter, personal communication). The study area was a 540×540 m (29.16 ha) area which was placed under experimental management for the sustainable production of timber in 1989 (full details are given by Quiros and Finegan 1994). Timber was harvested from the whole area under strict planning and control in 1989 and 1990. The area was divided into nine 180×180 m (3.24 ha) plots and three different regimes of post-harvest silvicultural intervention were applied, using a complete randomised block design (three replicate plots per silvicultural regime), in 1991 and 1992. Forest dynamics are monitored in a square 1.0 ha permanent sample plot (PSP) in the centre of each 3.24 ha plot.

The present study was made during 1994 in two PSPs, one which received no silvicultural treatment after timber harvesting (plot 8), and another in which a liberation thinning, designed to improve growing conditions for selected commercial trees, was applied (plot 5). As a result of the liberation thinning, mean basal area ≥10 cm dbh in the plots so treated declined to 17.9 m^2 ha^{-1} (s.d. 1.29) in 1994 and mean stand density to 397 trees ha^{-1} (s.d. 55) as opposed to 22.9 m^2 ha^{-1} (s.d. 0.76) and 518 trees ha^{-1} (s.d. 96) in the plots with timber harvesting only (Camacho *et al.* 1999). As may be expected on the basis of these figures, the canopy of plot 5 was markedly more open than that of plot 8 during the study. Microclimatic and photosynthetic measurements were done first during April-May ('first period', normally the driest period of the year) and the second during June-July ('second period', during the relatively wet season).

Eight species were selected for the investigation on the basis of their contrasting ecological characteristics and abundances in the two study plots (Table 1). A roughly circular study area of approximately 30 m diameter was selected in each PSP for the study of microclimate and photosynthesis. Selection criteria were the presence of saplings of as many species as possible, accessibility in early morning and late afternoon, and ease of movement through the forest with instruments (see below). In each plot, the study area was centred around a trail used for the extraction of timber, but included closed forest understorey adjacent to the trail. Photosynthetic measurements were done on individuals between *ca.* 0.5 and 1.8 m total height and although we aimed for five individuals per species in each plot, the number of individuals measured for each species was inevitably variable (see Table 1) and only four species could be studied in both plots, *S. amara, V. ferruginea, Q. paraense,* and *P. macroloba.* Photosynthetic and microclimatic measurements were taken simultaneously in each plot, the two plots being assessed on alternate days.

Table 1. Details of the eight Costa Rican tree species investigated in the study. SLI - short-lived intolerant, LLI - long-lived intolerant, I - intermediate, T - tolerant; JDG # - voucher numbers of specimens of seedlings and saplings collected at La Tirimbina by Juan Díaz González and deposited in the National Herbarium, San José, Costa Rica. Guilds were subjectively delimited by B.F. (unpublished). Growth is given by median annual diameter increment [mm] ≥10 cm dbh, 1990-1996 (Camacho *et al.* 1999). *N* is number of saplings used in the determination of gas exchange.

Species and voucher number	Family	Guild	Growth	*N*	
				plot 5	plot 8
Calophyllum brasiliense Standl. (JDG 954)	*Guttiferae*	I	-	-	5
Croton killipianus Croisat (JDG 962)	*Euphorbiaceae*	SLI	16.5	5	-
Laetia procera (Poepigg) Eichl. (JDG 959)	*Flacourtiaceae*	LLI	5.0	5	-
Minquartia quianensis Aubl. (JDG 957)	*Olacaceae*	T	2.0	-	2
Pentaclethra macroloba Kuntze. (JDG 963)	*Mimosaceae*	T	6.0	5	5
Qualea paraense Ducke (JDG 953)	*Vochysiaceae*	I	8.0	3	5
Simarouba amara Aubl. (JDG 958)	*Simaroubaceae*	LLI	15.5	5	5
Vochysia ferruginea Mart (JDG 952)	*Vochysiaceae*	LLI	15.0	3	5

Photosynthetic characteristics of saplings were measured on each sapling at intervals of 2-3 h, following a fixed route through each study area. During the first period, work was usually possible between about 08:00 and 16:00 h. Values were obtained for a total of 5 d per plot during the first period of the study, though few photosynthetic measurements were possible in the second period due to a persistent heavy rain. P_N and g_s were taken using a portable open gas exchange system, with an infrared gas analyser *LCA-3* and Parkinson broadleaf chamber (*Analytical Development Co.*, Hoddesdon, U.K.). Measurements were made on the third fully expanded leaf from the shoot apex in each case, using natural daylight only. The leaf area measured was 6.2 cm^2 in all species except *P. macroloba*, where because of the bipinnate leaf form, areas used were around 4.9 cm^2. The measurements were made at ambient CO_2 concentrations from air taken at a height of 3 m; mean CO_2 concentration entering the chamber was 236±0.8 $cm^3\,m^{-3}$ (95 % confidence interval). Relative humidity of the air entering the chamber was dried to 10-20 % below ambient (mean value of 40.0±1.0 %). The humidity sensors were cross-calibrated prior to use. PPFD was measured during each photosynthetic measurement using the sensor attached to the leaf chamber. The chamber was kept open between readings to maintain the temperature within close to ambient. Air and leaf temperatures during measurement were uncontrolled, but remained closely coupled; mean leaf temperature (measured with a thermocouple) was 24.9±0.6 °C. P_N and g_s were calculated using Eq. II of Caemmerer and Farquhar (1981).

For estimation of photosynthetic parameters, P_N was plotted as a function of I and P_N/I curves were fitted. Curves were fitted on values pooled from all the measurements of each species within each plot using the equation:

$$P_N = P_{max}\,\alpha\, I/(P_{max} + \alpha\, I) - R_D$$

where α is the apparent quantum efficiency (initial slope). This equation describes a rectangular hyperbola and is derived from the non-rectangular hyperbola model described by Jarvis *et al.* (1985), modified following Meir (1996) by omission of the convexity parameter.

Forest microclimate and irradiance of saplings were measured using a data logger (*21X Micrologger, Campbell Scientific*, Loughborough, U.K.). Air temperature was measured using thermocouples (type *K chromel-alumel*; *T.C.*, Uxbridge, U.K.), humidity using a thermistor probe (*MP. 100 Rotronic* probe, *Campbell Scientific*, Loughborough, U.K.), soil temperature using a *107*-thermistor probe (*Campbell Scientific*, Loughborough, U.K.), and PPFD using quantum sensors (*Skye Instruments*, Llandrindod Wells, U.K.). All sensors of each type were cross-calibrated prior to use. The logger was programmed to record each sensor every 10 s, and to calculate and store mean readings every 5 min. The data logger was located in a fixed point in each plot near to a path (with relatively open canopy above) and one set of sensors placed nearby; the other sensors were positioned 5.4 m away in the forest understorey. The *107*-thermistor probes were inserted in the soil to a depth of 2-3 cm; other sensors were placed on 1.3 m tall wooden posts. For measuring the leaf temperature, the thermocouples were attached to the abaxial leaf surface of a shrub species of *Melastomataceae* present near the measurement positions in both plots. Measurements of microclimate were taken daily for 7-8 h starting between 07:00 and 08:00 h in plots 5 and 8 on 7 and 10 d in the first period, and 5 and 8 d in the second period, respectively.

During the second period, a hemispherical photograph was taken just above the growing point of each of the 53 saplings used for measurement of photosynthesis, using a *Nikon FM2* camera with a *Nikkor* 8 mm F/2.8 fisheye lens and *Kodak Tri-X 400 ASA* film. The photographs were analysed using the 'Canopy' digital analysis system (Rich 1989) to calculate direct (DIRsf) and diffuse (DIFsf) site factors, respectively, the proportions of direct and diffuse radiation which potentially reach the point at which the photograph is taken, in relation to a point in the open. Global site factor (Gsf), which is analogous to the proportion of PPFD reaching the point at which the photograph is taken, relative to a point in the open (Rich 1989, Mitchell and Whitmore 1993) was calculated as:

$$\mathrm{Gsf} = \mathrm{a\ DIFsf} + \mathrm{b\ DIRsf}$$

using the coefficients a = 0.55 and b = 0.45 (P.M. Rich, personal communication).

Statistical analysis was carried out using the statistical package *SAS* (SAS Institute 1980). We used the non-parametric Kruskal-Wallis analysis of variance to test for differences between species in crown irradiation, and compared irradiances between plots with Mann-Whitney tests. Because of the non-independence of repeated measurements on the same small groups of saplings, we do not present statistical comparisons of PPFD recorded during measurement of gas exchange, or of P_N and g_s. Instead, we grouped all individual measurements of these variables for each species in each plot, and prepared box-and-whisker plots for quantitative evaluation of gas exchange performance.

Table 2. Measurements of photosynthetic photon flux density (PPFD) [μmol m^{-2} s^{-1}] in two plots of Costa-Rican lowland rain forest subjected to different silvicultural treatments. Means, ranges are in parentheses.

Plot	Period	Sensor position Trail	1	2	3	4	5
5	first	87 (1-1472)	31 (4-857)	29 (3-306)	107 (11-2188)	57 (5-1026)	44 (6-624)
	second	79 (6-1023)	22 (2-264)	26 (3-184)	81 (7-857)	37 (2-841)	35 (3-1089)
8	first	92 (10-1271)	25 (3-667)	27 (3-492)	23 (3-680)	22 (1-867)	70 (6-1469)
	second	48 (4-965)	16 (1-473)	17 (1-796)	14 (1-473)	16 (2-355)	36 (3-848)

Results

Microclimate and irradiance: Most values of PPFD and their means were <100 μmol m^{-2} s^{-1} in both plots in both measurement periods, while most shortlived (usually <5 min) peaks in irradiance were 100-600 μmol m^{-2} s^{-1} (Fig. 1*B*). In plot 5, occasional short peaks of PPFD reached 2000 μmol m^{-2} s^{-1} or more. During the second period, mean values were consistently and substantially lower in plot 8 than in plot 5 (Table 2). Similarly, comparable values of relative humidity were recorded in both plots (Fig. 1*A*) in the first period with mean values of 76.1 and 73.9 % for plots 5 and 8, respectively. During the second period, mean and minimum values of humidity were substantially higher than in the first period in both plots, reflecting the generally overcast and rainy conditions (Table 3). Mean air and leaf temperatures (Fig. 1*C*) were very similar in both plots, both tending to be 1-2 °C lower during the second period than the first. The leaf temperatures were closely coupled to air temperatures (means between 25-27 °C, maximum of 34.2 °C was recorded in plot 5, cf. Table 3). Soil temperature remained very consistent throughout, with mean values around 24 °C in both plots during both periods (Table 3).

Table 3. Measurements of relative humidity [%] and air, leaf, and soil temperatures [°C] in two plots of Costa-Rican lowland rain forest subjected to different silvicultural treatments. Means, ranges in parentheses.

Plot	Period		Relative humidity	Temperature		
				air	leaf	soil
5	first	trail	75.0 (37.8-98.1)	26.2 (21.8-36.9)	26.9 (21.2-34.2)	24.7 (22.8-25.7)
		under canopy	76.1 (52.9-97.8)	25.9 (21.4-30.3)	26.2 (21.4-34.2)	24.7 (23.0-27.8)
	second	trail	91.3 (80.8-99.1)	24.7 (22.7-27.1)	25.1 (23.2-28.3)	24.4 (23.6-25.4)
		under canopy	93.3 (80.3-98.3)	24.8 (23.0-27.5)	25.3 (23.4-30.3)	24.3 (23.7-27.2)
8	first	trail	73.3 (53.2-96.1)	27.4 (22.1-32.1)	27.1 (22.4-32.6)	24.6 (23.4-26.1)
		under canopy	73.9 (55.3-98.0)	27.0 (22.4-31.4)	27.4 (22.9-32.0)	25.3 (23.7-27.0)
	second	trail	88.2 (67.4-97.8)	25.1 (21.8-29.1)	25.3 (22.4-33.4)	24.3 (22.9-25.7)
		under canopy	88.3 (66.1-97.3)	25.4 (22.3-29.5)	25.7 (22.1-32.7)	24.6 (23.4-25.9)

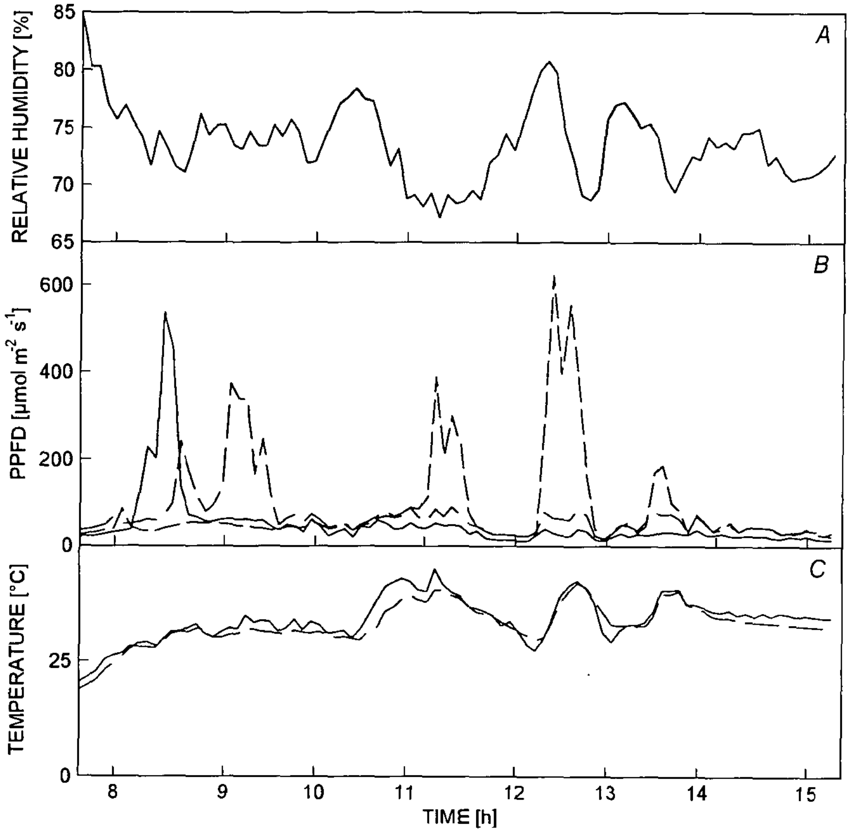

Fig. 1. Variation in microclimate in the understorey of a lowland rain forest in Costa Rica during a single, typical day. *A*: relative humidity, measured from a single position. *B*: photosynthetic photon flux density (PPFD), measured from three different positions within 5 m of the humidity sensor. *C*: leaf (————) and air (— — —) temperatures, measured adjacent to the relative humidity sensor. Measurements were taken in plot 5 between 07:30 and 15:30 h on April 20, 1994.

Differences in irradiance between the two plots were further illustrated by values of Gsf, DIRsf and DIFsf, which were each significantly lower in plot 8 than plot 5 (Mann-Whitney test, $p<0.01$; median values in plots 8 and 5, respectively, were 0.048 *versus* 0.086 for Gsf, 0.027 *versus* 0.052 for DIRsf, and 0.020 *versus* 0.036 for DIFsf). The measurements of PPFD made during the photosynthetic measurements with the sensor attached to the infra-red gas analyser also indicated higher I in plot 5 than 8 (overall median PPFD 99 or 88 μmol m^{-2} s^{-1}, respectively; Fig. 2*A*,*B*). PPFD values showed numerous outliers for all species in both plots, with maxima in the 200-250 μmol m^{-2} s^{-1} range, in spite of the median values <100 μmol m^{-2} s^{-1}. These outliers presumably reflect the incidence of sunflecks.

Differences in irradiance between species within plots were not large. There were no significant between-species differences in Gsf or DIRsf in either of the two plots, though in plot 5, *S. amara* showed a higher DIFsf than any of the other species, except *C. killipianus* ($p<0.05$). In terms of PPFD recorded during measurements of P_N, highest median irradiance was shown by leaves of *C. killipianus* and *S. amara* in plots 5 and 8, respectively, and lowest by *V. ferruginea* in plot 5 and *C. brasiliense* in plot 8 (Fig. 2*A*,*B*).

Photosynthetic characteristics: As in the case of PPFD, there was considerable overlap between species in P_N (Fig. 2*C*,*D*). However, differences between species were more evident in P_N than in PPFD. The highest median P_N 1.26 μmol m^{-2} s^{-1} was recorded in the pioneer *C. killipianus* in plot 5 (Fig. 2*C*), where overall ranges of P_N, similar to those of *C. killipianus*, but with slightly lower medians, were exhibited by *S. amara* and *P. macroloba*. The two species of *Vochysiaceae* (*Q. paraense* and *V. ferruginea*) showed P_N markedly lower than that of the other species (Fig. 2*D*). In general, P_N was markedly lower in plot 8 than in plot 5 (Fig. 2*D*). *S. amara* saplings in this plot, which received higher irradiance during measurements of photosynthesis than those of the other species (Fig. 2*B*), also had the highest P_N with a median of 0.81 μmol m^{-2} s^{-1} (Fig. 2*D*). The tolerant *M. guianensis* and the putatively intermediate species, *C. brasiliense* and *Q. paraense*, showed the lowest P_N in this plot.

The g_s was more clearly differentiated among species than either PPFD or P_N in plot 5 (Fig. 2*E*). Highest median g_s, by a large margin, was shown by *C. killipianus*, while *S. amara, P. macroloba,* and *L. procera* exhibited intermediate values and the lowest g_s were shown by *V. ferruginea* and *Q. paraense* (Fig. 2*E*). In plot 8, g_s was lower overall than in plot 5, as in the case of PPFD and P_N (Fig. 2*E*). Highest g_s was exhibited by *S. amara* and *P. macroloba* and lowest by *C. brasiliense* and *Q. paraense* (Fig. 2*E*). The g_s was consistently higher in *M. guaianensis* than in the latter two species, even though the three differed little in terms of P_N.

The degree of fit in P_N/I curves varied markedly between species ($r^2 = 0.09$-0.51; Table 4). Most of the P_N/I plots were characterised by a high scatter (Fig. 3). Error associated with the curve fitting procedure was also increased by the restricted range of I values in a number of cases; because the range of I values was wider in plot 5, the fits were better than for the latter plot. For *V. ferruginea* and *S. amara* in plot 8, the lack of measurements at sufficiently high I resulted in a straight line being fitted, making P_{max} impossible to estimate (Fig. 3*G*,*H*).

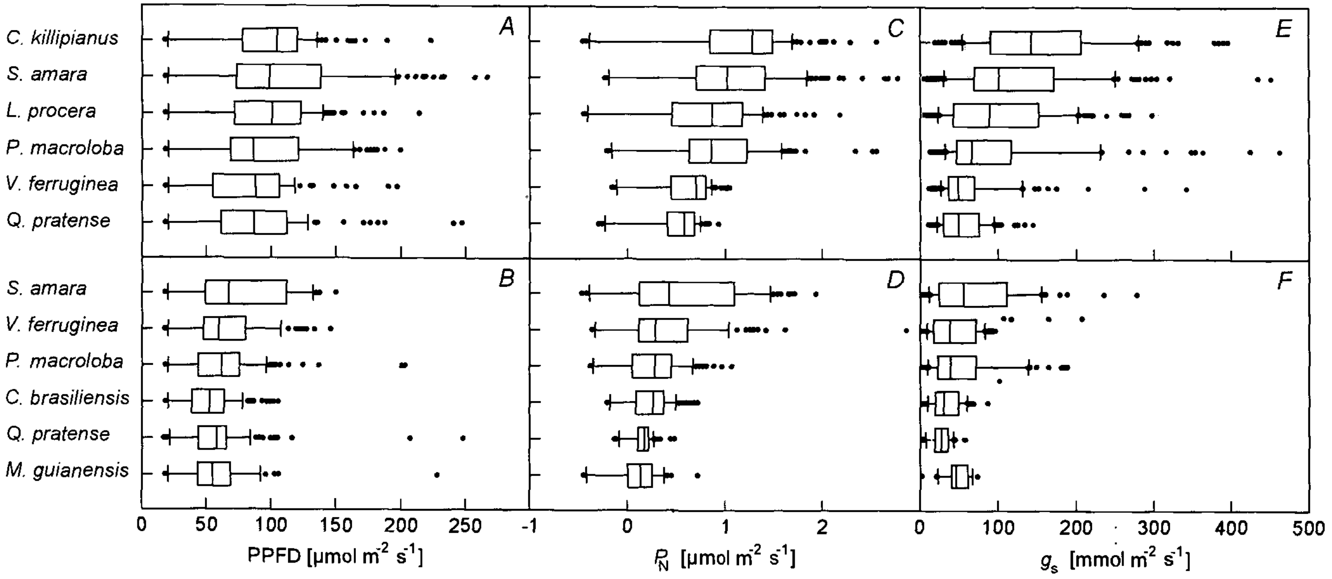

Fig. 2. Box and whisker plots of (*A*, *B*) photosynthetic photon flux density (PPFD; µmol m^{-2} s^{-1}), (*C*, *D*) net photosynthetic rates (P_N; µmol m^{-2} s^{-1}), and (*E*, *F*) stomatal conductances (g_s; mmol m^{-2} s^{-1}) measured during recording of photosynthesis of saplings of canopy tree species in plots 5 (*A*, *C*, *E*) and 8 (*B*, *D*, *F*) of a disturbed Costa-Rican rain forest, April-May 1994. Vertical lines within box indicate median, left and right edges of box indicate 25th and 75th percentiles, and horizontal line indicates range from 10th to 90th percentile; black dots are outliers. Species are ordered from top to bottom for each plot by median P_N.

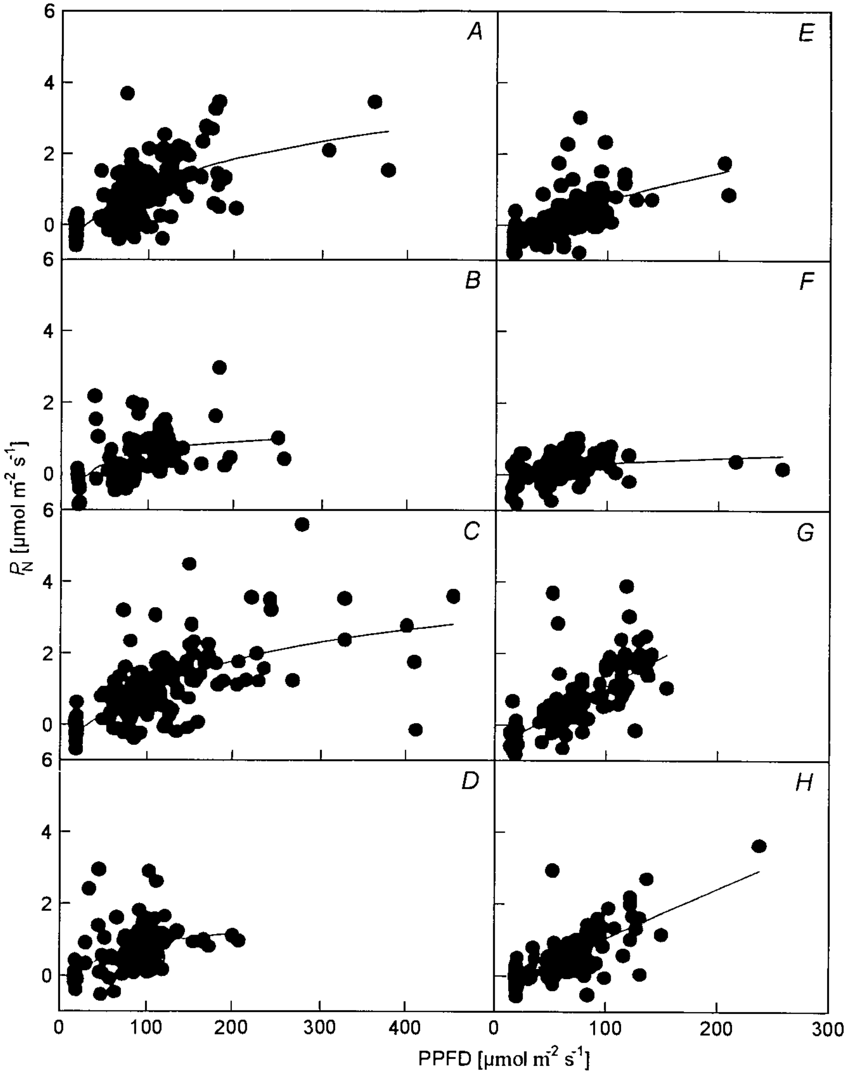

Fig. 3. Relationship between net photosynthetic rate (P_N) and photosynthetic photon flux density (PPFD) in saplings of four canopy tree species in a disturbed Costa Rican rain forest. *A* to *D*: plot 5, *E* to *H*: plot 8. Species: *Pentaclethra macroloba* (*A*, *E*), *Qualea paraense* (*B*, *F*), *Simarouba amara* (*C*, *G*), and *Vochysia ferruginea* (*D*, *H*). For details of curve fitting procedure, see text. Each point represents an instantaneous reading of the sapling *in situ* in the forest understorey.

As the estimated values of P_{max} were subject to a relatively high error, no significant differences between species were recorded. The general trend of the fitted P_{max} values is nevertheless similar to that of field measurements of P_N; for plot 5, a high value was shown by *C. killipianus*, intermediate values by *S. amara* and *P. macroloba*, and lowest values by *V. ferruginea* and *Q. paraense*. The only exception to this trend was the fitting of the highest P_N to P_N/I curves for *L. procera*, but P_{max}

in this species also showed the highest error by a large margin. For plot 8, fitted P_{max} values, as in the case of the field measurements of P_N, varied much less between species.

Table 4. Photosynthetic characteristics of seedlings of nine species in two plots of Costa Rican lowland rain forest subjected to different silvicultural treatments. Results of curve fitting of net photosynthetic rate [μmol m^{-2} s^{-1}] *versus* irradiance. Abbreviations: α, apparent quantum efficiency (initial slope) [mol mol^{-1}(photon)]; r^2, regression coefficient; R_D, dark respiration rate [μmol m^{-2} s^{-1}]. Predicted means ± 95 % confidence limit.

	r^2	n	P_{max}	α	R_D
Plot 5					
Calophyllum brasiliense	-	-	-	-	-
Croton killipianus	0.51	158	7.0 ± 5.2	0.03 ± 0.02	1.00 ± 0.56
Laetia procera	0.46	159	9.2 ± 13.5	0.02 ± 0.01	0.79 ± 0.47
Minquartia quianensis	-	-	-	-	-
Pentaclethra macroloba	0.43	156	4.8 ± 2.1	0.03 ± 0.02	0.62 ± 0.49
Qualea paraense	0.23	92	2.4 ± 2.0	0.09 ± 0.32	1.26 ± 2.64
Simarouba amara	0.42	161	4.9 ± 1.7	0.03 ± 0.02	0.66 ± 0.57
Virola koschnyi	0.00	105	0.2 ± 0.8	0.00 ± 0.08	-0.28 ± 1.31
Vochysia ferruginea	0.19	96	2.3 ± 1.1	0.06 ± 0.18	0.87 ± 2.0
Plot 8					
Calophyllum brasiliense	0.32	124	3.0 ± 3.9	0.02 ± 0.03	0.64 ± 0.64
Croton killipianus	-	-	-	-	-
Laetia procera	-	-	-	-	-
Minquartia quianensis	0.24	50	2.5 ± 2.1	0.07 ± 0.33	1.46 ± 3.23
Pentaclethra macroloba	0.33	125	4.7 ± 4.9	0.02 ± 0.02	0.84 ± %.55
Qualea paraense	0.09	133	1.1 ± 0.6	0.03 ± 0.08	0.51 ± 1.12
Simarouba amara	0.24	122	n.d.	0.02 ± 0.03	0.85 ± 0.96
Virola koschnyi	-	-	-	-	-
Vochysia ferruginea	0.51	113	n.d.	0.02 ± 0.01	0.73 ± 0.36

Species also demonstrated little variation in the predicted values of R_D (between -0.51 and -1.46 μmol m^{-2} s^{-1} in *Q. paraense* and *M. guianensis*, respectively; Table 4). Similar values of R_D were obtained in the field during the first period by covering the leaf chamber with alumium foil (N. Vera, unpublished). The fitted values of apparent quantum efficiency were also rather uniform, divergences from the prevailing values of 0.02-0.03 mol(CO_2) mol^{-1}(photon) were accompanied by wide confidence limits (Table 4).

Relatively few P_N values were obtained in the second period, for the reasons mentioned earlier; the measurements were restricted to plot 8. In all species, the mean values of P_N were significantly lower than those recorded during the first period ($p<0.01$). The maximum median P_N was again in *S. amara* (0.7 μmol m^{-2} s^{-1}); values for all the other species were <0.3 μmol m^{-2} s^{-1}.

Discussion

Forest microclimate: As concerns skewed distributions of PPFD with occasional high values associated with sunflecks, and daily patterns of temperature and relative humidity of the air, understorey microclimates at La Tirimbina forest were similar to those described from other neotropical forests (Chazdon and Fetcher 1984, Fetcher *et al.* 1985, Raich 1989, Smith *et al.* 1992; see the review by Chazdon *et al.* 1996). The hotter, drier conditions and generally higher PPFDs of the first period of our study reflected normal seasonal climatic trends of northeastern Costa Rica (Fetcher *et al.* 1985, 1994, Rich *et al.* 1993). Marked short-term microclimatic changes owing to local canopy closure have been demonstrated in secondary and old-growth vegetation (Fetcher *et al.* 1985, Rich *et al.* 1993). Increases in canopy cover between the two periods of our study, particularly in the more haevily disturbed plot 5, might have contributed to the changes between periods observed at La Tirimbina.

The radiant energy availability recorded in plot 5, both during measurements of P_N and determined by hemispherical photography, reflect the consequences of canopy opening due to the silvicultural treatment. The treatments applied are designed to benefit commercial trees $\geq$10 cm dbh (Hutchinson 1988), and their effect on understorey microclimates is indirect. The lower relative humidities and higher air temperatures recorded for plot 8 are perhaps unexpected, given the differences in solar radiation regimes. The soil temperature was constant in spite of the variations between plots and periods shown by other variables. Irradiance in the understorey at La Tirimbina during the present study was greater than in the similar, but undisturbed forest at nearby La Selva, where daily mean instantaneous PPFD values <10 μmol m^{-2} s^{-1} are the norm (Chazdon and Fetcher 1984). Relative humidities and air temperatures in understorey of our experiments were similar to those for gap environments at La Selva (Fetcher *et al.* 1994).

Irradiance and photosynthetic characteristics of saplings: Four putative guilds were represented among the eight study species, but sapling I varied little between species within each of the two plots, with only a slight tendency towards association of higher median PPFDs during measurements of photosynthesis with intolerant species (cf. Oberbauer *et al.* 1993). Low values of PPFD and P_N prevailed in many microsites: in plot 8 of the present study, median P_N was <0.5 μmol m^{-2} s^{-1}, similar to that for saplings of three canopy tree species at La Selva (Oberbauer *et al.* 1993). Low PPFDs limited the scope for modelling gas exchange which helps in the simulation and prediction of regeneration patterns, variations in productivity, or forest ecology (Landsberg 1986, Riddoch *et al.* 1991). Greater precision in model fitting requires a wider range of PPFD values than that encountered at La Tirimbina (cf. Riddoch *et al.* 1991). For a given I, P_N and g_s showed wide ranges in our study, as in field investigations of Riddoch *et al.* (1991) or Oberbauer *et al.* (1993). This reflects the influence of factors other than PPFD on P_N in tropical forest understoreys, among which may be plant water status and gradients of temperature, humidity, and CO_2 concentration in the understorey (Riddoch *et al.* 1991). The P_N/I curves for La Tirimbina saplings showed that the large number of outliers in the upper ranges of PPFD values during measurements of P_N (presumably from sunflecks) were often associated with high P_N. This result indicates a certain capacity to respond to sunflecks through increased P_N, in spite of the predominance of low PPFD values (Chazdon *et al.* 1996).

The comparison of sapling P_N in plots 5 and 8 is confounded with the greater P_N of some of the species found only in plot 5 (see below). The very presence in the latter plot of saplings of *C. killipianus* and *L. procera*, however, is undoubtedly a consequence of the greater canopy opening there. Thus the higher I in plot 5, presumably brought about by the silvicultural treatment, made possible higher P_N among saplings. All the species present in both plots, even those classified as intermediates or tolerants, showed higher P_N and g_s in plot 5 than in plot 8. Hence shade is tolerated, rather than required, by saplings growing under closed canopies. Such a response of sapling P_N to different canopy opening may be a generalised, albeit rarely documented, component of forest response to drastic disturbance.

In autecological terms, the saplings of different tropical rain forest tree species growing within small areas may show markedly different gas exchange characteristics; these differences may or may not correspond to expectations based on subjective guild classifications. P_N at all but the lowest PPFD decreased from "weeds of gaps" to pioneer trees to "climax trees" in the Nigerian semi-deciduous forest studied by Riddoch *et al.* (1991), while g_s did not differ between weeds of gaps and pioneer trees, but was considerably higher in both these groups than in climax trees. At La Selva, P_{max} was highest in *P. elegans* and *S. amara*, previously considered relatively light-demanding, and P_N in diffuse radiation (PPFD 15-20 μmol m^{-2} s^{-1}) highest in *L. ampla*, previously considered shade-tolerant (Oberbauer *et al.* 1993). Similarly, our highest values of P_N and g_s were shown—with one exception—by species previously considered light demanding: the pioneer *C. killipianus* and the long-lived *S. amara* and *L. procera*. The differences in P_N between these species and, for example, *Q. paraense*, were more marked than for PPFD measured simultaneously with P_N and g_s, and represent the expression of fundamental ecophysiological differences between the species in the disturbed forest habitats at La Tirimbina.

The estimation by modelling of parameters such as R_D and α was intended to contribute to understanding of between-species differences in regeneration pattern. For reasons already discussed, we were unable to estimate R_D with any precision. For α, other studies have, just like ours, yielded values in the general range of 0.02-0.03 μmol(CO_2) mol^{-1}(photon), with little variation between species (Ramos and Grace 1990, Riddoch *et al.* 1991, Ackerly 1996). Quantum efficiency does not, therefore, appear to make an important contribution to differences between species in regeneration strategy (Riddoch *et al.* 1991).

Similar to other field and laboratory studies, we found some divergences of gas exchange characteristics from expectations derived from subjective guild classifications. In particular, there is little support for the idea that a single ecological temperament is expressed throughout the life cycle: the ranking of our study species on the basis of median leaf P_N, for example (Fig. 2), is different from one based on growth rates of trees ≥10 cm dbh (Table 1). Some species are ranked lower in terms of sapling P_N than in terms of growth rates of established trees, while others showed the reverse trend. For example, detailed ecophysiological studies have confirmed that the canopy dominant *P. macroloba* is a shade-tolerant species (see Hartshorn 1983, Oberbauer and Strain 1986, Fetcher *et al.* 1987, Lieberman *et al.* 1990), but we found for this species P_N indistinguishable from that of *L. procera* and greater than that of *V. ferruginea*, both putatively intolerant (P_N and g_s of saplings of *V. ferruginea* were among the lowest in both plots). *P. macroloba* grows relatively fast in diameter (Lieberman *et al.* 1990), and in some circumstances it may dominate young secondary forest (Werner 1984, Finegan 1992). For trees ≥10 cm dbh, however, its diameter growth rate at La Tirimbina during the period 1988-1996 was lower than that of *V. ferruginea* and *S. amara* (Camacho *et al.* 1999; Table 1), and in secondary forest at the site it was always overtopped by *S. amara* when coexisting with them (Finegan *et al.*, unpublished). Similarly, P_N of the two species previously classified as intermediates, *C. brasiliense* and *Q. paraense*, differed little from those of the tolerants *P. macroloba* and *M. guianensis* in the more shaded plot 8, while *Q. paraense* showed markedly lower P_N and g_s than *P. macroloba* in plot 5. Individuals ≥10 cm dbh of *Q. paraense* nevertheless show diameter increments similar to or greater than those of *P. macroloba*, and always greater than in *M. guianensis* (Camacho *et al.* 1999; Table 1).

How might these varying expressions of ecological temperament be interpreted? Firstly, it is far from safe to assume that the gas exchange characteristics of individual leaves are simply related to the growth rates of saplings or trees, and the apparently conflicting signals given by sapling P_N and tree growth may be due to differences between species in patterns of allocation of the assimilated carbon, a poorly documented aspect of the biology of tropical trees (Ramos and Grace 1990, Oberbauer *et al.* 1993). Generally, ontogenetic patterns in ecological temperament may be involved. Clark and Clark (1992) stressed the need to determine whether the requirements and tolerances of tree species change during ontogeny. They indicated that the developmental stage represented by individuals <1 cm dbh (which includes all those used for our P_N measurements) is particularly critical in the life histories of canopy and emergent trees, being characterised by slow growth and high mortality. The predominance of low PPFD microsites in tropical forest understories is undoubtedly linked to the critical nature of this life-cycle stage, and means that survival of most saplings probably depends on a low compensation irradiance, efficient use of radiant energy from sunflecks, and the prevention of damage by herbivores and pathogens, much more than on the P_{max} (Chazdon *et al.* 1996, Kitajima 1996). In such circumstances, strong selection for "understorey-tolerant" characteristics at the sapling level may affect even essentially light-demanding species. The "seedling bank" strategy exhibited by some *Dipterocarpaceae*, which otherwise behave as relatively intolerant species (Whitmore 1984), may be a consequence of such selection. The decoupling of sapling ecophysiological characteristics from those of later developmental stages, in response to the prevailing understorey I, could have led to similarity of P_N of *V. ferruginea* and *Q. paraense* and of slower-growing species such as *M. guianensis* and *P. macroloba*.

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