

# Photosynthetic Traits of Five Neotropical Rainforest Tree Species: Interactions between Light Response Curves and Leaf-To-Air Vapour Pressure Deficit

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## ABSTRACT

*Measurements of leaf gas exchange at different photosynthetic photon flux density (PPFD) levels were conducted in order to compare the photosynthetic traits of five neotropical rainforest tree species, with a special emphasis on empirical mathematical models to estimate the light response curve parameters incorporating the effects of leaf-to-air vapour pressure deficit (D) on the saturated photosynthetic rate ( $A_{max}$ ). All empirical mathematical models seemed to provide a good estimation of the light response parameters. Comparisons of the leaf photosynthetic traits between different species needed to select an appropriate model and indicated the microenvironmental conditions when the data were collected. When the vapour pressure deficit inside the chamber was not controlled, the incorporation of linear or exponential functions that explained the effects of D on leaf gas exchange, was a very good method to enhance the performance of the models.*

**Key words:** Brazilian atlantic rainforest; ecosystem process models; net photosynthetic rate

## INTRODUCTION

Tropical rainforests represent a great proportion of the terrestrial biomass productivity (Malhi and Grace, 2000) and studies that evaluate leaf photosynthetic characteristics of tree species are needed to quantify the carbon dynamics at regional and global scales. Knowledge of leaf photosynthetic traits is needed to understand the carbon cycles of a particular forest ecosystem, to evaluate theoretical aspects of ecological succession, to select intercrop species in agroforestry (Bazzaz and Pickett, 1980; Barker et al., 1997; Lüttige, 1997), and to parameterize ecosystem process models that are used as tools for the assessment of sustainable yields from natural and planted forests, or to estimate the total

net primary productivity as the stand grows (Running and Coughan, 1988; McMurtrie, 1993; Aber et al., 1996; Landsberg and Gower, 1997).

It is well established that photosynthesis responds to light or photosynthetic photon flux density (PPFD), expressed as the moles of photons between 400-700 nm per square meter per second in a non-linear mathematical function (Nobel, 1991). Different empirical (Thornley, 1976; Leverenz, 1994; Ögren and Evans, 1993) and mechanistic models (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982) to estimate photosynthesis have been proposed and discussed in the literature. Despite some differences between the formulas, all these models were ultimately proposed with the same objective, i.e. to estimate photosynthetic light response parameters, such as

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the light saturated photosynthetic rate ( $A_{\max}$ ) and the apparent quantum yield ( $\alpha$ ) that explained the responses of photosynthesis to environmental variables and permitted modelling leaf to canopy carbon exchange (Beyshlag and Ryel, 1998). Despite of the high accuracy of the mechanistic models, empirical mathematical models have the advantage that they are easily parameterized from the data collected in field conditions. Empirical models are currently used and the derived parameters have been presented and discussed in several studies about different aspects of tree and forest ecophysiology (Prado et al., 1994; Kubiske and Pregitzer, 1996; Sullivan et al., 1996; Kitajima et al., 1997; Valladares et al., 1997; Eschenbach et al., 1998; Evans et al., 2000; Hiremath, 2000). However, there are no reports on the forest ecophysiology comparing these models and the associated light response curve parameters.

Other environmental factors also affect the net photosynthetic rate such as air temperature, atmospheric  $\text{CO}_2$  molar fraction and vapour pressure deficit (Nygren, 1995; Pachepsky and Acock, 1996; Day, 2000). In tropical rainforests, vapour pressure deficit changes at temporal and spatial scales (Lüttige, 1997). Because the vapour pressure deficit is directly dependent on relative humidity and air temperature (Landsberg, 1986), this microenvironmental factor is highly variable during the day or between days (Granier et al., 1996; Ishida et al., 1996) and depends on growth environmental conditions, such as forest gaps, abandoned agricultural lands or forest understory (Barker et al., 1997; Loik and Holl, 2001). High vapour pressure deficit values can induce stomatal closure and limits the influx of  $\text{CO}_2$ , with a strongly effect on the diffusive phase of photosynthesis. For many tropical and temperate tree species, the closing of the stomata has been observed as a function of the increases in the evaporative demand of the atmosphere (Dolman and Van Den Burg, 1988; McCaughey and Iacobelli, 1993; Landsberg and Gower, 1997; Yang et al., 1998; Mielke et al., 1999). Also, the sensitivity of the stomata to the vapour pressure deficit is largely variable between different plant species (Franks and Farquhar, 1999).

The aim of this study was to compare the photosynthetic traits of five neotropical rainforest tree species with a special emphasis on the use of empirical models to estimate light response curve parameters and the effects of the leaf-to-air vapour

pressure deficit on the light saturated photosynthetic rates ( $A_{\max}$ ).

## METHODS

The measurements were performed in the arboretum of the Universidade Estadual de Santa Cruz (UESC) and at the Centro de Pesquisas do Cacau (CEPEC)/CEPLAC, both located in the county of Ilhéus (14°47'S, 39°10'W, 15 masl), and at the Estação Experimental Lemos Maia (ESMAI)/CEPLAC, located in the county of Una (15°15'S, 39°05'W, 105 masl), Bahia, Brazil. The studied species were *Caesalpinia peltophoroides* Benth. (Caesalpinaceae), *Macrolobium latifolium* Vog. (Caesalpinaceae), *Manilkara salzmannii* (DC.) Lamb. (Sapotaceae), *Theobroma cacao* L. (Sterculiaceae) and *Theobroma grandiflorum* (Wild. ex Spring) Schumann (Sterculiaceae). The first three species were grown in the UESC's arboretum, while *T. cacao* was grown in a shade house in the nursery of CEPEC/CEPLAC and *T. grandiflorum* in an agroforestry system, partially shaded by a *Cocos nucifera* L. plantation, in ESMAI/CEPLAC. Among the species studied, *C. peltophoroides*, *M. latifolium* and *M. salzmannii* were native to the southern Bahian atlantic rainforest and have been very important, both economically and ecologically. *C. peltophoroides* and *M. latifolium* are fast-growing secondary species that naturally grows at moderate shade to full sunlight, and *M. salzmannii* is a slow-growing late successional species. *T. cacao* and *T. grandiflorum* are shade tolerants late secondary species. These species are native to the Amazon basin, being cultivated in agroforestry systems.

Leaf gas exchange was measured in one single mature and completely expanded leaf of several individuals per species, always between 930-1330. Light response curves were obtained using a Portable Photosynthesis System LI-6400 (Li-Cor, USA), equipped with an artificial light source 6400-02B RedBlue. Leaf gas exchange measurements at different levels of photosynthetic photon flux density incident at leaf surface (PPFD) were made using the "Light curve" routine of the *Open 3.3* software (Li-Cor, USA). Measurements were taken at eight levels of PPFD, i.e. 0, 50, 100, 200, 400, 800, 1200 and 1600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for the species growing at arboretum conditions (*C. peltophoroides*, *M. latifolium* and *M. salzmannii*) and at seven levels of PPFD, i.e. 0, 50,

100, 200, 400, 800 and 1200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for the species growing in shaded and partially shaded environments (*T. cacao* and *T. grandiflorum*). The measurements were always performed from the upper to the lower values of PPFD. The minimum time allowed for the reading stabilization at each level of PPFD was 120s, and the maximum time for saving each reading was 150s. The maximum coefficient of variation allowed for each reading's save was set to 1%. Seven to nineteen light response curves per species were obtained, depending on the species and sites: *C. peltophoroides* (n = 7), *M. latifolium* (n = 10), *M. salzmannii* (n = 10), *T. cacao* (n = 7) and *T. grandiflorum* (n = 19).

The net photosynthetic rate by unit of leaf area (A) and the stomatal conductance to water vapour (gs) were calculated, respectively, using the values of CO<sub>2</sub> and humidity variation inside the chamber, both measured by the infrared gas analyzer of the portable photosynthesis system. Dark respiration (Rd) corresponded to readings of PPFD = 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . With the exception of PPFD, no microenvironmental variable inside the chamber was controlled. Values of atmospheric CO<sub>2</sub> molar fraction (Ca), leaf (T<sub>L</sub>) and air temperature inside the chamber (T<sub>A</sub>) were obtained from the sensors of the equipment, while leaf-to-air vapour pressure deficit (D) and intercellular air space CO<sub>2</sub> molar fraction (Ci) were estimated by the *Open 3.3* software. The ratios of intercellular to atmospheric CO<sub>2</sub> molar fractions were calculated by dividing Ci by Ca.

To estimate photosynthetic light response parameters a simple rectangular hiperbola, described by Thornley (1976) and Landsberg (1986), was rewritten and used in the form:

$$A = A_{\max}[\text{PPFD}/(\beta + \text{PPFD})] - R_d \quad (\text{Model 1})$$

where A is the net photosynthetic rate, A<sub>max</sub> is the light saturated photosynthetic rate, β is the point of inflexion of the curve, which was defined as one half of the saturated PPFD, and R<sub>d</sub> is the dark respiration rate. Three variations of this model were tested, incorporating mathematical functions that explain the effects of D on A<sub>max</sub>:

$$A = A_{\max}[\text{PPFD}/(\beta + \text{PPFD})](1 - D/\gamma) - R_d \quad (\text{Model 2})$$

$$A = A_{\max}[\text{PPFD}/(\beta + \text{PPFD})]\exp(-\gamma D) - R_d \quad (\text{Model 3})$$

$$A = A_{\max}[\text{PPFD}/(\beta + \text{PPFD})](D^{-\gamma}) - R_d \quad (\text{Model 4})$$

where γ is a coefficient that indicates the sensitivity of leaf gas exchange to D.

A Gauss-Newton non-linear estimate routine of Statistica for Windows, version 5.0 (StatSoft, 1995) was used to obtain the best fittings for all the models. After this procedure, the values of A<sub>max</sub> from the models 2, 3 and 4 were corrected based on the mean value of D observed in all of the measurements (1.70 ± 0.02 kPa, n = 388). In all models, the values of the apparent quantum yield (α) were estimated as:  $\alpha = A_{\max}/\beta$ .

The results were interpreted and discussed based on the different light response curve parameters estimated from the models and species environmental growth conditions. Simple statistical comparisons between the models were made by comparing the values of regression coefficients (r<sup>2</sup>) and the graphical analysis. Residual analysis were also conducted in order to interpret the effects of D on the values of A estimated from the different models.

## RESULTS

Measurements of leaf gas exchange made at different days and environmental conditions generated differences in the microenvironmental variables inside the chamber (Table 1). The maximum mean values of D and T<sub>A</sub> were observed for *T. grandiflorum*, whereas the minimum values of these variables were observed for *C. peltophoroides*. The mean values of Ca varied from 373.6 to 380.1  $\mu\text{mol mol}^{-1}$ , for *C. peltophoroides* and *M. latifolium*, respectively. The average maximum values of the saturated net photosynthetic rate, measured at 1600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for *C. peltophoroides*, *M. latifolium* and *M. salzmannii* and at 1200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for *T. cacao* and *T. grandiflorum*, were observed in the species that were growing in arboretum conditions. The maximum and minimum mean values of A<sub>sat</sub> were observed for *C. peltophoroides* and *T. cacao* (10.51 and 5.69  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ , respectively). Similarly, the maximum and minimum values of stomatal conductance measured simultaneously with A<sub>sat</sub> (gs<sub>sat</sub>) were also observed for these two species (0.238 mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup> for *C. peltophoroides*, and 0.086 mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup> for *T. cacao*). The maximum values of the Ci/Ca ratio were also observed in *C.*

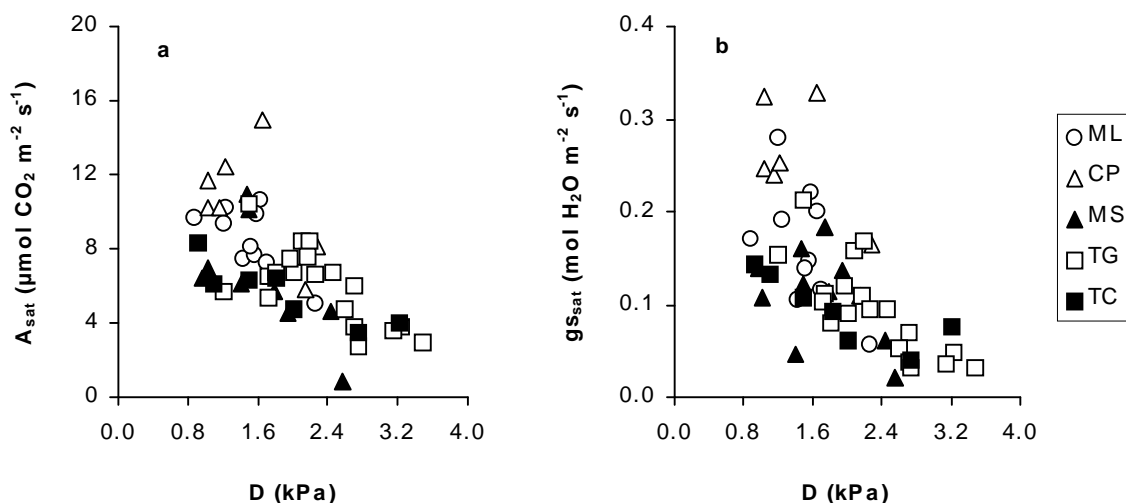
*peltophoroides* (0.72) and the minimum values were observed in *T. grandiflorum* (0.61).

Based on all species, strong effects of D on  $A_{\text{sat}}$  and  $g_{\text{sat}}$  were observed, in which the linear and exponential functions provided the highest values of  $r^2$  (Fig. 1). Direct relationship was also observed between  $g_{\text{sat}}$  and  $A_{\text{sat}}$  (Fig. 2), indicating a strong dependence of the saturated net photosynthetic rates to stomatal conductance.

The best fittings for Model 1 were observed for *M. latifolium* (Table 2). When the growth conditions of the species were compared, large differences between the statistical parameters were observed, but when the models were compared within the same species, little differences were observed for the regression coefficients ( $r^2$ ).

**Table 1** - Leaf-to-air vapour pressure deficit (D), air temperature ( $T_A$ ) and atmospheric  $\text{CO}_2$  molar fraction (Ca), saturated values of net photosynthetic rate ( $A_{\text{sat}}$ ) and stomatal conductance ( $g_{\text{sat}}$ ), ratio between intercellular air space and atmospheric  $\text{CO}_2$  molar fraction (Ci/Ca), and dark respiration rate (Rd) for each of the studied species. For microclimatic variables each value represents a mean of 46 to 128 repetitions  $\pm$  SE (see Table 1). For the leaf gas exchange variables each value represents a mean of 7 to 19 repetitions  $\pm$  SE: *C. peltophoroides* (CP, n = 7), *M. latifolium* (ML, n = 10), *M. salzmannii* (MS, n = 10), *T. cacao* (TC, n = 7) and *T. grandiflorum* (TG, n = 19). The values of  $g_{\text{sat}}$  and Ci/Ca were measured simultaneously with  $A_{\text{sat}}$ , at 1600 or 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , depending on the species.

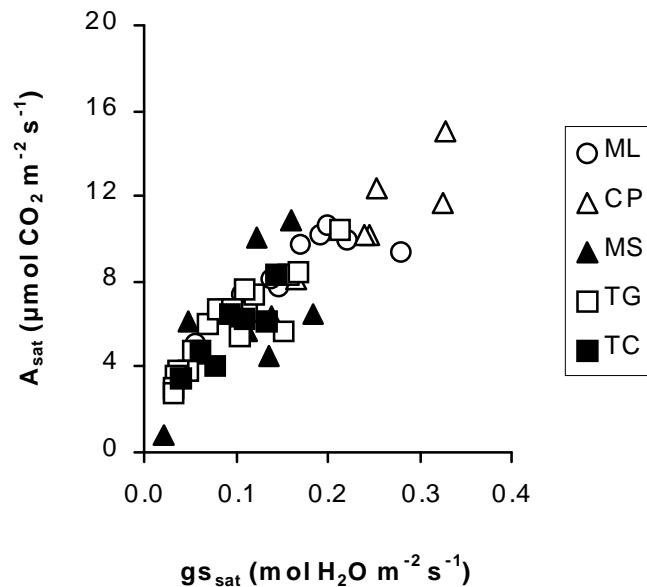
Species	D (kPa)	$T_A$ ( $^{\circ}\text{C}$ )	Ca ( $\mu\text{mol mol}^{-1}$ )	$A_{\text{sat}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$g_{\text{sat}}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	Ci/Ca	Rd ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
CP	1.42 $\pm$ 0.40	29.9 $\pm$ 1.8	373.6 $\pm$ 3.7	10.51 $\pm$ 1.12	0.238 $\pm$ 0.030	0.72 $\pm$ 0.01	1.38 $\pm$ 0.16
ML	1.42 $\pm$ 0.27	30.6 $\pm$ 1.3	380.1 $\pm$ 3.9	8.69 $\pm$ 0.53	0.159 $\pm$ 0.021	0.67 $\pm$ 0.02	0.83 $\pm$ 0.11
MS	1.53 $\pm$ 0.43	30.1 $\pm$ 2.0	374.6 $\pm$ 2.1	6.70 $\pm$ 0.72	0.109 $\pm$ 0.016	0.63 $\pm$ 0.05	1.05 $\pm$ 0.10
TC	1.83 $\pm$ 0.70	29.9 $\pm$ 3.1	376.9 $\pm$ 11.2	5.69 $\pm$ 0.60	0.086 $\pm$ 0.013	0.64 $\pm$ 0.02	1.19 $\pm$ 0.18
TG	2.20 $\pm$ 0.51	33.6 $\pm$ 1.5	377.1 $\pm$ 6.2	6.35 $\pm$ 0.43	0.095 $\pm$ 0.011	0.61 $\pm$ 0.02	1.24 $\pm$ 0.08



**Figure 01** - Relationships between the leaf-to-air vapour pressure deficit (D), the saturated net photosynthetic rate (a,  $A_{\text{sat}}$ ) and stomatal conductance (b,  $g_{\text{sat}}$ ). The values of A and gs were both measured at 1600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *C. peltophoroides* (CP), *M. latifolium* (ML) and *M. salzmannii* (MS) or 1200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *T. cacao* (TC) and *T. grandiflorum* (TG).  $A_{\text{sat}} = 12.27 - 2.77D$  ( $r^2 = 0.44$ );  $A_{\text{sat}} = 15.79\exp(-0.48D)$  ( $r^2 = 0.44$ );  $A_{\text{sat}} = 10.37D^{-0.83}$  ( $r^2 = 0.39$ );  $g_{\text{sat}} = 0.27 - 0.07D$  ( $r^2 = 0.44$ );  $g_{\text{sat}} = 0.41\exp(-0.72D)$  ( $r^2 = 0.54$ ); and  $g_{\text{sat}} = 0.22D^{-1.27}$  ( $r^2 = 0.49$ ). (n = 53)

**Table 2** - Characteristics of the light response curves. For models 2, 3 and 4, the values of light response curve parameters were calculated before correcting  $A_{\max}$  based on the mean values of  $D$  observed for all of the studied species ( $1.70 \pm 0.02$  kPa,  $n = 388$ ). *C. peltophoroides* (CP), *M. latifolium* (ML), *M. salzmannii* (MS), *T. cacao* (TC) and *T. grandiflorum* (TG).

Species	Model	$A_{\max}$	$\beta$	$\alpha$	Rd	$\gamma$	$r^2$
CP	1	12.86	142.9	0.09	1.38	-	0.84
	2	12.36	163.4	0.08	1.36	5.94	0.87
	3	12.39	161.1	0.08	1.38	0.21	0.87
	4	12.27	158.7	0.08	1.38	0.28	0.87
ML	1	9.79	122.4	0.08	0.81	-	0.89
	2	9.19	132.1	0.07	0.75	4.64	0.92
	3	9.50	130.4	0.07	0.77	0.28	0.92
	4	9.22	127.6	0.07	0.78	0.39	0.78
MS	1	7.51	107.3	0.07	1.06	-	0.69
	2	7.37	128.8	0.06	0.97	4.71	0.76
	3	7.32	123.1	0.06	1.02	0.28	0.75
	4	7.32	120.0	0.06	1.02	0.33	0.73
TC	1	6.81	61.9	0.11	1.21	-	0.82
	2	7.10	62.5	0.11	1.23	6.31	0.94
	3	7.00	61.8	0.11	1.23	0.24	0.94
	4	6.74	59.3	0.11	1.23	0.42	0.94
TG	1	8.03	89.2	0.09	1.34	-	0.77
	2	9.47	95.1	0.10	1.31	5.30	0.88
	3	9.43	92.7	0.10	1.34	0.30	0.87
	4	9.19	91.1	0.10	1.35	0.57	0.86



**Figure 02** - Relationship between saturated stomatal conductance ( $g_{s_{\text{sat}}}$ ) and net photosynthetic rate ( $A_{\text{sat}}$ ). The values of  $A$  and  $g_s$  were both measured at  $1600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *C. peltophoroides* (CP), *M. latifolium* (ML) and *M. salzmannii* (MS) or  $1200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *T. cacao* (TC) and *T. grandiflorum* (TG). ( $n = 53$ )

Differences between the values of light response curve parameters were also observed. For all the species, the very best fittings were obtained with Models 2 and 3, in which the smallest value of  $r^2$  was observed in *M. salzmanii* (0.75). The fitted data based on Model 3 and the measured values are presented in Fig. 3.

The smallest differences between measured and estimated values of A, in all classes of D (Table 3) were observed in models in which the microenvironmental parameter was included. Model 1, on the other hand, had a tendency to underestimate A at low D and overestimate A at high D (i.e. below and above 1.5 and 3.0 kPa, respectively). The highest mean values of the residuals were also observed for the Model 1, above 2.5 kPa.

All models provided good estimates of Rd (Table 4), but a poor relationship between measured and estimated values of  $A_{\text{sat}}$  was observed for the Model 1. In this case, the best results were observed in Models 2 and 3, in which linear or exponential functions that explained the effects of the leaf-to-air vapour pressure deficit on leaf gas exchange, were incorporated.

## DISCUSSION

The observation of the highest values of  $A_{\text{sat}}$  and  $g_{\text{sat}}$  in trees growing at arboretum conditions was expected because the leaves of these trees were constantly exposed to full sunlight and all were canopy trees; moreover, the environmental conditions, especially light and atmospheric  $\text{CO}_2$ , have strong influences on the leaf gas exchange characteristics of the leaves (Kubiske and

Pregitzer, 1996; Sullivan et al., 1996; Evans, 2000). The average maximum values of A measured in this study were similar to those of other neotropical forest tree species in field conditions, for instance the values measured by Hogan et al. (1995) in leaves of *Anacardium excelsum* (8.62), *Cecropia longipes* (12.4), *Dydimopanax morototoni* (14.5), *Ficus obtusifolia* (13.8), *Luehea seemannii* (10.43) and *Pseudobombax septenatum* (13.1), during the wet season in a Central American semi-deciduous tropical forest in Panama, and the values measured by Hiremath (2000) in leaves of tropical fast-growing native trees of Costa Rica, *Cedrela odorata* (10.10) *Cordia alliodora* (12.12) and *Hyeronima alchorneoides* (8.07).

At the normal growth conditions, the values of the  $\text{Ci}/\text{Ca}$  ratio were nearly constant but variable depending on the terrestrial biome types, with a tendency to be relatively higher in tropical rainforest species than xerophytic or tropical dry forest tree species (Lloyd and Farquhar, 1994; Ehleringer and Cerling, 1995). The  $\text{Ci}/\text{Ca}$  ratio is also considered as a good indicator of the stomatal limitation of photosynthesis (Farquhar and Sharkey, 1982). In the case of plant species that are more conservative in relation to water use, the lower the values of the  $\text{Ci}/\text{Ca}$  ratio, the higher is the stomatal limitation of photosynthesis. As shown in Table 1, the maximum values of  $\text{Ci}/\text{Ca}$  ratios were observed at low values of D and high values of  $g_s$ . For example, the maximum mean values of A and  $g_s$  were observed for *C. peltophoroides*. At the same time, high values of the  $\text{Ci}/\text{Ca}$  ratio and low values of D were observed in this species.

**Table 3** - Mean values of the residuals ( $A_{\text{measured}} - A_{\text{estimated}}$ ) for five classes of the leaf-to-air vapour pressure deficit (D). The analysis are related to all of the values collected from the five species studied.

Model	Classes of D (kPa)					
	0.0-1.0	1.1-1.5	1.6-2.0	2.1-2.5	2.6-3.0	3.1-3.5
1	0.41	0.60	-0.06	-0.41	-1.15	-1.77
2	-0.55	0.17	0.04	0.03	-0.21	-0.19
3	-0.53	0.14	0.01	-0.02	-0.30	-0.43
4	-0.51	0.23	0.07	-0.01	-0.39	-0.67
n	35	129	116	64	34	10

**Table 4** - Relationships between measured and modelled values of the dark respiration rate (Rd) and the saturated net photosynthetic rate ( $A_{\text{sat}}$ ). The measured and modelled values of  $A_{\text{sat}}$  were obtained at 1600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *C. peltophoroides*, *M. latifolium* and *M. salzmannii*, or 1200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for *T. cacao* and *T. grandiflorum*. (n = 53)

Model	Rd ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$A_{\text{sat}}$ ( $\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$ )
1	$y = -0.09 + 1.09x$ ( $r^2 = 0.97$ )	$y = 4.39 + 0.36x$ ( $r^2 = 0.37$ )
2	$y = -0.25 + 1.23x$ ( $r^2 = 0.96$ )	$y = 2.54 + 0.61x$ ( $r^2 = 0.63$ )
3	$y = -0.21 + 1.19x$ ( $r^2 = 0.96$ )	$y = 2.80 + 0.59x$ ( $r^2 = 0.61$ )
4	$y = -0.19 + 1.18x$ ( $r^2 = 0.96$ )	$y = 3.12 + 0.54x$ ( $r^2 = 0.56$ )

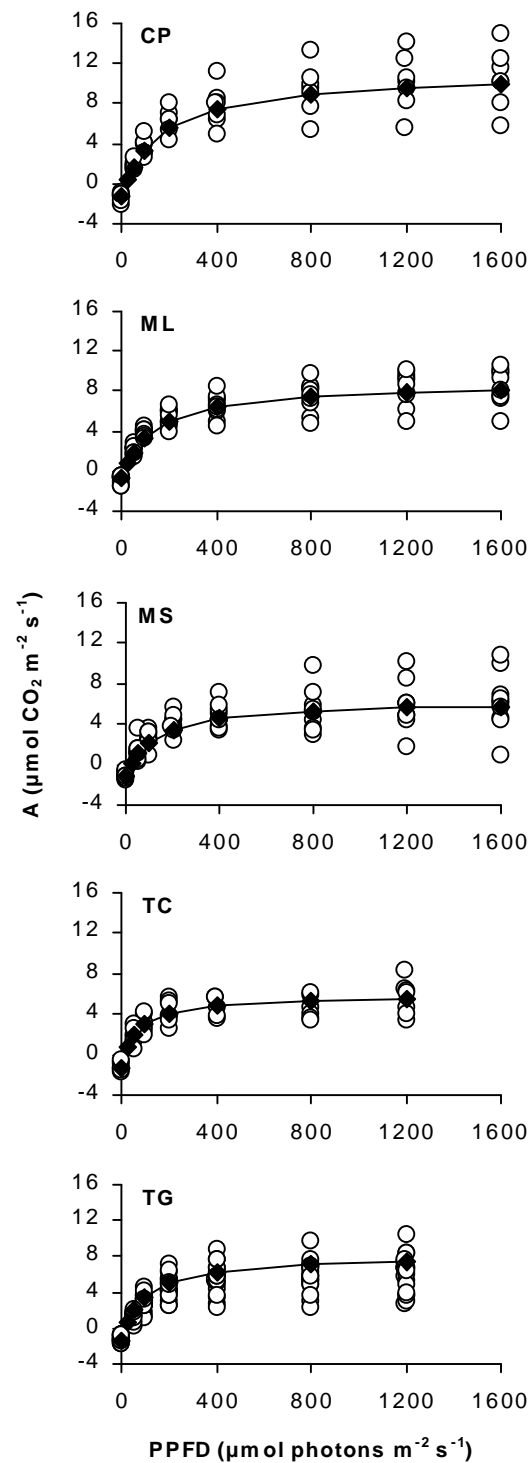
Different equations were proposed in order to estimate the responses of stomatal conductance to the vapour pressure deficit, such as linear (Dolman and Van Den Burg, 1988; McCaughey and Iacobelli, 1993) or exponential (Dye and Olbrich, 1993) functions. According to Landsberg and Hingston (1997), exponential equations are advantageous to linear ones because the latter can estimate unrealistic negative values of stomatal conductance at high values of the vapour pressure deficit.

By contrast, the linear form permits the extrapolation of the values of D, when the estimated values of A or  $g_s$  are near to zero. For stomatal conductance to water vapour, these values (estimated in our present study as  $\gamma$ ) were between 2 and 5 kPa in several tropical and temperate forest trees (Dolman and Van Den Burg, 1988; McCaughey and Iacobelli, 1993; Landsberg and Gower, 1997; Mielke et al., 1999). Because the stomata controls the exchange of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  between the leaf and the atmosphere, and the relationship of diffusion coefficients of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  is 1.6 (Nobel, 1991), we predicted that the estimated values of  $\gamma$  for photosynthesis would be higher than the values estimated for the stomatal conductance to water vapour. Confirming these expectations, the estimated values of  $\gamma$  for the Model 2 in our study varied between 4.64 for *M. latifolium*, and 6.31 kPa, for *T. cacao* (Table 2).

The best fittings obtained for Models 2 and 3 (Tables 2, 3 and 4) can be explained by the effects of D on stomatal conductance and net photosynthesis (Fig. 1). This occurred because a direct relationship between  $g_{\text{sat}}$  and  $A_{\text{sat}}$  was observed for all studied species (Fig. 2) in a way similar to that which demonstrated for a countless

number of tropical forest tree species (Hogan et al., 1995; Ishida et al., 1996; Kitajima et al., 1997). The values of  $A_{\text{max}}$ ,  $\alpha$  and Rd were related to the successional status of an individual species, or group of species (Bazzaz and Pickett, 1980; Lüttige, 1997). According to Lüttige (1997), the values of  $A_{\text{max}}$  in tropical plants were between 10 and 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for sun plants, and between 1 and 3  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for shade plants. We also need to consider that sunlight or shade tolerance varies if species are pioneer, late successional, understory or emergent canopy-dominant species. In this study, despite the fact that the trees of the different species analyzed were growing at different environmental conditions, it was clear that the highest value of  $A_{\text{max}}$  was observed in a fast-growing secondary species (*C. peltophoroides*) and the lowest value of  $A_{\text{max}}$  was observed in a typical late successional species (*T. cacao*). After correcting for the effects of D (based on the mean value of D for the all data collected, i.e. 1.70 kPa), the values of  $A_{\text{max}}$  estimated from the Model 3, for example, ranged from 7.00 up to 12.39  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *T. cacao* and *C. peltophoroides*, respectively.

In summary, the empirical mathematical models seemed to provide a good estimation of the light response photosynthetic parameters. When different photosynthetic characteristics of a particular species (or group of species) are to be compared, it is important to select an appropriate model and carefully indicate the environmental conditions at the moment in which the data are collected.



**Figure 03** - Response of net photosynthetic rate (A) to changing photosynthetic photon flux density (PPFD) for five neotropical rainforest tree species: *C. peltophoroides* (CP), *M. latifolium* (ML), *M. salzmannii* (MS), *T. cacao* (TC) and *T. grandiflorum* (TG). The solid lines denote fitted data based on Model 3 (see Table 2). Open symbols are the measured values.



When the vapour pressure deficit inside the chamber is not controlled, the incorporation of linear or exponential functions that explains the effects of the leaf-to-air vapour pressure deficit on leaf gas exchange is a very good method to enhance the performance of the models.

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## RESUMO

Medições das trocas gasosas foliares em diferentes níveis de densidade de fluxo de fótons fotossinteticamente ativos (PPFD) foram realizadas com o objetivo de comparar as características fotossintéticas de cinco espécies arbóreas de florestas úmidas neotropicais, com especial ênfase em modelos matemáticos empíricos para estimativa de parâmetros derivados das curvas de resposta à radiação luminosa e dos efeitos da diferença de pressão de vapor entre a folha e o ar ( $D$ ) na taxa fotossintética em saturação luminosa ( $A_{\max}$ ). Os modelos analisados proporcionaram boas estimativas para os parâmetros derivados das curvas de resposta à radiação luminosa. Comparações entre as características fotossintéticas de diferentes espécies devem sempre considerar os modelos utilizados, seguidas de indicações pormenorizadas das condições microambientais no momento em que os dados foram coletados. Quando a diferença de pressão de vapor não for controlada artificialmente durante as medições, a incorporação de uma função linear ou exponencial, explicando os efeitos de  $D$  nos parâmetros de trocas gasosas, é um excelente método para incrementar a performance dos modelos.

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