GENOTYPIC VARIATION IN CANOPY PHOTOSYNTHESIS, LEAF GAS EXCHANGE CHARACTERISTICS AND THEIR RESPONSE TO TAPPING IN RUBBER (*HEVEA BRASILIENSIS*)

By H. K. L. K. GUNASEKARA, W. A. J. M. DE COSTA† *and* E. A. NUGAWELA§

Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya 20400, Sri Lanka and §*Rubber Research Institute, Agalawatta, Sri Lanka*

SUMMARY

The main objective of this study was to quantify the genotypic variation of photosynthetic and gas exchange parameters of *Hevea* and to examine their relationships to dry rubber yield and its components. Canopy photosynthesis (P_c) of the genotype RRISL 211 was 20 % greater than that of RRIC 121. This was primarily due to RRISL 211's greater light-saturated leaf photosynthetic rates and a greater leaf area index in the top canopy stratum. Tapping significantly increased P_c in RRISL 211, but not in RRIC 121. The genotypic variation in photosynthetic capacity was not reflected in the overall dry rubber yield, which did not differ between the two genotypes. However, analysis of yield components showed that while RRISL 211 may have preferentially partitioned a greater proportion of its additional assimilates to increasing the latex volume and extending the root system, RRIC 121 partitioned more assimilates to increasing its dry rubber content through greater biosynthesis of rubber. The higher plugging index and the greater post-tapping girth increment of RRIC 121 were probably responsible for observed increases in its dark respiration following tapping. Although RRISL 211 had a greater transpiration efficiency, this did not provide a yield advantage as the trees were growing in an environment with adequate rainfall throughout the year.

INTRODUCTION

Latex is the economically important product of the rubber tree (*Hevea brasiliensis*). Carbohydrates produced through photosynthesis by the foliage canopy of *Hevea* are the primary material for latex production through metabolism. The rate of latex production in the latex vessels of *Hevea* has been related to the supply of sucrose from the adjacent sieve tubes (Gomez, 1983) indicating a close link between CO_2 assimilation capacity and rubber yield. In addition to latex production, carbohydrates from photosynthesis have to be allocated for tree growth as well. Exploitation, i.e. tapping of the rubber tree for latex, is known to retard drastically the girthing of the tree and its biomass production (Templeton, 1969). Loss of latex by tapping triggers its re-synthesis (George *et al.*, 1984). Gunasekara *et al.* (2007) demonstrated significant genotypic variation in the response of tree girth increment to tapping, and in latex volume per tree per tapping and the dry rubber content; the significant negative correlation between these two variables showed that both depend on a common pool

†Corresponding author: janendrad@yahoo.com

of assimilates coming from photosynthesis. The objective of the present study was to relate these genotypic variations in latex production, dry rubber content and girthing to those in photosynthetic capacity and gas exchange characteristics and their response to tapping.

<div align="center">MATERIALS AND METHODS</div>

A detailed description of the experimental site, the *Hevea* genotypes used and the management practices was given in Gunasekara *et al.* (2007). The essential details and methodology specific to this paper are summarized below.

The present study was a supplement to a longer (July 1999–January 2003) experiment to determine the feasibility of early commencement of tapping in three contrasting *Hevea* genotypes. Mature eight-year-old trees, from two *Hevea* genotypes, RRIC 121 and RRISL 211 (Gunasekara *et al.*, 2007), were selected. All cultural practices were performed according to recommendations of the Rubber Research Institute of Sri Lanka. All gas exchange and related measurements were made during the period November–December 2002, which are the peak yielding months of the year. Four tapped and four untapped trees from each of the two genotypes were selected. The tapped trees had been opened at a girth of 50 cm in April 2001 and were under the $\frac{1}{2}$S d/3 + Ethrel system (i.e. low frequency tapping with yield stimulation; Gunasekara *et al.*, 2007).

Measurement of photosynthesis

Photosynthesis and associated gas exchange characteristics (stomatal conductance, transpiration rate and transpiration efficiency) were measured using a portable Infra Red Gas Analyzer (IRGA; Model LI 6400, LI-COR Inc., Lincoln, NE, USA). Because it was extremely difficult to reach the leaves of a mature rubber canopy with the above instrument, measurements were made on detached leaves. The canopy of each tree was visually divided into three strata as upper (at approximately 18–22 m above ground level), middle (14–18 m) and lower (10–14 m). Twigs were cut from each stratum with a sharp knife and immediately put into a bucket of water. Thereafter, the middle leaflet of a healthy, bright green, mature leaf was separated (about 2 cm above the leaf base) from the petiole using a sharp blade, and it was then cut across the lamina under water. A further cut was made very close to the first after two minutes to remove any latex coagulated at the cut end of the leaf lamina. The cut ends were immediately put into a small beaker of water and taken to the laboratory in an air-tight container. The leaves sampled were kept for about two hours in controlled environment at 30 °C with low light (approximately 100 μmol m^{-2} s^{-1}) before photosynthesis was measured. Nugawela (1989) has shown that photosynthetic rates of leaves detached and kept as described above were similar to intact *Hevea* leaves attached to the tree. Similarity of photosynthetic rates of carefully detached and stored tree leaves to intact leaves have also been shown by Aylett (1985), Pereira *et al.* (1986) and Masuzawa (1987).

Photosynthesis measurements were done on four separate days. Each day, leaflets were sampled from two trees (tapped and untapped) of each genotype. On any given

Table 1. Starting sequence for the measurement of light response of photosynthesis in detached leaves of *Hevea* on the first day of measurement.

Sequence order	Genotype	Tapping treatment	Canopy stratum
1	RRISL 211	Tapped	Upper
2	RRIC 121	Tapped	Upper
3	RRISL 211	Untapped	Upper
4	RRIC 121	Untapped	Upper
5	RRISL 211	Tapped	Middle
6	RRIC 121	Tapped	Middle
7	RRISL 211	Untapped	Middle
8	RRIC 121	Untapped	Middle
9	RRISL 211	Tapped	Lower
10	RRIC 121	Tapped	Lower
11	RRISL 211	Untapped	Lower
12	RRIC 121	Untapped	Lower

day, measurements were made sequentially on 12 leaves (Table 1), which represented the two genotypes, the three canopy strata and the two tapping treatments. The sequence was reversed on the following day. Measurements made on the four days constituted four replicates for the 12 genotype × canopy stratum × tapping treatment combinations.

Photosynthetic light response of individual leaves from different canopy strata

Photosynthetic rate, measured as the rate of CO_2 uptake, of individual leaves was measured at different levels of photosynthetically active radiation (PAR), i.e. 25, 50, 75, 100, 200, 400, 800 and 1200 μmol m^{-2} [leaf area] s^{-1} by varying the incident photosynthetic photon flux density (PPFD) using an in-built artificial light source, 6400 – 02B Red/Blue (LI-COR Inc., Lincoln, NE, USA) under ambient CO_2 levels. Leaf temperature and water mole fraction were controlled at 30 °C ($\pm$0.01) and 25 mmol H_2O mol^{-1} air ($\pm$0.02) respectively throughout the experiment. Net photosynthetic rate per unit leaf area (P_n) was computed according to equation 1 given by Von Caemmerer and Farquhar (1981) as:

$$Pn = \{F(C_r - C_s)/100\,S\} - C_s\,E \tag{1}$$

where P_n is net photosynthetic rate (μmol [CO_2] m^{-2} [leaf area] s^{-1}), F is the molar flow rate of air going through the leaf chamber (μmol s^{-1}), C_r and C_s are the respective mole fractions of CO_2 in the reference and sample airflows (μmol [CO_2] mol^{-1} air), S is the area of leaf (cm^2) in the chamber and E is the transpiration rate (mol [H_2O] m^{-2} [leaf area] s^{-1}).

Photosynthetic light response of individual leaves was characterized by fitting the asymptotic exponential function (Boote and Loomis, 1991), thus:

$$P_n = P_{max} - (P_{max} + R_d)e{-}^{CI} \tag{2}$$

where P_n is the net photosynthetic rate (μmol [CO_2] m^{-2} [leaf area] s^{-1}), I is the light intensity in terms of PPFD, P_{max} is the light-saturated maximum P_n, and R_d is the dark respiration rate (i.e. P_n at zero I). C is a parameter related to the quantum efficiency, ϕ (initial slope of the curve at zero I), given by:

$$C = \phi/(P_{max} + R_d) \tag{3}$$

The parameters of equation 2 were estimated by non-linear regression using the PROC NLIN procedure (Marquardt method) of the SAS statistical package (Anonymous, 2000). Curves were first fitted for individual replicate measurements made on the four separate days. As the estimated parameters did not differ significantly (based on their 95 % confidence intervals) between the four replicates, light response curves were fitted for the averaged replicate measurements of each treatment combination.

Measurement of other gas exchange characteristics

Stomatal conductance for water vapour transfer (E) and transpiration efficiency (TE) were also measured simultaneously with photosynthesis measurements. E (mol [H_2O] m^{-2} [leaf area] s^{-1}) was calculated as:

$$E = F(w_s - w_r)/100\,S(1000 - w_s) \tag{4}$$

where w_s and w_r, the respective mole fractions of H_2O in the sample and reference airflows (mmol [H_2O] mol^{-1} air), and F and S are as defined for equation 1. Stomatal conductance (g_s) was calculated, in principle, as the difference between the total leaf conductance to water vapour (g_t) and the boundary layer conductance (g_b) after adjusting for differences in stomatal densities on the two sides of the leaf. In principle, g_t was computed as the ratio between transpiration rate and the water vapour concentration difference between the leaf interior and the outside air. The exact equations for calculation of g_s and g_t are given in LI-COR 6400 reference manual (Anonymous, 1998). TE was computed as the ratio between P_n and E.

Calculation of canopy photosynthesis

Canopy gross photosynthesis (P_c) was computed as the sum of photosynthesis of three canopy strata. Daily gross photosynthesis of a given canopy stratum (P_s) was computed using an equation given by Charles-Edwards (1982) as:

$$P_s = \Delta F + \Delta R = \frac{\phi\,s\,P_{max}\,h[1 - \exp(-kL)]}{\phi\,k\,s\,+\,h\,P_{max}} \tag{5}$$

where, ΔF is the daily net photosynthetic integral (μmol [CO_2] m^{-2} d^{-1}), ΔR is the daily respiratory integral (μmol [CO_2] m^{-2} d^{-1}), ϕ is the quantum (photochemical) efficiency (μmol [CO_2] μmol [PAR]$^{-1}$), s is the daily light integral (μmol [PAR] m^{-2} d^{-1}), P_{max} is the maximum light saturated net photosynthetic rate (μmol [CO_2]

$m^{-2}\ s^{-1}$), h is the day length ($s\,d^{-1}$), k is the canopy light extinction coefficient and L is the leaf area index of the canopy stratum. The day length (h) was taken as 10 h, and converted to seconds, i.e. $10\ h \times 60 \times 60\,s\,d^{-1} = 36\ 000\,s\,d^{-1}$. The daily light integral (s) was taken as $20\,MJ\,m^{-2}\,d^{-1}$, i.e. $40 \times 10^6\ \mu mol\ (PAR)\ m^{-2}\,d^{-1}$. The canopy extinction coefficient (k) was assigned a value of 0.6 for all genotypes. Nugawela (1989) and Nugawela *et al.* (1995a) adopted a similar procedure to compute canopy photosynthesis of *Hevea* genotypes growing in the same agro-ecological zone as those of the present study.

Measurement of leaf area index (LAI)

Measurement of the LAI of different canopy strata was necessary to compute P_s and P_c. Defoliation of *Hevea brasiliensis* is rapid and complete, typically occurring each year over a period of 2–3 weeks. Thus, leaflets collected during defoliation provide a means of determining the LAI (Nugawela, 1989). Six rectangular litter traps (45 cm × 45 cm) were positioned at random within each stand of the two genotypes. The total area of the leaflets within each litter trap was measured using a portable leaf area meter (Series LI – 3000, LI-COR Ltd., Lincoln, NE, USA) and the number of leaflets was also counted to estimate the mean leaflet size. The LAI of the whole canopy was estimated as the ratio between the total area of leaflets per litter trap (m^2) and the ground area covered by the litter trap (m^2).

The proportions of the total LAI found in the three different canopy strata, top, middle and bottom, of the two genotypes were estimated using a point quadrat inclined at an angle of 32.5° (Nobel and Long, 1985). A long piece of twine was tied onto one end of a 2-m long pole and placed on top of the canopy by an experienced tree climber. The free end of the twine was fixed at a random point on the ground at an angle of 32.5° to the horizontal with the help of a protractor attached to a leveling device. The number of contacts the twine made with leaves at the top (22–18 m), middle (18–14 m), and bottom (14–10 m) strata of the canopy were counted. Five measurements were made for each clone. The proportions of the LAI at different heights in the canopy were estimated as described by Nobel and Long (1985).

Trunk girth and girth increment

Trunk girth at a height of 150 cm from the bud union was measured in 10 trees under each tapping treatment at three-monthly intervals during the 42-month period (from July 1999 to January 2003). Rate of girth increment was estimated as the slope of the linear regression of trunk girth against time.

Yield and yield components

Cumulative dry rubber yield, dry rubber yield and latex volume per tree per tapping and the dry rubber content were measured as described in Gunasekara *et al.* (2007).

Statistical analysis

The precision with which the asymptotic exponential curve fitted the observed light response was assessed by the R^2-values (ratio between regression and total sums of

Table 2. Estimated parameters for the photosynthetic light response curves of leaves from different canopy strata for two *Hevea* genotypes under tapped and untapped conditions.

Genotype	Tapping treatment	Canopy stratum	P_{max} (μmol $[CO_2]$ m^{-2} s^{-1}) $\pm$ CI	R_d (μmol $[CO_2]$ m^{-2} s^{-1}) $\pm$ CI	ϕ (μmol $[CO_2]$ μmol^{-1} [PAR])	$C \pm CI$[†]
RRISL 211	Tapped	Upper	7.00 ± 0.25	0.112 ± 0.050	0.051	0.0071 ± 0.0012
		Middle	5.68 ± 0.21	0.183 ± 0.031	0.031	0.0053 ± 0.0008
		Lower	4.58 ± 0.23	0.187 ± 0.029	0.022	0.0046 ± 0.0009
	Untapped	Upper	7.67 ± 0.26	0.613 ± 0.038	0.032	0.0039 ± 0.0006
		Middle	3.56 ± 0.12	0.296 ± 0.030	0.028	0.0072 ± 0.0018
		Lower	2.91 ± 0.14	0.285 ± 0.028	0.022	0.0070 ± 0.0015
RRIC 121	Tapped	Upper	4.44 ± 0.27	0.708 ± 0.045	0.031	0.0060 ± 0.0014
		Middle	4.04 ± 0.16	1.023 ± 0.029	0.033	0.0066 ± 0.0009
		Lower	3.30 ± 0.11	0.317 ± 0.026	0.015	0.0041 ± 0.0009
	Untapped	Upper	5.93 ± 0.30	0.338 ± 0.030	0.023	0.0037 ± 0.0006
		Middle	3.49 ± 0.15	0.519 ± 0.049	0.028	0.0070 ± 0.0011
		Lower	2.80 ± 0.11	0.229 ± 0.029	0.015	0.0049 ± 0.0014
			Tapping treatment means			
RRISL 211	Tapped		5.75	0.161	0.035	
	Untapped		4.71	0.398	0.028	
RRIC 121	Tapped		3.93	0.683	0.026	
	Untapped		4.07	0.362	0.022	
			Genotypic means			
RRISL 211			5.23	0.279	0.031	
RRIC 121			4.00	0.522	0.024	

[†]CI: 95 % confidence interval for parameter estimates. Parameters P_{max}, R_d and C are described in equation 2 in the text; ϕ was estimated using equation 3.

squares). Curves were fitted separately for the measurements made on the four different days. The significance of treatment differences between the estimated parameters was determined by their respective 95 % confidence intervals.

<div align="center">RESULTS</div>

Light response curves and their parameters

The asymptotic exponential function fitted the light response of net photosynthetic rate (P_n) well with the R^2 value being above 0.90 in all genotype × canopy stratum × tapping treatment combinations (Figure 1). In both genotypes, photosynthetic rates were highest in leaves of the upper stratum and lowest in those of the bottom stratum. RRISL 211 showed greater P_n than RRIC 121 throughout the range of light intensities in all strata and in both tapped and untapped treatments.

Table 2 shows the estimated parameters of the light response curves for different treatment combinations. In both genotypes, a clear reduction of P_{max} was evident from leaves in the upper strata through the middle to the bottom strata of the canopy. P_{max} of leaves from all strata of RRISL 211 were greater than the corresponding strata of RRIC 121. When averaged across different strata, P_{max} of tapped trees was
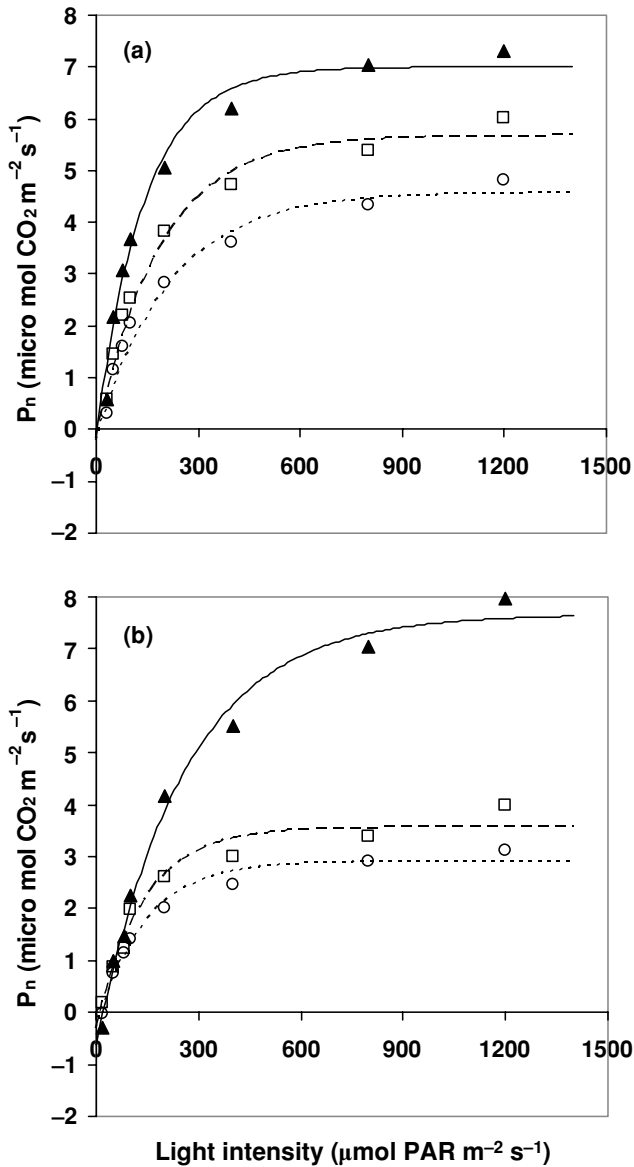
Figure 1. The response of net photosynthetic rate (P_n) to light intensity in leaves from different canopy strata (▲: upper; □: middle; ○: lower) of tapped (a, c) and untapped (b, d) trees in genotypes RRISL 211 (a, b) and RRIC 121 (c, d). Measurements were made under controlled conditions optimal for photosynthesis (temperature = 30 °C and VPD < 1.2 kPa). Each point is the mean of four observations. Best-fitting asymptotic exponential curves are also shown.

22 % greater than that of untapped trees in RRISL 211. However, there was a 4 % reduction in P_{max} due to tapping in RRIC 121.

There was a gradual reduction in ɸ from the upper through the middle to the lower canopy strata of RRISL 211 in both tapped and untapped treatments. In contrast,
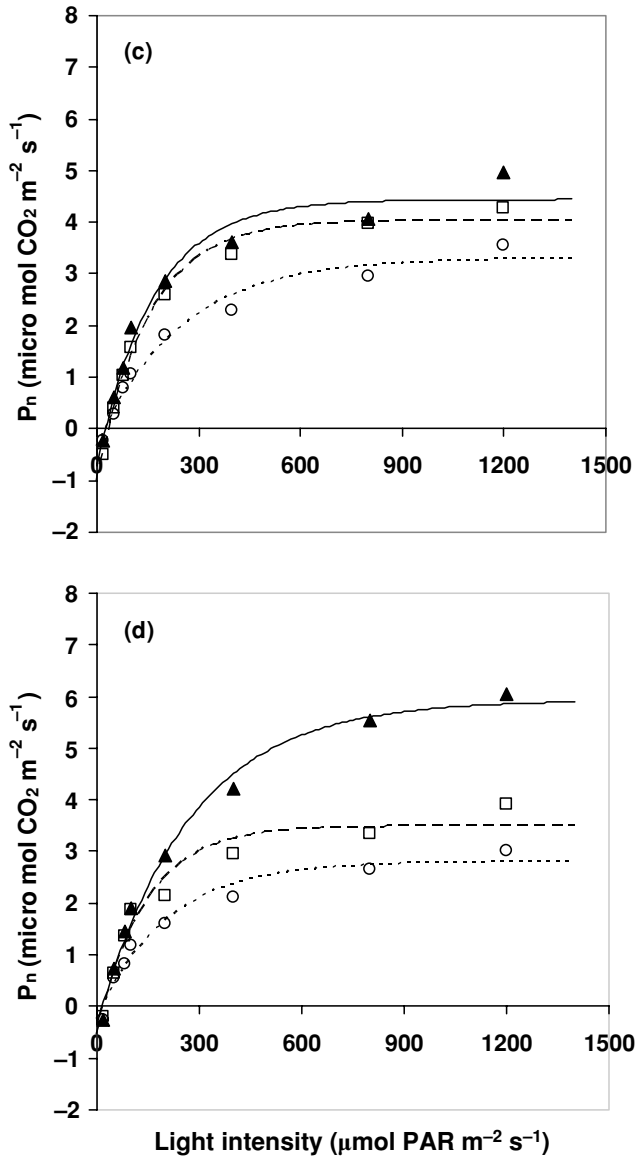
Figure 1. Continued.

RRIC 121 had the highest ϕ in the middle stratum. Within each genotype, in the upper and middle strata, tapped trees had a greater ϕ than the untapped. No such difference was observed in the lower stratum. When averaged across canopy strata, RRISL 211 had a greater mean ϕ than RRIC 121 in both tapping treatments.

The variation pattern of R_d differed between genotypes and tapping treatments. While tapping increased R_d relative to the untapped trees in all canopy strata in RRIC 121, the opposite was observed in RRISL 211. In tapped trees, when averaged across

Table 3. Estimated daily gross photosynthesis of different canopy strata and total canopy photosynthesis for two *Hevea* genotypes under tapped and untapped conditions. The percentage contribution from each stratum to the total is given in parentheses.

| Genotype | Tapping treatment | Daily gross photosynthesis (μmol [CO_2] m^{-2} d^{-1}) $\times 10^{4}$ [†] | | | |
		Upper	Middle	Lower	Total
RRISL 211	Tapped	28.38 (51 %)	16.83 (30 %)	10.60 (19 %)	55.81
	Untapped	29.72 (56 %)	15.70 (30 %)	7.42 (14 %)	52.84
	Mean	29.05	16.27	9.01	54.33
	s.e. (d.f.=9)	1.642	0.551	1.408	1.080
RRIC 121	Tapped	20.67 (45 %)	17.91 (39 %)	6.96 (15 %)	45.54
	Untapped	21.01 (46 %)	18.42 (41 %)	5.87 (13 %)	45.30
	Mean	20.84	18.17	6.42	45.42
	s.e. (d.f.=9)	0.922	0.835	0.447	0.540

[†]The values are based on light response curves measured on four separate days. Each value is the mean of separate calculations for the four days.

Table 4. Distribution of leaf area index (LAI) in different canopy strata for two *Hevea* genotypes. The percentage contribution from each stratum to the total LAI is given in parentheses.

| Genotype | Partial LAI in different canopy strata[†] | | | |
	Top	Middle	Bottom	Total
RRISL 211	1.98 (47 %)	1.27 (30 %)	0.94 (22 %)	4.19
RRIC 121	1.79 (42 %)	1.66 (39 %)	0.80 (19 %)	4.25
s.e. (d.f. = 5)	0.079	0.124	0.074	0.094

[†]Total LAI is the mean of six measurements through litter traps. See text for a detailed description of the estimation of partial LAI of different canopy strata.

canopy strata, R_d of RRIC 121 was more than three times (325 %) that of RRISL211. However, there was no substantial difference between R_d of the two genotypes in the untapped trees.

Canopy photosynthesis

When averaged across tapping treatments, the P_c of RRISL 211 was 20 % greater than that of RRIC 121 (Table 3). Tapping increased P_c by 6 % in RRISL 211. On the other hand, RRIC 121 showed only a 1 % increase in P_c in response to tapping. There was a clear difference between the two genotypes in the proportional contributions from different canopy strata to the total P_c. In RRISL 211, the upper stratum contributed proportionately more and the middle proportionately less to the total when compared to RRIC 121. This mirrored the genotypic variation in the distribution of LAI in the different canopy strata (Table 4). RRISL 211 had a proportionately greater LAI in the top stratum, while having a proportionately lower LAI in the middle stratum as compared to RRIC 121.
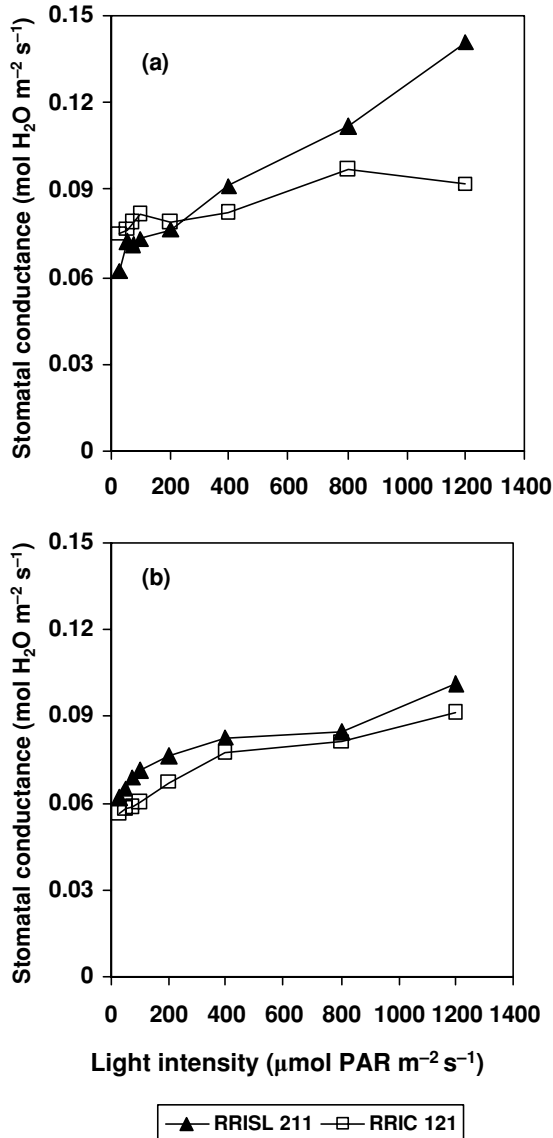
Figure 2. Variation in the mean stomatal conductances with light intensity for two *Hevea* genotypes under tapped (a) and untapped (b) conditions. Each point is the mean of measurements on leaves from the three canopy strata on four days.

Other gas exchange characteristics

There was a very gradual increase in g_s with increasing light intensity (Figure 2) in both genotypes under both tapping treatments. When g_s of all three canopy strata were pooled, in the tapped treatment RRISL 211 showed a greater g_s than RRIC 121 at higher light intensities (Figure 2a). No such difference between the two genotypes was observed in the overall g_s of the untapped treatment (Figure 2b). There was also a gradual increase of E with increasing light intensity in both genotypes (Figure 3).
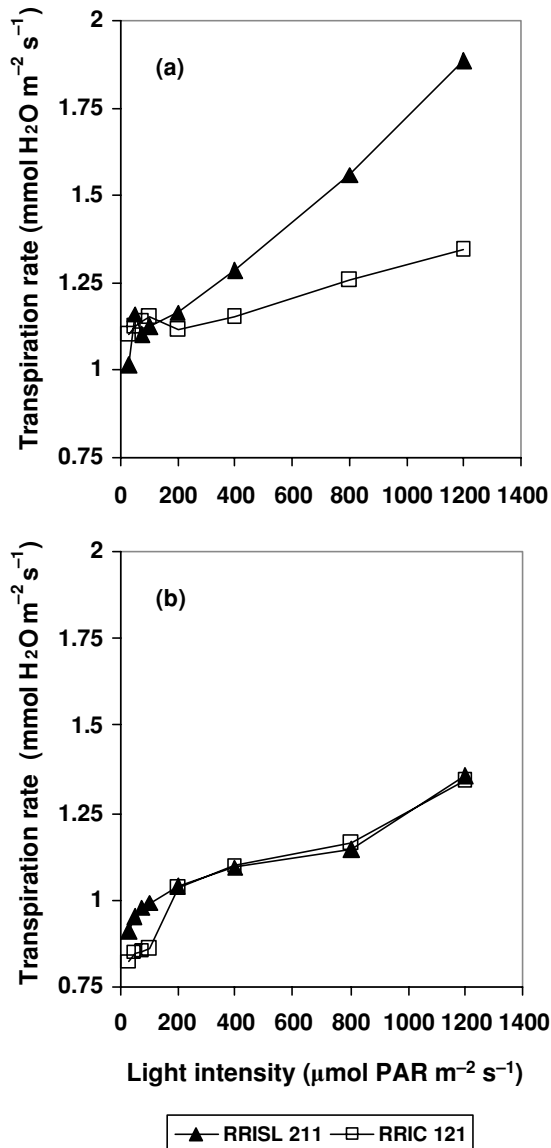
Figure 3. Variation in the mean transpiration rates with light intensity for two *Hevea* genotypes under tapped (a) and untapped (b) conditions. Each point is the mean of measurements on leaves from the three canopy strata on four days.

When the data for all canopy strata were pooled, the overall E in the tapped trees of RRISL 211 was greater than that of RRIC 121; no such variation could be observed between the two genotypes in the untapped treatment. TE showed a similar pattern of variation with light intensity in both genotypes in the tapped and untapped trees (Figure 4). TE increased with increasing light intensity up to about 200 μmol m^{-2} s^{-1} and remained approximately constant thereafter. When the data of all canopy strata were pooled, TE in the tapped treatment was greater in RRISL 211 than that of
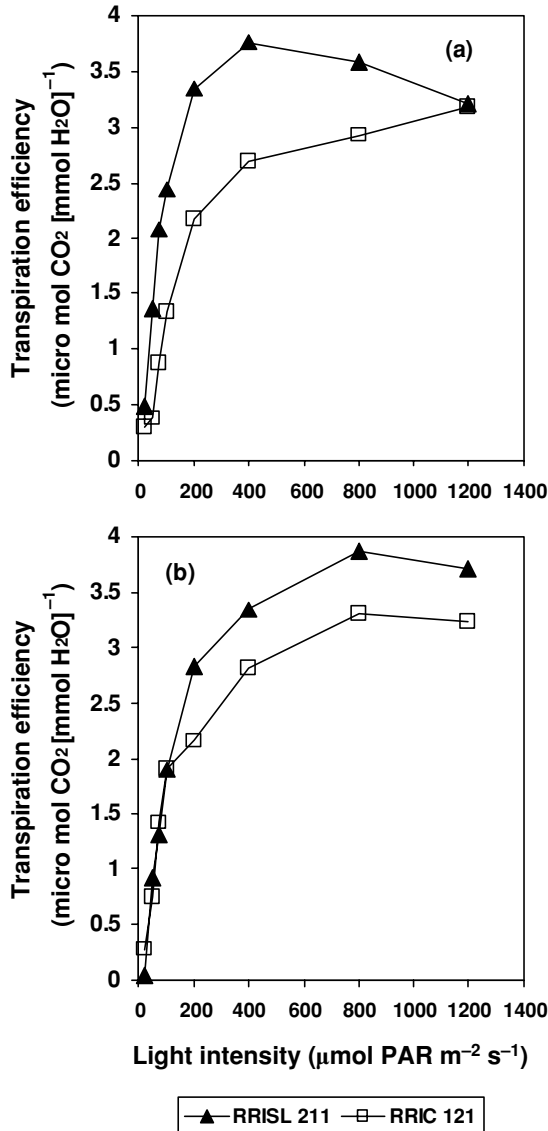
Figure 4. Variation in the mean transpiration efficiency with light intensity for two *Hevea* genotypes under tapped (a) and untapped (b) conditions. Each point is the mean of measurements on leaves from the three canopy strata on four days.

RRIC 121 at all light intensities except at 1200 μmol m^{-2} s^{-1} where, both genotypes had similar values (Figure 4a). On the other hand, in the untapped treatment TE of both genotypes did not vary significantly in the lower range of light intensities from 0–100 μmol m^{-2} s^{-1}. However, at light intensities above 100 μmol m^{-2} s^{-1}, the TE of untapped RRISL 211 was greater than that of RRIC 121 (Figure 4b). Overall, there were no significant differences in TE between tapped and untapped treatments of both genotypes at all light levels considered.

Table 5. Trunk girth and rate of girth increment for two *Hevea* genotypes.

Genotype	Tapping treatment	Trunk girth[†] (cm)	Rate of girth increment (cm month^{-1}) $\pm$ (CI)[‡]
RRISL 211	Tapped	50.85	0.29 ± 0.031
	Untapped	52.21	0.34 ± 0.015
RRIC 121	Tapped	60.50	0.52 ± 0.023
	Untapped	61.12	0.56 ± 0.019

[†]Measured as a mean of 10 trees in January 2003.
[‡]Estimated through linear regression of tree girth against time (July 1999 and January 2003). CI: 95 % confidence interval of the estimate.

Table 6. Mean dry rubber yield and yield components[†] of the two *Hevea* genotypes investigated (April 2001–January 2003).

Genotype	Latex volume per tree per tapping (ml)	Dry rubber content (%)	Dry rubber yield per tree per tapping (g)	Cumulative dry rubber yield (kg tree^{-1})
RRISL 211	152 (+63 %)	30.6 (−23 %)	39.6 (−6 %)	7.81 (−6 %)
RRIC 121	93	39.9	42.1	8.30
s.e.	12 (18 *d.f.*)	0.43 (2 *d.f.*)	3.40 (18 *d.f.*)	0.669 (18 *d.f.*)

[†]All values were obtained from trees opened at a girth of 50 cm and tapped under the $^{1}/_{2}$S d/3 + Ethrel system. Each value is the mean of 10 replicate trees.

Trunk girth and rate of girth increment

Trunk girth at the end of the study and rate of girth increment during the 42-month experimental period were significantly greater in RRISL 211 than in RRIC 121 (Table 5). Reductions in trunk girth and rates of girth increment due to tapping were greater in RRISL 211 than in RRIC 121.

Yield and yield components

Table 6 shows the cumulative dry rubber yield and its yield components for the two genotypes during the experimental period. The dry rubber yield, both cumulative and on a per tapping basis, did not vary significantly between the two genotypes. However, the latex volume per tree per tapping and the dry rubber content showed significant genotypic variation. While RRISL 211 had 63 % greater latex volume, its dry rubber content was 23 % lower than that of RRIC 121.

DISCUSSION

Genotypic variation in canopy photosynthesis of rubber

Results of the present study showed that there is appreciable variation in canopy photosynthesis between different genotypes of rubber. The greater P_c of RRISL 211 was primarily due to its greater P_{max} (maximum light saturated net photosynthetic rate) in all three canopy strata in comparison to the corresponding values for RRIC 121. Moreover, RRISL 211 had a greater proportion of its total LAI in the upper canopy

stratum (Table 4), which receives the highest light intensities. This meant that a larger proportion of the canopy of RRISL 211 was able to make use of its greater photosynthetic capacity (as indicated by P_{max}) by photosynthesizing at higher light intensities.

The P_c values of genotypes (Table 3) were about 15–40 % higher than those reported by Nugawela (1988) and Nugawela et al. (1995a) for mature stock (38–39×10^4 μmol CO_2 m^{-2} d^{-1}). This is understandable as the genotypes of the present study, especially RRISL 211, have been introduced recently after intensive selection for high yield potential. While the values of P_{max} and ϕ of our genotypes were similar to those reported by Nugawela et al. (1995a), the dark respiration rates (Table 2) were much lower than their values (2.5–2.8 μmol CO_2 m^{-2} s^{-1}). In addition, the LAI (Table 4) were also greater than those reported by Nugawela et al. (1995a) (2.42–3.31). Therefore, the lower R_d and greater LAI were probably the major reasons for the greater P_c of our genotypes.

In the present study, significant genotypic variation was observed for P_{max}. Nugawela (1989) and Nugawela et al. (1995a; b) also observed genotypic variation in P_{max}. The gradual reduction of P_{max} from upper through middle to lower canopy strata agrees with the expected variation of these parameters with increasing canopy depth. Similar reductions in P_{max} in one-year old rubber plants have been observed with increasing natural shade (Senevirathna et al., 2003). Greater P_{max} values in the top canopy stratum have been correlated with higher concentrations and activities of photosynthetic enzymes, photosystems and compounds of the electron transport chain (Beadle et al., 1985). These have been observed to decline with increasing canopy depth and consequently a decrease in P_{max}. This is regarded as an adaptation of leaves to their light environment by optimizing the allocation of the photosynthetic apparatus to maximize canopy photosynthesis (Beadle et al., 1985; DeJong and Doyle, 1985; Evans, 1988).

Differing patterns of variation between canopy strata were observed for ϕ in the two genotypes. A similar phenomenon was observed by Nugawela (1989) for two genotypes growing in the field. Although Ehleringer and Pearcy (1983) and Beadle et al. (1985) concluded that ϕ remains stable across genotypes, both the present study and Nugawela (1989) indicate the possibility of variation in ϕ between genotypes and in response to tapping. Both Ceulemans et al. (1984) and Nugawela (1989) observed significant genotypic variation in R_d. Although R_d showed significant genotypic variation in our study (Table 2), a significant interaction was also observed between genotype and tapping. Implications of this interaction in yield determination are discussed below.

Response of photosynthesis to tapping

Both leaf and canopy photosynthesis of RRISL 211 responded positively to tapping. With the removal of latex through tapping, the demand for assimilates from latex-producing tissue increases. This increased sink demand stimulates assimilate synthesis in the photosynthetic tissue. Such stimulation of photosynthesis due to increased sink demand has been reported in many crop species (Evans, 1993). It is notable that tapping increased dark respiration only in RRIC 121. This could have contributed to the absence of a response in P_c to tapping in this genotype. Moreover, Samsuddin and

Impens (1978) speculated that a significant amount of respiratory energy is needed for healing the tapping wound. RRIC 121 had a larger plugging index (Table 6), which is a measure of how quickly the tapping wound is healed, than RRISL 211. This could have contributed to the greater dark respiration rates of the tapped RRIC 121 trees. Measurements of tree girth increment since the commencement of tapping showed that RRIC 121 was able to maintain a greater rate of girthing than RRISL 211 (Table 5). This could also have caused the higher dark respiration rates for RRIC 121 as more respiratory energy would be required for both growth and maintenance of a larger tree.

Possible role of photosynthetic parameters in yield determination of rubber

Despite the genotypic variation in canopy photosynthesis, P_{max} and ϕ, the two genotypes investigated did not differ significantly in their dry rubber yield, either on per tapping or cumulative basis (Table 6). The absence of significant yield variations between the two genotypes was primarily because genotypic variation of the two principal yield components, latex volume per tree per tapping (vtt) and dry rubber content (DRC), approximately cancelled each other out. As indicated by its greater vtt, the additional carbohydrate resulting from the greater P_c of RRISL 211 was probably partially utilized for greater latex production. However, the greater stomatal conductance and consequently the higher transpiration rates of RRISL 211 also could have contributed to the increment in latex volume. The greater DRC of RRIC 121 showed that despite a lower P_c and a lower latex production capacity, RRIC 121 was able to partition a larger proportion of its photosynthates to synthesis of rubber than RRISL 211.

It is possible that partitioning of the common pool of primary assimilates between latex production and the synthesis of rubber is genetically determined so that it is an inherent characteristic of each genotype. On the other hand, the differences in trunk girth and rates of increment between the two genotypes (Table 5) could also have contributed to the absence of a clear relationship between yield and photosynthetic capacity. A close relationship exists between trunk girth and rubber yield (Narayanan and Ho, 1970). The inherently lower rate of girth increment and the greater post-tapping girth depression of RRISL 211 (Figures 2 and 3 of Gunasekara *et al.*, 2007), meant that at a given time point within the first eight years after planting, the capacity for biosynthesis of rubber was lower in RRISL 211 than RRIC 121. This could also have been a reason why the higher photosynthetic capacity of RRISL 211 was not reflected in its yield.

The greater transpiration rates of RRISL 211, in comparison to RRIC 121, indicate a greater water absorption capacity through a more extensive and/or deeper root system. Hence, it is also possible that at this stage of its life cycle, RRISL 211 may be partitioning a greater proportion of its assimilates to roots and thereby preventing an increase in yield despite an increase in photosynthesis. However, more in-depth investigations on rooting capacity and water relations of these *Hevea* genotypes are needed to confirm this.

Our results appear to contradict the results of Nugawela (1989) and Nugawela *et al.* (1995a) who observed a positive relationship under field conditions between P_c

and yield potential for two *Hevea* genotypes at the mature stage (10 years old) and for 10 genotypes at the juvenile stage (8–12 months old). However, as outlined above, there could be many reasons why such a relationship was not shown in our study. Similarly, Ceulemans *et al.* (1984) and Samsuddin et al. (1985) did not observe correlations between photosynthetic characteristics and the yield of rubber. Nugawela et al. (1995b) showed that there was significant variation in the photosynthetic capacity of different rubber genotypes to respond to the fluctuating light environments that are found under natural growing conditions. This is especially relevant in the humid tropical environment where the present experiment was conducted. In this environment, rapid and substantial reductions in irradiance due to clouds are frequent throughout the year. Estimations of P_c are based on steady-state photosynthetic rates under constant light levels. On the other hand, as shown by Nugawela *et al.* (1995b), genotypic variation in non-steady state photosynthetic rates in response to fluctuating light intensities under actual field conditions could also be a reason for the absence of a correlation between photosynthetic capacity and yield.

Similar to P_c, other parameters of gas exchange such as TE and g_s did not show a clear correlation with yield. However, this is not surprising as genotypic variations in TE and g_s become significant yield determinants only under water-limited growing conditions (Monteith, 1986). The rubber trees of the present experiment were grown in a humid tropical environment with an annual rainfall of 2500 mm, well-distributed throughout the year. The ranges of values for the gas exchange parameters reported were similar to those observed by Nugawela (1989).

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