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Clonal differences in photosynthesis in *Hevea brasiliensis* Müll. Arg.

K.N. NATARAJA and J. JACOB*

Division of Plant Physiology, Rubber Research Institute of India, Kottayam, Kerala, India 686 009

Abstract

The objective of the present investigation was to examine the extent of variations in single leaf net photosynthetic rate (P_N) and its relative dependence on stomatal conductance (g_s) and the mesophyll capacity to fix carbon in 12 clones of the natural rubber plant. There were significant variations in P_N measured at low and saturating photon flux density (PFD); the extent of variation was larger at low than at saturating PFD. The compensation irradiance (CI) and apparent quantum yield of CO_2 assimilation (ϕ_c) calculated from the P_N/PFD response curves showed significant variations among the clones. P_N at low irradiance was positively correlated with ϕ_c. Thus a clone with large P_N at low irradiance, high ϕ_c, and low CI may tolerate shade better and thus produce a high tree stand per hectare. A strong positive correlation existed between P_N saturated with radiant energy (P_{sat}) and carboxylation efficiency (CE) estimated from the response curves of P_N on intercellular CO_2 concentration (C_i), but g_s showed a poor correlation with P_{sat}. High CO_2 compensation concentration (Γ) led to low CE in *Hevea* clones. A clone with large P_{sat}, high CE, low g_s, and low Γ is the one in which photosynthesis is more dependent on the mesophyll factors than stomata. Such a clone may produce relatively high biomass and maintain high water use efficiency.

Additional key words: apparent quantum yield; carboxylation efficiency; CO_2 compensation concentration; compensation irradiance; dark respiration; intercellular CO_2 concentration; irradiance; quantum yield of CO_2 fixation; stomatal conductance; water use efficiency.

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*Author for correspondence; fax: 91-481-578317; e-mail: rubrind@giasmd01.vsnl.net.in.

Abbreviations: C_a, ambient atmospheric CO_2 concentration; C_i, intercellular CO_2 concentration; CE, dP/dC_i, *in vivo* carboxylation efficiency; CI, compensation irradiance; g_s, stomatal conductance; L_s, stomatal limitations to photosynthesis; PFD, photon flux density; P_{maxCi}, photosynthesis at saturating irradiance and C_i; P_N, net photosynthetic rate at ambient conditions; P_{sat}, net photosynthetic rate at saturating irradiance and ambient CO_2 concentration; R_D, leaf dark respiration rate; RuBPCO, ribulose-1,5-bisphosphate carboxylase/oxygenase; VPD, vapour pressure deficit; WUE, water use efficiency; ϕ_c, $dP/dPFD$, apparent quantum yield of CO_2 fixation; Γ, CO_2 compensation concentration.

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Introduction

Hevea brasiliensis, the most important source of natural rubber, is a perennial tree crop grown under different agroclimatic zones of the world (Archer and Audley 1973). Considerable efforts are being made through breeding and selection to improve rubber productivity to meet increasing demand (Anonymous 1997). There are many *Hevea* clones that are bred to suit different agroclimatic conditions. Rubber yield, biomass production, water use efficiency (WUE), and the associated physiological traits of these clones vary. Physiological characterization of the clones is important in designing further breeding strategies.

Studying the yield/biomass production or WUE of any perennial species like *Hevea* requires experiments of long duration. To overcome this problem one can look into the behaviour of certain physiological parameters which can be effectively used to assess the relative performance of any clone. Net photosynthetic (P_N) and transpiration rates of leaves and total leaf area per plant are the important factors that determine the biomass production and WUE of a species. Significant differences in leaf P_N and g_s exist across tree species (Nataraja 1991, Zipperlen and Press 1996). Similarly, significant genotypic variations in photosynthesis and g_s are reported in annual crop plants (*e.g.*, sunflower, Virgona and Farquhar 1996; *Miscanthus*, Weng and Ueng 1997) and in tree species (*e.g.*, *Eucalyptus camaldulensis*, Farrell *et al.* 1996; *Populus*, Kalina and Ceulemans 1997; *Prunus amygdalus*, Matos *et al.* 1997). A positive correlation between photosynthesis and biomass has been reported in chickpea (Mythili and Nair 1996). In several *Poa* species, relative growth rate was positively related to photosynthesis (Atkin *et al.* 1997). High P_N is important in increasing yield in cotton (Gerik *et al.* 1996). The productivity of hazelnut may be increased *via* increased canopy photosynthesis by improving the radiant energy distribution inside the canopy (Hampson *et al.* 1996). In *Hevea* clonal variations in photosynthesis have been observed (Samsuddin 1986, Dey *et al.* 1995, Nugawela *et al.* 1995), but a poor positive correlation between photosynthesis and yield has been observed in this species (Samsuddin *et al.* 1987).

Photosynthesis at low PFD is important in a plantation crop such as *Hevea*, because most of the leaves in the mature canopy are exposed to very low PFD throughout the day. The relative dependence of P_N on g_s and the biochemical efficiency of mesophyll to fix carbon determine the biomass production in relation to WUE. We studied on young bud grafted plants of 12 different clones of *Hevea* the extent of variations in P_N and its relative dependence on mesophyll efficiency and g_s.

Materials and methods

All experiments were made at the Rubber Research Institute of India, Kottayam located at 76°36'E and 9°32'N at an altitude of 73 m a.s.l. Twelve different commercially popular clones of *Hevea brasiliensis* Müll. Arg., namely, RRII 51, RRII 105, RRII 176, RRII 203, RRIC 100, RRIM 600, PB 217, 82/14, 82/17, 82/22, 82/29, and 82/30 were grown in large pots (0.75 m^3) filled with garden soil (equal mixture of red laterite soil, river sand, and farm yard manure) following all standard agronomical practices (Anonymous 1995).

Gas exchange measurements (P_N and transpiration rate, g_s, leaf-air vapour pressure difference, VDP) were made using a portable photosynthesis system (*LI6400, LI-COR*, Logan, USA) on intact, fully mature top leaves of 18 months-old plants. The observations were made at saturating PFD of 1000 μmol m^{-2} s^{-1} (red radiation from an LED source having a centre wavelength of 660 to 675 nm; *LI 6400-02, LI-COR*, Logan, USA), leaf temperature of 30±1.5 °C, and leaf-air VPD of around 1.0-1.2 kPa. Each leaf was allowed to stabilize for 5-8 min before measuring the P_N and g_s.

Photosynthetic response to leaf C_i was measured at saturating PFD by step changes in the CO_2 concentration (C_a) in the measurement cuvette. Different CO_2 concentrations were generated inside the leaf chamber by using a CO_2 injector (*LI 6400-01, LI-COR*, Logan, USA). C_i was calculated from the steady state measurement of gas exchange according to Farquhar and Sharkey (1982). The response of P_N to step changes in PFD was examined using an LED source fitted to the leaf chamber of the photosynthesis system.

P_N/C_i and P_N/PFD response curves were made by fitting an asymptotic function [$P_N = a\ (1 - e^{-bx}) + c$] between P_N, the dependent variable, and C_i or PFD, the independent variable (Jacob *et al.* 1995) by using the least square method. The r^2 was always >98 % for all the curves. *In vivo* carboxylation efficiency (CE) was computed as the initial slope of the P_N/C_i response curve [*i.e.*, $dP_N/dC_i = (a+c)\ b$, at $P_N = 0$]. The ϕ_c was estimated by calculating the initial slope of P_N/PFD response curve [*i.e.*, dP_N/dPFD = $(a+c)\ b$, at $P_N = 0$]. Irradiance and CO_2 saturated P_N (P_{sat} and P_{maxCi}, respectively) values were calculated as $a+c$. The values of Γ and CI were derived from the P_N/C_i and P_N/PFD curves, respectively, by computing the value of the independent variable at $P_N = 0$ $\{x = -[\ln(a+c) - \ln(a)]/b\}$.

Stomatal limitation to photosynthesis (L_s) was calculated according to Farquhar and Sharkey (1982) as $(P_0-P_N)/P_0$ where $P_0 = P_N$ at $C_i = 350$ μmol mol^{-1}, P_N = photosynthesis at $C_a = 350$ μmol mol^{-1}. Dark respiration rate of the leaf (R_D) was measured directly with the portable photosynthesis measurement system at zero PFD.

Results were subjected to analysis of variance (ANOVA) test and least significant differences (LSD) between the means were estimated at 95 % confidence level.

Results

Photosynthetic rate at saturating PFD (P_{sat}) computed from the P_N/PFD response curves (Fig. 1) ranged from 11 (RRII 51) to 15 μmol m^{-2} s^{-1} (RRII 203; Table 1). The clone RRII 51 maintained the lowest and RRII 203 the highest P_N when measured at a low PFD (80 μmol m^{-2} s^{-1}) and C_a (350 μmol mol^{-1}, Table 1). Significant differences in ϕ_c were also noticed among the clones (Table 1). The maximum ϕ_c was recorded in RRII 203 and the minimum in RRII 51. Significant variations in the CI were also recorded, ranging from 25 in RRIC 100 to 36 μmol m^{-2} s^{-1} in clone 82/22 (Table 1).

Detectable differences were found in the response of P_N to C_i (Fig. 2). The calculated values of P_N at saturating C_i (P_{maxCi}) ranged from 20 in RRII 51 to 26 μmol m^{-2} s^{-1} in RRII 105 (Table 1). The *in vivo* carboxylation efficiency (CE) calculated from the P_N/C_i response curves was the highest in RRIM 600 and the lowest in 82/17 (Table 1). The leading clone RRII 105 had a minimum and the clone 82/30 had a maximum Γ (Table 1). The R_D in the leaves of the *Hevea* clones ranged

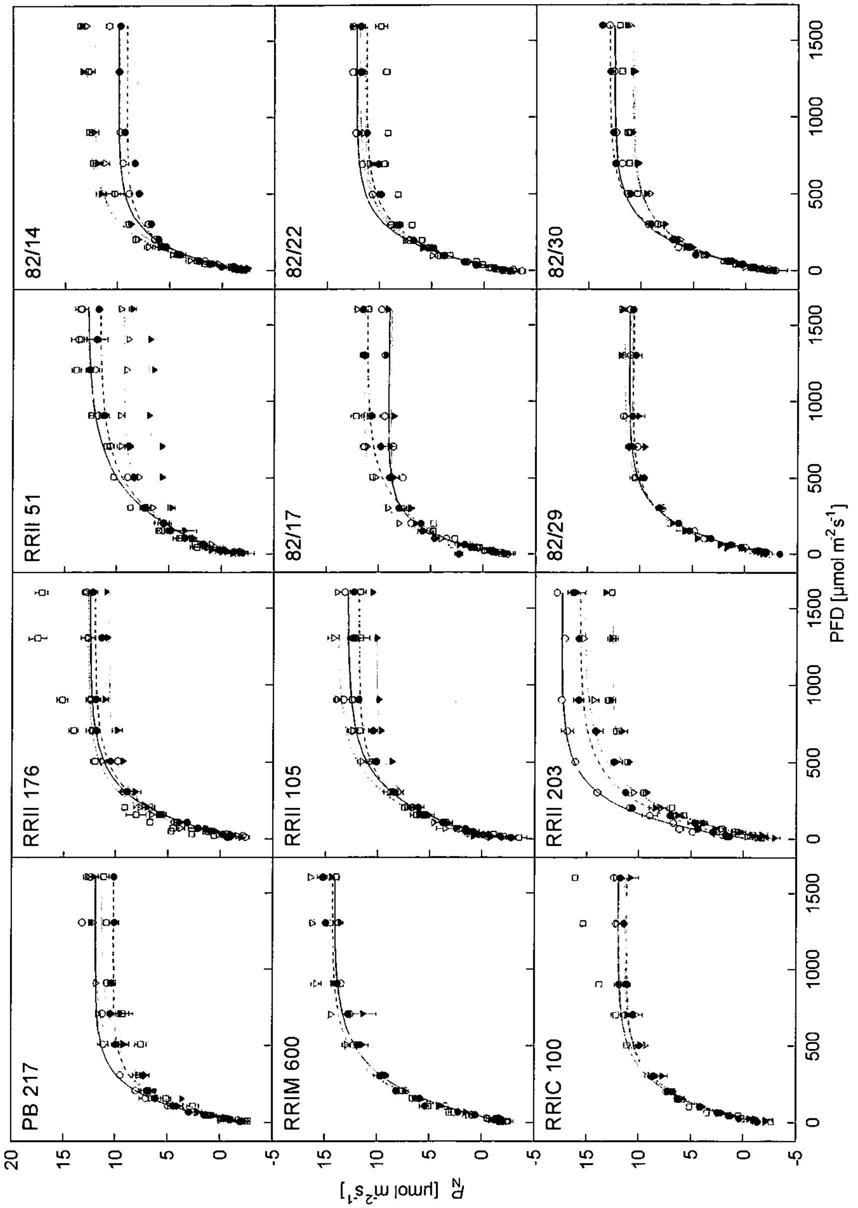

Fig. 1. Photosynthetic response (P_N) to irradiance of 12 different *Hevea* clones. Each line represents different plants in each clone. r^2 >98 %; each point is a mean of 5-8 observations; SE are shown.

from 1.57 in RRII 176 to 2.71 μmol(CO$_2$) m^{-2} s^{-1} in 82/22 (Table 1).

A positive correlation between P_N at low PFD and the ϕ_c was found (r = 0.70, p = 0.012, Fig. 3*A*). Also a positive correlation between P_{sat} and CE was observed (r = 0.73, p = 0.007, Fig. 3*B*). P_N measured at low PFD and P_{sat} were also significantly correlated (r = 0.73, p = 0.008, Fig. 3*C*). The CE was negatively related to Γ (r = -0.7, p = 0.011, Fig. 3*D*).

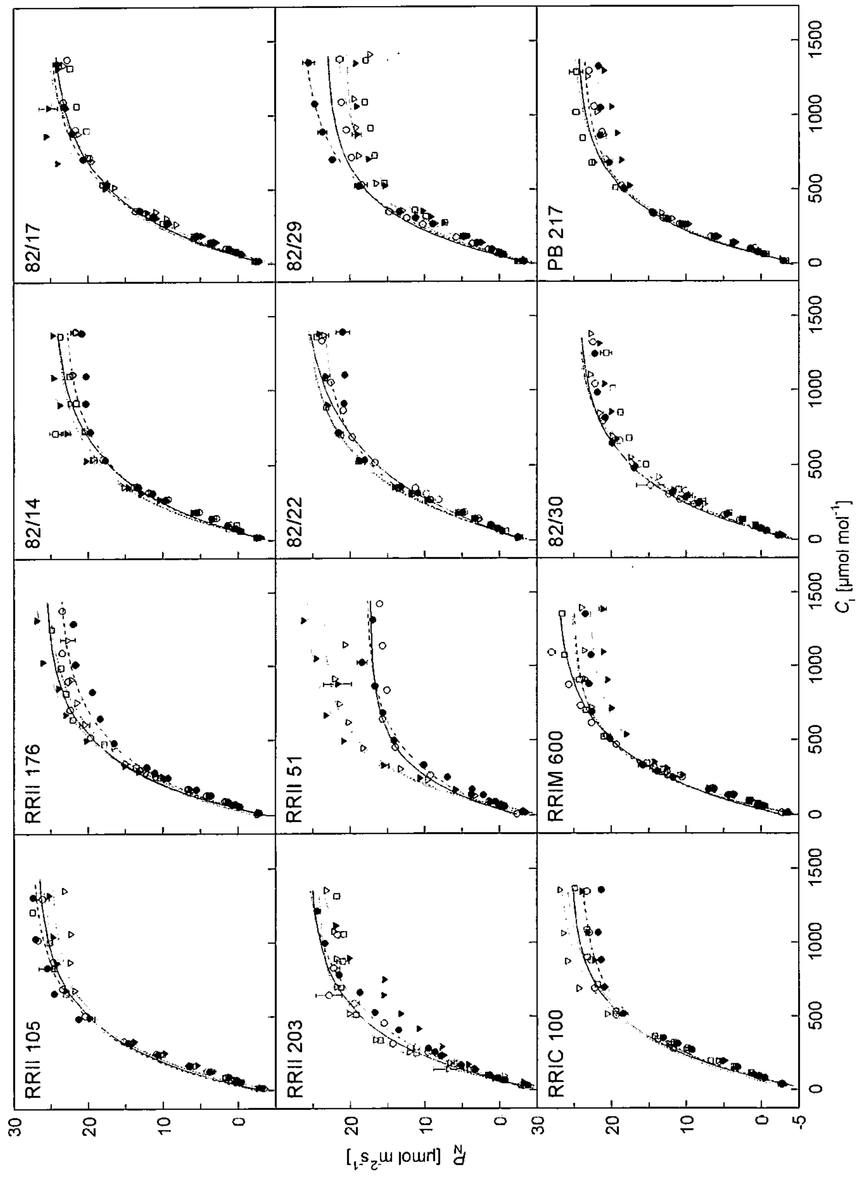

Fig. 2. Net photosynthetic rate/intercellular CO$_2$ concentration (P_N/C_i) response curves of 12 different *Hevea* clones. Each line represents different plants in each clone. r^2 >98 %; each point is a mean of 5-8 observations; SE are shown.

Table 1. Net photosynthetic rate saturated with irradiance, P_{sat} [μmol(CO_2) m^{-2} s^{-1}], or measured at a PFD of 80 μmol m^{-2} s^{-1}, P_{80} [μmol(CO_2) m^{-2} s^{-1}], apparent quantum yield for CO_2 fixation, ϕ_c [mmol(CO_2) mol^{-1}(PFD)]; compensation irradiance, CI [μmol m^{-2} s^{-1}]; CO_2-saturated rate of photosynthesis, P_{maxCi} [μmol(CO_2) m^{-2} s^{-1}]; *in vivo* carboxylation efficiency, CE [mmol(CO_2) m^{-2} s^{-1}]; Γ, CO_2 compensation concentration [μmol mol^{-1}]; leaf dark respiration rate, R_D [μmol(CO_2) m^{-2} s^{-1}]; stomatal limitation to photosynthesis, L_s [%]; and the ratio of photosynthesis to stomatal conductance, P_N/g_s [μmol(CO_2) μmol^{-1}(H_2O)] of 12 different clones of *Hevea* (values in the parentheses indicate standard error).

Clone	P_{sat}	P_{80}	ϕ_c	CI	P_{maxCi}	CE	Γ	R_D	L_s	P_N/g_s
RRII 51	10.8 (1.21)	2.1 (0.16)	0.419 (0.041)	27.3 (1.01)	19.5 (1.85)	0.651 (0.043)	58.4 (3.37)	1.83 (0.16)	13.3 (1.07)	6.8 (0.06)
RRII 105	12.2 (0.62)	2.8 (0.13)	0.587 (0.039)	29.5 (2.49)	25.9 (0.53)	0.739 (0.015)	53.2 (4.48)	2.44 (0.48)	17.8 (4.45)	8.0 (0.03)
RRII 176	12.7 (0.85)	3.2 (0.43)	0.629 (0.026)	27.7 (2.43)	24.8 (0.58)	0.694 (0.018)	59.6 (3.27)	1.57 (0.32)	15.3 (4.35)	14.1 (0.56)
RRII 203	14.7 (0.94)	3.8 (0.64)	0.708 (0.058)	29.2 (1.74)	24.3 (0.63)	0.710 (0.087)	65.6 (0.94)	1.61 (0.37)	20.7 (3.66)	13.6 (0.72)
RRIC 100	12.1 (0.73)	2.8 (0.12)	0.590 (0.023)	25.1 (1.99)	24.9 (0.53)	0.710 (0.017)	62.3 (3.77)	1.96 (0.27)	16.6 (3.23)	12.1 (0.03)
RRIM 600	14.4 (0.45)	2.6 (0.13)	0.615 (0.022)	32.5 (1.02)	24.5 (0.76)	0.774 (0.023)	58.3 (3.59)	2.29 (0.19)	8.5 (2.05)	7.3 (0.17)
PB 217	11.1 (0.41)	2.7 (0.29)	0.607 (0.046)	29.2 (2.52)	23.7 (0.74)	0.729 (0.009)	62.2 (1.61)	2.49 (0.16)	10.8 (2.79)	12.0 (0.06)
82/14	11.4 (0.79)	2.8 (0.16)	0.625 (0.058)	26.5 (1.13)	24.0 (0.57)	0.679 (0.018)	64.3 (1.54)	1.96 (0.13)	8.0 (0.66)	6.3 (0.14)
82/17	11.2 (0.61)	2.7 (0.19)	0.597 (0.032)	30.7 (1.16)	25.2 (0.56)	0.618 (0.023)	66.8 (2.89)	2.22 (0.09)	13.6 (3.98)	7.8 (0.15)
82/22	11.3 (0.48)	2.4 (0.09)	0.613 (0.009)	35.9 (1.08)	24.3 (0.69)	0.638 (0.024)	64.7 (0.72)	2.71 (0.31)	12.6 (1.17)	9.1 (0.09)
82/29	10.9 (0.26)	2.4 (0.13)	0.610 (0.064)	34.2 (2.49)	21.9 (1.25)	0.623 (0.042)	68.1 (2.46)	2.33 (0.22)	8.9 (1.15)	7.4 (0.09)
82/30	11.8 (0.44)	2.5 (0.047)	0.663 (0.019)	32.6 (1.26)	23.4 (0.56)	0.619 (0.021)	73.4 (1.72)	2.48 (0.16)	21.1 (3.83)	12.8 (0.93)
$LSD_{0.05}$	2.01	0.76	0.116	5.16	2.49	0.102	7.96	0.79	8.69	1.56

The different clones of *Hevea* showed significantly different stomatal limitations to photosynthesis (L_s). Clones 82/14 and 82/30 had the minimum and maximum L_s, respectively (Table 1). Significant differences in the ratio of P_N/g_s were also noticed in the *Hevea* clones (Table 1).

Discussion

The significantly wide variations in P_{sat} (34 %) and P_{maxCi} (30 %) observed in the 12 clones (Table 1) indicated a large genetic variability in photosynthetic capacity in this species. In the field, the leaves in the upper layers of a mature *Hevea* plantation with a leaf area index of above six may intercept as much as 75 % of the incident PFD (unpublished results) and a significant portion of the total leaf area that is present in the lower layers of the canopy is exposed to sub-saturating PFD of about 100-200 µmol m^{-2} s^{-1}. Thus, low PFD which limits the productivity in different tree crops (*e.g.*, hazelnut, Hampson *et al.* 1996) and forest ecosystems (Anten *et al.* 1996) can be a limiting factor in *Hevea* plantations also. Therefore, under field conditions, photosynthesis of shaded leaves is very important for the total carbon budget of the plantations. The extent of variations in low irradiance P_N was greater than the extent of variations in P_{sat} in the 12 clones, but there was a positive correlation between low irradiance P_N and P_{sat} (Fig. 3*C*).

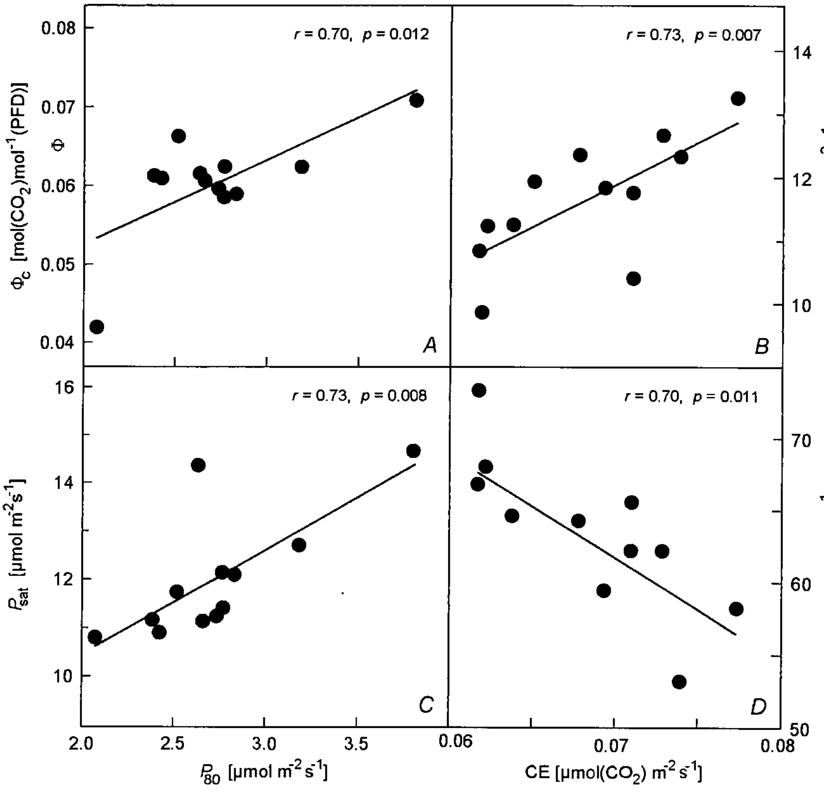

Fig. 3. Linear regression between photosynthesis at a PFD of 80 µmol m^{-2} s^{-1} (P_{80}), and apparent quantum yield, ϕ_c (*A*) or PFD-saturated net photosynthetic rate, P_{sat} (*C*), and *in vivo* carboxylation efficiency, CE and P_{sat} (*B*) or CO_2 compensation concentration, Γ (*D*).

The ϕ_c, which differed significantly among the clones (Table 1), was positively correlated with P_N at low irradiance (Fig. 3*A*), but weakly correlated with P_{sat} (values not shown). The total canopy photosynthesis and dry matter production may be determined more by ϕ_c than P_{sat} (Long 1985). Significant positive correlation between ϕ_c and rubber yield potential has been reported in *Hevea* (Nugawela *et al.* 1995). Because of their high P_N at low PFD and high ϕ_c, clones such as RRII 203 and

RRII 176 may tolerate shade and therefore withstand high density planting compared to a clone like RRII 51 which has relatively small P_N at low PFD and small ϕ_c. In general, clones with relatively large P_N at low PFD had low CI. In the shaded part of the canopy, low CI is beneficial for high photosynthetic productivity. Attempts to improve the capacity of the mesophyll to fix more carbon efficiently at low PFD may be rewarding in *Hevea* crop improvement programme.

The wide variations in Γ observed in the present study (Table 1) imply appreciable variations in photorespiration which decreases the photosynthetic productivity by decreasing the CE (Fig. 3*D*). In addition to photorespiration, carbon lost through dark respiration can also be significant (Morgan and Austin 1983). The R_D of leaves showed a marked variation (73 %) in the 12 *Hevea* clones (Table 1).

In vivo CE is a measure of the activity of the primary carboxylase enzyme RuBPCO in the leaves (Farquhar *et al.* 1980, Long 1985). Under non-stress conditions, most of the mesophyll control on photosynthesis is operated at the RuBPCO site, because it is a rate limiting enzyme in photosynthetic biochemistry (Farquhar *et al.* 1980, Woodrow and Berry 1988). Therefore, CE is an index of the mesophyll capacity for photosynthesis. The CE, which was significantly different among the clones studied here, showed a strong positive correlation with P_{sat} (Fig. 3*B*), but g_s showed a poor correlation with it (values not shown). Relative stomatal limitations to P_N were also comparatively small in this species (Table 1). These results suggest that the mesophyll factors play a much more important role than g_s in regulating P_N in *Hevea.*

When photosynthesis is controlled more by mesophyll factors and less by stomata, there would be relatively more carbon fixed per unit g_s. This will lead to improved WUE. Most often, genotypes with high WUE have poor crop growth rates resulting in poor biomass production (Udaya Kumar *et al.* 1998). This is because of the larger dependence of P_N on g_s than on the mesophyll capacity for CO_2 assimilation in the genotypes with high WUE (Ehleringer 1993, Pereira 1995). In the present experiment we showed that at least two clones of *Hevea* (RRII 203 and RRIC 100) which have been categorized as high biomass types by Licy and Premakumari (1988) and Saraswathy Amma *et al.* (1990) had relatively high P_N per unit g_s. This suggests that in these clones there is a greater dependence of P_N on mesophyll (than stomata) as indicated by their relatively high CE. These clones may be potential parents for breeding for high biomass and WUE in *Hevea.*

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