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Photosynthetic Capacity and Effect of Drought on Leaf Gas Exchange in Two Rubber (*Hevea brasiliensis*) Clones

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ABSTRACT

Photosynthetic capacity, water-use efficiency and nitrogen-use efficiency were compared between two different rubber clones, PB 260 and PB 217. Plants were grown in 50 dm^3 pots in a greenhouse at Clermont-Ferrand, France under controlled condition. Net CO_2 assimilation rate at 1800 ppm CO_2 (A_{1800}) and at 360 ppm CO_2 (A_{360}), maximum carboxylation rate (V_{cmax}), electron transport capacity (J_{max}) and nitrogen-use efficiency (A_{1800}/N_a, A_{360}/N_a, V_{cmax}/N_a and J_{max}/N_a) of clone PB 260 were significantly higher than those of clone PB 217. However, the dark respiration rate (R_d), the ratio of light-saturated rate of electron transport and maximum rate of carboxylation (J_{max}/V_{cmax}), leaf mass per area (M_a), leaf nitrogen content (N_m), leaf nitrogen per area (N_a), water use efficiency (*WUE*), SPAD value (SPAD) and chlorophyll fluorescence ratio (F_v/F_m) were non- significantly different between these clones. Effects of drought on leaf gas exchange rates was also studied. Net CO_2 assimilation rate (*A*), stomatal conductance (g_s) and transpiration rate (*E*) showed a declining curve as a function of increased water stress. *WUE* was high under severe stress, due to a more rapid decrease of *E* than *A*. At 14 days after stress, g_s and *E* decreased by 80-85%, while *A* decreased by 60-70%. Drought also reduced leaf water potential, which was possitively related to stomatal conductance. These results confirmed the potential genotypic variability of some photosynthetic traits under non-water-limited condition and stomatal behavior related with hydraulic properties during water stress in rubber trees.

Key words: photosynthesis, respiration, leaf nitrogen, stomatal conductance, rubber

INTRODUCTION

Rubber is a major plantation crop covering 9.76 millions hectares worldwide (RRIT, 1999). Due to lack of available land and competition with other crops, many countries tend to extend rubber plantations toward non-traditional zones characterised by soil and climate limitations e.g, Northeastern Thailand (Intraskul *et al*., 1992; Manmeun *et al*., 1993; Prasertsuk, 1997) India (Rao *et al*., 1990; Krishna *et al*., 1991; Chandrashekar, 1997; Chandrashekar *et al*., 1998;

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Vijayakumar *et al*., 1998) Indonesia (Karyudi *et al*., 2001). Severe growth reduction and longer immaturity periods due to soil moisture stress has been reported (Wichitchonchai and Manmeun, 1992; Manmeun *et al*., 1993; Chandrashekar *et al*., 1998; Vijayakumar *et al*., 1998) under such conditions. In order to assess and forecast rubber performance in these environments, better understanding of tree functionning is required. Particularly, the ability of trees to assimilate carbon should be assessed. It is well kown that canopy architecture and the associated microclimate, responses to environmental conditions, source-sink regulations of photosynthetic performance at the whole plant scale, and long-lasting effects of carbon partitioning and soil-plant interactions under field conditions are of paramount importance in determining plant growth and yield (Peng, 2000). However, a better knowledge of leaf photosynthetic activity and water- and nitrogen-use efficiencies remains necessary to understand differences in growth and yield between plant species or between clones of a given species. Most models used to simulate assimilate acquisition at plant scale require the description of gas exchange activities at leaf-scale (Sinoquet *et al*., 2001).

In rubber tree, only a few studies have already compared leaf characteristics such as photosynthetic capacity and water- or nitrogen-use efficiencies between clones exhibiting different growth rate and latex production. Samsuddin and Impens (1978a and b) showed that net photosynthesis-light response curves, stomatal conductance and water-use efficiency differed among four rubber clones (GT 1, PB 5/51, RRIM 600, and Tjir 1) under laboratory conditions. Correlation between photosynthetic rates and yield over five years was found by Samsuddin *et al*. (1987). Differences in net photosynthesis-light response curves among clones under field conditions have also been reported (Ceulemans *et al*., 1984). Recently, Nataraja and Jacob (1999) found significant differences in photosynthesis response curves to light and CO_2 among twelve rubber clones. However, differences in leaf photosynthetic capacity in rubber have never been related to anatomical or biochemical characteristics e.g., leaf mass-to-area ratio, nitrogen concentration, or leaf grenness. To present knowledge, nitrogen-use efficiency has never been compared between rubber clones.

Under water stress conditions, very low stomatal conductance (Chandrashekar *et al*., 1998) and severe inhibition of photosynthesis and transpiration (Krishna *et al*., 1991) were reported. Net photosynthesis and stomatal conductance showed a sigmoid shaped declining curve as a function of increasing water stress situations (Ceulemans *et al*., 1983). Leaf water potential, leaf resistance and trunk diameter changed according to soil moisture status (Resnik and Mendes, 1979). However, gas exchange parameters during drought cycle of rubber are still poorly documented. In particular, some gas exchange parameters have never been correlated with leaf water potential.

Clonal variations were evident in yield and yield components and associated physiological parameters in response to soil moisture status and meteorological factors (Rao *et al*., 1990). However, complex regulation of rubber biosynthesis and latex flow made it difficult to directely relate yield to leaf photosynthesis. Low dry rubber yield was associated with high plugging index and low initial flow rate of latex in dry season (Devakumar *et al*., 1988; Rao *et al*., 1990). Such parameters were closely linked to phloem turgor pressure and depending on stomatal conductance therefrom (Chandrashekar, 1997).

The objectives of this study were (1) to compare the leaf photosynthetic capacity, stomatal conductance, leaf mass-to-area ratio, nitrogen concentration, leaf greeness, and quantum yield of energy conversion by photosystem II between two rubber clones (PB 260 and PB 217) exhibiting differences in growth rate. Differences in leaf

water-use and nitrogen-use efficiencies were also tested. (2) to investigate variation of leaf gas exchange parameters during drought stress. (3) to correlate some leaf gas exchange parameters with leaf water potential.

MATERIALS AND METHODS

Plant material

The experiment was conducted with two rubber (*Hevea brasiliensis* Muell. Arg.) clones, PB 260 and PB 217. When grown together in the field, the growth of PB 260 was higher than that of PB 217 (average growth at 1 m from soil at 5 years were 46.4 and 43.2 cm respectively) (RRIT, 1993). Two year-old budded rubber trees of each clone were obtained from Michelin Company in Clermont-Ferrand, France. The rubber plants selected for this study were around 1.5 m high and 1 m^2 leaf area. They were planted in 50 dm^3 pots filled with 40% blond peat, 40% brown peat and 20% podzolane. They were grown in a greenhouse in Clermont-Ferrand under controlled conditions (air temperature ranging from 23 to 32°C, maximum *PPFD* around 2451 µmol/m^2/s, relative humidity ranging from 73 to 84 %) (Figure 2). Six plants of each clone were separated into 2 groups, i.e. control and stress. Control plants were daily watered, while stress plants were not watered during 14 days (drought cycle).

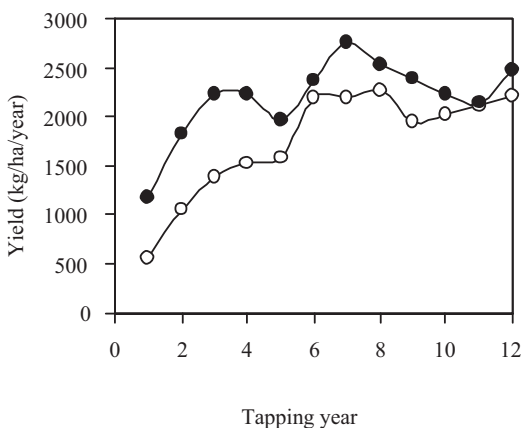

Figure 1 Variations in yield of rubber clone PB 260 (close symbols) and PB 217 (open symbols) during the tapping year. Data are derived from a field trial in Malaysia (source: CIRAD).

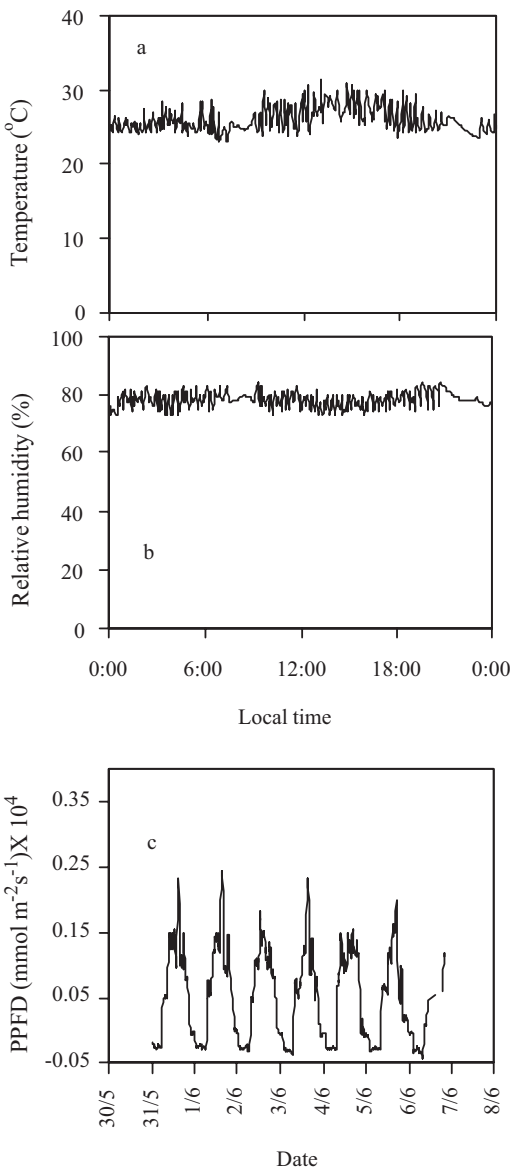

Figure 2 Typical daily variations in environmental conditions in the greenhouse (air temperature, a; air relative humidity, b and Photosynthetic Photon Flux Density, c).

Photosynthetic capacity

Net CO_2 assimilation rate (A), stomatal conductance (g_s), and CO_2 partial pressure in the substomatal spaces (C_i) were measured with a portable photosynthesis system model Li-6400 (Li-Cor Inc., Lincoln, NE, U.S.A.). Measurements were made on ten fully expanding leaves for each clone from 20 July to 2 August 2000. The key parameters of the Farquhar photosynthesis model (Farquhar *et al.*, 1980; version proposed by Harley *et al*., 1992) were determined for each leaf. An A-C_i response curve measured at $PPFD$ = 900 µmol/m^2/s was used to infer the best fit value of maximum carboxylation rate V_{cmax} and electron transport capacity J_{max} by non-linear least squares regression (SAS Inst. Inc., 1990). For each response curve, eight measurements were acquired (C_a = 100, 35, 30, 20, 15, 10, 7.5 and 5 Pa). A 10-min equilibration time was allowed before any measurement. Values of leaf dark respiration R_d were estimated by measurements of the CO_2 evolution rates after 20 min in darkness. During A-C_i responses and R_d determinations, leaf temperature and air water vapour pressure deficit at the leaf surface were 28.5 ± 0.4°C and 1.2 ± 0.2 kPa, respectively. A detailed description of the version of the Farquhar photosynthesis model used is given by Harley *et al.* (1992), and model primary parameters including the kinetic constants for Rubisco were tabulated as in Le Roux *et al*. (1999).

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured with a portable fluorometer (PAM 2000, Walz, Effeltrich, Germany). Measurements were made at predawn (around 4 AM) and at maximum solar elevation (around 2 PM) on the leaves for which the parameters of the photosynthesis submodel were determined (i.e., 10 leaves per clone). The chlorophyll fluorescence ratio $\Delta F/F'_m$ ($\Delta F = F'_m - F_s$, where F_s and F'_m were the steady state fluorescence during photosynthesis and during a saturating flash, respectively) was used as a reliable estimate of Φ_{II} i.e., the quantum yield of energy conversion by photosystem II PS_{II} (Genty *et al*., 1989).

Leaf mass per area, nitrogen and leaf greenness

Leaf greenness was measured on the leaflet using a SPAD-502 Chlorophyll Meter (Minolta Camera Co., Ltd., Japan).

The area of each sampled leaf was measured with a leaf area meter (Delta T Devices, Hoddeston, U.K.). Leaves were dried in the oven (48 hours at 65°C), and leaf dry mass was measured. Total leaf nitrogen concentration was determined with an elemental analyser (Carlo Erba Instruments, Milano, Italy).

Drought effect on leaf gas exchange study

A, g_s and transpiration rate (E) were measured with a portable photosynthesis system model Li-6400 (Li-Cor Inc., Lincoln, NE, U.S.A.). Continuous measurements were ramdomly made on 6 fully expanded leaves of each treatment every day after drought started (2 leaflets/plant). For each leaf, measurement was done at $PPFD$ = 900 µmol/m^2/s. Leaf temperature and air water vapour pressure deficit at the leaf surface were maintained at 28.5 ± 0.4°C and 1.2 ± 0.2 kPa, respectively. Water use efficiency was calculated from A devided by E. Midday leaf water potential was daily measured on one leaflet sample per plant with a pressure chamber during drought cycle.

RESULTS

Photosynthetic capacity

Net CO_2 assimilation rates at 1800 ppm CO_2 (A_{1800}) of clone PB 260 (25.2 µmol CO_2/m^2/s) was significantly greater than that of clone PB217 (21.2 µmol CO_2/m^2/s). At 360 ppm CO_2, A_{360} was approximately 38.8% and 40% of A_{1800} for clone PB 260 and PB 217, respectively (Table 1). Detectable differences between the two clones

were found in the response of *A* to *Ci* (Figure 3). At high *Ci*, the value of *A* was saturated at 26 and 23 μmol $CO_2/m^2/s$ in PB 260 and PB 217, respectively (Figure 3, see model).

The maximum carboxylation rate (V_{cmax}) and electron transport capacity (J_{max}) of clone PB 260 (53.96 and 147.67 μmol $CO_2/m^2/s$) were significantly greater than those of clone PB 217 (41.02 and 110.92 μmol $CO_2/m^2/s$, respectively) (Figure 4, top panel). The ratio between J_{max} and V_{cmax} was not significantly different between PB 260 (2.78) and PB 217 (2.80) (Figure 5).

The dark respiration rate was not significantly different between clone PB 260 (1.06 μmol $CO_2/m^2/s$) and PB 217 (1.03 μmol $CO_2/m^2/s$).

Chlorophyll fluorescence

Chlorophyll fluorescence was not significantly different between these clones. At predawn $\Delta F/F'_m$ predawn was 0.8429 for clone PB 260 and 0.8435 for clone PB 217, and at maximum solar elevation $\Delta F/F'_m$ afternoon was 0.7276 for clone PB 260 and 0.7342 for clone PB 217, respectively. The chlorophyll fluorescence of both clones was higher at predawn than at maximum solar elevation (Table 1).

Table 1 Net CO_2 assimilation rate at CO_2 1800 ppm, A_{1800} (μmol $CO_2/m^2/s$) or measured at CO_2 360 ppm, A_{360} (μmol $CO_2/m^2/s$); dark respiration rate, R_d (μmol $CO_2/m^2/s$); quantum yield of energy conversion by photosystem II at predawn (4.00 A.M.), ($\Delta F/F'_m$ predawn) and at afternoon (2.00 P.M.), ($\Delta F/F'_m$ afternoon); water use efficiency, *WUE* (μmol CO_2/m mol H_2O); leaf nitrogen concentration, N_m (%); leaf mass per area, M_a (g/m^2); leaf nitrogen per area N_a (gN/m^2) ; leaf nitrogen use efficiency expressed as net CO_2 assimilation rate divide by N_a at CO_2 1800 ppm, A_{1800}/N_a (μmol CO_2/gN/s) and at CO_2 360 ppm, A_{360}/N_a (μmol CO_2/gN/s); leaf greenness, SPAD (SPAD unit) of two rubber clones (± standard error of mean n=10). p is significant level.

Parameters	PB 260	PB 217	p
Photosynthetic capacity			
A_{1800}	25.19±0.66	21.21±0.48	0.0001
A_{360}	10.26±0.46	8.23±0.42	0.0001
R_d	1.06±0.01	1.03±0.09	0.83
$\Delta F/F'_m$ predawn	0.4829±0.0023	0.8435±0.0043	0.90
$\Delta F/F'_m$ afternoon	0.7276±0.0126	0.7342±0.0129	0.70
Water use efficiency			
WUE	5.06±0.26	5.30±0.22	0.50
Nitrogen concentration			
N_m	3.47±0.15	3.15±0.05	0.07
M_a	51.52±2.01	55.41±1.94	0.18
N_a	1.77±0.08	1.74±0.05	0.71
SPAD	52.37±2.19	48.42±1.29	0.14
Nitrogen use efficiency			
$A1800/N_a$	14.43±0.85	12.29±0.47	0.04
$A360/N_a$	5.91±0.43	4.75±0.25	0.03

Leaf mass per area, and nitrogen, nitrogen use efficiency and leaf greenness

Leaf nitrogen concentration (N_m) and leaf nitrogen per area (N_a) for PB 260 (3.47 % and 1.77 gN/m^2) tended to be greater than for PB 217 (3.15 % and 1.74 gN/m^2) but were not statistically different (p=0.07 and 0.71, respectively). Leaf mass per area (M_a,) was not significantly different between the two clones. However, clone PB 217 (55.41 g/m^2) tended to have a higher weight per area than that of clone PB 260 (51.52 g/m^2) (Table 1).

Leaf nitrogen use efficiencies (*NUE*) expressed as ratio between net CO_2 assimilation rate and N_a (A_{1800}/N_a and A_{360}/N_a) for clone PB 260 (14.43 and 5.91 µmol CO_2/gN/s) were

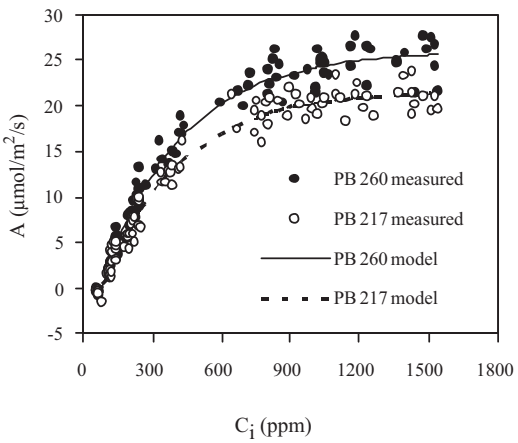

Figure 3 Net CO_2 assimilation rate (A) and intercellular CO_2 concentration (C_i) response curves of two rubber clones. Measurement was made on 10 leaflets per clone. Lines are fit through the data from equation y= a (1-e^{-bx}) + c (Nataraja and Jacob, 1999).

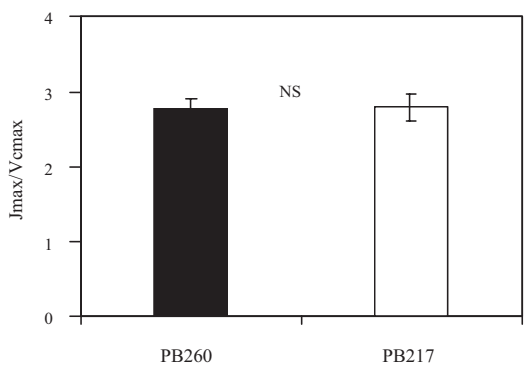

Figure 5 Comparison the ratio of light-saturated rate of electron transport J_{max} and maximum rate of carboxylation V_{cmax} between the two rubber clones. Means (n=10) and confidence intervals are presented (NS: non-significant at level p=0.05).

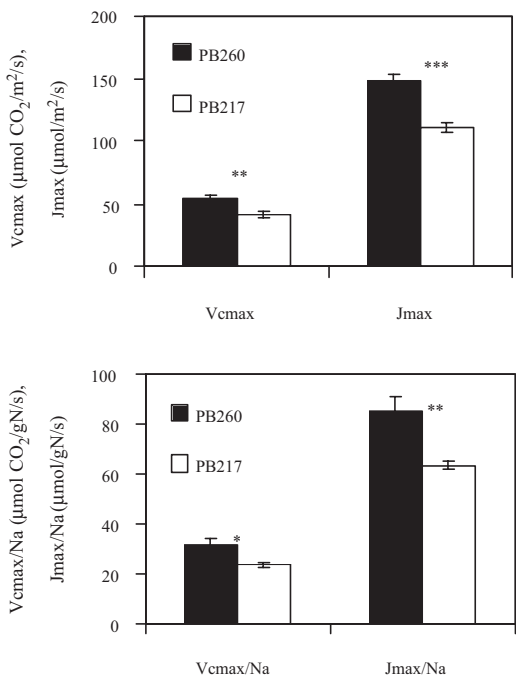

Figure 4 Comparison of maximum rate of carboxylation (V_{cmax}), light-saturated rate of electron transport (J_{max})(upper panel), and nitrogen use efficiency expressed as V_{cmax}/N_a and J_{max}/N_a (lower panel) between the two rubber clones. Means (n=8) and confidence intervals are presented (*: significant at the level p=0.05, **: significant at the level p=0.01, ***: significant at the level p=0.001).

significantly greater than for clone PB 217 (12.29 and 4.7591 µmol CO_2/gN/s) (Table 1).

NUE expressed as V_{cmax}/N_a for clone PB 260 (31.22 µmol CO_2/gN/s) was significantly greater than for clone PB 217 (23.38 µmol CO_2/gN/s). J_{max}/N_a of PB 260 (85.20 µmol CO_2/gN/s) was also significantly greater than clone PB 217 (63.90 µmol CO_2/gN/s) (Figure 4, bottom panel).

Leaf greenness measured by SPAD was not significantly different between clone PB 260 (52.4 SPAD unit) and clone PB 217 (48.4 SPAD unit) (Table 1).

Water use efficiency

Water use efficiency (*WUE*) was expressed as the ratio between A_{360} and E (A_{360}/E). In non-stress condition, *WUE* was not significantly different between clone PB 260 (5.06 µmol CO_2/mmol H_2O) and clone PB 217 (5.30 µmol CO_2/mmol H_2O) (Table 1).

Drought effect on leaf gas exchange

A, g_s and E values during 14 days of drought cycle are shown in figure 6. Daily variations in E and g_s in control plants were similar in both clones. However, g_s and E in PB 260 (202-252 mmol $H_2O/m^2/s$ and 2.0-2.6 mmol $H_2OH_2O/m^2/s$, respectively) were greater than in PB 217 (94-157 mmol $H_2O/m^2/s$ and 1.1-1.7 mmol $H_2O/m^2/s$, respectively). In stressed plants, g_s and E were generally high during 4-5 days after stress. But, g_s and E decreased daily from 5 days of stress until 14 days of stress. At the end of drought, cycle, g_s of PB 260 and PB 217 were 31 and 20 mmol $H_2O/m^2/s$ respectively, while E of PB 260 and PB 217 were 0.38 and 0.24 mmol $H_2O/m^2/s$, respectively (Figure 6).

A values in control plant were greater in PB 260 (7.9-9.8 µmol $CO_2/m^2/s$) than those in PB217 (7.1-8.2 µmol $CO_2/m^2/s$). For stress plants, A of both clones was nearly constant during 6 days after stress, and began to decrease at 7 days after stress. At 11 days after stress, A decreased by 70% when

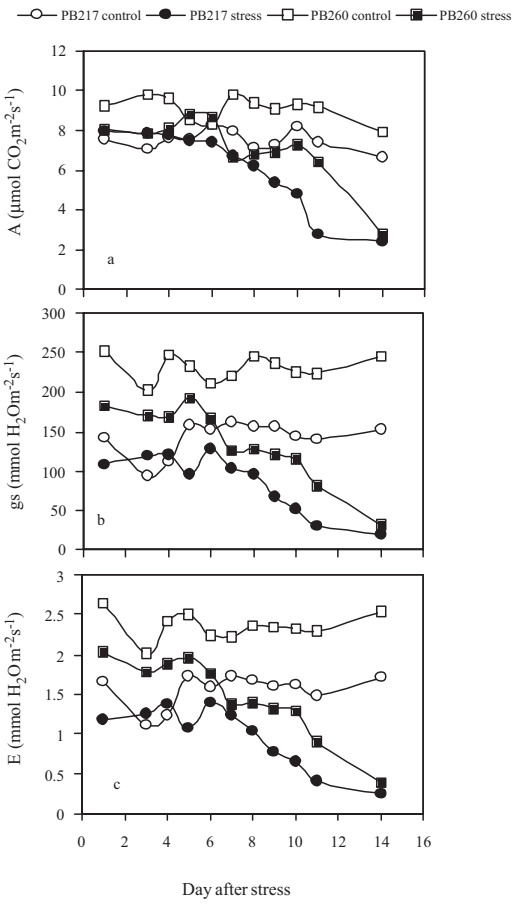

Figure 6 Net CO_2 assimilation rate (a), stomatal conductance (b) and transpiration rate (c) of the two rubber clones during drought cycle compared with control. Data points are the mean of 6 measurements.

compared to the control plant for PB 217 and 30 % for PB 260. However at the end of drought cycle, the results showed similar A (2.8 µmol $CO_2/m^2/s$) in both clones (Figure 6).

Water use efficiency (*WUE*) during drought stress is shown in Figure 7. In the control plants, *WUE* had no specific trends during the drought cycle ranging from 3.1-7.0 µmol CO_2 / mmol H_2O. In stress plant, *WUE* increased progressively from 7 days after stress. At the end of drought cycle, WUE were 9.4 and 10.1 µmol CO_2 / mmol

H_2O in PB 260 and PB 217, respectively. *WUE* increased 255 % when compared with control plant for PB 217 and 300 % for PB 260 (Figure 7).

Leaf water potential (*LWP*) in the control plants of both clones ranged from – 0.7 to –1.3 MPa. In stress plant, *LWP* declined progressively with time after stress. *LWP* of PB 260 was -1.27 MPa before stress and it was –2.1 MPa after 14 days of stress. *LWP* of PB 217 was –1.7 MPa before stress and it was –1.95 MPa after 14 days of stress (Figure 8).

Positive correlation between g_s and *LWP* was found in both clones. However, this correlation was weaker in PB 217 than in PB 260. From the equations, stomata would be closed (g_s = 0 mmol $m^{-2}s^{-1}$) when *LWP* reached –2.3 MPa in PB 260 and reached –2.2 MPa in PB 217 (Figure 9).

DISCUSSION

Photosynthetic capacity

The significant variations in A_{1800} and A_{360} observed in two clones indicated an important genetic variability in photosynthetic capacity among rubber clones as previously reported (Nataraja and Jacob, 1999; Ceulemans *et al*., 1984; Nugawela *et al*., 1995). Thus it is possible to use variations of the single-leaf net photosynthesis and light response as a screening tool among clones (Samsuddin and Impens, 1978b).

The R_d in this experiment was not significantly different between clone PB 260 and clone PB 217. In contrast, Nugawela *et al*. (1995) showed that the R_d was significantly different

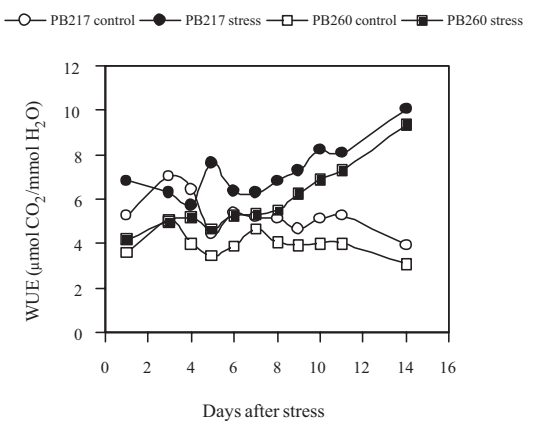

Figure 7 Water use efficiency of the two rubber clones during a drought cycle compared with control. Data points are the mean of 6 measurements.

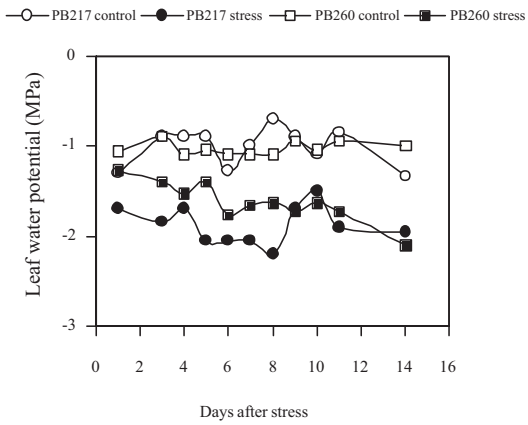

Figure 8 Leaf water potential of the two rubber clones during a drought cycle compared with control. Data points are the mean of 6 measurements.

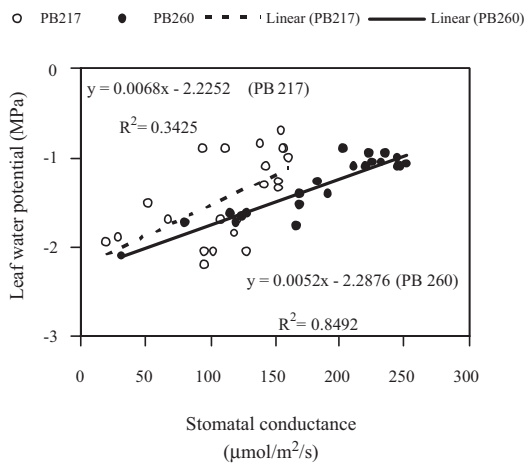

Figure 9 Relationship betaween leaf water potential and stomatal conductance during a drought cylel for the two rubber clones.

among ten genotypes contrasting in yield potential. The R_d of clone PB 217 (1.03 µmol/m^2/s) obtained in this experiment was lower than those reported by Nataraja and Jacob (1999) (2.49 µmol m^{-2} s^{-1}). The reason could be that the experiments differed in microclimate conditions. However, *A* and R_d of rubber leaf were affected by other plant factors such as leaf age (Samsuddin and Impens, 1979).

Although, leaf nitrogen concentration usually varies according to plant species, nevertheless leaf photosynthetic capacity is strongly correlated with leaf nitrogen on both N_m, and N_a (Reich *et al*., 1991; Wilson *et al*., 2000). In the experiment, the M_a, N_m, and N_a were not significantly different between clone PB 260 and clone PB 217 whereas significant differences were found in *A*. However, N_m and N_a in high photosynthetic capacity clone (PB 260) were higher than that of low photosynthetic capacity clone (PB 217). This could not showed correlation between *A* and leaf nitrogen in each clone because of a small number of leaves and a little diffence in leaf nitrogen concentration.

Water-use efficiency (*WUE*) is defined at the leaf level as ratio of photosynthetic carbon gain to transpirational water loss (*A*/E) based on a general expectation that increased *WUE* is associated with increased carbon gain and biomass accumulation (Donovan and Ehleringer, 1994). However the *WUE* obtained in non-water limited condition was non-significantly different between PB 260 (5.06 µmol CO_2/ m mol H_2O) and PB 217 (5.30 µmol CO_2/ m mol H_2O) clones.

The chlorophyll meter (SPAD) provides a simple, quick and nondestructive method to estimate leaf *N* status. There was a linear relationship between leaf *N* concentration on a dry-weight basis (N_{dw}) with the chlorophyll meter r^2=0.51 when made on the flag leaves of rice (Peng *et al*., 1993). However the SPAD value in this experiment showed non-significant difference between the two rubber clones, indicating that the leaf *N* concentration was nearly the same in these clones.

Chlorophyll fluorescence was used to estimate the maximal quantum yield of PSII photochemistry in dark-adapted cedar needles and the quantum yield of PSII electron transport in the light (Epron, 1997). The maximum quantum yield ($\Delta F/F'_m$), indicating the efficiency of excitation energy captured by open photosystem II reaction center, was not significantly different between PB 260 and PB 217 clones. *Fv/Fm* of rubber in the study was similar to value reported in the other plants i.e., cedar (*Cedrus atlantica* and *C. libani)* (Epron, 1997) and Quercus *suber L.* (Faria *et al*., 1996).

A, A-Ci curve, Vcmax, Jmax and Nitrogen concentration

A, A-Ci response**,** V_{cmax}, J_{max} and *NUE* were greater significantly different in PB 260 than those in PB 217 while N_a and SPAD were non-significantly different between these clones. However N_a and SPAD of PB 260 tended to be higher than that of PB 217. To obtain a correlation between *N* and the main parameters of Faquhar model such as V_{cmax}, J_{max} like Le Roux *et al*. (1999) indicated that noumerous rubber clones should be added and varied in leaf nitrogen concentration.

Drought effect on leaf gas exchange

A and g_s of rubber tree was found to show a declining curve as a function of increasing of water stress. The result was similar with to RRIM 701, PR 107 and FX 25 clones (Ceulemans *et al*., 1983). Stomata function was closely related to leaf water status similar to other species e.g., avocodo (Chartzoulakis *et al*., 2002), walnut (Cochard *et al*., 2002), olive (Giorio *et al*., 1999).

In severe stress conditions, *E* is more rapidly decreased than *A* (80-85% and 60-70%, respectively). Consequently, *WUE* is generally high under stress conditions when calculated from *A* devided by *E*.

From the relationship between leaf water potential and stomatal conductance, stomatal would be closed to zero when leaf water potential reached to –2.2 MPa, expressing similar results in these two clones. This result suggested that stomatal conductance related with hydraulic behavior in rubber (Sangsing *et al*., 2004). However, the degree of drought tolerance of these clones will be required on additional studies concerning plant hydraulic architecture.

CONCLUSION

Two rubber clones that exhibited diffent in growth and yield were compared in this study. Net CO_2 assimilation rate (A_{1800} and A_{360}), nitrogen-use efficiency (A/N_a, V_{cmax}/N_a, J_{max}/N_a) of clone PB 260 were greater than those of PB 217. However, the respiration rates, chlorophyll fluorescence, water-use efficiency and leaf greenness were non-significantly different between two clones. Drought caused stomatal closure, less transpiration, and reduced photosynthesis, but greater water use efficiency. After 14 days without watering, stomatal conductance and transpiration rate reduced by 80 to 85%, while net photosynthesis rates reduced by only 60 to 70%. Drought also reduced leaf water potential, which was possitively related to stomatal conductance. Additional study is required to compare and contrast the response of leaf water potential to drought between the two clones. The response of gas exchange physiology to drought is the basis for the development of rubber in the Northeastern provinces of Thailand, which are characterized with low rainfall and long period of drought.

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