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 dm³ pots in a greenhouse at Clermont-Ferrand, France under controlled condition. Net CO₂ assimilation rate at 1800 ppm CO₂ (A₁₈₀₀) and at 360 ppm CO₂ (A₃₆₀), maximum carboxylation rate (Vcmax), electron transport capacity (Jmax) and nitrogen-use efficiency (A₁₈₀₀/Nₐ, A₃₆₀/Nₐ, Vcmax/Nₐ and Jmax/Nₐ) of clone PB 260 were significantly higher than those of clone PB 217. However, the dark respiration rate (Rd), the ratio of light-saturated rate of electron transport and maximum rate of carboxylation (Jmax/Vcmax), leaf mass per area (Mₐ), leaf nitrogen content (Nₘ), leaf nitrogen per area (Nₐ), water use efficiency (WUE), SPAD value (SPAD) and chlorophyll fluorescence ratio (Fv/Fm) were non-significantly different between these clones. Effects of drought on leaf gas exchange rates was also studied. Net CO₂ assimilation rate (A), stomatal conductance (gs) 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, gs and E decreased by 80-85%, while A decreased by 60-70%. Drought also reduced leaf water potential, which was positively 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;
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 functioning is required. Particularly, the ability of trees to assimilate carbon should be assessed. It is well known 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 CO₂ 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 greenness. 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 directly 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 greenness, 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 m² leaf area. They were planted in 50 dm³ 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/m²/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](image1.png) **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](image2.png) **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\textsubscript{2} assimilation rate \( (A) \), stomatal conductance \( (g_s) \), and CO\textsubscript{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 \( PPFD = 900 \) \( \mu \)mol/m\textsuperscript{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 \( (C_a = 100, 35, 30, 20, 15, 10, 7.5 \text{ and } 5 \) 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\textsubscript{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 \( \frac{\Delta F}{F_m'} = \frac{F_m - F_s}{F_m'} \) was used as a reliable estimate of \( \Phi_{II} \) i.e., the quantum yield of energy conversion by photosystem II PS\textsubscript{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 randomly made on 6 fully expanded leaves of each treatment every day after drought started (2 leaflets/plant). For each leaf, measurement was done at \( PPFD = 900 \) \( \mu \)mol/m\textsuperscript{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 \( A/ E \). 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\textsubscript{2} assimilation rates at 1800 ppm CO\textsubscript{2} \( (A_{1800}) \) of clone PB 260 (25.2 \( \mu \)mol CO\textsubscript{2}/m\textsuperscript{2}/s) was significantly greater than that of clone PB217 (21.2 \( \mu \)mol CO\textsubscript{2}/m\textsuperscript{2}/s). At 360 ppm CO\textsubscript{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 $\mu$mol CO$_2$/m$^2$/s in PB 260 and PB 217, respectively (Figure 3, see model).

The maximum carboxylation rate ($V_{c\text{max}}$) and electron transport capacity ($J_{\text{max}}$) of clone PB 260 (53.96 and 147.67 $\mu$mol CO$_2$/m$^2$/s) were significantly greater than those of clone PB 217 (41.02 and 110.92 $\mu$mol CO$_2$/m$^2$/s, respectively) (Figure 4, top panel). The ratio between $J_{\text{max}}$ and $V_{c\text{max}}$ 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 $\mu$mol CO$_2$/m$^2$/s) and PB 217 (1.03 $\mu$mol 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).

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**Table 1** Net CO$_2$ assimilation rate at CO$_2$ 1800 ppm, $A_{1800}$ ($\mu$mol CO$_2$/m$^2$/s) or measured at CO$_2$ 360 ppm, $A_{360}$ ($\mu$mol CO$_2$/m$^2$/s); dark respiration rate, $R_d$ ($\mu$mol 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, $WUE$ ($\mu$mol CO$_2$/m mol H$_2$O); 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, $A_{1800}/N_a$ ($\mu$mol CO$_2$/gN/s) and at CO$_2$ 360 ppm, $A_{360}/N_a$ ($\mu$mol CO$_2$/gN/s); leaf greenness, SPAD (SPAD unit) of two rubber clones (± standard error of mean n=10). p is significant level.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>PB 260</th>
<th>PB 217</th>
<th>p</th>
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<tr>
<td><strong>Photosynthetic capacity</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$A_{1800}$</td>
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<td>$A_{360}$</td>
<td>10.26±0.46</td>
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<td>0.8435±0.0043</td>
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<tr>
<td>$\Delta F/F_m'$ afternoon</td>
<td>0.7276±0.0126</td>
<td>0.7342±0.0129</td>
<td>0.70</td>
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<tr>
<td><strong>Water use efficiency</strong></td>
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<td>5.06±0.26</td>
<td>5.30±0.22</td>
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<tr>
<td>$M_a$</td>
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<td>55.41±1.94</td>
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<td>1.74±0.05</td>
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<td><strong>SPAD</strong></td>
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<tr>
<td>$A_{1800}/N_a$</td>
<td>14.43±0.85</td>
<td>12.29±0.47</td>
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<td>$A_{360}/N_a$</td>
<td>5.91±0.43</td>
<td>4.75±0.25</td>
<td>0.03</td>
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</table>
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/m²) tended to be greater than for PB 217 (3.15 % and 1.74 gN/m²) 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/m²) tended to have a higher weight per area than that of clone PB 260 (51.52 g/m²) (Table 1).

Leaf nitrogen use efficiencies ($NUE$) expressed as ratio between net CO₂ assimilation rate and $N_a$ ($A_{1800}/N_a$ and $A_{3600}/N_a$) for clone PB 260 (14.43 and 5.91 μmol CO₂/gN/s) were

**Figure 3** Net CO₂ assimilation rate ($A$) and intercellular CO₂ 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 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 $p=0.001$).

**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 $p=0.05$).
significantly greater than for clone PB 217 (12.29 and 4.7591 μmol CO₂/gN/s) (Table 1). 

\( NUE \) expressed as \( V_{c,max}/N_a \) for clone PB 260 (31.22 μmol CO₂/gN/s) was significantly greater than for clone PB 217 (23.38 μmol CO₂/gN/s). \( J_{max}/N_a \) of PB 260 (85.20 μmol CO₂/gN/s) was also significantly greater than clone PB 217 (63.90 μmol CO₂/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 CO₂/ mmol H₂O) and clone PB 217 (5.30 μmol CO₂/ mmol H₂O) (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 H₂O/m²/s and 2.0-2.6 mmol H₂O/H₂O/m²/s, respectively) were greater than in PB 217 (94-157 mmol H₂O/m²/s and 1.1-1.7 mmol H₂O/m²/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 H₂O/ m²/s respectively, while \( E \) of PB 260 and PB 217 were 0.38 and 0.24 mmol H₂O/m²/s, respectively (Figure 6).

\( A \) values in control plant were greater in PB 260 (7.9-9.8 μmol CO₂/m²/s) than those in PB217 (7.1-8.2 μmol CO₂/m²/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 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 CO₂/ m²/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 CO₂ / mmol H₂O. 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 CO₂ / mmol
H₂O 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 gs 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 (gs = 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 A₁₈₀₀ and A₃₆₀ 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 Rₐ in this experiment was not significantly different between clone PB 260 and clone PB 217. In contrast, Nugawela et al. (1995) showed that the Rₐ was significantly different

**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 between leaf water potential and stomatal conductance during a drought cycle for the two rubber clones.
among ten genotypes contrasting in yield potential. The $R_d$ of clone PB 217 (1.03 μmol/m²/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 difference 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 CO₂/ mmol H₂O) and PB 217 (5.30 μmol CO₂/ mmol H₂O) 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 ($ΔF/ΔF’_m$), 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 numerous 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 RRM 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., avocado (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, stomata 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 different in growth and yield were compared in this study. Net CO₂ assimilation rate ($A_{1800}$ and $A_{3600}$), 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 positively 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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