

Respiration Rate and a Two-component Model of Growth and Maintenance Respiration in Leaves of Rubber (*Hevea brasiliensis* Muell. Arg.)

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ABSTRACT

The future information of leaf selection for studies on respiration rate and leaf greenness, and position variations of different rubber clones was investigated. Respiration rate and greenness were non-significantly different between leaf position (leaf No. 1, 2 and 3) and leaflet position (left, middle and right), but they were significantly different among clones. During leaf expansion, respiration rate per unit leaf area declined with leaf age, but the differences were not obviously detected among clones. Leaf expansion rate was sigmoid shaped curves, and increased with leaf age. Relative growth rate on an area basis (RGR_{area}) of leaf declined with age. At fully expanded leaf of PB 235, RRIM 600, PB 260 and GT 1 clones, the greatest leaf area was found in PB 235, and the least in GT 1. For crop growth model development and environmental response studies, a two- component model of growth and maintenance respiration was used in leaves of rubber. Growth respiration coefficients were non-significantly different (ranging from 4.928×10^5 to $5.678 \times 10^5 \mu\text{molCO}_2 \text{ m}^{-2}$) among 4 rubber clones. While, the greatest maintenance coefficients were in RRIM 600, PB 60, GT 1, the least was in PB 235. In particular, strong positive correlation between respiration rate and RGR_{area} was found for all clones. Maintenance respiration was weakly related with leaf temperature, but growth respiration was not significantly related with leaf temperature.

Key words: relative growth rate, leaf expansion, growth respiration, maintenance respiration, leaf greenness, hevea and rubber

INTRODUCTION

Respiration is an important process to transform the substrate into necessary intermediates and transform some of stored energy into usable energy. These products are necessary for growth, maintenance, uptake of nutrient and transport of materials. However, the process often uses a

significant fraction of the carbon fixed daily via photosynthesis and it is an important component of plant productivity and carbon balance (Amthor, 1989). Carbon loss from respiration process accounts for over 50% of gross primary productivity. Respiration is widely recognized as an important process in studies of plant response to environmental change (Wullschleger *et al.*, 1992).

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Total respiration is the sum of growth respiration and maintenance respiration. Growth respiration is the respiration required in the synthesis of new phytomass, while maintenance respiration supplies the energy to keep existing phytomass in a healthy state (Amthor, 1989). Growth respiration can be used to calculate the conversion efficiency and maintenance respiration is used to determine the maintenance coefficient. Both the conversion efficiency and maintenance coefficient are important parameters in crop growth models (Iersel, 2000). Moreover, respiration model has been used in the study of plant response to water deficit, salinity and ozone (Amthor, 1988; Wullschleger *et al.*, 1996) CO₂ (Hrubec *et al.*, 1985; Wullschleger *et al.*, 1992; Thomas *et al.*, 1993; Ziska and Bunce, 1993; Thomas and Griffin, 1994; Wullschleger *et al.*, 1994; Bunch, 1995).

A positive correlation between respiration and growth rates is commonly observed (Amthor, 1989; Poorter *et al.*, 1990). However, a negative correlation between yield and respiration is found in forage crop, and the respiration rate has been used as an index for breeding selection in this species (Wilson and Jones, 1982; Kraus *et al.*, 1993).

Rubber tree is a major natural rubber resource. Presently, over 9.76 million hectares of rubber tree are cultivated in the world (RRIT, 1999b). Photosynthetic rate in several rubber clones has been reported (Samsuddin and Impens, 1978 a-b, 1979; Ceulemans *et al.*, 1984; Samsuddin, 1987; Nataraja and Jacop, 1999). Nonetheless, respiration rate and partitioning of respiration into the components contributing to the growth respiration and maintenance respiration are still poorly documented. The respiration knowledge in rubber leaves is required for studies on carbon balance, plant growth model development and plant environmental response. Moreover, respiration performance may be used as an early parameter in rubber breeding program.

The objectives of this study were (1) to

compare respiration rate and leaf greenness between leaf position and leaflet position and also among rubber clones, (2) to partition respiration model into leaf growth respiration and leaf maintenance respiration.

MATERIALS AND METHODS

Plants materials

Experiments were conducted between October 2000 and April 2001 on six different rubber (*Hevea brasiliensis*) clones in growth rate and yield (RRIT, 1993; 1999a). The clones RRIM 600, PB 260, PB 235 PR 255, BPM 24 and GT 1 were selected. For RRIM 600, PB 260 PR 255 and BPM 24 are in the first class, while the PB 235 is the second class, and the GT 1 is not recommended clone in categorized class among clones recommended for commercial plantation of Rubber Research Institute of Thailand (RRIT, 1999a). Budded scions were grown in small containers until they produced two flushes of leaves and then transplanted in August 2000 into a 2.55 × 3.25 m² block containing Pakchong soil serie with 75 × 75 cm plant spacing. In addition, some plants were transplanted in February 2001 into the 150 l plastic pots containing Pakchong soil serie. Plants were placed in the nursery under natural conditions at Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand. All plants were daily watered to saturation and cultivated following the RRIT recommendations.

Experimental design

Two separate experiments were carried out. Experiment one was designed to investigate the influence of leaf position on respiration rate and leaf greenness among 5 rubber clones (BPM 24, RRIM 600, PB 235, PR 255 and GT 1). The position included three leaf positions (leaf number No.1, 2 and 3 upward from the bottom to the top in the flush) and three leaflet positions (leaflet position as right, middle and left position when see the leaf

from the stem). Definition, number of leaf and leaflet position are shown in Figure 1.

Experiment two was conducted to compare leaf respiration rates among 4 rubber clones (RRIM 600, PB 235, PB 260 and GT 1) and partitioning into growth and maintenance respiration.

Leaf growth measurements

In experiment two, two leaves per plant (leaf position 1 and 3) were selected for leaf area determination. Leaf area was daily estimated (non destructive) on expanding leaves as well as fully expanded leaves by drawing on intact leaves under overhead projector film, and calculated leaf area from overhead projector film weight. Leaf area was estimated several days approximately 12 hours before and after gas exchange measurement. Measurement was done until leaf fully expanded.

Gas exchange measurements

For experiment one, respiration measurements were carried out between 18.00-20.00 h using a portable photosynthesis system model Li-6400 (LiCor Inc., Lincoln, Nebraska, USA). For each leaf, respiration rate were measured

at $PPFD = 0 \mu\text{mol m}^{-2}\text{s}^{-1}$ and $\text{CO}_2 = 350 \text{ ppm}$. Leaf temperature and humidity in the leaf chamber were maintained at $27 \pm 2^\circ\text{C}$ and 45-60 % RH, respectively. Following each respiration measurement, leaf greenness on the leaflet was measured using a SPAD-502 Chlorophyll Meter (Minolta Camera Co., Ltd., Japan).

For experiment two, dark respiration rate (R_d) or CO_2 efflux during the night on individual trifoliate leaf was measured using a portable photosynthesis system model Li-6200 (LiCor Inc., Lincoln, Nebraska, USA). The difference between CO_2 concentration entering leaf chamber and sampling from leaf chamber was measured. Measurements on the same leaf used for leaf area estimation were made daily during 18.00-21.00 h. Respiration chambers were constructed of PVC pipe and completely enclosed one trifoliate leaf. Chamber volume was 604 or 1816 cm^3 depending on leaf area. Air entering the system passed through a 5 l buffer volume and flowed through the chamber at $1000 \mu\text{mol s}^{-1}$. The CO_2 partial pressure during measurement was approximately 360 ppm. Leaf temperature was measured by Noncontact Thermometer model Raynger® ST (Raytek Cor.,

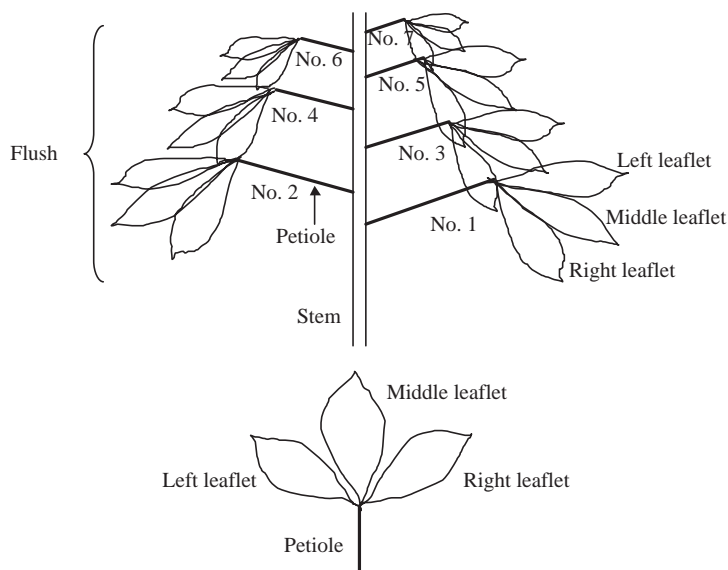


Figure 1 Leaf and leaflet characteristics of rubber and the definition of leaf and leaflet name.

CA., USA.) immediately after R_d measurement. Following each temperature measurement, leaf greenness on the leaf was measured using a SPAD-502 Chlorophyll Meter (Minolta Camera Co., Ltd., Japan).

R_d was calculated using equation,

$$R_d = \frac{\Delta CO_2 F}{L_A} \quad (1)$$

where ΔCO_2 = the difference in CO_2 concentration between sample and reference ($\mu mol CO_2 \mu mol gas^{-1}$)

F = flow rate through the desiccant ($\mu mol gas s^{-1}$)

L_A = leaf area (m^2)

The leaf area in equation (1) was calculated as

$$\text{Leaf area} = \frac{L_{Aa} + L_{Ab}}{2} \quad (2)$$

where L_{Aa} = the leaf area after gas exchange measurement (m^2)

L_{Ab} = the leaf area before gas exchange measurement (m^2)

Dark respiration was partitioned into functional components of growth and maintenance using the following equation, modified from that of Amthor (1988)

$$R = m + gRGR_{area} \quad (3)$$

where R = dark respiration rate expressed on a leaf area basis ($\mu mol CO_2 m^{-2} s^{-1}$)

RGR_{area} = relative growth rate of leaf on an area basis ($m^2 m^{-2} s^{-1}$)

Based on the regression equation of respiration rate versus RGR_{area} , the maintenance coefficient, m ($\mu mol CO_2 m^{-2} s^{-1}$), or y intercept, is the amount of carbon respired to support the existing amount of leaf area, and the growth coefficient, g ($\mu mol CO_2 m^{-2}$) or slope, is the amount of carbon respired per unit increase in leaf area. The RGR_{area} was calculated by using the equations of Thomas and Griffin (1994), Thomas *et al.* (1993), and Wullschleger *et al.* (1996):

$$RGR_{area} = \frac{\ln L_{Aa} - \ln L_{Ab}}{t} \quad (4)$$

where L_{Aa} = the leaf area after gas exchange measurement (m^2)

L_{Ab} = the leaf area before gas exchange measurement (m^2)

$t = M$ time between leaf area measurement in seconds (s)

Data analysis

Analyses of variance of the effect of leaf position, leaflet position and clone on respiration rate and leaf greenness were analyzed using Statistical Analysis System, SAS (Institute, North Carolina, USA). Growth and maintenance coefficients were estimated using linear regression. Standard errors of mean of measurement parameters were also analyzed using the Statistical Analysis System, SAS (Institute, North Carolina, USA).

RESULTS

Effect of leaf position on respiration rate and leaf greenness

Leaf position (node No. 1, 2 and 3) and leaflet position (left, middle and right) did not significantly affect leaf respiration rate and leaf greenness. However, leaf respiration rate and leaf greenness were significantly different among rubber clones. The clone GT 1 and PR 255 showed higher respiration rate than the two groups made of BPM 24, RRIM 600 and PB 235. GT 1 showed higher greenness than all the other clones. Leaf of PB 235 was greener than those of BPM 24 and RRIM 600. PR 255 was in between these two groups (Table 1).

Leaf area expansion and relative growth rate

From data collected over leaf expansion period, leaf area expansion showed similar trends, sigmoid increasing curves for all clones. During the first 5 days after leaf unfolding, leaf area

Table 1 Analysis of variances and effects of clone, leaf position, leaflet position on leaf respiration rate and leaf greenness measured on 5 rubber clones.

Effect	Respiration rate (mmol CO ₂ m ⁻² s ⁻¹)	Leaf greenness (SPAD Unit)
Clones		
BPM 24	1.17 b	22.86 c
RRIM 600	1.13 b	22.03 c
PB 235	0.57 c	26.48 b
PR 255	1.60 a	24.64 bc
GT 1	1.67 a	33.64 a
	p= 0.0001	p= 0.0001
	n= 27	n= 27
Leaf position (node)		
1	1.32 a	26.09 a
2	1.26 a	25.21 a
3	1.10 a	26.43 a
	p= 0.2726	p= 0.5908
	n= 45	n= 45
Leaflet position		
Left	1.23 a	25.88 a
Middle	1.21 a	25.98 a
Right	1.24 a	25.88 a
	p= 0.9705	p= 0.9949
	n= 45	n= 45
CV%	54.71	22.37

For each effect, data with common letters were not different at the 0.05 level by DMRT.

expansion increased slowly and then rapidly from 5-12 days. Thirteen days after leaf unfolding, leaf becomes fully expanded. Mean areas of leaf No.1 and No. 3 of the top flush, clone PB 235 and RRIM 600 were significantly greater than those of PB 260 and GT 1 (Figure 2). Relative growth rate on an area basis (RGR_{area}) of rubber leaves declined with leaf age, but there were not obvious differences among clones. At fully expanded leaf (about 13 days after unfolding), RGR_{area} became zero (Figure 3).

Respiration rate and leaf age relationship

The relationships between respiration rate and leaf age appeared to have similar trends for the 4 clones. During the first period of 2-3 days after unfolding, leaf respiration rates of GT 1, PB 235 and RRIM 600 were high about 9-11 $\mu\text{molCO}_2 \text{ m}^{-2}\text{s}^{-1}$. The rate of respiration rapidly decreased during 5-10 days. At 13 days after unfolding, respiration rates of all clone ranged about 1-2 $\mu\text{molCO}_2 \text{ m}^{-2}\text{s}^{-1}$ (Figure 4).

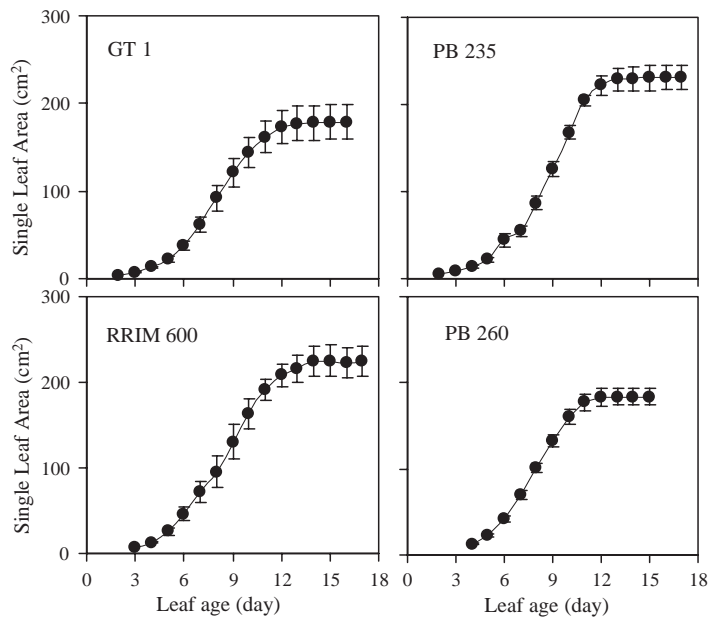


Figure 2 Mean leaf area expansion rates (leaf No. 1 and No. 3) with leaf ages of 4 rubber clone. Error bars represent one standard error of mean (n=4).

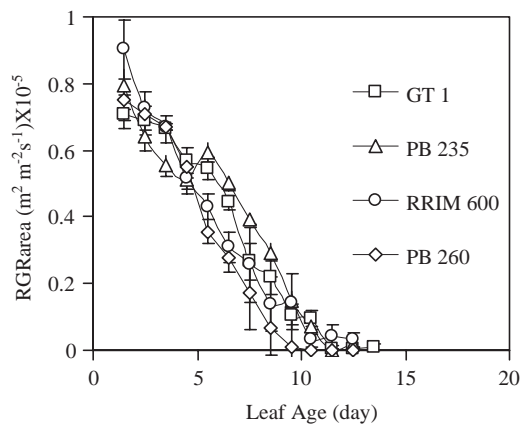


Figure 3 Relative growth rates on an area basis with leaf ages of 4 rubber clone. Error bars represent one standard error of mean (n=4).

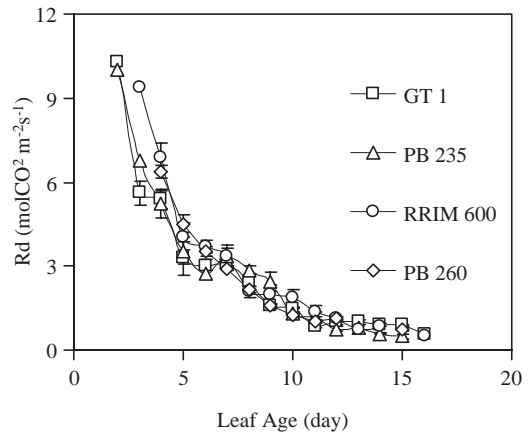


Figure 4 Relationship between respiration rates per unit of area and ages of leaf in 4 rubber clones. Error bars represent one standard error of mean (n=4).

Two components model of respiration rate

As predicted by the two-component model of growth and maintenance respiration, there was a strong positive relationship between respiration rate and RGR_{area} for all clones (Figure 5). Growth

respiration coefficients estimated from the slope of this relationship were non-significantly different among 4 rubber clones (4.928×10^5 to $5.678 \times 10^5 \mu\text{molCO}_2 \text{ m}^{-2}$) (Table 2, line in Figure 5). In particular, growth respiration coefficients during

Table 2 Growth and maintenance coefficient respiration, leaf greenness and mean fully expanded leaf area (leaf No. 1 and 3) of 4 rubber clones.

Clone	Growth coefficients ($\mu\text{mol CO}_2 \text{ m}^{-2} \times 10^5$)	Maintenance coefficients ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Leaf area (cm^2)
RRIM 600	5.224 \pm 1.119a	0.620 \pm 0.1233a	224 \pm 36ab
PB 260	4.928 \pm 0.485a	0.617 \pm 0.127a	184 \pm 20ab
PB 235	5.376 \pm 0.373a	0.367 \pm 0.098b	231 \pm 28a
GT 1	5.678 \pm 0.663a	0.613 \pm 0.073a	178 \pm 39b

Values are means \pm SE. Means within a column with the same letters are not significantly different at 0.05 (n=4).

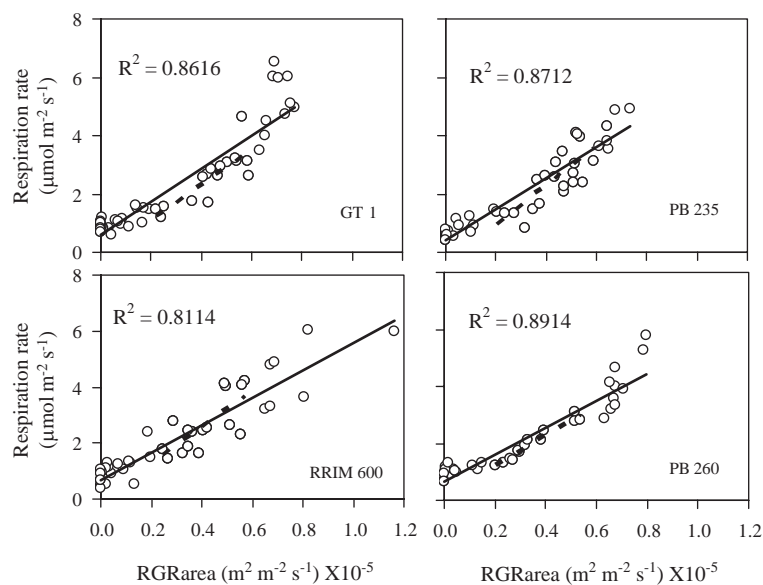


Figure 5 Respiration rates (R_d) as a function of relative growth rate on an area basis (RGR_{area}) of 4 rubber clones. Lines and statistics are linear regression of all values. Dash lines are linear regression of RGR_{area} during 0.2×10^{-5} to $0.6 \times 10^{-5} \text{ m}^2 \text{ m}^{-2} \text{ s}^{-1}$.

liner phase of growth expansion rates (leaf ages between 6 to 10 days and RGR_{area} between 0.2×10^{-5} to $0.6 \times 10^{-5} \text{ m}^2 \text{ m}^{-2} \text{ s}^{-1}$) are presented in dash lines (Figure 5). The slopes were $5.38 \mu\text{molCO}_2 \text{ m}^{-2}$, $5.97 \mu\text{molCO}_2 \text{ m}^{-2}$, $6.52 \mu\text{molCO}_2 \text{ m}^{-2}$ and $6.76 \mu\text{molCO}_2 \text{ m}^{-2}$ in PB 260, PB 235, RRIM 600 and GT 1, respectively. However, growth respiration coefficients were non-significantly different between estimated from all expansion periods (line, Figure 5) and estimated during linear phase (dash line, Figure 5). Estimates of the

maintenance coefficient (the y- axis intercept) were significantly different among 4 rubber clones. Clone PB 235 ($0.367 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was almost 2 times lower than those of other clones for this parameter (0.613 to $0.620 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Table 2). Measurement respiration rates at $RGR_{\text{area}} \leq 0.01 \times 10^{-5} \text{ m}^2 \text{ m}^{-2} \text{ s}^{-1}$ (just fully expanded), PB 235 ($0.57 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were also lower than those of other clones (0.90 , 0.87 and $0.70 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in PB 260, GT 1 and RRIM 600, respectively).

Temperature effect

When partitioning respiration rate into growth and maintenance respiration, maintenance respiration was weakly related with leaf temperature, while growth respiration was not significantly related with leaf temperature (Figure 6).

DISCUSSION

The significantly wide variations in leaf respiration rate and leaf greenness observed among 5 clones (Table 1) indicated a large genetic variability in carbon exchange capacity in this species. The result was similar to that of Nugawela *et al.* (1995) and Nataraja and Jacob (1999). It is very important for next carbon balance study in rubber.

However, node and leaflet position did not significantly affect leaf respiration and leaf

greenness. According for the specific growth pattern of this species (Samsuddin *et al.*, 1978), six to ten leaf emerged in the same type and in the same time in each growth flush. Thus, each node and leaflet was not different in age and development. In next respiration and greenness studies in a given clone, any leaves in the same flush could be used as a good random sample.

Leaf area expansion had similar result to the other tree species such as yellow poplar (Wullschleger *et al.*, 1992), northern red oak (Wullschleger *et al.*, 1996). Relative growth rate of rubber leaf declined with age was as observed on many species (Bunce, 1995). It closed to zero at fully expanded leaf.

Average leaf areas of leaf No. 1 and No. 3 of the third flush of a given tree were used to estimation. Among 4 clones, PB 235 had the highest leaf area and GT 1 has the lowest. It was well known that PB 235 leaf area was higher than those of other clones. However, Gomez and Hamzah (1980) investigated variation in leaf morphology and anatomy in 11 clones. There were no significant differences between clones and mean surface area per leaflet.

The clone GT 1 and PR 255 ($1.6\text{--}1.7\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$) showed higher respiration rate than two groups made of BPM 24, RRIM 600 ($1.13\text{--}1.17\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$) and PB 235 ($0.57\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$). While, Ceulemans *et al.* (1984) observed that respiration rates of 20 rubber clone varied from $1.5\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$ to $7.9\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$. For consideration about the same clones, PR 255 showed higher respiration rate than RRIM 600, PB 235 and GT 1. Compare only RRIM 600 to those in the literature, respiration rate in this study was lower ($1.13\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$) than those of observed by Nataraja and Jacob (1999), Nugawela *et al.* (1995) and Ceulemans *et al.* (1984) (2.29 , 3.12 and $4.95\ \mu\text{mol CO}_2\ \text{m}^{-2}\text{s}^{-1}$, respectively).

According to the two-component model of growth and maintenance respiration, there was a

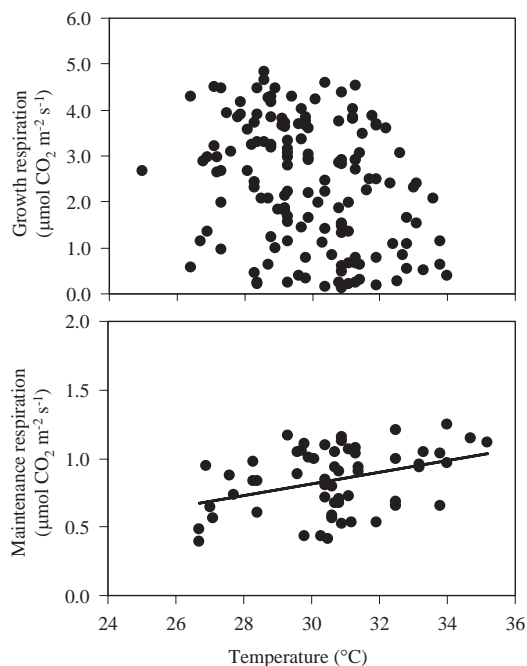


Figure 6 Relationship between growth respiration (top panel), maintenance respiration (bottom panel) and leaf temperature of rubber.

strong positive relationship between respiration rate and RGR_{area} in rubber leaves. Here was very similar to those reported on other species such as yellow poplar (Wullschleger *et al.*, 1992), northern red oak (Wullschleger *et al.*, 1996), cotton (Thomas *et al.*, 1993) and soybean (Thomas and Griffin, 1994; Bunce, 1995). In particular, the maintenance coefficients of rubber leaf showed clonal variation. There has been few reports of clonal variation for this parameter in the literature. These results indicated that when using two-component respiration model in rubber crop modeling, such parameter should be determined for each clone.

Maintenance respiration rate of PB 235 leaf was low as compared to the others. PB 235 is known to grow very fast before tapping (RRIT, 1999a). Due to success in use of maintenance respiration as an index for breeding selection for high growth in rye grass (Wilson and Jones, 1982, Kraus *et al.*, 1993), this parameter must be tested again in widely different growth performance in rubber clones. This is very interesting information.

Difference of leaf greenness among clones, GT 1 and PR 255 were higher greenness than that of RRIM 600, which was similarly by reported by Dansagoonpon (1997).

For an example of temperature effect, the result suggested that growth respiration was not affected by temperature, but only maintenance respiration affected by temperature. However Amthor (1989) reported that temperature very strongly influenced respiration rate. Thus, the knowledge of the effect of temperature on respiration rate in rubber tree is important to understanding of the relationship between respiration and productivity in the future.

CONCLUSIONS

The main conclusions of this study were (1) leaf position and leaflet position in the same flush of rubber did not affect respiration rate and leaf greenness; (2) a linear function of respiration

rate and relative growth rate obtained a two-component model of growth and maintenance respiration; (3) differences of maintenance coefficient were found among rubber clones and might be used as an index for breeding selection for high growth clone; and (4) leaf maintenance respiration affected by temperature.

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