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Gas Exchange of Three Dipterocarp Species in a Reciprocal Planting

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Abstract: Gas exchange is important for determining the species plasticity. However, study on gas exchange in dipterocarp is almost non-existence and this study may provide useful information for future references. The study was conducted at the Compartment 14, Ayer Hitam Forest Reserve, Puchong and Selangor, Malaysia. The main objective of this study was to determine the leaf gas exchange of three dipterocarps, *Shorea platyclados* V. SI. ex Foxw. (meranti bukit), *Shorea assamica* Dyer forma *globifera* (Ridl) Sym. (meranti pipit) and *Anisoptera marginata* Korth. (mersawa paya) planted in different sizes of gap. The results showed that the gas exchange parameters were not significantly different between species except stomatal conductance (Gs) and transpiration rate (E_L). Insignificant differences of all the gas exchange parameters were also observed between planting designs. Meanwhile, the correlation analysis showed that insignificant effect of design on species for net photosynthesis (A_{net}) is due to the effect of internal CO_2 concentration (Ci). However, the significant difference observed for transpiration rate (E_L) between species might be due to the significant roles of stomata conductance (Gs). Overall, the higher tropical species plasticity by introducing reciprocal planting in rehabilitation programme has produced mixed results.

Key words: Net photosynthesis, stomata conductance, *Shorea* species, plasticity, genecology

INTRODUCTION

Knapp and Smith (1990) hypothesized that plants in habitats experiencing high daily sunlight variability should demonstrate rapid recovery in photosynthesis and stomata conductance after a shading event in order to maximize carbon gain. Conversely, photosynthesis may respond more slowly to changes in isolation in plants native to environments with less variable solar radiation. Typically, the total light energy received during the day has a greater influence on acclimation than peak levels of photon flux density (Chabot *et al*., 1979). However, the timing and duration of sun flecks and or sun patches (longer, minutes to hour's exposure) and the pattern of alternation between high and low light are influential in the dynamics of photosynthetic and stomata responses to changes in light intensity (Allen and Pearcy, 2000). Individuals of plant species growing in arid land inter-shrub spaces will receive higher and more constant light levels than individuals located under a shrub canopy or under forest gap. The balance between stomata and photosynthetic response to light can play an important role not only in the amount of CO_2 that is captured during alternating periods of high and low light.

Forest gap is a condition on open surface area of the forest. The size of the gap is of particular importance, since research has shown that trees partition the gaps of different size (Brown and Whitemore, 1992). Gap size has not only been positively correlated with resources availability, but gradients of gap size have also been proposed as important elements in determining the composition of gap-filling species in tropical forest (Brokaw, 1985). Moreover, these different types of also induce a series of conditions for forest regeneration, not only inside the perpendicular projection of the gap perimeter, but also in the adjacent gap edge area or microclimate influenced area (Popma *et al*., 1988).

There are few studies involving the responses of different tropical tree species to a similar light regime, especially when forest gaps are considered. Furthermore, there is no study related to the plasticity potential of tropical species when 'reciprocal' planting is considered. Therefore, the aim of this study is to determine the gas exchange of tropical tree species namely *Shorea platyclados* (meranti bukit), *Shorea assamica* (meranti pipit) and *Anisoptera marginata*

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(mersawa paya) planted under different sizes of forest gap in a lowland forest.

Ang and Maruyama (1995) suggested that *S. platyclados* has a great potential as forest plantation species as it established well in open areas. The species recorded a survival rate of 92.2% in 26 months after planting and collar diameter and height increments of 35 mm and 2.5 m, respectively. In Bogor, Indonesia, Masano and Harun (1991) found that growth of the species in planting trials was exceptional and recorded a mean height of 25 m in and mean dbh of 41 cm after 25 years. In North Sumatra, Indonesia, *S. platyclados* plantations of 37, 38 and 40 years recorded MAI of DBH of 1.03 to 1.16 cm yr^{-1} (Butarbutar and Supriana, 1998). In Malaysia, this species normally grow at hill forest area and confined to the upper dipterocarps forest zone, having a higher altitudinal distribution than any other *Shorea* whereas *S. assamica* and *A. marginata* can be found at abundance in areas between lowland and hill forest areas. With the lack of these species distribution in other areas rather than higher altitude, reciprocal planting by introducing new environment to these species is needed in genecology study. Such study can be acted as a step in *ex-situ* conservation since more areas in higher altitude are degraded due to the housing and agricultural developments.

The physiological attributes of these species by measuring gas exchange is important in determining the species plasticity. However, the record on these species adapted in lowland environment is almost non-existence and this study may provide useful information for future reference. Hence, the objective of this study was to determine the gas exchange of three Dipterocarps sp. namely *Shorea platyclados, Shorea assamica* and *Anisoptera marginata* planted under forest gap at Ayer Hitam Forest Reserve, Selangor.

MATERIALS AND METHODS

Study site: The study was conducted in Compartment 14, Ayer Hitam Forest Reserve (AHFR). AHFR is a 1, 248 ha of land situated about 20 km from Kuala Lumpur, the capital city of Malaysia which includes compartment 1, 2, 12, 13, 14 and 15. This forest is the only well-managed Lowland Dipterocarps Forest in the Klang Valley besides Bukit Nenas Forest in Kuala Lumpur. This forest was selectively logged several times between 1936 to 1965. It is presently being used for research, education and extension in UPM. This forest has two series of soil that are Serdang and Durian series which is a combination of alluvium-colluviums soil.

The climate of AHFR area is typically tropical. The average temperature is 25.3°C with maximum is 27.2°C and minimum 22.9°C. The relative humidity is 87.6% with the maximum and minimum relative humidity is 97.8 and 77.4%. The wind speed is between 0.15 to 2.17 m sec^{-1} and soil temperature from 25.5 to 24.2°C. The average annual rain fall is 2178 mm in this forest area (Ainuddin and Salleh, 1999). There are three major rivers namely Sungai Rasau, Sungai Bohol and Sungai Biring which flow in this forest. The altitude ranges between 5-213 m a.s.l. with the highest peak at Permatang Kuang. The terrain is principally moderate with slopes ranging from 10 to 30%, the average slope is about 20% and there are many flat areas. The normal stream velocity is less than 15 cm^{-1} and occasionally increases with heavy rain (Ismail, 1999).

Plant material: Three dipterocarps species namely *Shorea platyclados* (meranti bukit), *Shorea assamica* (meranti pipit) and *Anisoptera marginata* (Mersawa paya) seedlings aged one year-old were used for this experiment. The seedlings were obtained from Lentang Forest Reserve on May and planted on June 2007 at four locations with different sizes of gaps in AHFR. The age of the seedlings planted at the area at the time of study is about 2 years and the height is about 1.5 to 2 m.

Planting design: The study area comprised of four planting designs established in 2007 with a total size of 4 ha. Each design consisted of different number of subplots and sizes. Three species which are *S. assamica*, *S. platyclados* and *A. marginata*were planted in each subplot with spacing at 2.5×2.5 m. Design 1 comprised of nine subplots sized 10×10 m and each subplot comprised nine seedlings. Design 2 has nine subplots sized 20×20 m and each subplot comprised 49 seedlings. Design 3 has five subplots sized 10×10 m and each subplot comprised nine seedlings. Design 4 has five subplots sized 20×20 m and each subplot was planted comprised 49 seedlings.

Data collection

Random sampling method: Random sampling method was used in this study. The sampling was based on random table and the numbers were generated using random number generator. Sixty seedlings were selected randomly from each design. For each design, 15 seedlings were sampled per plot. This includes five seedlings per species.

Gas exchange measurement: Three fully expanded and non senescing leaves were selected for each seedling. Five parameters were taken from each sample. They were net photosynthesis (A_{net}), stomata conductance (Gs), internal sub-stomata CO_2 (Ci), transpiration rate (E_L) and leaf to air vapour pressure deficit (D). Climate control was used due to the environmental fluctuation where CO_2

concentration was set at ~360 μmol moL^{-1}. Light intensity was set at light saturated photosynthesis using external LED red and blue unit. Trials were carried out to determine the level of quantum before the actual measurement was done. Measurements were taken from 08:00 to 12:30 to avoid the midday depression. Three sampling dates were determined randomly throughout the study.

Data analyses: All the data were subjected to Two-way analysis of variance (ANOVA). Normality and Equal Variance Test were done prior to ANOVA. If the result of normality test failed, the data were transformed until the results of normality test were passed. Statistical Package of Social Science (SPSS) version 15.0 packages were used for analyses and Duncan's New Multiple Range Test was further used to evaluate the multiple comparisons or mean separation. In all data analyses, means differing at a probability of <0.05 were considered being different. Correlation analyses were also done to determine the relationship between parameters.

RESULTS

Physiological attributes: Table 1 shows the summary of ANOVA for net photosynthesis (A_{net}), stomata conductance (Gs), internal sub-stomata CO_2 (Ci), transpiration rate (E_L) and leaf to air vapour pressure deficit (D) between species and design. There were no significant differences observed for all the gas exchange parameters between species. Similar results were also found in the interaction between two main factors. For planting design, however, stomata conductance (Gs) and transpiration rate (E_L) were found significantly different at $p<0.001$.

Table 2 shows the mean values of physiological parameters among dipterocarps species and planting design. From the results obtained, *S. assamica* recorded the highest mean values for net photosynthesis (A_{net}), stomata conductance (Gs), internal sub-stomata CO_2 (Ci), transpiration rate (E_L) and leaf to air vapour pressure deficit (D) than *S. platyclados* and *A. marginata.* The lowest mean for all parameters were recorded by *A. marginata*. Meanwhile, the mean values of all parameters were found higher for planting Design 1 except D. The lowest mean values of A_{net}, Gs, Ci and E_L were observed in planting Design 4.

Correlation analyses: The results from the ANOVA revealed that Gs and E_L were only found significantly different among dipterocarps species studied. Hence, correlation analyses were carried out to find the factors affecting these results. The gas exchange between the leaves and the atmosphere is primarily controlled by stomata conductance. Normally, the relationship between stomata conductance and net photosynthesis is positively linear provided that other factors such as physical environments and leaves characteristics are constant. If the leaf characteristics such as hairy and too waxy, mesophyll conductance in the leaves can play a major role in determining the rate of photosynthesis leaving the internal subcellular CO_2 (Ci) as a main factor.

The correlation analyses were carried out to examine the roles of Gs, Ci and D on A_{net} and E_L. No significant correlations were found between Gs and A_{net} and between D and A_{net}. However, significant negative linear correlation was found between Ci and A_{net} (Fig. 1). Highly significant logarithmatic correlation was found between Gs and E_L with $R^2 = 0.89$ but no significant correlation was observed between D and E_L (Fig. 2).

Table 1: Summary of ANOVA for net photosynthesis (A_{net}), stomatal conductance (Gs), internal sub-stomatal CO_2 (Ci), transpiration rate (E_L) and leaf to air vapour pressure deficit (D) between species and design

		A_{net} (μmol m^{-2} sec^{-1})		Gs (mol m^{-2} sec^{-1})		Ci (mol m^{-2} sec^{-1})		E_L (μmol m^{-2} sec^{-1})		D (kPa)	
Source of variation	df	MS	F	MS	F	MS	F	MS	F	MS	F
Species	2	1.953	0.253^{ns}	0.066	1.637^{ns}	12680.00	1.923^{ns}	4.960	2.255^{ns}	0.288	1.120^{ns}
Design	3	4.334	0.561^{ns}	0.256	6.385***	4001.979	0.607^{ns}	16.369	7.442***	0.035	0.134^{ns}
Species * Design	6	4.244	0.550^{ns}	0.043	1.069^{ns}	4211.461	0.639^{ns}	1.250	0.568^{ns}	0.384	1.492^{ns}

Note: ns: Not significant,***Significant different at $p<0.001$

Table 2: Mean of physiological parameters among three dipterocarp species

Source of variation	A_{net} (μmol m^{-2} sec^{-1})	Gs (mol m^{-2} sec^{-1})	Ci (mol m^{-2} sec^{-1})	E_L (μmol m^{-2} sec^{-1})	D (kPa)
Species					
S. platyclados	4.44±0.35	0.15±0.03	238.88±10.32	2.12±0.19	1.930±0.06
S. assamica	4.56±0.36	0.21±0.03	265.75±10.45	2.65±0.20	1.81±0.07
A. marginata	4.22±0.35	0.17±0.03	259.06±10.36	2.36±0.19	1.90±0.07
Design					
1	4.65±0.42	0.27±0.03A	264.88±12.29	3.03±0.22A	1.85±0.08
2	4.50±0.41	0.18±0.03B	250.67±12.01	2.56±0.22B	1.90±0.08
3	4.54±0.41	0.17±0.03B	244.37±12.10	2.36±0.22B	1.86±0.08
4	3.98±0.40	0.09±0.03C	258.02±11.50	1.64±0.21C	1.90±0.08

Note: ±represent mean standard error

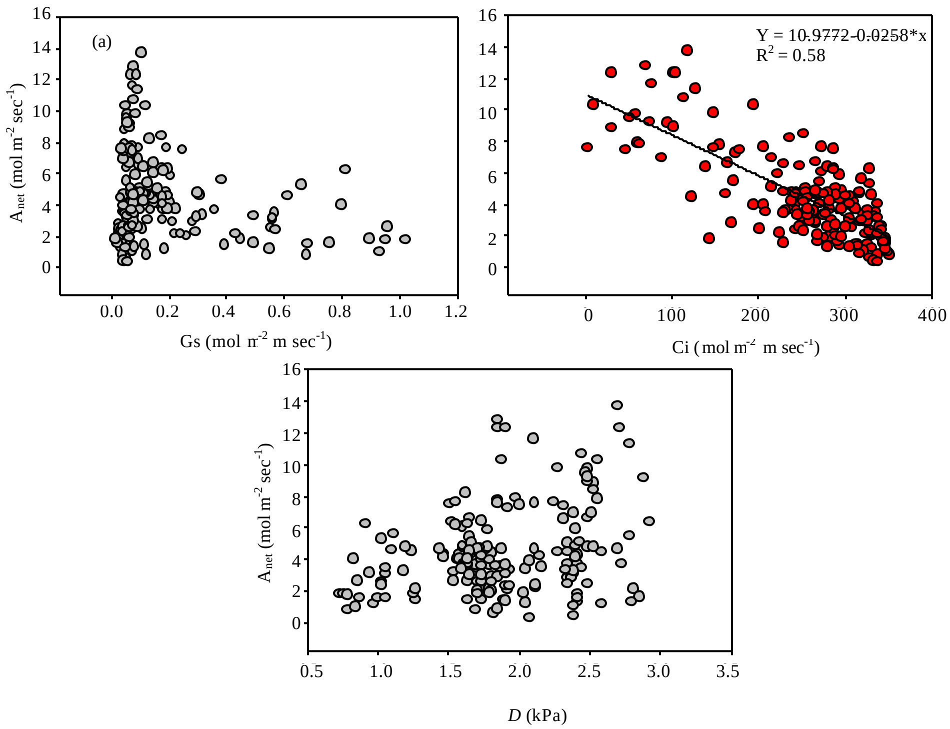

Fig. 1: Correlations between (A) net photosynthesis and stomatal conductance, (B) net photosynthesis and internal CO_2 concentration and (C) net photosynthesis and leaf to air vapour pressure deficit

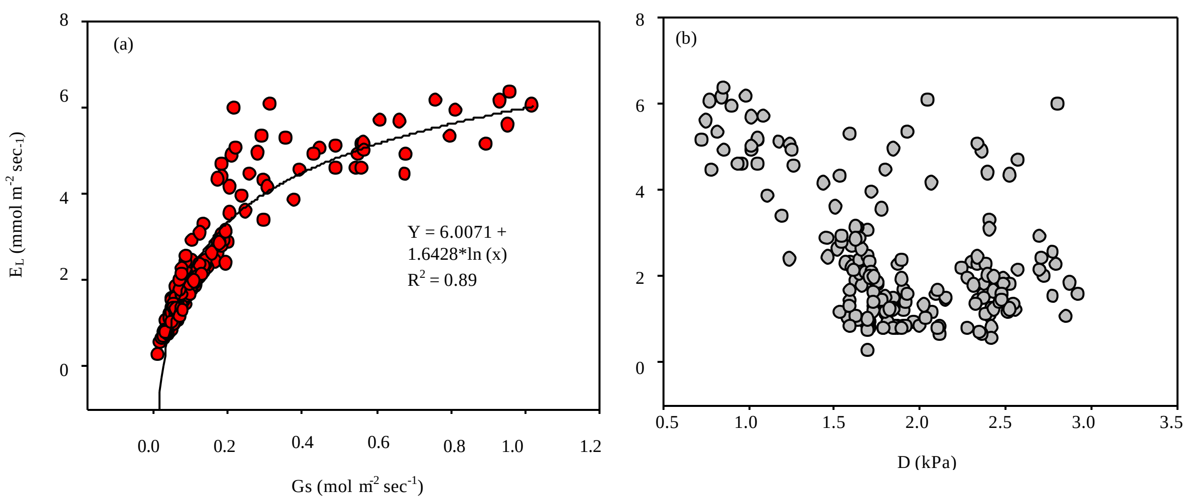

Fig. 2: Correlations between (A) transpiration rate and stomatal conductance and (B) transpiration rate and leaf to air vapour pressure deficit

DISCUSSION

Generally, gas exchange results of three dipterocarps species seedlings did not strongly support the plasticity of tropical tree seedlings as tropical rainforest seedlings require a high plasticity in terms of their physiology and morphology as they encounter contrasting environments. Thus measurements of gas exchange by assessing net photosynthesis and stomata conductance on the leaf level do not easily allow for conclusions to be reached on tree adaptation (Kuppers and Kuppers, 2003). The contrasting results found in this study for net photosynthesis and stomata conductance were not as expected. It could be due to the stomata conductance depends on guard cell and epidermal turgor. Consequently, the regulation of turgor in these cells requires metabolic energy depends on the balance between losses of water through transpiration (Franks *et al*., 2001). Due to that, transpiration rate was the only parameter affected by stomata conductance. Moreover, insignificant difference of net photosynthesis between species might be related to the role of intercellular CO_2 (Ci). The values of Ci were also not significantly different between species. The regulation of gas exchange between the leaf and the atmosphere is frequently affected by the leaf to air vapour pressure deficit (D). However, no significant correlations were found between vapour pressure deficit and net photosynthesis and also transpiration rate in this study and these results have leaving us with no clues. In reference to the combined stomata-photosynthesis model that had been used by Uddling *et al*. (2005) there was a striking pattern of net photosynthesis (A_{net}) rate being underestimated at low leaf to air vapour pressure deficit (D). This is probably occurred because of the changes in physiological capacities of photosynthesis and patchy stomata closure. Moreover, low leaf water potential has been reported to cause inhibition of almost all photosynthesis process (Kramer and Boyer, 1995) and it is a shame that no leaf water potential was taken in this study.

The 'reciprocal' planting introduced in this study in different sizes of gap also resulted in insignificant different of all physiological attributes between designs. The planting design did not affect the values of $A_{net,}$ Gs, Ci, E_L and D in this study. Similar results were also found on photochemical efficiency by Hazandy *et al*. (2009). Furthermore, the means values of net photosynthesis and transpiration rate of *S. platyclados* and *S. assamica* planted in different sizes of gap in AHFR were found far lower than those recorded by Ang and Maruyama (1995) planted in an open planting at FRIM. The mean values of net photosynthesis and transpiration rate were 10.19± 0.45 and 4.69±0.10 μmol m^{-2} sec^{-1} for *S. platyclados* and 11.66±0.90 and 6.10±0.12 μmol m^{-2} sec^{-1} for *S. assamica*, respectively (Ang and Maruyama, 1995).

Overall, the higher tropical species plasticity by introducing reciprocal planting in rehabilitation programme has produced mixed results. This is due to the fact that the survival rates for *A. marginata* is 98% followed by *S. assamica* (73.5) and *S. platyclados* (62%) but no significant differences for physiological parameters found in this study.

CONCLUSION

Gas exchange measurement on three dipterocarps species originated from different environmental conditions planted at a lowland forest did not produce outstanding results on the high plasticity potential for tropical rainforest seedlings. There were no significant differences of gas exchange parameters between species except stomata conductance and transpiration rate but no significant differences were found between planting design for all the gas exchange parameters. Insignificant difference for net photosynthesis between species might be due to the effect of intercellular CO_2 rather than stomata conductance. Stomata conductance was only affected the rate of transpiration. Different sizes of gap were not also affected the values of leaf gas exchange attributes across species studied.

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