

## E-2.2 Ecophysiological Research on Adaptation of Tropical Tree Species to Environmental Stress

**Contact Person** Yoosuke Matsumoto

Laboratory Chief

Ecophysiology Laboratory, Forest Environment Division,

Forestry and Forest Products Research Institute

Ministry of Agriculture, Forestry and Fisheries

Tsukuba Norin Kenkyu Danchi-nai P.O. Box 16, Ibaraki 305, Japan

Phone:+81-298-73-3211(Ext. 354), Fax:+81-298-73-1542

E-mail: YMAT@ffpri.affrc.go.jp

**Total Budget for FY1993-FY1995** 28,455,000 Yen (FY1994 7,450,000 Yen)

**Abstract** Biological processes of tropical tree species in growth and development are strongly influenced by environmental factors. To estimate effects of environmental factors and ecophysiological processes, water relation characteristics of 5 dipterocarp species were studied using P-V method. And light- and temperature- photosynthesis relation of 6 dipterocarp species, photosynthesis and water use efficiency of 17 tropical species, diurnal changes in transpiration rate( $Tr$ ), leaf conductance to water vapor( $G_w$ ), and water potential on *Shorea leprosula* and *Acacia mangium* saplings, diurnal changes in  $P_n$ ,  $Tr$ ,  $G_w$ , and water potential of 3 dipterocarp species, and diurnal changes in  $P_n$  and  $G_w$  of *Dryobalanops aromatica* mature tree were studied.

**Key Words** Tropical rain forest tree, Dipterocarps, Gas Exchange Rate, Water Relation

### 1. INTRODUCTION

Tropical rain forest is composed of dipterocarps the main trees of timber produce in Malaysia. Their biological processes in growth and development are strongly influenced by environmental factors. To estimate effects of environmental factors, water relation characteristics and ecophysiological processes were studied for several dipterocarp tree species, and adaptabilities were compared among species.

### 2. MATERIAL AND METHODS

#### 2.1 Water relation parameters of seedlings and mature trees

One-year-old seedlings of *Shorea assamica*, *S. platyclados*, *Dryobalanops aromatica*, *Hopea odorata*, and *Neobalanocarpus heimii* were used in this study. Also used were open-planted juvenile trees of *S. assamica*, *S. platyclados*, and *H. odorata*, and mature tall trees of *D. aromatica* and *N. heimii*.

Branches of 40 to 60cm long were collected from nursery and open site within FRIM campus. After being fully hydrated, single fully expanded mature leaves were cut from the branches and were used to

generate pressure-volume curves (Schorander *et al.* 1964, Tyree and Hammel 1972). Several water relation parameters were determined from the pressure-volume curves following Maruyama and Morikawa (1983).

## 2.2 Light- and temperature-photosynthesis relations

Net photosynthetic rate (Pn) of detached leaves of *S. assamica*, *S. platyclados*, *S. macroptera*, *D. aromatica*, *H. odorata*, and *N. heimii* was measured under controlled condition using Portable Photosynthesis and Transpiration Measurement System (PPTMS, H-2, ADC, UK). Branches were collected from upper crowns growing at FRIM campus and light- and temperature-photosynthesis curves were determined for single detached leaves. To control the light intensity, temperature, and humidity, a small box-type phytotron designed and made by Dr. Matsumoto was used.

## 2.3 Photosynthesis and water use efficiency

Pn and transpiration rate (Tr) of seedlings of *S. accuminata*, *S. assamica*, *S. curticii*, *S. leprosula*, *S. macroptera*, *S. ovalis*, *S. parvifolia*, *S. pauciflora*, *Dipterocarps comutus*, *Hopea odorata*, *Neobalanocarpus heimii*, *Acacia mangium*, *Alstonia angustiloba*, *Azadirachta excelsa*, *Cinnamomum iners*, *Endospermum malaccensis*, *Intsia palembanica*, *Khaya ivorensis*, and *Tectona grandis* were measured. These potted seedlings were grown at Chikus nursery of Multi-Storied Forest Management Project (MSFM project) carried by Forest Department Peninsular Malaysia (FD) and the Japan International Cooperation Agency (JICA).

From each seedling, five fully expanded mature leaves were selected and Pn and Tr were measured with PPTMS (H-2, ADC, UK). Measurements were carried out in the morning when stomatal conductance and Pn were relatively high.

## 2.4 Diurnal changes in transpiration, stomatal conductance, and leaf water potential of *Shorea leprosula* and *Acacia mangium* Saplings

Diurnal changes of Tr, stomatal conductance (Gw), and leaf water potential ( $\Psi_w$ ) of *Shorea leprosula* and *Acacia mangium* saplings were measured.

The study site is located in Chikus Forest Reserve where the MSFM project is being carried. Under the project, experimental plots were established in a three-year-old *A. mangium* plantation by thinning one (plot A), 2 (plot B), 4 (plot C), 8 (plot D), and 16 (plot E) rows of the *A. mangium* trees. A detail description of the project was reported by Iwasa *et al.* (1993).

In this study, planted seedlings of *S. leprosula* and naturally regenerated *A. mangium* in plot C (4 rows removed) and plot E (16 rows removed) were used. For each species, six fully matured single leaves were selected from two seedlings (three leaves per seedling) at each site.

Tr, Gw, and leaf temperature (Tleaf, °C) were measured with a Steady-State Diffusion Porometer (SDP, Li-1600, Li-Cor, USA) and  $\Psi_w$  was measured with a pressure chamber (Soil Moisture, USA). Measurements were carried on 24 to 26 January 1994.

## 2.5 Diurnal changes in photosynthesis, transpiration, stomatal conductance, and

### leaf water potential of *Shorea assamica*, *S. platyclados*, and *H. nervosa* young trees

Diurnal changes in Pn, Gw, and  $\Psi_w$  were measured for fully expanded young and mature leaves at upper canopy of *Shorea assamica*, *S. platyclados*, and *H. nervosa* young trees in Ang Li Hoe's experimental plot (Ang and Maruyama, 1995), located in FRIM campus.

Pn was measured with PPTMS(H-2, ADC, UK) and Tr, Gw, and leaf temperature (Tleaf) were measured with a SSDP(Li-1600, Li-Cor, USA) and  $\Psi_w$  was measured with a pressure chamber (Soil Moisture, USA). Measurements were carried on 24 and 25 June 1993.

### 2.6 Diurnal changes in photosynthesis and stomatal conductance of

#### *Dryobalanops aromatica* mature tree

Diurnal changes in Pn and Gw were measured for fully expanded immature and mature leaves at uppermost canopy (35 m above ground) of a *Dryobalanops aromatica* mature tree, using a scaffolding tower of 40 m high installed within FRIM campus.

Pn and Gw were measured every 15 to 20 minutes for six or seven leaves with PPTMS(H-4, ADC, UK). Measurement were carried out on 20 to 21 October, and 11 November 1994.

## 3. RESULTS AND DISCUSSION

### 3.1 Water relation parameters of seedlings and mature trees

Water potential at turgor loss ( $\Psi_w^{tLP}$ ) and osmotic potential at full turgor ( $\Psi_o^{tFT}$ ) of mature leaves of forest tree species are reported to be -1.83 to -3.40 MPa and -1.18 to -2.13 MPa, respectively (Hinkley *et al.* 1978). In this study,  $\Psi_w^{tLP}$  and  $\Psi_o^{tFT}$  of seedlings were within narrow range of -1.43 to -1.66 MPa and -1.23 to -1.39 MPa, respectively (Table 1). These high values of  $\Psi_w^{tLP}$  and  $\Psi_o^{tFT}$  found in this study indicate that the capacity for maintaining positive turgor is relatively low in leaves of these dipterocarp seedlings.

The maximum values of bulk modulus of elasticity ( $\epsilon_{max}$ ) were smaller in the seedlings than in the open trees. This suggests that the leaf cells of the seedlings were more elastic than those of the open trees. More elastic cells permit larger change in cell volume with smaller change in pressure potential ( $\Psi_p$ ), which results in lower RWC<sup>tLP</sup> (Maruyama & Morikawa 1983; Davis & Mooney 1986). In this study, except for *S. assamica*, although leaf cells were more elastic in the seedlings than in the open trees, lower  $\Psi_o^{tFT}$ , and thus higher  $\Psi_p$  at full turgor, contributed to lower RWC<sup>tLP</sup> in the open trees.

Lower  $\Psi_o^{tFT}$  in the open trees is mainly due to greater number of osmoles (Ns, solute accumulation) in *S. platyclados* and in *N. heimii* and to smaller symplasmic water volume at full turgor ( $V_o$ , solute concentration) in *S. assamica* and *D. aromatica*. In *H. odorata*, both greater Ns and smaller  $V_o$  contributed to lower  $\Psi_o^{tFT}$  in the open trees.

Leaf dry weight per unit leaf area (DW/LA) was greater in the open trees than in the seedlings (Table 1). This result indicates that the leaves of the open trees had more cell wall material than those of the seedlings. The greater values of DW/LA in the open trees would be due to the water stress.

From these results it might be concluded as follows. The capacity for maintaining positive turgor appeared to be low in nursery seedlings of dipterocarp. Open-planted juvenile trees and the mature trees

had adapted to stress of water deficiency morphologically as well as by maintaining positive turgor through osmotic adjustment. But the adaptability to the water stress was lower in *S. assamica* compared to the other species.

### 3.2 Light- and temperature-photosynthesis relations

Maximum rate of Pn varied 5.6 to 10.8  $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . These values are corresponding to those reported by Koyama(1981), and are relatively high compared to those of seedlings(Mori *et al.* 1990). Among these species, *N. heimii*, *S. macroptera* and *D. aromatica*, which are comparatively slow growing species, had lower Pn than those of *H. odorata* and *S. assamica*. *S. platyclados*, which is normally found in hill forests, also had low Pn.

Optimum temperature for maximum Pn was between 28 and 35 °C, and was highest in *S. platyclados* and lowest in *S. assamica* (Fig. 1). Reduction of Pn by increasing temperature was large in *S. macroptera*, *S. assamica*, *D. aromatica*, and *N. heimii*. In *H. odorata*, which is known as drought tolerant species, and in *S. platyclados*, reduction of Pn by both increasing and decreasing temperature was relatively small.

Light saturation point for Pn was between 400 and 620  $\mu \text{ mol m}^{-2} \text{ s}^{-1}$  in photosynthetically active photon flux density(PPFD). The highest light saturation was observed in *S. assamica*(Fig. 2), which is relatively more light demanding species(Symington 1943). According to Mori *et al.*(1990), light saturation is low in *N. heimii*, which is well known as a shade tolerant and slow growing species. But in this study, light saturation in *N. heimii* was not lower compared to the other species. Lower light saturation point in Mori *et al.*(1990) may be caused by lower light intensity under which plants were grown.

### 3.3 Photosynthesis and water use efficiency

Pn was highest in *Acacia mangium*, which is well known as a fast growing and light demanding species. *Hopea odorata*, *Tectona grandis*, and *Cinnamomum iners* also showed relatively high Pn(Fig. 3). Pn of dipterocarps with the exception of *H. odorata* was lower compared to that of fast growing species. *Intsia palembanica*, which is known as a slow growing species, also had low Pn.

Water use efficiency(WUE), i. e., ratio of Pn and Tr, was high in *I. palembanica* and *T. grandis*. *H. odorata* which occur naturally in northern part of Peninsular Malaysia where dry spells are more pronounced, also had high WUE. WUE was lowest in *S. assamica*, which occurs in low-lying land and in the vicinity of streams.

Among fast growing species, *A. excelsa*, *K. ivorensis*, and *E. malaccensis* had relatively low WUE, suggesting that they need large amount of water for maintaining their rapid growth. However, highest leaf area weight(LAW), i. e., leaf dry weight per unit leaf area, of *K. ivorensis* would enable this species to minimize transpirational water loss.

Among dipterocarps, both WUE and LAW were highest in *H. odorata*. *S. curticii*, which is normally found on ridges and hill tops, also had high WUE. In contrast, *S. leprosula* and *S. ovalis*, which are relatively faster growing species among red meranti group, had low WUE, suggesting that these species are not suitable for open planting. According to these characteristics of gas exchange, *I. palembanica*, *H. o*

*dorata*, and *S. platyclados* could be recommended as possible species for establishment in plantation.

### 3.4 Diurnal changes in transpiration, stomatal conductance, and leaf water potential on *Shorea leprosula* and *Acacia mangium* Saplings

In *S. leprosula*, Gw continued to increase gradually after 10:30, reached peak of  $410 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1}$  at 12:00, and then decreased rapidly in plot C (more shaded site where only 4 rows were removed) (Fig. 4). While, in plot E (almost open site where 16 rows were removed), Gw reached peak of  $350 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1}$  at 10:30, and then continued to decrease (Fig. 4). These differences in stomatal responses between two sites suggest that gas exchange through stomata was limited more strongly in plot E than in plot C, and seem to be a major factor causing better growth of *S. leprosula* in more shaded site than in more open site.

In *A. mangium*, Gw remained relatively constant throughout the daytime irrespective of changes of PPFD in plot C (Fig. 5). As a result, Tr followed the pattern of VPD, i. e., continued to increase until about 14:00 and then decreased. On the other hand, Gw and Tr closely reflected the pattern of PPFD in plot E (Fig. 5). And even under direct sunlight, Tleaf and VPDleaf remained lower than Tair and VPDair, respectively, due to evaporative cooling via rapid transpiration.

Maximum Gw of 480 and  $600 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1}$  and maximum Tr of 8.2 and  $11.1 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1}$  were recorded for *A. mangium* in plot C and in plot E, respectively. These values are much higher when compared to those of *S. leprosula*.

In many species, Gw decreases with increasing vapour pressure deficit (VPD) independent of leaf water status (Turner *et al.* 1984). In this study, Gw of *S. leprosula* also decreased when vapour pressure deficit of the ambient air (VPDair) reached above 10 hPa. But Gw of *A. mangium* was not limited by vapour pressure deficit, and the values of Gw obtained here were higher than those reported by Turner *et al.* (1984). These characteristics of Gw could explain the fast growing and light demanding characteristics of *A. mangium*.

Soil-to-leaf hydraulic conductance (L) of *S. leprosula* was  $6.4$  and  $5.4 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  for plot C and plot E, respectively, and L of *A. mangium* was  $10.1$  and  $12.2 \text{ mmolH}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  for plot C and plot E, respectively. In *A. mangium*, higher L resulted in less negative  $\Psi_w$  for same transpiration rate when compared to *S. leprosula*. This result indicates that water availability is higher in *A. mangium* than in *S. leprosula*. High L enabled *A. mangium* to maintain high Gw during daytime when transpiration rate was high.

### 3.5 Diurnal changes in photosynthesis, transpiration, stomatal conductance, and leaf water potential of *Shorea assamica*, *S. platyclados*, and *H. nervosa* young trees

In *S. Assamica*, and *S. platyclados*, Gw increased with increasing PPFD in the morning, followed by rapid decrease after reaching maximum on 25th June (Fig. 5). Midday depression in Gw of *H. nervosa* was smaller compared to the other species, and Gw remained relatively constant in the afternoon on 25th June. On 24th June, Gw of *S. assamica* showed a similar diurnal changes as on 25th June. But Gw of *S. platyclados*, and *H. nervosa* remained low and relatively constant during daytime on 24th June. Among

g all the species studied here, *S. assamica* had highest Gw.

Tr and Pn coincided with the diurnal changes of Gw irrespective of species and days. But decrease of Tr during midday was smaller compared to that of Gw because of increasing vapour pressure deficit (VPD). Both Tr and Pn were highest in *S. assamica*. Pn of *S. assamica* studied here is much higher compared to that of nursery seedlings. Mori(1980) also reported low Pn for dipterocarp seedlings grown under controlled environment. These differences would be caused by light intensity under which plants were grown. In these juvenile trees studied here, photosynthetic CO<sub>2</sub> uptake appeared to be strongly influenced by stomatal opening.

### 3.6 Diurnal changes in photosynthesis and stomatal conductance of *Dryobalanops aromatica* mature tree

Diurnal Pn and Gs varied considerably among leaves in a canopy. Maximum Pn reached  $12.0 \mu \text{mol m}^{-2} \text{s}^{-1}$  with mean value of about  $6.0 \mu \text{mol m}^{-2} \text{s}^{-1}$  (Fig. 6). Under light saturated condition, Pn related linearly to Gw, especially in the mature leaves. The coefficient of variation(C. V.) among canopy leaves in the difference between CO<sub>2</sub> concentrations of the ambient air and the leaf intercellular air space(Ca-Ci) was smaller than the degree of C. V. in both Pn and Gw.

These results suggest that maximum Gw in each leaf was mainly controlled by mesophyll assimilation(Pn/Ci) through some mechanisms such as keeping Ci at a constant or near-constant value. Although diurnal Gw decreased when leaf-to-air vapor pressure deficit(leaf-to-air VPD) exceeded  $0.025 \text{ kPa kPa}^{-1}$ , such high leaf-to-air VPD was seldom observed during the daytime because of dew in the early morning and regular rain in the afternoon.

This resulted in high Ci/Ca ratios(0.69-0.73) in canopy leaves, suggesting a small stomatal limitation to Pn by drought and non-conservative water-use in uppermost canopy leaves of *D. aromatica*

## 4. ACKNOWLEDGEMENTS

We wish to express a sincere appreciation to all the staff of the Multi-Storied Forest Management project which is carried by Forestry Department Peninsular Malaysia and Japan International Cooperation Agency(JICA) for their warm and kind support. We also would like to thank Mr. Ang Lai Hoe for his kind suggestions and for permission to use his experiment site.

## 5. REFERENCES

- Ang, L. H. and Maruyama, Y. (1995) Survival and early growth of *Shorea platyclados*, *S. macroptera*, *S. assamica* and *Hopea nervosa* in open planting. *Journal of Tropical Forest Science*.
- Davis, S.D. & Mooney, H.A. (1986) Tissue water relations of four co-occurring chaparral shrubs. *Oecologia* 70:527-535.
- Hinckley, T.M., Lassoie, J.P. & Running, S.W. (1978) Temporal and spatial variations in the water status of forest trees. *Forest Science Monograph* 20:1-72.
- Iwasa, M., Roslan, A., and Mangsor, M. Y. (1993) The establishment of multi-storied forests in Peninsula Malaysia. -Underplanting of Dipterocarpaceae in *Acacia mangium* plantation-. Proc. Inter. Workshop BIO-REFOR, Yogyakarta p.66-68
- Koyama, H. (1981) Photosynthetic rates in lowland rain forest trees of Peninsular Malaysia. *Japanese*

- Journal of Ecology 31:361-369
- Maruyama, Y. & Morikawa, Y. (1983) Measurement of leaf water relations using the pressure-volume technique. *Journal of Japanese Forest Society* 65:23-28. (in Japanese with English summary)
- Mori, T. (1980) Physiological studies on some dipterocarp species of Peninsular Malaysia as a basis for artificial regeneration. Research Pamphlet No.78. Forest Research Institute Malaysia, Kepong.
- Mori, T., Nakashizuka, T., Sumizono, T. & Yap, S.K. (1990) Growth and photosynthetic responses to temperature in several Malaysian tree species. *Journal of Tropical Forest Science* 3(1):44-57.
- Scholander, P.F., Hammel, H.T., Hemmingsen, E.A. & Bradstreet, E.T. (1964) Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proceedings of National Academy Science, U.S.A.* 52:119-125
- Symington, F.C. (1943) Forester's manual of dipterocarps. Malayan Forest Records Number 16. University of Malaya Press, Kuala Lumpur, Malaysia
- Turner, N. C., Schulze, E. D., and Gollan, T. (1984) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. *Oecologia* 63:338-342
- Tyree, M.T. & Hammel, H.T. (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* 23:267-282

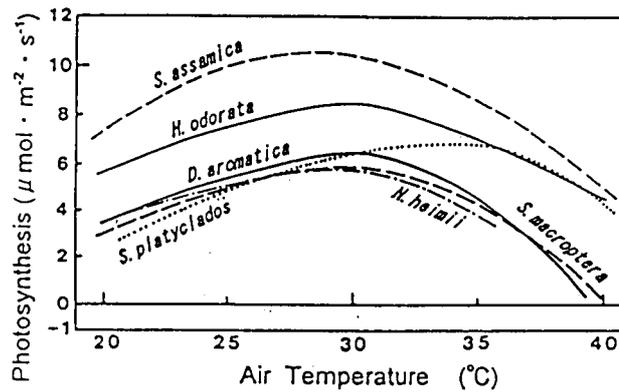


Fig. 1 Temperature-photosynthesis curves of *S. assamica*, *S. platyclados*, *S. macroptera*, *D. aromatica*, *H. odorata*, and *N. heimii*

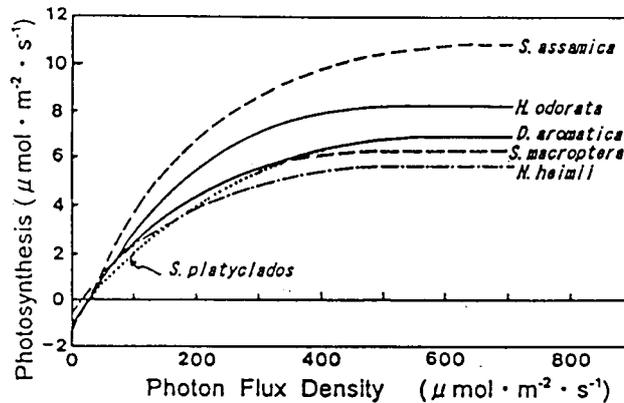


Fig. 2 Light-photosynthesis curves of *S. assamica*, *S. platyclados*, *S. macroptera*, *D. aromatica*, *H. odorata*, and *N. heimii*

Table 1. Water potential at turgor loss ( $\Psi_w^{tlp}$ ), osmotic potential at full turgor ( $\Psi_o^{sat}$ ), relative water content at turgor loss ( $RWC^{tlp}$ ), maximum value of bulk modulus of elasticity ( $\epsilon_{max}$ ), volume of symplasmic water per unit leaf dry weight ( $V_o/DW$ ), number of osmoles per unit leaf dry weight ( $N_o/DW$ ), leaf dry weight per unit leaf area ( $DW/LA$ ) and total volume of water per unit leaf area ( $V_t/LA$ )

species	$\Psi_w^{tlp}$ -MPa	$\Psi_o^{sat}$ -MPa	$RWC^{tlp}$ %	$\epsilon_{max}$ MPa	$N_o/DW$ OS/kgDW	$V_o/DW$ lH <sub>2</sub> O/kgDW	$DW/LA$ mgDW/cm <sup>2</sup>	$V_t/LA$ $\mu$ lH <sub>2</sub> O/cm <sup>2</sup>
Nursery seedlings								
<i>S. assamica</i>	1.66	1.32	84.1	23.9	0.64	1.20	6.97	12.37
<i>S. platyclados</i>	1.47	1.18	88.9	10.6	0.44	0.92	8.31	13.31
<i>H. odorata</i>	1.43	1.23	91.1	23.7	0.65	1.30	6.27	12.50
<i>D. aromatica</i>	1.66	1.39	87.6	18.0	0.73	1.31	6.88	11.65
<i>N. heimii</i>	1.50	1.28	89.3	23.1	0.41	0.80	7.72	8.52
Open-planted trees								
Juvenile								
<i>S. assamica</i>	1.75	1.42	86.3	25.6	0.60	1.05	7.73	11.29
<i>S. platyclados</i>	2.10	1.48	74.1	15.6	0.74	1.28	9.41	14.14
<i>H. odorata</i>	2.35	1.64	74.3	29.5	0.77	1.16	8.91	12.26
Mature								
<i>D. aromatica</i>	2.58	1.87	80.2	18.7	0.64	0.84	15.74	18.60
<i>N. heimii</i>	2.42	1.95	85.2	81.4	0.66	0.84	9.00	10.09

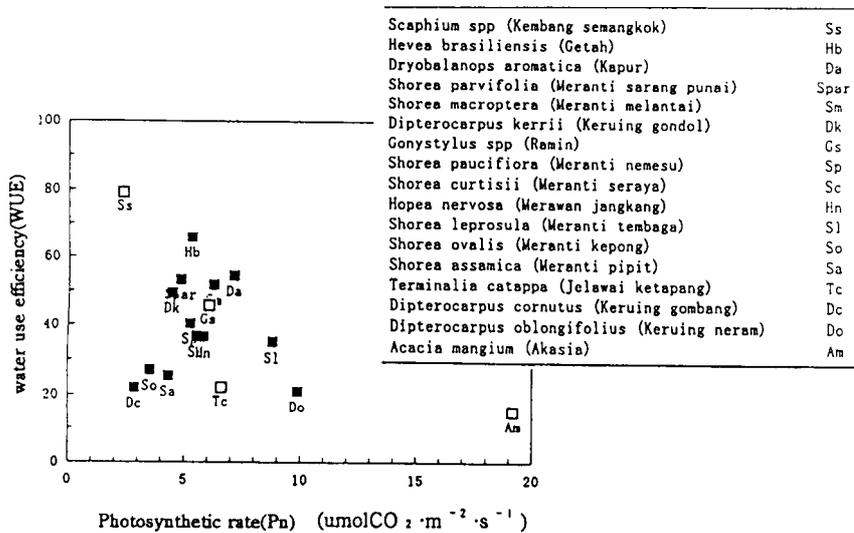


Fig. 3 Photosynthetic rate(Pn) and water use efficiency(WUE)

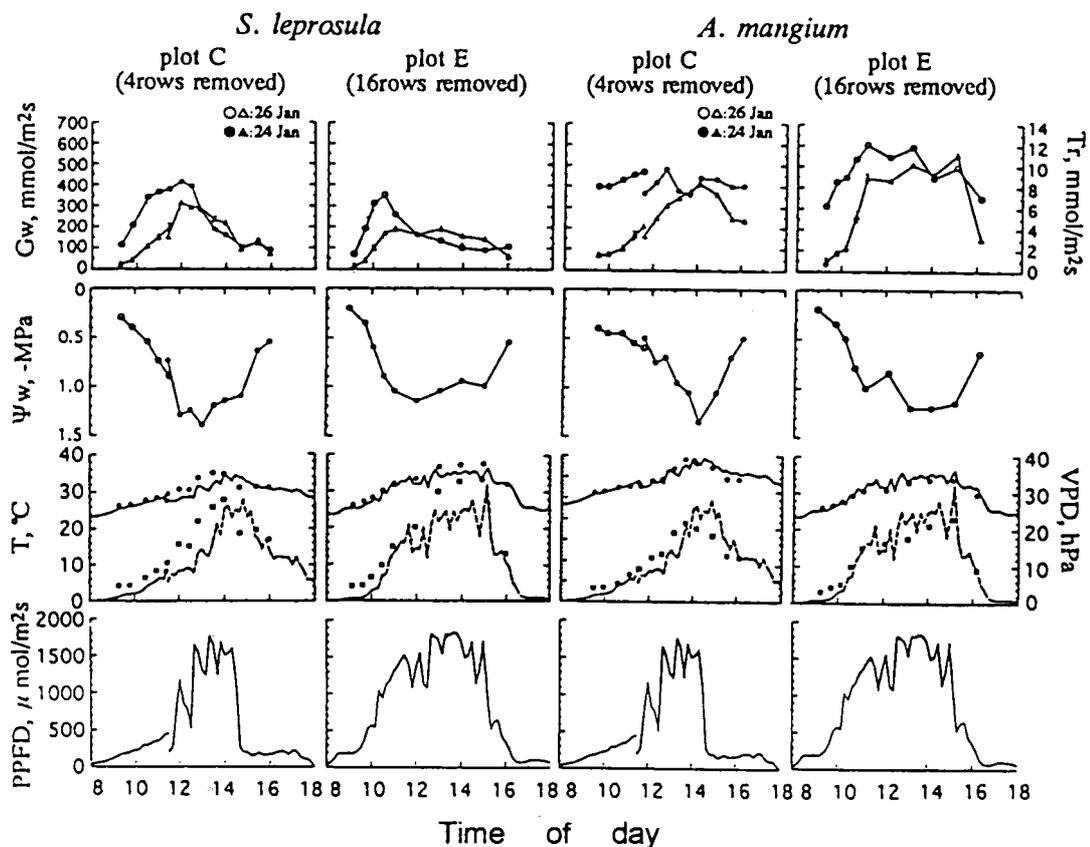


Fig. 4 Diurnal changes of water vapor conductance( $G_w$ , circles), transpiration rate ( $T_r$ , triangles), leaf water potential ( $\Psi_w$ ), air temperature( $T$ , solid line), leaf temperature(solid circles), vapour pressure deficit(VPD) of air(broken line) and leaf-to-air(solid squares), and photosynthetically active photon flux density(PPFD) on *S. leprosula* and *A. mangium*  
 ●▲ : January 24, 1994, ○△ : January 26, 1994

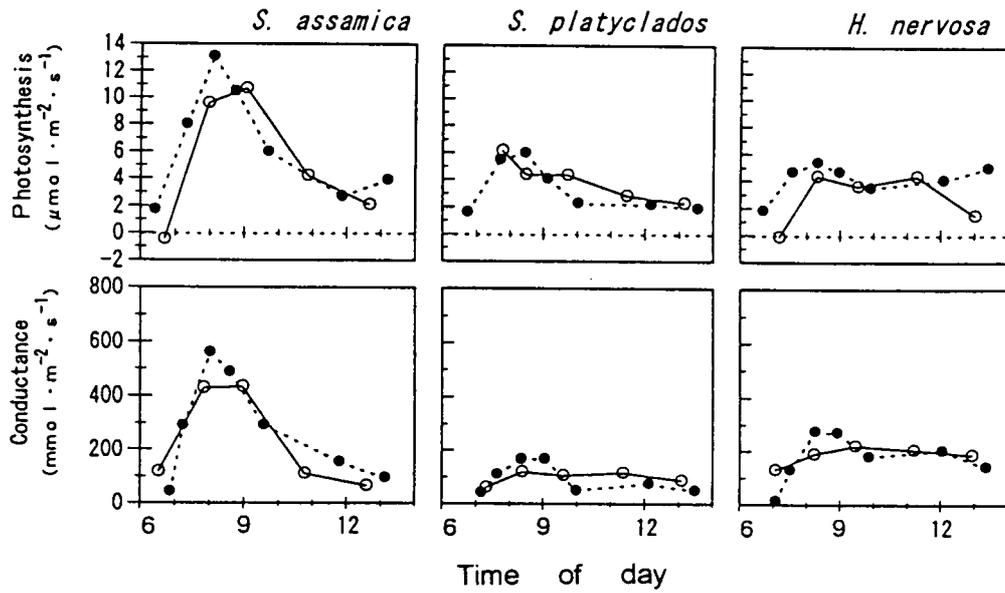


Fig. 5 Diurnal changes of water vapor conductance and photosynthetic rate of *S. assamica*, *S. platyclados*, and *H. nervosa*  
 ○ : June 24, 1993, ● : June 25, 1993

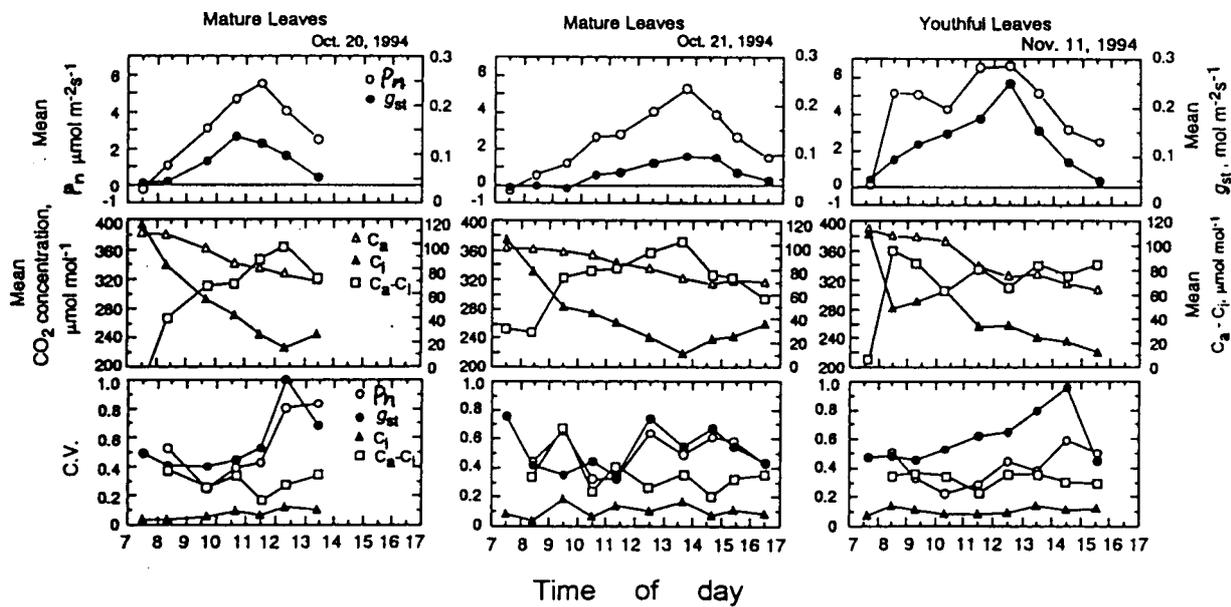


Fig. 6 Diurnal changes of photosynthetic rate ( $P_n$ , ○), water vapor stomatal conductance ( $g_{st}$ , ●),  $CO_2$  concentration of ambient ( $C_a$ , Δ), leaf intercellular  $CO_2$  Concentration ( $C_i$ , ▲), the differences between  $C_a$  and  $C_i$  ( $C_a - C_i$ , □), and each coefficients of variations (C.V.) in the uppermost canopy leaves of *Dryobalanops aromatica*