

## Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture

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*(Accepted 2nd August 1999)*

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**ABSTRACT.** Leaf water and osmotic potentials and gas exchange were monitored during a prolonged El Niño drought in 1998 for saplings of seven species in a Bornean heath forest and compared with measurements taken during a subsequent wet period. The four dipterocarp species maintained reasonably good water status throughout the drought, especially *Dipterocarpus borneensis* which had thick and deep tap roots. In contrast, two of three non-dipterocarp species, *Cleistanthus baramicus* and *Tristaniaopsis obovata* displayed predawn leaf water potentials approaching their turgor-loss points. During the drought, all species except *D. borneensis* displayed strongly reduced stomatal conductance after a brief exposure to sun, and all displayed lower maximum rates of stomatal conductance and net photosynthesis than during the wet period. Only *Cotylelobium burckii* displayed significant osmotic acclimation to the drought. *T. obovata* possessing a superficial root system suffered a high mortality due to the drought, but recovered faster after the first rains than the other species all of which had tap roots. Deep roots and strong stomatal control favour trees in tropical heath forests where water deficits probably occur regularly.

**KEY WORDS:** dipterocarps, drought tolerance, El Niño drought, haze, leaf water potential, osmotic potential, photosynthesis, root architecture, stomatal conductance, tropical heath forest

### INTRODUCTION

Although northern Borneo lies in the aseasonal tropics (Whitmore 1984), moderate droughts are frequent, and prolonged droughts occur occasionally (Walsh 1996). Drought affects the species composition, structure and reproduction of

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forests in northern Borneo (Ashton 1988, Becker *et al.* 1999; Brünig 1974, 1996). Occasional extreme drought conditions in this region are often associated with the complex atmospheric and oceanic anomaly known as the El Niño–Southern Oscillation phenomenon, which is responsible for worldwide climatic anomalies (Diaz & Markgraf 1992). A description of the El Niño phenomenon can be found in Diaz & Markgraf (1992).

From early September (or early December in Brunei) 1997 through to the middle of May 1998, a prolonged El Niño-associated drought occurred in the Borneo region. During this period, numerous extensive wildfires occurred in southern Sumatra, and central and eastern Kalimantan, Indonesia (Dennis 1999, Laumonier & Legg 1998), and in Brunei as well. Most of the fires were associated with agricultural and land-clearing operations or other human-induced fire accidents. The burnt lands included rain forests, bushlands, and deforested peat soils. Dense haze covered large parts of Borneo and surrounding regions for several months. The dense haze greatly affected the air quality and irradiance intensity and quality. For example, on dense hazy days (without clouds) in Brunei, photosynthetic photon flux density was reduced by about 50% compared to that on clear days, and there was also proportionally a greater scattering in the shorter wavelengths of the visible spectrum (W. E. Booth, unpubl. data).

Trees can survive drought using a variety of strategies (Jones 1992, Smith & Griffiths 1993). Stomatal closure is the first line of plant defence against water loss and the negative effect of water stress (Jones & Sutherland 1991, Schulze 1993, Tyree & Sperry 1988). Maintenance of turgor by means of osmotic adjustment is a common plant adaptation to drought (Jones 1992, Turner & Jones 1980, Wright *et al.* 1992). Deep-rooted trees are able to access deeper underground water and should be more resistant to drought than shallow-rooted ones (Becker & Castillo 1990, Becker *et al.* 1999, Hinckley *et al.* 1983, Wright *et al.* 1992). Trees of small size in a heath forest are highly susceptible to prolonged drought due to their shallower root systems (Becker & Wong 1993) and the limited water holding capacity of sands.

The objectives of the present study were: (1) to compare water status, stomatal conductance and photosynthetic rates of saplings in a heath forest during the drought and a subsequent wet period; (2) to clarify whether there were osmotic adjustments in the saplings to cope with the drought; (3) to determine whether the water status of saplings during the drought were related to root architecture.

#### METHODS

The research was conducted in the Research Forest at Bukit Sawat (4° 34'37" N, 114° 30'11" E, 11–23 m asl) in Brunei, a heath forest (kerangas) on a Pleistocene terrace with an albic arenosol soil type. The forest was selectively logged in the late 1960s. In a 0.96-ha plot, 1613 woody plants with DBH (diameter at

1.3 m height) > 5 cm were found, which included 171 species from 48 families (Davies & Becker 1996). Important canopy trees are *Gluta beccarii*, *Dipterocarpus borneensis*, *Shorea multiflora*, *Copaifera palustis* and *Calophyllum ferrugineum*. Mean annual temperature is 28.1 °C (1983–1988), a value which is even throughout the year (mean daily maxima = 32.0 °C, mean daily minima = 24.2 °C; Anon. 1990). The mean annual precipitation is 2920 mm (range = 1730–4252 mm; 1958–1988).

The present study was initially planned to compare water status, stomatal conductance, photosynthetic rates and osmotic potentials during the drought and wet (sliding 30-d rainfall > 100 mm; cf. Brünig 1974) periods for the saplings of the following four dipterocarp species: *Dipterocarpus borneensis*, *Cotylelobium burckii*, *Shorea multiflora* and *Hopea pentanervia*. For comparison, three non-dipterocarp species, *Cleistanthus baramicus* (Euphorbiaceae), *Tristaniopsis obovata* (Myrtaceae) and *Fordia splendidissima* (Leguminosae) were included in the study at a late stage of the drought period. Hereafter, only the generic names are used for the study species, except for *Hopea* and *Shorea* species.

Predawn leaf water potential ( $\Psi_{PD}$ ) is considered to be a good indicator of soil water availability (Jones 1992). From early February 1998 to the end of the drought,  $\Psi_{PD}$  was measured once every 1 or 2 wk for dipterocarp saplings growing on the edge of a path and in the understorey, using a pressure chamber (PMS 600, Meiwa Shoji Co. Ltd., Osaka, Japan). The path has been deserted since the logging in the late 1960s and is now only occasionally used by researchers and visitors. The dense hazy conditions in March and April restricted the field work. Midday leaf water potentials ( $\Psi_{MD}$ ) were also monitored but less frequently because of the time conflict with measurement of gas exchange. To determine  $\Psi_{PD}$  and  $\Psi_{MD}$ , leaves were used for *Dipterocarpus* and shoots for the other three dipterocarp species. Different plants were measured on different days, because many saplings had only a single shoot suitable for the  $\Psi$  determination.

On 15 March and 26 April,  $\Psi_{PD}$  was determined for saplings of the two non-dipterocarp trees, *Tristaniopsis* and *Cleistanthus*, growing on the edge of the path.  $\Psi_{PD}$  and  $\Psi_{MD}$  was also determined on two days in February for several plants of *Melastoma* sp. (a shrub species) growing in a large gap. These plants died shortly afterwards.

The moisture of soil (0–30 cm depth) at the edge of the path and inside the forest was measured occasionally during the drought period using a moisture point system (Environmental Sensors, Victoria, Canada). For comparison,  $\Psi_{PD}$ ,  $\Psi_{MD}$  and soil moisture was also determined on 11 October when the soil was well watered.

Leaf osmotic potentials at full saturation ( $\Psi_{\pi}^{100}$ ) and at turgor loss point ( $\Psi_{\pi}^0$ ) were determined for saplings of the seven species growing on the edge of the path, once in late May at the end of the drought, and once in late August and early September in the wet period, by means of pressure-volume (P-V)

analysis (Koide *et al.* 1989). Shoots or leaves from three to five plants of each species were collected and hydrated overnight with distilled water under a plastic bag in an air-conditioned laboratory.

Stomatal conductance ( $g_s$ ) and net photosynthetic rates ( $A$ ) were measured for insolated saplings of the seven species on the edge of the path on most of those days when  $\Psi$  was determined during the drought, using a closed portable photosynthesis system (LICOR 6200, USA) with a 1-l leaf chamber. These saplings were not used for the  $\Psi$  determination.  $g_s$  and  $A$  were also measured during a subsequent wet period.

Roots of three to seven saplings (0.5–2.5 m height) per species growing on the edge of the path and in the understorey were excavated. Root excavation included additional two dipterocarp species, *Hopea vacciniifolia* (understorey species) and *Shorea pachyphylla* (canopy species). Rooting depth was measured, and root types were described. When rooting depth exceeded 1.5 m, the depth and biomass of the deeper parts were roughly estimated based on the diameters of the broken ends of the unearthed roots. Harvested roots and shoots were oven-dried (80 °C) to constant weight, and root/shoot biomass ratios were determined.

Daily rainfall data during the period from 1 July 1997 to 31 July 1998 were provided by the Agricultural Meteorological Station at Sungai Liang (4° 40' 37" N, 114° 29' 21" E, 9 m asl), which is *c.* 14 km north of the study site. Sliding 30-d rainfall values were calculated for the period 1 December 1997 to 10 June 1998. Total rainfall in terms of sliding 30-d measure < 100 mm indicates drought in the tropics (Brünig 1974).

Pearson's correlation analyses were applied to analyse the relationships among net photosynthetic rates ( $A$ ), stomatal conductance ( $g_s$ ), leaf-to-air (bulk air in the leaf chamber) vapour pressure difference (VPD), and leaf temperature ( $T$ ). Anova was applied to compare the difference in  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^0$  among species. For each species, Mann–Whitney U-test was used to compare  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^0$  between the drought and wet periods, and root/shoot biomass ratios between the saplings in the understorey and on the edge of the path.

## RESULTS

$\Psi_{PD}$  of dipterocarp species growing both on the edge of the path and in the forest understorey remained reasonably high (> -0.5 MPa mostly) throughout the drought period (Figure 1), except for some saplings of *Hopea pentanervia* and *Shorea multiflora*. *Dipterocarpus* saplings, in particular, always displayed  $\Psi_{PD}$  close to zero throughout the drought period. The differences in  $\Psi_{PD}$  and  $\Psi_{MD}$  among the other three dipterocarp species were small. However, the  $\Psi$  variance among saplings became larger at the later stage of the drought period (Figure 1). There was almost no difference in  $\Psi_{PD}$  between the dipterocarp saplings on the edge of the path and in the understorey.  $\Psi_{MD}$  was lower than

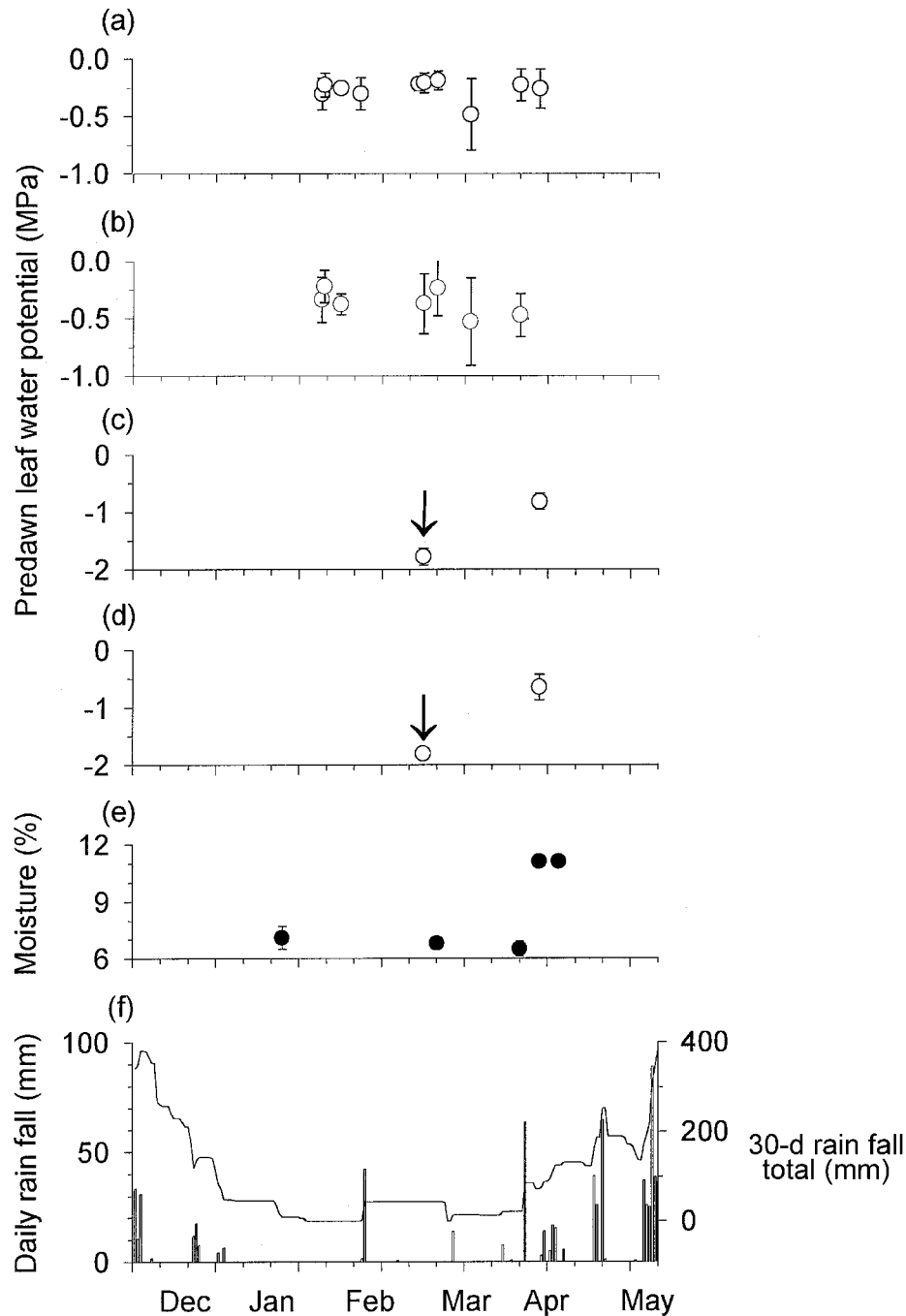


Figure 1. During the drought period, predawn leaf water potentials ( $\Psi_{PD}$ ) for the saplings of *Cotylelobium burckii*, *Hopea pentanervia* and *Shorea multiflora* (a) on the edge of the path, (b) in the understorey, (c) for *Tristaniopsis obovata*, (d) for *Cleistanthus baramicus* on the edge of the path; and (e) soil moisture (0–30 cm depth) at the edge of the path. As the differences in  $\Psi_{PD}$  among the three dipterocarp species were small, for clarity, their  $\Psi_{PD}$  data were combined. Data are mean  $\pm$  SD, the bars (SD) that are smaller than symbols are not visible. Arrows indicate the  $\Psi_{PD} \leq$  the turgor-loss point. (f) Daily rainfall (bars) and sliding 30-d rainfall (line) from 1 December 1997 to 10 June 1998 based on data from the Sungai Liang Meteorological Station.

Table 1. Leaf osmotic potentials at full saturation ( $\Psi_{\pi}^{100}$ , means  $\pm$  SD,  $n = 3-5$ ) and at the turgor-loss point ( $\Psi_{\pi}^0$ ) in the drought and wet periods, the lowest  $\Psi$  (leaf water potential) during the drought, and  $\Psi$  on 11 October 1998. Means within columns sharing a common superscript letter were not significantly different ( $P > 0.05$ , Anova-test).  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^0$  values between the drought and wet periods differed significantly only for CB ( $P < 0.05$ , Mann-Whitney U-test). Bold  $\Psi$  values  $\leq \Psi_{\pi}^0$ . CB = *Colytebium burekii*, DB = *Dipterocarpus borneensis*, HP = *Hopea pentanervia*, SM = *Shorea multiflora*, FS = *Shorea splendiddissima*, TO = *Tristanopsis obtusata* and CL = *Cleistanthus baramicus*.

Species	$\Psi_{\pi}^{100}$ (MPa)		$\Psi_{\pi}^0$		lowest $\Psi$ in drought		$\Psi$ on 11 October	
	Drought	Wet	Drought	Wet	Predawn	Midday	Predawn	Midday
<b>Dipterocarps</b>								
CB	-1.76 <sup>ab</sup> $\pm$ 0.09	-1.09 <sup>bc</sup> $\pm$ 0.06	-2.01 <sup>ab</sup> $\pm$ 0.10	-1.36 <sup>a</sup> $\pm$ 0.06	-0.60	-0.60	-0.23 $\pm$ 0.08	-0.18 $\pm$ 0.03
DB	-1.15 <sup>c</sup> $\pm$ 0.07	-0.96 <sup>c</sup> $\pm$ 0.11	-1.35 <sup>c</sup> $\pm$ 0.13	-1.26 <sup>a</sup> $\pm$ 0.19	-0.45	-0.50	-0.00 $\pm$ 0	-0.00 $\pm$ 0
HP	-1.91 <sup>a</sup> $\pm$ 0.23	-1.63 <sup>a</sup> $\pm$ 0.32	-2.18 <sup>b</sup> $\pm$ 0.13	-2.05 <sup>b</sup> $\pm$ 0.19	-1.45	<b>-2.20</b>	-0.25 $\pm$ 0.05	-0.43 $\pm$ 0.23
SM	-1.54 <sup>b</sup> $\pm$ 0.09	-1.63 <sup>a</sup> $\pm$ 0.18	-1.82 <sup>a</sup> $\pm$ 0.05	-1.78 <sup>b</sup> $\pm$ 0.17	-0.50	-1.20	-0.22 $\pm$ 0.03	-0.20 $\pm$ 0.10
<b>Non-dipterocarps</b>								
FS	-1.61 <sup>ab</sup> $\pm$ 0.04	-1.67 <sup>a</sup> $\pm$ 0.11	-1.73 <sup>a</sup> $\pm$ 0.04	-1.83 <sup>b</sup> $\pm$ 0.09	nd	nd	-0.17 $\pm$ 0.04	-0.75 $\pm$ 0.48
TO	-2.11 <sup>ab</sup> $\pm$ 0.35	-1.57 <sup>ab</sup> $\pm$ 0.16	-2.02 <sup>ab</sup> $\pm$ 0.20	-1.83 <sup>b</sup> $\pm$ 0.15	<b>-1.95</b>	<b>-2.40</b>	-0.13 $\pm$ 0.03	-1.05 $\pm$ 0.09
CL	-1.72 <sup>ab</sup> $\pm$ 0.09	-1.78 <sup>a</sup> $\pm$ 0.13	-1.83 <sup>a</sup> $\pm$ 0.11	-1.91 <sup>b</sup> $\pm$ 0.17	<b>-1.90</b>	<b>-3.40</b>	-0.35 $\pm$ 0.05	-1.37 $\pm$ 0.12

nd = no data.

$\Psi_{PD}$  for the dipterocarp saplings both on the edge of the path and in the understorey (data not shown). There was large variation in  $\Psi_{MD}$  among saplings. *Hopea pentanervia* displayed relatively lower  $\Psi_{MD}$  values compared to other dipterocarp species, and was the only dipterocarp that had some insulated saplings showing  $\Psi_{MD}$  lower than its  $\Psi_{\pi}^0$  (Table 1).

The water status of the non-dipterocarp species examined during the drought period strongly contrasted with that of the dipterocarp species (Figure 1, Table 1). As the drought progressed, leaf water potentials ( $\Psi$ ) of the dipterocarp saplings remained relatively high, while leaf wilting was observed for some adjacent non-dipterocarp species. On 6 February, the shrubs of *Melastoma* sp. in a large gap still displayed mean  $\Psi_{PD}$  of  $-0.3$  MPa and mean  $\Psi_{MD}$  of  $-1.2$  MPa. However, 1 wk later on 13 February, these shrubs showed mean  $\Psi_{PD}$  of  $-1.0$  MPa and wilted at midday. They died shortly afterwards. On the same day (13 February), a  $\Psi_{MD}$  of  $-3.4$  MPa was observed for *Cleistanthus* on the edge of the path, and a  $\Psi_{MD}$  of  $-2.4$  MPa for *Tristaniopsis*. These  $\Psi_{MD}$  values were lower than the respective turgor loss points ( $\Psi_{\pi}^0$ , Table 1), and these plants wilted at midday. On 15 March, both *Cleistanthus* and *Tristaniopsis*, displayed mean  $\Psi_{PD}$  approaching their  $\Psi_{\pi}^0$  values (Figure 1) and  $\Psi_{MD}$  lower than  $\Psi_{\pi}^0$ . A number of *Tristaniopsis* saplings up to 5 m in height on the edge of the path died in a late stage of the drought.

From 4 December 1997 to 30 April 1998, the total rainfall was 200 mm, of which 92% occurred in 9 d (Figure 1). The sliding 30-d rainfall was lower than 100 mm for the period from 1 January to 30 April (mean = 30.8 mm, SD = 24.5). The longest rainless period lasted for 49 d (3 January to 20 February). On 23 January, 20 March and 19 April, the soil moisture (0–30 cm depth) was 6–7% for sites both on the edge of the path (Figure 1) and inside the forest. After substantial rainfall, on 26 April, 3 May and 11 June, the soil moisture was uniformly at 11.1%, both at the edge of the path and inside the forest. The same soil moisture was recorded on 11 October when the soil was well watered.

In the drought period *Dipterocarpus*, and in the wet period *Dipterocarpus* and *Cotylelobium*, displayed the highest  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^0$  values (Table 1), indicating that their leaves were the least tolerant to plant water deficit in these periods. In the drought period, *Hopea pentanervia*, *Tristaniopsis* and *Cotylelobium* displayed the smallest  $\Psi_{\pi}^0$ , and *Shorea multiflora*, *Cleistanthus* and *Fordia* showed intermediate values, although the differences were hardly statistically significant. In the wet period, the differences in  $\Psi_{\pi}^0$  among species were even smaller than in the drought period. *Cotylelobium* showed significantly smaller  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^0$  values in the drought period than in the wet period (Table 1). *Dipterocarpus*, *Hopea pentanervia* and *Tristaniopsis* also displayed smaller  $\Psi_{\pi}^{100}$  in the drought period than in the wet period, but at statistically non-significant levels. This was, however, complicated by the fact that some leaves used for P-V analyses in the wet period were newly produced and younger than those used in the

drought period. The other three species did not show osmotic adjustment to cope with the drought. The P-V analyses were unsuccessful for some leaves or shoots of *Dipterocarpus*.

The saplings of most of the study species on the edge of the path were able to photosynthesize for a short period of the day during the drought, even at the peak of the drought (data not shown). After insolation for 1–2 h, dipterocarps, except for *Dipterocarpus*, strongly reduced their  $g_s$  and  $A$  rates. The two non-dipterocarp species closed their stomata after even shorter exposure to sun. In contrast, *Dipterocarpus* maintained relatively high  $A$  and  $g_s$  rates throughout the day and throughout the drought period. During the drought period all species displayed reduced maximum  $A$  and  $g_s$  rates compared to those during the wet period (Figure 2). The reduction in *Tristaniopsis* was the greatest.

$A$  was strongly correlated with  $g_s$  for each of the seven species during the drought and wet periods, respectively (Table 2). Both  $A$  and  $g_s$  in turn were

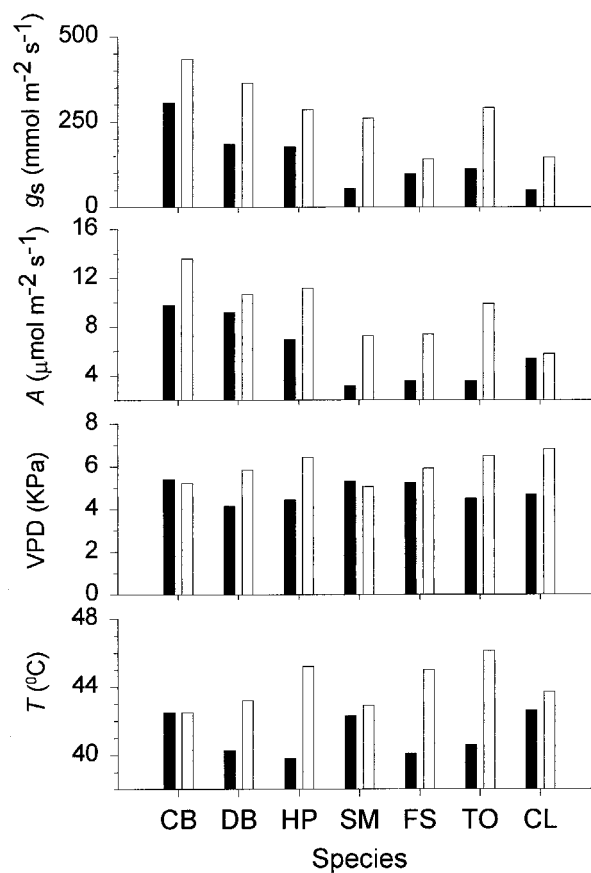


Figure 2. Comparison of maximum values of stomatal conductance ( $g_s$ ), net photosynthetic rate ( $A$ ), leaf-to-air vapour pressure difference (VPD) and leaf temperature ( $T$ ) recorded during the drought (filled bars) and wet periods (open bars) for *Cotylelobium burckii* (CB), *Dipterocarpus borneensis* (DB), *Hopea pentanervia* (HP), *Shorea multiflora* (SM), *Fordia splendidissima* (FS), *Tristaniopsis obovata* (TO) and *Cleistanthus baramicus* (CL).



Table 2. Pearson's correlation coefficients for net photosynthetic rates ( $A$ ) with leaf stomatal conductance rates ( $g_s$ ),  $A$  with leaf-to-air (bulk air in the leaf chamber) vapour pressure difference (VPD),  $g_s$  with VPD, and  $A$  with leaf temperature ( $T$ ). The measurements used were taken when the irradiance exceeded 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (mean = 760.5, SD = 190.4, maximum = 1180) for the drought period and exceeded 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (mean = 1530.3, SD = 327.4, maximum = 1947) for the wet period. The correlation coefficients are significant ( $P < 0.05$ ), except for those indicated with ns. Abbreviations for species follow Table 1.

Species	Period	N	$A$ vs. $g_s$	$A$ vs. VPD	$g_s$ vs. VPD	$A$ vs. $T$
CB	drought	34–53	0.85	–0.87	–0.73	–0.66
	wet	47–50	0.91	–0.59	–0.54	–0.33
DB	drought	22–31	0.85	0.10 <sup>ns</sup>	0.04 <sup>ns</sup>	0.30 <sup>ns</sup>
	wet	34	0.83	–0.86	–0.80	–0.77
HP	drought	36	0.87	–0.60	–0.44	–0.59
	wet	30	0.88	–0.87	–0.93	–0.81
SM	drought	22–24	0.76	–0.22 <sup>ns</sup>	–0.17 <sup>ns</sup>	–0.07 <sup>ns</sup>
	wet	41	0.79	–0.70	–0.87	–0.69
FS	drought	24–27	0.78	–0.41	–0.44	–0.32 <sup>ns</sup>
	wet	26	0.88	–0.77	–0.79	–0.57
TO	drought	27	0.89	–0.75	–0.87	–0.73
	wet	49	0.88	–0.81	–0.79	–0.84
CL	drought	20	0.88	–0.87	–0.80	–0.34 <sup>ns</sup>
	wet	44–47	0.88	–0.75	–0.59	–0.67

significantly correlated with VPD, except for *Dipterocarpus* and *Shorea multiflora* in the drought period (Table 2, Figure 3). For the same VPD, the leaves in the wet period had much higher  $A$  (Figure 3) and  $g_s$  values (not shown) than those in the drought period for all species except for *Dipterocarpus* that showed, during the drought, no correlation of  $A$  and  $g_s$  with VPD. VPD was to a large extent influenced by leaf temperature. For example, using the pooled data from the wet period, the correlation coefficient of VPD with leaf temperature was 0.952 ( $P < 0.001$ ). Apparently, the correlation of  $A$  and  $g_s$  with VPD could be partly due to the response of  $A$  and  $g_s$  to leaf temperature (Table 2).

In late April and early May, several substantial rains occurred (Figure 1). On 15 May, stomatal conductance rates exceeding 200  $\text{mmol m}^{-2} \text{s}^{-1}$  and photosynthetic rates of 7–8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  were recorded for *Tristaniaopsis* saplings. Such high rates were not recorded during the drought period (Figures 2 and 3). In contrast, other species did not increase stomatal conductance and photosynthetic rates on the same day (data not shown).

Saplings of all of the six dipterocarp species had tap root systems (Table 3). *Dipterocarpus* and *Shorea pachyphylla* had thick tap roots, while the other dipterocarp species had thin tap roots. The species differed in rooting depth regardless of the thickness of their tap roots. A 2-m-tall *Dipterocarpus* sapling had a thick tap root of 2 m in depth. Both *Hopea vacciniifolia* and *Shorea multiflora* had thin but also deep tap roots. The tap roots of the other dipterocarp species did not extend beyond 80 cm in depth for saplings shorter than 2.5 m.

*Fordia* had thick and deep tap roots, and notably a root/shoot biomass ratio larger than one as a result of dieback of aboveground shoots and subsequent re-sprouting. *Tristaniaopsis* and *Melastoma* spp. had typical superficial root systems confined to the upper 20 cm soil. *Cotylelobium burckii* was the only species that showed significant greater root/shoot biomass ratio for the saplings in the

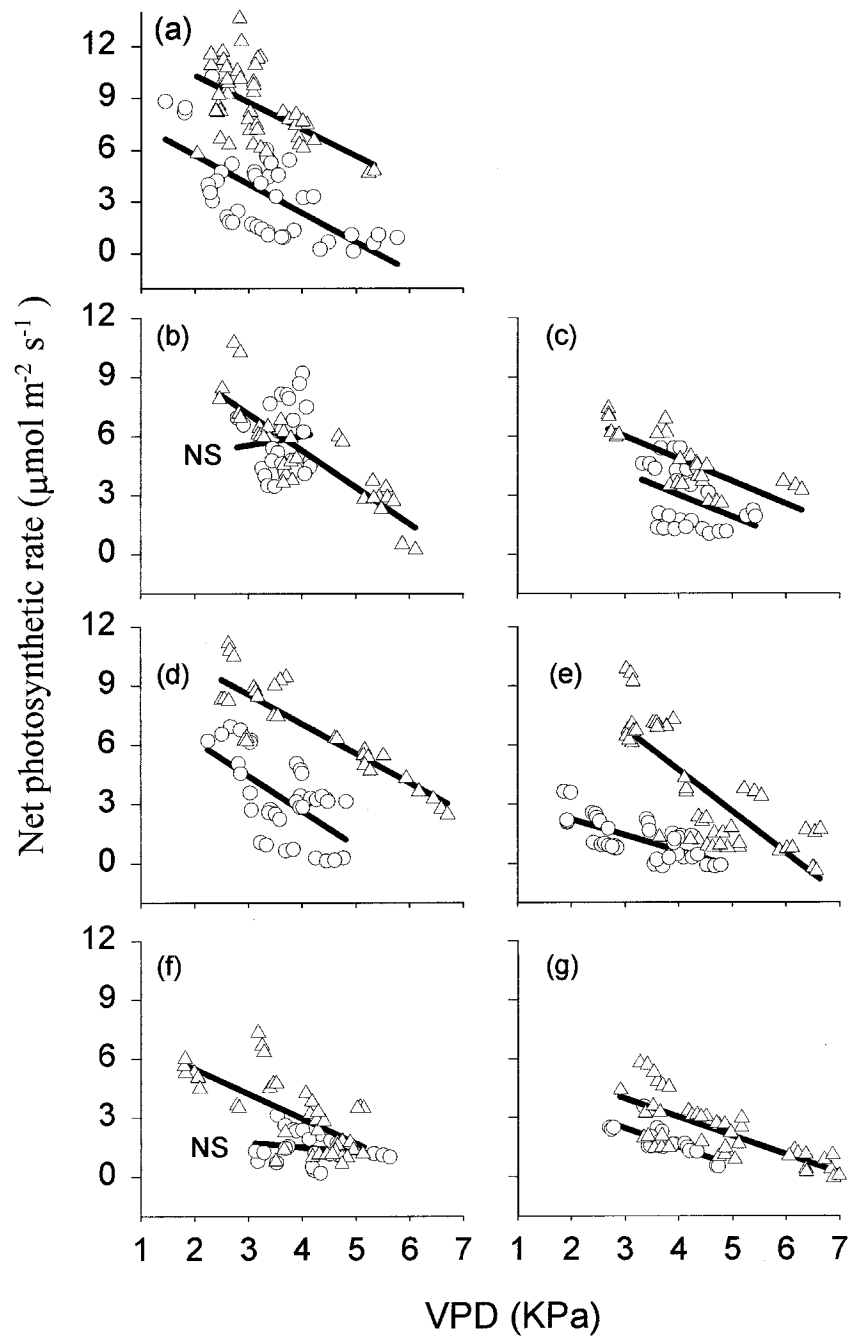


Figure 3. The dependence of net photosynthetic rate ( $A$ ) on VPD (leaf-to-air vapour pressure difference) during the drought (circles) and wet (triangles) periods for the saplings of (a) *Cotylelobium burckii*, (b) *Dipterocarpus borneensis*, (c) *Fordia splendidissima*, (d) *Hopea pentanervia*, (e) *Tristaniopsis obovata*, (f) *Shorea multiflora* and (g) *Cleistanthus baramicus*. The correlation coefficients are given in Table 2. The linear regression lines are shown in order to compare the trends between the drought and wet periods, although non-linear regressions may better fit some data sets. NS denotes non-significance of the regression line.

Table 3. Root system types, range of rooting depth, and root/shoot biomass ratios for saplings (45–250 cm tall) growing on the edge of the path (open) and in the understorey for the dipterocarp and non-dipterocarp species. HV = *Hopea vacciniifolia*, SP = *Shorea pachyphylla*. Abbreviations for other species follow Table 1. N = 3–7 per species per growth condition. Only CB's mean root/shoot ratio for the saplings in the understorey was significantly greater than for those at the edge of the path ( $P < 0.05$ , Mann–Whitney U-test). + indicates that a larger value could be possible.

Species	Root type	Range of rooting depth (cm)	Root/shoot ratio (mean $\pm$ SD)	
			Open	Understorey
Dipterocarps				
CB	thin-tap	30–70	0.21 $\pm$ 0.03	0.36 $\pm$ 0.06
DB	thick-tap	100–200 <sup>+</sup>	0.39 $\pm$ 0.03	0.40 $\pm$ 0.07
HP	thin-tap	30–60	0.37 $\pm$ 0.06	0.47 $\pm$ 0.14
HV	thin-tap	80–200 <sup>+</sup>	0.34 $\pm$ 0.07	0.29 $\pm$ 0.17
SM	thin-tap	80–150	0.43 $\pm$ 0.16	0.34 $\pm$ 0.09
SP	thick-tap	45–60	nd	0.37 $\pm$ 0.07
Non-dipterocarps				
FS	thick-tap	200 <sup>+</sup>	2.01 $\pm$ 0.42	1.74 $\pm$ 0.57
TO	superficial	10–20	0.35 $\pm$ 0.09	0.23 $\pm$ 0.05
CL	thin-tap	45–75	0.41 $\pm$ 0.10	0.35 $\pm$ 0.02

nd = no data.

understorey than for those on the edge of the path (Table 3). Root/shoot biomass ratio was negatively correlated with plant height for *Cotylelobium*, *Hopea pentanervia* and *Shorea multiflora* (Figure 4). Rooting depth was positively correlated with plant height for *Hopea vacciniifolia* ( $r = 0.94$ ,  $P = 0.006$ ) and *Shorea multiflora* ( $r = 0.83$ ,  $P = 0.011$ ).

#### DISCUSSION

High  $\Psi_{PD}$  in dipterocarp saplings throughout the drought period (Figure 1) suggested there was still water available for the plants, even at the later stage of the prolonged drought. Tyree *et al.* (1998) observed that in the heath forest at Badas near the present study site, there were still substantial water reserves above a hardpan at 2-m depth after two nearly rainless months in 1997, although extractable water in the top 1.2 m of soil was almost exhausted after 35 d. Brünig's (1996) suggestion of soil water exhaustion of tropical heath forests after 33–50 rainless days probably gives an underestimation of the soil water storage (Tyree *et al.* 1998). The prolonged hazy conditions in the late half of the 1998 drought could possibly mitigate drought severity as the haze strongly reduced the intensity of irradiance and evapotranspirational loss. An intensity of irradiance of 2400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on a clear day was measured (K.-F. Cao, unpubl. data). This was twice the intensity of maximum irradiance recorded on the hazy days but without clouds during the drought period.

The deep root systems apparently allowed the saplings to access deep underground water. *Dipterocarpus* saplings of 2 m in height had thick tap roots of 2 m in depth. They maintained  $\Psi_{PD}$  close to zero, and relatively high  $g_s$  and  $A$  rates throughout the drought period (data not shown). However, although the

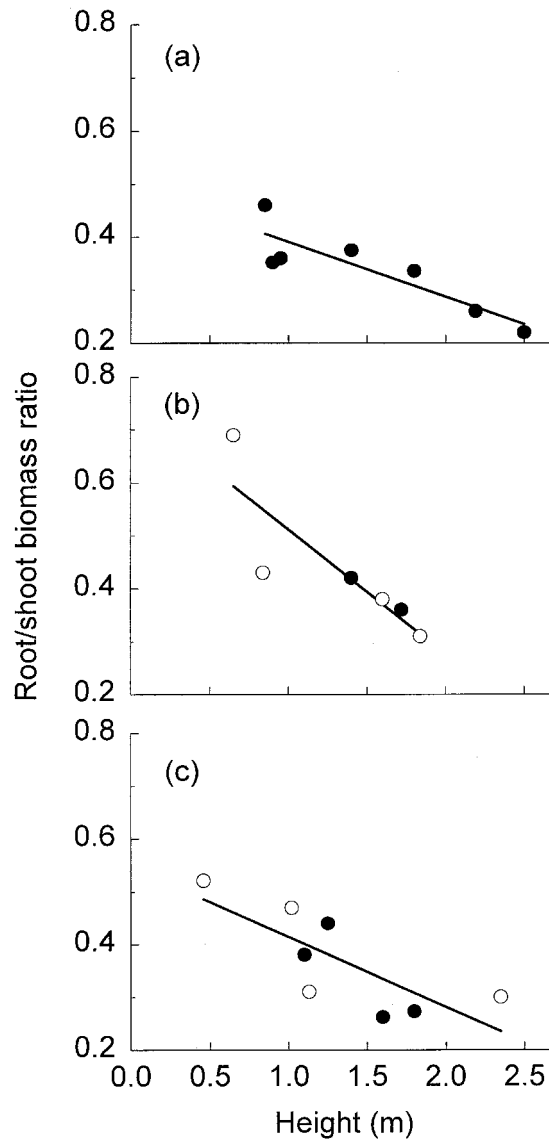


Figure 4. The dependence of root/shoot biomass ratio on sapling height for (a) *Cotylelobium burckii* ( $r = -0.87$ ,  $P = 0.01$ ), (b) *Hopea pentanervia* ( $r = -0.86$ ,  $P = 0.03$ ), and (c) *Shorea multiflora* ( $r = -0.79$ ,  $P = 0.02$ ). Open circles are for the saplings on the edge of the path, filled circles for those in the understorey.

roots of *Cotylelobium* and *Hopea pentanervia* saplings did not penetrate deeper than 70 cm (Table 3), they also maintained relatively high  $\Psi_{PD}$  (Figure 1). Dawson (1993) suggested the shallower-rooted plants' usage of the deep soil water which was brought to the drier upper soil at night by deep roots of other plants. This process of vertical translocation of soil water, known as hydraulic lift, is probably an explanation of the maintenance of good water status of the shallower-rooted dipterocarps (*cf.* Becker *et al.* 1999).

The plants possessing superficial or shallow root systems were susceptible to the prolonged drought. *Tristaniopsis* saplings, which were characterized by a typical superficial root system (Table 3), had  $\Psi_{PD}$  approaching their turgor loss points at the peak of the drought (Figure 1) and suffered a high mortality (K.-F. Cao, *pers. obs.*). The shrub *Melastoma* sp., which also had a superficial root system, suffered a similarly high mortality due to the drought. Seedlings of *Ternstroemia* sp., *Shorea multiflora*, *S. pachyphylla* and *Hopea pentanervia* shorter than 50 cm suffered a high mortality as well (K.-F. Cao, *pers. obs.*). These observations are consistent with Becker & Wong's (1993) finding that small trees or shallow rooted trees in the heath forest at Badas suffered the highest mortality during a prolonged drought in 1992.

However, *Tristaniopsis* saplings with superficial root systems recovered faster than saplings with deep root systems after the first rains following the drought. This could be because the first rains did not penetrate deeply, but they were retained in the upper soil that is associated with litter and humus. The saplings with superficial root systems associated with abundant fine roots apparently have an advantage in being able to absorb the water retained in the upper soil.

The root/shoot ratios in the study species except for *Fordia* (Table 3) were comparable to those in the understorey saplings in a nearby mixed dipterocarp forest and a nearby heath forest in Brunei (Becker *et al.* 1999) and, in a temperate forest in Japan (Cao & Ohkubo 1998). Decrease of root/shoot ratios with increase of sapling height in the three study species (Figure 4) is consistent with Cao & Ohkubo's (1998) finding for understorey saplings in central Japan. Relatively greater biomass allocation to root system in small saplings is thought to be beneficial for their establishment (T. Poulson, *pers. comm.*).

Strong stomatal response to water stress was a common feature in the study species. This was indicated by the fact that, during the drought period, the saplings of most of the study species strongly reduced their photosynthetic rates and stomata conductance rates or shut down their stomata after a short exposure to sun. Also, the  $A$  or  $g_s$  rates were closely responsive to the change of VPD for most of the study species during both the drought and wet periods (Figure 3, Table 2).

The strong inverse correlation of  $A$  and  $g_s$  with VPD in the wet period (Figure 3, Table 2) could suggest that some degree of water stress also develops in the insolated saplings on clear days (see  $\Psi_{MD}$  on 11 October for non-dipterocarps, Table 1). It is suggested that plants that are experiencing intermediate water stress are responsive to VPD (Nanomi *et al.* 1990, Schulze 1993). The water stress can be induced by high evapotranspiration, resulting from high leaf temperature (Figure 2) and intense irradiance (Table 2). The water stress during the wet period was certainly less severe than that during the drought period as indicated by high  $\Psi_{PD}$  values in the wet period (Table 1), and by the fact that for the same VPD, the saplings in the wet period had much greater  $A$  and  $g_s$  rates than in the drought period (Figure 3).

The maximum values of VPD and leaf temperature recorded in this study during the wet period were quite high (Figure 2). High leaf temperature and lower air humidity could cause some plants to partly close their stomata as well (Tenhunen *et al.* 1987), and high light intensity may cause decrease of the quantum efficiency of photochemistry (Baker 1993). Productivity of tropical trees in the canopy and in canopy openings is probably limited to some extent by negative effects of high temperature, intense irradiance and lower air humidity under bright sun (Ramos & Grace 1990, Tenhunen *et al.* 1987). Field measurements showed that on a clear day in a wet period, the saplings notably increased their stomatal conductance and photosynthetic rates following a brief midday shower. This could probably be because the shower caused a decrease in leaf temperature and increases in air humidity and leaf water potential.

Osmotic adjustment in response to drought conditions has been found to be a common phenomenon in tropical trees (Wright *et al.* 1992 and references therein). In contrast, most of the species in the present study did not show significant osmotic adjustments in response to the drought conditions (Table 1). One reason for this could be that the saplings of the present study in the white-sand heath forest could have regularly experienced some degree of water stresses even in the normal climatic conditions (Brünig 1996) so that their leaf osmotic potentials have already acclimated to certain degree of water stress.

A number of other plant features are also involved in resistance to water loss (Brünig 1996, Jones 1992). The shoots and probably also leaves of all the dipterocarp species studied contained oily resin (K.-F. Cao, *pers. obs.*, cf. Burkill 1966), the oil can be separated from the resin (Burkill 1966). In hot and dry conditions, this oil may evaporate, resulting in increase of the density of the boundary layer at the leaf surface and thus increase of resistance to diffusion of water vapour (Blackmore & Tootill 1988). Waxy leaves in dipterocarps and *Fordia splendissima*, and hairy leaves in *Cotylelobium burckii* and *Dipterocarpus borneensis*, change of leaf orientation to parallel solar rays (leaf tip pointing to the ground) under bright sun as in all the leaves of *Hopea pentanervia* and in young leaves of *Cotylelobium burckii* (K.-F. Cao, *pers. obs.*), and a low stomatal density in *Shorea multiflora* (K.-F. Cao, unpubl. data), certainly should help to reduce plant water loss (Brünig 1974, Jones 1992).

In summary, the saplings of all dipterocarp species examined had tap root systems but differed in rooting depth. They maintained good water status throughout the drought period. *Dipterocarpus borneensis* possessing a thick and deep tap root, suffered the least from the drought. The two non-dipterocarp species, *Tristaniopsis obovata* and *Melastoma* sp. both of which had superficial root systems suffered severe water stress during the drought. Survivors of *T. obovata* recovered fast after the first rains following the drought. Another non-dipterocarp species, *Cleistanthus obovata*, also suffered severe water stress during the drought in spite of its tap root system. Strong stomatal control, and deep root systems seem to be favourable plant adaptations in tropical heath forests where water deficits probably occur regularly.

## ACKNOWLEDGEMENTS

Sincere thanks are due to W. E. Booth and P. Becker for their helpful advice, technical assistance and comments on an earlier manuscript. The author is grateful to I. M. Said, J. A. Ahmad and A. Kalat for identification of the study species, and to M. A. Suleman for assistance in excavation of roots. Acknowledgements are extended to the Department of Forestry, Brunei Darussalam, for permission to conduct the research in the Research Forest at Bukit Sawat, and to the Sungai Liang Agricultural Meteorological Station for providing the unpublished rainfall data. Financial support was provided by the Universiti Brunei Darussalam.

## LITERATURE CITED

- ANONYMOUS. 1990. *The climate supplement of Brunei Darussalam*. ASEAN Secretariat, Jakarta. 142 pp.
- ASHTON, P. S. 1988. Dipterocarp reproductive biology. Pp. 219–240 in Lieth, H. & Werger, M. J. A. (eds). *Tropical forest ecosystems B. biogeographical and ecological studies. Ecosystems of the world 14b*. Elsevier, Amsterdam.
- BAKER, N. R. 1993. Light-use efficiency and photoinhibition of photosynthesis in plants under environmental stress. Pp. 221–235 in Smith, J. A. C. & Griffiths, H. (eds) *Water deficits, plant responses from cell to community*. BIOS Scientific Publishers, Oxford.
- BECKER, P. & CASTILLO, A. 1990. Root architecture of shrubs and saplings in the understorey of tropical moist forest in lowland Panama. *Biotropica* 22:242–249.
- BECKER, P. & WONG, M. 1993. Drought induced mortality in tropical heath forest. *Journal of Tropical Forest Science* 5:416–419.
- BECKER, P., SHARBINI, N. & YAHYA, R. 1999. Root architecture and root:shoot allocation of shrubs and saplings in two lowland tropical forests: implications for life-form composition. *Biotropica* 31:93–101.
- BLACKMORE, S. & TOOTILL, E. (eds). 1988. *The Penguin dictionary of botany*. Penguin Group, London. 391 pp.
- BRÜNIG, E. F. 1974. *Ecological studies in the Kerangas forests of Sarawak and Brunei*. Borneo Literature Bureau, Kuching, Malaysia. 237 pp.
- BRÜNIG, E. F. 1996. *Conservation and management of tropical rainforests, an integrated approach to sustainability*. CAB International, Wallingford, UK. 339 pp.
- BURKILL, I. H. 1966. *A dictionary of the economic products of the Malay Peninsula. Vol. I–II*. Ministry of Agriculture and Co-operatives, Kuala Lumpur. 2444 pp.
- CAO, K.-F. & OHKUBO, T. 1998. Allometry, root/shoot ratio and root architecture in understorey saplings of deciduous dicotyledonous trees in central Japan. *Ecological Research* 13:217–227.
- DAVIES, S. J. & BECKER, P. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* 8:542–569.
- DAWSON, T. E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95:565–574.
- DENNIS, R. 1999. A review of fire projects in Indonesia (1982–1998). Center for International Forestry Research, Bogor. 105 pp.
- DIAZ, H. F. & MARKGRAF, V. (eds). 1992. *El Niño: historical and paleoclimatic aspects of the Southern Oscillation*. Cambridge University Press, Cambridge.
- HINCKLEY, T. M., DUHME, F., HINCKLEY, A. R. & RICHTER, H. 1983. Drought relations of shrub species: assessment of mechanisms of drought resistance. *Oecologia* 59: 344–350.
- JONES, H. G. 1992. *Plants and microclimate, a quantitative approach to environmental plant physiology* (2nd edn.). Cambridge University Press, Cambridge. 428 pp.
- JONES, H. G. & SUTHERLAND, R. A. 1991. Stomatal control of xylem embolism. *Plant Cell and Environment* 14:607–612.
- KOIDE, R. T. ROBICHAUX, R. H., MORSE, S. R. & SMITH, C. M. 1989. Plant water status, hydraulic resistance and capacitance. Pp. 161–183 in Percy, R. W., Ehleringer, J. R., Mooney, H. A. & Rundel, P. W. (eds). *Plant physiological ecology, field methods and instrumentation*. Chapman and Hall, London.
- LAUMONIER, Y. & LEGG, C. 1998. Le suivi des feux en Indonésie. *Bois et Forêts de Tropiques* 258:5–18. (with English summary)

- NANOMI, H., SCHULZE, E.-D. & ZIEGLER, H. 1990. Mechanisms of stomatal movement in response to air humidity, irradiance and xylem water potential. *Planta* 183:57–64.
- RAMOS, J. & GRACE, J. 1990. The effects of shade on the gas exchange of seedlings of four tropical trees from Mexico. *Functional Ecology* 4:667–677.
- SCHULZE, E.-D. 1993. Soil water deficits and atmospheric humidity as environmental signals. Pp. 129–145 in Smith, J. A. C. & Griffiths, H. (eds). *Water deficits, plant responses from cell to community*. BIOS Scientific Publishers, Oxford.
- SMITH, J. A. C. & GRIFFITHS, H. (eds). 1993. *Water deficits, plant responses from cell to community*. BIOS Scientific Publishers, Oxford. 345 pp.
- TENHUNEN, J. D., PEARCY, R. W. & LANGE, O. L. 1987. Diurnal variations in leaf conductance and gas exchange in natural environments. Pp. 323–351 in Zeiger, E., Farquhar, G. D. & Cowan, I. R. (eds). *Stomatal function*. Stanford University Press, Stanford.
- TURNER, N. C. & JONES, M. M. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. Pp. 87–103 in Turner, N. C. & Kramer, P. J. (eds). *Adaptation of plants to water and high temperature stress*. Wiley, New York.
- TYREE, M. T. & SPERRY, J. S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* 88:574–580.
- TYREE, M. T., PATIÑO, S. & BECKER, P. 1998. Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. *Tree Physiology* 18:583–588.
- WALSH, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:385–407.
- WHITMORE, T. C. 1984. *Tropical rain forests of the Far East*. Clarendon Press, Oxford. 352 pp.
- WRIGHT, S. J., MACHADO, J. L., MULKEY, S. S. & SMITH, A. P. 1992. Drought acclimation among tropical forest shrubs (*Psychotria*, Rubiaceae). *Oecologia* 89:457–463.