Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest

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Abstract

The water relations of two tree species in the Euphorbiaceae were compared to test in part a hypothesis that the forest understorey plays an integral role in drought response. At Danum, Sabah, the relatively common species *Dimorphocalyx muricatus* is associated with ridges whilst another species, *Mallotus wrayi*, occurs widely both on ridges and lower slopes. Sets of subplots within two 4 -ha permanent plots in this lowland dipterocarp rain forest, were positioned on ridges and lower slopes. Soil water potentials were recorded in 1995–1997, and leaf water potentials were measured on six occasions. Soil water potentials on the ridges (−0.047 MPa) were significantly lower than on the lower slopes (−0.012 MPa), but during the driest period in May 1997 they fell to similarly low levels on both sites (−0.53 MPa). A weighted 40-day accumulated rainfall index was developed to model the soil water potentials. At dry times, *D. muricatus* (ridge) had significantly higher pre-dawn (−0.21 *v.* −0.57 MPa) and mid-day (−0.59 *v.* −1.77 MPa) leaf water potentials than *M. wrayi* (mean of ridge and lower slope). Leaf osmotic potentials of *M. wrayi* on the ridges were lower (−1.63 MPa) than on lower slopes (−1.09 MPa), with those for *D. muricatus* being intermediate (−1.29 MPa): both species adjusted osmotically between wet and dry times. *D. muricatus* trees were more deeply rooted than *M. wrayi* trees (97 *v.* 70 cm). *M. wrayi* trees had greater lateral root cross-sectional areas than *D. muricatus* trees although a greater proportion of this sectional area for *D. muricatus* was further down the soil profile. *D. muricatus* appeared to maintain relatively high water potentials during dry periods because of its access to deeper water supplies and thus it largely avoided drought effects, but *M. wrayi* seemed to be more affected yet tolerant of drought and was more plastic in its response. The interaction between water availability and topography determines these species' distributions and provides insights into how rain forests can withstand occasional strong droughts.

Introduction

Until relatively recently tropical forests regions were widely viewed as having a constant climate which was either annually seasonal (C. America and most of Africa) or largely aseasonal (much of S. America and SE Asia) (Walsh 1996a). It is now becoming clear that the regional climate varies significantly on a time-scale of several years to several decades (Brünig 1969; Walsh 1996b). These variations are stochastic in nature, occurring unpredictably, and are often characterized by the occasional extreme event (Newbery et al. (1992, 1999)). A substantial part of the climate variation has been linked to the supra-annual El Niño Southern Oscillation (ENSO) and in parts of SE Asia this results in temporarily strong droughts (Walsh 1996b; Walsh and Newbery 1999).

The local distributions of different tree species in SE Asian tropical rain forest are often strongly associated with topography (Austin and Greig-Smith

1968; Newbery 1991; Ashton and Hall 1992; Newbery et al. 1996). Change in topography is primarily associated with change in soil water availability, this being lower on ridges than on lower slopes (Whitmore 1984). A strong dry period may cause soil water potentials on ridges to become low enough to limit tree growth and cause deaths. If droughts are frequent enough over centuries to millennia then selection of drought-tolerant species on the ridges would be expected, and forest composition on ridges should be different from that on the generally wetter lower slopes (Newbery et al. 1996).

In NE Borneo, in Sabah (Malaysia), intensity and frequency of dry periods decrease inland (Walsh 1996a). In the area around the Sesama river, *c*. 65 km from the East coast, forest composition, structure and dynamics suggest a vegetation whose species are adapted to a regime of occasional moderate to strong droughts every decade or so, with perhaps an extreme event every century or two (Newbery et al. (1992, 1999); Walsh 1996b; Walsh and Newbery 1999). Newbery et al. (1999) have suggested that high abundance of Euphorbiaceae in the mature primary forest understorey is a characteristic feature of this disturbance regime and that many species of the family are adapted to temporary drought. Airy Shaw (1975) gives many descriptive notes to the taxonomy of the Euphorbiaceae to support this idea.

Understorey species have the greatest ridge-lower slope floristic differentiation at Danum (Newbery et al. 1996). If the hypothesis, that the these species are generally more shallowly rooted than the overstorey ones applies here, then the understorey should experience water limitation more frequently and for longer periods than the overstorey, and hence be more drought-tolerant. Furthermore, the understorey is thought to play a very important role in protecting the saplings of all (under- and overstorey) species during periods of drought disturbance (Newbery et al. 1999). It has been inadequately appreciated to date, however, that *c*. 90% of small stems (10 – < 50 cm gbh [girth at breast height], or 3.2–15.9 cm dbh [diameter at bh]), i.e. the structural understorey in lowland dipterocarp forest, consists of understorey species *per se*, and the rest of these small stems, some of which become overstorey canopy trees (> 50 cm gbh) form only *c*. 10%.

Detailed ordination analyses of the species' compositional patterns in two replicate 4-ha permanent plots at Danum, in which all trees ≥ 10 cm gbh were first enumerated in 1986, showed a strong floristic gradient from lower slope to ridge and highlighted a key group of understorey tree species on the ridges. In the absence of any significant correlations with soil chemistry, the suggestion was that this drought-tolerant understorey guild was an indicator of climatic selection of the form proposed above (Newbery et al. 1996). The three ridge-occurring species abundant enough to provide convincing trends in both plots were *Cleistanthus glaber* Airy Shaw (Euphorbiaceae), *Dimorphocalyx muricatus* (Hk. f.) Airy Shaw (Euphorbiaceae) and *Lophopetalum beccarianum* Pierre (Celastraceae). Several abundant species grew widely and independently of topographic position, notably *Ardisia colorata* Roxb. (Myristicaceae), *Fordia splendidissima* (Miq.) Buijsen (Leguminosae) and *Mallotus wrayi* King ex Hk. f. (Euphorbiaceae). There were no abundant understorey species growing only on lower slopes.

The aim of the work here reported was to test part of the hypothesis of Newbery et al. (1992, 1996), by asking the questions:

1. Are areas where ridge species occur drier than lower slopes, and do any differences in water availability become greater at drier times?
2. Are ridge species better adapted than ubiquitous species in tolerating and/or avoiding the effects of drought?

Materials and methods

Study site

Fieldwork was conducted in two 4-ha permanent plots (Figure 1) *c*. 500 m west of the Segama River at the eastern perimeter of the Danum Valley Conservation Area, Sabah (4°58′ N, 117°46′ E; Marsh and Greer (1992)), over the three periods: 4 December 1994 to 26 October 1995, 15 January to 12 December 1996, and 9 April to 30 June 1997. A full description of the site, plots and enumerations are given in Newbery et al. (1992, 1996, 1999). The forest is of the *Parashorea melanonaan* Blanco lowland dipterocarp type (Fox (1972, 1978)), and the soils are an orthic acrisol and dystric cambisol mixture (Bang association: Leong (1974) and Wright (1975)).

Mean annual rainfall recorded at the Danum Valley Field Centre (DVMC) from 1986 to 1998 was 2667 mm (Walsh and Newbery 1999). It varied considerably from year to year, ranging from 2378 mm
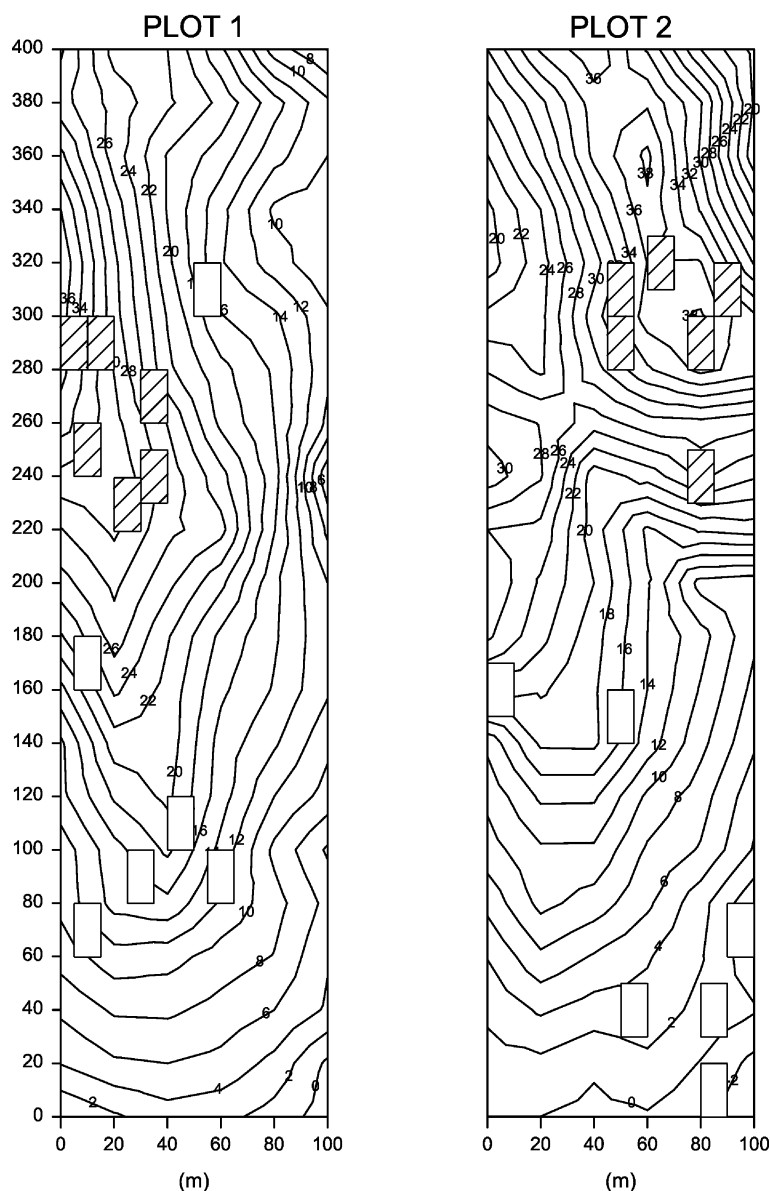
Figure 1. Contour maps of the two 4-ha permanent plots of Newbery et al. (1992) at Danum, Sabah, and locations of the ridge (hatched) and lower slope (open) subplots within them.

in 1987 to 3294 mm in 1995. Whilst 1987 was the driest year in terms of annual rainfall, 1992 had the most months with rainfall less than 100 mm. In this period the mean monthly rainfall was 231 mm. The driest month, both in terms of average rainfall and the larger number of months with less than 100 mm rainfall was April. The second driest month was August. The wetter periods corresponded to the two monsoons (the northeast one in November to March, and the southeast one in June to July) which affect the area

(Walsh 1996b). With a strong annual variation in monthly rainfall and the limited data for Danum it is not yet possible to predict which months will be drier or wetter than average. For example, the normally relatively dry April was one of the wettest months in 1996.

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Table 1. Criteria for the selection of the ridge and lower slope 10-m × 20-m subplots within the main 4-ha plots at Danum, Sabah, based on the presence or absence of six understorey species. For a subplot to be considered it had to contain the shown number of trees ⩾ 10 cm gbh at the time of the 1986 enumeration. A '–' indicates that no criterion was applied.

Species	Site Ridge	Lower slope
Ardisia colorata	–	> 1
Cleistanthus glaber	> 1	0
Dimorphocalyx muricatus	> 7	0
Fordia splendidissima	–	> 1
Lophopetalum beccarianum	> 1 [a]	0
Mallotus wrayi	–	> 7

[a] 0 trees accepted as valid for one subplot of plot 1

Species and subplot selection

A subplot size of 10 m × 20 m was chosen to give sufficient numbers of individuals (⩾ 10 cm gbh) per subplot of each of the aforementioned six species, and to achieve adequate subplot replication within each plot. Taking the enumeration data of 1986, and 5-m steps in both plot directions, a FORTRAN_77 program was used to find the numbers of trees per species in each of the 1368 possible subplots. Subplots containing the six species at or above the threshold densities given in Table 1 were selected. Presence or absence of clustered species was used to determine 'ridge' versus 'lower slope' sites rather than selecting from the contour maps available for the plots. From this reduced list of subplots, six ridge and six lower slope subplots were selected at random in each plot, making 24 subplots in total (Figure 1). Overlapping subplots were rejected, as were most contiguous subplots, where alternatives existed. Because of the relatively small areas in which clustered species occurred, it was nevertheless necessary to accept three pairs of contiguous ridge subplots (Figure 1). Using these criteria only five possible ridge subplots were offered for plot 1. For the final selection of subplots the criteria were relaxed slightly so that subplots with just one *Lophopetalum beccarianum* could be accepted. Interpolating approximately from the contours in Figure 1, the maximum elevation difference between subplots was *c.* 37 m. Mean (and range) elevations were 30.7 (17–36) m and 33.0 (23–36) m on the ridges of plot 1 and 2 respectively, and 16.5 (12–24) m and 6.5 (−2–21) m for the corresponding lower slopes. Differences in elevation were thus 14.2 and 26.5 m for plots 1 and 2 respectively.

This approach reconfirmed the association between species and topography: the selected subplots fitted well to the ridge and lower slope parts of plots 1 and 2 (Figure 1). An alternative approach would have been to define ridge and lower slope areas based on the elevation and slope data first, and then to have sought subplots within them. The results would have certainly converged to a similar selection of subplots but the advantage of our approach was that species' sample sizes per subplot were optimized and slightly different elevational ranges were allowed for the two plots.

Subplot enumeration

Each selected subplot was divided into eight 5-m × 5-m squares with strings. Within each square all individuals of the target species ⩾1 cm basal diameter were tagged and measured (dial callipers, accuracy of ± 1 mm) and individuals < 1 cm basal diameter were tallied. This minimum 1-cm size limit was set much lower than that in the 1986 enumeration of the whole plots (viz. 3.1 cm dbh) so that saplings could be sampled. Individuals were labelled with aluminium number-tags secured with nylon fishing line. It was important that species were identified accurately, and a few doubtful individuals were excluded. (The identifications from the 1986 enumeration were available so that trees ⩾ 3.1 cm dbh could be rechecked.)

Soil water status

Soil water potential was measured with soil psychrometers (P55T, Wescor Inc, USA; Briscoe (1984) and Rundell and Jarrell (1989)). Each psychrometer was calibrated in four different KCl solutions (0.05, 0.3, 0.5 and 0.8 molal) at 25 °C. Readings were taken using a dewpoint microvoltmeter (P33T, Wescor Inc, USA) in both dewpoint and psychrometer modes (Anon. 1979). Water potentials for the KCl solutions were obtained from Campbell and Gardner (1971). Linear regression, with the line constrained through zero, was used to find the slope of the line for each probe, in each mode, in order to calibrate meter readings to water potentials ($r^2 = 0.97$, df = 3 P < 0.001; for all probes).

On 24 and 25 March 1995 one soil psychrometer was installed at 20 cm depth, at a random location in each subplot (> 1 m in from the edge). This depth was chosen because the majority of root endings are at, or

Table 2. Dates of measurement of leaf water potentials (LWP) and construction of pressure-volume curves (PVC), together with the soil water potentials (SWP) at those times. Each collection number is a sample from both 4 -ha plots at Danum, Sabah. SWPs are the means of the previous and subsequent week's measurements. For each type of leaf water measurement, a '+' indicates that a sample was taken and '−' that no sample was taken. Least significant differences are given below the table for comparing SWP values.

| No. | Date | SWP (MPa) | | LWP at: | | PVC |
		Ridge	Lower slope	Pre-dawn	Mid-day	
1	2–4 May 1995	−0.08	−0.02	+	−	−
2	7–9 June 1995	−0.03	−0.01	+	−	+
3	19–21 September 1995	−0.03	−0.01	+	−	+
4	16–18 April 1996	−0.19	−0.07	+	−	+
5	23–26 July 1996	−0.08	−0.01	+	+	−
6	13–14 May 1997	−0.51	−0.55	+	+	−

LSDs (at $P = 0.05$) for comparison of sites = 0.035, and for dates within site = 0.027 (based on SEs from the restricted ANOVA with 26 dates – see text)

above, it. In an earlier study of root distribution and dynamics at Danum, using three observational plots just to the north of the main 4 -ha ones in the present study, Green (1992) showed that 90% of tree roots > 2 mm diameter and 89% of tree roots > 2 mm were in the top 15 cm of the soil profile. For each subplot, soil temperature and soil water potential were recorded at weekly intervals, in dewpoint mode, until 6 June 1997.

Plant water status

Trees were sampled for their water status on six occasions (Table 2). Pre-dawn water potential was measured on each occasion, mid-day water potential on two occasions and pressure volume curves were constructed on three occasions.

Due to logistical constraints of sampling, the need for sufficient individuals per subplot, and the requirements for leaves with long enough petioles yet these leaves not being too large for the pressure apparatus, plant water status was measured on just the two most important of the six species: *D. muricatus* (showing the strongest ridge association) and *M. wrayi* (the commonest, ubiquitous species in the plots at Danum).

For each set of measurements of plant water status (Table 2), 12 trees per plot were selected (i.e. 24 trees in total), four each of *D. muricatus* and of *M. wrayi* from ridge subplots and four of *M. wrayi* from lower slope subplots. The selection was at random from tagged trees in the 10–24.9 -mm dbh size class within each plot. Any individuals sampled in previous predawn measurements were excluded (Table 2) so that trees selected over time were independent.

Owing to the difficulty of locating trees in the predawn darkness and the limited sampling time, each plot was sampled on successive days. The day before, a healthy well-lit branch (at 2–4 m height) was selected on each tree that was to be sampled. Pre-dawn sampling started at 04:00. Two leaves were cut from each marked branch and immediately sealed in a ziplock bag in which the atmosphere was kept humid by moist tissue paper. The bag was then placed in a chilled, insulated bucket until the time of measurement; the method following Parker and Pallardy (1985). Pre-dawn water potential was later measured for each leaf using a Scholander pressure chamber (model SKPM1400, Skye Instruments, UK) at the DVMC (see Ritchie and Hinckley (1975) and Turner (1981)). Before measurement each leaf was wrapped in polythene film to prevent water loss. Mid-day water potentials were taken from 12:00 onwards, in the same manner as the pre-dawn ones, and from the same individual, on the same day. The data used in the analysis were the means of the water potentials for the two leaves cut from each tree.

Pressure-volume curves (see Milburn (1979) and Kramer (1983)) were constructed for leaves sampled on the previous day for pre-dawn measurements. The leaves were rehydrated for *c.* 24 h in deionized water. Only six leaves could be processed in one day and they were selected as two each of *D. muricatus* and *M. wrayi* from the ridge subplots and two of *M. wrayi* from the lower slope subplots. Selection was not completely at random, rather undamaged leaves of a suitable size were selected, but two leaves from the same tree were never used. Each leaf was weighed on a balance (model TS120S, Ohaus Corporation, USA) to an accuracy of ± 1 mg, wrapped in polythene film

and the water potential determined with the pressure chamber (as described above). The leaf was then reweighed. Between each of the readings leaves were allowed to dry. Eight measurements were taken per leaf. The leaves were finally dried for 24 h at 80 °C and again reweighed. In this way leaf moisture content at each point of measurement could be calculated.

Rooting depth

Root systems of *M. wrayi* and *D. muricatus* were excavated on 20–24 March 1996, and measurements of the excavated systems made within the following week. As far as possible all roots > 2 mm in diameter were recovered. To allow comparison, representative ridge and lower slope sites were selected. As no destructive sampling was desirable in the plots, these sites were outside of, but adjacent to, them. At the ridge site five trees each of *M. wrayi* and of *D. muricatus* were excavated, while at the lower slope site five of *M. wrayi* were excavated. All trees were of 25–45 mm dbh. Once the height and dbh of each tree had been recorded, the tree was felled by cutting the stem at *c*. 30 cm above ground level. Before excavation proceeded the position of the ground level and the direction of magnetic north, were marked on the trunk. The tree was then dug up by hand, aided by a small trowel; secateurs (hand clippers) were used to cut roots from neighbouring trees. Starting at ground level, for each lateral root, the diameter (where it joined the tap root), soil depth, and total length were measured. The lateral root was cut off and discarded. This procedure was the repeated until all lateral roots had been measured. The depth of the tap root (now without its laterals) was finally recorded.

Statistical analysis

Soil water potential data were analysed using a modified repeated measures analysis of variance (RM ANOVA) procedure. Unfortunately, available statistical software carried out RM ANOVA on unbalanced data sets (i.e. those with 'missing values') in an inefficient manner because subplots containing any missing values were completely excluded from the analysis. To overcome this problem, the data were analysed as a 'split-plot' design using GENSTAT 5.32 (Payne 1993) which use an iterative procedure to estimate missing values. These missing values were inserted into the data set and, this now complete data set was used to calculate estimates of ϵ, the asymmetry of the repeated-measures covariance matrix (Winer et al. 1991), with SuperANOVA (rel. 1.1, Abacus Concepts, USA). GENSTAT calculated F- and P-values for date (i.e. time point of measurement) and date × site interaction which were then adjusted using the corrected degrees of freedom. A maximally balanced subset of the data was also analyzed by residual maximum likelihood analysis (REML) in GENSTAT to confirm the robustness of this first *ad hoc* procedure.

A weighted rainfall index, w_{40}, was found for each day for which there were soil water potential values, as the sum of each preceding day's rainfall divided by its day number (n), where n = 1 was the previous day and n = 40 the fortieth day before:

$$W_{40} = \sum_{n=1}^{40} \left(\frac{r_n}{n} \right)$$

Soil water potential was fitted to w_{40} as a power equation: $SWP = a + c \cdot b^{w40}$ using GENSTAT. Pre-dawn and mid-day plant water potentials were subjected to ANOVA with collection time as a fixed factor and the (main) plots as blocks (measurements were not repeated at subplot or individual levels). As there were no individuals of *D. muricatus* from lower slope sites, two separate analyses were carried out, one comparing *D. muricatus* with *M. wrayi* from ridge sites, and the other comparing *M. wrayi* from ridge and lower slope sites.

Water potential parameters were obtained from the pressure-volume curve (PVC) data using non-linear regression which defines the turgor loss point. The fitted equation had two components representing turgor and osmotic pressure. Schulte and Hinckley (1985) suggested several alternative models, but the modified exponential function was applied because it has the fewest parameters and it provided a good fit to Schulte & Hinckley's test data. The data for each site-and-species combination were grouped for each collection number, plotted, the obvious outliers removed, and the model fitted with SPSS 6.0 (Norusis 1993). The fitting procedure provided 95% confidence intervals for each of the estimated parameters. Non-overlap of intervals for sites gave a conservative test of significance at P = 0.05.

Analysis of the root depth data followed the same approach as for the plant water potentials. For each lateral the cross-sectional area at the tap-root join was calculated. ANOVAs were used to compare sites and
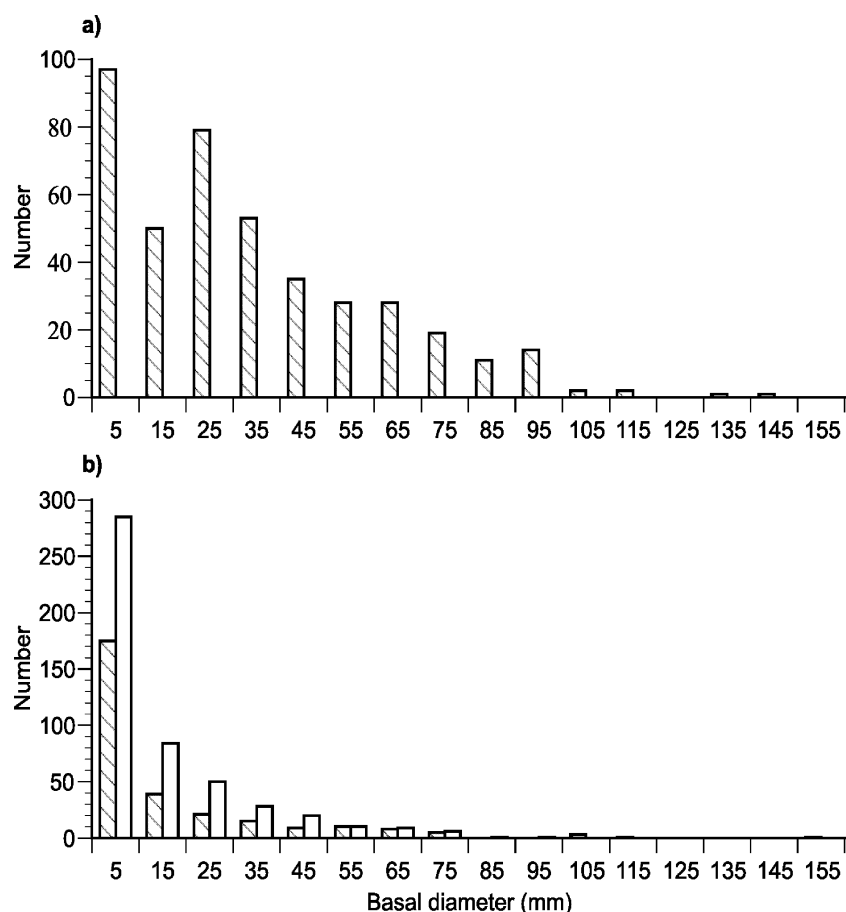
Figure 2. Basal diameter size class distribution of (a) *Dimorphocalyx muricatus* and (b) *Mallotus wrayi* in ridge (hatched bars) and lower slope (open bars) subplots, at Danum, Sabah.

species in terms of mean tap-root length, total lateral-root cross-sectional area and lateral-root depth (weighted by cross-sectional area). As a positive relationship between tree height and tap-root depth seemed likely, where significant differences in tree height between groups were found tree height was used as a covariate.

Results

Size class distribution

Out of 1870 individuals of the study species enumerated in the subplots there were 304 *A. colorata*, 95 *C. glaber*, 420 *D. muricatus*, 201 *F. splendidissima*, 69 *L. beccarianum* and 781 *M. wrayi* individuals. These numbers roughly reflected their abundance in the main 4 -ha plots (Newbery et al. 1996). There were

fewer individuals of *M. wrayi* in the ridge subplots than in the lower slope subplots (Figure 2). This was largely due to the contributions made by the smaller size-classes since there were similar numbers of larger trees. No individual of the ridge species was found in the lower slope plots.

Soil water potential

Trends in soil water potentials were similar to the rainfall data (Figure 3). The lowest water potentials were recorded in the driest year (1997) and high water potentials were recorded in the wettest year (1995). Lowest water potentials occurred at the same times as lowest running totals (April–May and August). However, differences between years, especially those between 1996 and 1997, were much greater than would be predicted from the running rainfall totals alone. Gaps in the record of soil psychrometer
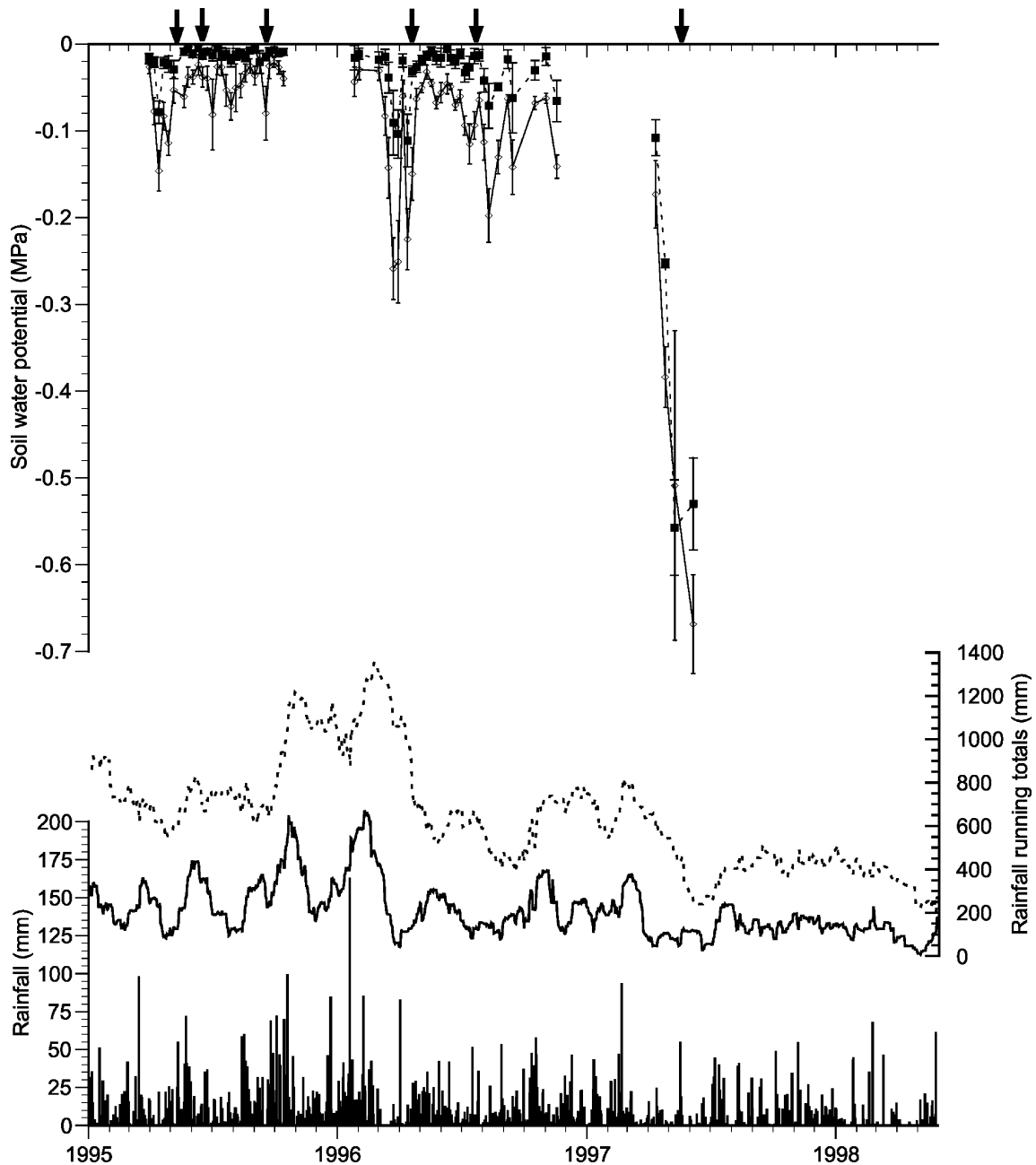
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Figure 3. Weekly soil water potentials (top) from ridge (solid line and open triangles) and lower slope (dashed line and closed squares) sites, daily rainfall (bottom) and 30- and 90-day running totals (middle) recorded at the Danum Valley Field Centre. The arrows indicate the dates of leaf sampling (see Table 2).

readings were at times of high rainfall when soil water potentials would have been at or near to zero.

Apart from one point in time, mean ridge site water potentials were consistently below those for lower slope sites. This difference between ridge and lower slope became greater during dry periods, except for

the driest period in 1997 when ridge and lower slope site water potentials were both similarly low. At this time only two lower slope, and four ridge, psychrometers remained undamaged. Given the within-site variability and small sample sizes, the data of 1997 were excluded from data analysis. These 1997 values
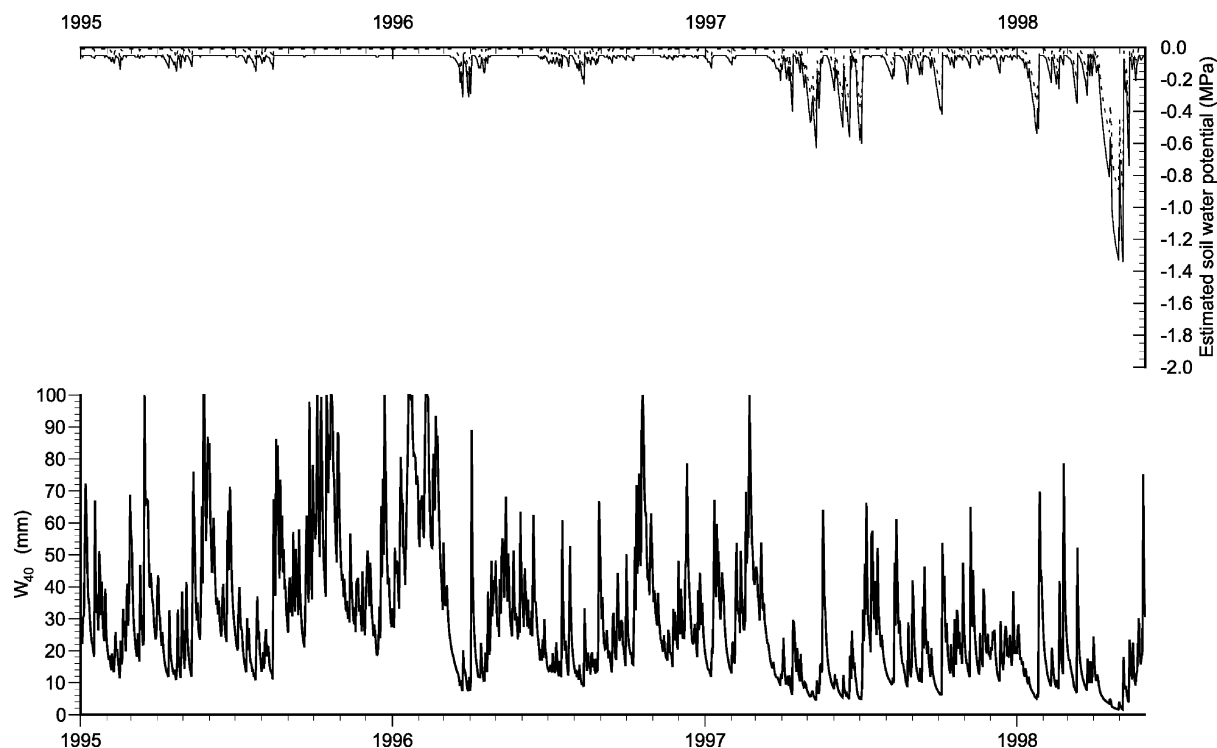
Figure 4. Weighted rainfall index (w_{40}) and estimated soil water potential for ridge (solid line) and lower slope subplots (dashed line), at Danum, Sabah.

are presented nevertheless in Figure 3 because they provide an estimate of the magnitude of the only severely dry period encountered. During the dry periods of 1996, ridge water potentials fell below the level at which water is considered easily available (−0.2 MPa) while lower slope water potentials remained above this level. The variability in the data suggest that wet microsites may exist in the ridge subplots as well as dry microsites in the lower slope subplots.

Variances in soil water potential were not significantly heterogeneous (Cochran's C, P > 0.05). There was a significant difference in water potential between sites (F = 16.2; df = 1,20; P < 0.001), date (F = 24.5; df = 59,853; P < 0.001) and site × date (F = 4.9; df = 59,853; P = 0.002). Results for the REML analysis confirmed the effect of site (Wald's statistic, W = 23.3, P < 0.001), date (W = 1035.6, P < 0.001) and site × date (W = 190.7, P < 0.001). The ANOVA of all of the data involved extensive missing-value estimation because of the large imbalance in the data set (n = 446 missing from 1440 or 31%). The longest-run, optimally-balanced subset was achievable for 26 dates using 4 and 5 (out of the 6) ridge and lower

subplots respectively for plot 1, and 5 and 4 (out of the 6) corresponding subplots for plot 2. This led to 468 values in total. The effect of site remained significant (F = 8.94; df = 1,15; P < 0.01; ridge mean water potential = −0.0465 MPa, lower slope = −0.0118 MPa), as did date and date × site interaction (F = 4.07 and 2.38 respectively; df = 13,206; P < 0.01).

Rainfall index and estimated soil water potentials

Since the soil analyses of Newbery et al. (1996) showed no textural differences, lines were fitted for ridge and lower slope subplots separately but constrained to a common value of b which (with SE) was 0.7554 ± 0.0086 (r^2 = 0.584, F = 358, df = 4,1013; P < 0.001). The equations were:

$$SWP = -0.0525 - 2.0280b^{w40} \quad \text{for ridge sites, and}$$

$$SWP = -0.0096 - 1.4070b^{w40} \quad \text{for lower slope sites.}$$

The lowest values of SWP were *c*. −0.80 MPa so predictions lower than this must be viewed with caution. (The range in w_{40} was 5 to 81 mm.) Figure 4 con-
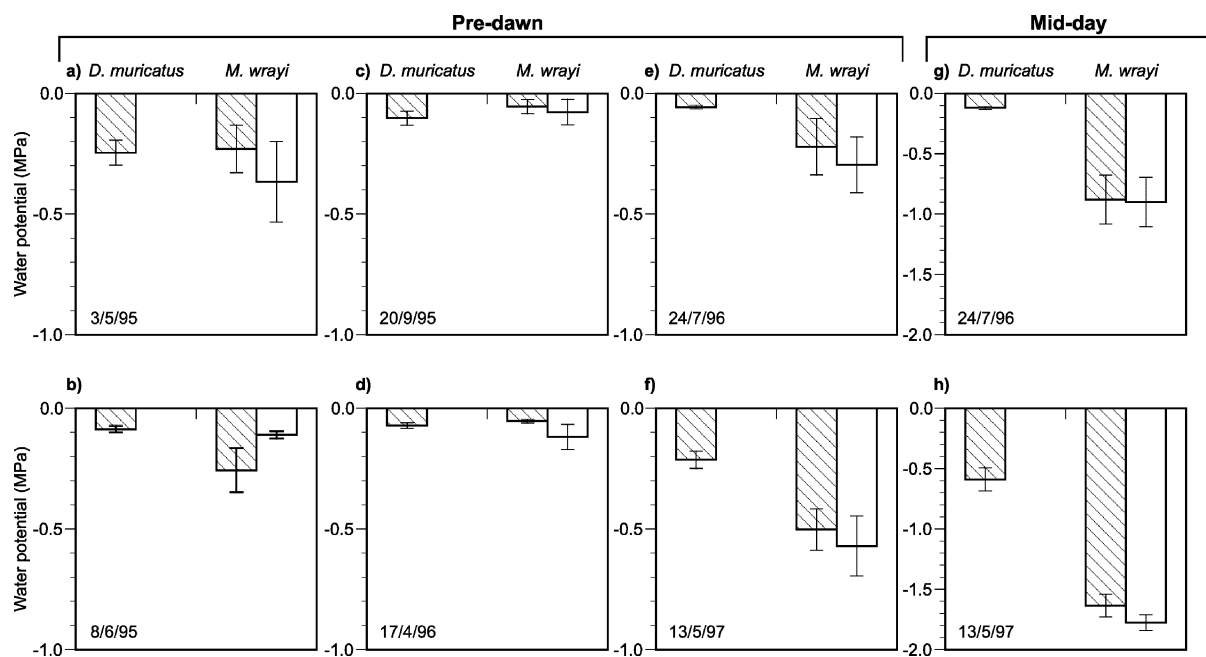
Figure 5. Pre-dawn (a-f) and mid-day (g,h) leaf water potentials of *Dimorphocalyx muricatus* and *Mallotus wrayi*, from ridge (hatched bars) and lower slope (open bars) sites, at six collection times (a-d, e+g, f+h), at Danum, Sabah. Bars are ± SE, *n* = 8. The estimated SWP values at these six times are given in Table 2.

firms that the 1997 soil water potentials (in Figure 3) very likely did reach their lowest values at that time, although no data were recorded to show them returning later to higher values. Predicted SWPs indicate that there were two short dry periods in early 1997: the observed SWPs presented in Figure 3 came from the second period. The model shows a much drier period in March-April 1998, and estimates that ridge values would have been close to −1.3 MPa and lower slope ones close to −0.9 MPa.

Pre-dawn and mid-day leaf water potentials

Measured leaf water potentials (Figure 5) were generally lower at times of low soil water potential than at times of high soil water potential. An exception was April 1996 where it appears that sampling may have taken place during a wet period between two dry periods. At the wettest time, June 1995, the pre-dawn leaf water potential of *D. muricatus* was −0.09 MPa, and that of *M. wrayi* −0.26 MPa (ridge) and −0.11 MPa (lower slope). At the driest time, May 1997, potentials fell to −0.21, −0.50 and −0.57 MPa respectively. The water potentials of *M. wrayi* fluctuated more than those of *D. muricatus.* Also, water potentials of *M. wrayi* were different among times where

soil water potentials were similar. It is notable however, that at the driest time, water potentials of *D. muricatus* remained well above the soil water potential at 20 cm, whilst those of *M. wrayi* were similar to the potentials found in the soil. There was a weak relationship between plant pre-dawn water potential and soil water potential at 20 cm (r^2 = 0.14, df = 186, P < 0.001).

Comparing *D. muricatus* and *M. wrayi* on the ridges, there was a significant difference in water potential among collection times (*F* = 6.60; df = 5,82; P = 0.001), and the water potentials of *D. muricatus* were significantly higher than those of *M. wrayi* (*F* = 6.57; df = 1,82; P = 0.012). There was a significant interaction between collection time and species (*F* = 2.54; df = 5,82; P = 0.034): the difference was larger at the drier time. Comparing *M. wrayi* between ridge and lower slope sites there was again a significant difference in water potential among collection times (*F* = 7.37; df = 5,81; P < 0.001), but not between the sites (*F* = 0.49; df = 1,81; P = 0.486), nor for the collection time × site interaction (*F* = 0.49; df = 5,81; P = 0.725).

For two leaf collections mid-day water potentials were also measured on the same day, and for the same trees as pre-dawn water potentials. In July 1996 plant

water potentials were much higher than in May 1997 (Figure 5). Each of the grouped water potentials fell below those found in the soil at 20 cm depth, both at the wet and dry collection times (wet, *D. muricatus* ridge, −0.12 MPa, *M. wrayi* ridge, −0.88 MPa and *M. wrayi* lower slope, −0.90 MPa; dry −0.59 MPa, −1.64 MPa and −1.77 MPa, respectively). Plant water potentials were significantly lower at the dry collection time compared to the wet one (*D. muricatus v. M. wrayi* ridge, $F = 24.6$; df = 1,27; P < 0.001; *M. wrayi* ridge *v. M. wrayi* lower slope, $F = 26.8$; df = 1,27; P < 0.001). As with the pre-dawn data, mid-day leaf water potentials of *D. muricatus* were significantly higher than those of *M. wrayi* on the ridge sites ($F = 53.5$; df = 1,27; P < 0.001) but there was no significant difference between *M. wrayi* individuals growing at different sites ($F = 0.26$; df = 1,27; P = 0.612).

Pressure-volume curves

A non-linear regression model, consisting of an osmotic and pressure function, was fitted to the pressure-volume curve data obtained at two of the six collection times, from *D. muricatus* and *M. wrayi* trees, on ridge and lower slope sites (Table 3). (At a third collection time the model failed to converge and the estimated values are not reported.) Soil water potentials were high for c. 2 wk before collection two and relatively low for a similar period before collection four so useful comparisons can be made between the estimates at these times. At collection two, leaf osmotic potentials at full hydration ($\Psi_{\pi,\mathrm{sat}}$) and at zero turgor (Ψ_0) were significantly (P < 0.05) lower for *M. wrayi* ridge than both *D. muricatus* and *M. wrayi* lower slope (Table 3). *D. muricatus* lost turgor at a high water content (R^*) so there was little difference between $\Psi_{\pi,\mathrm{sat}}$ and Ψ_0. At the drier collection time four, compared to collection time two, both $\Psi_{\pi,\mathrm{sat}}$ and Ψ_0 were significantly (P < 0.05) the lowest for *M. wrayi* ridge and highest for *M. wrayi* lower slope, with *D. muricatus* being intermediate (Table 3). Values of bulk modulus of cell elasticity at full hydration (ϵ'_{sat}) did not differ significantly between *D. muricatus* and *M. wrayi* (either site) at either collection time, though *D. muricatus* at the wet collection time had a relatively high value. All three species-site combinations had correspondingly lower R^*-values at the drier than at the wetter collection time. At both collection times Ψ_0-values were much lower than pre-dawn water potentials (Figure 5), and for the other times recorded. However, recorded mid-day
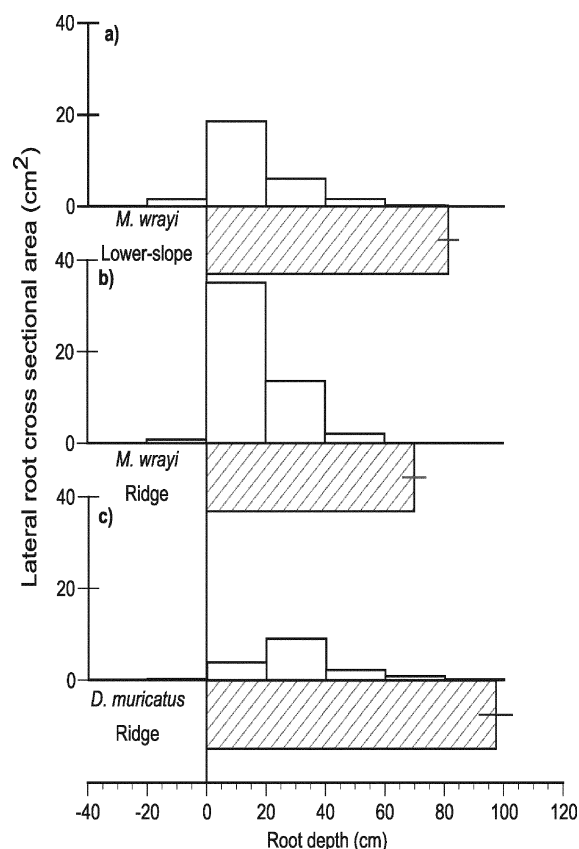

Figure 6. Root depths of *Dimorphocalyx muricatus* and *Mallotus wrayi* from ridge and lower slope sites, at Danum, Sabah. Vertical bars are total lateral root cross-sectional areas with depth. Horizontal bars (hatched) are mean tap-root depths (± SE, $n = 5$). Note that some roots originated above ground level.

values for *M. wrayi* for both sites (Figure 5) during dry periods approached the estimates of Ψ_0 suggesting that leaves of *M. wrayi* had low turgor pressures during the day.

Root depth

M. wrayi ridge trees were significantly shorter (3.4 m) than *M. wrayi* lower slope trees (4.2 m; $F = 5.32$; df = 1,8; P = 0.050) but *M. wrayi* ridge trees were not significantly different in height from *D. muricatus* trees (3.1 m; $F = 0.57$; df = 1,8; P = 0.473). Both species had tap-roots, and the tap-roots branched in some trees of each of the groups. Tap-root length and lateral root cross-sectional area are shown in Figure 6. *D. muricatus* was significantly more deeply rooted than *M. wrayi* on ridge sites ($F = 20.7$; df = 1,8; P = 0.002), but while it appears that *M. wrayi* ridge and *M. wrayi* lower slope means differed, the difference

Table 3. Non-linear regression estimates of osmotic potential at full hydration ($\Psi_{\pi,sat}$), relative water content at zero turgor (R^*), water potential at zero turgor (Ψ_0) and bulk modulus of elasticity (ϵ'_{sat}) for *Dimorphocalyx muricatus* and *Mallotus wrayi* leaves from ridge (R) and lower slope (LS) sites at Danum, Sabah. Collection number 2 was at a wet time of the year while number 4 was at a dry time of the year. (There were six collection times for plant water status – see text and Table 2.) Values with different small letters, within a collection time, differ significantly from one another at P ≤ 0.05, as judged by the lack of overlap in 95% confidence intervals.

Species	$\Psi_{\pi,sat}$ (MPa)	R^*	Ψ_0 (MPa)	ϵ'_{sat} (MPa)	r^2
Collection no. 2					
D. muricatus (R)	−1.12 a	0.95 a	−1.38 a	17.47 a	0.90
M. wrayi (R)	−1.56 b	0.81 b	−2.07 b	5.94 a	0.82
M. wrayi (LS)	−1.12 a	0.85 b	−1.56 a	7.28 a	0.91
Collection no. 4					
D. muricatus (R)	−1.45 b	0.83 b	−1.75 b	7.90 a	0.77
M. wrayi (R)	−1.69 c	0.73 c	−2.32 c	6.41 a	0.95
M. wrayi (LS)	−1.05 a	0.71 c	−1.48 a	3.64 a	0.60

was not significant when height was included as a covariate ($F = 1.59$; df = 1,7; P = 0.284).

Mean lateral-root cross-section area for each tree of *M. wrayi* on ridge sites (10.29 cm²) was significantly higher ($F = 8.62$; df = 1,8; P = 0.019) than that of *D. muricatus* (3.23 cm²) but there was no significant difference ($F = 2.84$; df = 1,7; P = 0.136) between *M. wrayi* on ridges and *M. wrayi* on lower slopes (5.59 cm). However, mean *D. muricatus* lateral-root depth (311.9 cm), weighted by cross-sectional area, was significantly higher ($F = 55.7$; df = 1, 121; P < 0.001) than *M. wrayi* on the ridges (116.5 cm), although again there was no significant difference ($F = 0.08$; df = 1,132; P = 0.782) between *M. wrayi* on ridges and *M. wrayi* on lower slopes (137.9 cm).

Discussion

The relationship between pre-dawn water potentials and soil water potential at 20 cm depth was weak, although plant water potentials were lower at drier times than wetter times (Figure 5). Pre-dawn plant water potentials were also usually higher than soil water potentials. These findings indirectly suggest that both *D. muricatus* and *M. wrayi* root into soil with greater water potentials greater than those at 20 cm. Measured root depths confirm that both species root to well below 20 cm (Figure 6).

Despite the differences in soil water potential between ridge and lower slope sites there were no differences in *M. wrayi* pre-dawn or mid-day water potentials between sites, while there was a difference between *M. wrayi* and *D. muricatus* on ridge sites

(Figure 5). A possible explanation for the lack of difference for *M. wrayi* between sites lies with the difference in lateral root cross-sectional area (Figure 6). *M. wrayi* trees from ridge sites had a greater area than those from lower slope sites. This increased water uptake capacity may have allowed *M. wrayi* trees growing on ridge sites to maintain high leaf water potentials. The pre-dawn water potential values measured here for *M. wrayi* were indeed similar to those previously recorded both in the wet and seasonal tropics, but measured mid-day values were lower than those for all of the other tropical wet forest species compared from the literature (Table 4). By contrast, *D. muricatus* pre-dawn and mid-day values were higher; the mid-day water potential at the wet time of year very much so.

At all measured times both species maintained pre-dawn water potentials well above the turgor loss point (Ψ_0). At mid-day, with low soil water potentials, *M. wrayi* leaves had turgor potentials which may have been low enough to reduce assimilation rates on ridge sites. At Danum, Zipperlen (1997) found that soil water potentials as high as −0.08 MPa were sufficient to reduce stomatal conductance in dipterocarp seedlings: much lower potentials are reported in the present study. *D. muricatus* mid-day water potentials furthermore never approached the estimated values of Ψ_0. Measurements at another nearby site to Danum additionally suggested that *M. wrayi* seedling assimilation rates were being periodically limited by water availability on ridge sites (Gibbons 1998).

D. muricatus was clearly deeper rooted than *M. wrayi* and had a greater proportion of lateral root cross-sectional area at greater depths, although total *D. muricatus* root cross-sectional area was lower than

Table 4. Published values of water potential (Ψ), osmotic potential at full hydration ($\Psi_{\pi,sat}$), water potential at zero turgor (Ψ_0), bulk modulus of elasticity (ϵ_{sat}) and root depth, for understorey or small-stature trees, from ridge (R) and lower-slope (LS) sites (or their equivalent), at wet and dry times of year, in the wet and moist tropics. Numbers given to one decimal place precision were estimated from figures. Wet and dry points are the extremes for each site, a dry time at a wet forest site being wetter than a dry time at a moist forest site.

Site	Species	Pre-dawn Ψ (Mpa)		Mid-day Ψ (MPa)		$\Psi_{\pi,sat}$ (Mpa)		Ψ_0 (Mpa)		ϵ_{sat} (MPa)		Root depth (cm)
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Wet Forest												
Costa Rica[1]	*Pentaclethra macroloba* [11]	−0.3	−0.33	−1.2	−1.2	−1.13	−1.21	-	-	12.7	9.8	-
Hawaii[2,10]	*Dubantia ciliolata*	-	−0.61	−1.13	−1.57	-	−1.08	-	−1.5	-	2.22	-
	Dubantia scabra	-	−0.11	−0.50	−0.78	-	−0.81	-	−0.9	-	10.23	-
Jamaica[3]	*Chaetocarpus globosus*	−0.66	-	−0.74	-	-	-	-	-	-	-	-
	Cyrilla racemiflora	-	−0.38	-	−0.74	-	-	-	-	-	-	-
	Ilex macfadyenii	−0.28	-	−1.10	-	-	-	-	-	-	-	-
	Podocarpus urbanii	−0.68	-	−1.30	-	-	-	-	-	-	-	-
	Vaccinium meridinale	−0.50	-	−1.70	-	-	-	-	-	-	-	-
Malaysia[4]	*Dimorphocalyx muricatus* (R)	−0.09	−0.21	−0.12	−0.59	−1.11	−1.44	−1.38	−1.75	17.47	7.90	97.4
	Mallotus wrayi (R)	−0.26	−0.50	−0.88	−1.64	−1.58	−1.69	−2.07	−2.32	5.94	6.41	69.8
	Mallotus wrayi (LS)	−0.11	−0.57	−0.90	−1.77	−1.20	−1.05	−1.38	−1.47	7.28	3.64	81.4
Moist Forest												
Australia[5]	*Castanospermum australe*	-	−0.4	-	−0.9	-	−0.80	-	−1.01	-	-	-
Ghana[6]	*Entandrophragma utilo* [12]	−0.9	−2.7	−1.4	−3.1	-	-	-	-	-	-	-
	Terminalia superba [12]	−1.0	−2.5	−1.3	−3.0	-	-	-	-	-	-	-
Panama[7]	*Psychotria chagrensis*	−0.1	−1.1	−0.8	−1.7	−0.9	−1.3	−0.9	−1.3	10	14	51
	Psychotria furcata	−0.2	−0.7	−0.7	−1.7	−0.9	−1.7	−1.0	−2.1	5	18	29
	Psychotria horizontalis	−0.1	−0.8	−0.7	−1.4	−1.1	−1.4	−1.3	−1.6	6	20	33
	Psychotria limonensis	−0.1	−0.7	−0.4	−1.0	−1.0	−1.1	−1.1	−1.2	8	12	92
	Psychotria marginata	−0.1	−0.6	−0.6	−1.3	−1.3	−1.5	−1.4	−1.7	13	27	38
Panama[8]	*Psychotria horizontalis* (R)	−1.7	−2.5	-	-	-	-	−1.88	−2.29	-	-	30 [12]
	Psychotria horizontalis (LS)	−0.6	−0.9	-	-	-	-	−1.67	−1.95	-	-	30 [12]
	Trichilia tuberculata (R)	−1.1	−2.0	-	-	-	-	-	-	-	-	80 [12]
	Trichilia tuberculata (LS)	−0.6	−1.1	-	-	-	-	-	-	-	-	80 [12]
Panama[9]	*Cordia alliodora*	−0.1	−0.6	−1.0	−2.0	-	-	-	-	-	-	-
	T. cipo (= T. tuberculata)	−0.4	−2.5	−1.5	−4.0	-	-	-	-	-	-	-

[1] Oberbauer et al. (1987)
[2] Robichaux (1984)
[3] Kapos and Tanner (1985)
[4] this study
[5] Myers et al. (1987)
[6] Veenendaal et al. (1995)
[7] Wright et al. (1992)
[8] Becker et al. (1988)
[9] Fetcher (1979)
[10] two species from different sites
[11] understorey saplings of a canopy species
[12] seedlings; data from Becker and Castillo (1990)

those of *M. wrayi* (Figure 5). The difference in pre-dawn water potentials is, probably, accounted for by *D. muricatus* rooting into soil with higher water potentials than those available to *M. wrayi*. The differences in mid-day water potentials and root cross-sec-

tional areas suggest that *D. muricatus* had either a higher root-and-shoot conductivity or a reduced desiccation rate (or both) than *M. wrayi*.

Nevertheless, the differences between sites were surprisingly small even in the dry periods and the

predicted soil water potential for 1997 only marginally approached values which would cause wilting (Figure 4). In a separate field experiment which induced tree water stress, achieved by placing plastic sheeting on the forest floor in 5-m × 5 -m quadrats of a set of satellite plots, Gibbons (1998) was able to reduce the soil water potential from −0.2 MPa down to only −0.5 MPa. One possibility is that hydraulic lift (Dawson 1993) was resetting surface soil water potentials at night in the dry period, this operating up to the time at which the large trees stop transpiring. Whether this is an important process in tropical forests during dry periods in general remains to be investigated in detail.

Differences in hydraulic architecture between various species have been recorded in several other studies, temperate and tropical, and high leaf-specific conductance has been proposed as a drought adaptation as long as soil water supply is maintained (e.g. Tyree et al. (1991)). The low leaf water potentials that develop in *M. wrayi* trees during the day suggest that there is a high water potential gradient between leaf and stem, which may increase the risk of xylem cavitation and embolism under normal conditions (Tyree and Ewers 1991; Sperry 1995). Walsh and Newbery (1999) reviewed the literature on conductance and risk of embolism in relation to the tropical forest at Danum. Specifically, they drew attention to a "trade-off" between increases in potential vessel conductance (e.g., through increased vessel diameter) and increases in the risk of embolism during times of plant water shortage. Drought-adapted canopy-trees at Danum may largely be able to contain embolisms in terminal branches which can be later replaced. Drought-tolerant understorey species could be similarly adapted. It is important to be clear though that this model applies to drought-tolerant species (species that directly experience and survive water shortage) and not to drought-evading species (species that survive drought by, for example, accessing additional supplies of water). The limited evidence here of low mid-day leaf-water potentials suggests that *M. wrayi* may fit more the drought-tolerance model with low apical stem conductances. By contrast, it seems that the deeper rooted *D. muricatus* is to some extent a drought-avoider and may lack these particular drought adaptations. Additional nursery experiments have demonstrated that *D. muricatus* seedlings are more drought-tolerant than those of *Baccaurea stipulata* J.J. Sm. (Euphorbiaceae), a less common species confined unusually to lower slope sites at Danum

(Gibbons 1998). Further investigations are required on this topic, ideally with *in situ* measurements of tree conductance.

The findings of Wright et al. (1992) confirm the importance of root depth. Of their study species in moist forest on Barro Colorado Island (BCI), Panama, the deepest rooting one, *Psychotria limonensis*, had water potentials which were the most similar to those of *D. muricatus* (Table 4). Jackson et al. (1995), working in the same forest, found differences between species in terms of the stable isotopic hydrogen ratio (δD) of their xylem water. Since δD values declined with soil depth (sharply in the top 30 cm), Jackson et al. (1995) suggested that different species were utilising water from different depths in the forest soil profile. Values of δD in xylem water were also negatively correlated with stomatal conductance rate and leaf water potential indicating that species using deeper water had higher rates of water use and higher leaf water potentials (Jackson et al. 1995). This accords with interpretation above for *M. wrayi* and *D. muricatus*.

Little information is available unfortunately on rooting depth for individual tropical species. Becker and Castillo (1990) measured root lengths in another Panamanian moist forest. Their architectural drawings suggest that there were differences in rooting depth between species, and that canopy species' saplings were more deeply rooted than treelets and shrubs of the same height. In Borneo, Baillie and Mamit (1983) observed roots along a road cutting in Sarawak. Most of the trees measured (dbh range 11–105 cm) were canopy species and some had root depths maximally of almost 4 m. Mean rooting depth was 2.35 m, this being 1.05 m above the weathered rock. Three trees in the 10–20 cm dbh range had rooting depths ranging from 1.55 to 2.54 m. Green (1992) at Danum (in the study mentioned above in the Methods) found root endings ⩽ 2 mm and > 2 mm diameter down to 120 cm with a small mode at 90 cm for roots > 2 mm diameter.

Excavation still remains the most reliable, though laborious, means of determining tree root architecture. In Amazonian seasonal forests, roots of larger trees were found at depths up to 18 m (Nepstad et al. 1994) – a maximum depth far greater than that possible at Danum – but Sternberg et al. (1998) found that roots of trees and saplings at one of the sites were quite heterogeneously distributed in the top 4 m of soil and individuals' root systems could not be readily differentiated by δ^{13}C ratios.

Both *D. muricatus* and *M. wrayi* osmotically adjusted their cell solute concentrations between wet and dry times. Estimated values of osmotic potential at full hydration ($\Psi_{\pi,\text{sat}}$), for both species, are similar to other published values (Table 4). Becker et al. (1988) found similar differences in $\Psi_{\pi,\text{sat}}$ to *M. wrayi* for *Psychotria horizontalis* when comparing plateau and slope sites. Although *M. wrayi* had similar values of Ψ at pre-dawn and mid-day on ridge and lower slope sites, differences in $\Psi_{\Pi,\text{sat}}$ between sites suggest that trees on the ridge sites most likely experience lower-soil water potentials at other times.

There was no clear pattern in change in bulk modulus of elasticity at full hydration (ϵ'_{sat}) between wet and dry times. By contrast Wright et al. (1992) found a clear increase in ϵ'_{sat} between wet and dry times of year. Differences in ϵ'_{sat} may be accounted for by leaf age. Both of the species in the present study and those of Wright et al. (1992) produced the majority of new leaves during or immediately after the annual dry spell. Therefore, if new, fully expanded leaves were selected, leaves sampled during the dry period would be almost 1 yr old whereas leaves sampled during a wet period would be younger. In the present study, it is likely that the ages of compared leaves were similar because newly flushed leaves during the wet sample time were not fully expanded and mostly older expanded leaves were used for the water potential measurements. Stomatal function and water status properties of leaves of tropical tree species have been shown to change with leaf age (Reich and Borchert 1988). Wright et al. (1992) also found a decrease in stomatal conductance with leaf age. It is possible then that loss of stomatal function may be a consequence of increasing $\varepsilon'_{\text{sat}}$ with age.

At times drier than those which occurred during this study it seems likely that *M. wrayi*, on ridge sites, has suffered severer drought stress. Drier times have been recorded at DVFC in the 10 yr prior to 1995 and comparative rainfall data from other sites in Sabah provide strong evidence that relatively severe droughts do occur with moderate frequency at Danum (Walsh 1996b; Walsh and Newbery 1999). Although *M. wrayi* trees could maintain turgor by further increasing cell solute concentrations, the values of $\Psi_{\pi,\text{sat}}$ measured were already towards the lower range found in tropical moist forest species (Table 4), so that further adjustment in this respect may not be possible. As well as accessing deeper supplies of water it appears that *D. muricatus* is still able to maintain high water potentials during the day. Therefore,

during a severe drought *M. wrayi* on ridge sites may be expected to have a higher incidence of apical embolism, and consequently a higher tree mortality rate, than *D. muricatus* and *M. wrayi* on lower slope sites. The deeper-rooted *D. muricatus* would be less vulnerable to drought stress *per se* at these drier times. However, if a drought occurred that was severe enough to dry the deeper soil layers both species might be equally vulnerable on ridge sites. Interestingly, in Panamanian moist forest (BCI), the mortality of both slope and generalist species increased during a severe drought (Condit et al. 1995). A higher mortality of slope specialists than generalists was expected as it was hypothesized that the specialists were transient and ill-adapted to drought conditions (Condit et al. 1996). However, if as at Danum during a drought slopes stay wetter than ridges, and the difference between sites becomes greater as the drought advances, mortality on the lower slope might not be higher because the different groups experience different degrees of water shortage.

Although there is some evidence that *D. muricatus* is more drought-adapted than *M. wrayi* (higher pre-dawn and mid-day water potentials at dry times and greater rooting depth) and that stronger effects of droughts occur on ridge than lower slope sites, *M. wrayi* trees are still found on ridge sites albeit less commonly than on lower slope ones. Therefore, either severe droughts do not occur with sufficient regularity to completely exclude *M. wrayi*, or possibly *M. wrayi* trees grow in relatively wet microsites on the ridges, or further *M. wrayi* is able to contain embolisms; or all three factors play a role. The within-site variability in soil water potential measured at Danum does suggest the existence of wet microsites. Both study species, as shallowly rooted seedlings, would be expected to be vulnerable to drought, but if both tend to fruit after a dry spell (J.M. Gibbons, *pers. obs.*) then probably they have enough time to root to sufficient depths before the next severe drought occurs. Differences in water relations and root architecture between *M. wrayi* on ridge and on lower slope sites suggest a high degree of physiological and morphological plasticity. *M. wrayi* is the commonest species in the plots (trees $\leq$ 10 cm gbh, Newbery et al. (1992, 1999)) and its dominance in the understorey may well be the result of this proposed plasticity.

Leaf anatomy gives only partial clues to mechanisms of drought tolerance. Gibbons (1998) recorded that *D. muricatus* had thicker leaves (212 μm, leaf area 348 cm^2, specific leaf area 286 cm^2 g^{-1}) com-

pared with *M. wrayi* (correspondingly: 79 μm, 274 cm^2, 332 cm^2 g^{-1}), but there were no consistent patterns for other ridge, non-ridge or ubiquitous species. This is a further indirect pointer to the important role of rooting and water uptake in differentiating the ecologies of *M. wrayi* and *D. muricatus*.

Newbery et al. (1999) reported on forest dynamics in the plots between the full 1986 and 1996 enumerations. This period, apart from one moderately dry spell in early 1992 (Walsh and Newbery 1999), was free of severe droughts. Recruitment and mortality of the study species over this period can be compared. (Note that recruitment refers to new trees entering the $\geq$ 10 -cm-gbh size class, not to seedlings.) Whilst there were differences between the plots in absolute numbers, the general trend was that the recruitment rate of *M. wrayi* was equal to or slightly below its mortality rate, while for *D. muricatus* mortality rate was twice the recruitment rate (see Newbery et al. (1999)). Of the other species selected in the present study, the recruitment rates of *A. colorata*, *L. beccarianum* and *F. splendidissima* exceeded their mortality rates, while the reverse was true of *C. glaber*. In general, over this relatively wet period (excepting for *L. beccarianum*) numbers of ubiquitous species remained constant or increased while numbers of clustered species declined. Further enumerations are required to see whether this pattern is long-term, but it suggests that in stress-free periods the drought-tolerant (or -avoiding) species might be at a competitive disadvantage.

To study the water relations of trees in response to periods of water shortage, one of the most essential variables, highlighted again in the present study, is root distribution. Estimation of root abundance and activity with depth for individual trees has indeed considerable practical difficulties, particularly in vegetation such as species-rich tropical forest. Without this information, however, it is not possible to quantify the distribution of active roots with depth for a given species of tree, in the same way for instance that foliage distribution can be determined at different tree heights with regard to light. These root data together with measurements of plant and soil water potentials would allow drought-avoidance (through architecture below ground) and drought-tolerance (through physiological mechanisms) to be better distinguished. The results presented in this paper show that this is a feasible approach and it can give important insights into the role of the understorey in response of tropical forest ecosystems to drought.

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