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Research paper

Effects of rainfall exclusion on leaf gas exchange traits and osmotic adjustment in mature canopy trees of *Dryobalanops aromatica* (Dipterocarpaceae) in a Malaysian tropical rain forest

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Climate change exposes vegetation to unusual levels of drought, risking a decline in productivity and an increase in mortality. It still remains unclear how trees and forests respond to such unusual drought, particularly Southeast Asian tropical rain forests. To understand leaf ecophysiological responses of tropical rain forest trees to soil drying, a rainfall exclusion experiment was conducted on mature canopy trees of *Dryobalanops aromatica* Gaertn.f. (Dipterocarpaceae) for 4 months in an aseasonal tropical rain forest in Sarawak, Malaysia. The rainfall was intercepted by using a soft vinyl chloride sheet. We compared the three control and three treatment trees with respect to leaf water use at the top of the crown, including stomatal conductance ($g_{s_{max}}$), photosynthesis (A_{max}), leaf water potential (predawn: Ψ_{pre} ; midday: Ψ_{mid}), leaf water potential at turgor loss point (π_{tip}), osmotic potential at full turgor (π_{100}) and a bulk modulus of elasticity (ϵ). Measurements were taken using tree-tower and canopy-crane systems. During the experiment, the treatment trees suffered drought stress without evidence of canopy dieback in comparison with the control trees; e.g., Ψ_{pre} and Ψ_{mid} decreased with soil drying. Minimum values of Ψ_{mid} in the treatment trees decreased during the experiment, and were lower than π_{tip} in the control trees. However, the treatment trees also decreased their π_{tip} by osmotic adjustment, and the values were lower than the minimum values of their Ψ_{mid} . In addition, the treatment trees maintained g_s and A_{max} especially in the morning, though at midday, values decreased to half those of the control trees. Decreasing leaf water potential by osmotic adjustment to maintain g_s and A_{max} under soil drying in treatment trees was considered to represent anisohydric behavior. These results suggest that *D. aromatica* may have high leaf adaptability to drought by regulating leaf water consumption and maintaining turgor pressure to improve its leaf water relations.

Keywords: Borneo, drought tolerance, experimental drought, osmotic adjustment, photosynthesis, stomatal conductance.

Introduction

Climate change has impacts on many aspects of forest ecosystems throughout the world (Foley et al. 2007, Trumbore et al. 2015). It is expected that increasing tree mortality and declining forest functions in many different forest types will be caused in particular by increasing drought severity and frequency

with global warming (Allen et al. 2010, Lewis et al. 2011, Bonal et al. 2015). It appears that the effects of drought are more severe in tropical rain forests than in other forest types (Phillips et al. 2009, Zelazowski et al. 2011, Kumagai and Porporato 2012, Duffenbaugh and Field 2013, Corlett 2016), because tree species in tropical rain forests do not regularly experienced

severe drought (Phillips et al. 2010, Itoh et al. 2012). However, the area covered by tropical rain forests is likely to be exposed to more frequent and severe droughts as a result of climate change (Allen et al. 2010, Meir and Woodward 2010, Kumagai and Porporato 2012). In addition, most species from tropical rain forests have been found to be more vulnerable to drought-induced xylem embolism than species from seasonal tropical forests with very dry periods (Tyree et al. 1998). Some researchers have also reported that El Niño-related drought causes higher tree mortality in aseasonal tropical rain forests in Southeast Asia (Nakagawa et al. 2000, Newbery and Lingenfelder 2009, Itoh et al. 2012) and that trees in Borneo are more vulnerable to severe drought than those in the Amazon rain forest (Phillips et al. 2010). In particular, large canopy trees showed the highest mortality during droughts (Potts 2003, Slik 2004, Van Nieuwstadt and Sheil 2005, Phillips et al. 2010). For example, the mortality (%) of large trees (≤ 50 cm diameter at breast height (dbh)) was $\sim 30\%$ higher than that of small trees (> 10 cm dbh) during the El Niño-related dry period in 1997–1998 in East Kalimantan, Indonesia (Van Nieuwstadt and Sheil 2005). Moreover, larger canopy trees were limited in their growth rate compared with smaller trees under drought conditions (Nakagawa et al. 2000, Yoneda et al. 2000, Schuldt et al. 2011). However, the physiological mechanisms underlying such responses induced by drought are not well understood in canopy trees in tropical lowland rain forests in Southeast Asia (Schuldt et al. 2011).

How do canopy trees respond to severe drought in the aseasonal tropical rain forest environment? It is known that canopy trees usually experience severe water deficits during the day as a result of high temperature and irradiation (Walter 1973) combined with hydraulic constraints on the transport of water from roots to leaves (Ryan and Yoder 1997, Koch et al. 2004, Ishii et al. 2008, Kitahashi et al. 2008). Canopy trees are thus most vulnerable to the direct impact of droughts, including reduced growth and mortality, because of hydraulic limitations, higher radiation and more evaporative demand experienced by exposed crowns (Schuldt et al. 2011, Bennett et al. 2015). On the other hand, water use strategies in canopy trees seem to vary between species even within the same forest environment in an aseasonal tropical rain forest (Hiromi et al. 2012, Inoue et al. 2015). Hiromi et al. (2012) suggested that the daily pattern of leaf water use in some canopy species of the Dipterocarpaceae, which dominates the tropical rain forests of Southeast Asia, was correlated with their susceptibility to unusual drought events; species with high transpiration rates in the daytime suffered a higher mortality than those with low transpiration rates during the severe drought caused by El Niño in 1998. A reduction in water consumption (depressed transpiration rates) by stomatal regulation may be one mechanism for drought tolerance.

Leaf water retention capacity also closely relates to the mechanisms of drought resistance in tropical rain forest trees

(Maréchaux et al. 2015, Binks et al. 2016). Drought-resistant species have some specific strategies that promote drought avoidance and/or drought tolerance; the former strategy is mainly explained by morphological traits such as shedding leaves to save water and deep root systems to utilize ground water, including making use of physiological traits such as osmotic adjustment and changes in the elasticity of cell walls (Kozłowski and Pallardy 2002). Since it is well known that trees in aseasonal tropical rain forests are evergreen with shallow root systems, their physiological capacity to adjust leaf water potential at the turgor loss point (π_{tlp}), which has been recognized as an index of leaf- and plant-level drought tolerance that is changed by osmotic adjustment and cell wall elasticity during drought, may play a key role in their drought tolerance (Bartlett et al. 2012). Several studies have reported on the drought tolerance of mature trees, studied by excluding rainfall in Amazonian tropical rain forests where there is a short-term dry season (Maréchaux et al. 2015, 2016, Binks et al. 2016). Maréchaux et al. (2015) found that Amazonian trees showed a wide range of π_{tlp} values, and species with more negative π_{tlp} (i.e., with greater leaf-level drought tolerance) had a tendency to be found in drought-prone habitats where there were shallow soils and a high soil sand content. In addition, the plasticity of drought tolerance also varied across species, and species that normally had a more positive π_{tlp} exhibited higher plasticity of π_{tlp} during an experimental drought in an Amazonian forest (Binks et al. 2016). The differences in mortality rates among some dipterocarp species during the El Niño drought in 1997–1998 in an aseasonal tropical rain forest in Southeast Asia were closely related to the species' ecological and ecophysiological traits, such as leaf water use, wood density and habitat conditions (Hiromi et al. 2012, Itoh et al. 2012). Therefore, species with lower mortality under unusual drought conditions may have lower π_{tlp} and/or higher plasticity of π_{tlp} even in an aseasonal tropical rain forest. However, information on variations in the plasticity of π_{tlp} is still limited in tropical trees, and canopy tree species in particular, due to the difficulty of accessing their tree crowns (Binks et al. 2016).

In this study, we investigated leaf ecophysiological responses to drought conditions in *Dryobalanops aromatica* Gaertn.f. (Dipterocarpaceae), a dominant canopy species in the lowland tropical rain forests of Borneo. We conducted a rainfall exclusion experiment (RFE) involving mature canopy trees and investigated changes in leaf water use and water retention capacity under drought stress conditions. There are some reports that *D. aromatica* did not suffer any obvious increase in mortality during severe El Niño droughts compared with other dipterocarp species such as those in the genus *Shorea* (Becker et al. 1998, Hiromi et al. 2012). We thus hypothesized that this species could maintain leaf water retention capacity by osmotic adjustment with a reduction in water consumption achieved by closing stomata under drought conditions even in aseasonal tropical rain forests.

Materials and methods

Study site

The RFE was conducted in 2008 in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°12'N, 114°00'E, 150–250 m above seal level). The study area had a humid tropical climate, without clear intra-annual variations in rainfall and temperature (Kumagai and Kume 2012). The mean annual rainfall and temperature at Lambir Hills National Park from 2000 to 2009 were ~2600 mm and 25.8 °C, respectively (Kume et al. 2011). In the canopy and emergent layers, the daily maximum temperature and photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) were sometimes above 35 °C and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Kenzo et al. 2003, Hiromi et al. 2012). Our experiment was performed in a 4-ha Crane plot (CP) in the National Park. An 85-m-tall canopy crane with a 75-m-long rotating jib was constructed in the center of the plot to provide access to the top of the canopy (Sakai et al. 2002). To evaluate the effects of the RFE on leaf water use, we selected *D. aromatica* (Dipterocarpaceae), which grows up to 65 m tall and 2 m in diameter (Itoh 1995, Ashton 2004), and which was well distributed throughout and around the CP. We selected three experimental trees (D1, D2 and D3) and three control trees (no procedure; C1, C2 and C3), located on nearby flat land (Table 1). Since D2 and D3 were out of the reach of the crane, we erected ladders up to the crown with terraces on the branches, and further ladders from there up to the canopy.

Experimental design

We erected the equipment for the RFE over the ground surrounding the three experimental trees (Figure 1). This equipment was

Table 1. Height and dbh of the trees studied during the experiment.

Parameters/tree	Control			Drought		
	C1	C2	C3	D1	D2	D3
Tree height (m)	43.4	50.2	40.4	42.4	44.9	37.8
Dbh (cm)	52.0	95.3	58.4	64.4	105.6	59.2

shaped like an umbrella with a radius of 15 m and a height of ~7 m, and was constructed by mounting a soft vinyl chloride sheet on a frame made of wood. To avoid coinciding with a dry spell, the RFE period lasted 4 months from the middle of November 2008 to the middle of March 2009, which included the wetter period from October to January in the study area (Kumagai et al. 2009). During the experiment, most rain was intercepted by the equipment and drained to the outside of the umbrella. The procedure caused a significant reduction in the water available for the trees, because the majority of the root system of a mature tree of *D. aromatica* is within 15 m of the stem (Yamashita et al. 2012).

Meteorological and soil moisture measurements

A tipping bucket rain gauge (No. 34T, Ohta Keiki, Tokyo, Japan) was installed at the top of the crane, 85.8 m above the forest floor. In addition, at a separate tower located some 500 m southwest of the crane, the rainfall was measured using another tipping bucket rain gauge. Time and date stamps were stored for each tip event of the rain gauge (HOBO Event, Onset, Pocasset, MA, USA).

Volumetric soil moisture content (θ) and matric potential (ψ) were measured at depths of 10, 30 and 80 cm in soils in the D1 and D3 plots and at depths of 10, 20 and 50 cm in the D2 plot at 1-h intervals (CR1000, Campbell Scientific, Logan, UT, USA). Note that these measurements were conducted at both sites: in the area where rainfall was excluded and in the control. An amplitude domain reflectometer (SM200, Delta-T Devices, Cambridge, UK) and a dielectric aquameter sensor (EC-10, Decagon Devices, Inc., Pullman, WA, USA) were used to measure the time series of θ for the D1 and D3 plots, and the D2 plot, respectively. A tensiometer (Special order, Environmental Measurement Japan Co. Ltd, Fukuoka, Japan) was also used to monitor ψ at the same depth where θ was measured, thereby providing the necessary measurements to derive in-situ soil water retention curves at each depth and to consider the possible spatial variations in soil moisture conditions. The weighted average θ in the 0–80 (θ_{0-80}) and 0–50 (θ_{0-50}) cm soil layers

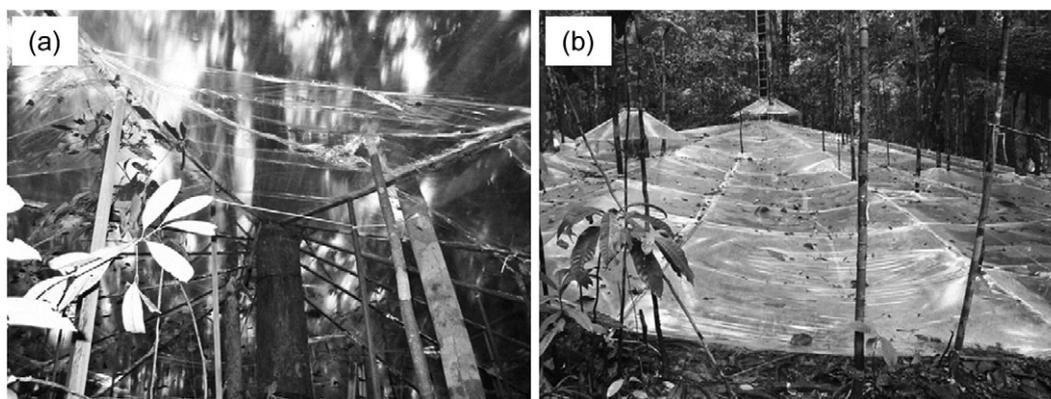


Figure 1. Rainfall exclusion equipment laid out like an umbrella around a treatment tree. Photos were taken from below (a) and beside (b) the equipment. See text for details of the equipment.

was calculated as $\theta_{0-80} = (20\theta_{10} + 35\theta_{30} + 50\theta_{50})/105$ and $\theta_{0-50} = (15\theta_{10} + 20\theta_{20} + 30\theta_{50})/65$ (where θ_x is volumetric soil moisture content at a depth of x cm, in $\text{m}^3 \text{m}^{-3}$), respectively. The relative extractable water in the soil (Θ ; $\text{m}^3 \text{m}^{-3}$) was calculated by using this average θ as: $(\theta - \theta_r)/(\theta_s - \theta_r)$, where θ_s and θ_r are the saturated water content and the residual water content averaged in the soil layer of the RFE for each plot, respectively.

A drastic increase in soil water content was occasionally observed in the treatment areas during the experiment because the vinyl umbrella sheets had been broken by fallen branches or heavy rainfall, resulting in leaks. Such a case was observed in D1 and D3 in the middle of December 2008, and in January and February 2009. We repaired the vinyl sheets each time.

Predawn and midday leaf water potential

Predawn and midday leaf water potentials (Ψ_{pre} and Ψ_{mid}) were measured between 06:00 and 07:00 h and between 12:00 and 14:00 h, respectively, in the field with a pressure chamber (Model 1002, PMS instruments, Corvallis, OR, USA). The measurements of Ψ_{pre} were conducted before the experiment commenced (October 2008) and from its beginning (November 2008) until the recovery of Ψ_{pre} in the treatment trees was observed. Three treatment and three control trees were repeatedly measured by sampling three to five sun-exposed shoots per individual about every 10 days.

For Ψ_{mid} , the measurements were conducted on days that were as clear as possible, although a totally cloudless day was very rare in the area and some overcast hours were included. The measurements of Ψ_{mid} were conducted from the experimental period (December 2008) until the recovery of Ψ_{mid} was observed in the treatment trees. The three treatment trees and one control tree (C2) were repeatedly measured by sampling three to five exposed shoots per individual about every 10 days. For the control trees C1 and C3, Ψ_{mid} was measured once during the experimental period on 1 March 2009 and twice after the experiment on 22 March and 21 April 2009.

Leaf photosynthesis and stomatal conductance at light saturation

Leaf photosynthetic rate (A_{max}) and stomatal conductance (g_{smax}) at light saturation in fully expanded and apparently non-senescent leaves were measured using a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE, USA). We conducted the measurements for 3 days before the experiment (1 week in advance), 3 days during the experiment and 2 days just after the experiment (within 1 month). Three to six shoots on the crown surface were selected and three to six leaves were measured in the morning (08:00–10:00 h) and around midday (12:00–14:00 h). Photosynthetic rates in the species under canopy conditions were saturated at $\sim 1200\text{--}1500 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ light intensity with 360 ppm CO_2 concentration (Kenzo et al. 2003, 2004).

Thus, the measured light intensity, CO_2 concentration and temperature were controlled at $\sim 1500 \mu\text{mol photon m}^{-2} \text{s}^{-1}$, 360 ppm, and 30 °C, respectively.

In addition to leaf gas exchange measurements, we conducted pressure-infiltration experiments to evaluate directly leaf stomatal openness at the whole-leaf level in the morning and at midday on sunny days during the experiment (Beyschlag and Pfanz 1990, Hiromi et al. 1999, Kenzo et al. 2007). In the method, the solution-infiltrated area in the leaf represents the distribution of open stomata. The measurements were conducted on three individuals in the treatment and control, respectively. We selected three to eight leaves which were fully expanded and apparently non-senescent and at the crown surface, for each measurement. The solution-infiltrated ratio in the leaf was analyzed with ImageJ software (<http://imagej.nih.gov/ij/>). To evaluate the relationship between g_{smax} and infiltrated ratio in the leaf, we conducted leaf gas exchange and pressure-infiltration measurements on the 25 leaves.

Diurnal changes in leaf gas exchange and water potential

Leaf gas exchange parameters, such as photosynthetic and transpiration rates (A and E , respectively) and stomatal conductance (g_s), were measured using a portable photosynthesis apparatus (LI-6400) on 1 March 2009 during the experimental period. All the measurements were made between 08:00 and 14:00 h at 2-h intervals. We measured three to five fully expanded and apparently non-senescent leaves at the top of the crown of one each of the treatment (D1) and control (C2) trees. The measured light intensity varied from 200 to 2100 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. The CO_2 concentration in the chamber was 360 ppm. Leaf water potential was also measured with a pressure chamber (Model 1002) every 2 h between 06:00 and 14:00 h on the same day. A total of three to five sun-exposed shoots from each measured individual (D1 and C2) were excised with pruning shears, and their water potential was determined immediately.

Pressure–volume curve

Water potential at the turgor loss point (π_{tlp}), osmotic potential at full turgor (π_{100}) and bulk modulus of elasticity (ϵ) on all treatment and control trees were determined from the pressure–volume curve (Tyree and Hammel 1972). Three branches ~ 50 cm long per individual were cut from each of the treatment and control trees for determining the time sequence of leaf water relations every month during the experiment. The sampled branches were bagged to prevent dehydration during transport back to the laboratory (Tyree et al. 1978, Hinchley et al. 1980). The base of each branch was then cut off in water and the branch was allowed to rehydrate in tap water for at least 12 h (Tyree et al. 1974). About 15 cm long shoots bearing 5–10 leaves were cut from the branches and measurements taken using a pressure chamber (Model 1002) to generate pressure–volume curves.

Statistical analysis

To compare differences in leaf water relation parameters between the experimental and control trees and between the measurement periods (pre-experimental period, experimental period and post-experimental period), we used one-way ANOVA. Differences between experimental and control trees with respect to infiltrated ratio in the leaf during the experimental period were also examined by one-way ANOVA. For all the statistical analyses, we used R version 2.15.1 (The R Foundation for Statistical Computing, Vienna, Austria).

Results

Meteorological and soil moisture conditions

Similarities in soil moisture response to rainfall before and after the RFE and the difference between the positions inside and outside the umbrella were clear (Figure 2). Note that leakages of rainwater through the plastic sheet occurred in the D1 and D3 plots in mid-January (Figure 2b), and mid-December and

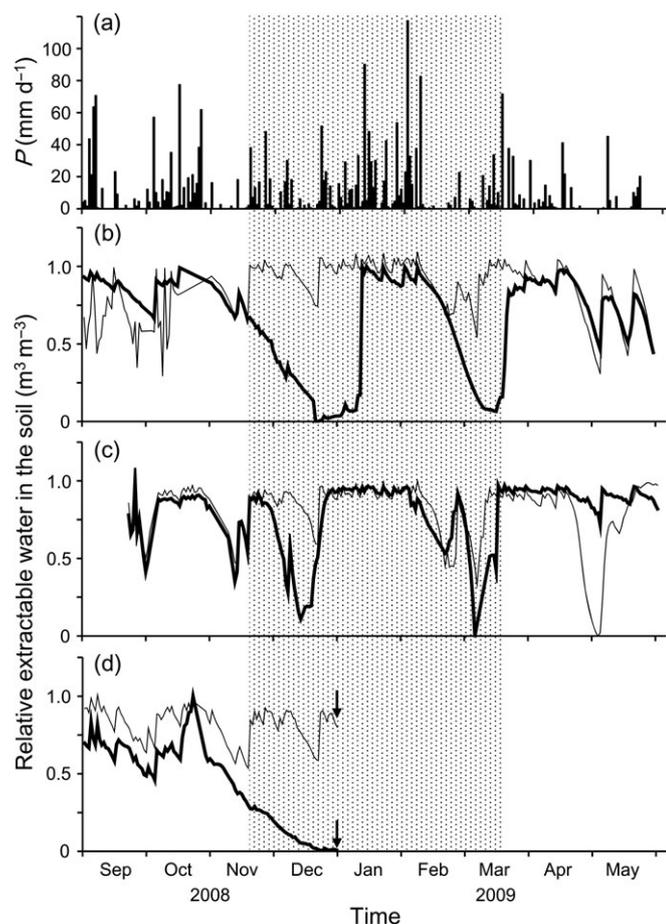


Figure 2. Daily precipitation (P) (a), and relative extractable water in the soil of the RFE (thick line) and control (thin line) positions for D1 (b), D3 (c) and D2 (d) plots. The shaded block represents the experimental period. Due to damage to the soil moisture sensor in D2 (indicated by arrows), the data after 30 December are missing (d).

mid-February (Figure 2c), respectively. Average volumetric soil water content of the shallow soil layer (at a depth of 10 cm) during the RFE was 32.3% outside and 13.7% under the shelter (Ohashi et al. 2015). The values for the deeper soil layer (30 cm) were 32.6% outside and 20.5% under the shelter.

Changes in leaf gas exchange traits and water potential

The leaf maximum photosynthetic rate (A_{\max}) and stomatal conductance ($g_{s\max}$) at light saturation clearly decreased in the treatment trees compared with the control trees at midday during the experiment (Table 2). However, there was no difference between the treatment and control trees in either parameter in the morning, and for A_{\max} and $g_{s\max}$ in the pre- and post-experimental periods (Table 2).

The infiltrated ratio in the leaf also supported this tendency. It was significantly correlated with $g_{s\max}$ ($g_{s\max} = 0.0063 \times$ infiltrated ratio in the leaf $- 0.1255$; Kendall tau = 0.576, $P < 0.001$), consistent with strong relationships between the infiltrated ratio and stomatal conductance and/or transpiration ratio found in previous studies (e.g., Beyschlag and Pfanz 1990, Hiromi et al. 1999, Kamakura et al. 2015). Infiltrated area in the leaf and estimated $g_{s\max}$ in treatment trees were also significantly lower at midday compared with control trees, whereas neither values differed between the treatment and control in the morning (Table 2; see Figure S1, Table S1 available as Supplementary Data at *Tree Physiology Online*). We also found significant stomatal patchiness in treatment trees at midday during the experiment (see Figure S1 available as Supplementary Data at *Tree Physiology Online*).

Predawn leaf water potential (Ψ_{pre}) in the treatment trees clearly decreased just after the experiment started and corresponded with a decrease in soil moisture content during the experiment (Figure 3, Table 3). Mean Ψ_{pre} values in the treatment trees significantly changed by ~ 0.14 MPa during the experiment, while the control trees showed constant mean Ψ_{pre} values and only a 0.01 MPa difference during the experiment. The treatment trees also exhibited significantly lower values of Ψ_{mid} than the control trees during the experiment, but recovered quickly up to the same level that the control trees exhibited just after the experiment (Figure 3, Table 3).

Diurnal changes in leaf water use

Diurnal changes in leaf water potential, stomatal conductance, transpiration and photosynthetic rates were lower in the treatment tree than in the control tree during the experiment (Figure 4). Leaf water potentials in both control and treatment tree were high early in the morning (06:00–08:00 h), but declined sharply between 10:00 and 12:00 h, and exhibited the lowest values around midday. The treatment tree showed clearly lower values in midday leaf water potential than the control tree, although they recovered slightly at 14:00 h. Diurnal changes in all the gas

Table 2. Changes in the maximum photosynthetic rate (A_{\max}), maximum stomatal conductance ($g_{s_{\max}}$) and leaf infiltrated ratio in the morning and at midday during the pre-experimental, experimental and post-experimental periods.

	Pre-experimental period		Experimental period		Post-experimental period	
	Control	Drought	Control	Drought	Control	Drought
Number of measured leaf ¹						
Morning	34	13	9	9	10	9
Midday	11	4	14	15	9	10
A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
Morning	13.2 \pm 2.7	12.7 \pm 2.8	14.7 \pm 2.9	13.9 \pm 1.9	10.8 \pm 2.8	10.9 \pm 3.3
Midday	12.5 \pm 2.3	13.3 \pm 1.8	13.8 \pm 3.2	7.3 \pm 3.9	11.2 \pm 2.1	10.7 \pm 4.1
$g_{s_{\max}}$ ($\text{mmol m}^{-2} \text{s}^{-1}$)						
Morning	0.27 \pm 0.07	0.31 \pm 0.05	0.45 \pm 0.19	0.40 \pm 0.10	0.40 \pm 0.21	0.46 \pm 0.13
Midday	0.22 \pm 0.06	0.31 \pm 0.05	0.40 \pm 0.16	0.19 \pm 0.11	0.25 \pm 0.21	0.26 \pm 0.25
Infiltrated ratio in the leaf (%)						
Morning	–	–	89.0 \pm 8.5 ns	95.2 \pm 6.8 ns	–	–
Midday	–	–	78.7 \pm 10.1*	52.9 \pm 11.0*	–	–

Values given are mean \pm standard deviation. Gas exchange measurements were conducted during the pre-experimental period for each of the three control and one treatment trees and during the experimental period and post-experimental period for one control and one treatment tree. Gas exchange measurements were conducted on 2–3 days for all individuals. Measurements for pressure-infiltration were conducted on 1 day for each of the three control and treatment trees.

¹Leaf number in the table is indicated for gas exchange measurements. Values with asterisks (*) are significantly different among treatments at $P < 0.05$, ns = $P > 0.05$ (one-way ANOVA).

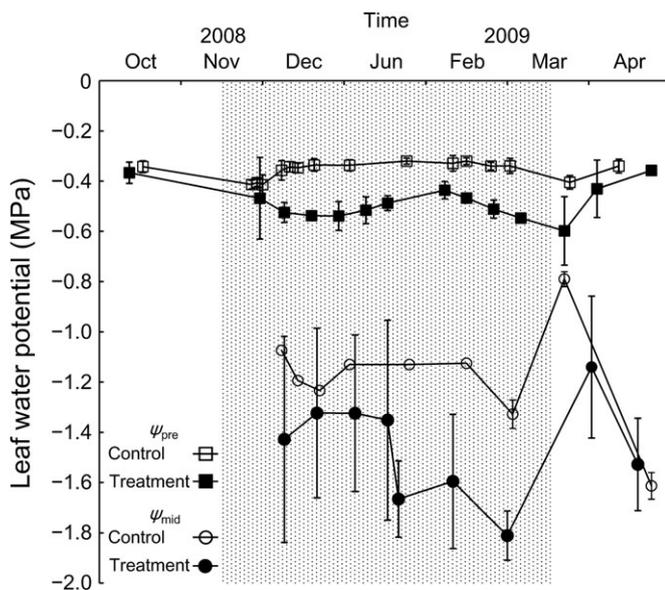


Figure 3. Changes in leaf water potential at predawn and midday in the RFE. Values of Ψ_{pre} and Ψ_{mid} indicate average (mean \pm SE; three trees with three shoots per treatment) for the control and treatment. The values of Ψ_{mid} in the control from December 2008 to February 2009 indicate averages of three shoots in C2. The shaded block represents the experimental period.

exchange parameters (A , E and g_s) peaked in the morning in both control and treatment trees, but rapidly declined between 12:00 and 14:00 h in the treatment tree, which displayed only about half the values of all the parameters in the control tree (Figure 4). On the other hand, the control tree showed a moderate midday depression in all the parameters.

Changes in leaf water retention capacity by osmotic adjustment

Leaf water potential at the turgor loss point (π_{tlp}) and osmotic potential at full turgor (π_{100}) decreased and the bulk modulus of elasticity (ϵ) increased <1 month after the RFE started (Figure 5). The lowest leaf water potential at the turgor loss point (π_{tlp}) and osmotic potential at full turgor (π_{100}) were observed in the treatment trees during the experiment (Table 3, Figure 5). Even the minimum value of midday leaf water potential in the treatment trees was over the value of π_{tlp} in the control trees. The midday leaf water potential in the treatment trees never dropped below π_{tlp} . The ϵ values of the treatment trees clearly increased during the experimental period and were significantly higher than those of the control trees. All the values related to leaf water recovered rapidly just after the experiment (Table 3, Figure 5). Only π_{100} exhibited slightly but significantly lower values in the treatment trees even after the experiment than in the pre-experimental period.

Discussion

Although soil moisture in the shallow soil layer (i.e., <10 cm) during the experimental period dropped to a similar value to that recorded during the El Niño-related dry period in 1997–1998, the deeper soil layer during the RFE contained much more abundant water compared with the El Niño period. In fact, volumetric soil water content at 10 cm during the RFE and the El Niño period was 13.7% and 14%, respectively (Ishizuka et al. 2000, Ohashi et al. 2015). In contrast, the values in the deeper soil layer were 20.5% during the RFE (at 30 cm) and 17% during

Table 3. Changes in the leaf water relation parameters during the period of the RFE.

Parameter (MPa)	Pre-experimental period		Experimental period		Post-experimental period	
	Control	Drought	Control	Drought	Control	Drought
Ψ_{pre}	-0.34 ± 0.02 b	-0.37 ± 0.04 b	-0.35 ± 0.02 b	-0.51 ± 0.02 a	-0.34 ± 0.03 b	-0.36 ± 0.02 b
Ψ_{mid}	-1.35^1	-1.22^1	-1.27 ± 0.05 b	-1.62 ± 0.07 a	-1.20 ± 0.04 b	-1.22 ± 0.15 b
π_{tip}	-1.67 ± 0.03 c	–	-1.84 ± 0.03 b	-2.50 ± 0.06 a	-1.73 ± 0.03 c	-1.81 ± 0.02 bc
π_{100}	-1.34 ± 0.06 c	–	-1.60 ± 0.04 b	-2.25 ± 0.11 a	-1.47 ± 0.07 bc	-1.57 ± 0.02 b
ϵ	2.46 ± 0.13 b	–	3.90 ± 1.22 b	9.69 ± 0.15 a	3.67 ± 1.30 b	3.69 ± 1.16 b

Values given are mean \pm standard deviation, $n = 3$. Values with different letters are significantly different among treatments and periods at $P < 0.05$ (Tukey's HSD test).

¹The mean value in C2 and C3 for control trees, and value in treatment tree D1.

the El Niño period (at 40 cm, Ishizuka et al. 2000). Despite the weaker drought in the deep soil layer compared with the El Niño period, treatment trees suffered drought stress without canopy dieback and adjusted their leaf traits to the experimental soil drying mainly by two methods: (i) regulating water consumption by closing stomata and (ii) increasing plasticity of drought tolerance by osmotic adjustment and increasing cell wall rigidity to improve its leaf water retention.

Changes in leaf water use

The leaves in the upper part of the crown of treatment trees suffered drought stress during the experiment. It is well known that species with a shallower root system, including most tropical rain forest trees in Borneo (Baillie and Mamit 1983, Kenzo et al. 2009), must decrease leaf water potential for water transport from the soil under severe drought conditions, although species with a deeper root system can maintain high leaf water potential by water transport from deeper soil in the same environment (Davis and Mooney 1986).

Although it is known that tropical canopy trees tolerate daily fluctuations in water conditions and recover their water status overnight (Goldstein et al. 1998, Bucci et al. 2004, Kenzo et al. 2015), the treatment trees showed significantly lower values in Ψ_{pre} and Ψ_{mid} than the control trees during the experiment (Table 3). The Ψ_{pre} of the treatment trees decreased just after the experiment started and the lower values were maintained throughout the experiment. Although the cover leaked during this study, the effect on the treatment trees may have been small: Ψ_{pre} in trees generally represents the soil water potential that the root system is accessing and treatment trees were associated with a lower Ψ_{pre} than the control trees. Decreased Ψ_{pre} may also have contributed to successful water uptake from the dry soil by the shallow root system, despite the restricted transpiration activity by the decreased g_s . Also, the decreased g_s and/or the decreased leaf water potential in the treatment trees induced a midday depression in photosynthesis (e.g., 53% lower than the control) (Table 2, Figure 4). A similar reduction in photosynthesis and g_s was also observed in a canopy tree of a lowland dipterocarp forest (Ishida et al. 2000) and saplings of Bornean heath forest tree species (Cao 2000), including several dipterocarp species,

during the El Niño-related drought. Such midday depressions may also have limited the daily carbon balance and then induced the observed reduction in the growth rate in canopy trees during the El Niño-related drought (Nakagawa et al. 2000). On the other hand, the ability of this species to recover from severe drought may be high, because both gas exchange traits and Ψ_{pre} recovered rapidly, returning to previous levels within 1 month of end of the experiment. Similar high recovery ability was also reported in the shallow-rooted species compared with the deep-rooted species of Bornean heath forest saplings (Cao 2000).

Leaf water retention capacity by osmotic adjustment

Dryobalanops aromatica may achieve high plasticity in drought tolerance by a combination of regulating water consumption and maintaining turgor pressure to improve its leaf water retention capacity, allowing it to grow even in the aseasonal tropical rain forest environment. Cao (2000) also found that in a Bornean heath forest, there were various responses to El Niño-related drought with respect to leaf water use and osmotic adjustment among species at the sapling stage. In this study, the values of π_{tip} and π_{100} significantly decreased in both control and treatment trees compared with the control trees measured 6 months before the experiment (Table 3), mainly because of osmotic adjustment. However, both values of π_{tip} and π_{100} were significantly lower in the treatment trees than in the control trees during the experimental period. A reduction in leaf π_{tip} and π_{100} usually increases leaf water retention capacity and maintain turgor pressure through an enhanced ability for water uptake from drier soil (Bowman and Roberts 1985, Kramer and Boyer 1995). Significantly increased ϵ values in the treatment trees compared with those in the control trees may also contribute to preventing the collapse of mesophyll cells under low leaf water potential (Kramer and Boyer 1995).

Similar osmotic adjustment was observed in canopy trees subjected to experimental drought in the Amazonian tropical rain forest (Binks et al. 2016). The studied species clearly decreased its π_{tip} as a result of an increase in both osmotic adjustment and elasticity of cell walls (Table 3, Figure 5). The mean minimum π_{tip} was -2.5 MPa, and this value was clearly lower than the minimum value of Ψ_{mid} during the experiment (Figure 3). These results suggest that *D. aromatica* was able to maintain leaf turgor

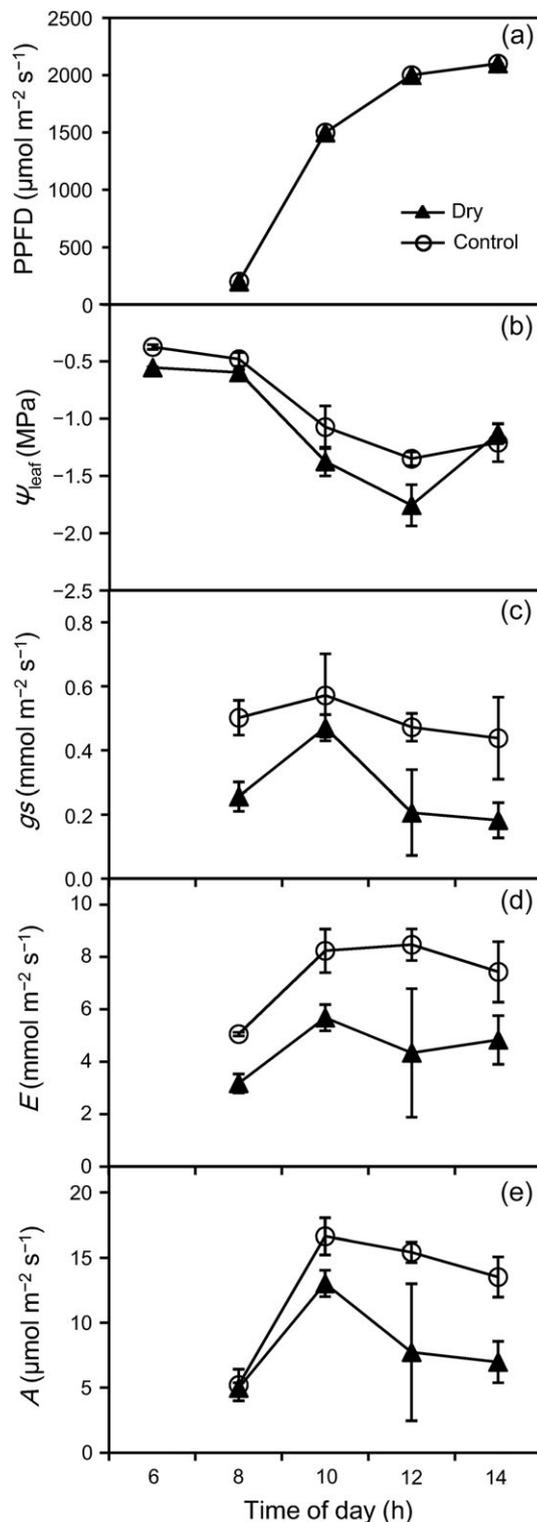


Figure 4. Diurnal changes in leaf water use in the RFE. PPFD = photosynthetic photon flux density. Values for all parameters indicate an average (mean \pm SE; three shoots per treatment) in D1 and C2.

pressure on soil drying, and thus it may be possible to achieve this enhanced water retention ability through osmotic adjustment when growing in sandy soil with its increased risk of drought, thus reducing mortality even under severe drought conditions

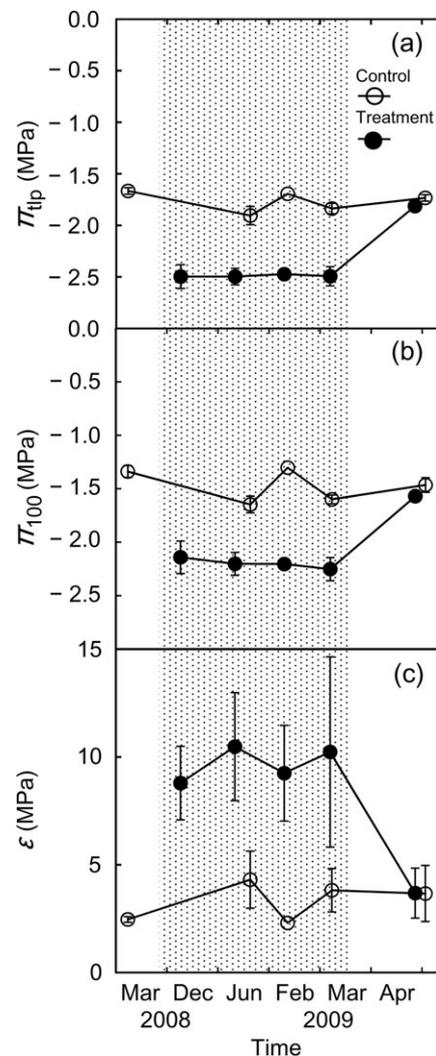


Figure 5. Changes in leaf water relation parameters in the RFE. Values of π_{tip} , π_{100} and ε indicate average (mean \pm SE; three trees with three shoots per treatment) in the control and treatment, though only the value for February 2009 in the control is the average of three shoots in C2. The shaded block represents the experimental period.

(Itoh 1995, Hirai et al. 1997, Ashton 2004, Hiromi et al. 2012). In fact, some studies reported that this species did not suffer any obvious increase in mortality even during the two severe El Niño droughts of 1993 and 1998 (Becker et al. 1998, Hiromi et al. 2012). Thus, we might assume prevention of hydraulic failure at the higher position of the stem, caused by the excess dehydration, by the osmotic adjustment and stomatal control in the upper part of the crown.

Relationship between ecological traits and response to drought in *D. aromatica*

Our target species, *D. aromatica*, has some specific drought tolerance mechanisms under canopy conditions in aseasonal tropical rain forest. Leaf water use in trees during the drought can be divided roughly into two types: in anisohydric species there is a

greater water potential gradient between soil and leaf with less stomatal regulation to maintain water uptake and photosynthesis; in isohydric species a constant leaf water potential is maintained with strong stomatal regulation but usually sacrificed photosynthesis (McDowell et al. 2008, Skelton et al. 2015). During the experiment, the study species showed anisohydric responses, e.g., decreased midday leaf water potential based on osmotic adjustment (down to -1.9 MPa) and maintenance of photosynthetic activity. However, during a non-drought period, Kitahashi et al. (2008) and Hiromi et al. (2012) reported isohydric-like behavior, with higher leaf water potential even at midday (higher than -1.3 MPa) compared with other canopy species (e.g., less than -2.0 MPa). According to Domec and Johnson (2012), some species have the potential to switch from isohydric to anisohydric behavior in order to prevent plant desiccation when soil moisture is low. Such switching may occur in *D. aromatica*. Further studies under more severe drought conditions could provide a better understanding of the drought response of *D. aromatica* in Borneo.

It should be noted that high wood density (~ 0.7 g cm $^{-3}$) and small vessel diameter in the species compared with other dipterocarp canopy species (Chu 1974, Hiromi et al. 2012, Inoue et al. 2015) may have afforded high tolerance to xylem cavitation, which is caused by a reduction in water potential during the experiment (Ishida et al. 2008, Chave et al. 2009). The strong negative relationship between drought-induced mortality and wood density during the El Niño-related drought in Borneo (Slik 2004, Van Nieuwstadt and Sheil 2005) was consistent with the present results. Although Meinzer et al. (2009) and Goldstein et al. (1998) noted the importance of xylem water storage to mitigate drought stress, *D. aromatica* may survive drought as a result of its plasticity with respect to leaf drought tolerance rather than wood water storage, which was limited by high wood density (Suzuki 1999, Osunkoya et al. 2007, Kenzo et al. 2016). In addition, Kume et al. (2008) also reported that daily fluctuation in sap flow in *D. aromatica* did not depend on stem water storage.

Conclusion

Our results demonstrate that a dominant canopy species in the study site, *D. aromatica*, may withstand drought with plasticity with respect to drought tolerance primarily by maintaining turgor pressure to improve its leaf water retention, and secondarily by regulating water consumption by stomatal closure at midday. However, we should recapture that there have been reported significant differences in drought tolerance and leaf water use traits among canopy tree species including *D. aromatica* in Borneo (Tyree et al. 1998, Hiromi et al. 2012, Inoue et al. 2015). Because this is a case study using a single tree species to examine drought responses with respect to leaf water use, further research under severe drought conditions, involving many other species and examining other physiological traits such as photoinhibition, hydraulic conductance in leaves and branches, P50

values and water permeability in fine roots, is required to provide a better understanding of forest and tree responses to severe drought in tropical rain forests in Southeast Asia.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology Online*.

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Conflict of interest

None declared.

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