

Effect of through-fall exclusion on leaf water use in the tropical canopy tree species *Dryobalanops aromatica*

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Abstract Climate change exposes vegetation to unusual drought, causing risk of a decline in productivity and increased mortality. It still remains unclear how trees and forests respond to such unusual drought, particularly in tropical rain forests. For a detailed study of tropical tree responses to soil drying, a through-fall exclusion experiment was conducted on three target trees of *Dryobalanops aromatica*, which is one of the dominant canopy tree species, for three months at Lambir Hills National Park. We compared the control and treatment trees regarding leaf water use at the top of the crown, including transpiration, stomatal conductance, photosynthesis, leaf water potential (predawn: Ψ_{pre} , midday: Ψ_{mid} and at turgor loss point: π_{tlp}), osmotic potential at full turgor (π_{100}), and a bulk modulus of elasticity (ϵ), by use of tree-tower and canopy-crane systems. During the experiment, there was no evidence of canopy dieback. However, the treatment trees showed higher water stress than the control trees, because predawn and midday leaf water potential decreased with soil drying. Additionally, the drought treatment led to a reduction in stomatal conductance (g_s), and the treatment trees showed about half the value of g_s compared with the control trees. Consequently, transpiration and photosynthetic rates clearly decreased compared with those in the control trees. Minimum values of midday leaf water potential in the treatment trees decreased during the drought, and were lower than π_{tlp} in the control trees. However, the treatment trees also decreased their π_{tlp} by osmotic adjustment, and their π_{tlp} values were lower than the minimum values of their midday leaf water potential. These results suggest that this species may have plasticity in drought tolerance by maintaining turgor pressure to improve its leaf water relations and regulating water consumption during severe drought.

Keywords Dipterocarpaceae, Drought tolerance, Leaf water use, Through-fall exclusion, Tropical rainforest

Introduction

Climate change has impacts on multiple aspects of forest ecosystems throughout the world (Foley et al. 2007, Trumbore et al. 2015). There are many reports on increasing tree mortality and declining forest functions in many different forest types caused by increasing drought severity and frequency with global warming (Allen et al. 2010). It seems that drought effects are more severe in tropical forests than in other forest types (Phillips et al. 2009, Zelazowski et al. 2011, Diffenbaugh and Field 2013). Recently, some researchers have reported that El Niño-related drought causes higher tree mortality in tropical rain forests in Southeast Asia (Nakagawa et al. 2000, Newbery and Lingenfelder 2009, Itoh et al. 2012). The tree mortality during an El Niño drought varied according to the tree size, and it was particularly high in canopy trees (Nakagawa et al. 2000, Potts 2003).

The upper canopy layers of tropical rain forests in Southeast Asia are dominated by trees of the family Dipterocarpaceae. It is known that their water use strategies seem to vary among different species even under the same canopy conditions (Hiromi et al. 2012, Inoue et al. 2015). Hiromi et al. (2012) suggested that the daily pattern of leaf water use in some dipterocarp canopy species was correlated with their susceptibility to unusual drought events; species with high transpiration rates in the daytime suffered a higher mortality than species with low transpiration rates during the severe drought caused by El Niño in 1998. Reduction of water consumption by lowering transpiration rates may be a mechanism of drought resistance.

Drought-resistant species have some specific strategies promoting drought avoidance and/or drought tolerance; the former strategy is mainly explained as being due to morphological traits such as leaf shedding for water saving and deep root systems for utilization of ground water, and the latter as due to physiological traits including osmotic adjustment and changes in elasticity of cell walls (Kozłowski and Pallardy 2002). Since it is well known that trees in tropical rain forests are evergreen with shallow root systems, the 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 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 been reported on drought tolerance of trees 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 wider range of π_{tlp} , and species with more negative π_{tlp} (i.e. with greater leaf-level drought tolerance) had a tendency to be distributed over drought-prone habitats affected by soil depth and soil sand content. In addition, the plasticity of drought tolerance also varied across species, and species that normally had a more positive π_{tlp} showed higher plasticity of π_{tlp} during an experimental drought in an Amazonian forest (Binks et al. 2016). On the other hand, in an aseasonal tropical rain forest in Southeast Asia, tree mortality varied among some dipterocarp species during the unexpected El Niño drought in 1997–1998, and the differences of mortality rate were closely related to the species' ecological and ecophysiological traits, such as leaf water use, wood density and habitat conditions (Hiromi et al. 2012). These results might suggest that species with lower mortality during unusual drought may have lower π_{tlp} and/or higher

plasticity of π_{tp} even in an aseasonal tropical rain forest. However, information on the variation of plasticity of π_{tp} is still limited in tropical trees, in particular in canopy tree species due to the difficulty of accessing their tree crowns (Binks et al. 2016).

In this study, we investigated the physiological response to a drought condition of *Dryobalanops aromatica*, a dominant dipterocarp canopy species in many forests in Borneo. We conducted a through-fall exclusion experiment and investigated changes of leaf water use and leaf water relations under water stress conditions. There are some reports that *D. aromatica* did not suffer any obvious increase in mortality during severe El Niño droughts (Becker et al. 1998, Hiromi et al. 2012). We then hypothesized that this species could change leaf water retention capacity by osmotic adjustment even under drought conditions.

Materials and methods

Study site

The through-fall exclusion experiment 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 a.s.l.). The study area had a humid tropical climate, with weak seasonal changes in rainfall and temperature (Kumagai and Kume 2012). The mean annual rainfall and temperature at Lambir Hills National Park from 2000–2009 were approximately 2600 mm and 25.8 °C (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 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Hiromi et al., 2012). Our experiment was performed at a 4-ha Crane plot (CP) in Lambir Hills National Park. An 85-m-tall canopy crane with a 75-m-long rotating jib was constructed in the center of the plot, so as to provide access to the top of the canopy (Sakai et al. 2002). To evaluate the effect of the drought experiment on leaf water use, we selected *Dryobalanops aromatica* Gaertn.f. (Dipterocarpaceae), which grows up to 65 m tall and 2 m in diameter (Itoh 1995), and which was well distributed throughout and around 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 set ladders up to the crown, terraces on the branches, and further ladders from there to the canopy.

Table 1 Height and DBH of the trees used for 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

Experimental design

We constructed equipment for through-fall exclusion on the three experimental trees (Fig. 1). This equipment was shaped like an umbrella with a radius of 15 m and a height of about 7 m, and was constructed by putting a soft vinyl chloride sheet on a frame made of wood. The term of through-fall exclusion was 5 months from the middle of November 2008 to the middle of March 2009. During the experiment, most rain was intercepted by the equipment and drained to the outside of the umbrella. The procedure cause significant reduction of the water available for the

trees, because majority of the root system of a mature tree of *D. aromatica* is within a range of 15 m from the stem (Yamashita et al. 2012).

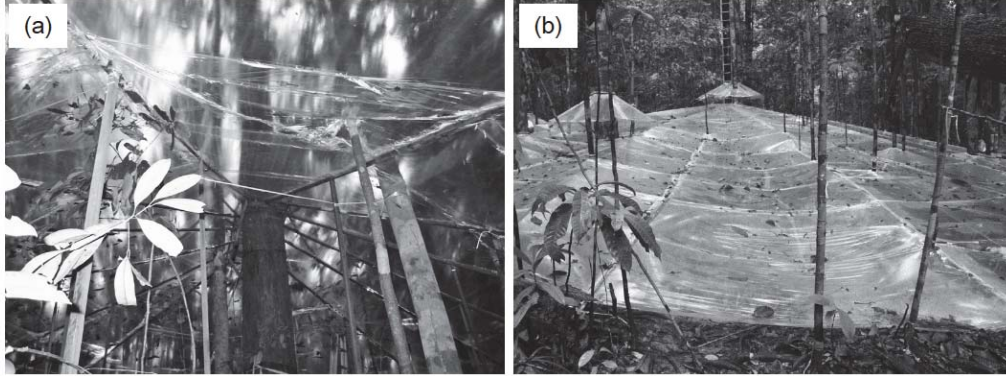


Fig. 1 Through-fall exclusion equipment spread like an umbrella around a treatment tree. Photos were taken from below (a) and beside (b) the equipment. See text for details of the equipment.

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 from the forest floor. Also, at a separate tower located some 500 m southwest of the crane, the rainfall was measured using a tipping bucket rain gauge (No.34T, Ohta Keiki). Time and date stamps were stored from each tip event of the rain gauge (HOBO Event, Onset, Pocasset, MA).

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-hour intervals (CR1000, Campbell Scientific, Logan, UT). Note that these measurements were conducted both in sites of the drought experiment and the control. An amplitude domain reflectometer (SM200, Delta-T Devices, Cambridge, UK) and a dielectric aquameter sensor (EC-10, Decagon Devices, Inc., Pullman, WA) were used to measure the time series of θ for the D1 and D3 plots, and D2 plot, respectively. A tensiometer (Special order, Environmental Measurement Japan Co. Ltd., Fukuoka, Japan) was also used to monitor ψ at the same depth as θ , thereby providing the necessary measurements to compute in-situ soil water retention curves at each depth or to consider the possible spatial variations in soil moisture condition. The weighted average θ in the 0–80 (θ_{0-80}) and 0–50 (θ_{0-50}) cm soil layers 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 m^3m^{-3}), respectively. The relative extractable water in the soil (Θ ; m^3m^{-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 drought experiment position for each plot, respectively.

Predawn and midday leaf water potential

Predawn and midday leaf water potential (Ψ_{pre} and Ψ_{mid}) were measured between 0600 and 0700h

and between 1200 and 1400h, respectively, in the field with a pressure chamber (Model 1002, PMS instruments, USA). The measurements of Ψ_{pre} were conducted before the drought experiment (October 2008) and from the beginning of the drought experiment (November 2008) until the time when 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 exposed shoots per individual about every ten days.

For Ψ_{mid} , 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 drought experiment period (December 2008) until the time when the recovery of Ψ_{mid} in the treatment trees was observed. The three treatment trees and one control tree (C2) were repeatedly measured by sampling three to five exposed shoots per individual about every ten days. For the control trees C1 and C2, Ψ_{mid} was measured once during the experimental period on 1 March 2009 and two times after the experiment on 22 March and 21 April 2009.

Diurnal changes in leaf water use

Leaf gas exchange parameters, such as photosynthetic and transpiration rates (A and E) and stomatal conductance (g_s) at light saturation, were measured by using a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE) on 1 March 2009 during the experiment. All measurements were made between 0800 and 1400 h at 2-hour intervals. We measured 3–5 fully expanded and apparently non-senescent leaves at the top of the crown of one individual each from 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, PMS instruments, USA), between 0600 and 1400 h, every 2 hours on the same day. A total of 3–5 exposed shoots from each individual (D1 and C2) were excised with pruning shears, and their water potential was measured immediately.

Pressure-volume curve

Water potential at turgor loss point (π_{lp}), osmotic potential at full turgor (π_{100}) and bulk modulus of elasticity (ϵ) were determined using the pressure-volume curve (Tyree and Hammel 1972, Maruyama and Morikawa 1983). A branch was cut from each of the treatment and control trees for determining the time course of leaf water relations every month during the experiment. The sampled branches were bagged to protect against dehydration during transport back to the laboratory. Then the base of each branch was cut in water and the branch was allowed to rehydrate in tap water for at least 12 hours.

Statistical analysis

To compare differences of water relation parameters between experimental and control trees and among measurement periods (pre-experimental period, experimental period and post-experimental period), we used one-way ANOVA. For all statistical analyses, we used R version 2.15.1 (The R foundation for statistical computing, Vienna, Austria).

Results and Discussion

Meteorological and soil moisture conditions

Similarities in soil moisture response to rainfall before and after the treatment and the difference between the positions inside and outside the umbrella were clearly identified (Fig. 2). During the experimental period, the peak conditions of soil drought inside the umbrella for the treatment trees were almost the same as the 1997/98 drought related to El Niño (Ishizuka et al. 2000).

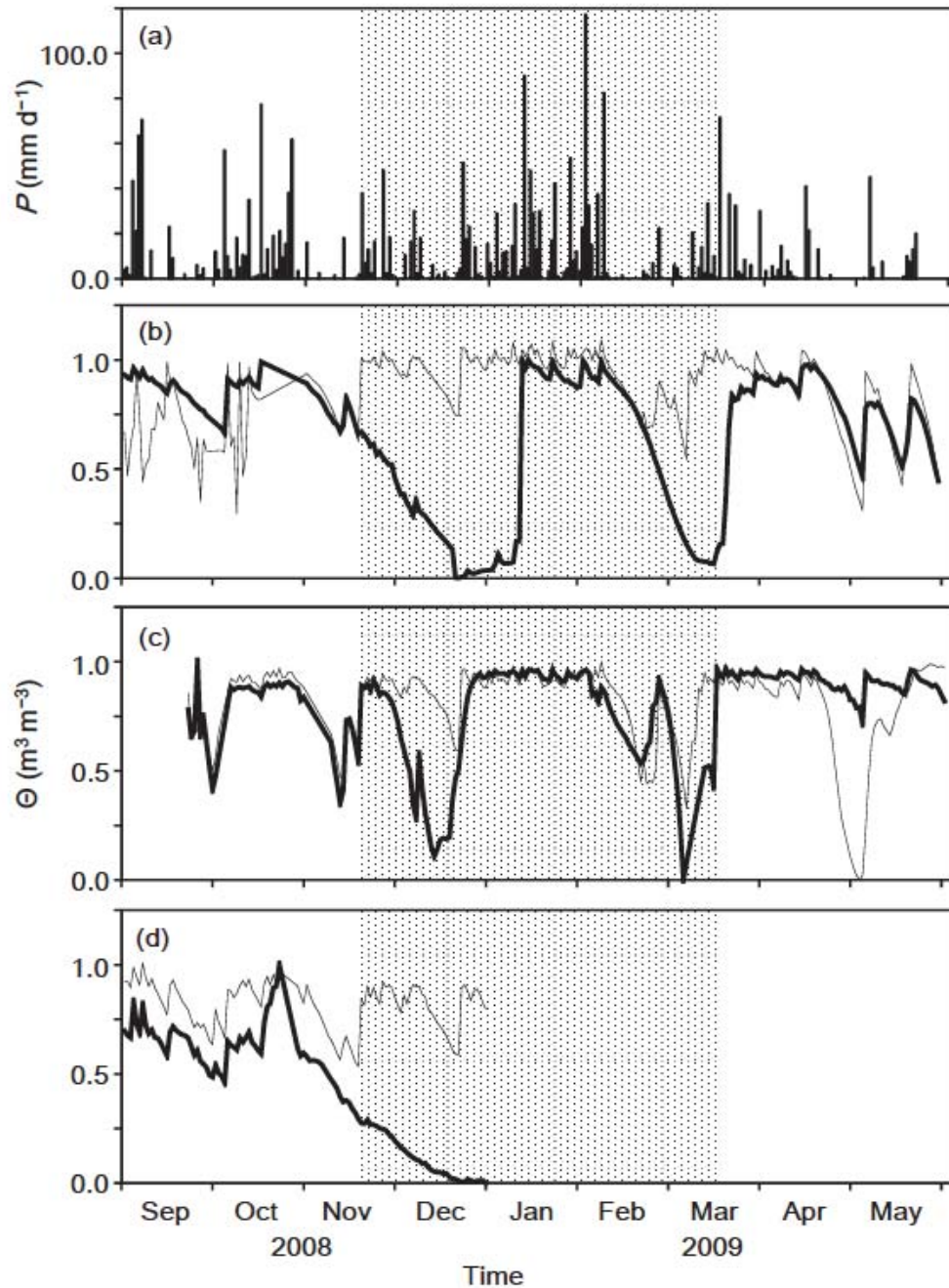


Fig. 2 Daily precipitation (P) (a), and relative extractable water in the soil (Θ) at drought-experiment (thick line) and control (thin line) positions for D1 (b), D3 (c), and D2 (d) plots. Shaded column represents the drought-experiment period.

Predawn and midday leaf water potential

During the experiment, Ψ_{pre} in the treatment trees decreased with soil moisture content (Table 2). Mean Ψ_{pre} values in the treatment trees clearly changed by about 0.14 MPa before compared to during the experiment, while the control trees showed constant mean Ψ_{pre} values and only a 0.01 MPa difference even during the experiment. It is known that tropical canopy trees tolerate daily fluctuations of water conditions and recover overnight (Bucci et al. 2004). However, the drought treatment caused clear water stress to the treatment trees; they showed notably lower values than the control trees during the experiment (Table 2).

Table 2 Changes in the leaf water relation parameters during the period of the through-fall exclusion experiment.

Parameter	Pre-experimental period		Experimental period		Post-experimental period	
	Control	Drought	Control	Drought	Control	Drought
Ψ_{pre}	-0.34 ± 0.02^a	-0.37 ± 0.04^a	-0.35 ± 0.02^a	-0.51 ± 0.02^b	-0.34 ± 0.03^a	-0.36 ± 0.02^a
Ψ_{mid}	-	-	-1.33 ± 0.06^a	-1.48 ± 0.21^a	-1.20 ± 0.04^a	-1.22 ± 0.15^a
π_{tlp}	-1.67 ± 0.03^a	-	-1.84 ± 0.03^b	-2.50 ± 0.06^c	-1.73 ± 0.03^a	-1.81 ± 0.02^{ab}
π_{100}	-1.34 ± 0.06^a	-	-1.60 ± 0.04^b	-2.25 ± 0.11^c	-1.47 ± 0.07^{ab}	-1.57 ± 0.02^b
ϵ	2.46 ± 0.13^a	-	3.90 ± 1.22^a	9.69 ± 0.15^b	3.67 ± 1.30^a	3.69 ± 1.16^a

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

Diurnal changes in leaf water use

A midday depression in leaf water potential and gas exchange parameters was observed in the control and treatment trees (Data not shown). Leaf water potential in both control and treatment trees was high early in the morning (0600–0800 h), but declined sharply between 1000–1200 h. The treatment trees in particular showed much lower values than the control trees. They commonly recovered slightly at 1400 h. All gas exchange parameters (A , E and g_s) peaked in the morning in both control and treatment trees, but rapidly declined between 1200–1400 h in the treatment trees, which displayed only about half the values of all the parameters in the control trees. On the other hand, the control trees showed a moderate midday depression in all the parameters. Hiromi et al. (2012) reported that *D. aromatica* is a water-saving type species with lower stomatal conductance than other dipterocarp species. However, even *D. aromatica* showed greater water consumption by adjusting stomatal regulation under water stress conditions.

Changes in leaf water relations in drought experiment

π_{tlp} and π_{100} significantly decreased in both control and treatment trees from the values in the control trees measured six months before the experiment (Table 2). However, both measurements were significantly lower in the treatment trees than in the control trees during the experimental period. Only the treatment trees showed significantly increased ϵ values during the experimental period compared with the control trees before and during the experiment. Even though the minimum value of midday leaf water potential in the treatment trees was over π_{tlp} in the control trees, there was no evidence of canopy dieback in the treatment trees during the experimental period. The midday leaf water potential in the treatment trees never dropped below π_{tlp} . These

results may suggest that the treatment trees could maintain their turgor potential under severe drought conditions.

Conclusions

Our results suggest that a dominant canopy species, *D. aromatica*, may have plasticity of drought tolerance by maintaining turgor pressure to improve its leaf water relations and regulating water consumption during severe drought. There is a consensus among scientists that further global warming will cause changes in precipitation patterns even in tropical rain forest areas (Asner et al. 2010, Hérault and Gourlet-Fleury, 2016). Although predictions about the changes in precipitation in Southeast Asia are still uncertain, irregular precipitation patterns may lead to increasing tree mortality and decreasing forest functions, such as forest production and carbon and water cycling, even if the total amount of annual precipitation may not change or may even increase in this area. Further studies using experimental approaches like this study on many other species would be required to provide a better understanding of forest and tree responses to severe drought.

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