



Limited stomatal regulation of the largest-size class of *Dryobalanops aromatica* in a Bornean tropical rainforest in response to artificial soil moisture reduction

Natsuko Yoshifuji^{1,5} · Tomo'omi Kumagai^{2,3} · Tomoaki Ichie⁴ · Tomonori Kume⁵ · Makiko Tateishi⁶ · Yuta Inoue^{1,7} · Aogu Yoneyama⁴ · Tohru Nakashizuka⁸

Received: 5 April 2019 / Accepted: 8 December 2019 / Published online: 19 December 2019
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Abstract

The physiological response of trees to drought is crucial for understanding the risk of mortality and its feedbacks to climate under the increase in droughts due to climate change, especially for the largest trees in tropical rainforests because of their large contribution to total carbon storage and water use. We determined the response of the mean canopy stomatal conductance per unit leaf area (g_s) and whole-tree hydraulic conductance (G_p) of the largest individuals (38–53 m in height) of a typical canopy tree species in a Bornean tropical rainforest, *Dryobalanops aromatica* C.F.Gaertn., to soil moisture reduction by a 4-month rainfall exclusion experiment (REE) based on the measurements of sap flux and leaf water potentials at midday and dawn. In the mesic condition, the g_s at vapor pressure deficit (D) = 1 kPa (g_{sref}) was small compared with the reported values in various biomes. The sensitivity of g_s to D (at a given g_{sref}) was ≥ 0.6 irrespective of soil moisture conditions, indicating intrinsically sensitive stomatal control with increasing D . The REE caused greater soil drought and decreased the mean leaf water potentials at midday and dawn to the more negative values than the control under the relatively dry conditions due to natural reduction in rainfall. However, the REE did not cause a greater decrease in g_s nor any clear alteration in the sensitivity of g_s to D compared with the control, and induced greater decreases in G_p during REE than the control. Thus, though the small g_s and the sensitive stomatal response to D indicate the water saving characteristics of the studied trees under usual mesic conditions, their limited stomatal regulation in response to soil drought by REE and the resulting decline in G_p might suggest a poor resistance to the unusually severe drought expected in the future.

Keywords Climate change · Emergent tree · Mean canopy stomatal conductance · Rainfall exclusion · Sap flow · Whole-tree hydraulic conductance

✉ Natsuko Yoshifuji
yoshifuji@ffpri.affrc.go.jp

¹ Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan

² Institute for Space-Earth Environmental Research, Nagoya University, Nagoya, Aichi 464-8601, Japan

³ Graduate School of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-ku, Tokyo 113-8657, Japan

⁴ Faculty of Agriculture and Marine Science, Kochi University, Nankoku, Kochi 783-8502, Japan

⁵ Kasuya Research Forest, Kyushu University, Sasaguri, Fukuoka 811-2415, Japan

⁶ Kyoto University Research Administration Office, Kyoto 606-8501, Japan

⁷ The United Graduate School of Agricultural Sciences, Ehime University, Matsuyama, Ehime 790-8566, Japan

⁸ Research Institute for Humanity and Nature, Kamigamo-Motoyama, Kyoto 603-8047, Japan

Introduction

Tropical forests account for 44% of the total global forest area (Keenan et al. 2015). Such forests play an important role in global carbon cycling (e.g. Beer et al. 2010) and are a major source of hydrologic flux that influences regional and global climate and water cycling (e.g. Kanae et al. 2001; Lean and Warrilow 1989; Spracklen et al. 2012). Tropical rainforests generally occur in humid environments that receive abundant annual rainfall with little or moderate seasonality (Kumagai et al. 2016). However, a dataset constructed from worldwide climate stations shows a long-term trend for decreasing rainfall in tropical rainforest regions in Africa and Asia during the late twentieth century (Malhi and Wright 2004). With regard to interannual variability, the El Niño-Southern Oscillation (ENSO) is the primary driver of rainfall fluctuations for large areas of Southeast Asia and central and northern South America (Malhi and Wright 2004). Reduced rainfall during El Niño events is observed in a band extending from Borneo to New Guinea and in northeast Amazonia (Malhi and Wright 2004). Furthermore, the results from climate models demonstrate that the frequency and intensity of El Niño events increase because of greenhouse warming in the future and that the effect continues even after the stabilization of greenhouse gas concentrations (Cai et al. 2014, 2018; Timmerman et al. 1999; Zheng et al. 2019).

Increases in tree mortality rates associated with intense drought during severe El Niño events have been reported for multiple tropical rainforests in Borneo, Amazonia and Central America (e.g. Clark 2004; Meir and Grace 2005; Nakagawa et al. 2000; van Nieuwstadt and Sheil 2005; Williamson et al. 2000). In the Amazon basin, severe drought in 2005, which was not driven by an ENSO event, caused an increase in the incidence of tree mortality and loss of aboveground biomass in many rainforest sites, thereby converting them from sinks to sources in carbon cycling (Phillips et al. 2009). These studies indicate that hydro-climatic change in the future may induce degradation of tropical forests (Feldpausch et al. 2016; Kumagai and Porporato 2012a; Phillips et al. 2009), in turn affecting feedbacks to the atmosphere (Bonan 2008; Kumagai et al. 2013; Meir et al. 2006; Takahashi et al. 2017). Fauset et al. (2015) demonstrated that, though the abundant species tends to contribute more to the total biomass and productivity in Amazonian forests, species maximum size also strongly influences biomass and productivity. The greater increases in mortality of large trees during unusually severe droughts were reported in tropical forests in Borneo and Central America (e.g. Condit et al. 1995; Nakagawa et al. 2000; van Nieuwstadt and Sheil 2005). Furthermore, Bennett et al. (2015), based on data

for tree growth and mortality in forests worldwide, concluded that droughts consistently had a more detrimental impact on the growth and mortality rates of larger trees. Therefore, to predict future carbon and water cycling in tropical rainforest ecosystems and their feedbacks to the local and global climate, an understanding of the ecological and physiological responses of large trees in tropical rainforest to drought is crucial.

Phillips et al. (2010) suggest that Bornean forests, which are located in the Southeast Asian tropics, show greater drought-sensitive mortality than Amazonian forests. This conclusion motivates greater consideration of the influence of drought on physiological response and water use of Bornean tropical forest trees. Bornean tropical rainforests are among the most humid biomes in the world and receive abundant rainfall throughout the year (see Kumagai et al. 2016). In such climatic conditions, water and carbon exchange between the atmosphere and the forest ecosystem is intense (Kumagai et al. 2004, 2005, 2009). Regulation of water use in these ecosystems tends to be limited on account of the usually abundant water resources, despite episodes of relatively severe drought (Kumagai and Porporato 2012b). However, water use and physiological response under drought are not yet well understood for these Bornean tropical rainforests, partly because of the irregular and infrequent occurrence of drought. In Southeast Asian tropical rainforests, it is common for trees to attain a maximum height of up to 70 m (see Yamakura et al. 1986). It was observed that only the upper 10–15% of the total number of largest trees in the present research plots in a Bornean tropical rainforest explained c. 75% of the total aboveground carbon storage and water use in the forest ecosystem (Tomo'omi Kumagai, unpublished). Thus, emergent tree species should be given higher priority to understand the response of water use to drought.

With regard to regulation of water status, plants can be categorized as 'isohydric' or 'anisohydric', which represent both ends of the water status regulation continuum rather than a dichotomy. Isohydric plants maintain a constant midday leaf water potential (Ψ_{l_day}) regardless of drought conditions by regulation of stomatal conductance and transpiration, whereas anisohydric plants allow Ψ_{l_day} to decline with decreasing soil moisture (see McDowell et al. 2008). This categorization has been associated with consideration of the causes of drought-induced tree mortality (McDowell et al. 2008). Namely, the constant Ψ_{l_day} of isohydric plants is advantageous for avoidance of drought-induced hydraulic failure, whereas stomatal closure during prolonged periods of drought can lead to carbon starvation. In contrast, hydraulic failure at a lower Ψ_{l_day} tends to occur more often for anisohydric plants than for isohydric plants (McDowell et al. 2008). We note that Martínez-Vilalta and García-Forner (2017) insisted that it is difficult to attribute

the potential cause of drought-induced mortality (hydraulic failure or carbon starvation) to iso/anisohydric regulation of Ψ_{1_day} because of the complexity of the relationship of Ψ_{1_day} with stomatal regulation and xylem vulnerability to drought. As for the vulnerability of hydraulic failure, recent studies investigated the hydraulic safety margins determined as the differences between xylem pressure at 50% loss of conductivity and minimum xylem pressure under natural condition rather than an iso/anisohydric categorization, and examined the differences between angiosperms and gymnosperms (Choat et al. 2012; Meinzer et al. 2009). Nevertheless, the concept of iso/anisohydric behavior is still a promising tool to understand the characteristics of drought responses of plants.

For this categorization and further examination of the environmental and biological control of plant water status and stomatal behavior, derivation of the mean canopy stomatal conductance per unit leaf area (g_s) at vapor pressure deficit (D) = 1 kPa (g_{sref}) and the sensitivity of g_s to D (m) from the observed g_s should be useful (Oren et al. 1999). The g_{sref} is considered to represent the intrinsic and maximal capacity of g_s . The m/g_{sref} ratio of 0.6 is predicted from the simple hydraulic model assuming perfect stomatal regulation of constant differences between leaf and soil water potentials with respect to D (Oren et al. 1999). An m/g_{sref} ratio larger (smaller) than 0.6 denotes more (less) strict regulation of the minimum leaf water potential (e.g. Ewers et al. 2005). Kumagai et al. (2015) showed that the 0.6 m/g_{sref} ratio may be a criterion for determining whether a studied plant shows isohydry or anisohydry. In addition, some observational studies have shown that it is possible for m/g_{sref} to change temporally (e.g. Ewers et al. 2005). Igarashi et al. (2015) reported a seasonal decline in m/g_{sref} in the leaf-senescence season in a deciduous teak plantation in northern Thailand, which suggests that stomatal sensitivity is altered in response to seasonal drought. Thus, the values of g_{sref} and m/g_{sref} and their responses to drought are useful measures to examine the characteristics of water-use regulations of plants based on the concept of iso/anisohydric categorization.

Observational study of the effects of unusual drought alone is challenging. Thus, field-based rainfall exclusion (canopy throughfall exclusion; TFE) experiments represent a promising approach to investigate the responses of tropical rainforest trees to soil moisture reduction (e.g. da Costa et al. 2010; Fisher et al. 2006; Nepstad et al. 2007; Rowland et al. 2015). We conducted a rainfall exclusion experiment (REE), which aimed to exclude c. 100% of incident rainfall from penetrating to the soil, with a typical canopy and emergent evergreen species in Bornean tropical rainforests, *Dryobalanops aromatica* C.F.Gaertn. (Dipterocarpaceae), to examine the response of their water use to artificial soil moisture reduction based on the concept of iso/anisohydric categorization. Though either isohydric or anisohydric

categorization is used to represent the strategy of one species in general, we examined the characteristics of the responses of water status to changing D and soil moisture using the words “isohydric-like” or “anisohydric-like” in this study. We derived g_s and whole-tree hydraulic conductance (G_p) based on the measurements of sap flow and leaf water potential. We investigated whether Ψ_{1_day} , g_s and its sensitivity to D changed in response to soil moisture reduction by comparing the changes in Ψ_{1_day} , g_s and m/g_{sref} between REE and control trees. We further investigated how G_p changed in response to the soil moisture reduction. The extent of the changes in g_s and G_p under the different extent of soil moisture reduction caused by naturally reduced rainfall and REE treatment was determined. In addition, we also examined the absolute values of g_{sref} and m/g_{sref} to determine the intrinsic stomatal regulation of *D. aromatica*.

Materials and methods

Study site

The study was conducted in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak (the north-western part of Borneo), Malaysia (4° 12' N, 114° 02' E). The continuous canopy height at the study site is about 40 m, but emergent trees attain a height of 50 m (Kumagai et al. 2004). The mean leaf area index was 6.2 m² m⁻² and ranged spatially between 4.8 and 6.8 m² m⁻² (Kumagai et al. 2004). Soils at the study site are classified as Red-Yellow Podzolic Soils (Malaysian classification) or Ultisols (United States Department of Agriculture Soil Taxonomy), with high sand content (62–72%) and high porosity (54–68%) (Ishizuka et al. 1998). The depth of the soil layer was 2.32 m on average and was around 1 m in shallow areas (Wakahara et al. 2014). The ground water table was not observed (Taeko Wakahara, personal observation). The mean annual rainfall was 2600 mm with interannual variation ranging between 2191 and 2944 mm (Kume et al. 2011). Rainfall was distributed through the year with no distinctive phase-locked dry seasons (Kume et al. 2011). The mean annual temperature from 2000 to 2009 was 25.4 °C, with seasonal variation of slightly higher temperature between July and September (Kume et al. 2011).

A 93-m-tall canopy crane with a 75-m-long rotating jib was constructed at the study site to provide access to the upper canopy. Rainfall and solar radiation (R_s) were measured at the top of the crane, 85.8 m above the ground, with a tipping bucket rain gauge (RS102, Ogasawara Keiki, Tokyo, Japan) and a solar radiometer (MS401, EKO, Tokyo, Japan), respectively. Air temperature (T_a), relative humidity (h), and wind speed (U) were measured at 60 m above the ground on the crane with a thermohygrograph (HMP35A, Vaisala

Co., Helsinki, Finland) and a cup-anemometer (AC750, Makino Instruments, Tokyo, Japan), respectively. Data loggers (CR10X, Campbell Scientific Inc., Logan, UT, USA) recorded R_s , T_a , h , and U every 5 s, and 10-min averages were calculated. Details of meteorological observations and data processing are provided by Kume et al. (2011). Net radiation (R_n) was estimated using the empirical relationship with R_s , obtained from intensive observations at the study site, as $R_n = 0.87R_s - 35.0$ ($R^2 = 0.99$; Kumagai et al. 2004).

Plant materials, rainfall exclusion experiment, and soil moisture measurement

We selected seven canopy or emergent trees of *D. aromatica* located within a distance of about 350 m from the crane. *D. aromatica* is a typical canopy evergreen species

Table 1 Stem diameter (D_S), tree height (H), and total leaf area (A_L) of *Dryobalanops aromatica* trees studied in the rainfall exclusion experiment (REE) in Lambir Hills National Park, Sarawak, Borneo

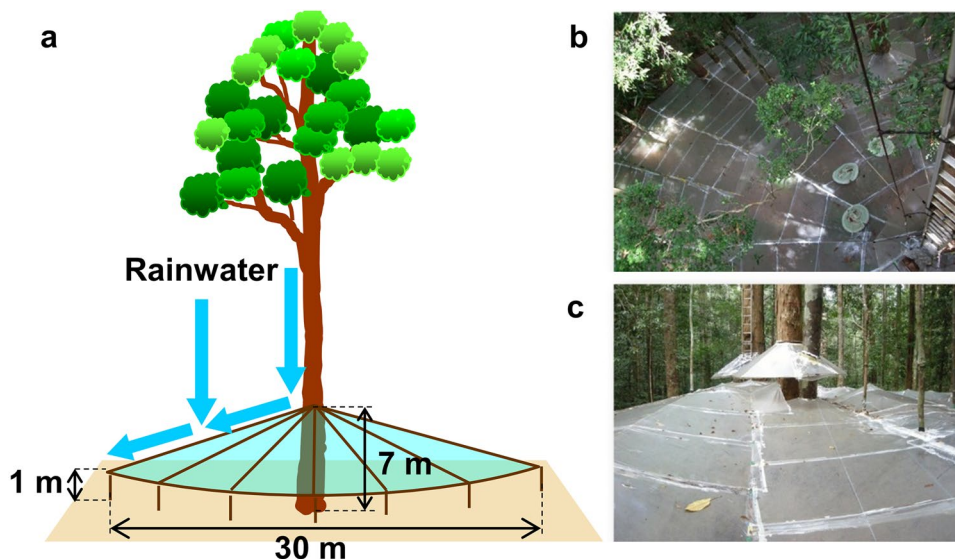
Tree#	D_S (m)	H (m)	A_L^a (m ²)	REE period
D1	0.64	42.4	272.3	15 Nov 2008–16 Mar 2009
D2	1.06	44.9	579.3	22 Nov 2008–17 Mar 2009
D3	0.59	37.8	222.5	28 Nov 2008–18 Mar 2009
C1	0.95	50.2	540.9	Control
C2	1.44	53.4	1021.0	Control
C3	0.58	40.4	226.2	Control
C4	0.52	43.4	203.6	Control

^a A_L of all sample trees was estimated from D_S and H using allometric equations proposed for a tropical lowland evergreen dipterocarp forest in East Kalimantan, Borneo (Yamakura et al. 1986), with leaf mass per area of *D. aromatica* measured at the study site (Kenzo et al. 2004).

distributed on the Malay Peninsula, Borneo, and Sumatra (Ashton 2004). The REE was conducted with three of the seven selected trees (D1–D3) from November 2008 to March 2009, and the remaining four trees were exposed to natural conditions as the control (C1–C4) (Table 1). For the REE, transparent and soft vinyl chloride sheeting of 30 m diameter was placed above the ground around the base of each selected tree (with the trunk located at the center of the sheeting), to function like a large umbrella to prevent rain water from reaching the ground (Fig. 1). Before installation of the sheeting, we confirmed that the maximum horizontal spread of the root system of *D. aromatica* was less than 15 m from the stem based on the survey of the rooting area by tracing the randomly selected roots from the sampled trees (Yamashita et al. 2012). The sheeting sloped from the center to the margin to ensure that rain water ran off the sheeting and away from the tree. The height of the sheeting above the ground was 7 m at the center and 1 m at the margin to allow aeration. Growth of understory trees was allowed by cutting a small slit in the sheet as appropriate. The rainfall that passed through each slit was captured by a funnel to prevent it reaching the soil.

It took several days to install the sheeting around an individual tree, therefore the starting date of the REE differed up to 13 days among the individual trees (Table 1). For the analysis of tree water-use behavior under different drought conditions, we delimited five observation periods: the period before the REE (B; from 1 October 2008 to the day preceding the REE starting date); the initial period of the REE (P1; from the REE starting date to 31 December 2008); the middle period of the REE (P2; from 1 January 2009 to 10 February 2009); the late period of the REE (P3; from 11 February 2009 to the end date of the REE); and the period after the REE (A; from the first day after the REE end

Fig. 1 a Schematic illustration of the rainfall exclusion experiment. Photographs of the experimental setup taken from b above and c the side



date to 31 May 2009) (see Table 1). For control trees, the same starting and end dates of periods as the REE-treated tree D2 were adopted (see Table 1). Note that all REE trees and control trees were exposed to the natural environmental conditions in the periods B and A, whereas only REE trees were exposed to artificial soil moisture reduction by REE in the periods P1 to P3.

The height (H) of the selected trees ranged from 37.8 to 53.4 m (Table 1). The girth of the stem of the selected trees was measured just above the buttress root. Stem diameter (D_S) was calculated assuming a perfect circle shape in cross-section, and varied from 0.52 to 1.44 m among the studied trees. The total leaf dry weight per tree was estimated from H and D_S using allometric equations determined for a lowland dipterocarp forest in East Kalimantan, the eastern portion of Borneo, of which the range of H and D_S were up to 70 m and 1.3 m, respectively, covering the range of our studied trees (Yamakura et al. 1986). Total leaf area per tree (A_L ; m²) was estimated by dividing total leaf dry weight by leaf mass per area of *D. aromatica* measured at the study site (160.4 g m⁻²; Kenzo et al. 2004) (Table 1).

Paired measurements of volumetric soil moisture content (θ) inside and outside the sheeting for REE were conducted using amplitude domain reflectometers (SM200, Delta-T Devices, Cambridge, UK) at the D1 and D3 plots and dielectric aquameter sensors (EC-10, Decagon Devices, Inc., Pullman, WA, USA) at the D2 plot. Two sets of three sensors were installed at each plot: one set was inside the sheeting for REE and the other was outside. The three sensors of each set were installed at depths of 0.1, 0.3, and 0.8 m in the soil of the D1 and D3 plots and 0.1, 0.2, and 0.5 m in the D2 plot. The θ was recorded at 1-h intervals with data loggers (CR1000, Campbell Scientific). Tensiometers (Special order, Environmental Measurement Japan Co. Ltd., Fukuoka, Japan) were also installed to monitor matric potential (Ψ_s) at the same depths 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 the soil moisture condition. The weighted average θ in the 0- to 0.8-m ($\theta_{0-0.8}$) and 0- to 0.5-m ($\theta_{0-0.5}$) soil layers was calculated as $\theta_{0-0.8} = (20\theta_{0.1} + 35\theta_{0.3} + 50\theta_{0.8})/105$ and $\theta_{0-0.5} = (15\theta_{0.1} + 20\theta_{0.2} + 30\theta_{0.5})/65$ (where θ_x is θ at a depth of x m, in m³ m⁻³), respectively. The relative extractable water in the soil (Θ ; m³ m⁻³) was calculated by using these weighted average θ as $\Theta = (\theta - \theta_r)/(\theta_s - \theta_r)$, where θ_r and θ_s are the residual and the saturated water content averaged in the soil layer for each plot, respectively (Inoue et al. 2017). We used Θ to estimate the soil moisture conditions of the upper soil layer because Ψ_s declined below the lower limit of the measurement range of a tensiometer, which is about -0.1 MPa. The Θ at the D3 site was available only until December 2008 because of problems in the measurement system.

Sap flow measurement

Sap flow was measured for all of the REE trees (D1–D3) and two control trees (C1 and C2) by the thermal dissipation method with self-made Granier-type sensors (Granier 1987). Each sensor consisted of a pair of heated and unheated probes (20 mm long and 2 mm diameter), each containing a needle with a thermocouple. The temperature difference between the heated and unheated probes (ΔT) was measured every 30 s, and the 30-min averages were recorded by a data logger (CR1000, Campbell Scientific). The xylem sap flux density (F_d ; mm s⁻¹) was calculated from ΔT using Granier's (1987) procedure. The details of the sensor structure, installation, and measurement system are identical to those of Tateishi et al. (2010).

A set of six sensors were inserted radially into the stem just above the buttress root in each studied tree. Three sensors were inserted at 0–20 mm depth in the sapwood in the southeast, northwest, and southwest or northeast directions; two sensors were inserted at 20–40 mm depth in the east and west directions; and one sensor was inserted at 40–60 mm depth in the east or northeast directions. The sensors were sufficiently separated to prevent the influence of the heated probe of a neighboring sensor. The portion of the trunk in which the sensors were inserted was insulated with an aluminum cover to avoid thermal influences from radiation. Thirty sensors in total were installed throughout the study period (October 2008–May 2009). Although damaged sensors were replaced as frequently as possible, long data gaps resulted from irregularity in the electricity supply as well as sensor failure because the studied trees were distributed over a wide area and were located far from the power source. As a result, F_d for D2 and C2 was measured only until December 2008 and January 2009, respectively.

Whole-tree transpiration (E_T ; kg s⁻¹) was calculated with consideration of radial profiles of sap flux density using Eq. (1):

$$E_T = \sum_i (A_{s_i} \overline{F_{d_i}}), \quad (1)$$

where A_{s_i} (m²) and $\overline{F_{d_i}}$ (mm s⁻¹) are the donut-shaped sapwood area and the circumferential mean F_d , respectively, at depth i ($i=0-20, 20-40,$ and $40-60$ mm). An additional intensive measurement of radial profiles of F_d up to 100 mm depth showed that the contribution of F_d at 60–100 mm depth was less than 8.8% (data not shown). Thus, $F_d > 60$ mm depth in the sapwood was ignored for estimation of E_T . We calculated E_T only when data for all of the six sensors per tree were available. The E_T per unit leaf area (E_L ; mm s⁻¹) was derived with the formula:

$$E_L = \frac{E_T}{A_L}. \quad (2)$$

If A_L changed during the observation period, we needed to take its effect on Eq. (2) into consideration. We monitored leaf-fall of the REE trees using litter traps installed on the sheeting, and confirmed that the amount of leaf litter did not change significantly even during the REE treatment periods (data not shown). Thus, we assumed A_L was constant for each studied tree throughout the observation period.

Leaf water potential measurement

Leaf water potential at dawn (Ψ_{1_dawn}) and Ψ_{1_day} were measured for all of the REE trees and three control trees (C1, C3, and C4) between 12:00 and 14:00 and between 06:00 and 07:00, respectively, using a Scholander-type pressure chamber (Model 1002, PMS Instruments, Corvallis, OR, USA) with N_2 balancing gas. We accessed the upper canopy to sample leaves with the gondola of the canopy crane except for D2 and D3, which were beyond the crane jib range. We, therefore, reached the upper canopy of D2 and D3 with ladders attached to the tree trunks. Three to five leaves per tree were sampled from sun-exposed shoots at almost the same height of the canopy of each tree at every measurement. Measurements of Ψ_{1_dawn} were recorded for the periods from B to A; the number of measurement days per tree per period varied from 1 to 8 d. Measurements of Ψ_{1_day} were recorded from P1 to A for D1–D3 and C1, and from P3 to A for C2 and C3; the number of measurement days per tree per period varied from 1 to 4 d.

Calculation and analysis of mean canopy stomatal conductance

The g_s ($m\ s^{-1}$) was calculated for each tree used for sap flow measurement with the simplified form of the Penman–Monteith equation (Kumagai et al. 2008; Oren et al. 2001; Pataki and Oren 2003):

$$g_s = \frac{\gamma \lambda E_L}{\rho_a c_p D}, \quad (3)$$

where γ is the psychrometric constant ($Pa\ K^{-1}$), λ is the latent heat of vaporization of water ($J\ kg^{-1}$), ρ_a is the density of dry air ($kg\ m^{-3}$), c_p is the specific heat of air at constant pressure ($J\ kg^{-1}\ K^{-1}$), and D is the vapor pressure deficit (Pa). Two important assumptions must be satisfied to use Eq. (3) for calculation of g_s : (1) the leaf boundary-layer conductance (g_{bl}) is large relative to leaf stomatal conductance, and (2) the time-lag between transpiration in the canopy leaves and F_d measured in the lower stem can be ignored. Assumption (1) means coupling between the leaf surface

and atmosphere and negligible effect of wind speed on transpiration. Assumption (1) can be justified because we examined the relationship between D and E_L under different wind speeds and observed little variation (data not shown). It has been considered that coniferous species can be expected to satisfy Assumption (1) because of the narrow leaves with small characteristic dimension (d) but not for broadleaf species, such as *D. aromatica*, because of the large d (Kume et al. 2015). However, on the basis of wind tunnel experiments and model calculations, Kume et al. (2015) revealed that the significance of the effect of wind speed on transpiration cannot be simply determined by d nor leaf type (coniferous or broadleaf) and that the species with low leaf stomatal conductance can satisfy Assumption (1) irrespective of leaf type. Assumption (2) can be also justified because less-than-20-min time-lag was observed in comparisons of the diurnal course of sap flow velocity in the basal stem above the buttress roots of a *D. aromatica* at the study site with that in a twig at the height of 52.4 m of the same tree and with the canopy-scale transpiration (Kume et al. 2008).

Responses of g_s to environmental variables are commonly described by a series of multiplicative functions of each variable (Jarvis 1976). Oren et al. (1999) focused on the relationship between g_s and D (kPa) under the condition of non-limiting light and modeled as:

$$g_s = g_{sref} - m \ln D. \quad (4)$$

In the present study, we determined g_{sref} and m for each studied tree in each observation period to facilitate the comparison of g_s response to D between the observation periods and between the REE and control trees. We used boundary line analysis, which allowed selection of data representing the maximum conductance without the effect of low light (e.g. Ewers et al. 2001; Schäfer et al. 2000). The upper boundary line was derived by regressing Eq. (4) with data obtained as follows: (1) partitioning g_s data into 0.2 kPa D intervals after excluding data when $D < 0.5$ kPa, $R_n \leq 0$ $W\ m^{-2}$ and under rainy conditions, (2) calculating the mean and standard deviation of g_s in each interval, (3) removing outliers ($P < 0.05$, Dixon's test: see Sokal and Rohlf 2012), (4) selecting the data falling above the mean plus one standard deviation, (5) averaging the selected data for each D interval with $n \geq 3$ for the remaining g_s values, and (6) g_{sref} and m were calculated as the intercept and slope of the linear regression line between the mean g_s values of all D intervals obtained in Step (5) and $\ln D$.

Calculation of whole-tree hydraulic conductance

Whole-tree hydraulic conductance (G_p ; $mm\ day^{-1}\ MPa^{-1}$) of each studied tree was calculated for each observation period using Eq. (5) following Wullschleger et al. (1998):

$$\begin{aligned}
 G_p &= \frac{\overline{E_L}}{\overline{\Psi_{\text{soil}}} - (\overline{\Psi_{1,\text{day}}} + \Psi_g)} \\
 &= \frac{\overline{E_L}}{(\overline{\Psi_{1,\text{dawn}}} + \Psi_g) - (\overline{\Psi_{1,\text{day}}} + \Psi_g)} \\
 &= \frac{\overline{E_L}}{\overline{\Psi_{1,\text{dawn}}} - \overline{\Psi_{1,\text{day}}}}, \quad (5)
 \end{aligned}$$

where $\overline{E_L}$, $\overline{\Psi_{1,\text{dawn}}}$ and $\overline{\Psi_{1,\text{day}}}$ are mean daily E_L , mean $\Psi_{1,\text{dawn}}$ and mean $\Psi_{1,\text{day}}$, respectively, in each observation period, $\overline{\Psi_{\text{soil}}}$ is mean soil water potential, and Ψ_g is gravitational potential at the tree height.

Results

Environmental conditions and whole-tree transpiration

Rainfall was observed through the whole study period with variations in daily depth and the number of days with no rainfall between the observation periods (Fig. 2a). Mean daily rainfall values were 10.4, 7.9, 19.1, 5.9, and 4.6 mm day⁻¹ in B, P1, P2, P3, and A, respectively, and gradually declined from B to A except in P2. Mean daily rainfall in P2 was the largest among the periods and was about 2.7 times the 10-year mean from 2000 to 2009 (7.1 mm day⁻¹) at the study site. Mean daily rainfall in P3 and A were smaller than the 10-year mean from 2000 to 2009. The Θ measured outside the sheeting for REE also declined gradually from B to A except in P2, indicating that the control trees were exposed to humid conditions in P2 but to relatively dry conditions in P3 and A because of naturally reduced rainfall (Fig. 2b–d). R_n and D declined from B to P2 then increased from P2 to A (Fig. 2a).

The values of Θ measured inside the sheeting for REE were not different from the values measured outside the sheeting in B and A. However, Θ measured inside the sheeting was considerably smaller than that measured outside the sheeting from P1 to P3, though temporal sudden increases were observed because of rainwater leakage caused by a partial breakage in the sheeting due to fallen branches or heavy rainfall (Fig. 2b–d). This indicates that REE treatment effectively caused greater soil moisture reduction around the REE trees during P1–P3 compared with the naturally reduced rainfall in A.

The mean $\Psi_{1,\text{dawn}}$ of control trees was less negative than -0.39 MPa throughout the observation periods and showed little or no variation. The mean $\Psi_{1,\text{dawn}}$ was slightly less negative in P2 than in the other periods (Fig. 3d, f, g)

because of the moist conditions due to the occurrence of high rainfall (Fig. 2). There were not significant differences between $\Psi_{1,\text{dawn}}$ of REE and the control trees in B ($P=0.14$). The mean $\Psi_{1,\text{dawn}}$ of the REE trees declined to between -0.43 and -0.59 MPa during REE treatment, from P1 to P3, although the differences among the observation periods were not statistically significant in D2 (Fig. 3a–c). $\Psi_{1,\text{dawn}}$ of the REE trees were significantly more negative than those of the control trees in P1, P2, and P3 ($P \leq 2.7 \times 10^{-13}$) even though the rainwater leakage caused temporal increases in Θ in the upper soil layer (0- to 0.8-m depth) around the REE-treated trees (Fig. 2b–d). These results indicate that the REE trees were exposed to a severer drought than the control trees during P1–P3.

The mean daily E_L of control trees showed small variation among the observation periods; a slight decline was observed between B and P2 in C1 (Fig. 3d), which may be affected by the declines in R_n , D , and rainfall in these periods (Fig. 2). The mean daily E_L of the REE trees significantly declined during REE treatment, with the smallest values observed in P2 (Fig. 3a–c).

Mean canopy stomatal conductance

In all studied trees, g_s decreased with increasing D . When compared at the same D , g_s declined from B to P1 in the REE trees and the control tree C1 (Fig. 4a–d). The g_s of all REE trees and C1 remained lower throughout the periods P1–P3 and A. The g_s of C2, which might be underestimated due to overestimation of A_L (see Table 1, Eqs. (2), (3)), was relatively constant over the observation periods (Fig. 4e). The g_{sref} and m of the REE trees declined during REE treatment (P1–P3) and remained small in A (Fig. 5a–c). For the control trees, g_{sref} and m of C1 also declined gradually, whereas those of C2 slightly increased (Fig. 5d, e). During the entire observation period, g_{sref} of the REE trees D1, D2, and D3 declined by 16.2%, 16.8%, and 27.9%, respectively, and m declines by 30.1%, 24.5%, and 46.0%, respectively. These values were not greater than those of C1 except for m of D3; g_{sref} and m of C1 declined by 29.9% and 33.0%, respectively. The values of m/g_{sref} differed among the studied trees; however, the time series showed no clear differences between the REE and the control trees (Fig. 6). Note that m/g_{sref} is unaffected by possible underestimation of g_s of C2 because its influence on both m and g_{sref} is cancelled by using their ratio. Thus, g_s , g_{sref} , and m for both the REE and the control trees except for C2 declined throughout the observation periods, and the rates of their temporal declines were not greater for the REE trees than for the control tree C1. These results suggest that, though the background trend of soil moisture caused by natural reduction in rainfall over the entire observation period (Fig. 2) likely caused a small

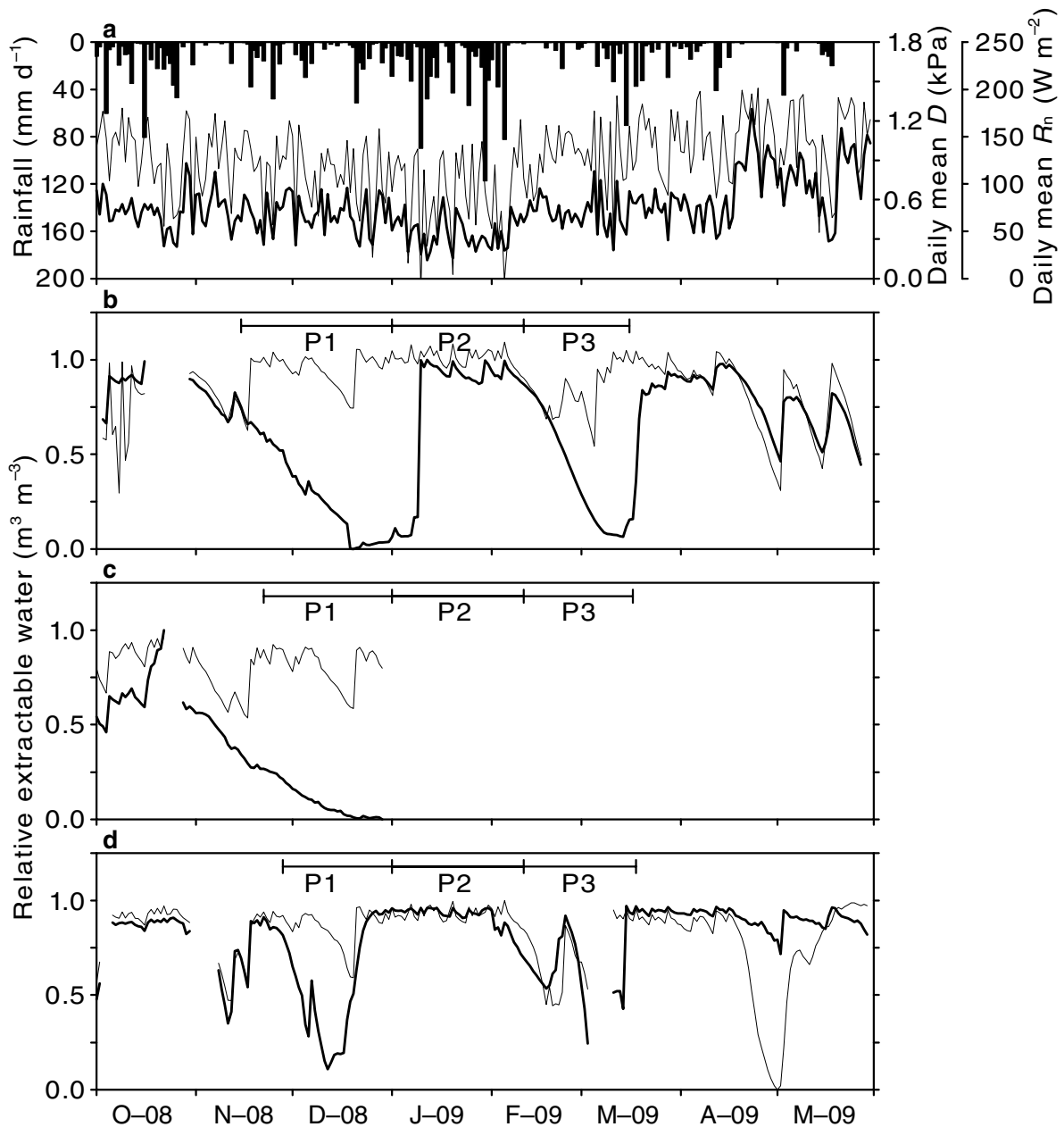


Fig. 2 Meteorological and soil moisture conditions from October 2008 to May 2009. **a** Daily rainfall (vertical bars), daily mean net radiation (R_n , thin line), and daily mean vapor pressure deficit (D , thick line). Relative extractable water (Θ) in the soil inside (thick

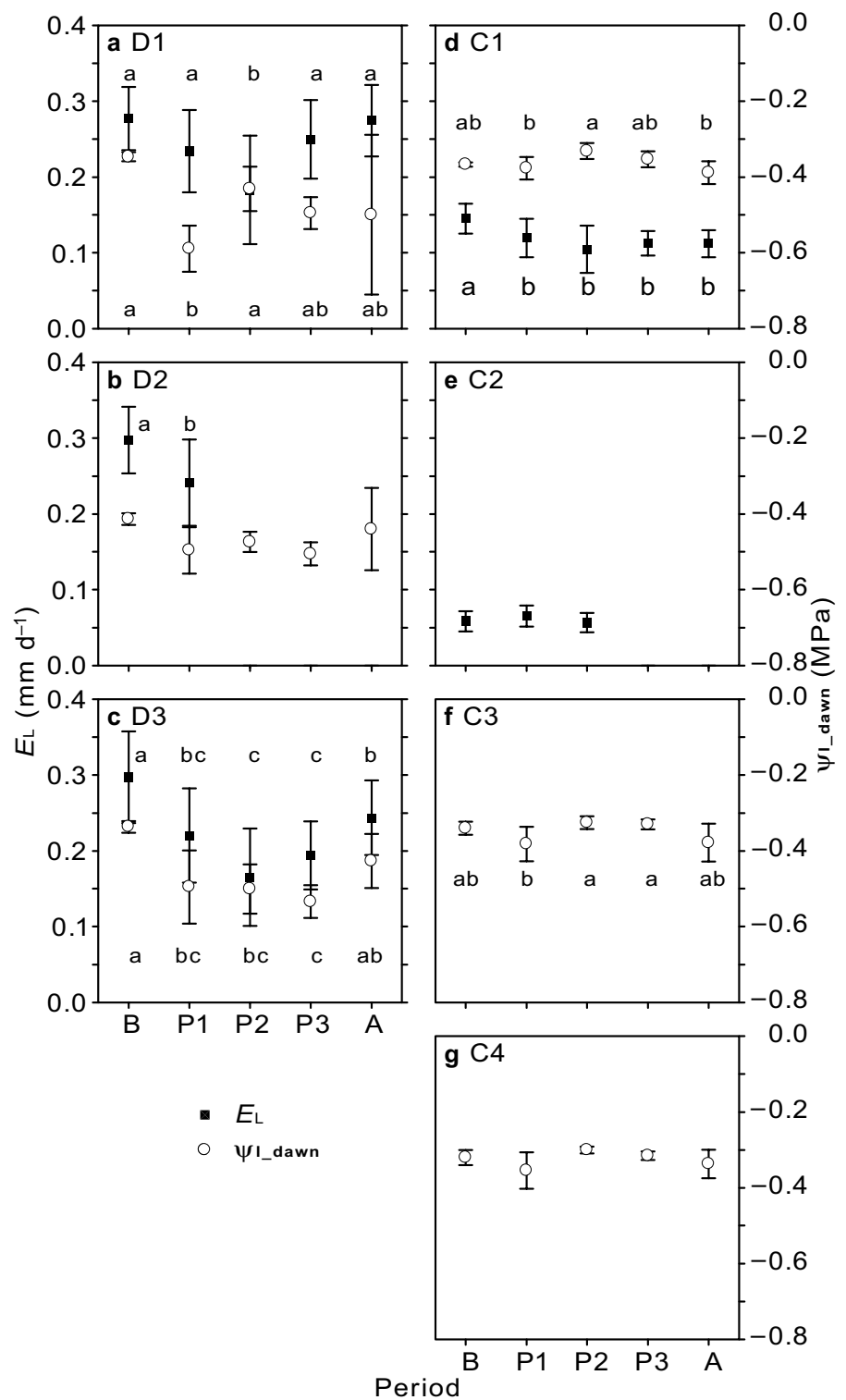
line) and outside (thin line) the sheeting for the rainfall exclusion experiment (REE) at the **b** D1, **c** D2, and **d** D3 plots. Horizontal bars in **b**, **c** and **d** show the initial, middle, and late periods of REE (P1, P2, and P3, respectively).

reduction in g_s of both the REE and the control trees (Fig. 4), greater soil moisture reduction caused by REE treatment had little influence on the values of g_s and the sensitivity of g_s regulation to D of the REE trees.

Whole-tree water status

The mean Ψ_{1_day} of the control trees varied between -0.76 and -1.30 MPa over the whole observation period and the value was lowest in P3 (Fig. 7d–f) during which the rainfall amount was small (Fig. 2). The mean Ψ_{1_day} slightly increased in P2 in response to the moist soil condition around the control trees due to the occurrence of high

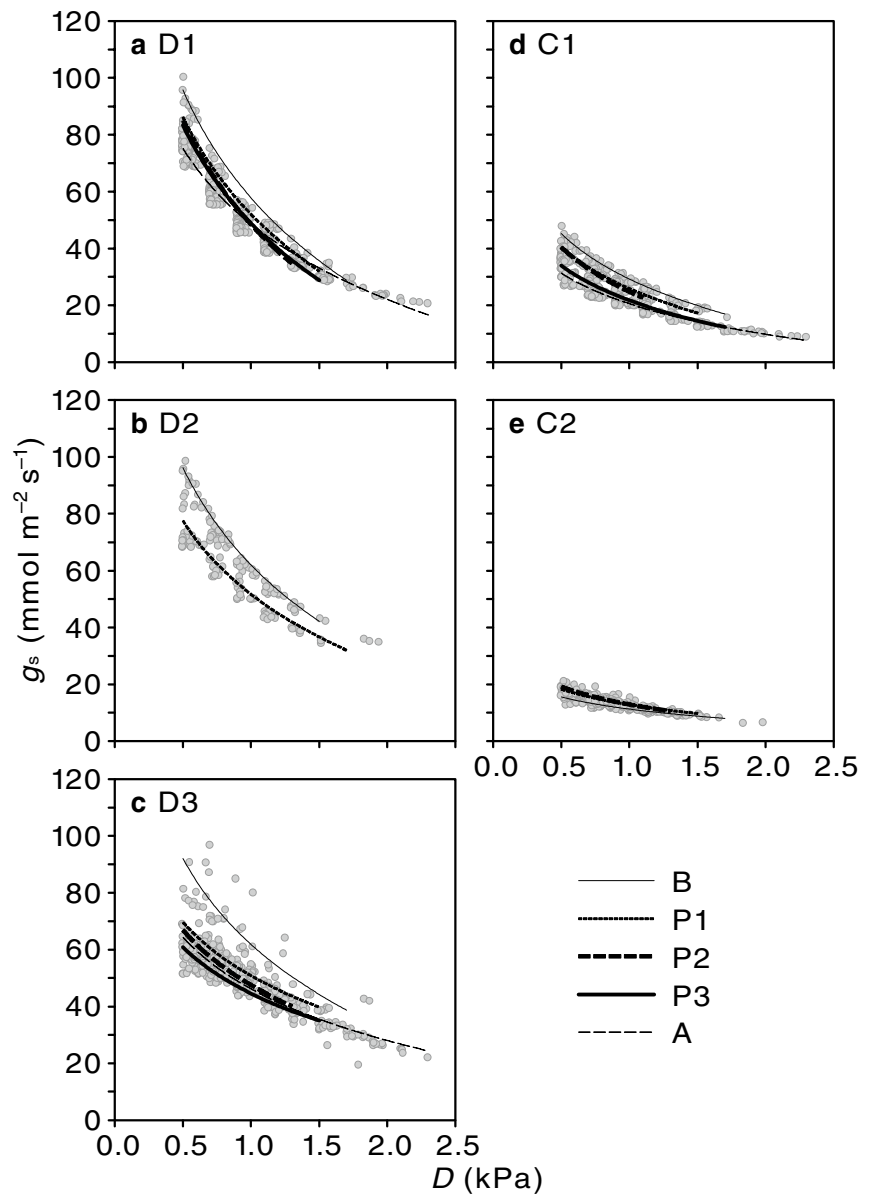
Fig. 3 Mean daily transpiration per unit leaf area (E_L , closed squares) and mean leaf water potential at dawn (Ψ_{L_dawn} , open circles) of *D. aromatica* trees in the rainfall exclusion experiment (a D1, b D2, and c D3) and control trees (d C1, e C2, f C3, and g C4) in each observation period: B is before the REE; P1, P2, and P3 are the initial, middle, and late periods of the REE, respectively; A is after the REE. Error bars represent the SD. Different letters indicate a significant difference between the periods within each studied tree ($P < 0.01$)



rainfall. The mean Ψ_{L_day} in A was less negative than that in other periods, although the mean daily rainfall in A was the smallest, probably because considerable rainfall occurred just before the measurement day. On the other hand, the mean Ψ_{L_day} of the REE trees significantly

declined during the REE treatment and was more negative than that of the control trees. The minimum mean Ψ_{L_day} values were -1.58 , -1.91 , and -1.60 MPa in P3 for D1, D2, and D3, respectively (Fig. 7a–c).

Fig. 4 Relationships between vapor pressure deficit (D) and mean canopy stomatal conductance (g_s) of *D. aromatica* trees in the rainfall exclusion experiment (a D1, b D2, and c D3) and control trees (d C1 and e C2). Closed circles represent the data selected by the upper boundary line analysis (see “Materials and methods”). The regression lines were determined for each observation period (B, thin solid line; P1, dotted line; P2, thick broken line; P3, thick solid line; A, thin broken line)



The G_p of the D1 and D3 trees declined markedly during the REE treatment (Fig. 8a, b). The G_p of the C1 tree also declined in P1 and P3, during which rainfall was lower than during the other periods (Fig. 8c). However, the extent of the decline in G_p was greater for D1 and D3 than for C1; the maximum ratios of the decline in G_p during the REE treatment to those in A were 60.2% and 63.6% for D1 and D3, respectively, which were much larger than the 53.1% for the C1 tree. The G_p of the control tree C1 increased in A, although the mean daily rainfall in A was the smallest, reflecting the increase in $\Psi_{L_{day}}$ due to the occurrence of rainfall just before the measurement day (see Fig. 7d and Eq. (5)). In contrast to the declines in G_p being greater for the REE trees than for the control tree C1, the changes in g_{sref} were small in both the control and

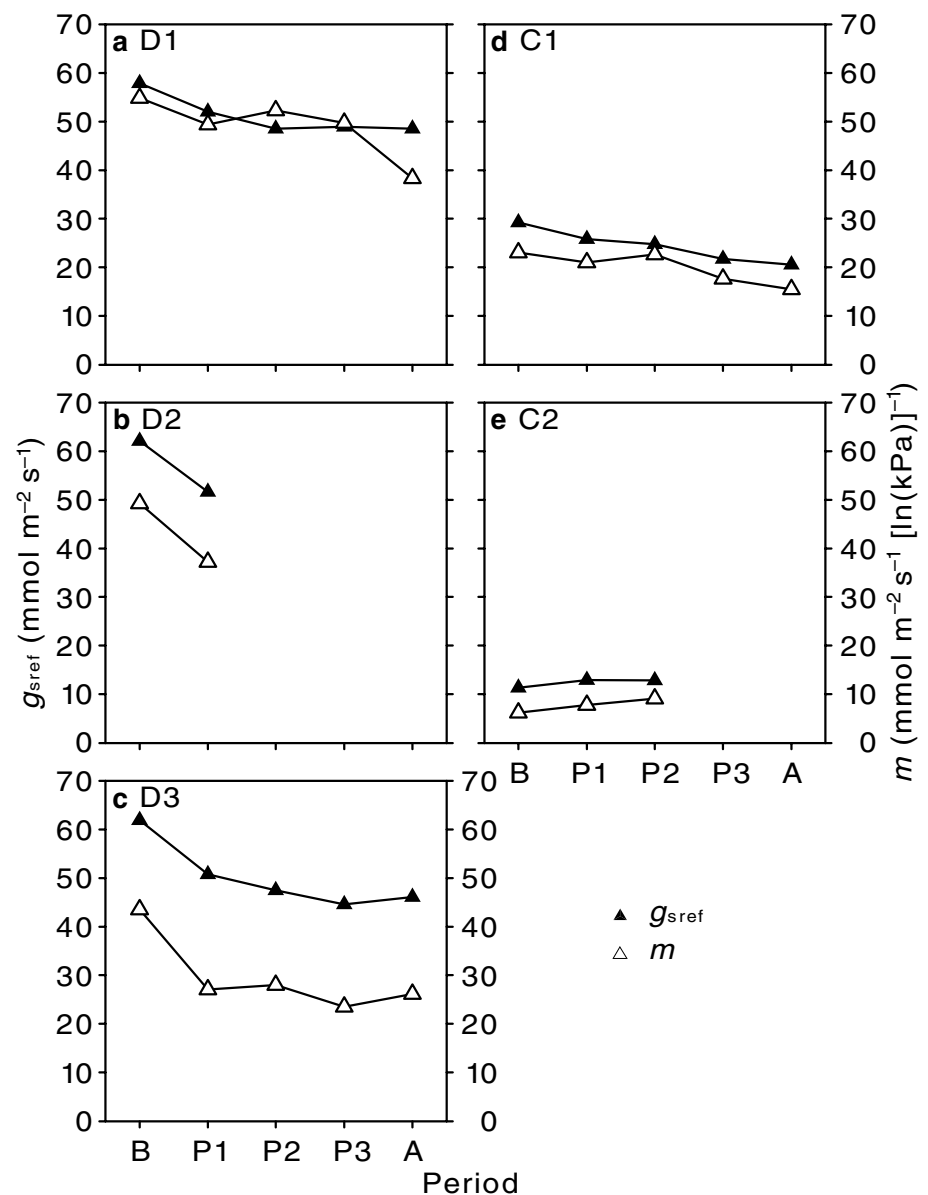
REE trees (Fig. 8). These findings indicate that soil moisture reduction induced only limited stomatal regulation, irrespective of the extent of the soil moisture reduction caused by background rainfall decline and REE treatment, and caused a greater decline in G_p corresponding to the greater soil moisture reduction caused by the REE treatment.

Discussion

Extent of drought caused by REE treatment

The 4-month REE effectively caused a drought for the REE trees, as indicated by the declines in Θ and $\Psi_{L_{dawn}}$ being

Fig. 5 Mean canopy stomatal conductance (g_s) at vapor pressure deficit (D)=1 kPa (g_{sref} , closed triangles) and the sensitivity of g_s to the natural log of D [$m = -dg_s/d\ln(D)$, open triangles] of *D. aromatica* trees in the rainfall exclusion experiment (a D1, b D2, and c D3) and control trees (d C1 and e C2) in each observation period



greater for the REE trees than for the control trees during the REE treatment (Figs. 2, 3). However, the extent of the drought was moderate, because the minimum values of the mean $\Psi_{L,dawn}$ and mean $\Psi_{L,day}$ of the REE trees during the treatment were only -0.59 and -1.91 MPa, respectively. This may be partly attributed to temporal rainwater leakage caused by a partial breakage of the sheeting. In addition, the water-holding capacity of the soil at the study site may also attribute to this moderate decline in $\Psi_{L,dawn}$. The Ultisols in this site have a very high sand content (62–72%), and therefore soil water drains rapidly at low tensions, but water might be held at higher tensions in these soils and does not drain easily, similar to clay soils (Kumagai et al. 2004, 2009), which could mitigate the minimum soil water potential. Considering the large size of the sampled trees,

there remains the possibility of soil water acquisition by the trees during the REE treatment from outside the sheeting for the REE and/or deeper soil layer than that where Θ was measured, though the size of the sheeting (15 m in radius) was determined to cover the rooting area based on the traced distance of the selected roots from the sampled trees (Yamashita et al. 2012) and the survey of the vertical profile of the roots indicated that the roots were not deep in this site (Tomonori Kume, unpublished data). The REE trees were selected among trees situated on upland or midslope, where the soil water tends not to converge. However, possible horizontal water exchange in deep soil layers between the inside and outside of the REE areas may also explain the moderate declines in $\Psi_{L,dawn}$ and $\Psi_{L,day}$.

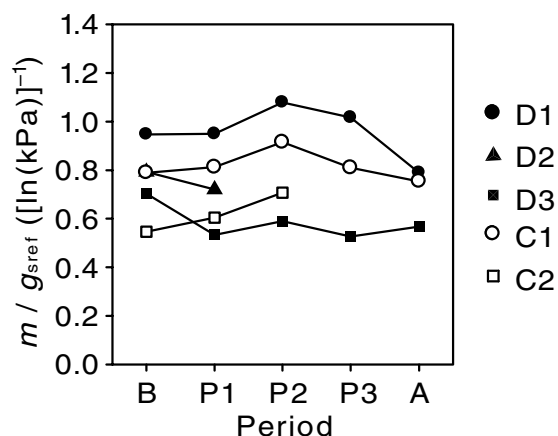


Fig. 6 Ratios of m [the sensitivity of mean canopy stomatal conductance (g_s) to the natural log of vapor pressure deficit (D); $-dg_s/d\ln(D)$] to g_{sref} (g_s at $D=1$ kPa) of *D. aromatica* trees in the rainfall exclusion experiment (D1, closed circles; D2, closed triangles; D3, closed squares) and control trees (C1, open circles; C2, open squares) in each observation period

Intrinsic stomatal regulation

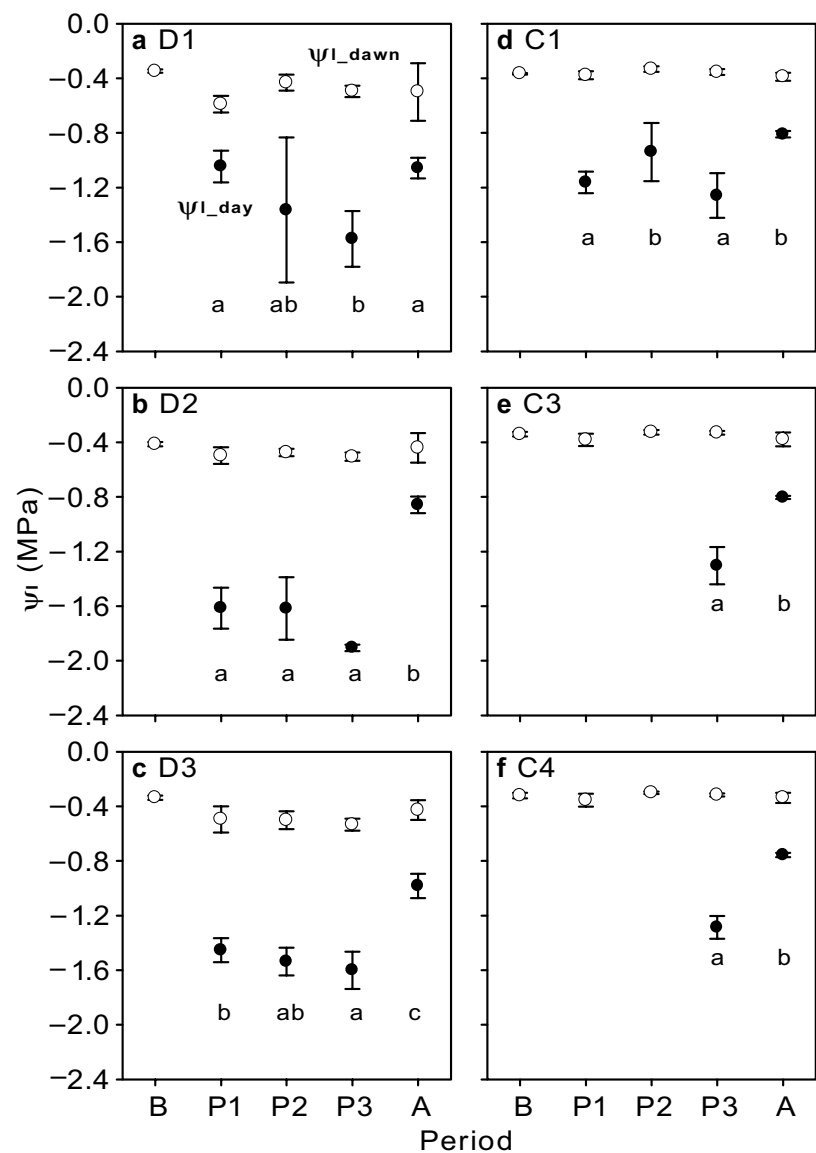
In the present study, the m/g_{sref} of all studied trees of *D. aromatica* in both REE and control plots was about or greater than 0.6, irrespective of soil moisture conditions, which implies that the trees were intrinsically isohydric-like (Fig. 6). However, this represents the sensitivity to increasing D , i.e. at a short time scale. Compared with reported values of g_{sref} recorded from a variety of biomes (Oren et al. 1999), the values observed in the present study were in the lower range, i.e. 45–62 $\text{mmol m}^{-2} \text{s}^{-1}$ for D1–D3, 21–29 $\text{mmol m}^{-2} \text{s}^{-1}$ for C1, and 11–13 $\text{mmol m}^{-2} \text{s}^{-1}$ for C2, even under mesic conditions (Fig. 5). Note that the heights of the studied trees were about 40 m or taller, and those of C1 and C2 were c. 50 and 53 m, respectively (cf. Table 1). Decreasing hydraulic conductance with tree height can reduce stomatal conductance to prevent the leaf water potential from becoming overly negative (Schäfer et al. 2000). Hence, the lower values of g_{sref} and the higher values of m , resulting in the higher m/g_{sref} ratio, might be due to the exceptional height of the trees observed in this study. The narrow range of D (see Fig. 4) may also contribute to the high m/g_{sref} ratio because of the deviation in the relationship between g_s and $\ln D$ from linearity, as described by Oren et al. (1999). However, no clear relationships between the range of D and the m/g_{sref} ratio values were observed in the present study (see Figs. 4, 6).

Effect of soil moisture reduction to stomatal regulation and G_p

Although the background trend of soil moisture caused by natural reduction in rainfall (Fig. 2) likely caused a small reduction in g_s of both the REE and the control trees (Fig. 4), the greater soil moisture reduction caused by the REE treatment did not induce larger declines in g_{sref} for the REE trees compared with those of the control trees. In addition, m/g_{sref} showed less variation under conditions of reduced soil moisture (Fig. 6). These results indicate that stomatal behavior was not altered in response to soil moisture reduction caused by the REE, which was consistent with the results of Kumagai and Porporato (2012b). This limited stomatal response allowed the decline in $\Psi_{L_{day}}$ corresponding to the extent of soil moisture reduction, which indicated that the studied trees of *D. aromatica* were anisohydric-like with respect to soil moisture reduction over a time scale of several months. Thus, the emergent *D. aromatica* trees were conservative in water use and caused little alteration in stomatal behavior in response to soil moisture reduction induced by the REE treatment, allowing $\Psi_{L_{day}}$ and G_p to decline (Figs. 6, 7, 8).

G_p includes several components, such as soil, root, stem, and leaf hydraulic conductances, and is affected by multiple factors relating the xylem and extra-xylem within the plant (Hacke 2014). Though the extent of soil moisture decline sensed by the REE-treated trees was moderate, the present study could not explicitly determine whether the plant hydraulic conductance was more responsible for the decline in G_p than the soil hydraulic conductance. The loss of xylem conductivity due to vascular damage in some components of the tree is a possible reason for the decline in G_p . However, the REE-treated trees did not die and the G_p value recovered in A with an increase in soil moisture (see Fig. 8), implying that fatal hydraulic failure such as irreparable vascular damage was avoided. Fisher et al. (2006) showed that the decrease in soil-to-leaf hydraulic conductance, rather than the decline in soil water potential, was the dominant cause of restricted water use under soil drought in an eastern Amazonian forest by comparing the observation data and the predictions of a soil–plant–atmosphere model with isohydric stomatal behavior. Thus, we inferred that the decrease in G_p (Fig. 8), in turn, might restrict water use of the REE-treated trees as a passive reaction (Fig. 3) at the same time that the opposite effect was induced by the increase in $\Psi_{L_{dawn}} - \Psi_{L_{day}}$ caused by the declines in $\Psi_{L_{day}}$ due to the limited stomatal control [see Eq. (5)], which might contribute to prevent hydraulic failure. In addition, Inoue et al. (2017) observed that the sun-exposed leaves at the top of the crown of the same trees of *D. aromatica* used in the present study decreased the leaf water potential at turgor loss point by osmotic adjustment during the REE treatment and

Fig. 7 Mean midday leaf water potential (Ψ_{l_day} , closed circles) of *D. aromatica* trees in the rainfall exclusion experiment (**a** D1, **b** D2, and **c** D3) and control trees (**d** C1, **e** C3, and **f** C4) in each observation period. Error bars represent the SD. Different letters indicate a significant difference in Ψ_{l_day} between the periods ($P < 0.01$). Mean leaf water potential at dawn (Ψ_{l_dawn} , open circles) is also shown for reference



enabled Ψ_{l_day} to decline without the loss of turgor pressure. This leaf adaptability should also contribute to the tolerance of the tree to soil moisture reduction. Declines in the leaf water potential at the turgor loss point in response to drought is reported with various species in diverse biomes (e.g. Bartlett et al. 2014; Johnson et al. 2018). Osmotic adjustment in response to the artificial long-term drought treatment was also observed with tropical rainforest trees in the Amazon (Binks et al. 2016).

Vulnerability to soil drought

Recent evidence suggests that avoidance of the risk of hydraulic failure is the optimal strategy for water use in both isohydric and anisohydric species. For example, Sevanto et al. (2014) and McDowell (2011) demonstrated

feedback between hydraulic conductivity and carbohydrate availability, and Meinzer et al. (2009) reported that a variety of mechanisms enable maintenance of hydraulic safety under dynamic conditions. This might partly explain why examination of hydraulic failure thresholds is a powerful means of predicting tree mortality (Anderegg et al. 2015). Furthermore, recent studies reported that the major cause of tree mortality under severe drought was deterioration of the hydraulic system (e.g. Anderegg et al. 2014; Rowland et al. 2015) and that drought results in the death of a greater number of large trees than of smaller trees (e.g. Bennett et al. 2015; Rowland et al. 2015). Manzoni (2014) collated published data on hydraulic traits of woody species growing in different biomes worldwide with contrasting climates and showed that the water potentials at 50% loss of xylem conductivity (Ψ_{50x}) were lower than those at 50% stomatal

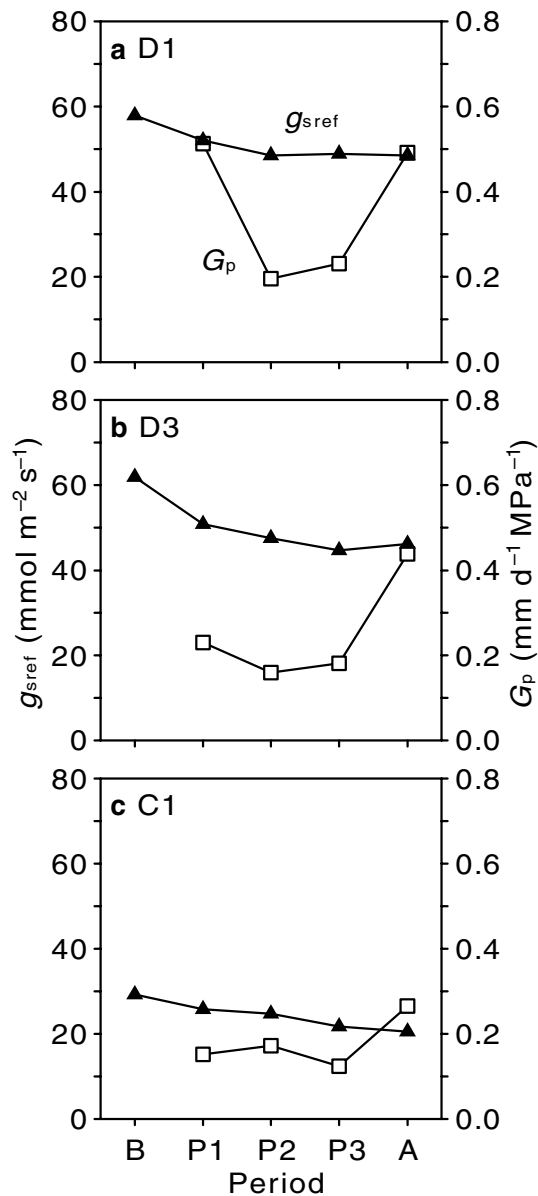


Fig. 8 Whole-tree hydraulic conductance (G_p , open squares) and mean canopy stomatal conductance at vapor pressure deficit = 1 kPa (g_{sref} , closed triangles) of *D. aromatica* trees in the rainfall exclusion experiment (a D1 and b D3) and control trees (c C1) in each observation period

closure (Ψ_{50s}) for most traits, consistent with a water-use strategy of first avoiding the risk of hydraulic failure.

In the present study, soil moisture reduction caused by the REE treatment resulted in limited stomatal regulation among the studied trees, allowing $\Psi_{l,day}$ to decline in response to the soil moisture reduction (Figs. 5, 7). As a result, G_p was reduced with constant g_{sref} under the reduced soil moisture (Fig. 8). Though it is unknown whether the G_p decline was attributed to the loss of xylem conductivity or for other reasons, our results seem to be

somewhat inconsistent with the conclusion of Manzioni (2014). It should be noted, however, that Manzioni (2014) did not include data from tropical rainforests. According to Choat et al. (2012), trees in tropical rainforests growing under abundant annual rainfall tend to show a less negative Ψ_{50x} because the trees do not have to maintain a large safety margin (i.e. the difference between Ψ_{50x} and actual minimum xylem pressure) under such humid conditions. Their results seem to suggest the higher vulnerability of tropical rainforests to hydraulic failure in case of unusually severe drought than the other biomes, and seem to be consistent with our results. More extensive and detailed studies are necessary to determine the responsibility of a loss of xylem conductivity to the decline in G_p of the emergent trees of *D. aromatica* and their vulnerability to hydraulic failure. In addition, because the extent of soil moisture reduction sensed by the REE-treated trees was still moderate and below the level at which their death is induced, further studies are necessary to determine the effects of much longer and severer soil drought than that caused by our REE on their water use regulation.

McDowell and Allen (2015) pointed out that mechanistic description of tree hydraulics can contribute to prediction of tree mortality and forest die-off induced by climate change. In addition, Mencuccini et al. (2015) suggested the possibility of modeling carbon starvation, hydraulic failure, and phloem transport failure to explore possible physiological vulnerabilities under severe drought. The results of the present REE provide information necessary for development and analysis of such mechanistic models. Because tropical rainforests contain a rich diversity of tree species and a variety of tree sizes, it is important to investigate the differences in the response of water use to drought among species and tree sizes within a forest to predict the impact on forest dynamics. At the present study site, Hiromi et al. (2012) investigated interspecific variation in water use at the leaf scale among four emergent dipterocarp species, including *D. aromatica*, under the natural environmental conditions. These authors reported that the leaf-scale transpiration rate, stomatal conductance, and midday decline in leaf water potential of *D. aromatica* were smaller than those of the other species. These responses may be advantageous to *D. aromatica* trees because they use less water, even though they are anisohydric-like for soil moisture reduction, whereas the other emergent tree species may be more vulnerable to drought (Hiromi et al. 2012). More extensive and complex experiments are needed to acquire detailed information on reproduction and prediction of vulnerability of tropical rainforests to climate change-related severe drought expected in future.

Acknowledgements We thank Kenji Tsuruta for assistance with field measurements, and Takao Itioka and Michiko Nakagawa for help with

logistics. We are grateful to the Sarawak Forestry Corporation and the Sarawak Forest Department for their cooperation. This work was supported in part by Grants-in-Aid for Scientific Research (#23255002, #19255006, #15H02645) from the Japan Society for the Promotion of Science and funding for the project “Program for Risk Information on Climate Change” from the Ministry of Education, Culture, Sports, Science and Technology, Japan.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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