



The exchange of water and energy between a tropical peat forest and the atmosphere: Seasonal trends and comparison against other tropical rainforests

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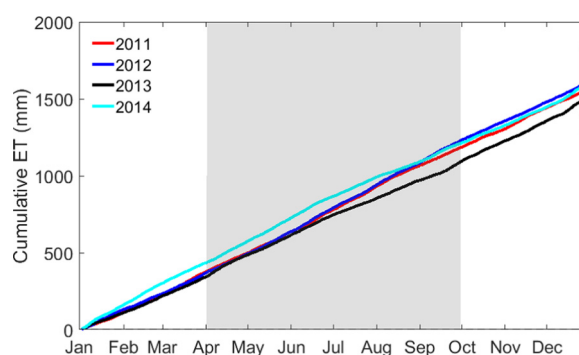
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HIGHLIGHTS

- Latent & sensible heat flux from a tropical peat forest were measured for 4 years.
- Turbulent fluxes at the tropical peat forest exhibited little seasonal variability.
- Some FLUXNET tropical forests exhibited pronounced seasonal variability.
- VPD and soil moisture helped explain the Bowen ratio at these forests.

GRAPHICAL ABSTRACT



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ABSTRACT

Tropical rainforests control the exchange of water and energy between the land surface and the atmosphere near the equator and thus play an important role in the global climate system. Measurements of latent (LE) and sensible heat exchange (H) have not been synthesized across global tropical rainforests to date, which can help place observations from individual tropical forests in a global context. We measured LE and H for four years in a tropical peat forest ecosystem in Sarawak, Malaysian Borneo using eddy covariance, and hypothesize that the study ecosystem will exhibit less seasonal variability in turbulent fluxes than other tropical ecosystems as soil water is not expected to be limiting in a tropical forested wetland. LE and H show little variability across seasons in the study ecosystem, with LE values on the order of $11 \text{ MJ m}^{-2} \text{ day}^{-1}$ and H on the order of $3 \text{ MJ m}^{-2} \text{ day}^{-1}$. Annual evapotranspiration (ET) did not differ among years and averaged $1579 \pm 47 \text{ mm year}^{-1}$. LE exceeded characteristic values from other tropical rainforest ecosystems in the FLUXNET2015 database with the exception of GF-Guy near coastal French Guyana, which averaged $8\text{--}11 \text{ MJ m}^{-2} \text{ day}^{-1}$. The Bowen ratio (Bo) in tropical rainforests in the FLUXNET2015 database either exhibited little seasonal trend, one seasonal peak, or two peaks. Volumetric water content (VWC) and VPD explained a trivial amount of the variability of LE and Bo in some of the tropical rainforests including the study ecosystem, but were strong controls in others, suggesting differences in stomatal regulation and/or the partitioning between evaporation and transpiration. Results demonstrate important

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differences in the seasonal patterns in water and energy exchange across different tropical rainforest ecosystems that need to be understood to quantify how ongoing changes in tropical rainforest extent will impact the global climate system.

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1. Introduction

Tropical ecosystems play a critical role in the global climate system by regulating the amount of heat and water that enters the atmosphere near the equator to drive deep convection. Ongoing changes to tropical forest extent (Kim et al., 2015) have impacted regional and global climate (Avisar and Werth, 2005; Bala et al., 2007; Medvigy et al., 2011; Werth, 2002), emphasizing the importance of understanding how tropical rainforests exchange water and energy with the atmosphere and how differences in their response to environmental variability may determine these dynamics.

Tropical rainforests exhibit seasonal patterns of energy and water exchange in response to wet and dry seasons; many studies report a doubling or more of the Bowen ratio (Bo , the sensible heat flux H divided by the latent heat flux LE) during the dry season (da Rocha et al., 2004; Gerken et al., 2018). These findings are consistent with the notion that tropical rainforest tree species are isohydric, meaning that they strictly regulate canopy conductance in response to water deficits (Fisher et al., 2006; Konings and Gentine, 2016). At the same time, other studies using modeling approaches suggest that some tropical forests should exhibit anisohydric water regulation strategies (Inoue et al., 2017; Kumagai and Porporato, 2012) if water stress is less of a risk. Yet others argue that different tree species exhibit a range of isohydric to anisohydric behavior (Klein, 2014), leaving it unclear if the conductance of diverse tropical forest canopies share similar responses to ongoing increases in the atmospheric vapor pressure deficit (VPD) (Novick et al., 2016; Sulman et al., 2016) and decreases in soil moisture (Jung et al., 2011). Gross primary productivity (GPP) varies considerably in response to increasing VPD across different tropical rainforests (Kiew et al., 2018; Wu et al., 2017); a recent synthesis of eddy covariance sites determined that VPD is significantly related to GPP across 12 tropical rainforest sites, but to a widely varying degree (Fu et al., 2018). Namely, VPD explained <4% of the variability in GPP across three ecosystems (GF-Guy, GH-Ank, and VU-Coc) that happened to be near the ocean where water may be assumed to be more available than the other nine ecosystems where VPD explained 20% of the variability of GPP on average (Fu et al., 2018). If the control over GPP by VPD is due to stomatal closure, energy balance partitioning may also be strongly constrained by VPD in tropical rainforests that are characterized by a large transpiration fraction. The response of eddy covariance-measured H and LE to seasonal water and energy availability across different tropical ecosystems has not been studied to date.

Here, we describe the seasonal variability in H and LE , and thereby the Bo , and their response to net radiation (R_n), VPD, and soil water availability (via volumetric soil water content, SWC) in a tropical peat rainforest ecosystem in Malaysian Borneo, hereafter abbreviated MY-MLM. We place these observations in the context of the seasonal variability of surface-atmosphere water and energy exchange measured at other tropical rainforest ecosystems across all five continents on which tropical rainforests exist. We hypothesize that the study ecosystem will exhibit less seasonal variability in water and energy exchange compared to other tropical rainforests because soil water is not expected to be limiting. We also hypothesize that VPD will be of lesser importance to LE and H in the study ecosystem versus other tropical rainforests given the findings of Fu et al. (2018). We place particular emphasis on eddy covariance energy balance closure and uncertainty estimation in the study ecosystem, noting that whereas tropical rainforest

ecosystems on average have higher energy balance closure than most other ecosystems (Gerken et al., 2018; Stoy et al., 2013); an analysis of energy balance closure cannot be excluded from a careful investigation of surface-atmosphere water and energy exchange using the eddy covariance technique.

2. Methods

2.1. Micrometeorological measurements at Maludam National Park, Malaysia

The primary study ecosystem, MY-MLM, is a tropical peat forest ecosystem in Maludam National Park in the Betong Division of Sarawak, Malaysia (Tang et al., 2018). Dominant vegetation in the overstory includes *Shorea albida*, *Gonystylus bancanus* and *Stemonurus* spp. (Anderson, 1972) with an average canopy height of 35 m. Peat thickness is 8 m in the vicinity of the eddy covariance tower at 1°27'13" N, 111°8'58" E. Mean annual precipitation during the measurement period was 2798 mm year⁻¹ and mean annual temperature was 26.9 °C.

R_n and global radiation (R_g) were measured at 41 m using a CNR4 net radiometer (Kipp & Zonen, Delft, The Netherlands). Two LI-190SB quantum sensors (LI-COR) were likewise mounted at 41 m and pointed downward and upward to measure incoming and outgoing photosynthetic photon flux densities (PPFD). Air temperature (T_{air}) relative humidity (RH) and thereby VPD were measured at 11 m and 41 m using CS215 temperature and relative humidity probes (Campbell Scientific). The tower was also equipped with a three-cup anemometer and wind vane (01003–5 R.M. Young Co., Traverse, MI, USA) at 41 m to measure wind speed (WS) and wind direction in addition to the sonic anemometer. P was measured by a TE525MM tipping-bucket rain gauge (Texas Electronics, Dallas, Texas, USA) 1 m above the ground surface in an open area located ca. 5 m from the tower. Soil temperature was measured with platinum resistance thermocouples at 5 and 10 cm below the ground surface. Volumetric soil water content was measured at a depth of 30 cm using time domain reflectometry (CS616, Campbell Scientific). All meteorological variables were continuously recorded using CR3000 and CR1000 dataloggers at a sampling frequency of 5 min and averaged over each 30 min period except WT, which was monitored on a half-hourly basis using a water level logger (DL/N 70 STS Sensor Technik Sirmach AG, Sirmach, Switzerland).

2.2. Eddy covariance measurements at MY-MLM

H and LE were measured at MY-MLM using the eddy covariance technique from 2011 to 2014 in the roughness sublayer at 41 m. The eddy covariance system was comprised of a LI-7500A open-path CO₂/H₂O analyzer (LI-COR Inc., Lincoln, NE, USA) coupled to a CSAT3 three-dimensional sonic anemometer (Campbell Scientific). 10 Hz observations were stored on a CR3000 Datalogger (Campbell Scientific) and half-hourly flux measurements were calculated using EddyPro (LI-COR) with WPL correction (Webb et al., 1980), block averaging, double rotation to align the sonic anemometer with the mean flow (Wilczak et al., 2001), and time-lag and frequency response corrections (Massman, 2000).

Table 1
Tropical rainforest eddy covariance sites in the FLUXNET2015 database including the MY-MLM site explored in the present study.

Site ID	Name	Latitude	Longitude	Observation period (years of measurement)	References
AU-Rob	Robson Creek, Australia	-17.1175	145.6301	2014–2014 (1)	Bradford et al. (2014)
BR-Sa1	Santarem-Km67-Primary Forest, Brazil	-2.8567	-54.9589	2002–2011 (9)	Martens et al. (2004)
BR-Sa3	Santarem-Km83-Logged Forest, Brazil	-3.0180	-54.9714	2000–2004 (5)	Goulden et al. (2006)
GF-Guy	Guyaflex, French Guyana	5.2777	-52.9288	2004–2014 (11)	Bonal et al. (2008)
GH-Ank	Ankasa, Ghana	5.2685	-2.6942	2011–2014 (4)	Albinet et al. (2015)
MY-PSO	Pasoh Forest Reserve, Malaysia	2.9730	102.3062	2003–2009 (7)	Kosugi et al. (2008)
PA-SPn	Sardinilla Plantation, Panama	9.3181	-79.6346	2007–2009 (3)	Wolf et al. (2011a), Wolf et al., 2011b, Wolf et al., 2011c)
MY-MLM	Maludam National Park, Malaysia	1.4536	111.1494	2011–2014 (4)	Tang et al. (2018)

2.3. Soil heat flux

Soil heat flux (G) was not measured at MY-MLM, so we estimated it using a model. Assuming that peat soils have a porosity of 80% and water content of 50% (Monteith and Unsworth, 1990), G can be calculated as the sum of the flux at depth z and the rate of change heat storage above the depth z :

$$G = -\lambda \frac{\partial T_{\text{soil}}}{\partial z} + c_s \left(\frac{\partial T_{\text{soil}}}{\partial t} \right) \Delta z \quad (1)$$

where λ is thermal conductivity ($0.29 \text{ W m}^{-2} \text{ }^\circ\text{C}^{-1}$), $\frac{\partial T_{\text{soil}}}{\partial z}$ is the temperature gradient (here between depths of 0.05 m and 0.1 m where T_{soil} measurements were available), c_s is the heat specific capacity ($2.31 \text{ MJ m}^{-3} \text{ }^\circ\text{C}^{-1}$), $\frac{\partial T_{\text{soil}}}{\partial t}$ is the average change in soil temperature with time (T) ($^\circ\text{C s}^{-1}$), taken here to be at depths of 0.05 m and 0.1 m, and Δz is the vertical distance between the ground surface and $z = 0.1 \text{ m}$.

2.4. Gap-filling and uncertainty analysis

Missing H and LE were gap-filled by fitting a daily linear regression with R_n that included a slope and an intercept parameter. We applied the approach of Richardson et al. (2006) (see also Hollinger and Richardson, 2005) to estimate the random uncertainty of H and LE . Random errors were inferred using the paired daily-difference approach in which a measurement pair was selected only if the mean half-hourly PPFD for two successive days differed by $<75 \mu\text{mol m}^{-2} \text{ s}^{-1}$, T_{air} differed by $<3 \text{ }^\circ\text{C}$, and WS differed by $<1 \text{ m s}^{-1}$. Random uncertainty was propagated through the gap-filling routines by perturbing the input flux observations with a random value drawn

from a normal distribution multiplied by the previously calculated random errors following the recommendations of Motulsky and Ransnas (1987). This procedure was iterated 100 times for each day such that 100 gap-filling models were fit for each day using least squares regressions (Vick et al., 2016). Missing H and LE data were filled using the mean of the 100 models, which were also used to quantify uncertainty due to gap-filling. The squared sum of random and gap-filling uncertainty was computed to calculate the total uncertainty.

2.5. FLUXNET2015

Observations of H , LE , and R_n from tropical forest ecosystems in the FLUXNET2015 database were compared against observations from MY-MLM, and their responses to VPD and VWC were explored to address the experimental hypotheses. The FLUXNET2015 database harmonizes, standardizes, and gap-fills half-hourly or hourly observations of H and LE submitted by Principal Investigators from regional flux networks using standard methods (Papale et al., 2006; Pastorello et al., 2017; Reichstein et al., 2005). The seven tropical rainforest eddy covariance sites come from all continents on which tropical rainforests exist: Africa, Asia, Australia, North America, and South America, as described in Table 1 and Fig. 1. We investigate the response of turbulent fluxes to VWC and VPD by modeling the linear relationship between turbulent fluxes and R_n and testing if the model residual is related to VWC and VPD for values of VPD $> 10 \text{ hPa}$, the value at which VPD often constrains canopy conductance to water vapor flux (Lasslop et al., 2010). We also investigate the relationship between VWC, VPD, and B_o for positive B_o values across the different tropical forest ecosystems to explore how variability in soil supply of water and atmospheric demand for water impact energy balance partitioning.

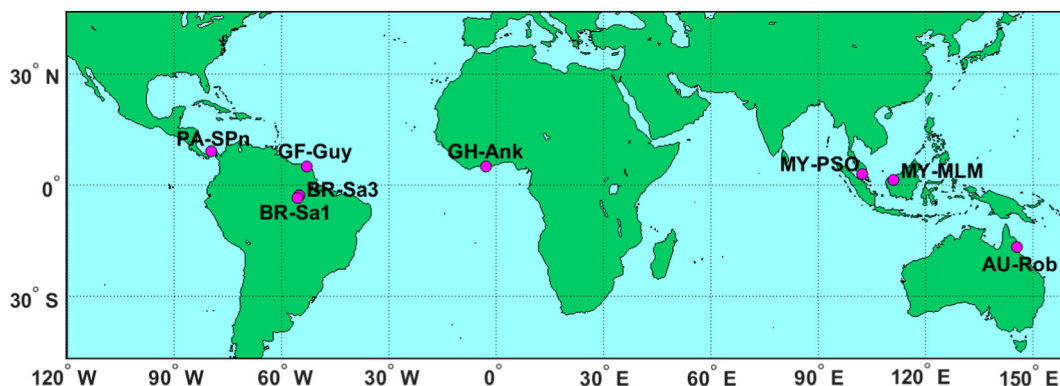


Fig. 1. Map of the Maludam National Park, Malaysia tropical peat forest research site (MY-MLM) and tropical rainforest FLUXNET tower sites used in this study (see Table 1).

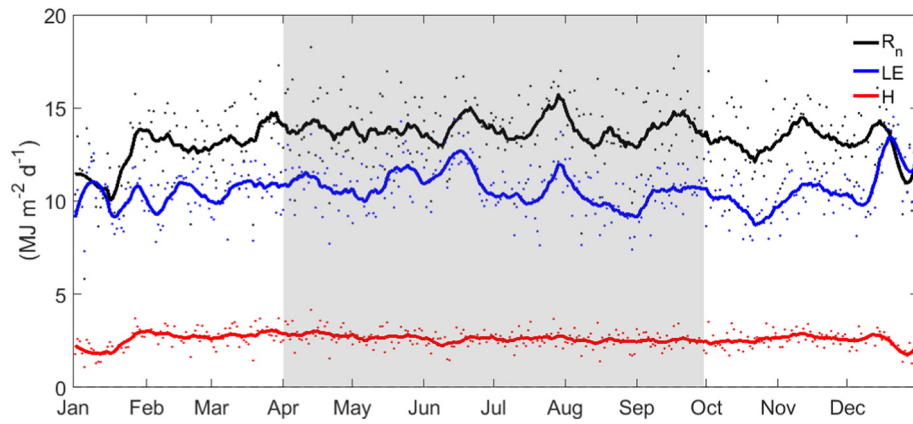


Fig. 2. The seasonal pattern of net radiation (R_n), latent heat flux (LE), and sensible heat flux (H) at the MY-MLM tropical peat forest ecosystem in Sarawak, Malaysian Borneo. Dots represent mean daily values for the four-year measurement period and lines represent a Savitzky-Golay filter applied to the average flux sum for each day of the calendar year.

3. Results

3.1. Water and energy fluxes from MY-MLM

LE at MY-MLM decreased from the wet season (with characteristic values on the order of $11 \text{ MJ m}^{-2} \text{ day}^{-1}$), to the dry season (with characteristic values on the order of $10 \text{ MJ m}^{-2} \text{ day}^{-1}$) (Fig. 2) and largely followed seasonal patterns in R_n , which varied from 13 to $14 \text{ MJ m}^{-2} \text{ day}^{-1}$ on average. H exhibited less seasonal variability with average daily sums on the order of $3 \text{ MJ m}^{-2} \text{ day}^{-1}$. Evapotranspiration (ET) calculated from LE measurements did not significantly differ among the study years and averaged $1579 \pm 47 \text{ mm year}^{-1}$ (mean \pm standard deviation) (Fig. 3). As a consequence, the evaporative fraction ($EF = R_n/LE$) and Bo exhibited little interannual differences (data not shown) nor differences during the daytime regardless of dry or wet season (Fig. 4). The EF was close to 0.74 and the Bo near 0.33 during daytime, and the Bo was more negative (and the EF more positive) during nighttime periods of the dry season across all years (Fig. 4). The Bo increased in response to R_n across both wet and dry seasons, indicating that additional energy is disproportionately partitioned to H as R_n increases (Fig. 5). Whereas ET did not exhibit annual differences as noted (Fig. 3), there was a decrease in shortwave albedo during the later years of measurement (2013–2014) from 8.5% during mid-day earlier in the measurement period to 8% later in the measurement period (Fig. 6).

LE did not decrease in response to increasing VPD during any year or season of measurement at MY-MLM (Fig. 7). Bo decreased during the dry season as VPD approached 1 kPa during the dry seasons of the first two years of the measurement record (Fig. 8), demonstrating that

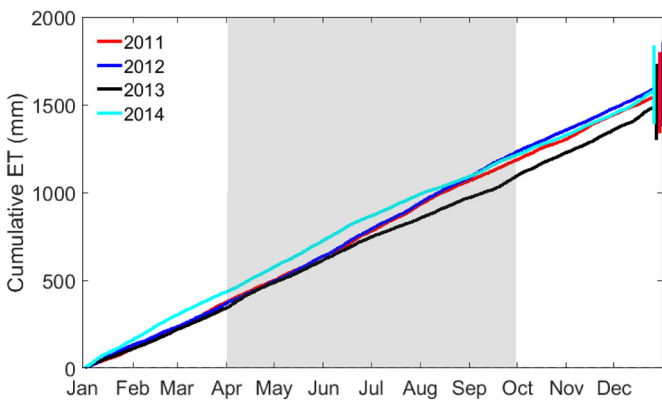
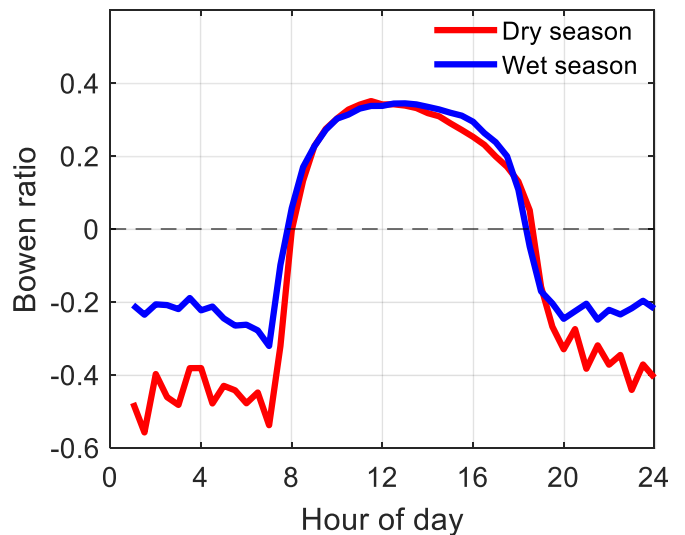
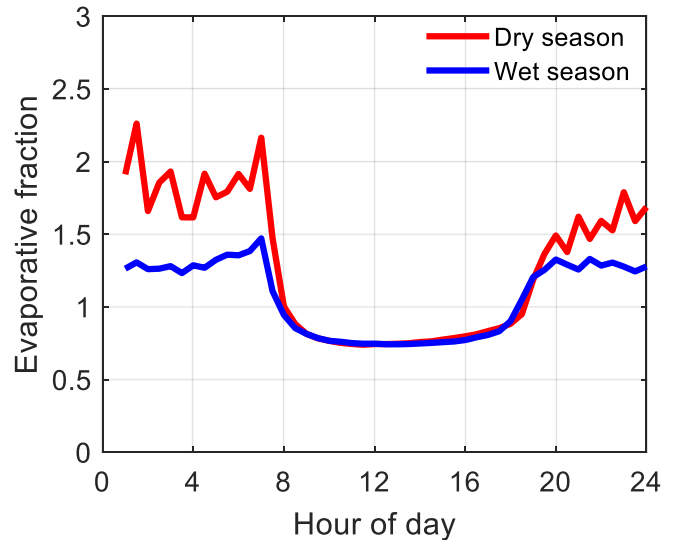


Fig. 3. The cumulative sum of evapotranspiration (ET) in a tropical peat forest ecosystem in Sarawak, Malaysian Borneo (MY-MLM) with uncertainty estimates displayed as ± 1 standard deviation from the annual sum. Shaded areas represent the dry season. Annual ET sums are not significantly different from each other.

Fig. 4. Mean diurnal evaporative fraction (top) and Bowen ratio (bottom) for the dry and wet season in a tropical peat forest ecosystem in Sarawak, Malaysian Borneo (MY-MLM).

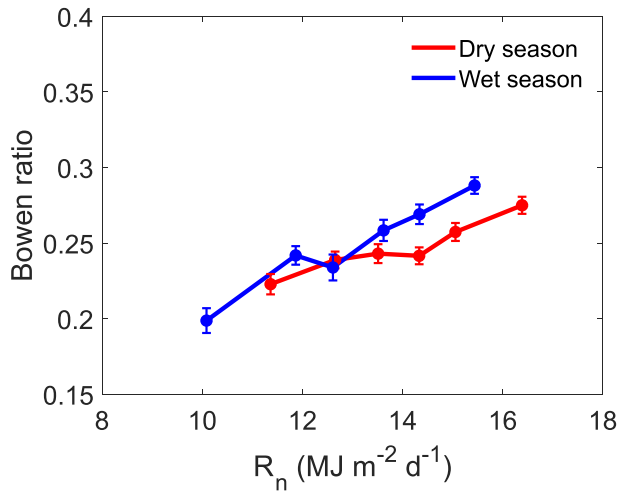


Fig. 5. The response of the Bowen ratio to net radiation (R_n) across the dry and wet seasons in a tropical peat rainforest ecosystem in Sarawak, Malaysian Borneo (MY-MLM). Vertical bars represent the standard error for each bin.

energy was partitioned even more toward LE during periods when VPD was high.

3.2. Energy balance closure at MY-MLM

The mean of the daily sum for G during the four years of measurement period was $-0.26 \pm 0.58 \text{ MJ m}^{-2} \text{ d}^{-1}$, indicating a net flow of heat from the soil to the atmosphere. Energy balance closure (calculated as the relationship between the daily sum of H plus LE versus R_n minus the model for G) increased from 67% during the wet season to 74% during the dry season (Fig. 9) and averaged 70% across the entire measurement period, somewhat less than globally-distributed eddy covariance sites from the FLUXNET La Thuile database ($84 \pm 20\%$) and tropical sites from the La Thuile database ($94 \pm 16\%$) (Stoy et al., 2013).

3.3. Water and energy fluxes from global tropical rainforest ecosystems

The magnitude of average daily LE across the calendar year tended to be higher at MY-MLM ($11 \text{ MJ m}^{-2} \text{ day}^{-1}$) than most other tropical rainforest ecosystems in the FLUXNET2015 database with the exception

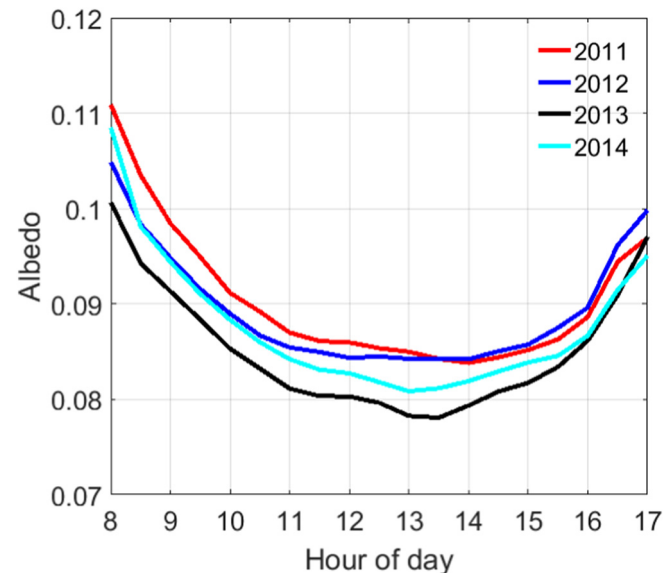


Fig. 6. The average diurnal pattern of the shortwave albedo for different measurement years in a tropical peat rainforest ecosystem in Sarawak, Malaysian Borneo (MY-MLM).

of GF-Guy in French Guyana (Fig. 10a). Mean daily LE across the calendar year exhibited diverse patterns across the different study ecosystems, with average daily fluxes differing by four times (ca. $2 \text{ MJ m}^{-2} \text{ day}^{-1}$) from dry to wet season at GH-Ank in Ghana to a seasonally invariant $8 \pm 1 \text{ MJ m}^{-2} \text{ day}^{-1}$ at a tropical rainforest on Peninsular Malaysia (MY-PSO).

H at MY-MLM was less variable than most other study ecosystems despite large differences in wet and dry season precipitation that differed for example from $>550 \text{ mm month}^{-1}$ in December 2013 to $<50 \text{ mm month}^{-1}$ in July 2013. Daily average H reached as high as ca $8 \text{ MJ m}^{-2} \text{ day}^{-1}$ at a tropical rainforest in Australia (AU-Rob), where net negative daily H values were also observed, similar to GF-Guy (Fig. 10b). As a consequence of the seasonal patterns in LE and H , the seasonal pattern of Bo can be characterized into sites that have two calendar year peaks (MY-PSO and PA-SPn), sites with little seasonal pattern in Bo (BR-Sa1 and BR-Sa3), and sites with characteristically low Bo values <0.25 early in the calendar year and larger values later (AU-Rob, GF-Guy, GH-Ank, and the study ecosystem, MY-MLM) (Fig. 10c).

3.4. The response of turbulent fluxes to variability in water supply and demand

The relationship between VPD (for VPD values $>1 \text{ kPa}$) and the residual of the relationship between R_n and LE was significant at the common $P < 0.05$ level but rarely explained $>2\%$ of its variance with the exception of GF-Guy and PA-SPn at which nearly 5% and over 11% of the variance of the model residual was explained by VPD, respectively (Fig. 11). $>10\%$ of the variability in the residual of the linear relationship between R_n and H is explained by VPD in these two ecosystems (data not shown). As a consequence, VPD explained 7% of the variability of Bo at GF-Guy and 20% of its variability at PA-SPn (Table 2). VPD also explained 19% of the variability of Bo at AU-Rob, which like MY-MLM demonstrated a positive relationship between VPD and Bo . VPD and VWC explained $<1\%$ of the variability in Bo at MY-MLM (Table 2), and VWC explained at most 6% of the variability in the residual of the relationship between R_n and LE across all sites.

4. Discussion

4.1. Water and energy fluxes from MY-MLM: energy balance closure and seasonal patterns

Annual rainfall decreased during the measurement period at MY-MLM (3290, 2941, 2688 and 2272 mm for 2011, 2012, 2013 and 2014, respectively), but annual ET was comparable between years; 1568, 1616, 1516 and 1614 mm for 2011, 2012, 2013 and 2014, respectively (Fig. 3). These observations suggest that ET was insensitive to observed variability in P , and also that water available for groundwater recharge of surface flow decreased across the measurement period from ca. 1700 mm in 2011 to ca. 660 mm in 2014. These observations are consistent with the notion that ET is a conserved quantity compared to other terms in the water balance in energy-limited ecosystems (Oishi et al., 2010).

Turbulent fluxes at MY-MLM were poorly related to water limitation across the observed range of variability of VWC and VPD. Daytime EF and Bo were insensitive to dry or wet season at MY-MLM (Fig. 4), but the surface cooled more quickly at night during the dry season, resulting in Bo values that were more negative. These observations are consistent with a more rapid nighttime cooling during the dry season when WT heights were characteristically beneath the soil surface at MY-MLM (Tang et al., 2018). In other words, the largest differences between the dry and wet season in LE and H occurred at night and are consistent with the influence of the heat capacity of standing water on ecosystem energy fluxes rather than the influence of this water on daytime energy partitioning.

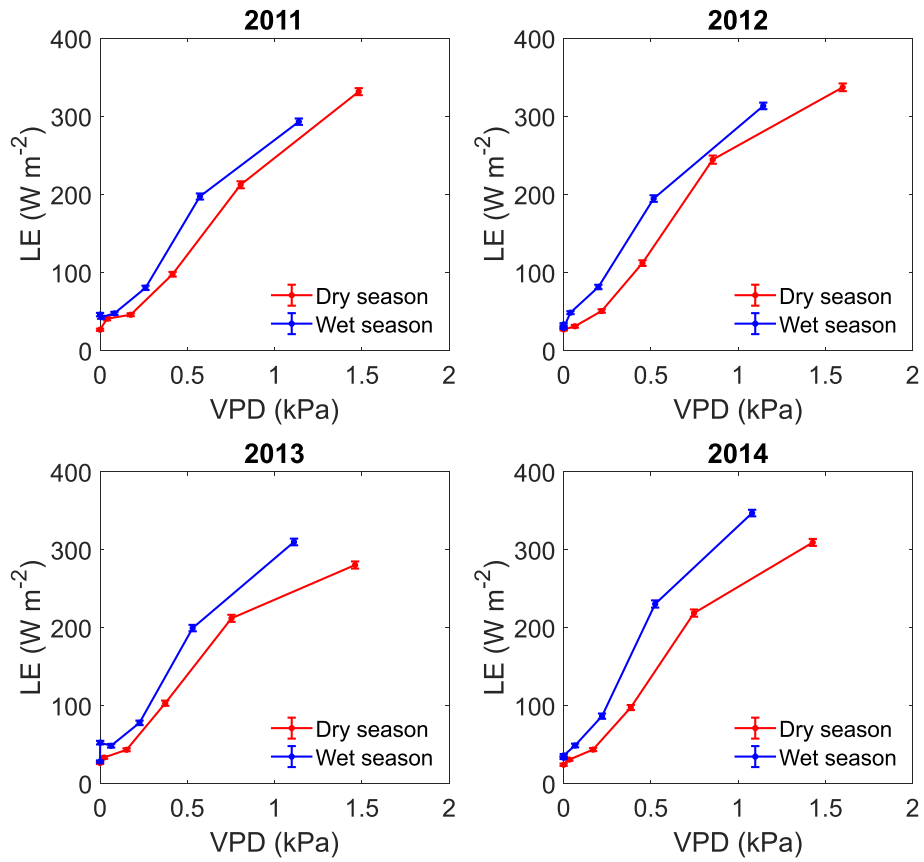


Fig. 7. Mean half-hourly LE against mean half-hourly VPD for dry and wet seasons for 2011, 2012, 2013 and 2014, respectively. Vertical bars represent the standard error for each bin.

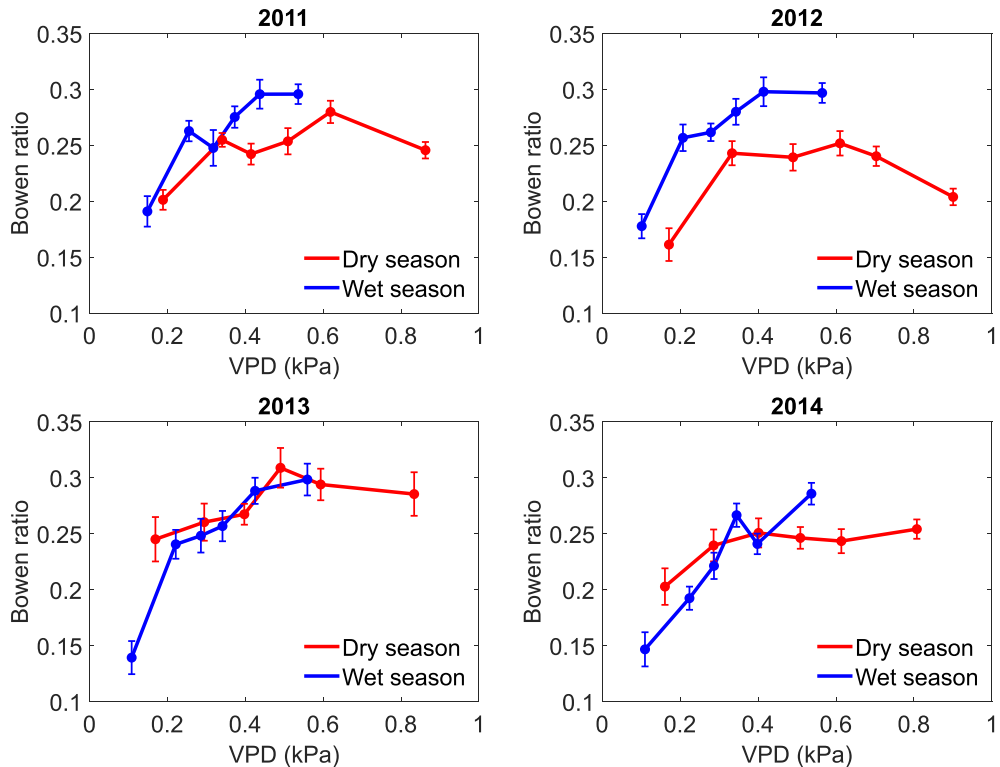


Fig. 8. Daily averaged Bowen ratio against daily averaged VPD for dry and wet seasons for 2011, 2012, 2013 and 2014, respectively. Vertical bars represent the standard error for each bin.

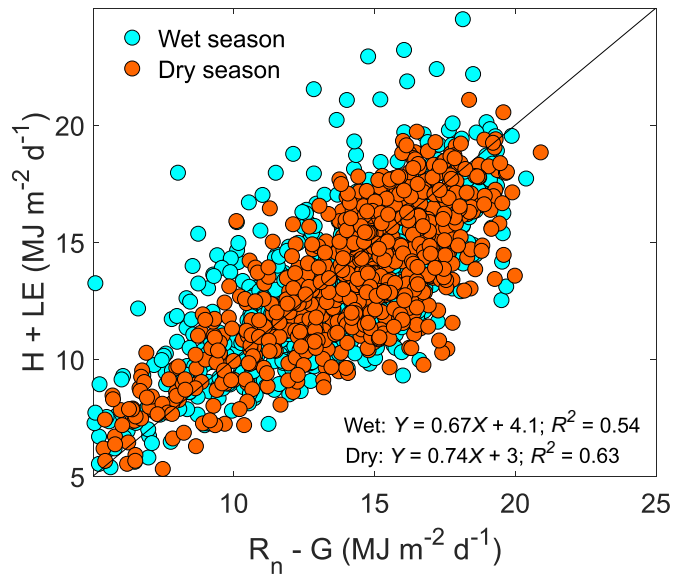


Fig. 9. Energy balance closure, calculated as the daily sum of sensible (H) and latent heat flux (LE) versus the daily sum of net radiation (R_n) minus the model for soil heat flux (G) across the dry and wet seasons for a four-year measurement period in a tropical peat rainforest ecosystem in Sarawak, Malaysian Borneo (MY-MLM).

The non-closure of surface energy balance is common in eddy covariance measurements (Stoy et al., 2013; Wilson et al., 2002) and is often attributed to a number of causes such as inadequacy of instrument system, mismatch in footprint between R_n and eddy fluxes, neglected energy sinks, advective flux divergence, low and high frequency loss of turbulent fluxes at individual sites (Foken, 2008; Wilson et al., 2002). We note that the present analysis of energy balance closure

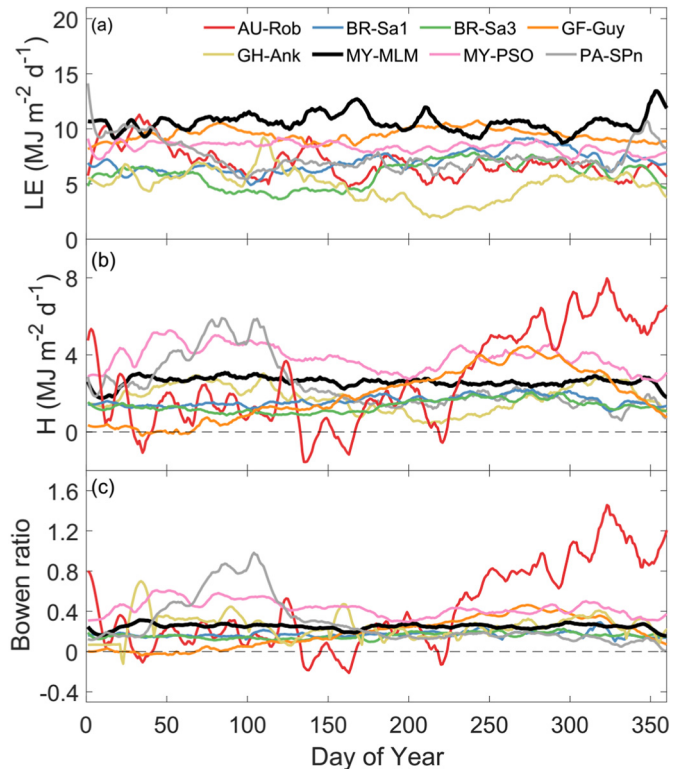


Fig. 10. The seasonal patterns of (a) latent heat flux (LE), (b) sensible heat flux (H), and (c) the Bowen ratio, across the eight eddy covariance research sites investigated here (see Table 1). Lines represent a Savitzky-Golay filter applied to average daily fluxes and ratios across all measurement years for each ecosystem. Values for MY-MLM follow Fig. 2.

excludes unmeasured ecosystem heat fluxes a model for G (Eq. (1)), which are minor terms in the energy balance at the diurnal time scales analyzed here (Leuning et al., 2012). Because energy balance closure was lower during the wet season when the water table characteristically exceeded the soil surface (Tang et al., 2018), our observations are consistent with the notion that the advective exchange of heat due to flowing water is a nontrivial term in the energy balance, as has been found in other wetland ecosystems (Barr et al., 2013). Energy balance closure values from the present analysis are similar to wetland ecosystems in the La Thuile FLUXNET database (0.76), which had the lowest average energy balance closure of any La Thuile database ecosystem (Stoy et al., 2013). Results of this study and others suggest that additional instrumentation is needed to capture advective energy flux in ecosystems characterized by flowing water.

4.2. Surface-atmosphere energy flux in tropical rainforest ecosystems

The mean annual ET at MY-MLM (1579 mm yr^{-1}) was similar to a hydrologically disturbed peat forest in Kalimantan, Indonesia (1636 mm yr^{-1} , Hirano et al., 2015) and a rainforest at Lambir Hills National Park in Sarawak, Malaysia (1545 mm yr^{-1} , Kumagai et al., 2005), but higher than a rainforest in Peninsular Malaysia (MY-PSO, 1287 mm yr^{-1} , Kosugi et al., 2012), central Amazonian forests (BR-Ma1, 1123 mm yr^{-1} , Malhi et al., 2002; Hutryra et al., 2007), and an afforested site (PA-SPn, 1114 mm yr^{-1}) and a pasture site (1034 mm yr^{-1}) in Panama (Wolf et al., 2011a, 2011b, 2011c). These observations are consistent with experimental hypothesis that LE (and by conversion ET) would be higher at MY-MLM than other tropical rainforest sites due to the consistent availability of water in a tropical peat forest wetland ecosystem and relative lack of seasonality, as also demonstrated by the insensitivity of daytime EF and Bo to wet and dry season. Tropical rainforests near the tropical/subtropical boundary, namely AU-Rob, exhibited daily average Bo approaching 1.5, and Amazonian *terra firme* rainforests exhibited sharp increases in Bo to ca. 0.7 during conditions of high R_n (exceeding 900 W m^{-2}) (Gerken et al., 2018), suggesting that reduction in LE in response to dry conditions is an important feature of these tropical rainforests, recalling that LE continued to increase in response to VPD at MY-MLM (Fig. 7). Bo rarely exceeded 0.3 at MY-MLM, even during the dry season, suggesting that water is consistently available for ET, and seasonal patterns of Bo in other tropical forested ecosystems indicates large differences in their hydrologic function with important implications for global heat and moisture transport (Fig. 8).

The residual of the relationship between LE and R_n as well as energy balance partitioning was poorly described by VPD and VWC across the range of forests and environmental variability explored here, except at AU-Rob and PA-SPn where they explained 19–30% of the variability in these terms and to a lesser degree GF-Guy, where they explained 4–7% (Table 1; Fig. 11). AU-Rob is near the tropical/subtropical ecotone and PA-SPn is a re-establishing forest with a developing root system (Wolf et al., 2011a, 2011b, 2011c), and VPD explained 11–32% of the variability of GPP in these ecosystems (Fu et al., 2018) suggesting a strong coupling between carbon dioxide, turbulent fluxes, and hydrologic variability. Turbulent fluxes at most other tropical forests studied here, including MY-MLM, were poorly related to VPD and VWC, and there is little evidence that the tropical peat forest MY-MLM is any less sensitive to water availability and demand given the range of environmental variability of the available data, and even though annual P was nearly 1/3 lower during the last year of measurement than the first.

The diversity of responses of turbulent fluxes to water availability across tropical forests could be due to a number of factors that require further investigation. Trees may have been insufficiently water stressed to elicit a substantial response in energy balance partitioning, but it is reasonably well-established that canopy conductance to water flux decreases in response to VPD, especially above 1 kPa (Lasslop et al., 2010), which was frequently exceeded in the observations (Fig. 11). Greater evaporation under elevated VPD may therefore be responsible for the

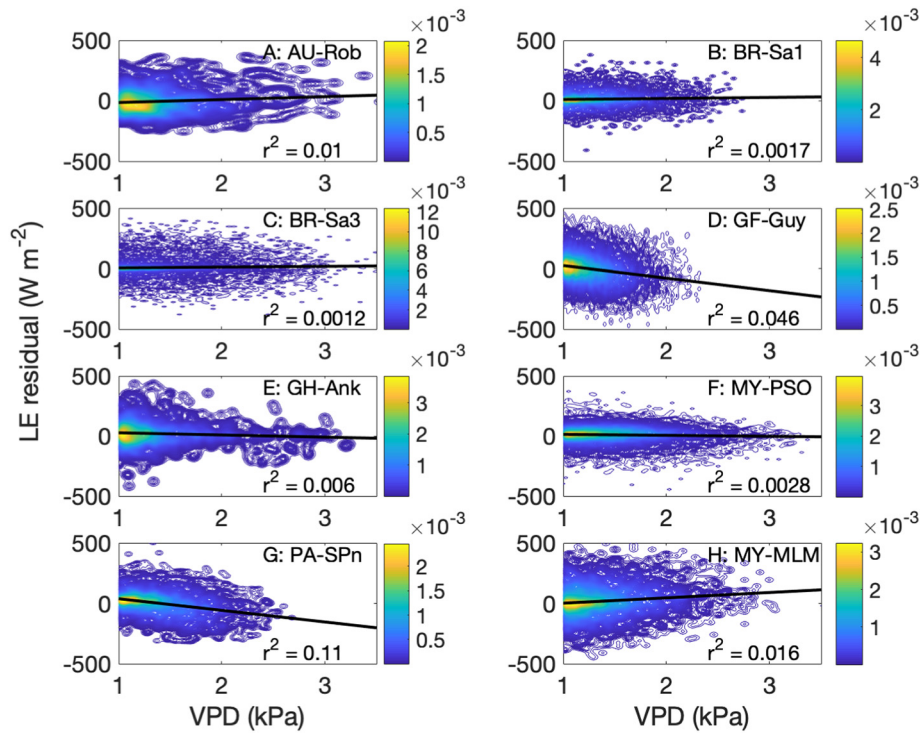


Fig. 11. The relationship between vapor pressure deficit (VPD) and the residual of a linear model between net radiation and latent heat flux (LE residual). Results are presented for VPD values >1 kPa for which canopy conductance is known to be sensitive to VPD across global ecosystems (Lasslop et al., 2010). All relationships were significant at the common $P < 0.05$ level.

observations, and the partitioning of evaporation and transpiration at the ecosystem scale remains a critical area of research for understanding the global water cycle. As noted above, variability in tree isohydricity (Klein, 2014) may be responsible for the observations as well as the physical and biological environment in which plants compete for water, which impacts the response of canopy conductance to water availability (Mrad et al., 2019).

5. Conclusion

The experimental hypothesis that H and LE would be less variable and less related to water availability at MY-MLM than other tropical rainforest ecosystems could not be falsified using observations and approaches used here. ET was relatively constant at MY-MLM despite decreasing rainfall over the four-year study period, consistent with the notion that ET is a conserved quantity in radiation-limited ecosystems. Results demonstrate important differences in the seasonal patterns in water and energy exchange in tropical rainforest ecosystems that exhibit large differences in the response of canopy processes to atmospheric moisture stress via VPD. These diverse responses of turbulent fluxes to hydrologic variability suggest considerable differences in

ecosystem hydrology among tropical rainforests that need to be understood to quantify how ongoing changes in tropical rainforest extent will impact the global climate system.

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Table 2

The amount of variability (r^2) of the Bowen ratio (Bo) explained by volumetric water content (VWC) and vapor pressure deficit (VPD) for the tropical forest ecosystems described in Table 1 and the study ecosystem, MY-MLM. VWC data were not available for BR-Sa1.

Site ID	VWC	VPD
AU-Rob	0.31	0.19
BR-Sa1	–	<0.01
BR-Sa3	0.05	0.01
GF-Guy	0.04	0.07
GH-Ank	<0.01	<0.01
MY-PSO	0.03	<0.01
PA-SPn	0.23	0.20
MY-MLM	<0.01	<0.01

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