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Title: Leaf surface water, not plant water stress, drives diurnal variation in tropical forest canopy water content

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Summary:

- Variation in canopy water content (CWC) that can be detected from microwave remote sensing of vegetation optical depth (VOD) has been proposed as an important measure of vegetation water stress. However, the contribution of leaf surface water (LW_s), arising from dew formation and rainfall interception, to CWC is largely unknown, particularly in tropical forests and other high-humidity ecosystems.
- We compared the AMSR-E VOD and CWC predicted by a plant hydro-dynamics model at four tropical sites in Brazil spanning a rainfall gradient. We assessed how LW_s influenced the relationship between VOD and CWC.
- The analysis indicates that while CWC is strongly correlated with VOD (R^2=0.62 across all sites), LW_s accounts for 61-76% of the diurnal variation in CWC despite being less than 10% of CWC. Ignoring LW_s weakens the near-linear relationship between CWC and VOD and reduces the consistency in diurnal variation. The contribution of LW_s to CWC variation, however, decreases at longer, seasonal to interannual, time scales.
- Our results demonstrate that diurnal patterns of dew formation and rainfall interception can be an important driver of diurnal variation in CWC and VOD over tropical ecosystems and therefore should be accounted for when inferring plant diurnal water stress from VOD measurements.

Key words: canopy water content, ED2, ecosystem modeling, leaf surface water, vegetation optical depth, X-band

Introduction

Climate change and the accompanying intensification of hydrological cycles are imposing strong and chronic stress on terrestrial ecosystems (Novick *et al.*, 2016; McDowell *et al.*, 2018). Enhancing our understanding of vegetation water dynamics is therefore critical to predictions of ecosystem sensitivity to global change (Fatichi *et al.*, 2016; Schimel & Schneider, 2019). Recent work has shown that vegetation optical depth (VOD) estimated from microwave remote sensing observations is a reliable proxy for the canopy water content (CWC) and a promising source of data for monitoring and understanding vegetation water dynamics (Konings *et al.*, 2019; Feldman *et al.*, 2020). Changes in VOD can reflect vegetation diurnal water stress patterns (Konings & Gentine, 2017; Li *et al.*, 2017; Anderegg *et al.*, 2018; Zhang *et al.*, 2019), seasonality in plant water potential and leaf area (Guan *et al.*, 2014; Momen *et al.*, 2017), and vegetation biomass changes at longer time scales (Liu *et al.*, 2015; Fan *et al.*, 2019). However, accurate and robust interpretation of VOD variability remains challenging because of the complex physiological and biophysical processes impacting vegetation water dynamics at a wide range of time scales (Grossiord *et al.*, 2017). Variation in VOD can be driven by canopy water interception due to rainfall and dew formation, plant hydraulics, phenology, and structural changes from growth and mortality (Konings *et al.*, 2019). These challenges have hindered direct use of VOD in understanding vegetation water dynamics.

Spatio-temporal variation in VOD have mostly been linked to changes in leaf and wood internal water content (Jackson & Schmugge, 1991; Cosh *et al.*, 2010; Tian *et al.*, 2016), but theoretically they are also sensitive to surface water arising from dew formation and intercepted rainfall. While a previous study at a temperate agricultural site found relatively little effect of dew on airborne X-band (10.7 GHz) measurements (Du *et al.*, 2012), diurnal changes in leaf surface water were found to modulate tower-based VOD measurements collected at a similar microwave frequency (11.4 GHz) in a tropical canopy in Panama (Schneebeli *et al.*, 2011). This latter study was performed at the scale of a few meters, however, which may show sensitivities not detectable at the ecosystem-scales (Wigneron *et al.*, 2017).

At the ecosystem-scale, the contribution of leaf surface water to VOD signals remains largely unknown despite leaf surface water being an important component of the moisture budget, particularly in rainforest ecosystems where significant diurnal and seasonal variation in CWC occurs because of frequent rainfall interception and dew formation (Junqueira Junior *et al.*, 2019; Binks *et al.*, 2021) and where measurements of leaf surface water beyond qualitative leaf wetness data (Binks et al. 2019) do not exist. Therefore, ignoring the contribution of leaf surface water to VOD can lead to overestimation of changes in leaf internal water, which potentially biases the interpretation of VOD data as a measure of vegetation water stress. On the other hand, the ability to separate leaf surface water from canopy water content in VOD data may provide additional information about plant water dynamics. Through its effects on stomatal conductance, leaf surface water influences key aspects of plant metabolism including carbon assimilation (Aparecido *et al.*, 2017; Gerlein-Safdi *et al.*, 2018a,b) and support several important, yet relatively unknown, eco-physiological processes such as leaf foliar water uptake (Eller *et al.*, 2013; Binks *et al.*, 2019) and epiphyte water use and survival (Lakatos *et al.*, 2012).

Recent advances in mechanistic representation of plant hydrodynamics in terrestrial biosphere models (Mencuccini *et al.*, 2019) provide a new avenue for interpreting VOD data: these models are now capable of explicit simulation of CWC dynamics from a set of biophysical descriptions and field-based plant functional traits. In turn, VOD data can provide valuable ecosystem scale evaluation data to hydrodynamic models, which are usually benchmarked by individual-level plant hydraulic measurements within forest plots (Xu *et al.*, 2016; Christoffersen *et al.*, 2016; Kennedy *et al.*, 2019; De Kauwe *et al.*, 2020). However, no studies to date have compared simulated CWC from terrestrial biosphere models with satellite VOD data.

In this study, we compare terrestrial biosphere model predictions of CWC and satellite VOD, and quantify the contribution of leaf surface water to VOD variation across diurnal to seasonal and inter-annual time scales. Specifically, we hypothesize:

(H1) CWC, summed over the representative penetration depth of VOD observations, scales linearly with VOD.

(H2) The contribution of leaf surface water to VOD is higher than leaf and wood internal water at diurnal time scale because leaf surface water usually accumulates at night and evaporates during the day while VOD at longer time scales is more likely controlled by changes in plant water stress and canopy biomass.

(H3) The contribution of leaf surface water to VOD is higher at moist sites than at dry sites because there is more rainfall interception and dew formation under humid conditions.

To evaluate these hypotheses, we compare VOD data derived from X-band (10.7 GHz) measurements by the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) (Du *et al.*, 2017) to predictions of CWC from a terrestrial biosphere model incorporating plant hydrodynamics, at four tropical forest and savanna sites in Brazil across a large rainfall gradient. AMSR-E VOD covers full annual cycles from 2003 to 2010 and has local bypassing times at 1:30AM and 1:30PM that can reasonably capture diurnal changes (Konings & Gentine, 2017; Li *et al.*, 2017) in addition to seasonal and inter-annual variation in CWC. The terrestrial biosphere model used in the study is the Ecosystem Demography version 2 (ED2). It is an ideal model platform to evaluate the relationship between CWC and leaf surface water with VOD because the model explicitly incorporates plant hydraulics and leaf energy budget (Xu *et al.*, 2016; Longo *et al.*, 2019) enabling it to simulate the dynamics of all of leaf surface water, leaf internal water, and wood internal water, as well as their vertical and horizontal heterogeneity within canopy.

Materials and Methods

Model description

ED2 (Medvigy *et al.*, 2009) is an individual-based terrestrial biosphere model that represents the dynamics of structurally and functionally-diverse plant canopies. The recent version of the model (ED-2.2, Longo *et al.*, 2019) has explicit representation of the leaf water and energy budget at sub-hourly resolution for each plant cohort. The model calculates changes of leaf surface water for each plant cohort as the balance of dew formation, evaporation, rainfall interception, and water shedding. Detailed description of the water fluxes that contribute to dynamics of leaf surface water in the model can be found in **SI Notes 1**.

ED2 is also one of the first models to couple trait-based plant hydraulics with vegetation demographic dynamics (Xu *et al.*, 2016). The hydraulics-enabled version (ED2-hydro) separates plant internal water pools into leaf and stem water pools at the cohort-level, and estimates sub-hourly water exchanges between these two pools using water potential gradient and cohort-specific stem water conductance following Darcy's law. The integration of plant hydraulics with stomatal conductance and rhizosphere water uptake enables cohort-level simulation of the dynamics of plant internal water content (see **SI Notes 1** for details). ED2-hydro has been calibrated and evaluated in several neotropical forests across a large precipitation gradient (Xu *et al.*, 2016; Powell *et al.*, 2017, 2018).

In this study, we used the functionality of ED-2.2-hydro to conduct mechanistic simulations of all major components of vegetation CWC. We updated key plant hydraulic parameters for tropical plant functional types (PFTs) based on a meta-analysis over tropical species (Christoffersen *et al.*, 2016) to incorporate the effects of plant functional diversity. Since vertical structure of vegetation biomass can influence interpretation of VOD data due to the limited penetration depth of microwave signals (Chaparro *et al.*, 2019), we also made several model updates in allometry, trait phenoplasticity, and mortality to improve simulated vegetation structure in tropical forests (details in **SI Notes S1**). The model parameterization (**Table S1**) used in this study are archived at https://github.com/xiangtaoxu/ED2/tree/VOD.

Model configuration and simulation setup

We conducted simulations for two tropical moist forests (Manaus K34 and Reserva Jaru) that both receive more than 2000 mm yr^{-1} mean annual rainfall and two tropical savanna sites (Brasília and Pé-de-Gigante) that both receive less than 1500 mm yr^{-1} mean annual rainfall (**Table 1**). These sites were selected based on the quality of AMSR-E VOD data available for these locations (in particular, minimal contamination from nearby rivers or other large water bodies), and the availability of in-situ meteorological data (Brasília: SONDA-INPE (2020); other sites: de Gonçalves *et al* (2013)).

Since the temporal coverage of in-situ meteorological data ranges from 1999 to 2012 depending on the site (see **Table 1** for details) but does not encompass the full length of AMSR-E VOD time series

(2003-2010), we integrated the ground measurements with climate reanalysis data from Modern-Era Retrospective analysis for Research and Applications, Version 2 (MERRA2) (Gelaro *et al.*, 2017). To avoid the known biases in MERRA2 precipitation over tropical regions (Beck *et al.*, 2019), we used precipitation data from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) (Funk *et al.*, 2015). To minimize the systematic biases in the reanalysis meteorology relative to local climate, and preserve monthly values, we calculated the difference between the monthly average of the reanalysis data and in-situ data for each variable over the years when in-situ data is available. We then applied the difference to modify the whole reanalysis time series to get the meteorological forcing (**Fig. S1**). The difference for precipitation is in logarithm space so that no rainfall was added to dry days when we applied the difference.

Simulations at each site consisted of a 400-year model spin-up to attain steady state vegetation structure and composition followed by a 30-year contemporary simulation (1981 to 2010) encompassing the AMSR-E measurements. For the spin-up simulation, we initialized the model with a small number of seedlings (0.1 individuals per m^2) of all four PFTs and ran the model with a cycling meteorological forcing from 1981 to 2000. Following up the spin-up simulations, we ran the model forced by meteorology from 1981 to 2010. For both sets of simulations, we used a constant rate of 1% of forest area experiencing windthrow disturbance (i.e 0.01 ha ha^{-1} yr^{-1}) and a constant atmospheric CO_2 at 380 ppm.

VOD retrievals

We used X-band (10.7 GHz) VOD retrieved from observations of the Japanese Aerospace Exploration Agency (JAXA) Advanced Microwave Scanning Radiometer for EOS (AMSR-E) instrument. Specifically, the VOD data were those retrieved by the Land Parameter Data Record (LPDR) version 2 (Jones & Kimball., 2012; Du *et al.*, 2017). The LPDR uses a multi-step procedure to disentangle the contributions of VOD, vegetation scattering, soil moisture, temperature, atmospheric humidity, and open water bodies to the observed radiometric brightness temperatures (Jones *et al.*, 2010).

Although the Amazon rainforest remains among the most challenging ecosystems for accurate VOD retrieval due to the large heterogeneity in canopy structure and the associated biophysical properties, interpretation of microwave radiometry has proven feasible even in highly complex canopies: for example, Calvet *et al* (1994) used a site-specific model to determine the relationship between Ka-band radiometry and stomatal resistance at Manaus. Nevertheless, the VOD retrievals are expected to be more accurate at the savanna sites than at the densely forested sites.

Model evaluation and comparison with VOD

We first evaluated the terrestrial biosphere model's predictions of vegetation structure and plant hydraulics because both of these characteristics directly affect CWC. We compared vertical profiles of leaf area index (LAI) profiles derived from the Geoscience Laser Altimeter System (GLAS) aboard the Ice, Cloud, and the Elevation Satellite (ICESat), which has previously been shown to capture variation in tropical forest structure (Tang & Dubayah, 2017; Yang *et al.*, 2018), with model simulated LAI profiles. Site-specific LAI profiles were derived from GLAS waveforms using a light-extinction model based on the MacArthur and Horn (1969) approach (Ni-Meister *et al.*, 2001; Tang *et al.*, 2014) using measurements collected between 2003 to 2008 (Zwally *et al.*, 2014) within a 50 km grid box centered around each study site. We extracted simulated average LAI profiles using model outputs from the same period of time for comparison. Both the GLAS and simulated LAI profiles were aggregated to a vertical resolution of 5 meters. LAI can show large seasonal changes especially in the two savanna sites. Therefore, we also compared the average seasonality of total LAI with Moderate Resolution Imaging Spectroradiometer (MODIS) LAI (Didan, 2015).

Unlike vegetation structure, there are no high-resolution and long-term measurements of plant hydraulic properties (e.g. leaf water potential) over tropical forests. Limited field measurements suggest leaf water potential for tropical canopy trees normally varies between 0 and -1 MPa within a day at moist sites (Fontes *et al.*, 2018) and can drop below -2 MPa at seasonally dry forest (Wu *et al.*, 2020) and cerrado sites (Bucci *et al.*, 2005). We therefore tested whether the simulated diurnal variation showed a similar range of variation.

For leaf surface water, there are no direct measurements on its diurnal and seasonal cycles in the tropics to the best of our knowledge. Limited measurements report predawn values for top canopy leaves ranging from 0.02 to 0.11 kg H_2O m^{-2} leaf in a tropical moist forest at Caxiuanã (personal communication with O. Binks) and from 0.02 to 0.08 kg H_2O m^2 leaf for five species in a tropical moist forest in Costa Rica (Aparecido *et al.*, 2017). Our simulated leaf surface water at predawn (6:00AM) in top canopy leaves showed a consistent range at a similarly wet forest site and predicted top canopy leaves are frequently wet at predawn (**Fig. S2**), which is consistent with a recent report at Caxiuanã using leaf wetness sensors (Binks *et al.*, 2021). Altogether, these consistencies suggest the model predictions on leaf surface water dynamics are realistic.

Following the model evaluation, we used daily AMSR-E VOD data at both 1:30AM and 1:30PM, and extracted the hourly average values of simulated leaf surface water (LW_s), leaf internal water (LW_i), and wood internal water (WW_i), the three components of CWC in ED-2.2-hydro, at the same time of VOD observations. We averaged both VOD and simulated CWC values into bi-weekly values to reduce high-frequency variation and noise in VOD (Konings *et al.*, 2016). In forests, X-band VOD is mostly sensitive to top canopy layers due to its high electromagnetic frequency (Macelloni *et al.*, 2001; Guglielmetti *et al.*, 2007). The depth at which significant canopy attenuation occurs, commonly referred to as the penetration depth, depends on both canopy structure and water status, and thus is variable in both space and in time. Spatial and temporal variation in penetration depth is generally not accounted for in retrieval algorithms (Konings *et al.*, 2016; Du *et al.*, 2017). Recently, Chaparro et al (2019) showed that X-band VOD values saturate when aboveground biomass (AGB) is higher than 1 kgC m^{-2}. Therefore, we chose a conservative average penetration depth by only including LW_s, LW_i, and WW_i for the top 1 kgC m^{-2} of biomass (leaf and wood, which corresponds to 2-10 meters depending on forest biomass vertical profiles) for each forest patch within site-level simulation results (**Fig. S3**) when comparing simulated CWC and AMSR-E VOD. Additionally, we also evaluated how VOD and CWC relationships vary with different assumptions of penetration depth.

We conducted analyses using the corresponding VOD data and CWC simulations across diurnal and bi-weekly time scales. First, we extracted the predicted diurnal cycle of LW_s, LW_i, and WW_i to investigate the roles of each water pool in determining CWC dynamics that emerge from ED-2.2-

hydro. Specifically, we derived the contribution of LW_s, LW_i, and WW_i to the variations in total CWC from the model at both diurnal and biweekly time scales by calculating the fractional contributions of each sub-component variance to the total CWC variance. For the diurnal-scale analysis, we quantified the variance as the value difference between 1:30AM and 1:30PM, since there are only two VOD observations within each diurnal cycle. For the biweekly-scale analysis, we calculated the variance of the mean of 1:30AM and 1:30PM for each biweekly (14 day) period.

Second, we compared the VOD measurements and CWC and assessed the role of leaf surface water in their relationships. To test our first hypothesis on the scaling between VOD and CWC (H1), we quantified the linear relationship between VOD and CWC using ordinary least squares (OLS) regression for each site and all sites combined. To test our second and third hypothesis on the contribution of leaf surface water to CWC and VOD dynamics and its variation across sites (H2 and H3), we compared VOD and two metrics of CWC: (1) CWC_{int} that only includes the internal water content of leaf and wood; and (2) CWC_{all} that includes both leaf and wood internal water and leaf surface water.

Specifically, we assessed the cross-site variation in isohydricity index, a widely-used metric to describe the diurnal behavior of plant water use (Martínez-Vilalta *et al.*, 2014; Konings & Gentine, 2017). This metric (σ) is calculated from the following regression equation:

$$X_{1:30PM} = \sigma \times X_{1:30AM} + \Lambda, \qquad \text{(eq 1)}$$

where σ is the isohydricity index, Λ is the regression intercept, and *X* is a state variable describing canopy water status. Low σ implies vegetation is more isohydric because daytime water status is relatively insensitively to nighttime water status due to stomatal control while higher σ implies vegetation is more anisohydric. We calculated *σ* values for observed VOD, simulated CWC, and leaf water potential to investigate whether and how VOD-based isohydricity (generally assumed to reflect leaf internal water stress) is affected by leaf surface water dynamics.

We then contrasted the average seasonality and deseasonalized multi-year variation of VOD and simulated CWC for each study site in terms of (1) absolute values at 1:30AM and (2) relative diurnal range (100% – $X_{1:30PM}$ / $X_{1:30AM}$ × 100%). Together with variance decomposition of the simulated CWC, the evaluation of these two metrics enables quantification of the impacts of leaf and wood water content and leaf surface water on VOD.

Results

Predictions of vegetation structure and plant water potentials

The long-term model equilibrium yielded LAI profiles that were generally consistent with GLAS estimates at the four evaluation sites (**Fig. 1a-d**). Individual-level competition in the model led to a general demographic size structure of a few big trees and many small trees, yielding decreasing leaf area density (LAD) from forest understory to canopy top that largely fall into the uncertainty of lidar-based estimates. At the two forest sites (M34 and RJA), top canopy height reached 35-40 meters while LAD became very small (<0.01 m2/m3) above 20 meters at the two savanna sites (PDG and BSB). However, the model tended to overestimate the total LAI at the sites by 0.3-0.5 m^2 m^{-2} (**Fig. 1a-d**), with the excess LAI arising mainly from overestimates of LAD in upper canopy layers. The model simulations also tended to underestimate LAD in the lowest (<5m) canopy layer at the two forest sites.

Seasonal changes of predawn leaf water potential govern the seasonal dynamics of canopy leaf phenology the model. As a result, seasonality of total leaf area was minimal at M34 where total rainfall is high and rainfall seasonality is mild. There were slight decreases of LAI at RJA (~0.2 m^2 m^{-2}), and larger (0.5-1 m^2 m^{-2}) decreases at PDG and BSB toward the end of the dry season (**Fig. 1e-f**). MODIS LAI exhibited qualitatively similar patterns of LAI seasonality between the wet and dry sites. However, at M34, the MODIS LAI estimates exhibit increases in LAI during the wet season, and earlier onset of leaf shedding around the start of dry season at PDG and BSB, compared to the model simulations. Overall, ED-2.2-hydro generated canopy vertical structure and increasing seasonal magnitude in canopy phenology from wet sites to dry sites, which are largely consistent with remote sensing observations.

The biosphere model simulations imply significant spatio-temporal variation in leaf water potential (Ψ_{leaf}) across all four sites (**Fig. 2**). For upper canopy leaves, the average maximum Ψ_{leaf} was close to zero for wet sites and for the wet season at dry sites (**Fig. 2e-f**), implying a full recharge of daytime water loss in the model. In the dry season at PDG and BSB, maximum Ψ_{leaf} dropped below -1 MPa, triggering leaf shedding in the model. The daily minimum Ψ_{leaf} of canopy leaves were generally 1-1.5 MPa lower than maximum values depending on moisture supply. These average patterns in leaf hydrodynamics are consistent with observed variation in leaf water potentials over tropical forests (Bucci *et al.*, 2005; Fontes *et al.*, 2018; Wu *et al.*, 2020). Wood water potential at the base of stems (Ψ_{stem}) had similar diurnal cycles and seasonality as Ψ_{leaf} (**Fig. S4**). However, the simulated Ψ_{stem} was always close to zero at M34, the wettest site in our study (**Fig. S4a**), whereas at the two drier sites ψ_{stem} showed reduced diurnal variation during the wet season (**Fig. S4c-d**), but similar seasonal variation as Ψ_{leaf}.

While observations of diurnal and seasonal variation in plant water potential were not available, the model's predictions of evapotranspiration (ET) matched observed patterns of ET seasonality that were available from flux tower measurements at M34, RJA, and PDG (**Fig. S5**), providing additional support for the model's ability to capture key characteristics of vegetation hydrodynamics in our study sites.

Spatio-temporal variation in simulated CWC and VOD observations

The model simulations indicate that LW_s dominates the diurnal cycles of CWC, despite being less than 10% of total CWC of upper canopy layers on average (**Fig. 3**). Generally, LW_s accumulated from late afternoon, reached peak values in early morning, then declined to near zero by midday. In contrast, LW_i varied by only 10-15% within a day and WW_i had even smaller diurnal variation (**Fig. 3a-d**). As a result, LW_s showed substantial contribution to CWC diurnal variability (**Fig. 3e-h**), accounting for 76% of CWC differences between 1:30AM and 1:30PM at M34 (wettest site) and 61% at BSB (driest site). LW_i generally accounted for more of the remaining CWC diurnal variances than WW_i. At the biweekly timescale, the contribution of LW_s was considerably lower (18%-36% for RJA, PDG, and BSB), except for M34 where LW_s still drove seasonal and inter-annual variations in the simulated CWC. In addition, at this time scale, WW_i became the dominant driver of CWC variation except for the wettest site (M34). Increasing the penetration depth to 10 kgC m^{-2} of AGB did not qualitatively change these general cross-site and cross-time-scale patterns; it did however, increase the contribution of wood internal water pools to patterns of diurnal and seasonal patterns of CWC variability (**Fig. S6**).

We found a strong linear relationship between VOD and simulated CWC_{all} (top 1 kgC m^{-2} of AGB) with an R^2 of 0.62 (**Fig. 4a**). The relationship remained significant at site-level, but the regression R^2 and slopes varied: simulated CWC_{all} explained less than 20% of variance in VOD at the two moist forest sites M34 and RJA, but accounted for about 50% of variance at the two savanna sites PDG and BSB (**Fig, 4c,d**). At the same time, the sensitivity of VOD to CWC_{all} (indicated by the slope of the VOD regressed against CWC_{all}) increased by approximately 300% from the wettest site (M34; slope = 0.55) to the driest site (BSB; slope = 2.15), whereas the regression slope of data from all sites combined fell in-between these values (slope = 0.86). The relationship between CWC_{int} (CWC excluding leaf surface water) and VOD was weaker (R^2 = 0.60 for all data combined) and the site-specific R^2 values declined by 5-10% for M34, BSB, and PDG while RJA showed little change (**Fig. 4b,c**). The site-specific regression slopes of the VOD-CWC_{int} relationship all steepened due to increasing nonlinearity of the relationship while the cross-site variations did not change much (**Fig. 4b**). As a result, the VOD-CWC_{int} regression slope using data from all sites combined (0.96, black line in **Fig. 4**) became lower than site-specific regression slopes (1.2 – 2.8, colored lines in **Fig. 4**). Using a much deeper penetration depth that included the top 10 kgC m^{-2} of AGB yielded similarly high R^2 values (0.61 for both CWC_{all} and CWC_{int}), but the R^2 values were far lower (<10%) for the two moist forest sites, and the cross-site regression slope was much lower than all site-level regression slopes regardless of whether or not LW_s was included (**Fig. S7**). Overall, the model predictions of CWC that includes all forms of canopy water showed robust linear relationships with VOD, but the relationships were stronger at drier sites and across sites along a rainfall gradient.

We calculated isohydricity (σ) values from the variability in biweekly VOD estimates and calculated a similar metric from model simulations of bi-weekly variability in CWC_{all}, CWC_{int}, and canopy Ψ_{leaf}. Our VOD-based isohydricity values were comparable to the values estimated by Konings & Gentine, (2017) and Li *et al.*, (2017) from daily VOD observations. As seen in **Fig. 5a-d**, the VOD-based σ was low at the two wet sites (0.44 for M34 and 0.59 for RJA respectively) and higher at two dry sites (0.71 for PDG and 0.72 for BSB respectively). The largest difference between VOD-based and

CWC_{all}-based isohydricity occurred at M34, where the simulated isohydricity was considerably lower than the VOD-derived estimate (σ =0.18 and 0.44 respectively). However, the isohydricity values from the model predictions of CWC_{all} and VOD observations were very close at the other three sites (**Fig. 5a-h**). In contrast, dynamics of CWC_{int} and Ψ_{leaf} implied almost perfect to extreme anisohydric behavior across all sites with σ values very close to or larger than one (**Fig. 5i-p**), highlighting the significant contribution of LW_s to the diurnal variation in simulated CWC_{all}, and, by inference, to VOD measures of isohydricity.

We also compared the average seasonality of simulated CWC and observed VOD with respect to both their values at 1:30AM and their diurnal ranges (**Fig. 6**). At the two moist forest sites, 1:30AM VOD showed seasonal patterns that peaked in the middle of the dry season with a seasonal amplitude of ~10% at M34 and 20% at RJA (black lines in **Fig. 6,** panels **a** and **b,** respectively). Simulated CWC_{all} did not reproduce these patterns, however, showing minimal seasonality at M34 and a small and short decline in late dry season at RJA (green lines in **Fig. 6,** panels **a** and **b,** respectively). At the two savanna sites, 1:30AM VOD showed 20-25% seasonal variations, peaking in the late wet season, and reaching its lowest values in the late dry season (black lines in **Fig. 6,** panels **c** and **d** respectively). The simulated 1:30AM CWC_{all} showed similar seasonal patterns and amplitude (green lines in **Fig. 6c and d** respectively). As a result, the correlation between VOD and simulated CWC_{all} increased from around zero at wet sites to ~0.8 at the dry sites. Interestingly, CWC_{int}, which excludes the highly seasonal (vary by 30%-100%) LW_s that follows the seasonality of rainfall (**Fig. S8a-d**), exhibited stronger correlation with VOD seasonality particularly at the two wet sites (Pearson's r increased from ~0 to 0.4-0.5), but a reduction of seasonal amplitude by 5-10% at all sites.

The comparison of the seasonality in the diurnal range showed similar patterns with the model-data correlation increasing from wetter sites to drier sites (**Fig. 6e-h**). However, the influence of LW_s was more prominent at the savanna sites. At these two drier sites, the simulated diurnal range of CWC_{int} peaked in mid to late dry season when daytime atmospheric water demand was high and soil water supply was low. Inclusion of LW_s, whose diurnal range could reach 80-100% (**Fig. S8e-h**), resulted in shifts of the peak to late wet season for CWC_{all}, which is consistent with VOD seasonality, and resulted in comparable average diurnal range values (5-10%) as VOD data. At the two forest sites, the inclusion of LW_s reduced the temporal correlation of the diurnal range between VOD and CWC_{all} at M34 and reversed the correlation at RJA; however, it increased the average diurnal range to be closer with the VOD observations. The model-predicted diurnal range may bias low because WW_i is calculated from water potential at the base of the stem, which may have smaller diurnal range than branch water potential in nature. A post-hoc correction by assuming wood water potential is the same as leaf water potential increased the average diurnal range in CWC for 2-3% but did not change the seasonal patterns or the impact of LW_s (**Fig. S9**). Overall, these results suggest the ED-2.2-hydro did not capture the seasonality in canopy hydrodynamics and phenology at the forest sites; however, it performed well at the two savanna sites, where consideration of LW_s significantly improved the agreement between simulated CWC and VOD observations.

At the inter-annual timescale, VOD showed substantial variability relative to its average seasonality in both 1:30AM values and diurnal ranges (**Fig. 7**) due to changes in hydroclimatic conditions. Simulated anomalies of both CWC_{all} and CWC_{int} at 1:30AM were more correlated with anomalies of 1:30AM VOD at the drier sites (significant positive correlation with Pearson's r ranging from 0.36 to 0.53 for PDG and BSB) than at the wet sites (no significant correlations). While including LW_s increased the correlation coefficients by 0.05 to 0.2, it did not change the general cross-site pattern. The simulated diurnal range anomalies in CWC were not correlated with the diurnal range anomalies in VOD at inter-annual time scales no matter whether LW_s was included or not (**Fig. 7e-h**). The simulated diurnal range in CWC generally showed less inter-annual variability with standard deviation of 1.0-1.7% (CWC_{all}) and 0.19-0.37% (CWC_{int}) than the diurnal range in VOD, which had standard deviations ranging from 1.9% to 2.2%. Similar to the seasonal scale analysis, correcting for wood internal water did not change the simulated patterns of inter-annual variations in CWC (**Fig. S10**).

Discussion

Predicted Canopy Water Content (CWC) and its relationship with Vegetation Optical Depth (VOD)

The increasing use of Vegetation Optical Depth (VOD) to infer large-scale patterns of vegetation water stress builds on the mechanistic proportionality between VOD and Canopy Water Content

(CWC) (Konings *et al.*, 2019). However, quantitative assessments of this relationship have been lacking at the ecosystem scale – the scale at which remote sensing VOD measurements are made (tens of kilometers) – particularly in humid, high-biomass ecosystems such as tropical forests. This is mostly because ground-based measurements of CWC are generally made at the level of leaves or tree branches (Powers & Tiffin, 2010; Chavana-Bryant *et al.*, 2016; Martin *et al.*, 2018). Consequently, previous VOD field evaluation studies (Liu *et al.*, 2015; Fan *et al.*, 2019; Chaparro *et al.*, 2019) only examined the statistical associations between spatial variation in VOD and above-ground biomass, a quantity that is easier to measure at larger spatial scales via forest inventory and LiDAR measurements.

Our study evaluates, for the first time, the VOD-CWC relationship in both the spatial and temporal domains through novel application of a terrestrial biosphere model. Our analyses support the first hypothesis (H1) that VOD scales approximately linearly with CWC across space and time; however, it also reveals important sources of complexity in this relationship: the slope of VOD-CWC relationship varied across sites with different moisture conditions and vegetation structures (**Fig. 4**). While some variation in the slope with vegetation type is expected, a three-fold increase in the slope from savanna to forest sites (**Fig. 4d**) is far greater than previously estimated from radiometric experiments in non-forested ecosystems (Van De Griend & Wigneron, 2004) and leads to a relatively sigmoidal or saturating VOD-CWC relationship for cross-site variations.

VOD saturation at high aboveground biomass density (Chaparro *et al.*, 2019) should not be the primary factor driving variation in the VOD-CWC slopes because cross-site variation in penetration depth is explicitly considered in our analysis (**Fig. S3**) although our approach might not fully capture small seasonal changes of penetration depth within each site. The larger-than-expected variation in the VOD-CWC slope may reflect deficiencies in the model formulation: most notably, the model's drought-driven phenology scheme generated smaller-than-observed seasonal amplitudes in CWC at the two wet sites, compared to the seasonality in VOD (**Fig. 6**), which may explain the low regression R^2 and slope at M34 and RJA. The cross-site variation in the slopes of the VOD-CWC relationships could also be due to uncertainty in the VOD retrievals, particularly the uncertainty associated with surface temperature and single-scattering albedo in the densely forested M34 and RJA sites (Du *et al.*,

2017) or due to multiple scattering (Schwank *et al.*, 2018). Both explanations call for additional calibration of VOD with in-situ measurements of CWC, especially in moist, high-humidity ecosystems such as tropical forests.

The role of leaf surface water (LW_s) in CWC and VOD variation across different time scales

Our simulations explicitly consider dew formation, rainfall interception, and the resulting dynamics of LW_s. While no direct measurements of canopy LW_s temporal dynamics are available to evaluate the model's predictions, the simulated range of LW_s is consistent with sparse sampling from an Amazon moist forest (**Fig. S2**). In addition, a rare ground-based radiometer study in a Panamanian tropical moist forest (Schneebeli *et al.*, 2011) estimated that whole canopy LW_s could regularly reach 0.17 $kgH_2O\ m^{-2}$ (ground) at pre-dawn from dew formation and intensive rainfall events occasionally increased LW_s to 0.4-1 $kgH_2O\ m^{-2}$. The model generated comparable average predawn LW_s values of 0.21-0.23 $kgH_2O\ m^{-2}$ at the two tropical forest sites (**Fig. S6**). The simulated average predawn LW_s is close to the observed dew-driven value, but lower than the observed rainfall-driven values likely because reanalysis rainfall underestimates the diurnal cycle (**Fig. S11**).

In our model simulations, LW_s accounts for more than 50% of diurnal variation in CWC at all four of the study sites (**Fig. 3**). The large diurnal contribution from the relatively small LW_s pool (< 10% of total CWC) stems from its fast turn-over rate: by midday almost all LW_s accumulated during the night evaporates away (**Fig. 3**). In contrast, simulated LW_i varied by only 10-15% within a day and WW_i by even less. In nature and in the model, this occurs because plant stomatal control constrains daily minimum leaf water potential to be above, or not far below, the leaf turgor loss point (Brodribb & Holbrook, 2003; Fontes *et al.*, 2018), whose corresponding relative water content is approximately 90% for tropical wet forests (Bartlett *et al.*, 2012).

Consequently, our results call into question the ability to correctly infer spatial and temporal patterns of plant water stress from diurnal measurements of VOD in humid forest ecosystems such as tropical rainforests, as illustrated in our isohydricity analysis (**Fig. 5**). First, leaf surface water dynamics might contribute most to the VOD-based isohydricity. Second, isohydricity index based on water content is influenced by both leaf internal water stress and the seasonal variation in vegetation structure, and thus can deviate from the isohydricity index based on leaf water potential and converge to one (**Fig. 5i-p**). In addition, if VOD diurnal range reflects diurnal water stress, it should peak in the dry season in tropical forests when plant diurnal water stress is generally the highest -- as shown in both observations (Brodribb & Holbrook, 2004; Fisher *et al.*, 2006) and the biosphere model simulations conducted in this study (**Fig. 2**). However, at the two savanna sites, VOD diurnal range peaked in late wet season, which can only be explained by including LW_s (**Fig. 6**). Excluding rainy days (Konings & Gentine, 2017; Li *et al.*, 2017) is likely not enough to eliminate the effects because dew formation can also significantly contribute to LW_s and the simulated importance of LW_s only drops to a low level in months with both low rainfall and humidity (**Fig. S12**). Hence, the influence of LW_s on VOD retrievals may also be important in other humid ecosystems such as those found along the North American Pacific coast (Burgess & Dawson, 2004) and montane forests (Berry *et al.*, 2014).

The importance of LW_s decreases, however, at the seasonal and inter-annual time scales (**Fig. 6&7**), implying that failing to consider LW_s will have less effect in VOD-based inference of canopy phenology (Guan *et al.*, 2014; Wang *et al.*, 2020) and vegetation mortality (Rao *et al.*, 2019; Wigneron *et al.*, 2020). Therefore, our results support our second hypothesis (H2) that the contribution of leaf surface water is highest at the diurnal time scale.

In contrast, there is only partial support for our third hypothesis (H3) that the contribution of leaf surface water to diurnal VOD dynamics increases as precipitation increases: variance decomposition implies an increasing contribution from LW_s along the gradient from dry to wet sites (**Fig. 3**) and from wet to dry months (**Fig. S12**) is consistent with H3. However, it is difficult to draw strong conclusions regarding H3 given the large uncertainties in VOD retrievals and low level of seasonality in the model simulations compared to the observed seasonality of VOD values and diurnal ranges at the two moist forest sites (**Fig. 6**). In addition, the simulated cross-site variations in LW_s contribution might be biased because ED-2.2-hydro does not represent possible leaf trait adaptation across moisture gradients such as changes in leaf texture and trichome abundance that could regulate leaf surface water retention (Aparecido *et al.*, 2017) and thus influence LW_s dynamics. Further in situ data collection and model improvement and benchmark are necessary to accurately evaluate how LW_s contribution vary across moisture gradients.

Implications for tropical phenology in vegetation models

Our model-data analysis also provides a useful evaluation of the plant hydrodynamics and leaf phenology formulations in the ED-2.2-hydro terrestrial biosphere model. As anticipated, there was better agreement between the model predictions and the VOD measurements at the two drier sites where abiotic moisture conditions exhibit large variability that significantly affects canopy water content. However, the predicted seasonal decline of LAI is later than in MODIS LAI estimates (**Fig. 1**), and the relative magnitude of the seasonal decline in CWC was smaller than VOD observations (**Fig. 6**), suggesting that the model's drought-deciduous leaf phenology scheme may not be sufficiently responsive to seasonal water stress. In the current model formulation, leaf-drop is triggered when pre-dawn water potential falls below turgor loss point, whereas drought experiments on tropical seedlings suggest the average of pre-dawn and midday water potential can best predict leaf shedding (Wolfe *et al.*, 2016). Incorporating midday water potential into the drought-deciduous phenology scheme might therefore improve the seasonality at drier savanna sites.

Similarly, at the two wet sites, the predicted seasonality in canopy water content was lower than the seasonality in VOD (**Fig. 6**). This may be because the VOD seasonality is partially attributable to unknown retrieval errors caused by seasonally varying properties (e.g. changes in canopy structure) in densely vegetated areas (Konings *et al.*, 2016; Du *et al.*, 2017). Another possible explanation is that biotic factors, such as leaf ontogeny, can influence seasonal variation in canopy water content under moist conditions. For instance, leaf relative water content can change substantially with leaf age in tropical wet forests (Chavana-Bryant *et al.*, 2016) therefore seasonal changes in leaf demography at tropical moist forests (Wu *et al.*, 2016) may contribute to seasonal variation in CWC and resulting VOD measurements. A simple calculation of CWC changes based on published leaf demography and leaf ontogeny data at Manaus (Chavana-Bryant *et al.*, 2016; Wu *et al.*, 2016) suggests that seasonal variation in leaf age could explain the seasonal amplitude of VOD at M34, albeit with a 1-2 month lag in timing (**Fig. S13**).

Conclusions

Our analyses indicate a large contribution of leaf surface water to diurnal variation in landscape-scale canopy water content (CWC) and AMSR-E Vegetation Optical Depth (VOD) signals over tropical forests. This is important because diurnal variation in VOD has been proposed as a measure of canopy isohydricity, a metric widely used to diagnose the water status of plant canopies. Our analysis shows that leaf surface water also influences seasonal variation in VOD, but to a far lesser extent. In this analysis, we examined VOD measurements from X-band microwave instruments that have relatively low penetration into the dense canopies of tropical forests; however, our findings also apply to VOD measurements from lower (L-band) electromagnetic frequencies (e.g. SMAP and SMOS) because the simulated LW_s contributions remain high even when we evaluated deeper canopy penetration depth (**Fig. S6**). Therefore, future applications of microwave band measurements, as well as and other imaging spectroscopy-based estimates of canopy water content (Asner *et al.*, 2016) should carefully consider the effects of variation in leaf surface water, particularly during rainy and humid periods. In turn, the sensitivity of VOD to leaf surface water newly identified in this study provides new opportunities to understand leaf surface water dynamics and its impact on plant water use.

Our analyses also highlight the value of explicitly representing plant hydrodynamics in terrestrial biosphere model formulations. The consistency between VOD and model predicted CWC across diurnal, seasonal, and inter-annual timescales at the two tropical savanna sites suggests that the current model structure is able to capture important processes governing plant hydrodynamics; however, capturing diurnal and seasonal patterns of VOD in wet tropical forests is likely to require consideration of phenological processes affecting canopy water content, such as seasonal leaf demography and ontogeny.

Author Contributions

X.X., P.M., A.K., and S.S. designed the research. M.L. and X.X. processed the meteorology and flux tower data. A.K. and A.F. processed AMSR-E VOD data. L.X. and S.S. provided GLAS Lidar LAI. D.W. provided the MODIS data. J.W. provided the in-situ leaf trait and demography data. X.X.

performed model simulation, conducted analyses, and drafted the manuscript. All authors contributed to writing of the manuscript.

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Data Availability

The remote sensing data that support the findings of this study are openly available at http://files.ntsg.umt.edu/data/LPDR_v2/ for VOD, https://nsidc.org/data/icesat/data.html for GLAS, and https://lpdaac.usgs.gov/ for MODIS. The ED2 model codes are archived at https://doi.org/10.5281/zenodo.3978588. The meteorological forcing data used to drive ED2 are available from the corresponding author upon request.

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Supporting Information Legends

Fig. S1 Average monthly seasonality of the meteorological forcing used to drive the model simulations.

Fig. S2 Distribution of predawn leaf surface water (LW_s) in top canopy compared with observed ranges.

Fig. S3 Schematic diagram on penetration depth for CWC in ED-2.2-hydro.

Fig. S4 Vertical profile and average seasonality of simulated wood water potential at the base of tree stems.

Fig. S5 Average seasonality of evapotranspiration from ED-2.2-hydro simulations (red line) and flux tower data.

Fig. S6 Contribution of leaf surface water to canopy water content in model simulations using 10 kgC m^{-2} as penetration depth.

Fig. S7 Relationship between VOD and simulated CWC_{all} (including LW_s) and CWC_{int} (excluding LW_s) using 10 kgC m^{-2} as penetration depth.

Fig. S8 Average seasonality of simulated leaf surface water.

Fig. S9 Average seasonality of VOD and CWC corrected by leaf water potential.

Fig. S10 Deseasoned multi-year variability of VOD and CWC corrected by leaf water potential.

Fig. S11 Average diurnal cycles of precipitation rainfall from ground-observation (GRND) and reanalysis data (REAN) used in our simulations.

Fig. S12 Relative contribution of variance in LW_s to the diurnal variance in CWC_{all} as a function of precipitation and vapor pressure deficit.

Fig. S13 Average seasonality of midnight VOD at M34 compared with seasonality of leaf water concentration estimated from leaf demography data.

Notes S1 Additional model description for ED-2.2-hydro

Table S1 Key plant photosynthetic, structural, and hydraulic traits for the three tree plant functional types (PFTs) used in our simulations.

Tables and Figure Legends

Table 1 Description of climate and soil conditions used for ED-2.2-hydro simulations at the four study sites.

Site name	Location (lon, lat)	MAT (°C)	MAP (mm)	Soil Texture (% of sand and clay)*	Temporal coverage of *in situ* meteorology**
Manaus K34 (M34)	-60.21,-2.61	25.7	2673	0.2,0.68	1999-2006
Reserva Jaru (RJA)	-61.93,-10.08	25.0	2069	0.8,0.1	1999-2002
Pé-de-Gigante (PDG)	-47.65,-21.62	22.8	1453	0.85,0.03	2001-2003
Brasília (BSB)	-47.71,-15.60	21.7	1344	0.13,0.53	2010-2012

*We used the best estimates of soil texture following previous ED2 simulations (Longo, 2014; Restrepo-Coupe *et al.*, 2017) and we used the same soil depth of 10 meters.

** Meteorological variables necessary to drive the model include incoming shortwave and longwave radiation, temperature, humidity, pressure, precipitation, and wind speed

Figure 1 Evaluation of vegetation structure in ED-2.2-hydro across four study sites along a rainfall gradient. (**a-d**) The average profile of leaf area index (LAI) within forest canopy from the Geoscience Laser Altimeter System (GLAS) lidar inversion (red) and model simulations (black). Red error bars represent standard deviation of GLAS data within the 50km grid cell around each site. The x-axis represents leaf area density (LAD) for each 5 meter band from 0m to 50m above ground while the y-axis represents height of each band. Inset plots within each panel compare the total LAI from model and GLAS data. (**e-h**) Seasonality of monthly average canopy total LAI from model simulation (black) and observations from Moderate Resolution Imaging Spectroradiometer (MODIS, blue). Grey bars denote the average monthly rainfall in millimeters. Each column displays results for a study site with site acronym and mean annual rainfall at the top of each column.

Figure 2 Simulated leaf hydrodynamics in ED-2.2-hydro. (a-d) vertical distribution of daily maximum (blue) and minimum (red) leaf water potential. We averaged cohort-level leaf water potential for every 5 meter height bands, using cohort leaf area index as weighting factors. (e-h) seasonality of average daily maximum and minimum leaf water potential for upper canopy leaves. We define upper canopy as the top 1kgC m^{-2} biomass.

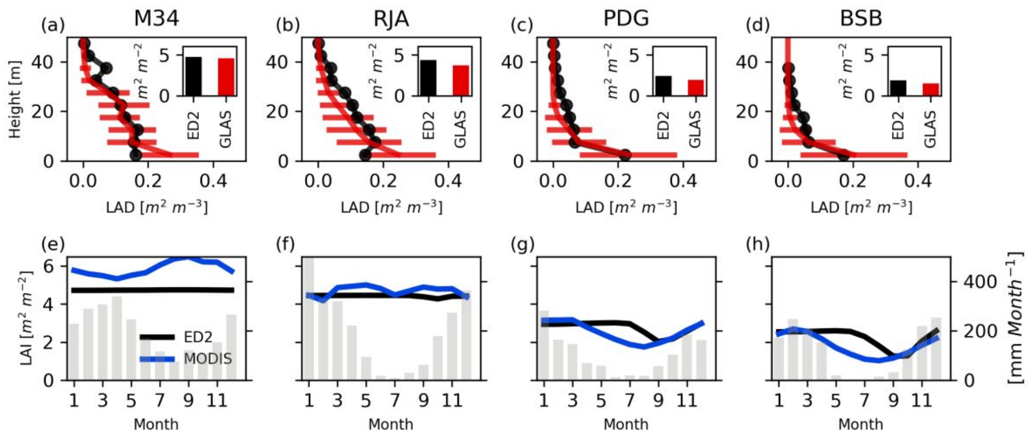
Figure 3 Contribution of leaf surface water to canopy water content (CWC) in model simulations. (**a-d**) Average diurnal cycles of CWC partitioned into wood internal water (WW_i, brown), leaf internal water (LW_i, green), and leaf surface water (LW_s, blue) for our four study sites. The vertical dashed lines represent the local bypassing time of vegetation optical depth (VOD) measurements (1:30AM and 1:30PM). (**e-h**) Variance decomposition of CWC temporal variations into the three sub-components at both the diurnal scale (black bars) and biweekly scale (red bars). We only used the simulated CWC at the same time as VOD measurements (dashed lines in panels a-d) for this analysis.

Figure 4 Relationship between vegetation optical depth (VOD) and **(a)** simulated CWC_{all} (canopy water content including leaf surface water) and (**b**) CWC_{int} (canopy water content excluding leaf surface water). Each dot represents bi-weekly average of 1:30AM or 1:30PM values, with the colors indicating the different study sites, M34 (brown), RJA (red), PDG (purple), and BSB (blue). Solid black lines represent ordinary least square linear regression between VOD and CWC using all data combined while solid color lines represent regressions for each site. Regression R^2 (**c**) and slopes (**d**) are also shown for each site and all sites combined. We only include CWC dynamics from the top 1kgC m^{-2} biomass in the simulations.

Figure 5 Isohydricity index (σ) from vegetation optical depth (VOD, **a-d**), canopy water content including leaf surface water (CWC_{all}, **e-h**), canopy water content excluding leaf surface water (CWC_{int}, **i-l**), and leaf water potential (**m-p**, Ψ in MPa). Each column represents results from one study site. Each dot represents a biweekly average of VOD, CWC_{all}, CWC_{int} or Ψ. CWC and Ψ values represent water contents and average leaf water potential of the upper canopy layers (top 1 kgC m^{-2}). Red lines represent linear regression results with σ values shown on top of each panel. All regressions are significant.

Figure 6 Comparison of average seasonality between vegetation optical depth (VOD) and simulated canopy water content (CWC) across four study sites. (**a-d**) seasonality of 1:30AM VOD (black), CWC_{all} (including leaf surface water, green), and CWC_{int} (excluding leaf surface water, purple). To facilitate comparison, we normalized the seasonality by dividing the maximum seasonal values for each variable. (**e-h**) similar to **a-d** but for diurnal ranges calculated as $(1 - X_{1:30PM} / X_{1:30AM}) \times 100\%$, where X denotes either VOD or CWC. We calculated Pearson's r between the average seasonality in VOD and the simulated CWC (with and without leaf surface water) and showed the correlation coefficients using the same color as the different CWC lines. Significant correlation ($p < 0.05$) was marked with *. In all panels, we only included water from the top 1 kgC m^{-2} biomass within the canopy and gray bars represent average monthly rainfall.

Figure 7 Comparison of interannual -year variability between vegetation optical depth (VOD) and simulated canopy water content (CWC) after removing average seasonality across four study sites. (**a-d**) variability of 1:30AM VOD (black), CWC_{all} (including leaf surface water, green), and CWC_{int} (excluding leaf surface water, purple). We normalized the time series by dividing the maximum as in Figure 6. (**e-h**) similar to **a-d** but for diurnal ranges calculated as $(1 - X_{1:30PM} / X_{1:30AM}) \times 100\%$, where X denotes either VOD or CWC. We calculated Pearson's r between the average seasonality in VOD and the simulated CWC (with and without leaf surface water) and showed the correlation coefficients using the same color as the different CWC lines. Significant correlation ($p < 0.05$) was marked with *. In all panels, we only included water from the top 1 kgC m^{-2} biomass. Due to high-frequency variation in the simulated CWC, we averaged the biweekly data into bimonthly values to facilitate comparison.



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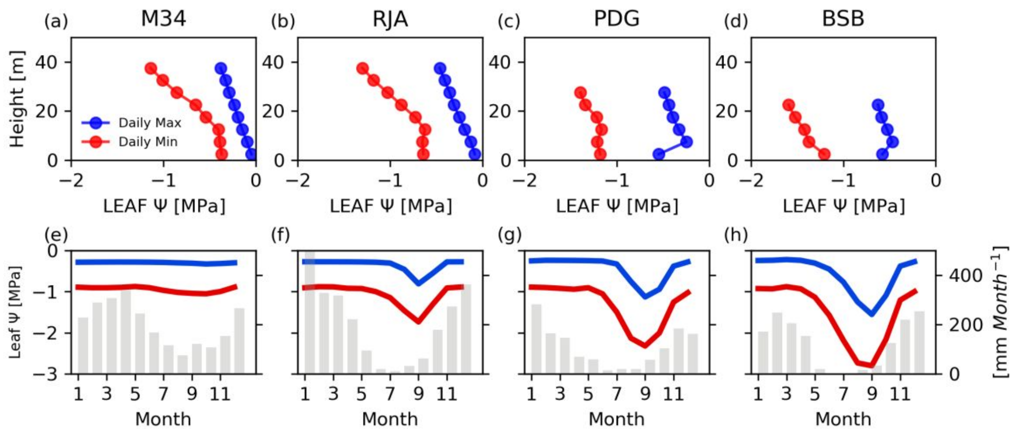

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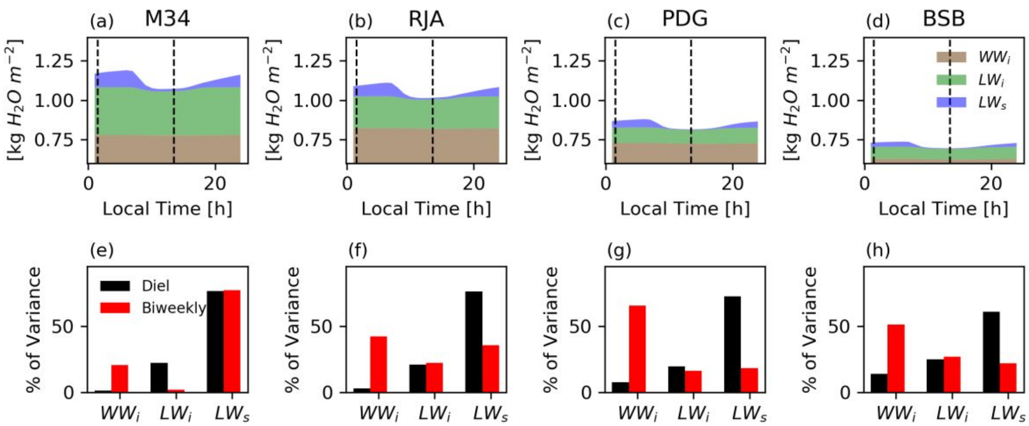

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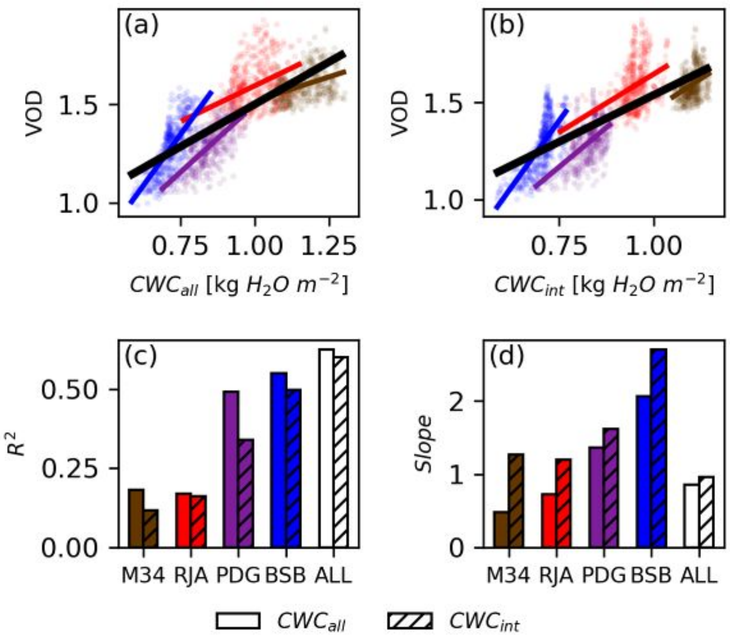

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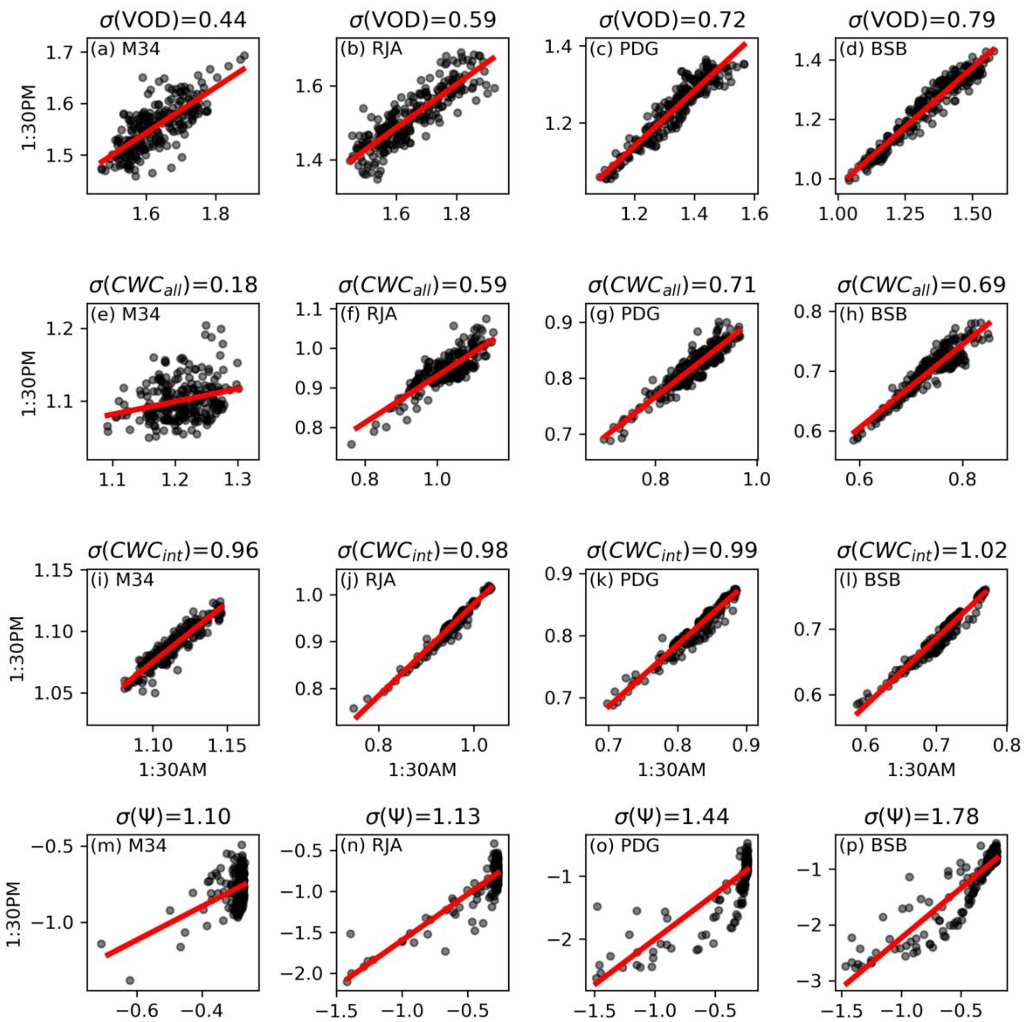

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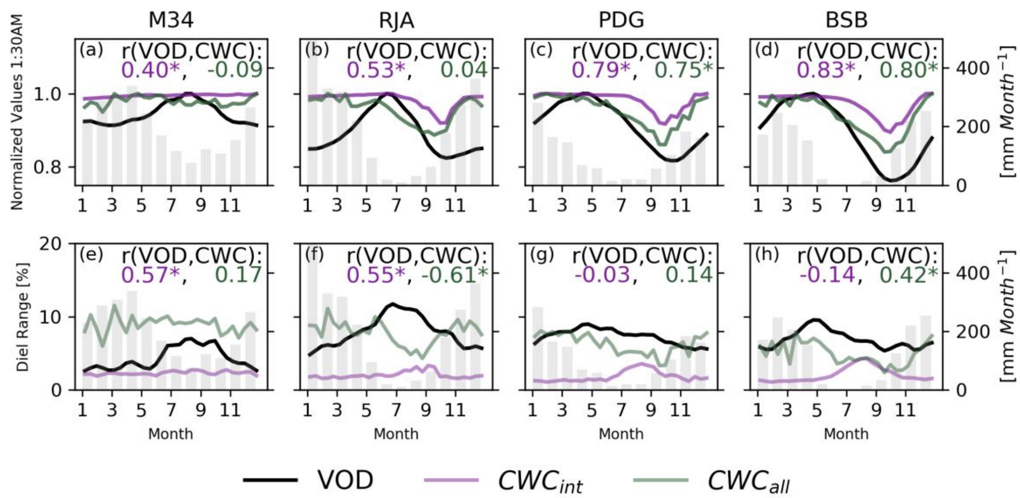

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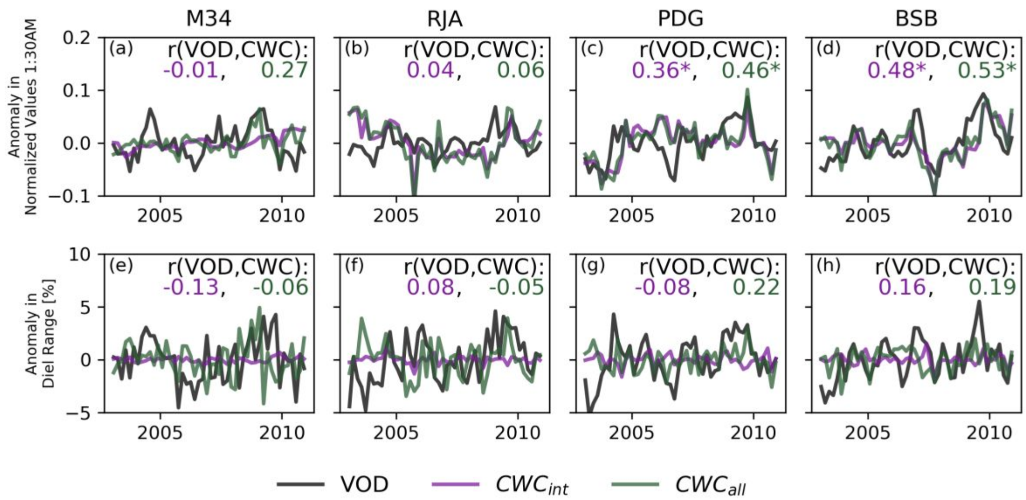

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