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Soil moisture variation drives canopy water content dynamics across the western U.S.

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ABSTRACT

Drought stress is a major contributing factor to plant mortality across the globe. Drought effects are often studied at the local scale, but recent advances in remote sensing allow for observations of plant water status across broad geographic scales. The vegetation optical depth (VOD) derived from satellite-based surface microwave emission has been shown to be sensitive to canopy water content, which is increasingly recognized as an important indicator of water relations and incipient mortality in plants. We develop an index which quantifies the normalized difference between night- and daytime diurnal VOD retrievals (nVOD_r) and apply it across the western U.S. to determine the relative sensitivity of plants to variations in water supply (soil moisture) and atmospheric water demand (vapor pressure deficit -VPD). Canopy water content dynamics were most sensitive to soil moisture variation at intermediate climatic water deficits where tree cover transitions to grass cover. These areas are in transitional climate zones and occur at ecotones between forest and non-forest vegetation where canopy water content dynamics are most sensitive to both soil moisture and VPD variation. Our results suggest that vegetation in semi-arid ecotones is likely to see the most proximal impacts of drought stress as the planet warms.

1. Introduction

Forest mortality rates have more than doubled in the western United States over the last 40 years (Van Mantgem et al., 2009). Elevated temperatures and increased water stress that characterize drought have been implicated as the largest contributing factors to rising mortality rates (Allen et al., 2015; Allen et al., 2010). Drought events are occurring more frequently and with higher severity, and these trends are projected to continue as climate change progresses (Meehl et al., 2007). While negative impacts of drought have been observed in most ecosystems, research suggests that populations at dry range edges are less buffered from climate impacts and are more likely to exhibit increased mortality and regeneration failure under drought stress (Anderegg et al., 2019; Davis et al., 2019; Young et al., 2017). These dry range edges are often transitional zones between plant physiognomic types where species live

near the boundary of their climatic tolerance. Moreover, these ecotones experience larger climatic variance due to greater land surfaceatmosphere coupling (Koster et al., 2004; Seneviratne et al., 2010; Seneviratne et al., 2006), which potentially exposes dry edge species to negative impacts under directional climate shifts towards hotter and drier conditions.

Plants experience drought when increasing evaporative demand through rising vapor pressure deficit (VPD) and/or decreasing available soil moisture lead to greater water loss through transpiration than can be replaced via water uptake from the soil. Although warm temperature can accelerate soil drying through evapotranspiration, precipitation can recharge soil moisture and is thus a first order control on soil moisture dynamics. Research addressing plant responses to drought often focus on temperature and/or VPD (Grossiord et al., 2020; Novick et al., 2016; Sulman et al., 2016; Williams et al., 2010) or precipitation and soil

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moisture dynamics (Goulden and Bales, 2019; Schwantes et al., 2018; Simeone et al., 2018), but both water supply and demand play a crucial role (Du et al., 2018; Perez-Martin et al., 2009; Stephenson, 1990). Indeed, water supply and atmospheric demand are fundamentally linked (Trenberth and Shea, 2005). Increasing atmospheric aridity across much of the western U.S. has resulted in decreasing summer precipitation, challenging our ability to attribute drought induced vegetation change to either supply or demand (Holden et al., 2018). Therefore, it is important to understand how vegetation sensitivity to VPD and soil moisture dynamics varies spatially and in time to better quantify regional drought susceptibility as the climate changes. Here, we examine the relative influence of soil moisture and VPD variation on plant water status in the western U.S via their effects on canopy water content dynamics.

There is mixed evidence on the relative importance of water supply and demand to plant growth and response to drought. Increasing temperatures and atmospheric demand have been identified as the primary contributing variables to tree drought mortality in the southwestern U.S. (Williams et al., 2013), as a greater contributing factor to evapotranspiration than soil moisture in mesic forests across the U.S. (Novick et al., 2016), and as the primary driver of interannual variation in forest productivity and transpiration at an Ameriflux site in Indiana (Sulman et al., 2016). However, soil moisture can impact vegetation productivity and transpiration regardless of VPD, especially at moderate to low levels of soil wetness (Körner, 2019; Seneviratne et al., 2010; Stocker et al., 2019). Papagiannopoulou et al. (2017) found that global vegetation dependence on water availability has been under reported with semiarid and transitional ecosystems being primarily water-limited, and Novick et al. (2016) showed greater soil moisture limitation to stomatal conductance at xeric sites. Limited water availability was also largely responsible for the extensive forest mortality during the 2012-2015 California drought (Goulden and Bales, 2019) and the reduced vegetation productivity during the 2003 European drought (Reichstein et al., 2007), while low soil moisture extremes were predominantly responsible for canopy loss during a 2011 drought in Texas (Swenson et al., 2017). Decreased supply and increased demand are often highly correlated over extended time periods, and land-atmosphere feedbacks between the two can magnify drought impacts (Holden et al., 2018; Martinez-Vilalta et al., 2019; Seneviratne et al., 2010; Zhou et al., 2019). However, VPD is more sensitive to temperature, which is widely predicted to increase globally as climate changes, while the impacts of climate change on precipitation and moisture availability are more variable and uncertain (Burke and Brown, 2008; Dannenberg et al., 2019; IPCC, 2013; Novick et al., 2016; Pendergrass et al., 2017).

Drought decreases growth and increases risk of mortality (Anderegg et al., 2015a; Berdanier and Clark, 2016; Bigler et al., 2007; Camarero et al., 2015; Carnicer et al., 2011; Guada et al., 2016). The imbalance between water uptake and loss that plants experience under drought increases xylem tension (decreases water potential) and can lead to cavitation and loss of water transport capacity (measured as percent loss of conductivity - PLC). Such hydraulic failure has been shown to be a strong driver of drought-induced mortality (Adams et al., 2017; Anderegg et al., 2013; Brodribb and Cochard, 2009). More recent studies have emphasized the utility of plant water content-related metrics (such as relative water content - RWC) as useful indicators of incipient mortality given its linkage to plant hydraulics, osmotic regulation, and our ability to measure water content at large scales using remote sensing (Martinez-Vilalta et al., 2019; Sapes et al., 2019). While direct measurements have been successful in parameterizing and simulating the effect of drought on plant water status at the watershed scale (Anderegg et al., 2015b; Simeone et al., 2018), remote sensing offers the possibility to expand monitoring to regional or larger scales.

Remotely sensed vegetation optical depth data (VOD) is derived from satellite-based surface microwave emission and is sensitive to canopy moisture, which depends on water content and biomass. Therefore, VOD has been identified as a means to retrieve broad-scale vegetation canopy

water dynamics. High frequency microwaves do not fully penetrate plant canopies, and therefore VOD retrievals using short wavelengths are minimally influenced by soil moisture, primarily picking up surface microwave emission from leaves and the upper canopy (Konings and Gentine, 2017; Konings et al., 2019). VOD has been related to multiple plant water status metrics including: 1) volumetric water content (VWC) (Konings and Gentine, 2017; Konings et al., 2019), 2) leaf water potential (LWP) and above ground biomass (Momen et al., 2017; Zhang et al., 2019), 3) RWC of plant canopies for predicting tree mortality from the 2012-2015 California drought (Rao et al., 2019), 4) a stomatal sensitivity index and drought coupling metric (Anderegg et al., 2018; Konings et al., 2017a; Konings and Gentine, 2017; Li et al., 2017), 5) and seasonal canopy water content patterns in the African tropics (Konings et al., 2017b). Negative anomalies in the diurnal differences between night and day VOD retrievals (which represents a decline in nighttime canopy rehydration) have also been shown to correlate with meteorological drought events over croplands in the USA, suggesting that the diurnal VOD signal is sensitive to drought stress when there is insufficient water available for plants to rehydrate (Schroeder et al., 2016).

In this study we seek to answer two questions. First, can we identify the relative sensitivity of canopy water content to VPD and soil moisture variation in the western U.S. using VOD retrievals? Although recent work has noted that VPD and soil moisture variation are often coupled (Novick et al., 2016; Seneviratne et al., 2010; Zhou et al., 2019), these drivers have different dynamics with VPD varying at higher temporal frequencies than soil moisture (Figs. 1a & S4; Koster et al., 2004). Extremes from higher frequency variation in VPD may quickly lead to responses that reduce stomatal conductance but increase plant water use, increasing the probability of hydraulic failure (Grossiord et al., 2020), while extended low soil moisture from slower frequency variation can lead to progressive loss of hydraulic conductance (Martinez-Vilalta et al., 2019; Sapes et al., 2019). Loss of hydraulic conductance from high VPD as well as from prolonged water can cause RWC to cross mortality thresholds. Disentangling their relative influence on canopy water content dynamics may provide context for interpreting the relative importance of mid to end of century projected temperature and precipitation changes on plant health. Second, does canopy water content sensitivity to soil moisture and VPD vary spatially and if so, where are the most sensitive sites? Identifying areas where canopy water content is particularly sensitive to variation in supply and demand of water is critical for identifying those regions in which we may expect near-term climate change impacts due to drought induced mortality.

2. Methods

2.1. Background

We utilize long term VOD retrievals to examine the relative influence of soil moisture and VPD variation on canopy water content in the western U.S. Because VOD is also sensitive to above-ground biomass (Momen et al., 2017; Tian et al., 2016; Tian et al., 2018), changes in biomass over space and time can obscure our understanding of changes in plant water status (Zhang et al., 2019). Consequently, we isolate the effects of varying biomass on VOD using a general additive model and focus on the model residuals in order to quantify changes in canopy water content. As in other studies, we assume that negative deviations of [night – day] VOD retrievals (Δ) during the study period signify that plants are unable to replace water lost to transpiration during the day and are therefore experiencing some degree of water stress (Frolking et al., 2011; Schroeder et al., 2016). After accounting for the influence of LAI variation we anticipate that positive diurnal anomalies in VPD (drier atmosphere) will result in negative diurnal anomalies in VOD (Fig. 2a), whereas we expect positive anomalies in soil moisture (greater soil moisture) will result in positive anomalies in VOD (Fig. 2b). If canopy water content is insensitive to supply/demand then we expect the relationships with VOD to be decoupled (Fig. 2).



Fig. 1. a) Daily time series of standardized scores from 2003 to 2018 for normalized diurnal variability in canopy water content (nVOD; in red) against vapor pressure deficit (VPD; top in yellow), soil moisture (SM; middle in blue), and leaf area index (LAI; bottom in green) for an example point shown in red in (b) along with the spatial distribution of all sites used in this analysis. c) example temporal distribution of nVOD values for sample point shown in red in (b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 2. Potential responses of $nVOD_r$ (normalized measure of diurnal variations [night-day] in VOD retrievals with the influence of biomass removed) to changes in VPD/soil moisture when plant water status is sensitive to changes in water demand/supply (left column) and when water status is decoupled from changes in water demand/supply (right column).

2.2. Data

VOD data used in this study comes from the X-band (10.7 GHz) of the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) sensor that launched in May 2002 and failed in October 2011, and the Advanced Microwave Scanning Radiometer 2 (AMSR2) on the Global Change Observation Mission-1st Water (GCOM-W1) satellite that launched in July 2012. The data includes 25 km resolution ascending (daytime at 1:30 pm local time) and descending (nighttime at 1:30 am local time) daily overpasses for the complete years 2003 to 2018 (Owe et al., 2008), cropped to the Western United States (latitudes from 31° - 50° N, longitudes from $102^{\circ} - 125^{\circ}$ W). Continuity between both sensors was achieved using the X-band VOD from the land parameter data record (Du et al., 2017) (LPDR). The intercalibration removed noted biases in AMSR2 retrievals and allowed for a homogeneous and cohesive dataset spanning the duration of both products. Data used in this study spanned from 2003 to 2018, with a gap between October 4, 2011 and May 18, 2012 when AMSR-E was out of operation and AMSR-2 had not yet launched. The LPDR product flags and removes pixels where land surface temperature < 273 K (assumed frozen soil) and pixels with strong precipitation as defined by Jones et al., 2010. We then also removed daily observations where either day or night retrievals were not present.

Within the western U.S., we randomly subset 1000 points meeting the criteria above (corresponding to 33.9% of suitable pixels) and extracted the LPDR VOD difference between night and day (Δ) for each pixel to include the full cohesive AMSR-E and AMSR2 record.

Daily VPD data was retrieved from the gridded meteorological climatology database gridMET (Abatzoglou, 2013) at a 4 km resolution spanning the full years 2003–2018. The VPD grid was aggregated to the 25 km resolution of the VOD data.

To assess changes in biomass, we used LAI data retrieved across the years 2003–2018 from the 1 km resolution NASA MCD15A3H MODIS product (Myneni et al., 2015), which combines the best acquisitions from the sensors on both the Terra and Aqua satellites to retrieve data over a 4-day period. The data was filtered using the quality assurance data field to filter out LAI retrieval pixels with high cloud cover and errors in the main retrieval algorithm. Filtered LAI retrievals were then aggregated to 25 km resolution, and linearly interpolated to daily observations to match the VOD data.

Soil moisture data across the years 2003–2018 was taken from daily grids with 250-m resolution from TOPOFIRE (Holden et al., 2019). Due to the large size of the dataset, soil moisture for the 25 km pixel was characterized by averaging 30 randomly selected points that fell within the larger domain of each 25 km pixel for each of the 1000 pixels utilized for the study. The soil moisture grids contained in TOPOFIRE were developed using a single layer daily soil water balance model, with terrain-resolved radiation, temperature and humidity grids as inputs, and a snow model described by Holden et al. (2018). Evapotranspiration was modeled using the Penman-Monteith equations (FAO; Allen et al., 1998) and adapted from the monthly model described by Dobrowski et al. (2013). For validation purposes, in situ soil moisture data was also accessed through TOPOFIRE (Holden et al., 2019) for 331 sites from snow telemetry (SNOTEL) and soil climate analysis network (SCAN) stations across the western U.S. that collected soil volumetric water content measurements at 8-in. depth across the years 2015-2018.

To determine the degree of water stress in a plant in response to changes in soil and atmospheric drought, we examined the sensitivity of the normalized difference between night and day VOD (nVOD; Eq. 1) during months in which drought stress is most likely to occur (April to September) to changes in normalized VPD, soil moisture, and LAI (Eqs. 2–4). Seasonally normalized daily standardized scores were calculated using the formulas:

$$nVOD = \frac{\Delta_{i-mcan_{j}(\Delta_{i})}}{s_{j}(\Delta_{i})}$$
(1)

$$VPD \ standardized \ score = \frac{vpd_{i-mean_j(vpd_i)}}{s_i(vpd_i)}$$
(2)

LAI standardized score =
$$\frac{lai_{i-mean_j(lai_i)}}{s_j(lai_i)}$$
 (3)

$$SM \ standardized \ score = \frac{sm_{i-mean_j(sm_i)}}{s_i(sm_i)} \tag{4}$$

where Δ = the difference between night and day VOD retrievals; *s* = standard deviation; *i* represents daily observations during months in which drought stress is most likely to occur (April – September) across the study period (2003–2018); and *j* = +/- 5 day window centered on *i* across all years in the study period.

To analyze how model coefficients vary over climate deficit gradients we used fields of annual climate normals for climatic water deficit (CWD) over the study period. CWD represents the evaporative demand that is not met by available water. This product is modeled on a monthly timestep and when summed annually varies from 0 mm at the wettest sites to roughly 2300 mm at the driest sites. Monthly derived estimates of CWD for the western U.S. were acquired from TerraClimate (Abatzoglou et al., 2018) covering the period 2003–2017 (2018 data was not available at time of access) at 4 km resolution and were aggregated to 25 km to match the VOD data resolution. Monthly values were summed each year to get annual CWD, and then averaged to get mean annual CWD for the western U.S. at 25 km resolution.

Percent tree cover was taken from the MODIS MOD44B vegetation

continuous fields (VCF) data product at 250-m resolution for the year 2016 (Dimiceli et al., 2015). Percent forb, grass, and shrub cover was taken from the Rangeland Analysis Platform data product at 30-m resolution for the year 2016 (Jones et al., 2018). Data was aggregated to 25 km to match the VOD data.

Land cover type data (e.g. plant physiognomic types and land use) was taken from the National Lands Cover Database (NLCD) 2016 (Yang et al., 2018). The data was resampled from 30 m to 100 m using nearest neighbor interpolation and then aggregated to 25 km to get fractional cover for each classification type. All data sources in this study are summarized in Table 1.

2.3. Analysis

All analysis was done in R (R Core Team, 2018), and all variables and climate information were prepared using the raster package (Hijmans, 2017). We extracted the LPDR VOD, LAI, VPD, and soil moisture data at a subset of 1000 points. From those 1000 points, 8 were removed as the soil moisture returned NA due to the presence of water bodies in some of the subset of 30 randomly selected pixels. The remaining 992 25 km pixels (Fig. 1b) across the western US are treated as independent 'sites' over which we examine the relationship between nVOD and drought metrics.

At each site, daily time series (Fig. 1a) were developed for nVOD and biophysical drivers (soil moisture and VPD). To eliminate variations induced by plant phenological cycles and isolate effects of soil moisture and VPD, we first removed the effect of LAI on nVOD by fitting a general additive model (GAM) relating nVOD to LAI standardized scores and then extracted the residuals of this fit from the nVOD time series. These standardized residuals will be referred to as nVOD_r. We used the GAM function from the mgcv package (Wood, 2011) and limited the basis function to 4 degrees of freedom to avoid model overfitting.

After removing the effect of LAI on the nVOD dataset (nVOD_r), we

Table 1

Summary table of data products used in the study and their time basis, native resolution, and what these data were used for.

Data Product	Time Basis	Native Resolution	Study Use
AMSR-E Vegetation Optical Depth (VOD)	Daily	25 km	VOD as a proxy for canopy water content
AMSR2 VOD	Daily	25 km	VOD as a proxy for canopy water content
gridMet vapor pressure deficit (VPD)	Daily	4 km	Atmospheric water demand as expressed by VPD
MODIS leaf area index (LAI)	4-day	1 km	Above-ground biomass as expressed by LAI
TOPOFIRE soil moisture	Daily	250 m	Water supply as expressed by soil moisture
TerraClimate climatic water deficit (CWD)	Monthly	4 km	Mean site climate as expressed by mean yearly CWD
MODIS vegetation continuous fields (VCF) percent tree cover	Yearly	250 m	Percent tree cover to characterize site vegetation
NLCD land cover type classification	Yearly	30 m	Land cover classification to filter out urban and agricultural areas
TOPOFIRE SNOTEL/ SCAN soil moisture	Daily	N/A	In situ soil moisture measurements taken from individual stations to validate results using modeled soil moisture product
Rangeland Analysis Platform percent vegetation cover	Yearly	30 m	Percent vegetation cover to further characterize site vegetation composition along with tree cover

then fitted a multiple linear regression using soil moisture and VPD standardized scores as predictors and nVODr as the response variable. We used standardized coefficients from the linear model to assess the relative importance of each variable, and calculated corellograms for each time series to visualize serial autocorrelation. We then determined whether the coefficients were significantly different than a value of 0 (pvalue < .05) after accounting for serial autocorrelation in residuals by correcting coefficient variance estimates using a Newey West estimator (Newey and West, 1986). We initially included an interaction term between the two predictor variables in our multiple linear regression, which proved largely insignificant with only 127 (12.8%) meeting the significant threshold of p < .05 and the individual variable standardized coefficients showing no change (linear model coefficients of 0.988 and 0.999 for soil moisture and VPD respectively when forcing the intercept through 0). Since all variables are standardized, the coefficients can be interpreted as dimensionless sensitivity indices of the response variable to the predictors.

We compared standardized regression coefficients to mean annual CWD to examine how $nVOD_r$ sensitivity differed across a water availability gradient. We additionally examined how the model coefficients varied as a function of inter-annual climate variability using the standard deviation of annual CWD values. The relationships between the coefficients and climate conditions were curvilinear and were fitted with GAMs. Lastly, we examined relationships between the most 'sensitive sites', defined as sites with coefficients greater than the absolute value of the 90th percentile, and site climate and vegetation cover. To determine if the site conditions of the most 'sensitive' sites were different from our background population we ran a non-parametric Mann-Whitney-Wilcoxon Test for percent tree cover, percent grass cover, and mean annual CWD comparing 'sensitive' sites to all other sites.

To corroborate the linear regression analysis and account for potential nonlinear relationships between nVOD and our predictors, we constructed a separate boosted regression tree (BRT) analysis. At each site we fit a BRT model to the response and predictor time series using the gbm.step function from the *dismo* R package (Hijmans et al., 2017). We utilized a learning rate and bag fraction set to 0.005 and 0.6 respectively to model the sensitivity of nVOD to daily LAI, soil moisture, and VPD standardized scores. We extracted relative variable influences, cross validation correlation means, and partial dependence plots for the BRTs at each site.

To further corroborate our results obtained using modeled soil

moisture as a predictor, we repeated both the regression and BRT analysis using nVOD, LAI, and VPD data at pixels containing SNOTEL soil moisture measurements. In this analysis, nVOD, LAI, VPD, and soil moisture standardized scores were calculated over the years of available SNOTEL observational data (2015–2018).

3. Results

Linear model (LM) coefficients, representing the sensitivity of nVOD_r to variation in soil moisture and VPD standardized scores, were significant (p-value < .05) at 889 and 600 of the 992 sites (90% and 60%) respectively. Of the 992 sample sites, 918 (93%) exhibited greater sensitivity to soil moisture than to VPD, with larger standardized coefficient absolute values than VPD. The difference in variable influence can be observed in the example time series (Fig. 1a) and regression results (Fig. 3) for a single site. The time series shows that daily nVOD dynamics more closely resemble those of normalized soil moisture than VPD. This is further reflected in regression results that display a tighter LM fit between nVOD_r and soil moisture (Fig. 3a) where low nVOD_r values are primarily concentrated at the lowest soil moistures regardless of the corresponding VPD value.

The correlograms also reflected the difference in variation constants of nVOD and soil moisture compared to VPD. The average variable autocorrelation lag for nVOD was much closer to soil moisture than that of VPD (Fig. S1), with a slower rate of autocorrelation reduction as the lag increases. When comparing the average nVOD autocorrelation lag to that of soil moisture the slope was very close to a one to one relationship at 0.92. The slope of the VPD autocorrelation relationship with nVOD was 0.02, with VPD showing a much faster rate of variation than the other two variables.

Our interpretation of variable contributions to the nVOD_r response is further reinforced by the site partial dependence plots from our BRT analysis (Fig. 4). While some nonlinearity in the relationships with nVOD is evident, the responses generally resemble the relationships conceptualized in Fig. 2. Further, BRT variable influence is consistent with our LM coefficients (Figs. 5 & S8). Moving forward, we focus primarily on the strength of LM coefficients as these are more easily comparable between sites than diagnostics from the BRT models.

VPD standardized coefficients exhibited greater absolute values in the Southwestern states of Arizona, Utah, New Mexico, and Colorado, while the bulk of both insignificant VPD and soil moisture coefficients



Fig. 3. Linear relationship at sample site in Fig. 1 between $nVOD_r$ and a) soil moisture and b) VPD standardized scores, and c) the continuous response of $nVOD_r$ to daily VPD and soil moisture standardized scores. The relationships in a and b were derived from a time series spanning 15 years and comprised of 1839 days of observations during the months April–September.



Fig. 4. Boosted regression tree partial dependence plots relating nVOD to a) soil moisture, b) VPD, and c) LAI for all sites. Grey lines represent the partial response curves for each individual site (n = 992) while the black line represents the average response across all study sites.



Fig. 5. Geographic distribution of $nVOD_r$ sensitivity relating $nVOD_r$ to VPD (left column) and soil moisture (right column). $nVOD_r$ sensitivity is represented by standardized regression coefficients from multiple linear regression models in a) and b) and represents % variable influence extracted from boosted regression tree models in c) and d). Colored circles in a) and b) represent coefficients that are statistically significant (p < .05) after accounting for serial autocorrelation, grey circles represent insignificant coefficients. Coefficient color gradient in a) and b) is opposite for VPD and soil moisture so that relative variable influence for the expected response can be compared using the same color scale.

occurred along the Cascades and Northern Rockies (Fig. 5).

LM VPD and soil moisture coefficients exhibited respective minimums (large negative coefficients) and maximums (large positive coefficients) at a similar mean CWD of roughly 800 mm; the absolute value of the coefficients declined as CWD increased (drier) and leveled off for both soil moisture and VPD between 1200- and 1500-mm (Fig. 6). Soil moisture coefficients were better explained by CWD than VPD coefficients; GAM deviance explained (D^2) values were 0.30 and 0.18 respectively. The general patterns observed in both the relative influence of coefficients and the coefficient relationship with CWD are also present in the SNOTEL analysis using in situ soil moisture measurements (Fig. S1). There is, however, more uncertainty in these models given that D.S. Lyons et al.



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Fig. 6. Linear model coefficient (nVOD_r sensitivity) variation along a hydroclimatic gradient (climatic water deficit; CWD) for a) VPD and b) soil moisture. The red line represents a generalized additive model (GAM) fit. CWD represents the evaporative demand that is not met by available water. CWD varies from 0 mm for moist conditions to 2300 mm at the driest sites. Mean annual CWD represents the average annual value for the years 2003–2017. D² (deviance explained) is shown to illustrate GAM fit. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

they were fit using 4 years of data. Moreover, SNOTEL stations are limited to more hygric, high elevation areas with lower deficits. Thus, we do not observe leveling off in the coefficient relationship with CWD (Fig. S1).

LAI correlation coefficients with both soil moisture and VPD correlation coefficients showed a strong relationship with mean annual climate, having GAM D^2 values of 0.44 and 0.73 respectively. The correlations between LAI and VPD transitioned from positive to negative at a similar intermediate CWD value of ~800 mm where we observed relative maximum and minimum of the LM coefficients (Fig. S7).

Mean site CWD showed a strong relationship with percent tree cover (GAM $D^2 = 0.68$), with tree cover declining as CWD increases (Fig. 7c). Percent tree cover approaches a value of 0% at ~800 mm deficit (Fig. 7c). Mean site CWD is less strongly linked with percent grass and forb cover (GAM $D^2 = 0.26$), with low cover at low and high CWD and a peak with wide variability at ~750 mm deficit (Fig. 6b). Both of these respective minima/maxima occur at a similar deficit value where soil moisture and VPD LM coefficients exhibit their respective maximum and

minimum values (Fig. 5). The Mann-Whitney-Wilcox tests showed that the most 'sensitive' coefficients (absolute value of coefficients >90th percentile) occurred under different conditions than the background population (Fig. 8). They primarily occurred at lower tree cover for both soil moisture and VPD (Wilcoxon P < .05 for both) and occurred at lower grass cover for VPD and higher grass cover for soil moisture (Wilcoxon p < .05 for both) than the background population (Figs. 8b & 8c). CWD at the sensitive VPD sites was higher than the background population (Wilcoxon p < .05), while the sensitive soil moisture sites had a slightly higher mean CWD that was marginally significant (Wilcoxon p = .067), but had a much narrower interquartile range than the background population (Fig. 8a).

Contrary to our expectations, we observed a positive response to VPD and negative response to soil moisture at 48 (5%) and 85 (9%) sites respectively. These sites were primarily located in the Pacific Northwest and were concentrated at values of CWD below 500 mm and higher tree cover (Figs. 5 & 6;). Of the sites that exhibited these unexpected patterns, 19 and 5 sites fell below the significance threshold of P < .05 for



Fig. 7. Percent cover distribution along mean site annual climatic water deficit (CWD) for a) all vegetation types with color coded curves fit using smoothed means and then specifically for b) percent grass/forb cover and c) percent tree cover where curves to show relationships were fit with a general additive model (GAM).



Fig. 8. Distribution of the 90th percentile of standardized coefficients ('sensitive sites') vs all other sites ('background') for VPD (left column) and soil moisture (right column). Distribution is shown for a) mean annual climatic water deficit (CWD), b) percent tree cover, and c) percent grass and forb cover. Mann-Whitney-Wilcoxon tests were conducted across both 'sensitive sites' and 'background' sites for the variables CWD, tree cover, and grass and forb cover. Actual values are jittered over the boxplots for clarity.

VPD and soil moisture respectively.

4. Discussion

4.1. Canopy water content shows greater relative sensitivity to soil moisture than VPD

Plant canopy water content dynamics across the western U.S.

responded to both VPD and soil moisture variation. However, knowing the relative sensitivity of water content dynamics to variations in these two variables provides important context for understanding potential future impacts of changing temperature and precipitation on plant water relations.

Soil moisture variability emerged as the dominant driver of canopy water content dynamics $(nVOD_r)$ at 93% of sites, although there also remains important joint influence with VPD at non energy-limited sites.

These results are consistent with research that identifies soil moisture as a primary control on vegetation growth (Littell et al., 2008; Papagiannopoulou et al., 2017; Reichstein et al., 2007; Stocker et al., 2019; Wurster et al., 2020), and studies that suggest that the impacts of anomalies in VPD are generally short term compared to the persistent effects of soil moisture anomalies (Koster et al., 2004). Even after normalization, it is evident from our example time series (Fig. 1a) and the site correlograms (Fig. S3) that soil moisture and nVOD have lower frequency variation and retain a degree of memory, while VPD standardized scores exhibit higher frequency variation. Soil moisture deficits can impact plant water status regardless of VPD as soil moisture and VPD become decoupled under dry conditions (Stocker et al., 2019), as even small water losses that occur when stomata are closed can lead to dehydration when there is no soil water supply (Körner, 2019). Our results suggest that this is the case with canopy water content dynamics as well as the lowest values of nVOD_r primarily occurred at the lowest soil moisture standardized scores, regardless of corresponding VPD values (Fig. 3c). Nonetheless, soil moisture and VPD cannot be treated as entirely independent due to their inherent correlation (Fig. S5; Holden et al., 2018; Seneviratne et al., 2010; Zhou et al., 2019), and therefore their influence cannot be fully separated into unique contributions to changing vegetation water status.

Greater nVOD_r sensitivity to soil moisture likely arises from plant hydraulic dependence on water availability (Grossiord et al., 2018). Loss of canopy water content is driven by a combination of reduced water supply from soil and transpiration, and depends on bulk soil-plant hydraulic conductance (including stomatal responses) and VPD. When soil moisture is low, soil-plant hydraulic conductance decreases and xylem tension and resistance to water flow increases resulting in embolism. Loss of hydraulic function associated with reduced soil-plant conductance leaves plants unable to replace water lost to transpiration during the day and, therefore, leads to decreased canopy water content (Martinez-Vilalta et al., 2019; Sapes et al., 2019). Low soil moisture also reduces the pressure gradient between the leaf and soil water. This reduces the amount of rehydration that can occur as water potentials must become increasingly negative in order to drive water uptake and will also result in decreased canopy water content. Hydraulic limitation to water uptake can occur regardless of VPD (Körner, 2019) and while VPD may fluctuate day to day, periods of low soil moisture are persistent until a precipitation event. The difference between day and night canopy water content will decline due to plants' inability to rehydrate while the soil remains dry (Frolking et al., 2011; Schroeder et al., 2016). Additionally, the difference between night and day plant water content, the basis of our normalized index, may also be influenced by stomatal response to soil moisture availability (Mcdowell et al., 2008; Sperry et al., 2002; Sperry and Love, 2015). When soil is well-watered, transpiration is unregulated and plant water content fluxes are greater (Hochberg et al., 2018). However, when the soil is relatively dry, plants may close their stomata to downregulate transpiration and minimize water lost regardless of the strength of evaporative demand (Hochberg et al., 2018). This mechanism would also cause reduced diurnal differences in water content due to greater flow resistance associated with tighter stomatal control. Further, decreased carbon assimilation from tighter stomatal control and the downregulation of transpiration can lead to depleted carbon reserves and reduced osmotic regulation, which leads to loss of cell turgor, decreased hydraulic conductance, and further reductions in water content (Martinez-Vilalta et al., 2019; Sapes et al., 2019

Sites where VPD emerged as a dominant constraint on canopy water content dynamics were located in the southwestern U.S. However, our results suggest that a larger proportion of sites in the southwestern U.S. are more sensitive to variations in soil moisture. This is corroborated by results from our BRT analysis (Fig. S6) which also show a larger influence of LAI on nVOD dynamics in the southwestern region (Figs. S6 & S7). This may be driven partially by a monsoon effect that might conflate the effects of biomass variation and soil moisture variation. Vegetation growth in this region is sensitive to pulses of moisture that come from summer precipitation events during the North American monsoon (Tang et al., 2012; Watts et al., 2007). By removing the influence of biomass variation from the nVOD signal, we likely lose some portion of the nVOD response to soil moisture due to variable correlation (Fig. S7).

4.2. Canopy water content sensitivity is greatest at mesic hydroclimatic settings

Diurnal differences in canopy water content showed the most sensitivity to soil moisture variation at intermediate levels of climatic water deficit (Figs. 5 & 6). These intermediate levels of water availability occur at values of CWD that exhibit the highest nVOD_r sensitivity to both soil moisture and VPD and represent climatic transition zones from areas that are wetter and more energy limited to drier and more water limited. These occur at CWD values where we see a transition from forest cover towards grass cover consistent with ecotones between forest and non-forest vegetation (Fig. 7; Fig. S8).

Research has identified woody plant species' populations at dry range edge margins and transition zones as the most vulnerable to drought (Allen and Breshears, 1998; Anderegg et al., 2019; Davis et al., 2019; Young et al., 2017), and have suggested that this vulnerability may be due in part to high temporal climate variability (Anderegg et al., 2019). Areas of hydroclimatic transition zones, represented by an intermediate climate between moisture limited arid climates and energy limited hygric climates, have been identified as hotspots for landatmosphere coupling where soil moisture feeds back on both evapotranspiration and subsequent precipitation and results in enhanced climate variability (Koster et al., 2004; Seneviratne et al., 2010; Seneviratne et al., 2006). In these areas, low soil moisture decreases evapotranspiration which leads to increased atmospheric aridity, thus decreasing the atmospheric moisture that can recharge soil moisture through precipitation (Zhou et al., 2019). These zones represent a transition from energy limited to water limited systems, and the CWD where we observe a switch from a positive correlation to negative correlation between VPD and LAI suggests this occurs at a similar CWD where the VPD and soil moisture sensitivity curves peak (Fig. S8; Fig. 5). Our results suggest that plants in these hydroclimatic transition zones show the greatest sensitivity of canopy water content to soil moisture and VPD variation.

Given that nVOD_r represents the diurnal ability of plants to replace water lost via transpiration, it is not surprising that it is less sensitive at sites with low mean annual CWD. These sites are energy limited (Fig. S8) with more available water and lower atmospheric demand, and therefore are more likely to have sufficient soil water for maintaining canopy water content even during extended periods without precipitation. The Northwest and montane regions in the Northern Rockies represent the bulk of such areas where insignificant model coefficients were found (Fig. 5) and represent conditions where plant water status is decoupled from changes in daily supply/demand in our conceptual model (Fig. 2). Low CWD is also associated with low climatic variance, and therefore the standardized values representing deviations from mean seasonal conditions may not represent a sufficient imbalance in supply or demand to be reflected by a response in plant water content.

We also find a subset of sites in the Northwest with model coefficients that are opposite our expectations (difference between night and day increases despite negative soil moisture and positive VPD standardized scores). In these areas our models show a lack of significant positive VPD coefficients which suggests that the counter intuitive results may be more driven by moisture surplus and access to deep ground water. Evapotranspiration can become decoupled from soil moisture in areas that are not water limited (Seneviratne et al., 2010) and tree drought response in forested areas can be driven by the availability of deep ground water (Goulden and Bales, 2019). As these sites are located in energy limited hygric areas with low CWD and high forest cover (Figs. 6 & 7) it is possible that soil moisture depletion during the analysis period does not leave the deeper soil dry enough to inhibit plant rehydration. For these areas, canopy water content response to drought is likely to occur over multiple seasons that lead to depletions of long term water sources (as observed by Asner et al., 2016; Berdanier and Clark, 2016; Brodrick et al., 2019; Goulden and Bales, 2019), and are not likely to show up strongly in an analysis of responses to daily or even seasonal changes in water supply and demand.

Our results demonstrate that the sensitivity of canopy water content to soil moisture and VPD dynamics, is mediated by inter-annual hydroclimatic variation. Sites that have the lowest nVOD_r sensitivity to soil moisture and VPD variation also have the lowest interannual CWD variability (Fig. S3). These areas occur on the ends of the hydroclimatic spectrum; they can be consistently wet or dry.

4.3. Geographic variability in canopy water content sensitivity

The sites most 'sensitive' to soil moisture are defined by low tree cover and high grass cover (Fig. 8), leading us to hypothesize that canopy water content in these areas is more vulnerable to the increases in atmospheric water demand and reductions in water supply that are likely to accompany directional climate changes. Our LM coefficients are greatest at CWD values coinciding with sites where forest cover transitions to grass cover (Fig. 7a), suggesting that the highest sensitivity is occurring near transitional climate zones that occur along forest to nonforest ecotones. Fluctuations in canopy water content driven by soil moisture variation at these sites may push plants in these locations beyond hydraulic safety margins resulting in mortality (Brodrick and Asner, 2017; Choat et al., 2012; Martinez-Vilalta et al., 2019; Sapes et al., 2019). We hypothesize that the most 'sensitive' sites occur in transitional ecotones. However, the coarse resolution of our data makes it difficult to identify specific transitional zones. We provide a map of the combined interquartile ranges of tree cover, grass cover, and CWD for the 'sensitive' sites which identifies the spatial distribution of conditions where high nVOD sensitivity is most likely to occur (Fig. S9).

4.4. Implications for climate change

Canopy water content sensitivity to hydroclimate and hydroclimate variability has implications for understanding impacts of ongoing climate change. Hygric environments that experience decreases in available water may become more sensitive to anomalies in water supply and demand as moisture reserves are depleted. This greater sensitivity to drought could have implications for transitional ecosystems, as mortality at dry edges can lead to regeneration failure and range shifts (Allen and Breshears, 1998; Davis et al., 2019; Lenoir et al., 2008).

The greater relative importance of soil moisture variation on canopy water content dynamics also has implications for forecasting how plant water dynamics will be influenced under future climate change. VPD is projected to increase with temperature (IPCC, 2013). However, summer precipitation in the western U.S. is predicted to decrease in frequency and amount but increase in variability, reducing water supply and leaving longer periods between soil moisture recharge (Holden et al., 2018; Pendergrass et al., 2017; Rupp et al., 2017; USGCRP, 2017). Therefore, predicted precipitation trends are likely to reduce canopy water content and increase rates of drought-induced mortality (Sapes et al., 2019).

4.5. Caveats

There is uncertainty introduced by scale mismatches between our response variable and the functional resolution of the predictor variables we derive. However, these types of scale mismatches are relatively common to the application of VOD data for examining plant water relations. For example, previous research has shown reasonable agreement between in-situ soil moisture measurements and 25 km resolution satellite microwave soil moisture products (Draper et al., 2009; Njoku

et al., 2003; Reichle et al., 2007). Likewise, individual tree LWP and biomass measurements have been shown to correspond with 25 km resolution VOD and LAI dynamics (Momen et al., 2017; Zhang et al., 2019). Our analysis using SNOTEL soil moisture was also consistent with our broad scale results (Fig. S2). Additionally, VOD retrievals along steep slopes have been noted as less robust. As the LPDR product does not flag mountainous areas we were unable to remove them, and it is possible that VOD retrieval errors have contributed to the greater number of low and insignificant coefficients seen in wetter, energy-limited areas that appear to occur around mountainous regions (Fig. 5).

When we removed the direct influence of seasonality of biomass on nVOD dynamics, it is possible that in doing so we have also removed information on how canopy water content dynamics respond to drought. For instance, leaf shedding can be a physiological response to drought, and reduced growth and biomass can indicate higher susceptibility to a subsequent drought event (Camarero et al., 2015; Carnicer et al., 2011; Guada et al., 2016). Both soil moisture and VPD standardized scores are correlated to LAI standardized scores, and by treating LAI as a first order influence on nVOD we implicitly assume that any correlation between the variables is primarily driven by LAI. However, this approach is necessary to disentangle the influence of biomass dynamics on nVOD and put the focus of our analysis on canopy water content sensitivity. Critically, by removing the effect of seasonal LAI changes, our approach likely provides conservative estimates of the sensitivities to the drivers of drought. Moreover, correlation coefficients were greater between soil moisture and LAI standardized scores (Fig. S7) which suggests that the influence of soil moisture was more likely to be negatively impacted by removing biomass trends such as those observed in the southwest region. Further, information lost by removing the influence of biomass is unlikely to change the overall pattern of soil moisture coefficients. Our BRT analysis (that did not remove the influence of biomass variation and used LAI standardized scores as a predictor along with soil moisture and VPD) supports our regression-based results; soil moisture still emerged as the most influential variable at 90% of the sites with LAI replacing VPD in relative importance at some of the southwestern sites (Fig. S8).

Our study is constrained by the coarse resolution of the VOD data and does not parse out differential species-specific ranges or hydraulic traits and responses, which are known to influence drought susceptibility (Anderegg et al., 2019; Anderegg et al., 2018; Bréda et al., 2006). There is a great deal of variability in the linear model coefficients we quantify. The coarse resolution of our analysis and the inability to consider species-specific responses likely accounts for some of this variability. Further research examining how model coefficients vary by plant physiognomic types and species traits is warranted. Lastly, the coarse resolution of the analysis also limits our ability to account for top-oclimatic effects and the effect of enhanced supply in hydraulic convergence zones that are known to help buffer vegetation from climate variability (Dobrowski, 2011; McLaughlin et al., 2017; Simeone et al., 2018). Despite these caveats, coherent spatial patterns of canopy water content sensitivity still emerge.

5. Conclusion

We show that canopy water content dynamics have a stronger coupling to soil moisture than VPD variation at a majority of sites across the western U.S. Plant water content was decoupled from changes in both soil moisture and VPD at wetter environments with less climatic variance. In contrast, canopy water content showed the greatest sensitivity to VPD and soil moisture at sites with intermediate climatic water deficits - sites that represent climatic transition zones between energylimited and moisture-limited environments and exhibit strong landatmosphere coupling. These sites occur at CWD values where there is a transition from tree cover towards grass cover that are consistent with ecotones between forest and non-forest. These areas are likely to be more vulnerable to increases in drought frequency and severity projected with continuing climate change. Our study outlines large scale spatial and climatic patterns of daily canopy water responses to changing metrics of drought across the western U.S. Our findings highlight the importance of soil moisture dynamics to plant water relations, especially in transitional ecotones.

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2020.112233.

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