Patterns of plant rehydration and growth following pulses of soil moisture availability

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Abstract. Plant hydraulic and photosynthetic responses to individual rain pulses are not well understood because pulse experiments are sparse. Understanding individual pulse responses would inform how rainfall intermittency impacts terrestrial biogeochemical cycles, especially in drylands which play a large role in global atmospheric carbon uptake interannual variability. Using satellite-based estimates of predawn plant and soil water content from the Soil Moisture Active Passive (SMAP) satellite, we quantify the timescales of plant water content increases following rainfall pulses, which we expect bear the signature of whole-plant mechanisms. In wetter regions, we find that plant water content increases rapidly and dries along with soil moisture, which we attribute to predawn soil-plant water potential equilibrium. Global drylands, by contrast, show multi-day plant water content increases after rain pulses. Shorter increases are more common following dry initial soil conditions. These are attributed to slow plant rehydration due to high plant resistances using a plant hydraulic model. Longer multi-day dryland plant water content increases are attributed to pulse-driven growth, following larger rain pulses and wetter initial soil conditions. These dryland responses reflect widespread drought recovery rehydration responses and individual pulse-driven growth responses, which supports isolated field experiments. The response dependence on moisture pulse characteristics also implies ecosystem sensitivity to intra-annual rainfall intensity and frequency, which are expected to shift in a future climate.

1. Introduction

A changing climate is likely to shift not only mean annual rainfall, but also the frequency and intensity of rainfall events (Donat et al., 2016; Giorgi et al., 2019; Trenberth, 2011). Understanding the impacts of rainfall distribution shifts on the terrestrial biosphere is important because vegetation globally exerts a large control on terrestrial water and carbon balances (Ahlström et al., 2015; Jasechko et al., 2013; Poulter et al., 2014) and drives feedbacks with the lower atmosphere (Gentine et al., 2019; Green et al., 2017). Changing rainfall frequency with the same annual rainfall can impact terrestrial carbon uptake (Fay et al., 2003; Knapp et al., 2002), suggesting ecosystem sensitivity to characteristics of individual rain events. This motivates characterizing plant responses to individual moisture availability pulses across climates and biomes. This is especially the case for semi-arid herbaceous plants which respond primarily to individual pulses, likely occurring under a pulse-reserve paradigm of individual rainfall events triggering photosynthetic responses and storages (Collins et al., 2014; Feldman et al., 2018; Noy-Meir, 1973). However, vegetation responses on these shorter timescales are less well understood than the more commonly studied responses to monthly or annual water anomalies.

A major component of understanding moisture pulse responses is quantifying the duration over which plants take up and use the rain pulse water. These response durations bear the signature of, among others, plant rehydration in the soil-plant atmosphere continuum (SPAC), growth, and resource limitations such as drought (Manzoni et al., 2013; Ogle et al., 2015; Ogle and Reynolds, 2004; Sperry et al., 2016). Characterizing these timescales and their dependencies across biomes will

increase our understanding of whole-plant behavior and assist plant hydraulic parameterizations in land surface models to better assess plant water stress (Bonan et al., 2014; Fisher et al., 2018; Kennedy et al., 2019; Lin et al., 2019; Tai et al., 2017; Xu et al., 2016). However, the fundamentals of these pulse water use durations, especially soil to plant water storage timescales, remain unknown globally.

45   Soil and plant water content measurements can be used to characterize the soil-plant hydraulic system and understand plant water storage timescales, but are laborious and are thus often constrained to a single location. Alternatively, microwave remote sensing satellites provide plant water content observations across the globe at near-daily sampling frequencies (Entekhabi et al., 2010; Kerr et al., 2010; Konings et al., 2016). Although these observations are at a coarse resolution (10s of kilometers), their ecosystem scale resolution and relationship to leaf water potential (Momen et al., 2017; Zhang et al., 2019)
50 makes them a useful tool for studies of ecosystem plant-water relations (Feldman et al., 2018; Konings et al., 2019; Konings and Gentine, 2017). However, the plant water content measurements are a function of both relative water content and dry biomass, thus making them additionally sensitive to biomass and growth (Momen et al., 2017; Zhang et al., 2019). This is nevertheless an advantage because the plant water content sensitivity to both water potential and dry biomass allows evaluation of timescales of multiple whole plant mechanisms at the landscape-scale.

55   With regard to plant rehydration timescales, plant water uptake and storage timescales have been typically assessed using an electric circuit analogy, with the timescale of interest the plant resistance times capacitance, or RC time constant (Phillips et al., 1997, 2004; Ward et al., 2013). The RC time constant quantifies the time required for leaf or xylem water potential to reach 63% of its equilibrium value following a soil moisture or transpiration perturbation. Measured RC time constants vary from minutes for grasses to hours for trees (Hunt and Nobel, 1987; Nobel and Jordan, 1983; Phillips et al.,
60 1997, 2004; Ward et al., 2013). According to this theory, plant rehydration after rain pulses should occur within a day. By contrast, several field pulse experiments of grass and shrub species, primarily in dryland environments (broadly annual rainfall less than 500 mm), commonly show multi-day predawn water potential increases after rewetting pulses (Fravolini et al., 2005; Huxman et al., 2004; Ignace et al., 2007; West et al., 2007). Multi-day predawn water potential increases would lengthen plant water content timescales. These multi-day water potential increases appear to be related to recovery from water-limitation
65 between storms, which highlights the potential impact of antecedent moisture conditions on plant responses (Guo and Ogle, 2019; Ogle et al., 2015; Plaut et al., 2013). Hydraulic limitations from previously dry conditions have also been observed, driving multi-day recovery of leaf gas exchange after soil rewetting (Blackman et al., 2009; Brodribb and Cochard, 2009; Chen et al., 2009; Huxman et al., 2004; Martorell et al., 2014). These multi-day hydraulic response observations call into question whether hydraulic response timescales are consistently sub-daily across global biomes. They also highlight the unknown role
70 of moisture pulse characteristics (antecedent soil conditions and pulse magnitude) on these timescales.

     With regard to timescales of growth, while growth is known to occur on seasonal timescales, there is evidence that growth can occur following rainfall events as under the pulse-reserve hypothesis (Noy-Meir, 1973). Specifically, dryland measurements suggest that growth can occur over days to weeks following a pulse (Angert et al., 2007; Dougherty et al., 1996; Hermance et al., 2015; Novoplansky and Goldberg, 2001; Post and Knapp, 2019; Sher et al., 2004). Also, ecosystem growth
75 responses in drylands have been modeled previously with a 1-5-day lag (depending on plant type) and a decaying persistence over 1-2 week scales (Ogle and Reynolds, 2004; Reynolds et al., 2004). Ultimately, pulse driven growth following rainfall would lengthen plant water content timescales by increasing the total plant water storage capacity.

     Here, we evaluate the duration of total plant water content increases following rainfall pulse events. Under nominal moisture conditions with no growth, one would expect sub-daily plant water content increases based on RC time constants.
80 Slow rehydration and/or growth would likely extend these timescales to multiple days. We ask: across global biomes, do plant water uptake responses to soil moisture pulses ever occur beyond a day and what are these timescales? How do pulse characteristics (pulse magnitude, moisture pre-conditions) and growth influence these timescales? Do attributes of the moisture pulse (pulse magnitude, moisture pre-conditions) favor plant growth versus rehydration? To address these questions, we use microwave remote sensing of total plant water content, a combination of dry biomass and relative water content, following an

85 approach for rain pulse studies originally developed in Feldman et al. (2018). In order to better understand potential mechanisms underlying remote sensing observed timescale variations, we also discuss the observed timescales and their drivers in the context of a SPAC model.

2. Methods

90 **2.1 Datasets**

We use four years (April 1st, 2015 to March 31st, 2019) of soil moisture and plant water content observations from the Soil Moisture Active Passive (SMAP) satellite (Entekhabi et al., 2010). SMAP measures the low frequency microwave (1.4 GHz) radiation emitted from Earth's surface. The radiation signal is in units of temperature, or brightness temperature (TB). The radiation is polarized, where the emitted waves' oscillations have distinct horizontal (TB$_H$) and vertical (TB$_V$)

95 orientation. SMAP measures both TB$_V$ and TB$_H$. Both TB$_V$ and TB$_H$ magnitudes alone are sensitive to surface soil moisture (top ~5 cm). Furthermore, the difference between TB$_V$ and TB$_H$ is sensitive to how much the emitted waves are attenuated when traversing a vegetation canopy. The vegetation attenuation of the microwave radiation is called vegetation optical depth (VOD). More vegetation water content results in higher VOD (Jackson and Schmugge, 1991; Konings et al., 2019). An established radiative transfer equation can partition the TB$_V$ and TB$_H$ signals into soil moisture and VOD (Mo et al., 1982;

100 Wigneron et al., 2017). We use a recently developed algorithm, called the multi-temporal dual channel algorithm (MT-DCA), to robustly estimate soil moisture and VOD using this radiative transfer equation (Konings et al., 2017, 2016).

The SMAP satellite measurements occur at 6:00 AM (local time) everywhere on 9 km grids across the globe. 6:00 AM is approximately predawn, when plant water status is assumed to be maximal (due to nighttime plant rehydration). The satellite orbit is such that there is a one-, two-, or three-day revisit, depending on the day and latitude. Due to the orbit pattern,

105 higher latitudes are measured more frequently. This results in sampling frequencies of 1-2 days at midlatitudes and 2-3 days at the equator.

Since VOD has been shown to be nearly linearly proportional to total vegetation water content (Jackson and Schmugge, 1991), VOD is proportional to the product of relative water content and aboveground dry biomass (Konings et al., 2019; Momen et al., 2017; Zhang et al., 2019). Therefore, VOD can increase due to either rehydration of cell water storages

110 or biomass growth, as growth provides additional water storage capacity. While the low-resolution of VOD estimates hinders species-specific or stand-scale assessments, it provides the opportunity to assess integrated, landscape-scale vegetation behavior across global biomes (Feldman et al., 2018; Tian et al., 2018). VOD shows promise for use in monitoring plant water stress with recent findings showing VOD can monitor drought-induced mortality with loss of plant water storage (Martínez-Vilalta et al., 2019; Rao et al., 2019).

115 Soil moisture observations of the MT-DCA algorithm compare closely to other SMAP soil moisture products (which use different algorithmics) as well as to in-situ observations (Chan et al., 2016; Dadap et al., 2019; Feldman et al., 2018). Direct in-situ VOD information is unavailable, although SMAP VOD's mean and dynamics are comparable to another satellite VOD product (Kerr et al., 2010). For further discussion of SMAP VOD estimate performance and comparison with other products, we refer the reader to Konings et al. (2017) and Feldman et al. (2018).

120 To assist in discriminating VOD changes related to hydraulic or growth activity, we use the daily leaf area index (LAI) product from the EUMETSAT Satellite Applications Facility on Land Surface Analysis (LSA SAF; Trigo et al., 2011). These LAI observations serve as an indicator of above-ground biomass independent of VOD. While constrained primarily to Africa, these LAI observations are estimated from 15-minute geostationary observations which provide daily LAI fluctuations after cloud contamination mitigation and allow better resolution of the growth and senescence stages than most other global

125 LAI datasets (García-Haro et al., 2013; Gessner et al., 2013). Both VOD and LAI datasets together are required to determine the occurrence of pulse driven growth. Due to a non-linear averaging technique (García-Haro and Camacho, 2014), the LAI dataset may be partially smoothed over sub-weekly scales and may be less apt to determine whether detected growth over a week is associated with a given rain event. VOD increases can be associated with a given event, but are confounded by

rehydration. The LAI changes over the weekly scales of pulses can monitor canopy growth and are used to determine whether
130   the VOD increases following a given storm are influenced by growth or only due to water rehydration.

Ancillary data are used to evaluate climate and biome dependencies of the findings. Specifically, we compute mean
annual precipitation using the Global Precipitation Measurement IMERG product (Huffman, 2015) and tree cover from the
Moderate Resolution Imaging Spectroradiometer (MODIS) (Dimiceli et al., 2015) to evaluate VOD behavior across climate
gradients. International Geosphere-Biosphere Programme (IGBP) land cover maps are used to remove frozen and bare ground
135   (Kim, 2013). Tree cover is also used to remove densely vegetated forests where soil moisture and VOD satellite estimation are
uncertain.

2.2 Soil Moisture Pulse Identification

VOD behavior and response timescales are evaluated during soil moisture drydown periods that occur after rainfall
140   (Fig. 1). Drydown periods, or soil moisture pulses, are defined as an increase in soil moisture of at least 0.01 m^3/m^3 followed
by a drying period of at least four consecutive measurements (approximately 8-12 days). This approach is nearly identical to
previous approaches (McColl et al., 2017; Shellito et al., 2018). To remove seasonal drydowns less associated with an
individual rainfall event, drying periods of longer than twenty days are not included. Seasonal trends (periodic climatology)
are removed from soil moisture and VOD time series during drydowns, while preserving the magnitude of initial conditions
145   (Feldman et al., 2019). This procedure removes seasonal VOD growth trends to isolate short term increases due to pulse-driven
growth and/or slow rehydration. Note that differences persist in the literature on whether the rain event or plant response is
defined as the pulse (Reynolds et al., 2004). Both soil and plant responses are discussed as pulses here.

2.3 Vegetation Pulse Response Timescale Estimation and Analysis

150   For infiltrating water to ultimately reach the leaf, it must typically percolate from the soil surface to the roots, pass
through the root endodermis, and move up the xylem through the shoot to leaves (Mackay et al., 2015; Sperry et al., 2016,
1998). Given an identified soil moisture drydown period, the VOD response timescale, defined here as time-to-peak (t_p), is
estimated as the time from the beginning of the soil moisture drydown to the first local maximum value of VOD (Fig. 1). t_p
captures the aggregate rehydration and growth timescale during this soil-plant water transport process. The t_p estimation relies
155   on consecutive VOD increases, which provide more robust estimates than the global maximum during the drydown. To
increase sample size, we conduct the analysis on all pixels contained within a 0.5ºx0.5º domain (includes ~30 SMAP pixels).
Densely forested regions (>40% tree cover; such as the Congo and Amazon Basins) are masked because soil moisture and
VOD estimates are less certain due to radiative transfer limitations in dense canopies (Feldman et al., 2018; Konings et al.,
2017).

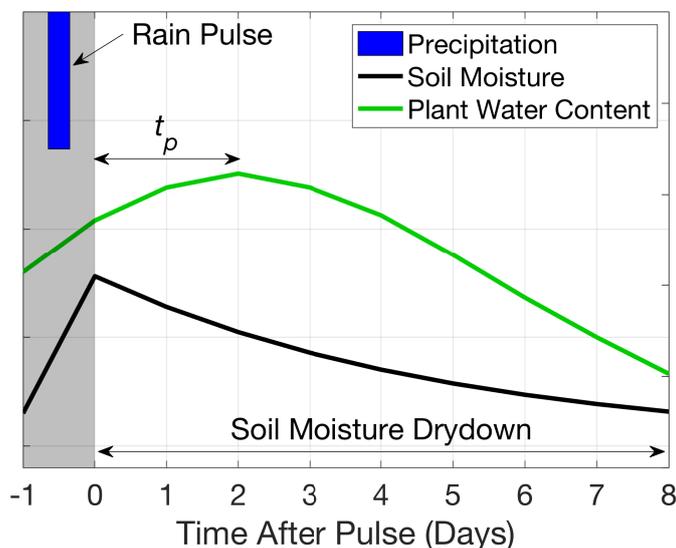
160   We compute the median t_p over all drydowns within each 0.5º x 0.5º pixel. The t_p probability mass function, within a
given pixel, typically has a mixed distribution with many zeros. The median t_p is chosen to describe this distribution because
it not only provides a typical timescale of VOD increase, but also indicates whether or not the majority of pulses resulted in
consecutive, multi-day VOD increases (as opposed to the mean, which can be greater than zero even if a majority of pulses
resulted in a t_p of zero). Several tests are performed to determine the effects of SMAP's irregular, above daily sampling period,
165   the algorithm, and measurement noise on t_p estimates for a given pulse.

The t_p definition evaluates continuous post rainfall VOD increases and potentially neglects the duration of plant water
content increases during the period of soil moisture increase (between the observations before the drydown beginning and at
the drydown beginning). We do not attempt to estimate the duration of VOD increase during the soil moisture increase period
because it is not possible to resolve when plant water content increases began due to the 1-3 day satellite sampling frequency.
170   Instead, the VOD behavior preceding the drydown is categorically evaluated by determining the frequency of plant water
content increases and decreases during the rain pulse. This allows evaluations of t_p of zero which can result from either a rapid

rehydration response during the rain storm (on the order of hours) or no rehydration response throughout the pulse (no VOD increase).

175 For each soil moisture pulse within a pixel, t_p is estimated along with the LAI change from beginning to end of the drydown (ΔLAI), antecedent surface soil moisture (soil moisture value before drydown beginning), soil moisture pulse magnitude (difference between initially pulsed and antecedent surface soil moisture), and antecedent VOD. Antecedent is defined here as the observation just preceding the peak soil moisture observation beginning the drydown. Each variable is binned into rapid VOD response (t_p=0), short VOD increase ($1 \leq t_p \leq 3$ days), and long VOD increase ($t_p > 3$ days) groups because they provide partitions consistent with the satellite sampling and because uncertainty analyses reveal that while a t_p estimate

180 for a given drydown is uncertain, there is more confidence in whether it exists within a given bin (see Sect. 3.4). The groups are then compared. Due to non-normality of groups based on Jarque-Bera normality tests (Jarque and Bera, 1980), Kruskal-Wallis non-parametric tests are performed to determine significance of difference in means between the groups. Also, correlation coefficients are computed between t_p and ΔLAI, antecedent moisture, and pulse magnitude to augment the categorical analyses.

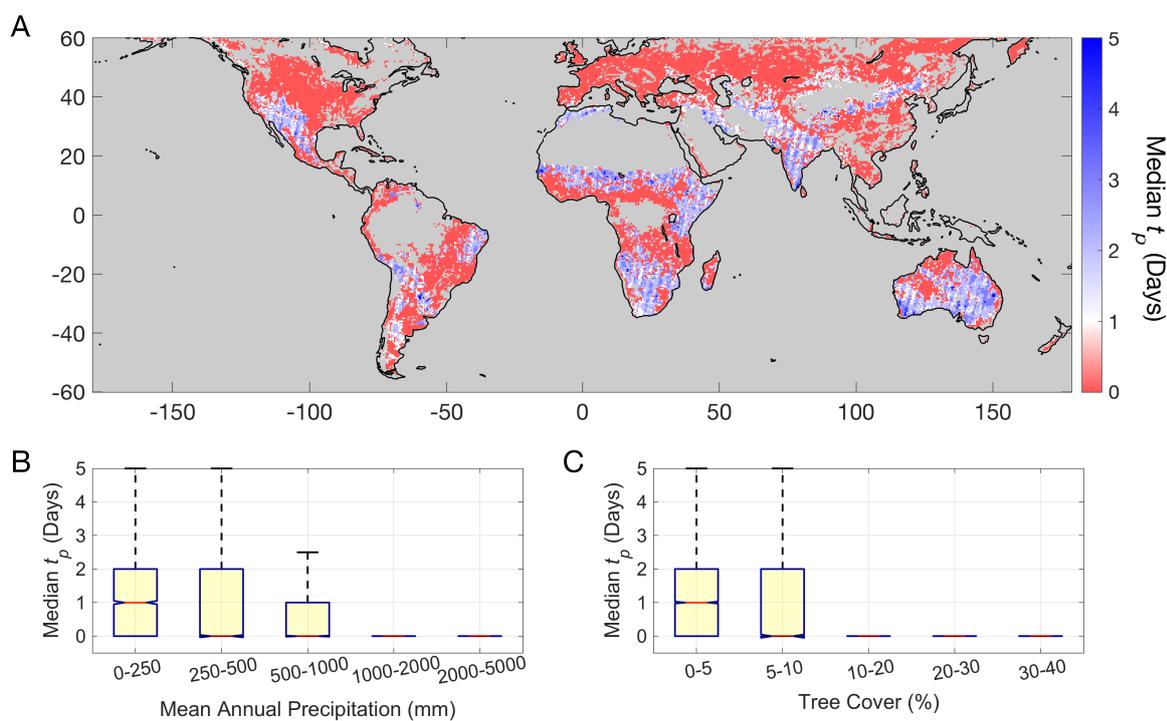
185 The seasonal timing of rapid, short, and long t_p values are assessed relative to peak seasonal moisture, or the proximity to the wet season. The peak seasonal soil moisture is determined by smoothing the soil moisture times series using a 90-day moving average window. This only provides a zeroth-order seasonal moisture peak approximation as many locations have intermittent rainfall or bimodal precipitation distributions.

190 Fig. 1. Schematic definitions of rain pulse, soil moisture drydown period, and time to peak plant water content (t_p).

3. Results
3.1 Global plant water content characteristic responses and timescales

The VOD data shows that more arid regions, with lower annual rainfall and tree cover (Fig. 2B and 2C), exhibit multi-

195 day vegetation water content increases following moisture pulses ($t_p \geq 1$ day, blue regions in Fig. 2A). That is, after soil moisture increases following a storm, vegetation water content increases for multiple days even while surface soil moisture begins to dry. Furthermore, in regions with $t_p \geq 1$ day, VOD typically begins increasing during the rain pulse period instead of with a lag after soil moisture drying begins (occurs in 77% of the pixels). Aggregated example time series of this nonzero t_p behavior can

be seen in drylands in the Sahel and Southwest United States (Figs. 3A and 3B). In the regions with multi-day VOD increases,
200   the spatial median t_p is two days. In subsequent sections, we evaluate the mechanisms underlying these multi-day plant water
content increases primarily in drylands (blue regions in Fig. 2A).

By contrast, more humid ecosystems with more woody plant coverage typically do not exhibit multi-day plant water
content increases (t_p=0; Fig. 2). They instead exhibit water loss following the pulse during soil drying (see average behavior
illustrated in Figs. 3C and 3D). In 83% of regions with t_p of zero (red regions in Fig. 2A), the plant drying responses are
205   typically preceded by an initial VOD increase, showing rapid water uptake during the storm period (Fig. S1). In contrast, a
minority of these regions typically show no VOD increases, suggesting plant water content continuously dries throughout the
pulse with no discernable hydraulic response (Fig. S1). We do not investigate regions with median t_p of zero further here
because their exact sub-daily timescales are unresolvable, but within expectations (see Discussion).

210   Fig. 2. Median time to peak plant water content (t_p) after soil moisture pulse. (A) Median t_p global distribution. Median t_p
binned as a function of (B) mean annual precipitation and (C) tree cover. Mostly bare surfaces with low vegetation density are
masked. Densely forested areas (tree cover > 40%) are masked due to limitations in VOD estimation for dense canopies.

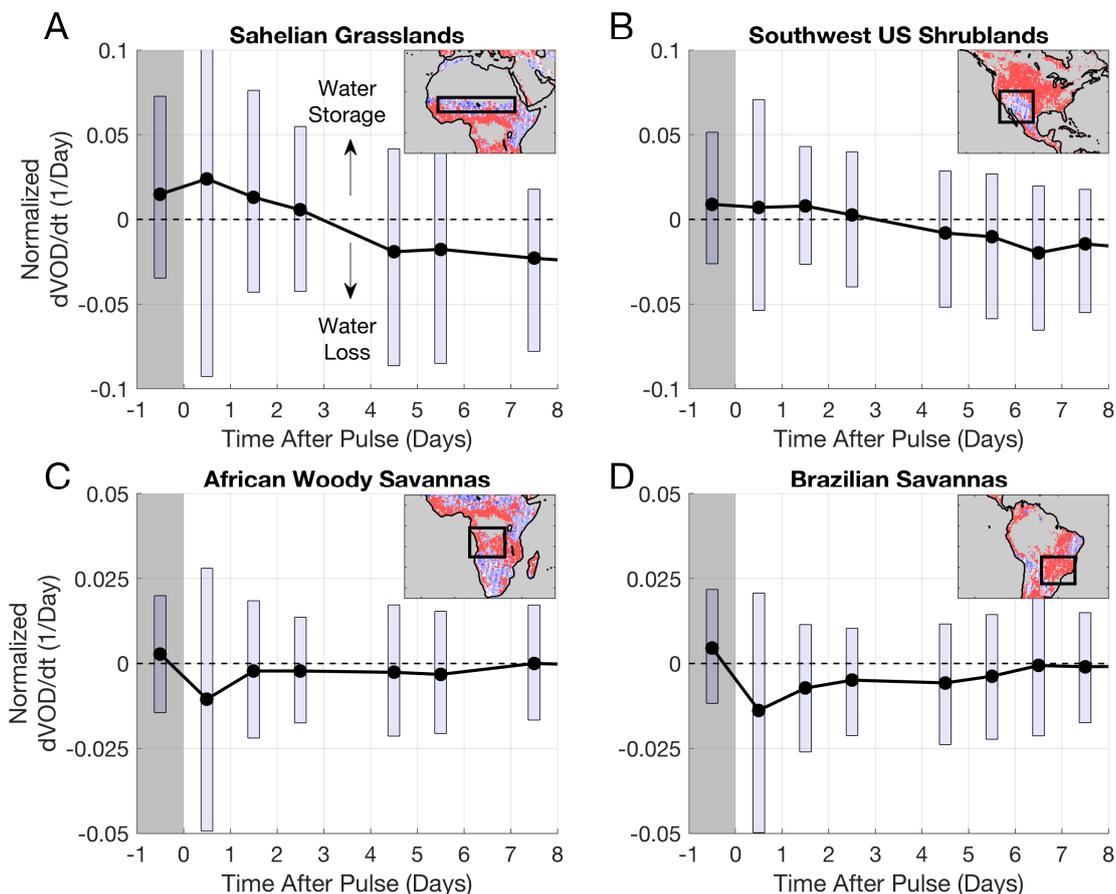



Fig. 3. Median VOD change rate on a given day after the pulse for regions outlined in the insets. Boxes delineate the interquartile range for each day. dVOD/dt is normalized by dividing by VOD time mean for a given pixel for consistent comparison across regions. dVOD/dt is reported as the average change rate over a given day (for example, from day 0 to day 1). All pixels with the noted dominant land cover (>75% IGBP land cover type) are used within the boxed region in the inset to create the distributions for each respective day after the pulse. Gray shading indicates the pulse period when soil moisture is increasing (Fig. 1). At time greater than zero, soil moisture is drying (drydown event; see Fig. 1). Behavior extends beyond a week in many cases, but only eight days following the pulse are shown here. Note that top and bottom panels have different y-axis limits.

3.2 Growth influence on plant water content increase timescales

A positive correlation between LAI rates of change and plant water content increase timescales is found in 72% of African pixels with median $t_p \geq 1$ ($p<0.05$). Calculating the LAI rates of change for the rapid VOD response ($t_p=0$), short VOD increase ($1 \leq t_p \leq 3$), and long VOD increase ($t_p>3$) groups reveals that growth tends to occur alongside plant water content increases longer than three days (Figs. 4A and 4D). These longer plant water content uptake timescales average 7 days and continue beyond a week 40% of the time. This growth influence means that rehydration alone cannot explain longer plant water content increase durations. Note that VOD increases during growth still demonstrate increased aboveground plant water content because more aboveground biomass results in water uptake to hydrate a greater volumetric plant storage capacity.

In general, growth does not influence shorter plant water content increase timescales. Indeed, LAI is often decreasing during short VOD increases (Fig. 4A). This suggests that plant water content increases over less than three days are mostly due to rehydration. Furthermore, when VOD increases do not extend beyond a day ($t_p = 0$), growth is also less frequently occurring.

The reoccurrence of growth influenced, multi-day VOD increases consistently following soil moisture pulses means that rainfall intermittently triggers growth throughout a year. This is because $t_p > 3$ coincide with increasing daily LAI (Fig. 4), consistently cooccur with a soil moisture pulse, and are separated from seasonal growth patterns. Seasonal trends were removed from VOD meaning that seasonal growth patterns are not confounding these VOD increases on sub-weekly timescales. The fact that seasonal trends were removed also means that deseasonalized VOD patterns show a close link to the moisture pulse with consistent multi-day increases and eventual decreases with water loss.

Although this daily LAI dataset is limited to Africa only, Africa contains one third of the world's regions with median $t_p \geq 1$ day (blue regions in Fig. 2A) and we expect similar results for the rest of the globe. Note that these results are not sensitive to the three-day threshold choice between long and short VOD increase groups; they are nearly identical if choosing a threshold of two, four, or five days.

On average, the short and long VOD increase bins occur approximately with equal frequency, both with seasonal variations (Fig. 4B). Longer duration VOD increases, influenced more by growth (Fig. 4A), appear to occur more frequently during times of the year when soil moisture is higher (Fig. 4B). In contrast, short VOD increases, associated more with rehydration, occur more often during drier times of the year (Fig. 4B). Furthermore, rapid rehydration responses occur 40-50% of the time throughout the year amongst the multi-day VOD increases.

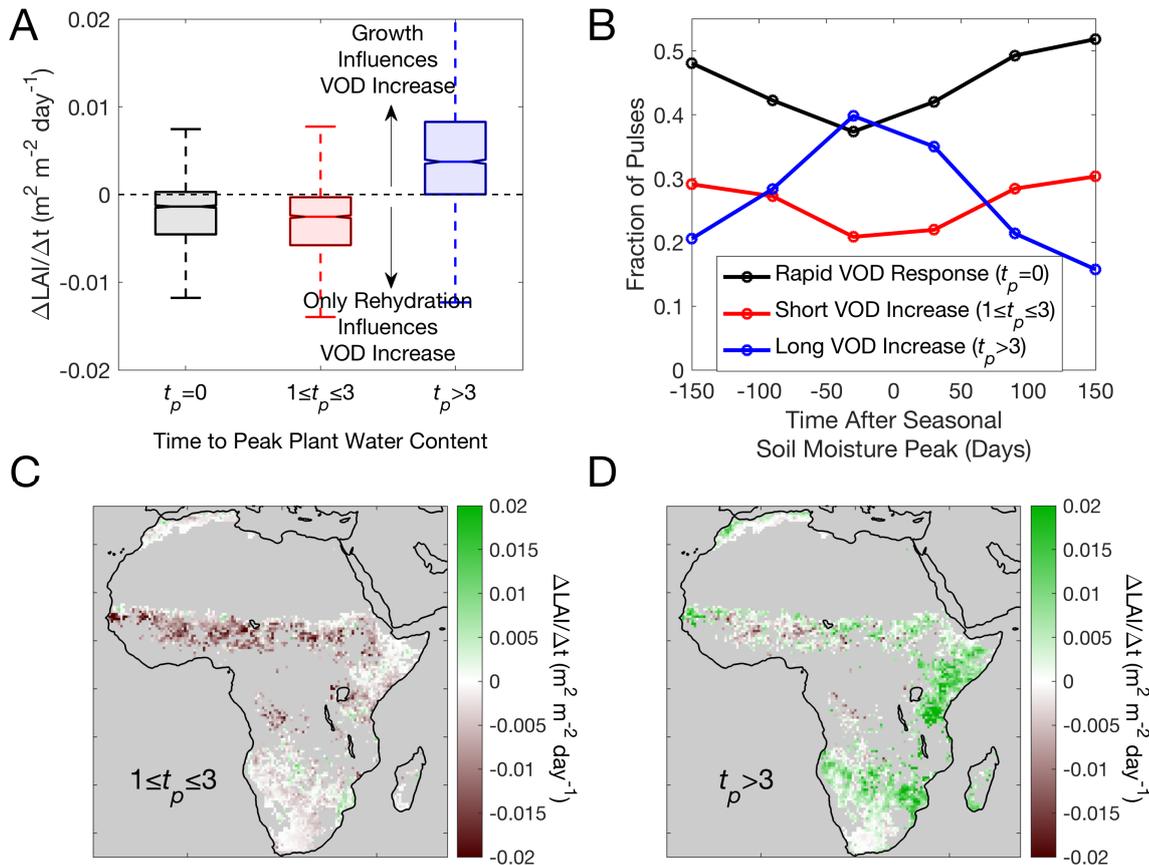
LAI growth rates average 0.005 m²/m² per day for these long VOD increases. On a mean percent change basis, there is a 15% LAI increase on average over the course of a week after a pulse. Note that LAI may not detect additional branch/stem biomass growth that VOD may detect.

255

Fig. 4. Timescale of plant water content increases relation to biomass changes and seasonality in African regions with median $t_p \geq 1$ day. Growth influences the plant water uptake timescale when $\Delta LAI/\Delta t > 0$. By contrast, only rehydration contributes to plant water content increases when $\Delta LAI/\Delta t < 0$. Only intermittent variability in VOD is used to produce t_p removing seasonal confounding connections with LAI (see text and SI). (A) Mean change in LAI per day over length of pulse period binned into
260 rapid responses ($t_p = 0$), short VOD increases ($1 \leq t_p \leq 3$ days), and long VOD increases ($t_p > 3$ days). A Kruskal-Wallis test indicates group means are all significantly different ($p \ll 0.01$; $\chi^2 = 2{,}576$, $\upsilon = 2$). (B) Seasonality of short and long VOD increase occurrences with respect to seasonal soil moisture peak. Positive and negative time indicates occurrence after and before the soil moisture seasonal peak, respectively. Plotted values are spatial medians in 60-day sized bins. Sample size in each bin (in a given pixel) is over 100, though pulses tend to be more frequent nearer to seasonal soil moisture peak. (C) Spatial distribution
265 of median $\Delta LAI/\Delta t$ for short VOD increases as binned in A. (D) Spatial distribution of median $\Delta LAI/\Delta t$ for long VOD increases as binned in A.

3.3 Pulse condition influence on plant water content increase timescales

Variations in VOD increase timescales across space and time likely occur as a result of differences in vegetation
270 traits, edaphic and topographic properties affecting soil moisture infiltration, and climatic properties. While an evaluation of

all of these factors is beyond the scope of this manuscript, we focus here on climatic drivers. To evaluate the climatic drivers of VOD increase timescales in regions with median $t_p \geq 1$ day (blue regions in Fig. 2A), we assess how t_p relates to rain pulse conditions: antecedent surface soil moisture, soil moisture pulse magnitude, and antecedent VOD. Growth-influenced VOD increases of longer duration are associated with initially wetter surface soil (Fig. 5A) as well as with larger pulse magnitudes

275   (Fig. 5B). This suggests that the surface must be sufficiently wet initially and a large enough pulse must occur to elicit a growth response. Conversely, shorter duration VOD increases associated primarily with rehydration frequently occur under drier initial soil conditions with smaller rewetting pulses (Fig. 5). This is consistent with short increase durations becoming more prevalent during drier periods and long increase durations becoming more prevalent in wet periods (Fig. 4B). Note that while we constrain results here to Africa for consistent comparison with the growth assessment (Sect. 3.2), the results are nearly identical

280   when calculated across the globe (not shown).

In assessing what differentiates rapid responses and short VOD increases that appear driven by only rehydration, we find short VOD increases have slightly larger pulse magnitudes (Fig. 5B) and drier antecedent soil moisture than rapid responses (Fig. 5A). Also, drier initial plant water status for short VOD increases (Fig. 5C) independently suggests a slightly drier root zone initially than for rapid responses (Fig. S12). Note that mean differences are small between these metrics, even

285   though they show statistical significance (likely effect of large sample size). Nevertheless, cases of vegetation water content increases on the order of 1-3 days, due primarily to rehydration, occur under dry soil conditions with small-to-moderate rewetting pulses.

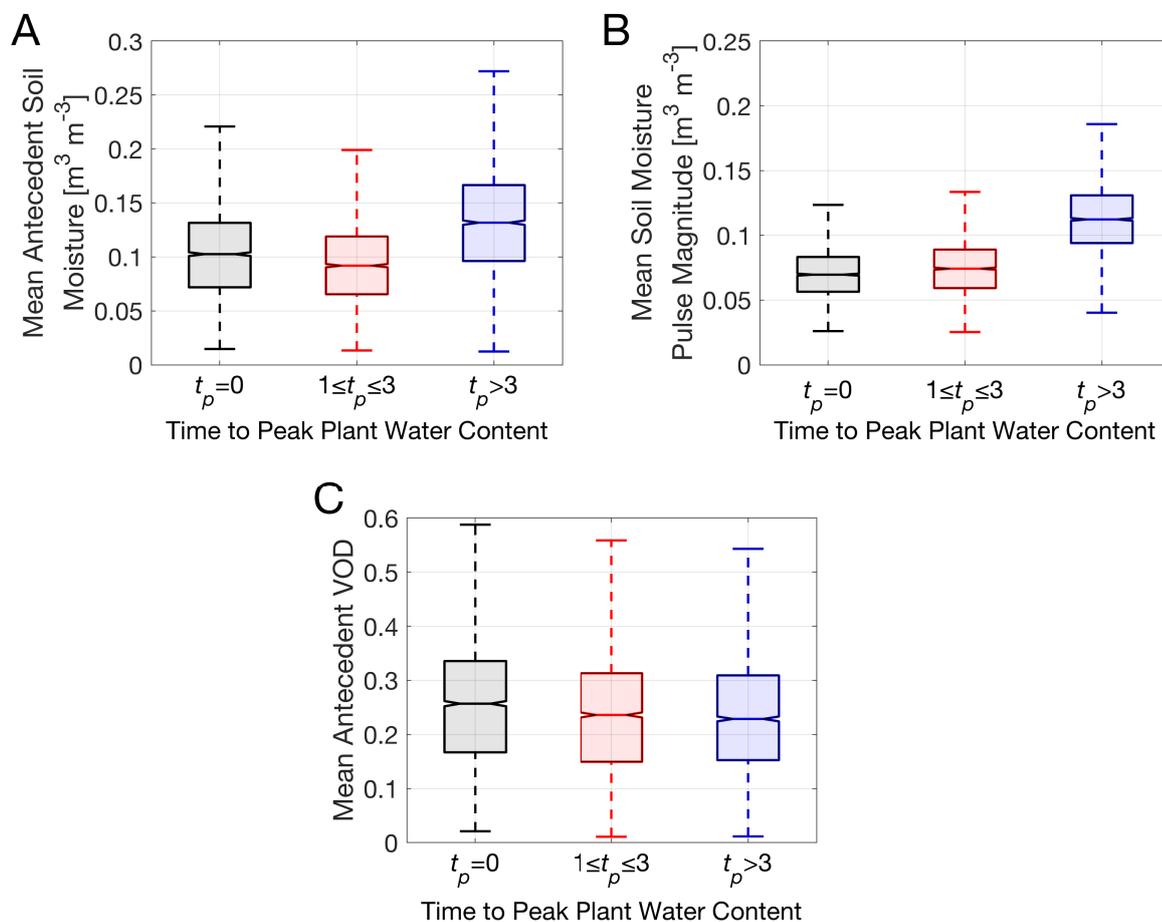



Fig. 5. Spatial distribution of pulse conditions binned as function of rapid VOD response (t_p =0), short VOD increases (t_p =1-3 days), and long VOD increases (t_p >3 days) in African regions with median $t_p \geq 1$ day. Kruskal-Wallis (KW) tests indicate all group means are significantly different within each panel. (A) Antecedent surface soil moisture (KW test p<<0.01; χ^2=944, υ=2). 77% of pixels have significantly positive linear relationships with t_p (p<0.05). (B) Surface soil moisture pulse magnitude (KW test p<<0.01; χ^2=3,582, υ=2). 86% of pixels have significantly positive linear relationships with t_p (p<0.05). (C) Antecedent VOD (KW test p<<0.01; χ^2=63, υ=2). 82% of pixels have significantly negative linear relationships with t_p (p<0.05).

3.4 Satellite plant water content response uncertainty analysis

Satellite t_p estimates here appear robust with effects of satellite sampling frequency, algorithmic estimation error, and measurement noise increasing t_p variance, but not introducing discernable biases. This is based on several tests conducted evaluating t_p sensitivity to 1-3 day satellite sampling frequency, soil moisture-VOD retrieval algorithm, and random instrument noise on order of that of SMAP radiometer (Piepmeier et al., 2017). A stochastic rainfall generator was used to simulate soil moisture and consequent drydowns. A range of "true" VOD behavior was considered such as perfect correlation with soil moisture (true t_p of zero) and multi-day VOD increases during drying (true t_p greater than zero). Analyses were conducted directly on these simulated time series, including converting these time series to TB measurements for implementation in the algorithm and comparing the original "true" time series to the algorithm-estimated time series as in Zwieback et al. (2019).

The SMAP sampling period of 1-3 days results in greater variance but no mean biases for t_p estimates below the Nyquist frequency of 4-6 days (Figs. S3 and S4). One can combine low frequency microwave measurements from similar satellites (Kerr et al., 2010) to increase the sampling frequency and reduce uncertainty in t_p estimates here. This is not attempted

310 due to complications in combining the datasets. The MT-DCA algorithm used here reduces sensitivity to noise within the simultaneous soil moisture-VOD estimation (Konings et al., 2016, 2015; Zwieback et al., 2019). We found that use of a traditional algorithm biases t_p towards zero (Fig. S6) because its greater sensitivity to noise will tend to spuriously induce positive correlation between soil moisture and VOD within the estimation procedure (Konings et al., 2016). Therefore, increases in VOD during soil drying and thus positive t_p are not a result of algorithmic artifacts (Feldman et al., 2018). It is

315 also unlikely that algorithmic noise is driving spatial patterns as both algorithms produce the same spatial pattern. Note that the MT-DCA algorithm can artificially increase t_p, though measurement noise may cancel this effect (Fig. S3). Finally, measurement noise primarily increases variance of t_p (Fig. S3).

Ultimately, while identifying precise t_p values for a given drydown may be hindered by these sources of uncertainty, median t_p for a pixel are likely not biased and more confidence is exhibited in whether t_p is zero or non-zero (Fig. S5). This

320 uncertainty analysis provides confidence in the global patterns of median t_p and results based on binned t_p where zero, short, and long t_p can be confidently partitioned.

4. Discussion
4.1 Plant water uptake timescale variation across climates

325 We observe a continuum of plant water uptake timescales from humid to dryland environments, with mainly drylands showing frequent multi-day plant water content increases (Fig. 2). Given that capacitance increases at least three orders of magnitude from grasses in drylands to trees in humid regions (Carlson and Lynn, 1991; Hunt Jr et al., 1991), one might expect, if at all, occurrence of multi-day responses in wooded regions. However, humid, wooded regions broadly exhibit peak plant water content during rather than after the storm event, before soil drying begins (Figs. 2 and S1). Plant water loss occurs

330 thereafter with soil drying (Figs. 3C and 3D). The initial VOD increase can be due to plant water uptake where pre-dawn water potential approaches equilibrium with soil moisture and/or due to plant interception of rainfall droplets. In some cases, no discernable VOD increases occur before or after the pulse which may be due to already well-watered conditions (Fig. S1). Even in drylands, pulse utilization decreases if the plant-soil system is initially sufficiently wet (Ehleringer et al., 1991; Gebauer et al., 2002; Ignace et al., 2007). Nevertheless, due to the 1-3-day satellite sampling, we are unable to resolve more

335 specific plant water content timescales and underlying mechanisms for these well-watered, wooded regions. During the drydown, VOD drying likely occurs along with loss of soil moisture due to transpiration while maintaining pre-dawn soil and plant-storage water potential equilibrium.

The consistent trend of multi-day plant water content increases, which are found broadly across dry regions (Fig. 2), is unexpected, at least in the context of nominal RC time constants. Field-based estimates of plant water uptake timescales (via

340 RC plant hydraulic time constants) typically do not exceed a day, regardless of species (Huang et al., 2017; Nobel and Jordan, 1983; Phillips et al., 1997, 2004; Ward et al., 2013). This is in part because plant capacitance and resistance tend to trade off with changes in plant architecture and moisture conditions (i.e., capacitance increases and resistance decreases generally with from grass to tree species) (Hunt Jr et al., 1991; Phillips et al., 1997; Richards et al., 2014; Ward et al., 2013). We discuss below both the influence of growth and slow plant rehydration on these observed multi-day VOD increases.

345

4.2 Growth impact on dryland plant water uptake timescales

As is evident in independent satellite LAI observations, growth influences plant water content increases of more than three days primarily in dryland regions (Fig. 4). These week-long consecutive plant water content increases occur when the soil is initially wetter and pulses are larger (Fig. 5). Therefore, plant rehydration alone cannot explain these longer duration

350 VOD increases. We further suspect rehydration is rapid under these well-watered conditions. While pulsed-growth is expected

to occur with a lag of 1-5 days (Ogle and Reynolds, 2004), these lags may be obscured in the sampling of VOD and initial VOD increases due to rehydration. Furthermore, these pulsed plant water content increases due to growth may continue for longer than detected here (beyond two weeks). However, continued water loss and VOD decreases through transpiration may eventually dominate over VOD increases due to growth, curtailing the peak VOD (resulting in behavior like that shown
355 schematically in Fig. 1). VOD ultimately shows sub-weekly growth temporal dynamics beyond those resolved from optical instruments.

These results indicate that large soil moisture pulses on initially wetter soils trigger dryland vegetation growth responses after storm events, as hypothesized under the pulse-reserve paradigm (Collins et al., 2014; Noy-Meir, 1973). This weekly variability may drive seasonal growth in these locations (Reynolds et al., 1999) where the seasonal growth cycles
360 appear to be made up of sub-weekly intermittent growth dynamics as modeled in Ogle and Reynolds, (2004). The growth occurrences under wetter conditions are expected given cell turgor must be high for cell expansion and rapid growth to occur (Kramer and Boyer, 1995). Furthermore, a recent study showed that larger pulses during the growing season resulted in 1-2 weeks of increasing leaf and stalk density in a semi-arid grassland, consistent with results here (Post and Knapp, 2019). Additionally, larger pulses have previously been shown to elicit greater plant photosynthetic responses (Chen et al., 2009;
365 Dougherty et al., 1996; Schwinning and Sala, 2004). Therefore, detection of pulse-triggered growth on timescales of drydowns here is consistent with previous results, although it is the first to show how widespread the pulse-triggered growth dynamics are in drylands. Additionally, the seasonal occurrence of growth-driven, longer t_p (Fig. 4B) supports that pulses will trigger growth primarily in the season when species are phenologically active and able to invest in aboveground biomass (Post and Knapp, 2019; Reynolds et al., 1999; Schwinning and Sala, 2004).
370

4.3 Slow dryland plant rehydration mechanisms
Over half of the moisture pulses, primarily in global drylands, result in multi-day satellite-observed plant water content increases (Fig. 2). These multi-day VOD increases are often only due to rehydration, especially the shorter VOD increases (1-3 day) following small-to-moderate pulses on initially dry soils (Figs. 4 and 5). They can occur even when biomass
375 is decreasing (Fig. 4; such as leaf off). For dryland ecosystems that include grass and shrub species with isolated forests, multi-day rehydration is generally unexpected with nominal RC time constants on the order of an hour (Carlson and Lynn, 1991; Hunt Jr et al., 1991). However, previous field studies often show 1-4-day rehydration of grasses and shrubs upon rewetting following dry conditions, especially in the southwestern United States, where multi-day VOD increases are observed (Briones et al., 1998; Fravolini et al., 2005; Huxman et al., 2004; Ignace et al., 2007; West et al., 2007).
380 To better understand the physiological drivers of multi-day rewetting, we assessed the potential hydrologic and physiological mechanisms driving slow rehydration using a plant hydraulic (SPAC) model and parameters within known bounds for semi-arid species (Figs. S7 to S13 and Table S1). Note that assimilating satellite VOD into a SPAC model is beyond the scope of this study and is hindered by the large number of unknown plant hydraulic parameters at global scales. After implementing randomized simulations using a Monte Carlo approach, we found that the sufficient conditions for multi-day
385 plant rehydration determined here include initially high soil-plant resistances decreasing over multiple days following a storm. These time-varying resistances can occur either in the soil, plant, or both (Figs. 6, S8, and S10). The possibility of multi-day rehydration due to these conditions suggests that RC timescales can greatly deviate from nominal conditions (Scholz et al., 2011), especially under drought scenarios where resistances are both higher and changing. Furthermore, after uncoupling effects of soil and plant resistances in the SPAC model, we suspect that multi-day rehydration as seen by VOD is likely
390 dominated by plant resistance limitations rather than soil resistance limitations for several reasons. First, high soil resistances reduce infiltration rates and result in a phase-lagged delay in plant rehydration (Fig. 6B), which is not observed in the satellite VOD behavior here. In the slow rehydration cases, VOD increases begin immediately during the storm and not with a phase lagged delay (Figs. 3 and S2), which more closely resembles slow plant rehydration dominated by plant resistance limitations rather than those dominated by soil resistance limitations (compare satellite VOD observations in Figs. 3A and 3B with SPAC

395 model simulations in Fig. 6A versus 6B). Second, the common existence of soil macropores and active root profiles partially near the surface would preclude infiltration delays to root systems even under the driest initial soil conditions (Kramer and Boyer, 1995).

The initially high, decreasing resistances, as determined from the SPAC model and likely influencing landscape scale plant water content behavior, are likely due to drought recovery of soil-root interface and xylem architecture. Initially high,
400 decreasing resistances has been observed in the field, where after rewetting of dry soil conditions, soil-root interface and xylem resistances can decrease by one to three orders of magnitude over a few days (Carminati et al., 2017; North and Nobel, 1995; Trifilò et al., 2004; West et al., 2007). Under prolonged dry conditions, a disconnect between soil and root interface can occur, and after rewetting, the soil-root and radial root hydraulic conductivity progressively increase (Carminati et al., 2009; North and Nobel, 1997). Similarly, xylem cavitation and embolism from drying lead to increased xylem resistance that can regain
405 conductance and refill after rewetting (Martorell et al., 2014), though noting controversies with existence of xylem repair and refilling (Charrier et al., 2016; Lamarque et al., 2018; Venturas et al., 2017). Recent evidence suggests that whole root resistance (i.e., soil-root interface, radial) rather than xylem resistance (from cavitation) dominate the whole plant resistance during these drying and rewetting cycles (Rodriguez-Dominguez and Brodribb, 2020).

We expect that VOD and thus ecosystem-scale relative water content are sensitive to plant rehydration. Many species
410 show little sensitivity of relative water content to changing water potential, especially under wetter plant water status. In this case, VOD changes would be less sensitive to changes in plant water potential. However, herbaceous species within drylands and many species under drier conditions tend to have near-linear relationships between relative water content and plant water potential (Jones, 2014; Jones and Higgs, 1979; Nobel and Jordan, 1983). Therefore, VOD increases in drylands investigated here will be a function of plant water potential and rehydration.

415

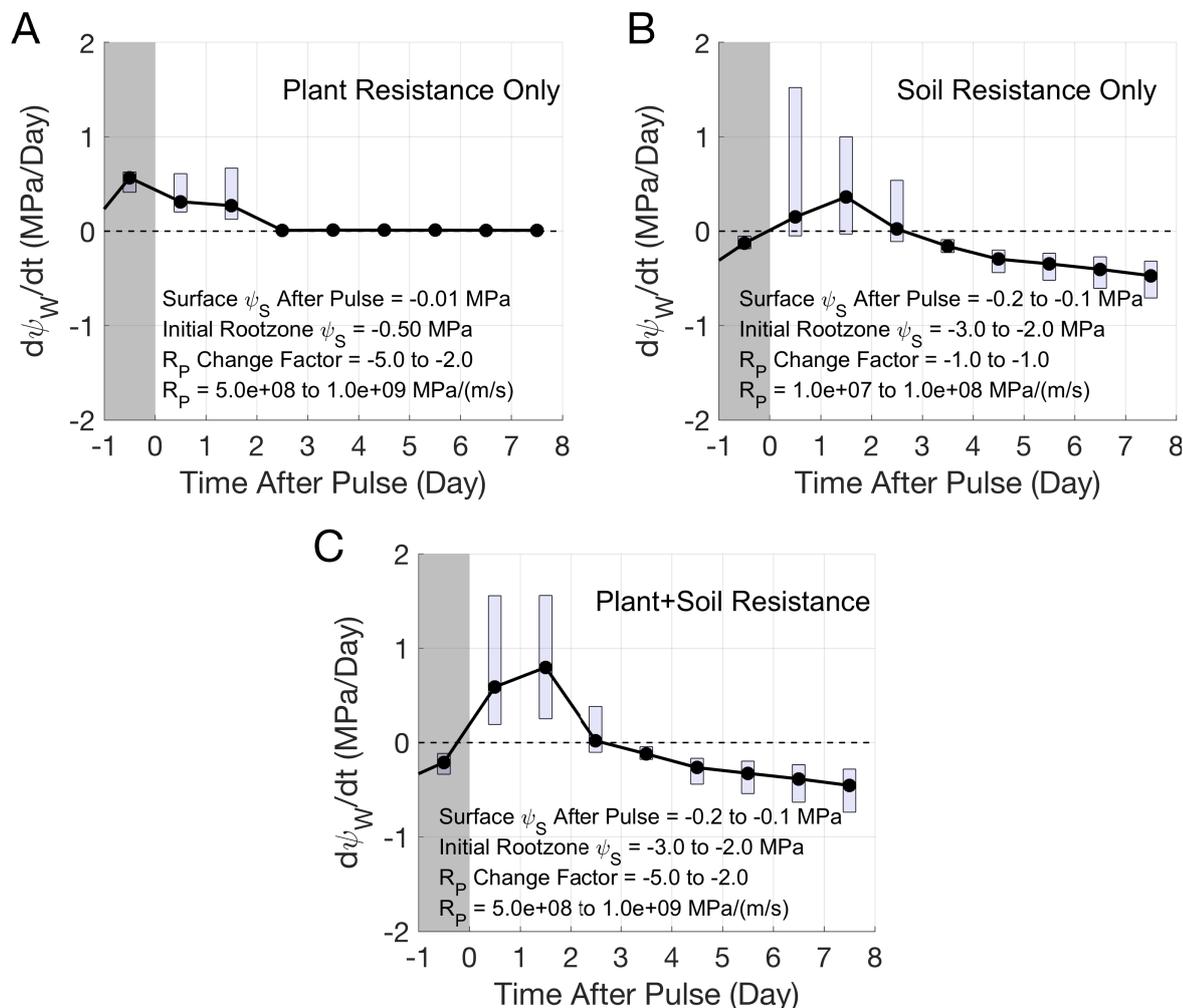



Fig. 6. SPAC model simulations of determined sufficient conditions driving slow rehydration (see text and SI) for semi-arid grass and shrub species. Rate of change in predawn plant-storage water potential (ψ_w) on a given day following a pulse where $d\psi_w/dt > 0$ indicates rehydration. Same format and conventions as Fig. 3. Parameter bounds determined to drive each slow rehydration scenario are shown in each panel. (A) Plant limitation only where plant resistance (R_P) is initially high and decreases. (B) Soil limitation only where rootzone soil moisture is initially dry and pulses are small to moderate, causing slow infiltration. (C) Both plant and soil limitations from A and B. Parameter ranges common amongst all simulations: rooting depth = 0.3 to 0.7 m, VPD = 1 to 5 kPa, wind = 1 to 8 m/s, C = 10^{-6} to 10^{-5} m/MPa, and R_S impairment factor = -10 to -1. See SI for more information on the SPAC model.

5. Conclusions

The globally-observed timescales of plant water content responses to moisture pulses here reveal a climate gradient of ecosystem-scale vegetation pulse water usage. The vegetation water content of more wooded, humid regions appears to respond rapidly to rain pulses, likely with rehydration responses occurring in less than a day (due to predawn equilibrium). By contrast, drier ecosystems more often show multi-day plant water uptake responses following moisture pulses with the timescale of the response indicative of underlying mechanisms. Specifically, longer plant water content increases are linked

to growth and follow larger pulses on wetter surfaces. Therefore, dryland vegetation intermittently upregulates and grows after individual rainfall events rather than continuously, demonstrating evidence for the pulse-reserve hypothesis and suggesting sub-weekly (rain pulse) rather than seasonal phenological controls on growth (Noy-Meir, 1973). Additionally, shorter plant
435 water content increases are indicative of slow plant rehydration responses and are linked here to hydraulic recovery from initially dry conditions. The slow rehydration responses indicate that plant water uptake timescales can frequently deviate from nominal RC time constants with greatly increased resistances under dry conditions, as observed previously in field experiments and demonstrated here using a SPAC model.

Our results also indicate that SMAP satellite vegetation optical depth observations hold biophysical information at
440 sub-weekly timescales. Namely, they show patterns of rehydration and growth responses and rain pulse dependencies consistent with that seen in field studies. This merits investigation of sub-monthly ecological processes using these 1-3 day sampled satellite microwave observations, which so far have been primarily used for seasonal and interannual VOD variability investigations (Brandt et al., 2018; Jones et al., 2014; Tian et al., 2018).

We show that global dryland ecosystems show a high sensitivity to the characteristics of individual moisture pulses.
445 Therefore, expected shifts in rainfall frequencies and intensity may influence arid to semi-arid vegetation hydraulic and growth processes, presenting potential feedbacks on biogeochemical cycles and changes in plant community composition (Giorgi et al., 2019; Knapp et al., 2002). These dry ecosystems cover 40% of the land surface, store significant amounts of carbon (Beer et al., 2010; Collins et al., 2014), regulate atmospheric carbon interannual variability (Ahlström et al., 2015; Poulter et al., 2014), and are projected to expand (Huang et al., 2016). Therefore, it is key to characterize the vegetation responses to rainfall
450 events – including their timescales - in these environments in the context of predicting future climate.

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Author Contribution

P.G. and A.F.F. conceived the study. D.E. led the project. A.F.F. conducted the analysis and wrote the manuscript. D.J.S.G.,
460 A.G.K., P.G., and D.E. contributed interpretations and numerous revisions to all versions of the analysis, figures, and manuscripts.

Data Accessibility

SMAP L1C brightness temperature used to retrieve soil moisture are available from the National Snow and Ice Data Center
465 (NSIDC) (https://nsidc.org/data/ SPL1CTB_E). LandSAF leaf area index is available from EUMETSAT (https:// landsaf.ipma.pt). Generated maps are available at https://github.com/afeld24/VOD_Timescales.

References

Ahlström, A., Raupach, M.R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J.G., Friedlingstein,
470   P., Jain, A.K., Kato, E., Poulter, B., Sitch, S., Stocker, B.D., Viovy, N., Wang, Y.P., Wiltshire, A., Zaehle, S., Zeng, N.,
        2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. Science (80-.). 348,
        895–900. https://doi.org/10.1002/2015JA021022

Angert, A.L., Huxman, T.E., Barron-Gafford, G.A., Gerst, K.L., Venable, D.L., 2007. Linking growth strategies to long-term

population dynamics in a guild of desert annuals. J. Ecol. 95, 321–331. https://doi.org/10.1111/j.1365-
475   2745.2006.01203.x

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan,
       G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W.,
       Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D., 2010. Terrestrial gross carbon
       dioxide uptake: Global distribution and covariation with climate. Science (80-.). 329, 834–838.
480   https://doi.org/10.1126/science.1184984

Blackman, C.J., Brodribb, T.J., Jordan, G.J., 2009. Leaf hydraulics and drought stress: Response, recovery and survivorship
       in four woody temperate plant species. Plant, Cell Environ. 32, 1584–1595. https://doi.org/10.1111/j.1365-
       3040.2009.02023.x

Bonan, G.B., Williams, M., Fisher, R.A., Oleson, K.W., 2014. Modeling stomatal conductance in the earth system: Linking
485   leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum. Geosci. Model Dev. 7, 2193–
       2222. https://doi.org/10.5194/gmd-7-2193-2014

Brandt, M., Wigneron, J.P., Chave, J., Tagesson, T., Penuelas, J., Ciais, P., Rasmussen, K., Tian, F., Mbow, C., Al-Yaari, A.,
       Rodriguez-Fernandez, N., Schurgers, G., Zhang, W., Chang, J., Kerr, Y., Verger, A., Tucker, C., Mialon, A., Rasmussen,
       L.V., Fan, L., Fensholt, R., 2018. Satellite passive microwaves reveal recent climate-induced carbon losses in African
490   drylands. Nat. Ecol. Evol. 2, 827–835. https://doi.org/10.1038/s41559-018-0530-6

Briones, O., Montaña, C., Ezcurra, E., 1998. International Association for Ecology Competition Intensity as a Function of
       Resource Availability in a Semiarid Ecosystem. Oecologia 116, 365–372.

Brodribb, T.J., Cochard, H., 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. Plant
       Physiol. 149, 575–584. https://doi.org/10.1104/pp.108.129783

495 Caldwell, M.M., Richards, J.H., 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by
       deep roots. Oecologia 79, 1–5. https://doi.org/10.1007/BF00378231

Carlson, T.N., Lynn, B., 1991. The effects of plant water storage on transpiration and radiometric surface temperature. Agric.
       For. Meteorol. 57, 171–186. https://doi.org/10.1016/0168-1923(91)90085-5

Carminati, A., Benard, P., Ahmed, M.A., Zarebanadkouki, M., 2017. Liquid bridges at the root-soil interface. Plant Soil 417,
500   1–15. https://doi.org/10.1007/s11104-017-3227-8

Carminati, A., Vetterlein, D., Weller, U., Vogel, H.J., Oswald, S.E., 2009. When roots lose contact. Vadose Zo. J. 8, 898–809.
       https://doi.org/10.2136/vzj2008.0147

Chan, S.K., Bindlish, R., O'Neill, P.E., Njoku, E., Jackson, T., Colliander, A., Chen, F., Burgin, M., Dunbar, S., Piepmeier,
       J., Yueh, S., Entekhabi, D., Cosh, M.H., Caldwell, T., Walker, J., Wu, X., Berg, A., Rowlandson, T., Pacheco, A.,
505   McNairn, H., Thibeault, M., Martinez-Fernandez, J., Gonzalez-Zamora, A., Seyfried, M., Bosch, D., Starks, P.,
       Goodrich, D., Prueger, J., Palecki, M., Small, E.E., Zreda, M., Calvet, J.C., Crow, W.T., Kerr, Y., 2016. Assessment of
       the SMAP Passive Soil Moisture Product. IEEE Trans. Geosci. Remote Sens. 54, 4994–5007.

https://doi.org/10.1109/TGRS.2016.2561938

Charrier, G., Torres-Ruiz, J.M., Badel, E., Burlett, R., Choat, B., Cochard, H., Delmas, C.E.L., Domec, J.C., Jansen, S., King,
510   A., Lenoir, N., Martin-StPaul, N., Gambetta, G.A., Delzon, S., 2016. Evidence for hydraulic vulnerability segmentation
        and lack of xylem refilling under tension. Plant Physiol. 172, 1657–1668. https://doi.org/10.1104/pp.16.01079

Chen, S., Lin, G., Huang, J., Jenerette, D., 2009. Dependence of carbon sequestration on the differential responses of ecosystem
        photosynthesis and respiration to rain pulses in a semiarid steppe. Glob. Chang. Biol. 15, 2450–2461.
        https://doi.org/10.1111/j.1365-2486.2009.01879.x

515   Collins, S.L., Belnap, J., Grimm, N.B., Rudgers, J.A., Dahm, C.N., D'Odorico, P., Litvak, M., Natvig, D.O., Peters, D.C.,
        Pockman, W.T., Sinsabaugh, R.L., Wolf, B.O., 2014. A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land
        Ecosystems. Annu. Rev. Ecol. Evol. Syst. 45, 397–419. https://doi.org/10.1146/annurev-ecolsys-120213-091650

Dadap, N.C., Cobb, A.R., Hoyt, A.M., Harvey, C.F., Konings, A.G., 2019. Satellite soil moisture observations predict burned
        area in Southeast Asian peatlands. Environ. Res. Lett. 14, 094014. https://doi.org/10.1088/1748-9326/ab3891

520   Dimiceli, C., Carroll, M., Sohlberg, R., Kim, D.H., Kelly, M., Townshend, J.R.G., 2015. MOD44B MODIS/Terra Vegetation
        Continuous Fields Yearly L3 Global 250m SIN Grid V006. 2015, distributed by NASA EOSDIS Land Processes DAAC,
        https://doi.org/10.5067/MODIS/MOD44B.006.

Donat, M.G., Lowry, A.L., Alexander, L. V., O'Gorman, P.A., Maher, N., 2016. More extreme precipitation in the world's
        dry and wet regions. Nat. Clim. Chang. 6, 508–513. https://doi.org/10.1038/nclimate2941

525   Dougherty, R.L., Lauenroth, W.K., Singh, J.S., 1996. Response of a Grassland Cactus to Frequency and Size of Rainfall Events
        in a North American Shortgrass Steppe. J. Ecol. 84, 177. https://doi.org/10.2307/2261353

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert
        plants. Oecologia 88, 430–434. https://doi.org/10.1007/BF00317589

Entekhabi, D., Njoku, E.G., O'Neill, P.E., Kellogg, K.H., Crow, W.T., Edelstein, W.N., Entin, J.K., Goodman, S.D., Jackson,
530   T.J., Johnson, J., Kimball, J., Piepmeier, J.R., Koster, R.D., Martin, N., McDonald, K.C., Moghaddam, M., Moran, S.,
        Reichle, R., Shi, J.C., Spencer, M.W., Thurman, S.W., Tsang, L., Van Zyl, J., 2010. The Soil Moisture Active Passive
        (SMAP) Mission. Proc. IEEE 98, 704–716. https://doi.org/10.1109/JPROC.2010.2043918

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a
        C 4-dominated grassland. Oecologia 137, 245–251. https://doi.org/10.1007/s00442-003-1331-3

535   Feldman, A.F., Short Gianotti, D.J., Konings, A.G., McColl, K.A., Akbar, R., Salvucci, G.D., Entekhabi, D., 2018. Moisture
        pulse-reserve in the soil-plant continuum observed across biomes. Nat. Plants 4, 1026–1033.
        https://doi.org/10.1038/s41477-018-0304-9

Feldman, A.F., Short Gianotti, D.J., Trigo, I.F., Salvucci, G.D., Entekhabi, D., 2019. Satellite-Based Assessment of Land
        Surface Energy Partitioning–Soil Moisture Relationships and Effects of Confounding Variables. Water Resour. Res. 55,
540   10657–10677. https://doi.org/10.1029/2019WR025874

Fisher, R.A., Koven, C.D., Anderegg, W.R.L., Christoffersen, B.O., Dietze, M.C., Farrior, C.E., Holm, J.A., Hurtt, G.C., Knox,

R.G., Lawrence, P.J., Lichstein, J.W., Longo, M., Matheny, A.M., Medvigy, D., Muller-Landau, H.C., Powell, T.L., Serbin, S.P., Sato, H., Shuman, J.K., Smith, B., Trugman, A.T., Viskari, T., Verbeeck, H., Weng, E., Xu, C., Xu, X., Zhang, T., Moorcroft, P.R., 2018. Vegetation demographics in Earth System Models: A review of progress and priorities.

545   Glob. Chang. Biol. 24, 35–54. https://doi.org/10.1111/gcb.13910

Fravolini, A., Hultine, K.R., Brugnoli, E., Gazal, R., English, N.B., Williams, D.G., 2005. Precipitation pulse use by an invasive woody legume: The role of soil texture and pulse size. Oecologia 144, 618–627. https://doi.org/10.1007/s00442-005-0078-4

García-Haro, F.J., Camacho, F., 2014. Algorithm Theoretical Basis Document for Vegetation parameters (VEGA) 401, 1–34.

550   García-Haro, F.J., Camacho, F., Meliá, J., 2013. The EUMETSAT Satellite Application Facility on Land Surface Analysis Product User Manual Vegetation Parameters (VEGA) 401, 1–46.

Gebauer, R.L.E., Schwinning, S., Ehleringer, J.R., 2002. Interspecific Competition and Resource Utilization between Bumblebees. Ecology 83, 2602–2616. https://doi.org/10.2307/3672007

Gentine, P., Green, J.K., Guérin, M., Humphrey, V., Seneviratne, S.I., Zhang, Y., Zhou, S., 2019. Coupling between the
555   terrestrial carbon and water cycles—a review. Environ. Res. Lett. 14, 083003. https://doi.org/10.1088/1748-9326/ab22d6

Gessner, U., Niklaus, M., Kuenzer, C., Dech, S., 2013. Intercomparison of leaf area index products for a gradient of sub-humid to arid environments in west africa. Remote Sens. 5, 1235–1257. https://doi.org/10.3390/rs5031235

Giorgi, F., Raffaele, F., Coppola, E., 2019. The response of precipitation characteristics to global warming from climate projections. Earth Syst. Dyn. 10, 73–89. https://doi.org/10.5194/esd-10-73-2019

560   Green, J.K., Konings, A.G., Alemohammad, S.H., Berry, J., Entekhabi, D., Kolassa, J., Lee, J.E., Gentine, P., 2017. Regionally strong feedbacks between the atmosphere and terrestrial biosphere. Nat. Geosci. 10, 410–414. https://doi.org/10.1038/ngeo2957

Guo, J.S., Ogle, K., 2019. Antecedent soil water content and vapor pressure deficit interactively control water potential in Larrea tridentata. New Phytol. 221, 218–232. https://doi.org/10.1111/nph.15374

565   Hermance, J.F., Augustine, D.J., Derner, J.D., 2015. Quantifying characteristic growth dynamics in a semi-arid grassland ecosystem by predicting short-term NDVI phenology from daily rainfall: a simple four parameter coupled-reservoir model. Int. J. Remote Sens. 36, 5637–5663. https://doi.org/10.1080/01431161.2015.1103916

Huang, C.W., Domec, J.C., Ward, E.J., Duman, T., Manoli, G., Parolari, A.J., Katul, G.G., 2017. The effect of plant water storage on water fluxes within the coupled soil–plant system. New Phytol. 213, 1093–1106.
570   https://doi.org/10.1111/nph.14273

Huang, J., Yu, H., Guan, X., Wang, G., Guo, R., 2016. Accelerated dryland expansion under climate change. Nat. Clim. Chang. 6, 166–171. https://doi.org/10.1038/nclimate2837

Huffman, G., 2015. GPM Level 3 IMERG Final Run Half Hourly 0.1 × 0.1 Degree Precipitation, version 05 (Goddard Space Flight Center Distributed Active Archive Center (GSFC DAAC), 2015).

575   Hunt, E.R., Nobel, P.S., 1987. Non-steady-state Water Flow for Three Desert Perennials with Different Capacitances. Aust. J.

Plant Physiol. 14, 363–375.

Hunt Jr, E.R., Running, S.W., Federer, C.A., 1991. Extrapolating plant water flow resistances and capacitances to regional scales. Agric. For. Meteorol. 54, 169–195.

Huxman, T.E., Cable, J.M., Ignace, D.D., Eilts, J.A., English, N.B., Weltzin, J., Williams, D.G., 2004. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: The role of native versus non-native grasses and soil texture. Oecologia 141, 295–305. https://doi.org/10.1007/s00442-003-1389-y

Ignace, D.D., Huxman, T.E., Weltzin, J.F., Williams, D.G., 2007. Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. Oecologia 152, 401–413. https://doi.org/10.1007/s00442-007-0670-x

Jackson, T.J., Schmugge, T.J., 1991. Vegetation effects on the microwave emission of soils. Remote Sens. Environ. 36, 203–212. https://doi.org/10.1016/0034-4257(91)90057-D

Jarque, C.M., Bera, A.K., 1980. Efficient test for normality, homoscedasticity and serial independence of regression residuals. Econ. Lett. 6, 255–259.

Jasechko, S., Sharp, Z.D., Gibson, J.J., Birks, S.J., Yi, Y., Fawcett, P.J., 2013. Terrestrial water fluxes dominated by transpiration. Nature 496, 347–350. https://doi.org/10.1038/nature11983

Jones, H.G., 2014. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology, 3rd ed. Cambridge University Press, Cambridge, UK.

Jones, H.G., Higgs, K.H., 1979. Water potential-water content relationships in apple leaves. J. Exp. Bot. 30, 965–970. https://doi.org/10.1093/jxb/30.5.965

Jones, M.O., Kimball, J.S., Nemani, R.R., 2014. Asynchronous Amazon forest canopy phenology indicates adaptation to both water and light availability. Environ. Res. Lett. 9, 124021. https://doi.org/10.1088/1748-9326/9/12/124021

Kennedy, D., Swenson, S., Oleson, K.W., Fisher, R.A., Lawrence, D.M., da Costa, A.C.L., Gentine, P., 2019. Implementing plant hydraulics in the Community Land Model, version 5. J. Adv. Model. Earth Syst. 1–29. https://doi.org/10.1029/2018ms001500

Kerr, Y., Waldteufel, P., Wigneron, J.-P., Delwart, S., Cabot, F., Boutin, J., Escorihuela, M.J., Font, J., Reul, N., Gruhier, C., Juglea, S.E., Drinkwater, M.R., Achim HReul, N., Boutin, J., Gruhier, C., Juglea, S.E., Drinkwater, M.R., Hahne, A., Neira, M.M.-, Mecklenburg, S., 2010. The SMOS Mission : New Tool for Monitoring Key Elements of the Global Water Cycle. Proc. IEEE 98, 666–687.

Kim, S., 2013. Ancillary Data Report: Landcover Classification. Jet Propuls. Lab. Calif. Inst. Technol., JPL D-53057.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science (80-.). 298, 2202–2205. https://doi.org/10.1126/science.1076347

Konings, A.G., Gentine, P., 2017. Global variations in ecosystem-scale isohydricity. Glob. Chang. Biol. 23, 891–905. https://doi.org/10.1111/gcb.13389

610 Konings, A.G., McColl, K.A., Piles, M., Entekhabi, D., 2015. How many parameters can be maximally estimated from a set of measurements? IEEE Geosci. Remote Sens. Lett. 12, 1081–1085. https://doi.org/10.1109/LGRS.2014.2381641

Konings, A.G., Piles, M., Das, N., Entekhabi, D., 2017. L-band vegetation optical depth and effective scattering albedo estimation from SMAP. Remote Sens. Environ. 198, 460–470. https://doi.org/10.1016/j.rse.2017.06.037

Konings, A.G., Piles, M., Rotzer, K., McColl, K.A., Chan, S.K., Entekhabi, D., 2016. Vegetation optical depth and scattering
615 albedo retrieval using time series of dual-polarized L-band radiometer observations. Remote Sens. Environ. 172, 178–189. https://doi.org/10.1016/j.rse.2015.11.009

Konings, A.G., Rao, K., Steele-Dunne, S.C., 2019. Macro to micro: microwave remote sensing of plant water content for physiology and ecology. New Phytol. 223, 1166–1172. https://doi.org/10.1111/nph.15808

Kramer, P.J., Boyer, J.S., 1995. Water Relations of Plants and Soils. Academic Press.

620 Lamarque, L.J., Corso, D., Torres-Ruiz, J.M., Badel, E., Brodribb, T.J., Burlett, R., Charrier, G., Choat, B., Cochard, H., Gambetta, G.A., Jansen, S., King, A., Lenoir, N., Martin-StPaul, N., Steppe, K., Van den Bulcke, J., Zhang, Y., Delzon, S., 2018. An inconvenient truth about xylem resistance to embolism in the model species for refilling Laurus nobilis L. Ann. For. Sci. 75. https://doi.org/10.1007/s13595-018-0768-9

Lin, C., Gentine, P., Frankenberg, C., Zhou, S., Kennedy, D., Li, X., 2019. Evaluation and mechanism exploration of the
625 diurnal hysteresis of ecosystem fluxes. Agric. For. Meteorol. 278. https://doi.org/10.1016/j.agrformet.2019.107642

Mackay, D.S., Roberts, D.E., Ewers, B.E., Sperry, J.S., McDowell, N.G., Pockman, W.T., 2015. Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models of tree response to drought. Water Resour. Res. 51, 6156–6176. https://doi.org/10.1002/2015WR017200.A

Manzoni, S., Vico, G., Porporato, A., Katul, G., 2013. Biological constraints on water transport in the soil-plant-atmosphere
630 system. Adv. Water Resour. 51, 292–304. https://doi.org/10.1016/j.advwatres.2012.03.016

Martínez-Vilalta, J., Anderegg, W.R.L., Sapes, G., Sala, A., 2019. Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. New Phytol. https://doi.org/10.1111/nph.15644

Martorell, S., Diaz-Espejo, A., Medrano, H., Ball, M.C., Choat, B., 2014. Rapid hydraulic recovery in Eucalyptus pauciflora after drought: Linkages between stem hydraulics and leaf gas exchange. Plant, Cell Environ. 37, 617–626.
635 https://doi.org/10.1111/pce.12182

McColl, K.A., Wang, W., Peng, B., Akbar, R., Short Gianotti, D.J., Lu, H., Pan, M., Entekhabi, D., 2017. Global characterization of surface soil moisture drydowns. Geophys. Res. Lett. 44, 3682–3690. https://doi.org/10.1002/2017GL072819

Mo, T., Choudhury, B.J., Schmugge, T.J., Wang, J.R., Jackson, T.J., 1982. A model for microwave emission from vegetation-
640 covered fields. J. Geophys. Res. 87, 11229. https://doi.org/10.1029/JC087iC13p11229

Momen, M., Wood, J.D., Novick, K.A., Pangle, R., Pockman, W.T., McDowell, N.G., Konings, A.G., 2017. Interacting Effects of Leaf Water Potential and Biomass on Vegetation Optical Depth. J. Geophys. Res. Biogeosciences 122, 3031–3046. https://doi.org/10.1002/2017JG004145

Nobel, P.S., Jordan, P.W., 1983. Transpiration stream of desert species: Resistances and capacitances for a c3, a c4, and a cam
645   plant. J. Exp. Bot. 34, 1379–1391. https://doi.org/10.1093/jxb/34.10.1379

North, G.B., Nobel, P.S., 1997. Root-soil contact for the desert succulent Agave deserti in wet and drying soil. New Phytol.
135, 21–29. https://doi.org/10.1046/j.1469-8137.1997.00620.x

North, G.B., Nobel, P.S., 1995. Hydraulic conductivity of concentric root tissues of Agave deserti Engelm. under wet and
drying conditions. New Phytol. 130, 47–57. https://doi.org/10.1111/j.1469-8137.1995.tb01813.x

650 Novoplansky, A., Goldberg, D.E., 2001. Effects of water pulsing on individual performance and competitive hierarchies in
plants. J. Veg. Sci. 12, 199–208. https://doi.org/10.2307/3236604

Noy-Meir, I., 1973. Desert Ecosystems: Environment and Producers. Annu. Rev. Ecol. Syst. 4, 25–52.

Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik, M.E., Tissue, D.T., 2015.
Quantifying   ecological   memory   in   plant   and   ecosystem   processes.   Ecol.   Lett.   18,   221–235.
655   https://doi.org/10.1111/ele.12399

Ogle, K., Reynolds, J.F., 2004. Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses,
thresholds, and delays. Oecologia 141, 282–294. https://doi.org/10.1007/s00442-004-1507-5

Phillips, N., Nagchaudhuri, A., Oren, R., Katul, G., 1997. Time constant for water transport in loblolly pine trees estiamted
from time series of evaporative demand and stem sapflow. Trees 412–419.

660 Phillips, N.G., Oren, R., Licata, J., Linder, S., 2004. Time series diagnosis of tree hydraulic characteristics. Tree Physiol. 24,
879–890. https://doi.org/10.1093/treephys/24.8.879

Piepmeier, J.R., Focardi, P., Horgan, K.A., Knuble, J., Ehsan, N., Lucey, J., Brambora, C., Brown, P.R., Hoffman, P.J., French,
R.T., Mikhaylov, R.L., Kwack, E.Y., Slimko, E.M., Dawson, D.E., Hudson, D., Peng, J., Mohammed, P.N., De Amici,
G., Freedman, A.P., Medeiros, J., Sacks, F., Estep, R., Spencer, M.W., Chen, C.W., Wheeler, K.B., Edelstein, W.N.,
665   O'Neill, P.E., Njoku, E.G., 2017. SMAP L-Band Microwave Radiometer: Instrument Design and First Year on Orbit.
IEEE Trans. Geosci. Remote Sens. 55, 1954–1966. https://doi.org/10.1109/TGRS.2016.2631978

Plaut, J.A., Wadsworth, W.D., Pangle, R., Yepez, E.A., Mcdowell, N.G., Pockman, W.T., 2013. Reduced transpiration
response to precipitation pulses precedes mortality in a piñon-juniper woodland subject to prolonged drought. New
Phytol. 200, 375–387. https://doi.org/10.1111/nph.12392

670 Post, A.K., Knapp, A.K., 2019. Plant growth and aboveground production respond differently to late-season deluges in a semi-
arid grassland. Oecologia 191, 673–683. https://doi.org/10.1007/s00442-019-04515-9

Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J.G., Chevallier, F., Liu, Y.Y.,
Running, S.W., Sitch, S., Werf, G.R. Van Der, 2014. Contribution of semi-arid ecosystems to interannual variability of
the global carbon cycle. Nature 509, 600–603. https://doi.org/10.1038/nature13376

675 Rao, K., Anderegg, W.R.L., Sala, A., Martínez-Vilalta, J., Konings, A.G., 2019. Satellite-based vegetation optical depth as an
indicator   of   drought-driven   tree   mortality.   Remote   Sens.   Environ.   227,   125–136.
https://doi.org/10.1016/j.rse.2019.03.026

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernández, R.J., 2004. Modifying the "pulse-reserve" paradigm for deserts of North America: Precipitation pulses, soil water, and plant responses. Oecologia 141, 194–210. https://doi.org/10.1007/s00442-004-1524-4

Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. Ecol. Monogr. 69, 69–106. https://doi.org/10.1890/0012-9615(1999)069[0069:IODODS]2.0.CO;2

Richards, A.E., Wright, I.J., Lenz, T.I., Zanne, A.E., 2014. Sapwood capacitance is greater in evergreen sclerophyll species growing in high compared to low-rainfall environments. Funct. Ecol. 28, 734–744. https://doi.org/10.1111/1365-2435.12193

Rodriguez-Dominguez, C.M., Brodribb, T.J., 2020. Declining root water transport drives stomatal closure in olive under moderate water stress. New Phytol. 225, 126–134. https://doi.org/10.1111/nph.16177

Scholz, F.G., Phillips, N.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., 2011. Size- and Age-Related Changes in Tree Structure and Function, in: Size- and Age-Related Changes in Tree Structure and Function. pp. 341–361. https://doi.org/10.1007/978-94-007-1242-3

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211–220. https://doi.org/10.1007/s00442-004-1520-8

Shellito, P.J., Small, E.E., Livneh, B., 2018. Controls on surface soil drying rates observed by SMAP and simulated by the Noah land surface model. Hydrol. Earth Syst. Sci. 22, 1649–1663. https://doi.org/10.5194/hess-22-1649-2018

Sher, A.A., Goldberg, D.E., Novoplansky, A., 2004. The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. Oecologia 141, 353–362. https://doi.org/10.1007/s00442-003-1435-9

Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: Results from a model. Plant, Cell Environ. 21, 347–359. https://doi.org/10.1046/j.1365-3040.1998.00287.x

Sperry, J.S., Wang, Y., Wolfe, B.T., Mackay, D.S., Anderegg, W.R.L., McDowell, N.G., Pockman, W.T., 2016. Pragmatic hydraulic theory predicts stomatal responses to climatic water deficits. New Phytol. 212, 577–589. https://doi.org/10.1111/nph.14059

Tai, X., Mackay, D.S., Anderegg, W.R.L., Sperry, J.S., Brooks, P.D., 2017. Plant hydraulics improves and topography mediates prediction of aspen mortality in southwestern USA. New Phytol. 213, 113–127. https://doi.org/10.1111/nph.14098

Tian, F., Wigneron, J.-P., Ciais, P., Chave, J., Ogée, J., Peñuelas, J., Ræbild, A., Domec, J.-C., Tong, X., Brandt, M., Mialon, A., Rodriguez-Fernandez, N., Tagesson, T., Al-Yaari, A., Kerr, Y., Chen, C., Myneni, R.B., Zhang, W., Ardö, J., Fensholt, R., 2018. Coupling of ecosystem-scale plant water storage and leaf phenology observed by satellite. Nat. Ecol. Evol. 2. https://doi.org/10.1038/s41559-018-0630-3

Trenberth, K.E., 2011. Changes in precipitation with climate change. Clim. Res. 47, 123–138. https://doi.org/10.3354/cr00953

Trifilò, P., Raimondo, F., Nardini, A., Lo Gullo, M.A., Salleo, S., 2004. Drought resistance of Ailanthus altissima: Root

hydraulics and water relations. Tree Physiol. 24, 107–114. https://doi.org/10.1093/treephys/24.1.107

Trigo, I.F., Dacamara, C.C., Viterbo, P., Roujean, J., Olesen, F., Barroso, C., Camacho-de-coca, F., Freitas, S.C., García-haro, J., Geiger, B., Ghilain, N., Meliá, J., Pessanha, L., Arboleda, A., 2011. The Satellite Application Facility for Land Surface Analysis. Int. J. Remote Sens. 1161. https://doi.org/10.1080/01431161003743199

Venturas, M.D., Sperry, J.S., Hacke, U.G., 2017. Plant xylem hydraulics : What we understand, current research, and future challenges. J. Integr. Plant Biol. 59, 356–389. https://doi.org/10.1111/jipb.12534

Ward, E.J., Bell, D.M., Clark, J.S., Oren, R., 2013. Hydraulic time constants for transpiration of loblolly pine at a free-air carbon dioxide enrichment site. Tree Physiol. 33, 123–134. https://doi.org/10.1093/treephys/tps114

West, A.G., Hultine, K.R., Jackson, T.L., Ehleringer, J.R., 2007. Differential summer water use by Pinus edulis and Juniperus osteosperma reflects contrasting hydraulic characteristics. Tree Physiol. 27, 1711–1720. https://doi.org/10.1093/treephys/27.12.1711

Wigneron, J.P., Jackson, T.J., O'Neill, P., De Lannoy, G., de Rosnay, P., Walker, J.P., Ferrazzoli, P., Mironov, V., Bircher, S., Grant, J.P., Kurum, M., Schwank, M., Munoz-Sabater, J., Das, N., Royer, A., Al-Yaari, A., Al Bitar, A., Fernandez-Moran, R., Lawrence, H., Mialon, A., Parrens, M., Richaume, P., Delwart, S., Kerr, Y., 2017. Modelling the passive microwave signature from land surfaces: A review of recent results and application to the L-band SMOS & SMAP soil moisture retrieval algorithms. Remote Sens. Environ. 192, 238–262. https://doi.org/10.1016/j.rse.2017.01.024

Xu, X., Medvigy, D., Powers, J.S., Becknell, J.M., Guan, K., 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. New Phytol. 212, 80–95. https://doi.org/10.1111/nph.14009

Zhang, Y., Zhou, S., Gentine, P., Xiao, X., 2019. Can vegetation optical depth reflect changes in leaf water potential during soil moisture dry-down events? Remote Sens. Environ. 234, 111451.

Zwieback, S., Bosch, D.D., Cosh, M.H., Starks, P.J., Berg, A., 2019. Vegetation–soil moisture coupling metrics from dual-polarization microwave radiometry using regularization. Remote Sens. Environ. 231. https://doi.org/10.1016/j.rse.2019.111257