



Carbon Fixation Pathways Drive Grassland Responses to Soil Moisture and Atmospheric Dryness

M. Reza Alizadeh^{1*}, Daniel Short Gianotti¹, Jan Adamowski², Alexandra G. Konings³, Dara Entekhabi¹

¹ Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA, United States.

² Department of Bioresource Engineering, McGill University, Quebec, Canada.

³ Department of Earth System Science, Stanford University, Stanford, CA, United States.

Correspondence to: M. Reza Alizadeh (alizade@mit.edu)

Abstract. Ecosystem water and carbon dynamics are controlled by the forcing-response characteristics of the vegetation-soil-atmosphere continuum. Soil moisture and atmospheric water demand are well established to regulate plant water uptake and carbon assimilation, but the specific causal mechanisms and magnitudes by which plants respond to either or both of these forcings, particularly during periods of soil moisture drydown between precipitation pulses, are less understood. We investigate the causal linkages in this continuum, focusing on the impact of vegetation water-use strategies on different causal regimes of land-atmosphere feedback during drydowns using observations of soil moisture, vapor pressure deficit, and vegetation water content across the Continental US. We identify two prevalent regimes in grasslands: (1) a soil-water limited regime where vegetation water content follows soil moisture closely, increasing atmospheric demand via transpiration and responding to aridity (65.8% of grasslands), and (2) a regime in which grasses retain water content under drying conditions, driven by adaptive traits related to the C4 photosynthetic carbon fixation pathway and high water-use efficiency (33.1% of grasslands). We demonstrate that the biological distinction between C3 and C4 photosynthetic pathways fundamentally alters causal feedbacks in the plant-soil-atmosphere system, governing grassland vulnerability to drought and modulating ecosystem resilience in a warming climate.

Keywords: Grassland, C3/C4 photosynthesis, Causal inference, Ecohydrology, Land-atmosphere feedbacks, Drought

1 Introduction

Soil water availability and atmospheric dryness both drive the flow of water through the plant-soil-atmosphere continuum (Jasechko et al., 2013; Silva and Lambers, 2021). Specifically, soil moisture (SM) and vapor pressure deficit (VPD) are critical physical variables that modulate plant physiological processes, thereby affecting carbon assimilation (Konings et al., 2017; Denissen et al., 2022; Li et al., 2025). These forcings are critical for accurate assessments of climate and hydrological variability on terrestrial carbon cycles (Liu et al., 2020; Xu et al., 2023). Plants can physiologically and structurally adapt their water uptake and carbon fixation to changing soil moisture and VPD through varied root behaviors, xylem hydraulics, stomatal actions and evolution of different types of photosynthesis pathways (C3/C4/CAM) (Martínez-Vilalta et al., 2014;



Fu et al., 2022b; Cai et al., 2024). C_3 plants fix CO_2 directly through Rubisco, whereas C_4 grasses use an additional pathway involving phosphoenolpyruvate carboxylase to concentrate CO_2 around Rubisco in bundle sheath cells. This CO_2 -concentrating mechanism suppresses photorespiration and allows C_4 grasses to achieve a given rate of carbon assimilation at lower stomatal conductance than C_3 grasses under warm, high-light conditions (Osborne and Sack, 2012; Taylor et al., 2012). Under comparable environmental conditions, C_4 grasses therefore generally assimilate more carbon per unit water transpired, giving them higher leaf-level water-use efficiency (Morison and Gifford, 1983; Way et al., 2014)

Ecosystem water uptake and carbon assimilation respond to pulses of resource availability. Water availability is intermittent and steadily decreasing during interstorm drydowns (defined here as periods of progressive soil moisture depletion following precipitation events (Feldman et al., 2024a, b)). Drydown periods of soil moisture offer natural stress tests for models of plant-soil-atmosphere interactions. During these periods the interactions between soil moisture, vegetation and atmospheric conditions are intensified (Silva and Lambers, 2021).

During drydowns, atmospheric dryness as represented by VPD steadily increases due to the coupling between the surface water and energy balance coupling with the overlying atmospheric boundary layer (Zhou et al., 2019). Vegetation physiology also responds to VPD (McAdam and Brodribb, 2015; Fu et al., 2022b). With both soil moisture and VPD changing during drydowns, it is not clear which dominates in regulating physiological response and regulation of carbon assimilation.

Previous work has shown that atmospheric demand can constrain surface conductance and evapotranspiration more strongly than soil moisture in several biomes (Novick et al., 2016), whereas satellite-based analyses identified soil moisture as the dominant driver of dryness stress on ecosystem production across much of the vegetated land surface (Liu et al., 2020). Flux-tower analyses have also shown that VPD reduces photosynthesis across a broad range of soil moisture conditions, while soil moisture limitation becomes more important as soils dry (Fu et al., 2022b). Recent work has tried to disentangle these effects by showing that soil moisture is the main driver of gross primary productivity (GPP) in water-limited regions, while VPD influence is greater in energy-limited systems (Liu et al., 2025). However, the role of the underlying ecophysiological mechanisms shaping the causal feedbacks between soil water, plant hydraulic status and atmospheric demand during interstorm drydowns is less clear.

Our study contributes to this knowledge by applying a data-driven causal discovery model to direct satellite observations of soil moisture and vegetation water content. We shift the focus from who is the dominant driver to how different plant functional strategies, particularly C_3 and C_4 photosynthetic pathways in grasslands, create fundamentally different causal regimes during critical inter-storm dry-down periods. Instead of attributing relative importance of drivers on photosynthesis as previously done (e.g., Konings et al., 2017; Liu et al., 2020; Liu et al., 2021; Liu et al., 2025).

We use data from the NASA Soil Moisture Active Passive (SMAP) satellite remote sensing mission, which provides estimates of surface soil moisture (SM) and vegetation optical depth (VOD – linearly related to above-ground vegetation water storage) (Jackson and Schmugge, 1991). These datasets are integrated with vapor pressure deficit (VPD) observations from gridded climate data for the Continental United States (CONUS) to examine causal relationships in plant-soil-



65 atmosphere water dynamics during drydowns in the warm season (June to August). This combination provides a unique
observational perspective on hydrological exchanges, allowing for the testing of causal pathways in the soil-vegetation-
atmosphere continuum. We employ a time series causality model to explore causal effects and interactions in this continuum.
Our analysis addresses two key questions: 1) What are the dominant causal regimes in soil-vegetation-atmosphere
interactions and how do these differ across climates and biomes? 2) How do plant traits (hydraulic and photosynthetic
70 strategies) control different SM-VPD-VOD dynamics, and how do those dynamics translate to differences in landscape
water, energy and carbon coupling? We work on grasslands, as these globally important ecosystems store up to a third of
terrestrial soil carbon, and are highly sensitive to hydrological variability, and thus are key to shaping land-atmosphere
feedbacks and the future trajectory of the global carbon cycle.

2 Materials and Methods

75 2.1 Datasets

We use L-band radiometry data obtained from the Soil Moisture Active Passive (SMAP) satellite gridded at a spatial posting
of 9 km and with a temporal revisit of 1-3 days (Entekhabi et al., 2010; O'Neill et al., 2020). Both SM and VOD are inferred
from the measurements. Vegetation Optical Depth (VOD) data are used as a proxy for vegetation water content, defined here
as the column-integrated canopy water mass sensed by passive microwave observations, including water in above-ground
80 vegetation tissues and related to canopy structure such as LAI (Jackson and Schmugge, 1991). VOD has been shown to be
highly effective for monitoring large-scale vegetation hydraulic status and its response to drought (Konings et al., 2021),
making it ideal for our analysis of drydown dynamics (Moesinger et al., 2020). VOD retrievals are derived from SMAP data
employing the multi-temporal dual channel algorithm (Feldman et al., 2021). Although passive-microwave soil-moisture
retrieval is known to degrade under dense forest vegetation, the L-band SMAP retrieval is well-constrained at low soil
85 moisture (the dielectric contrast between dry and wet soil is large and well-characterised), and SMAP shows good validation
performance over herbaceous land cover (Colliander et al., 2021). The MTDC dual-channel algorithm (Feldman et al.,
2021) retrieves SM and VOD jointly, mitigating vegetation-driven biases. Grasslands occupy the low-to-moderate VOD
range, well below the high-vegetation regime where retrievals are most uncertain.

Additionally, VPD data from the gridMET dataset (Abatzoglou, 2013) are incorporated as indicators of climate-driven
90 behavior. The gridMET dataset blends the high-resolution spatial information from PRISM with the high-frequency
temporal attributes of the NLDAS-2 reanalysis via climatically aided interpolation, and provides a continuous, 4 km daily
surface-meteorological record for the contiguous United States from 1979 to the present. Gridded daily Leaf Area Index
(LAI) data were obtained from the NOAA Climate Data Record (CDR) of Visible Infrared Imaging Radiometer Suite
(VIIRS) LAI and Fraction of Absorbed Photosynthetically Active Radiation (FAPAR), Version 1 (Claverie et al., 2023). The
95 product is provided on a $0.05^\circ \times 0.05^\circ$ grid. To ensure uniformity across the different datasets, all data were transformed and
regridged to match the 9 km SMAP Equal-Area Scalable Earth Grid, version 2.0 (EASE-Grid 2.0), over the period of SMAP



data availability. VIIRS LAI was regridded from its 0.05° product grid to the 9 km SMAP grid using area-weighted averaging. Nine-kilometre cells with fewer than 30 valid daily LAI observations during the June–August warm season were masked. Our investigation focuses on the warm season, which is June until August. The strongest connections between SM, VPD, and VOD are studied during this time since vegetative activity is at its highest during the peak growth season. The interannual mean is calculated by averaging soil moisture across all years of the SMAP record. Soil moisture anomalies are then calculated by subtracting this mean from the corresponding daily soil moisture values.

We used the global C4 vegetation classification data from Luo et al. (2024) to analyze how C3/C4 plants respond to environmental stressors of soil moisture and VPD changes during drydowns. They generate the C4 dataset by combining multiple data sources with a photosynthetic optimality model to estimate the global extent of C4 vegetation, natural C4 grasses and C4 crops. For natural grasses, their model mimics the ratio of the C4/C3 net-assimilation-rate under the key environmental drivers—ambient including CO₂ concentration, growing-season air temperature, photosynthetically active radiation, aridity (e.g., VPD), and soil nitrogen availability.

We use the global ecosystem-scale plant hydraulic trait dataset developed by Liu et al. (2021), which provides spatially explicit estimates of key hydraulic parameters including the stomatal sensitivity parameter (g_1). This dataset is produced using a model–data fusion approach that integrates a plant hydraulic model with observations of vegetation optical depth (VOD), surface soil moisture and evapotranspiration from satellite measurements to retrieve ecosystem-scale hydraulic traits across different biomes.

Grassland areas were masked using the 2021 National Land Cover Database (NLCD) (Dewitz, 2023), which provides consistent land-cover classifications at a 30 m resolution across the contiguous U.S. with an overall accuracy of Level I of ~91%. The NLCD 2021 includes an updated, high-confidence delineation of herbaceous (grassland/Herbaceous) classes.

To assess the potential influence of C4 crops (e.g., corn and sorghum) within the SMAP 9 km pixels, we used the USDA Cropland Data Layer (CDL; USDA NASS, 2015–2021), aggregated from its 30 m native resolution to fractional cover on the SMAP 9 km grid. For each 9 km pixel, we computed the fractional cover of grassland/pasture (CDL class 176), total cropland (CDL cultivated band), C4 crops (corn and sorghum), and C3 crops (soybean and winter/spring/durum wheat). We also defined a high-purity grassland subset by retaining only pixels that met all three criteria: $\geq 70\%$ grassland/pasture cover, $\leq 20\%$ total cropland cover, and $< 5\%$ C4-crop cover. This subset of pixels was used to re-test the association between the coupling regimes and C4 grass cover to assess whether the association persisted when cropland cover, particularly that of C4 crops, was limited.

In addition, to quantify irrigated area fractions within each coupling regime, we used the LANID Landsat-based irrigation maps (Xie et al., 2021), aggregated from 30 m to the SMAP 9 km grid by calculating the proportion of each 9 km pixel classified as irrigated. Pixels with $\leq 10\%$ LANID irrigated cover were considered predominantly rainfed. This filter was applied in combination with the high-purity grassland filter above.



2.2 Soil Moisture Drydown Detection

130 We define soil moisture drydowns as periods where at least four consecutive overpasses exhibit decreasing soil moisture measurements. We selected four consecutive overpasses as a compromise between avoiding short-term fluctuations in soil moisture that could be driven by noise, and not being biased toward only evaluating the transitions to dry seasons. To fill gaps in soil moisture data during drydown periods, we employ a method based on calculating the first-order autoregressive (AR(1)) coefficient, ρ_1 , for time series data with missing values (Short Gianotti et al., 2019). AR(1) infilling (Short Gianotti et al., 2019) is applied only within previously identified drydown segments, i.e., sequences of successively declining observed SMAP retrievals during rain-free intervals. Because the soil-moisture trajectory across any such segment is monotonically decreasing by construction and follows the well-characterised exponential recession of soil moisture below field capacity (McColl et al., 2017), the AR(1) procedure interpolates between observed declining endpoints along a physically constrained path. We therefore do not expect it to affect our results. Because interpolation may nevertheless smooth the retrieved microwave series. We also reproduced all core results using observed retrievals only, with every infilled sample excluded from the causal estimation (Sects. 2.5 and 3.6; Table S4).

2.3 Phase Space Reconstruction and Diagrams

The three states in the soil-vegetation-atmosphere continuum (SM, VOD, VPD) used in this study co-vary. In order to visualize their covariation and especially shifts in their linkages dependent on the states themselves, we transform the three time series into a phase space by eliminating time among them.

The diagrams of SM–VOD–VPD phase space are created by dividing the soil moisture and VPD ranges into 20 uniformly spaced intervals along each axis, forming the phase-space blocks. For consistent comparison across soil moisture drydowns, VOD, VPD and LAI are linearly interpolated as functions of soil moisture onto a common soil moisture grid with a spacing of $0.01 \text{ m}^3 \text{ m}^{-3}$. This allows drydowns with different soil moisture sampling points to be combined at the same soil moisture values when constructing the median trajectories. Similarly, VOD, VPD and LAI values are interpolated to align with these soil moisture increments at the same precision. We identified all soil moisture drydown The fill color denotes the median rate of change in VOD ($d\text{VOD}/dt$) or the median rate of change in LAI ($d\text{LAI}/dt$) for drydowns originating in each respective block. See Feldman et al. (2018) for further explanation and examples of phase diagrams and interpretation.

2.4 Causality Model

155 Pairwise Pearson correlations or mutual information assessed at zero lag are usually the first step in multivariate environmental time-series analysis (Camps-Valls et al., 2023). However, such measures cannot infer directionality as there is no inherent flow of information in a direction. Association measures including lagged dependencies and non-linear relationships (e.g., multivariate Granger causality) still do not recover contemporaneous causal links and are prone to spurious associations driven by latent confounders (von Storch and Zwiers, 2002; Richiardi et al., 2013). A synthetic



comparison shown in Fig. 1 demonstrates this and motivates alternative statistical approaches. The ground-truth time-series graph is generated by the reference structural causal model (SCM) (Fig. 1a). Lagged correlation does not recover any causal direction and injects spurious associations (Fig. 1b). Multivariate Granger causality recovers some lagged links, but does not recover the contemporaneous structure, and injects a spurious link from X_1 to Z (Fig. 1c). Conversely, momentary conditional independence (MCI) recovers both the lagged and contemporaneous causal structure and orients edges within the Markov equivalence class (Fig. 1d). In this study, we apply the Peter and Clark Momentary Conditional Independence (PCMCI) approach to identify the directional pathways and interaction strengths between SM, VOD and VPD during drydowns, controlling for confounding between the three water-state variables and (in sensitivity tests) other meteorological/energy-balance drivers.

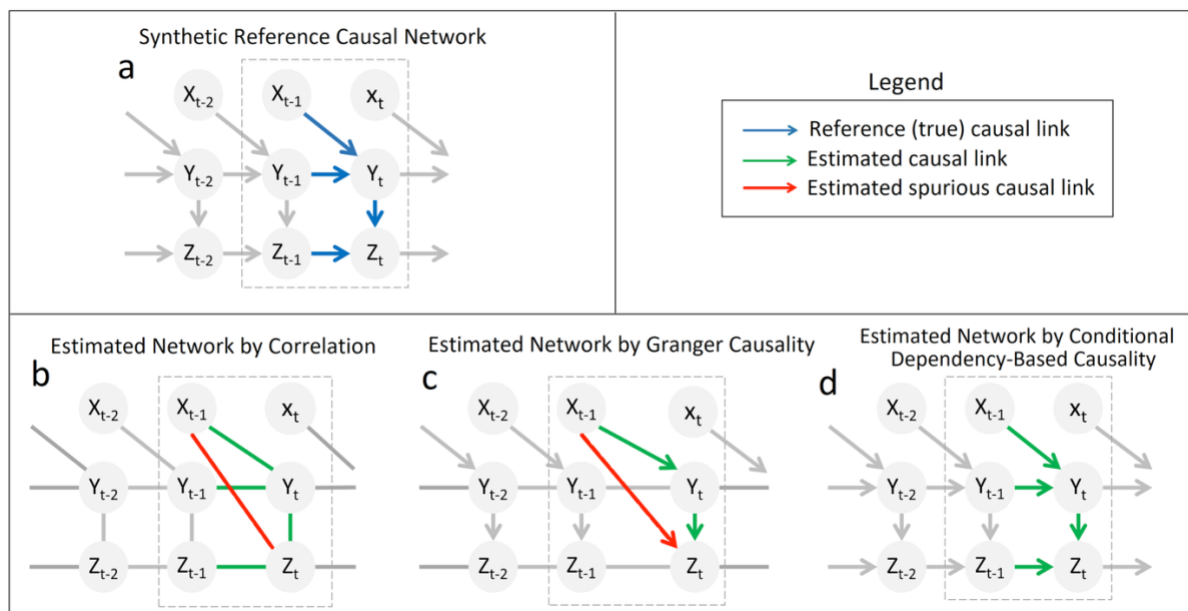


Figure 1: Comparison of causal structures and correlation on synthetic environmental time series. (a) The ground-truth time-series graph (actual temporal and causal relations between variables X , Y and Z over multiple time steps). (b) Recovered graph by lagged correlation, Dashed gray lines are spurious correlations (c) The directed graph from multivariate Granger causality. This graph captures some lagged links but ignores contemporaneous (instantaneous) connections and generates a spurious link from X to Z . (d) PCMCI recovers both lagged and contemporaneous causal links and orients edges within the Markov equivalence class, thus providing a more accurate representation of the underlying causal structure.

We use the PCMCI causality model (Runge et al., 2019a, b) to examine the causal relationships among environmental variables in our study. This model first identifies causal links between each variable by controlling for confounding effects from other drivers through the PCMCI method (Spirtes et al., 2001; Runge et al., 2019a). Within the PCMCI framework (Runge et al., 2019b), we use a conditional mutual information (CMI) approach to detect non-linear directional dependencies among environmental variables. CMI, grounded in information theory, is the broadest measure of dependency as it directly estimates the joint density without assuming a specific parametric form. This test relies on an estimator (Frenzel and Pompe,



2007) combined with a shuffle test, which constructs the distribution under the null hypothesis of independence (Runge et al., 2019a, b). CMI is defined by:

$$I(X; Y|Z) = \int p(z) \iint p(x, y|z) \log \frac{p(x, y|z)}{p(x|z)p(y|z)} dx dy dz \quad (1)$$

185 A uniform set of parameters and preprocessing choices was used for the application of PCMRI throughout the analysis. Testing for conditional independence was done using the Conditional Mutual Information (CMI) test. We used a maximum lag of $\tau_{\max} = 3$ overpasses, computed α_{pc} automatically, and applied a link-significance threshold of $\alpha = 0.05$. We then used the pixel-level PCMRI results to group pixels into coupling regimes with distinct patterns of significant relationships among SM, VOD and VPD during drydowns. These regimes distinguish different patterns of vegetation water content
 190 response to soil moisture and atmospheric demand.

2.5 Additional Analyses and Robustness Tests

To assess whether the inferred SM-VOD-VPD coupling regimes are artefacts of cropland mixing, irrigation, omitted meteorological drivers, uncorrected multiple testing, or the drydown definition, we compiled four auxiliary datasets and repeated the causal regime analysis under each.

195 To test whether our SM-VOD-VPD coupling regimes are sensitive to omitted meteorological drivers that might also affect land-atmosphere fluxes, we re-ran PCMRI with three candidate covariates: a 30-day Antecedent Precipitation Index (API; exponentially weighted gridMET daily precipitation, decay timescale $\tau = 30$ d) representing precipitation memory and deeper soil-moisture storage; Growing Degree Days (GDD; base 5 °C) computed from daily gridMET maximum and minimum air temperature, representing thermal forcing of vegetation activity; and incoming shortwave radiation (Srad,
 200 gridMET) representing radiative-energy supply. All three were aggregated to the SMAP 9 km EASE-2 grid and standardised to monthly z-scores.

To test whether our results contained inflated false positives under pixel-wise hypothesis testing, per-pixel link significance was additionally re-evaluated under a Benjamini-Hochberg (Benjamini and Hochberg, 1995) False Discovery Rate correction ($q = 0.05$) applied across all grassland pixels for each tested edge, and the coupling-regime map was reconstructed
 205 using the corrected significance flags. Also, to verify that the inferred regimes are not sensitive to the choice of drydown definition, we repeated the entire pipeline with the minimum-drydown-length criterion relaxed and tightened to 3 and 5 consecutive declining overpasses. Results of all robustness checks are reported in Sect. 3.6 and Supplementary Materials.

To analyze whether the coupling regimes depend on the inclusion of dates with limited canopy development, we used the VIIRS LAI record to define a pixel-specific climatological growing season within the warm-season analysis window (June–
 210 August). For this sensitivity test, growing-season dates were defined as those on which climatological LAI exceeded the midpoint between that pixel's minimum and maximum climatological LAI during June–August. The PCMRI analysis for each coupling regime was then restricted to dates on which at least 30% of pixels in that regime were within their



climatological growing season. The analysis was repeated using a 50% threshold, and a fixed peak-canopy window (1 July–15 August) was tested separately. Because each restriction shortens the record and can reduce the statistical power of conditional independence tests (Runge et al., 2019b), every restricted estimate was compared against estimates obtained from contiguous random windows matched in length and usable-sample count. Each restricted estimate is reported as a z score relative to that control distribution to assess whether the estimated coupling strength differs from that obtained from equally short records.

3 Results

3.1 Non-Linear Grassland Responses to Environmental Drying During Interstorms

Prior to the introduction of our causal analyses, we first stress the non-linearity of interactions between vegetation water content and the soil and atmospheric forcings. We specifically examine the large-scale response of vegetation to short-term variations in surface soil moisture and VPD. Figure 2 shows a phase-space plot illustrating the interactions between plant, soil and atmospheric variables during drydown periods in grasslands (see Sect. 2.3). The diagram illustrates time progression from right to left as soils dry following rain events.

The phase space analysis of SM–VOD–VPD reveals interesting covariations between these three variables during soil moisture drydowns (Fig. 2). Along the observed drydown trajectories, soil moisture declines monotonically with time (moving from right to left), while the direction and magnitude of VPD changes vary with the initial conditions. Drydowns beginning at lower VPD generally have steeper trajectories toward higher VPD, indicating a larger increase in VPD per unit decrease in soil moisture.

In Fig. 2, blue symbols ($dVOD/dt > 0$) represent vegetation water content increasing while soil moisture is decreasing, while red symbols represent the opposite ($dVOD/dt < 0$). Along the drydown trajectories, grasses tend to increase their water content (positive $dVOD/dt$) when soil moisture is available and then de-hydrate when soil moisture falls below a particular critical threshold (local maxima in the Fig. 2 curves, generally $\approx 0.05 - 0.15 \text{ m}^3/\text{m}^3$ volumetric soil moisture depending on the pixel). Plant water uptake behavior changes significantly when soil moisture levels fall below this threshold value. The rate of VOD loss becomes higher (darker red symbols) when initial VPD is high, and soil moisture is low. Plant stomata respond to high VPD by closing, reducing water loss and the risk of hydraulic failure. Concurrently, photosynthetic rates are generally down-regulated as internal leaf CO_2 concentrations drop. This covariation is a consequence of the inherent complexity and non-linear responses in the coupling of land and atmosphere; conventional bivariate, time-invariant models cannot capture these interdependencies (Budyko, 1963, 1974; Dirmeyer et al., 2021). While the phase plot (Fig. 2) captures the covariations among SM, VPD and VOD, it does not reveal which variable drives the others. The observed increases and decreases in vegetation water content during interstorm drydowns motivate us to characterize the causal relationships among vegetation water content, soil moisture and atmospheric aridity.

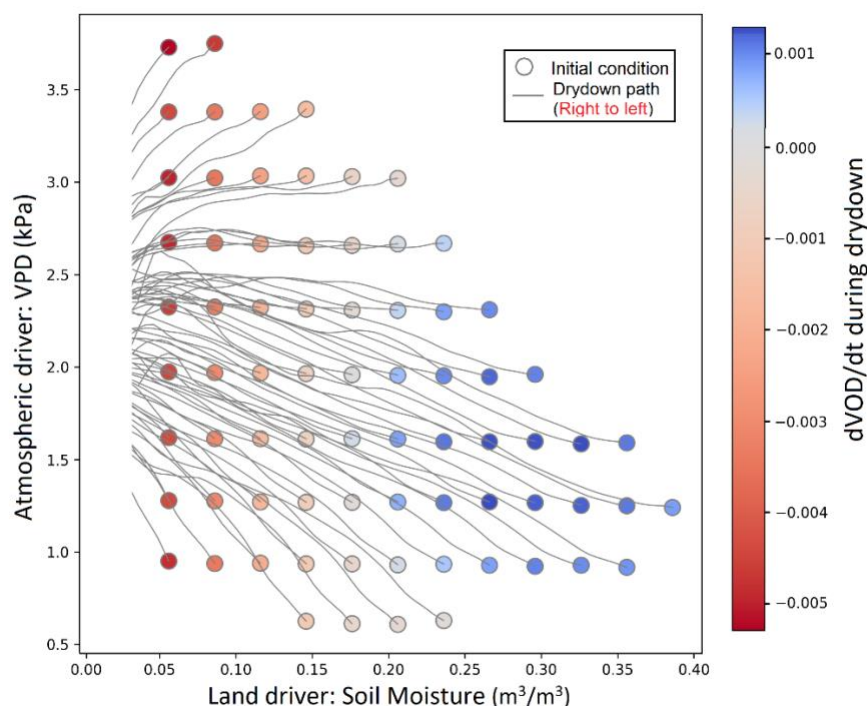


Figure 2: Phase-space dry-down dynamics of coupled soil–plant–atmosphere interactions in CONUS grasslands. Each curve traces in time from high to low soil moisture (right to left) and represents the median path of all drydowns starting from that initial condition (symbol) in the phase plot. The symbol fill colour is the median change of vegetation water content during drydowns ($dVOD/dt$) for the corresponding curve starting at that point in SM-VPD space. Vegetation water content (VOD) first increases as soils dry and then decreases as soils dry further.

3.2 Dominant Causal Regimes of Grasslands Response to Soil Moisture and Atmospheric Demand

We investigate the causal pathways between SM, VPD and VOD anomalies using the PCMCi causal model (see Methods). We identify four different coupling regimes (labelled, B, C, and D) with different causal structures between these variables (Fig. 3). These regimes show the different ways vegetation, especially grasslands, response to changes in soil moisture and atmospheric conditions.

The most extensive regime, Regime A, constitutes 65.8% of the grasslands area and is characterized by positive SM-VOD and negative VPD-VOD causal links. Such patterns indicate a high responsiveness of vegetation in these regions to supply and demand of soil moisture for atmospheric moisture. The positive SM-VOD link indicates that vegetation water content (VOD) decreases with decreasing soil moisture, implying a direct dependence of VOD on surface water availability. At the same time, the negative VPD-VOD relationship shows that as atmospheric demand (VPD) increases, vegetation loses water more quickly (presumably due to transpiration increases), which in turn reduces VOD. This regime identifies regions where vegetation is especially sensitive and vulnerable to drought stress due to coupled rapid declines in vegetation water content due to falling soil moisture and increasing VPD.



Regime B, which accounts for 33.1% of the grasslands in CONUS and is primarily distributed in the Great Plains, exhibits an opposite plant-water response with a negative SM-VOD and positive VPD-VOD causal link. Here, vegetation gains water content under decreasing soil moisture, possibly reflecting differences in growth and physiological responses to declining soil moisture and increasing atmospheric demand (D'Odorico et al., 2007; Anderegg et al., 2019).

The positive VPD-VOD relationship suggests that vegetation in these regions is resilient to atmospheric demand, which may be related to the presence of drought-tolerant species that can maintain water content and photosynthetic activity under higher VPD (Massmann et al., 2019; Zhang et al., 2019). These positive VPD-VOD and negative SM-VOD links are sustained at a one-day lag, emphasizing the persistent, lagged coupling of water-vegetation feedbacks in this regime (Fig. S1). Regime B therefore identifies ecosystems in which vegetation water content is less tightly aligned with short-term variations in surface soil moisture, enhancing resilience to extended dry periods (Fu et al., 2022a). Regime C covers only 1.1% of the CONUS area and Regime D covers only 0.01%. Given the minor spatial extent of Regimes C and D, our primary focus below will be on the dominant Regimes A and B.

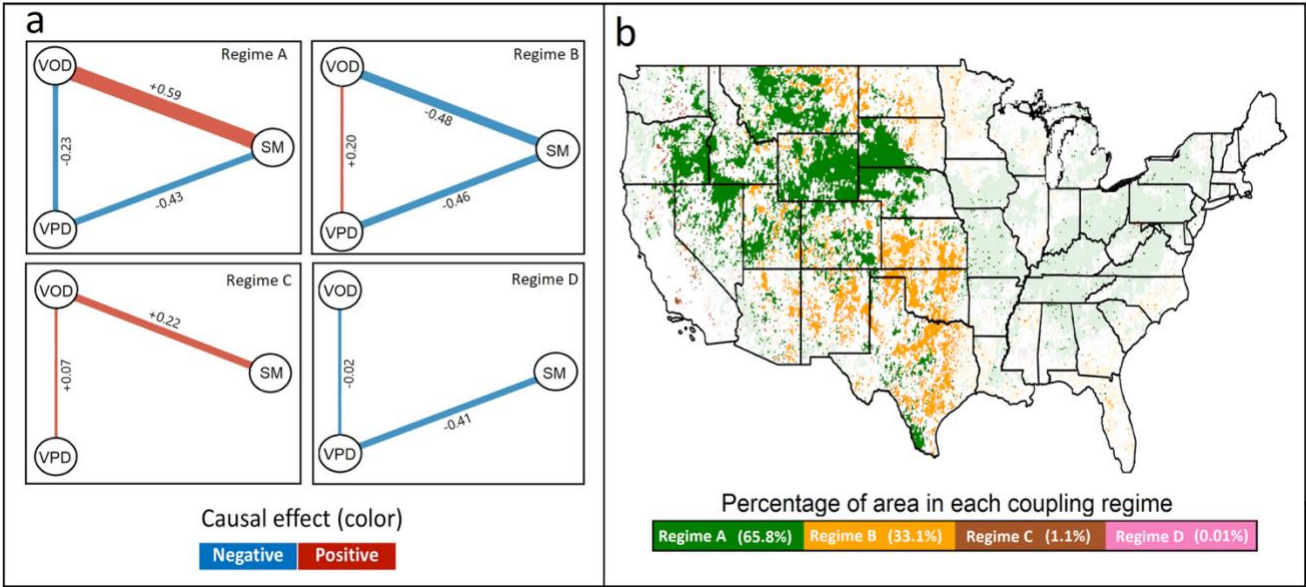


Figure 3: Spatial distribution and causal structures of dominant vegetation-soil-atmosphere causal regimes across the grasslands. Four distinct causal regimes among soil moisture (SM), vegetation optical depth (VOD), and vapor pressure deficit (VPD) across the CONUS are represented with their respective percentages shown in the legend. (a) displays the directed acyclic graphs (DAGs) illustrating the causal structure of each regime, with arrow colors indicating the type of causal effect (positive in red, negative in blue), and arrow width representing the causal strength. Numbers on the causal links indicate the causal strength of the link at concurrent lag time ($t=0$). (b) shows the spatial distribution of each regime, with non-significant causal strengths masked in white. The causal regimes in non-grassland areas across the CONUS are depicted with reduced opacity.

3.3 Contrasting Plant-Soil-Atmosphere Causal Dynamics Reveal Distinct Adaptive Strategies in Grasslands

We further investigate the strength of the causal dynamics for the two dominant regimes (A and B) in grassland areas and highlight the different physical processes that drive the vegetation responses to soil and atmospheric conditions (Fig. 4).

Regime A shows overall a more intense causal VOD-soil moisture and VPD relationship, indicating a higher sensitivity of vegetation to the immediate environmental conditions. Conversely, Regime B shows stronger evidence for SM-VPD linkages, where adaptive water-use strategies may improve resilience to variability in soil moisture and atmospheric conditions (Osborne and Sack, 2012; Leakey et al., 2019). Regime B is mainly present in the rainfed grasslands of the central Great Plains in transitional hydroclimate zones that are prone to oscillation between water-limited and energy-limited regimes, but it is not confined solely to these areas. By contrast, Regime A encompasses both water- and energy-limited environments, thus illustrating different ecological patterns beyond simple climatic boundaries.

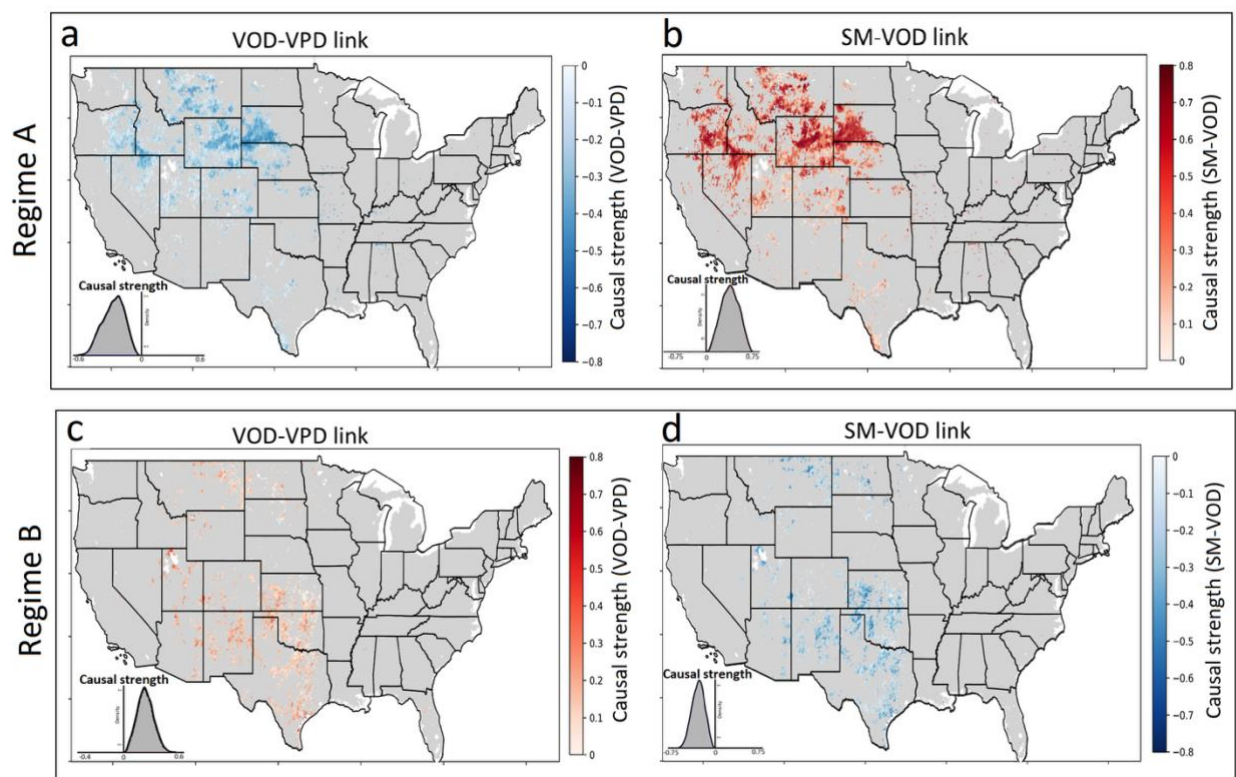


Figure 4: Spatial patterns of causal-link strength between SM, VOD, and VPD in the two dominant grassland regimes across CONUS. Maps show the causal strength for the diagnostic links defining Regime A and Regime B. Red indicates positive causal effects and blue indicates negative causal effects; color bars show causal-link strength for each panel. (a) Negative VOD–VPD link in Regime A; (b) positive SM–VOD link in Regime A; (c) positive VOD–VPD link in Regime B; and (d) negative SM–VOD link in Regime B. Non-significant causal strengths (P -value > 0.05) are shown in white. Gray pixels indicate areas outside the focal regime in each panel.

Several explanations are possible for the different patterns of co-variation of SM, VPD, and VOD observed in Regime B versus Regime A. Regime B may be associated with deeper root systems that can access moisture below the topsoil, which could help maintain vegetation water content as the surface soil dries because water stored at greater depth may remain available for longer periods. However, the prevalence of grasslands in these regions indicates that deep roots alone are unlikely to explain this widespread behavior (Nippert and Holdo, 2015; Chavez Rodriguez et al., 2024). Irrigation might in



305 principle supplement soil moisture in Regime B. However, the LANID-based irrigation analysis (Fig. S5; Table S2) shows that Regime B is overwhelmingly rainfed and is, if anything, slightly less irrigated than Regime A (mean irrigated cover of 1.9% in Regime B versus 2.3% in Regime A). These low irrigation fractions suggest that irrigation is unlikely to be the main driver of the negative SM–VOD coupling in Regime B.

To further examine whether differences in surface soil water availability could explain the Regime B response, we compared
310 the rate of surface soil moisture depletion between the two regimes. The magnitude of the surface soil moisture decline was approximately 84% greater in Regime B based on the event-mean estimate and 44% greater over the first three days of the drydown. The same contrast was retained after stratification by initial soil moisture and mean VPD (Tables S6 and S7). Surface sand fractions were also similar between the two regimes (median 42.5% in Regime A and 41.5% in Regime B), indicating that differences in surface soil texture are unlikely to explain the contrast. Despite this more rapid surface drying,
315 VOD increased during drydowns in 78% of Regime B pixels compared with only 3% of Regime A pixels. Thus, the Regime B response cannot be explained by slower depletion of the surface soil layer sensed by SMAP. This result does not exclude water uptake from deeper soil layers, which cannot be directly resolved from the surface soil moisture observations used here. The concurrent increases in VOD and LAI observed in Regime B (Figs. 2 and 6) further indicate that the Regime B signal is associated with vegetation responses during drydowns rather than slower surface drying alone.

320 The positive SM–VOD and negative VPD–VOD relationships in Regime A are consistent with vegetation water content declining as surface soil moisture decreases and atmospheric demand increases. By contrast, the negative SM–VOD and positive VPD–VOD relationships in Regime B are consistent with vegetation water content increasing under these drying conditions (Figs. 3 and 4). Differences in plant water regulation may contribute to this contrast, as plant hydraulics mediates transpiration responses to soil moisture and VPD (Liu et al., 2020).

325 **3.4 C3/C4 Photosynthetic Pathways Lead to Divergent Grassland Responses to Soil and Atmospheric Aridity**

It is known that the different photosynthetic pathways of C3 and C4 plants are involved in determining the vegetation responses to environmental stress. C4 plants are more efficient in water use under high light and temperature conditions (Ghannoum, 2009; Leakey et al., 2019). This higher efficiency is attributed to a CO₂-concentrating mechanism that reduces photorespiration and enables a lower stomatal conductance for a given rate of carbon assimilation (Way et al., 2014).
330 We therefore tested whether Regimes A and B differ in their prevalence of C3 and C4 photosynthesis. To ensure that this contrast reflects natural C4 grasses rather than C4 crops or cropland mixing within the 9 km pixels, we repeated the comparison using the CDL-derived high-purity grassland subset (Sect. 2.1). C4 crops were essentially absent in both regimes, with median C4-crop fractions of 0.0% in Regime A and 0.1% in Regime B. Within the high-purity grassland subset ($\geq 70\%$ grassland/pasture, $\leq 20\%$ cropland, and $< 5\%$ C4-crop cover), Regime B retained a significantly higher C4
335 fraction than Regime A (median 45.6% vs 30.9%; Kolmogorov–Smirnov $D = 0.51$, $p \approx 2 \times 10^{-95}$; $N = 1,706/528$). The contrast was similar when the analysis was further restricted to predominantly rainfed grassland pixels (median 45.6% vs 31.0%; $D = 0.51$, $p \approx 1 \times 10^{-94}$; $N = 1,651/524$; Fig. S6; Table S3). C4 grasses are common throughout CONUS grasslands



but are more prevalent in Regime B than in Regime A, suggesting that photosynthetic pathway may be a contributing factor to the contrasting VOD responses to soil moisture and VPD (Fig. 5a). The Kolmogorov-Smirnov test (statistic = 0.42, p-value = 1.8×10^{-13}) indicates that the two distributions are significantly different from each other, with lower C4 grass percentages in Regime A (red) and higher C4 grass percentages in Regime B (blue).

Regime B, with a greater proportion of C4 grasses, is less sensitive to both soil moisture and VPD. The prevalence of C4 grasses in these areas provides support for the hypothesis that high water-use efficiency (WUE) and reduced sensitivity to VPD enable these plants to uncouple their water status from surface drying (Morgan et al., 2004; Morgan et al., 2011; Hufkens et al., 2016). C4 plants are more adapted to the hot dry conditions that occur after long drydowns or in arid biomes and their higher WUE allows them to continue photosynthesizing in hot dry conditions (Wand et al., 1999; Taylor et al., 2012). This characteristic gives an advantage. Our finding is consistent with experimental studies where higher temperatures can alleviate desiccation stress in C4 species while increasing it in C3 species (Morgan et al., 2011). This feature coupled with possible lagged hydraulic responses could result in reduced water (VOD) loss at high VPD conditions (Osborne and Sack, 2012; Fridley et al., 2016; Knapp et al., 2020). Thus, Regime B is an ecosystem strategy where the vegetation sustains productivity by minimizing water loss and maximizing carbon assimilation during a decline in environmental water availability.

Conversely, vegetation in Regime A, dominated by C3 plants, shows strong dependence on soil moisture and vulnerability to increased atmospheric demand. The positive relationship between soil moisture and VOD means that decreases in soil moisture cause decreases in vegetation water content, which is characteristic of low drought resilience of C3 plants (Liu et al., 2020; Li et al., 2022). This increased sensitivity of grasslands to the availability of soil moisture, with a sudden shift in energy partitioning once a critical soil moisture threshold is crossed, has been documented in flux tower studies and is a key difference from more drought-resistant forest ecosystems (Fu et al., 2022a). This sensitivity is illustrated by the negative relationship between VPD and VOD, whereby greater VPD results in more water loss through transpiration, reducing VOD.

We also explore estimates of the slope parameter g_1 of the Medlyn stomatal conductance model (Medlyn et al., 2011) at the ecosystem level and examined the incorporation of climate variability in the development of these two different regimes. The g_1 parameter encapsulates fundamental differences in the marginal carbon cost of water and therefore in intrinsic water-use strategies. Lower g_1 indicates a more conservative (water-efficient) strategy, and higher g_1 corresponds to less conservative water use. Grasslands in Regime B exhibit more conservative stomatal behavior associated with greater C4 dominance, as evidenced by a tighter distribution of lower g_1 values suggesting greater closure under evaporative demand (Fig.5b). Regime A had a broader, right-shifted g_1 range, indicative of more relaxed stomatal control. This difference is significant ($K-S = 0.217$, $p \approx 5.4 \times 10^{-14}$) and supports the idea that Regime B grasses have a stronger stomatal control at similar atmospheric demand. Conversely, the two regimes show almost complete overlapping Aridity Index distributions ($K-S = 0.04$, $p = 0.28$), both with a peak at low values, indicating semi-arid conditions for both regimes (Fig.5c). This suggests that a local mean hydroclimate is not driving these functional causal differences.



Plant functional traits strongly influence ecosystem responses to soil moisture deficits and high vapor pressure deficit (VPD). For instance, hydraulic diversity of embolism resistance reduces the reduction of evapotranspiration during drought (Anderegg et al., 2018; Serra-Maluquer et al., 2022). Similarly, in grasslands, a mixture of C₃ and C₄ species could buffer sensitivity to soil moisture declines through diverse hydraulic strategies (e.g., ecosystem-scale isohydricity; Konings and Gentine, 2017). C₃ plants with higher stomatal conductances (g_i) are more likely to be anisohydric — less tightly regulating their internal water status and increasing their sensitivity to environmental water states, while C₄ plants could tend to be isohydric. Our findings provide new evidence at a continental scale that C₃-dominated grasses (Regime A) are more sensitive in a causal sense to changes in soil moisture and VPD. This is contrasted to the adaptability of Regime B to these fluctuations and highlights the role of photosynthetic pathways in mediating grassland responses to aridity during soil moisture drydowns.

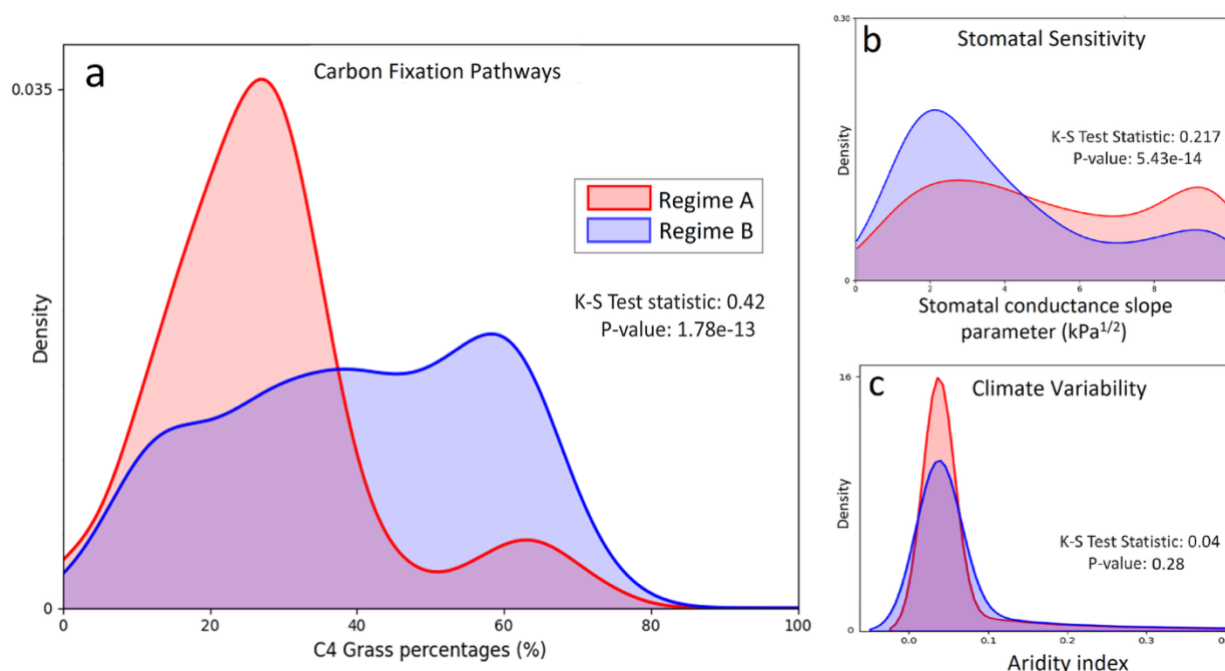


Figure 5: Probability density functions illustrating how distribution of C₄ photosynthetic pathways, leaf water-use strategy, and climate aridity differ between two causal regimes. (a) Distribution of percentage cover by C₄ grasses in Regimes A and B, (b) distribution of stomatal conductance slope parameter (g_i), and (c) distribution of the Aridity Index. Photosynthetic pathway composition—specifically the prevalence of C₄ versus C₃ grasses—underlies the divergent water-use strategies and vegetation–soil moisture coupling observed between the two regimes rather than broad climatic variability.

3.5 Contrasting Soil–Atmosphere Coupling and Growth Resilience in C₄- vs. C₃-Dominated Grasslands

We further highlight the distinct differences between Regimes A and B in their phase-space plot of plant–soil–atmosphere water relationships (Fig. 6). This phase plot includes the changes in Leaf Area Index over time ($dLAI/dt$) in order to isolate above-ground biomass growth from rehydration as parts of the $dVOD/dt$ signal.



In Regime B (Fig. 6b), where C4 grasses are more prevalent, drydown trajectories move from right to left as soils dry, and median dLAI/dt values are predominantly positive (green symbols, reaching approximately $+0.015 \text{ d}^{-1}$). Leaf area gains are evident even for drydowns beginning at lower soil moisture ($< 0.2 \text{ m}^3 \text{ m}^{-3}$) and elevated VPD ($\sim 2.5 \text{ kPa}$). These positive LAI changes are consistent with canopy growth contributing to the increases in VOD during drydowns, rather than rehydration alone (Feldman et al., 2021). In Regime A (Fig. 6a), where C3 grasses are more prevalent, dLAI/dt values are also predominantly positive, but leaf area gains are generally smaller than in Regime B. These observations should be used to evaluate whether land-surface and ecosystem models reproduce continued leaf area gains during interstorm drydowns and the differences in these responses between grassland systems (Feldman et al., 2024a).

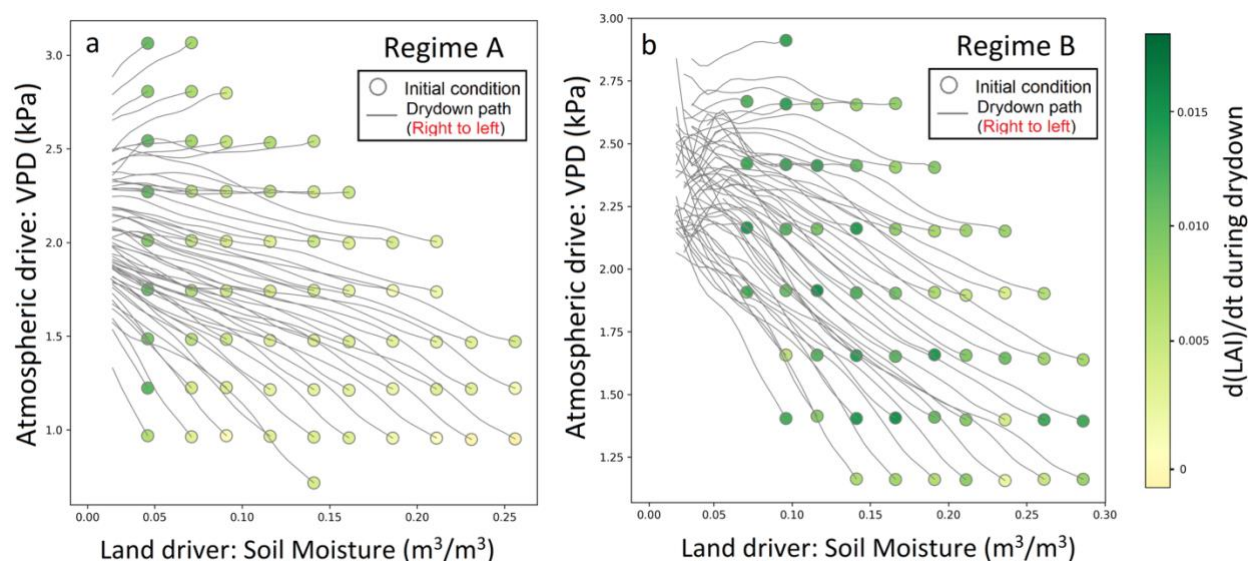


Figure 6: Phase-space drydown responses in C₃ and C₄ grasslands: C₄ water-use efficiency drives extended carbon uptake and sustains vegetation growth deep into soil moisture drydowns. Median drydown paths in volumetric soil moisture (SM) versus vapour-pressure deficit (VPD) space for: (a) Regime A (C₃-dominated grasslands); (b) Regime B (C₄-dominated grasslands), plotted from wet (right) to dry (left). Circles mark starting SM–VPD conditions, with fill color indicating the median rate of change of leaf area index (dLAI/dt)—a proxy for grass-cover growth or senescence—over each drydown. While both regimes maintain positive growth as soils dry, C₄ grasslands (Regime B) sustain higher dLAI/dt under lower soil moisture and higher VPD, reflecting their superior water-use efficiency and extended carbon uptake during drydowns.

3.6 Robustness of the Coupling Regimes and the C4 Association

We conduct several robustness analyses to rule out the main alternative explanations for Regime B. To verify that the coupling regimes are not artefacts of omitted meteorological or energy-balance drivers, we repeated the PCMCi estimation with API, GDD, and shortwave radiation (Srad) added as candidate covariates (Sect. 2.5; Figs. S2 and S3). In both Regime A and Regime B the core SM–VOD, VPD–VOD, and SM–VPD links retain their sign and change in magnitude by at most $\sim 10\%$ (typically 3–7%). Independently, the per-pixel coupling-regime map rebuilt after partialling out the influence of API, GDD, and incoming shortwave radiation (Srad) is essentially indistinguishable from the original: 98.8% of grassland pixels



classified in both maps retain their original regime label, with Regime A 65.8% → 64.0% and Regime B 33.1% → 35.1%
 415 (Fig. S4).

The robustness of the regime–C4 association to cropland mixing and irrigation is described in Sect. 3.4 and Fig. S6. The higher C4 fraction in Regime B persists after restricting the analysis to high-purity grassland and predominantly rainfed pixels.

To address concerns of inflated false positives in pixel-wise hypothesis testing, per-pixel link significance was additionally
 420 re-evaluate under a Benjamini–Hochberg False Discovery Rate correction ($q = 0.05$). Re-evaluating per-pixel link significance leaves the coupling-regime map essentially unchanged: 93.4% of grassland pixels retain their classification, every retained pixel keeps its original regime assignment (100% label agreement among co-classified pixels), and the regime area fractions shift by less than 0.5 percentage points (Fig. S7). The coupling regimes are therefore not artefacts of uncorrected multiple testing. Finally, Relaxing and tightening the drydown criterion to 3 and 5 consecutive declining
 425 overpasses yields regime area fractions that shift by less than 2.4 percentage points (Table S1) and core SM–VOD–VPD edge strengths that are preserved in sign and magnitude. The classification is therefore insensitive to the drydown definition. Because varying that criterion does not itself remove interpolated values, sensitivity to the AR(1) infilling step is assessed separately below.

We also repeated the causal estimation using observed retrievals only, excluding every sample that involved an infilled soil-
 430 moisture or VOD value (Sect. 2.5). Retaining 87.9% of the original conditioning windows, the regime-defining SM–VOD coupling keeps its sign and its dominant lag in both regimes and changes in magnitude by less than 3% (Table S4). The sign reversal that distinguishes Regime B from Regime A is therefore not generated by interpolated values. The secondary contemporaneous SM–VPD and VPD–VOD coefficients also retain their signs but change by approximately 9–12%, and are accordingly interpreted as secondary features of the network rather than as quantitatively invariant components.

435 A further possibility is that the negative SM–VOD coupling in Regime B arises from dates of limited canopy development rather than from vegetation behaviour during active growth. If this were the source of the signal, excluding dates with limited canopy development would be expected to weaken the coupling. Instead, restricting the analysis to dates on which at least 30% of pixels were within their climatological growing season, and separately applying a 50% criterion (Sect. 2.5), strengthened the Regime B coupling relative to matched random windows. The Regime B coefficient changed from $z =$
 440 -2.00 at the 30% criterion to $z = -3.89$ at the 50% criterion, while Regime A remains within its control distribution under every restriction (Table S5). Within the fixed peak-canopy window, when leaf area has largely plateaued, the Regime B coefficient remains negative but is not distinguishable from matched controls. The negative coupling is therefore most apparent during the period of active canopy development rather than being produced by dates with limited canopy development, although active growth and mid-summer climate remain partly inseparable in these observations.



445 4 Discussion and Conclusions

Our study shows how the pathways of photosynthetic carbon fixation, and in particular the differences between C3 and C4 grasses, strongly affect the coupling between soil moisture, vegetation water content and atmospheric dryness during the periods between precipitation pulses. We identified two dominant causal regimes in U.S. grasslands, each characterized by distinct vegetation responses to soil and atmospheric drying. In regime A, dominated by C3 vegetation, a positive coupling
 450 between soil moisture and VOD and a negative coupling between VPD and VOD are observed. This is the classic “environmental water as driver” framework for vegetation: as soils and atmosphere dry, plants lose water. In Regime B, vegetation exhibits resilience to desiccation that is related to the adaptive traits of C4 photosynthesis. This is the other popular view of plant-water relations, “plants as drivers of water fluxes”: vegetation takes up water as soils dry out. However, in both regimes, rather than decreasing as a result of any compensating boundary-layer cooling, VPD primarily
 455 rises as soils dry—driven by decreased evapotranspiration and increased surface heating. Such functional divergence has important implications for predicting future shifts in grassland composition. Our results suggest that warming and drying of the atmosphere could lead to large scale changes in the structure and function of ecosystems in transitional climate zones, favoring C4-dominated systems.

The energy exchanges between land and atmosphere at the soil-vegetation-atmosphere interface are highly non-linear and
 460 even small changes in the timing or intensity of water inputs (e.g., rain pulses and intervals of arid conditions) can lead to disproportionately large changes in evapotranspiration rates and surface-temperature regimes (Yang et al., 2016; Feldman et al., 2024b). These different energy flux responses directly impact ecosystem carbon uptake, as reduced latent cooling under low soil moisture conditions limits photosynthesis and changes in radiation budgets under high VPD conditions shift the balance between incoming and outgoing energy (Sellers et al., 1997; Dubbert and Werner, 2019). Ecosystems in Regimes A
 465 and B will differ in their effect on the surface energy budget and evaporative cooling of the lower atmosphere. Low soil moisture in Regime A limits evapotranspiration, resulting in an increase in sensible heat flux and surface temperatures. In contrast, Regime B shows strong stomatal control under high VPD, maintaining transpiration and latent cooling as the soil dries, buffering surface heating. Thus, small changes in the availability of water or in atmospheric demand can cause large regional differences in land carbon budgets. Our results demonstrate the significance of considering soil and atmosphere
 470 driven processes in predictions of grassland carbon dynamics in these regions.

Regime A could be characterized by stronger positive land-atmosphere feedbacks where low SM reduces evapotranspiration and enhances sensible heat flux, leading to accelerating drought intensification (Anderegg et al., 2019). Our results show Additionally, the increased VPD sensitivity in Regime A might enable the rapid onset of flash droughts through a tight coupling between soil drying and atmospheric aridity, as discussed in recent vegetation–climate interaction studies
 475 (Anderegg et al., 2019). The more resilient storage of regime B at high VPD may help to protect against such rapid drought intensification. Our results offer a possible ecophysiological mechanism based on plant hydraulic traits to explain the more general patterns reported by Liu et al. (2025), which found soil moisture, rather than VPD, is the dominant driver of



photosynthesis globally in water limited regions. Results suggest that the dominance of soil moisture observed here may be enabled by the high water-use efficiency of C4 grasses (Regime B) that can sustain their water status and function under high atmospheric demand. Therefore, our work complements their findings on GPP by showing how trait-based approaches at the landscape scale correspond to these global patterns of drought response, focusing on VOD during drydowns. Testing these implications with flux-tower observations and land-surface model experiments with photosynthetic pathway-specific hydraulic traits will be essential for understanding and predicting compound drought dynamics in grassland biomes.

Our robustness analyses rule out the main alternative explanations for Regime B. Irrigation cannot be the driver, since Regime B is overwhelmingly rainfed and is less irrigated than the water-limited Regime A. Phenological green-up is minimized by restriction to the warm season and by including Growing Degree Days as a candidate variable, and is dealt with directly using an independent optical LAI record: restricting the analysis to each pixel's climatological growing season strengthens rather than weakens the Regime B coupling relative to matched random windows (Sect. 3.6; Table S5). Although passive access to deeper soil-moisture storage is consistent with sustained vegetation water content, it is unlikely to explain alone the increase in both VOD and LAI observed in Regime B during surface drying (Figs. 2 and 6). The simplest form of this explanation predicts a slower erosion of the sensed surface layer in Regime B, but what is seen is the opposite: Surface soil moisture declines at least as fast in Regime B as in Regime A under matched initial wetness and evaporative demand, with similar soil texture between the regimes (Sect. 3.6; Tables S6 and S7). However, continued photosynthetic carbon gain is the defining advantage of the C4 water-use-efficiency pathway under surface drying. Surface recession is also related to evaporation, drainage, texture, lateral redistribution and root uptake, and rapid surface drying can coincide with deep water use. These observations therefore constrain uptake from deeper layers, shallow groundwater and laterally redistributed water. They may locally contribute within a pattern they do not seem sufficient to generate at continental scale. Using the crop-resolved USDA Cropland Data Layer to differentiate between C4 crops (corn, sorghum) and natural C4 grasses, we confirm that the higher C4 cover in Regime B is a property of natural grasses rather than irrigated agricultural pixels. The association Regime B C4 is significant and sharper on high-purity natural grassland than on the full domain. Together with the active growth of Regime B vegetation during drydowns, these results support the interpretation that Regime B is a signature of the natural c4 grassland physiology, and not a sampling artifact of cropland mixing, irrigated agriculture or passive deep water buffering.

These results emphasize the significance of plant physiological diversity in modulating land-atmosphere coupling and changes in the land carbon budget. The different responses in Regimes A and B highlight the importance of including ecophysiological diversity, particularly photosynthetic pathways, in models of soil-vegetation-atmosphere interactions. Recent global-scale analyzes have confirmed that soil moisture is the dominant driver of ecosystem productivity in water-limited regions (Liu et al., 2025). Our work, however, shows how this dominance is enacted at the landscape scale through the prevalence of drought-resilient C4 functional traits. Including these regime-dependent dynamics in Earth system models will improve understanding of the processes by which ecosystems balance water and carbon needs under changing



environmental stressors, and will inform future strategies for ecosystem management and adaptation in water-limited and transitional environments (Feng et al., 2018; Vicente-Serrano et al., 2013; Fu et al., 2022a, b).

We conclude that the biological difference between C3 and C4 photosynthetic pathways is the major factor controlling the response of grassland ecosystems to hydroclimatic stress. Expected shifts in the biogeography of these functional strategies, under increasing hydroclimatic stress, will have important implications for regional carbon cycling, surface energy balance, and ecosystem resilience (Havrilla et al., 2023; Finger Higgins et al., 2025). Accurate representation of these different trait-mediated causal regimes will improve the predictive ability of the next generation of Earth System Models to project terrestrial ecosystem dynamics under global change.

Code and data availability

All source datasets used in this study are publicly available from their original providers. The SMAP-derived 9 km surface-soil-moisture and vegetation-optical-depth data retrieved with the Multi-Temporal Dual Channel Algorithm (MT-DCA), version 5, are available from Zenodo at <https://doi.org/10.5281/zenodo.5619583>. The gridMET precipitation, maximum and minimum air temperature, vapour pressure deficit, and downward shortwave radiation data for 2015–2021 are available from the Climatology Lab at <https://www.climatologylab.org/gridmet.html>. The NOAA Climate Data Record (CDR) of Visible Infrared Imaging Radiometer Suite (VIIRS) Leaf Area Index (LAI) and Fraction of Absorbed Photosynthetically Active Radiation (FAPAR), Version 1, is available from the NOAA National Centers for Environmental Information at <https://doi.org/10.25921/9x3m-0e02> (Claverie et al., 2023). The global C4 vegetation dataset, version 2.2, is available from Zenodo at <https://doi.org/10.5281/zenodo.10516423>. The plant hydraulic trait dataset is available from Figshare at <https://doi.org/10.6084/m9.figshare.13350713.v2>. The 2021 National Land Cover Database is available from the U.S. Geological Survey at <https://doi.org/10.5066/P9JZ7AO3>. The USDA Cropland Data Layer is available at <https://doi.org/10.15482/USDA.ADC/1227096>. The Landsat-based Irrigation Dataset for the conterminous United States (LANID-US), version 3.0, is available from Zenodo at <https://doi.org/10.5281/zenodo.5548555>. The OpenLandMap sand-content data used in the Supplement are available from Zenodo at <https://doi.org/10.5281/zenodo.2525662>. The processed data underlying the figures and tables and the custom analysis scripts are not archived in a public repository and are available from the corresponding author upon reasonable request.

Supplement link

The supplement is available online.



Author contributions

M. Reza Alizadeh: conceptualization, data curation, formal analysis, methodology, software, investigation, validation, visualization, writing – original draft, writing – review and editing. Daniel Short Gianotti: investigation, writing – review and editing. Jan Adamowski: investigation, writing – review and editing. Alexandra G. Konings: investigation, writing – review and editing. Dara Entekhabi: conceptualization, investigation, supervision, writing – review and editing.

Competing interests

The authors declare no conflicts of interest.

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During the preparation of this manuscript, the authors used ChatGPT (OpenAI; Sol 5.6; accessed 2026) to assist with English-language editing, including grammar, spelling, sentence structure, and readability, and, to a limited extent, with developing literature-search terms and identifying potentially relevant publications. All candidate publications were independently located, read, evaluated, and verified by the authors before use or citation. ChatGPT was not used to generate data, analyses, results, scientific interpretations, or conclusions. The authors reviewed and approved the complete manuscript and take full responsibility for its content.

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