

RESEARCH ARTICLE

Uncovering the critical soil moisture thresholds of plant water stress for European ecosystems

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Abstract

Understanding the critical soil moisture (SM) threshold (θ_{crit}) of plant water stress and land surface energy partitioning is a basis to evaluate drought impacts and improve models for predicting future ecosystem condition and climate. Quantifying the θ_{crit} across biomes and climates is challenging because observations of surface energy fluxes and SM remain sparse. Here, we used the latest database of eddy covariance

measurements to estimate θ_{crit} across Europe by evaluating evaporative fraction (EF)-SM relationships and investigating the covariance between vapor pressure deficit (VPD) and gross primary production (GPP) during SM dry-down periods. We found that the θ_{crit} and soil matric potential threshold in Europe are 16.5% and -0.7 MPa, respectively. Surface energy partitioning characteristics varied among different vegetation types; EF in savannas had the highest sensitivities to SM in water-limited stage, and the lowest in forests. The sign of the covariance between daily VPD and GPP consistently changed from positive to negative during dry-down across all sites when EF shifted from relatively high to low values. This sign of the covariance changed after longer period of SM decline in forests than in grasslands and savannas. Estimated θ_{crit} from the VPD-GPP covariance method match well with the EF-SM method, showing this covariance method can be used to detect the θ_{crit} . We further found that soil texture dominates the spatial variability of θ_{crit} while shortwave radiation and VPD are the major drivers in determining the spatial pattern of EF sensitivities. Our results highlight for the first time that the sign change of the covariance between daily VPD and GPP can be used as an indicator of how ecosystems transition from energy to SM limitation. We also characterized the corresponding θ_{crit} and its drivers across diverse ecosystems in Europe, an essential variable to improve the representation of water stress in land surface models.

KEYWORDS

critical soil moisture threshold, drought, Europe, evaporative fraction, gross primary production, surface energy partitioning, vapor pressure deficit

1 | INTRODUCTION

The critical soil moisture (SM) threshold of plant water stress is the point when evapotranspiration starts to decrease due to the SM deficit (Feldman et al., 2019; Seneviratne et al., 2010). Below this threshold, exhaustion of SM leads to reduced evapotranspiration and increased partitioning toward sensible heat flux due to higher surface temperatures that lead to drier air and an increase in the vapor pressure deficit (VPD), which impairs important ecosystem functions like carbon dioxide uptake (Betts, 2004; Gentile et al., 2019; Granier et al., 2007; Seneviratne et al., 2010). SM therefore plays a crucial role in partitioning of available between latent and sensible heat fluxes from the land surface (Schwingshackl et al., 2017). This energy partitioning determines local climate and influences the terrestrial component of land-atmosphere coupling (Santanello Jr et al., 2018). Thus, it is imperative to quantify the critical SM thresholds (θ_{crit}) of plant water stress and surface energy partitioning characteristics for evaluating the drought impacts on ecosystem function and improving models to predict future climate accurately.

The evaporative fraction (EF) is the ratio of latent heat flux to the sum of latent and sensible heat fluxes, and EF-SM relationships are commonly used to quantify θ_{crit} and surface energy partitioning characteristics (Budyko, 1974; Koster et al., 2009; Seneviratne et al., 2010). SM directly limits evapotranspiration under SM-limited conditions, which increase surface temperature at a given level

of net radiation, driving a positive land-atmosphere climate feedback (Betts, 2004; Gentile et al., 2019; Seneviratne et al., 2010). At higher SM availability, the system is considered energy limited as more moisture does not necessarily lead to greater evapotranspiration, and the strength of the water, carbon, and energy cycle coupling is subdued (Feldman et al., 2019; Pendergrass et al., 2020). Evapotranspiration is at or near its potential value where net radiation and atmospheric resistance are instead limiting. This EF-SM framework is well established (Figure 1) but quantifying the θ_{crit} that determines the transition from energy to water-limited regimes across biomes and climates is challenging because surface energy fluxes and SM observations remain sparse (Baldocchi et al., 2004; Budyko, 1974; Feldman et al., 2019; Koster et al., 2009). The extreme drought events that help quantify θ_{crit} are, by definition, rare, and often require long observational time series.

Attempts have been made to characterize these different evapotranspiration regimes at submonthly scales using satellite greenness data and air temperature globally (Zscheischler et al., 2015), for North America (Short Gianotti et al., 2019), and on weekly scales for Africa using satellite remote sensing data of the diurnal amplitude of the land surface temperature and surface soil moisture (Feldman et al., 2019). These studies did not investigate the role of VPD, but recently, both observations and models showed that VPD increases tend to reduce gross primary production (GPP) across a large range of SM conditions, whereas the reduction of SM only reduces GPP

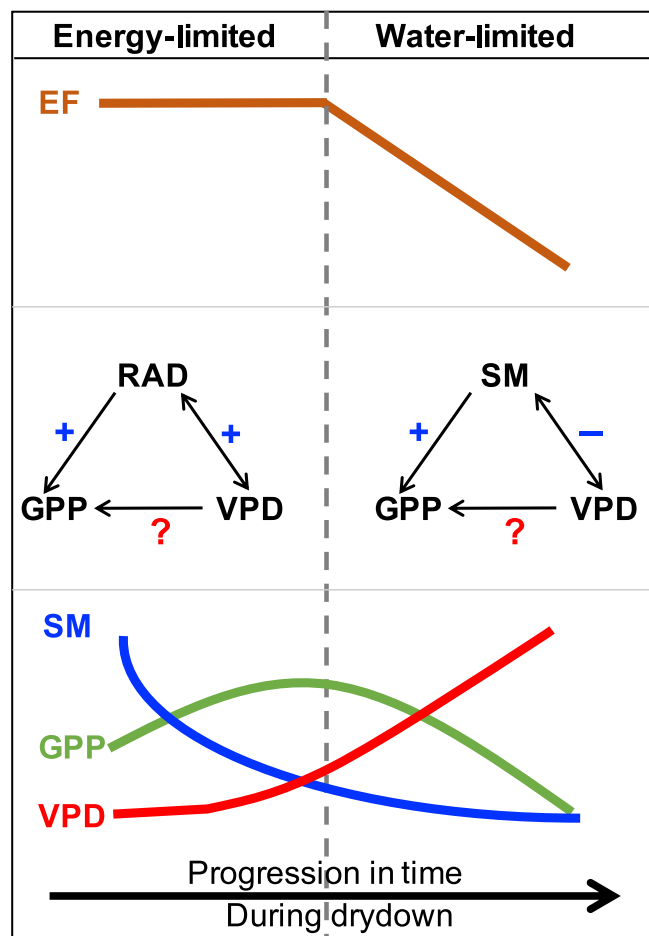


FIGURE 1 Schematic of the typical relationship between evaporative fraction (EF) and soil moisture (SM), as well as the changes in daily SM, gross primary production (GPP), and vapor pressure deficit (VPD) during soil moisture dry-down. We hypothesize that the covariance between daily VPD and GPP can be used to detect two regimes during dry-downs, that is, one regime with energy limiting conditions (positive covariance) and one regime with water limiting conditions (negative covariance). "+" and "-" represent the positive and negative correlation, respectively. RAD: incoming shortwave radiation. During a SM dry-down, there is generally an initial period of GPP increase due to available SM after rainfall if the ecosystem is already water limited before the dry-down counting started [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

below a critical SM threshold (Green et al., 2019; Grossiord et al., 2020; Kimm et al., 2020). GPP and evapotranspiration are tightly coupled on short timescales (Gentine et al., 2019), and we argue that the sign of the covariance between daily VPD and GPP can be an indicator of the relative strength between the water and energy limitation on ecosystem function. This is because VPD combines the effects of both water and enthalpy (via temperature) on GPP (Grossiord et al., 2020; Kimm et al., 2020; Novick et al., 2016). GPP is positively related to radiation under energy-limited regimes (Figure 1), and positively correlated with SM under water-limited regimes (Gentine et al., 2019; Seneviratne et al., 2010). However, it is unknown if the sign change of covariance between daily VPD and

GPP is also an effective metric to describe surface energy partitioning characteristics between water- and energy-limited regimes, and vice versa.

The dry-down periods following rainfall, that is, long periods without rainfalls when soil moisture decreases (Akbar et al., 2018; Feldman et al., 2018, 2019), provide a natural experiment for us to evaluate the EF-SM relationships and investigate how the sign of the covariance between daily VPD and GPP changes as SM declines and ecosystems shift from energy to water-limited states. During the course of a dry-down, an ecosystem with θ_{crit} will transition from a regime during which higher VPD is driven by incoming radiation which increases GPP, to another regime where SM reductions increase VPD but reduce GPP. During a SM dry-down, there is generally an initial period of GPP increase due to available SM after rainfall if the ecosystem is already water limited before the dry-down counting started, and is followed by a decline (Figure 1); but VPD keeps increasing if the incoming solar radiation (RAD) remains stable, for example, in the presence of anticyclonic conditions (Feldman et al., 2020). During the initial increasing GPP period, energy limitation (e.g., photosynthetically active radiation or temperature) is the major driver of GPP while SM becomes a key limiting factor during the following GPP decreasing stage (Seneviratne et al., 2010). However, the relationships between VPD and GPP in these two different stages may be different. We hypothesize that the covariance between daily VPD and GPP can be used to detect these two regimes during dry-downs, that is, one regime with energy limiting conditions (positive covariance) and one regime with water limiting conditions (negative covariance).

During a dry-down, EF first remains constant but then decreases when SM becomes lower than a given threshold (Figure 1). The EF-SM relationship is characterized by a transition point in SM separating the water and energy-limited regimes (Koster et al., 2009; Seneviratne et al., 2010). There is limited opportunity to test the appearance of SM limitations during dry episodes across a wide diversity of biomes and climates because EF-SM relationships are infrequently characterized due to the challenge of directly measuring surface energy fluxes and SM across sites (Baldocchi et al., 2004; Budyko, 1974; Feldman et al., 2019; Koster et al., 2009). To our knowledge, there is no observation-based assessment of the transition point of SM between demand and soil water supply limitation across Europe. Even less is known about the controlling factors and mechanisms in determining the θ_{crit} across diverse ecosystems. Climate models, on the other hand, rely on a parametric representation of SM-evaporation relationships to describe associations between water and energy cycles and predict future climate. However, due to difficulty in observing EF at large scales to constrain model results, and the lack of model simulation output at daily or hourly time steps, these relationships take different forms across climate models which contribute to divergences and uncertainty in making climate projections (Dirmeyer et al., 2006; Feldman et al., 2019; Schwingshackl et al., 2017).

The recently released ICOS (Integrated Carbon Observation System network of eddy covariance observations) (Centre, 2019) dataset with continuously measured CO_2 , water vapor, and energy

fluxes in Europe allows more direct observations of EF–SM relationships over various biomes and climates. Further, this dense network provides a unique opportunity to evaluate EF–SM relationships and change of the covariance between VPD and GPP during dry-downs. In recent years, Europe has experienced a series of extreme summer drought and heat events (e.g., 2003, 2010, 2015, and 2018), each characterized by record-breaking climate anomalies and extensive dry-down periods (Bastos, Ciais, et al., 2020; Bastos, Fu, et al., 2020; Fu et al., 2020). We can thus investigate the surface energy partitioning–SM relationship during these dry-downs (episodes with no rain for several consecutive days (Figure 1)), where SM shows a short term rise after rain and then decreases until the next rain event. There were many “dry-down” periods with no rain in Europe in recent years that can be used to detect the critical moisture value at the onset of water stress.

Focusing on SM dry-downs, this study uses the latest eddy covariance measurements from ICOS to quantify θ_{crit} across Europe and test the hypothesis that the sign change of covariance between daily VPD and GPP can be used to detect θ_{crit} . By evaluating the EF–SM relationships, we first quantify θ_{crit} values and the EF sensitivity to SM in the water-limited regime. Then, we investigate the changes of covariance between daily VPD and GPP during SM dry-downs and quantify θ_{crit} values with this second approach, which are compared with the θ_{crit} from the first approach. Last, we explore what factors drive the spatial variability of θ_{crit} and EF sensitivity to SM.

2 | MATERIALS AND METHODS

2.1 | Datasets

We used half-hourly SM, VPD, GPP, precipitation, latent heat flux, sensible heat flux, and incoming shortwave radiation from the recently released ICOS (Integrated Carbon Observation System) dataset (Centre, 2019). ICOS includes 52 eddy covariance sites in Europe with energy, water, carbon fluxes and meteorological data, which were processed following a consistent and uniform processing pipeline (Pastorello et al., 2020). We selected 31 sites with measurements for all above variables, including 22 forests, five grasslands, three savannas, and one shrubland (Table S1). Savanna sites include both trees and grasses and in our case are found in Mediterranean climate zones (El-Madany et al., 2020; Luo et al., 2018, 2020). Croplands were excluded due to the effect of management on the seasonal timing of ecosystem fluxes, both from crop rotations and from the varying timing of planting and harvesting. Wetland sites were also removed because they have a high water table and infrequently show soil moisture limitations.

SM was measured as volumetric soil water content (percentage) at different depths, varying across sites. Surface SM (SM_1: 0–5 cm) was measured at all sites and some sites also provided deeper SM measurements (e.g., SM_2: 5–20 cm; SM_3: 20–60 cm). We mainly used the surface SM observations but deeper SM measurements were also used when available. GPP estimates from the nighttime

partitioning method were used for the analysis (Reichstein et al., 2005). Data were quality controlled so that only measured and good-quality gap-filled data (QC = 0 or 1) were used. Daytime half-hourly data (9 am to 16 pm local standard time) were averaged to daily values while SM values were averaged over the full day.

Measured soil texture, mean annual precipitation, summer average of VPD, incoming shortwave radiation, and wind speed data at each site were also used to understand the drivers in determining the spatial variability of θ_{crit} and EF sensitivity to SM in water-limited stage.

2.2 | Soil moisture dry-down identification

Dry-downs following rainfall are episodes with no rain for several consecutive days during which SM shows a short-term “pulse” rise after rain and then decays until the next rain event. A dry-down is retained for our analysis when SM decreases consecutively for at least 10 days after rainfall (Akbar et al., 2018; Feldman et al., 2018; McColl et al., 2017; Shellito et al., 2018). We focused on the soil dry-downs during the summer (June–July–August) season for all available site-years. This resulted in 428 dry-down events that form the basis of our study.

2.3 | Critical SM threshold and evaporative fraction sensitivity to SM estimation

We calculated the daily EF as the ratio of observed latent heat flux to the sum of latent and sensible heat fluxes during each soil dry-down. Then, we characterized the EF–SM relationship at each site using all available soil dry-downs, from a regression between these two variables with a linear-plus-plateau model:

$$EF = \begin{cases} a + b(SM - c) & \text{if } SM < \theta_{crit} \\ a & \text{if } SM \geq \theta_{crit} \end{cases}$$

where a is the maximum value of EF in absence of SM stress (energy-limited stage), b represents the slope of the linear increase phase (water-limited stage), and c is the critical SM threshold. These three parameters were simultaneously estimated by least squares fit with the R software package “nlstools” (Baty et al., 2015) for each site, leading to site-specific estimated values of peak EF, slope, and θ_{crit} . θ_{crit} is the breakpoint until which EF increases linearly as a function of SM (Figure 1 and S1). The slope represents the EF sensitivity to SM in the water-limited regime, indicating the magnitude of EF increase for each additional 1% change of SM when SM is below its breakpoint. The plateau is the maximum EF value reached when SM exceeds its threshold. The time spent in the water-limited stage was computed as the ratio of the number of days with $SM < \text{threshold}$ divided by the total duration of the dry-down as in Feldman et al. (2019). SM threshold values were converted to soil matric potentials using soil retention curves and soil

texture data (Table S1) (Gourlez de la Motte et al., 2020; Granier et al., 2007; Marthews et al., 2014).

There were 23, 16, and 12 sites with the critical SM threshold estimates based on the first (SM_1), second (SM_2), and third (SM_3) soil water content measurement depth (Figures S1–S3), respectively. For the rest of sites, it was not possible to estimate a SM threshold using the EF–SM relationship because samples were too infrequent, deep SM measurements were missing, or there were no thresholds.

2.4 | Covariance between daily VPD and GPP during dry-down

We also calculated the covariance between daily VPD and GPP across 9-day moving windows during the dry-down (e.g., 1–9 days; 2–10 days; 3–11 days...). A positive covariance indicates that higher VPD is associated with increases in GPP (which we term “radiation effects”) while a negative covariance indicates that water stress limits GPP, that is, with a higher VPD caused by dryer soils results in a lower GPP. Here, we excluded some short dry-downs because their covariances during the dry-down are all positive or negative, suggesting the entire dry-down period is under energy-limited or water-limited stage. We only chose the long soil dry-downs with at least 15 days (with at least seven covariance values) and their covariances must include both positive and negative values to see if the change of covariance signs corresponds to the ecosystem transition from energy-limited into water-limited regime.

The evolution of covariance with moving window days during the dry-down periods allowed us to evaluate the joint variability of daily VPD and GPP change. Across all soil dry-downs, the median value of the VPD–GPP covariance was calculated for equal bins of 1-day change to identify the timing when the sign of covariance will change. Similar to the covariance, the average of SM during the moving window (e.g., 1–9 days; 2–10 days; 3–11 days...) were also calculated to detect the critical SM threshold when the sign of covariance changes. The correlation of Pearson and Spearman and their associated test were performed to compare the θ_{crit} values from this covariance method with the EF–SM method.

2.5 | Drivers of the spatial variability of critical SM thresholds and EF slopes

We evaluated the relative importance (RI) of soil texture, mean annual precipitation, summer average VPD, incoming shortwave radiation, and wind speed in determining the spatial variability of θ_{crit} and EF sensitivities to SM. We used a RI analysis approach to quantify the relative contributions of each factor to the SM thresholds or EF slopes, expressed as the Pearson correlation in a multiple linear regression (SM thresholds (or EF slopes) = $b_0 + b_1 \times \text{MAP} + b_2 \times \text{Clay fraction} + b_3 \times \text{VPD} + b_4 \times \text{radiation} + b_5 \times \text{wind} + \epsilon$). ϵ represents other drivers that were not considered but might contribute to the variability of SM thresholds or EF slopes. The algorithm was implemented

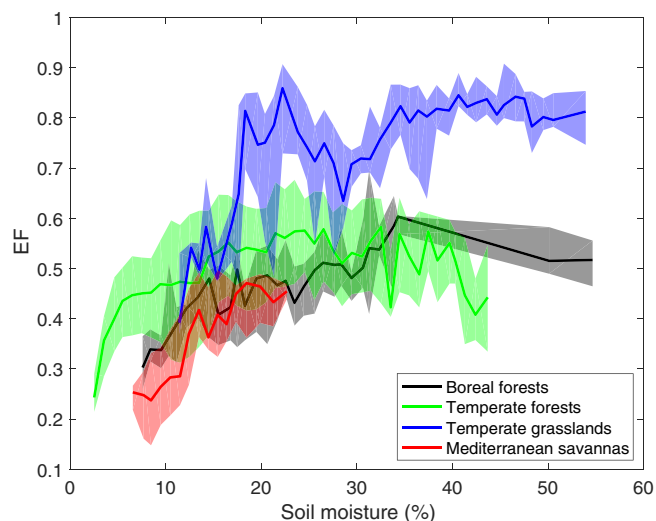


FIGURE 2 EF–SM relationships for different vegetation types. Bold lines indicate binned median values calculated in equal SM bins of 1% increments, while shading bounds the 25th and 75th percentiles of EF values within soil moisture bins. EF: evaporative fraction; SM: soil moisture [Colour figure can be viewed at wileyonlinelibrary.com]

with the “relaimpo” package in R (Grömping, 2006), which is based on variance decomposition for multiple linear regression models. The “relaimpo” package provides six different methods for analyzing the RI of each regressor in linear regression. We used “LMG” to quantify the contribution of different correlated regressors in a multiple linear regression (Huang et al., 2018). The LMG method estimates the RI of each variable by decomposing the sum of squares into non-negative contributions shared by each variable, and the LMG values were obtained by averaging the sequential sum of squares (r^2) for all possible orders. Finally, all RI values were normalized (divided by r^2) to sum to 1. We also repeated this analysis using the available energy (AE, the difference between net radiation and soil heat flux) instead of the incoming shortwave radiation to evaluate the relative role of AE.

3 | RESULTS

3.1 | Surface energy partitioning characteristics and critical SM threshold of plant stress

EF behavior during all dry-downs within each vegetation type is plotted together in Figure 2. The general behavior is in line with that shown in Figure 1. Temperate grasslands and Mediterranean savannas showed stronger EF–SM coupling (greater slope) at low soil moisture values than boreal and temperate forests. The AE is increasingly partitioned toward sensible heat flux with decreasing SM during the water-limited regime.

The surface SM thresholds (using SM_1) is highly correlated with the SM thresholds observed in deeper soil layers (using SM_2 and SM_3) (Figure S4). As surface SM measurements are available at all sites, we focused on surface SM thresholds. Across all sites, we found

that the critical SM threshold in Europe is $16.5 \pm 7.5\%$ (median $\pm$ SD, Figure 3a). Temperate grasslands ($27.0 \pm 10.6\%$) had higher SM thresholds than temperate forests ($16.5 \pm 5.5\%$) and Mediterranean savannas ($13.0 \pm 1.6\%$, Figure 3c). We also found that the soil matric potential threshold in savannas (-1.22 ± 0.21 MPa) is more negative than in forests (-0.64 ± 0.45 MPa) and grasslands (-0.37 ± 0.49 MPa, Figure 3c). Overall, we estimated that the critical soil matric potential threshold across all sites in Europe is -0.71 ± 0.46 MPa (Figure 3b).

The sensitivities (slopes) of EF to SM, time spent in water-limited stage, and the peak EFs are different among vegetation types (Figure 4). Across all sites, EF decreased by 0.03 per 1% SM decrease (Figure 4a). Savannas showed a higher sensitivity of EF to SM (slope 0.05 ± 0.02) than forests (slope 0.03 ± 0.02). We further found that the time spent in water-limited stage in savannas ($82.9 \pm 9.7\%$ of all dry-down durations) was nearly two times as long as in forests ($44.0 \pm 24.1\%$); across all European sites, it was about $48.3 \pm 27.0\%$ of the dry-down period duration (Figure 4b). However, the peak EF in energy-limited stage in forests (0.5 ± 0.1) tended to be higher than in savannas (0.4 ± 0.1 , Figure 4c).

3.2 | Covariance between daily VPD and GPP during SM dry-down

As an alternative to the EF-SM relationships, the change of the sign of the covariance between daily GPP and VPD during dry-down was used to detect the critical SM threshold. To explore the dynamics of the VPD-GPP relationships during dry-down, we first illustrated the changes in the covariance of daily GPP and VPD during a long soil moisture dry-down at CH-Cha (grassland, Figure 5a, b), as well as the coincident changes in surface energy partitioning-SM relationship (Figure 5c). Both the original data and moving average data found that daily GPP first increases but then decreases during the dry-down while daily VPD increases steadily (Figure 5a). The sign of covariance between

daily VPD and GPP changed from positive into negative around a SM threshold of 35% for this example (Figure 5b). The positive covariances suggested that positive radiation effects (VPD-radiation coupling) on GPP are stronger while negative covariances showed that SM limiting effects on GPP are stronger (VPD-SM coupling). The EF-SM relationship showed that the EF values remain relatively high (about 0.75) at high SM (35%–55%); however, under low SM (<35%), EF and SM were positively related in the interval during which reduced SM lowers EF (Figure 5c). These observations are consistent with the notion that the ecosystem shifted from an energy-limited regime to a water-limited regime during this dry-down such that the sign of covariance between daily VPD and GPP was related to surface energy partitioning. Another example in a forest site, DE-Hzd, yielded similar results (Figure S5).

We also examined the covariance between daily VPD and GPP for all soil dry-downs (Figure 6). All covariances consistently changed their signs from positive to negative during the dry-down (Figure 6a). We found that the median values of covariances across all dry-downs revealed that the breakpoint often occurs around the fourth moving window (the covariance is calculated using 9-day moving window, e.g., 1–9 days; 2–10 days; 3–11 days...). The changed covariance signs are also found in different vegetation types consistently (Figure 6b–d). The timing of the breakpoint in forests (fifth moving window, Figure 6b) is larger than in grasslands (third moving window, Figure 6c) and savannas (second moving window, Figure 6d), suggesting that it takes longer for the VPD-GPP covariance sign to change from positive to negative in forests compared to grasslands and savannas. As the savanna sites have Mediterranean climate and the peak growing season is mainly in spring (El-Madany et al., 2020; Luo et al., 2018, 2020), we performed the same analysis using both spring and summer and obtained similar results that the breakpoint in savannas is reached in shorter time than in forests (Figure S6).

Combining the SM data for each dry-down (Figure 6e–h), we then quantified the critical SM thresholds when the VPD-GPP

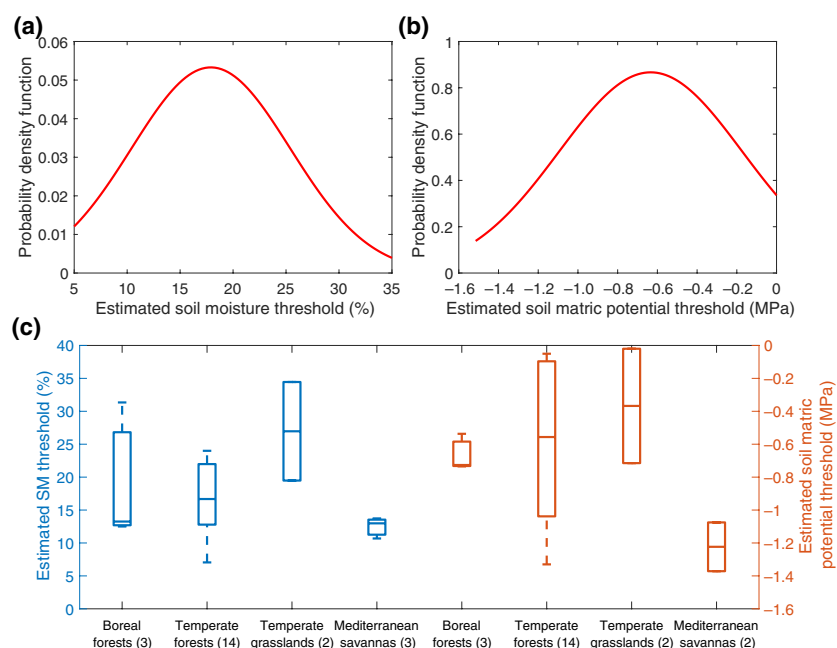
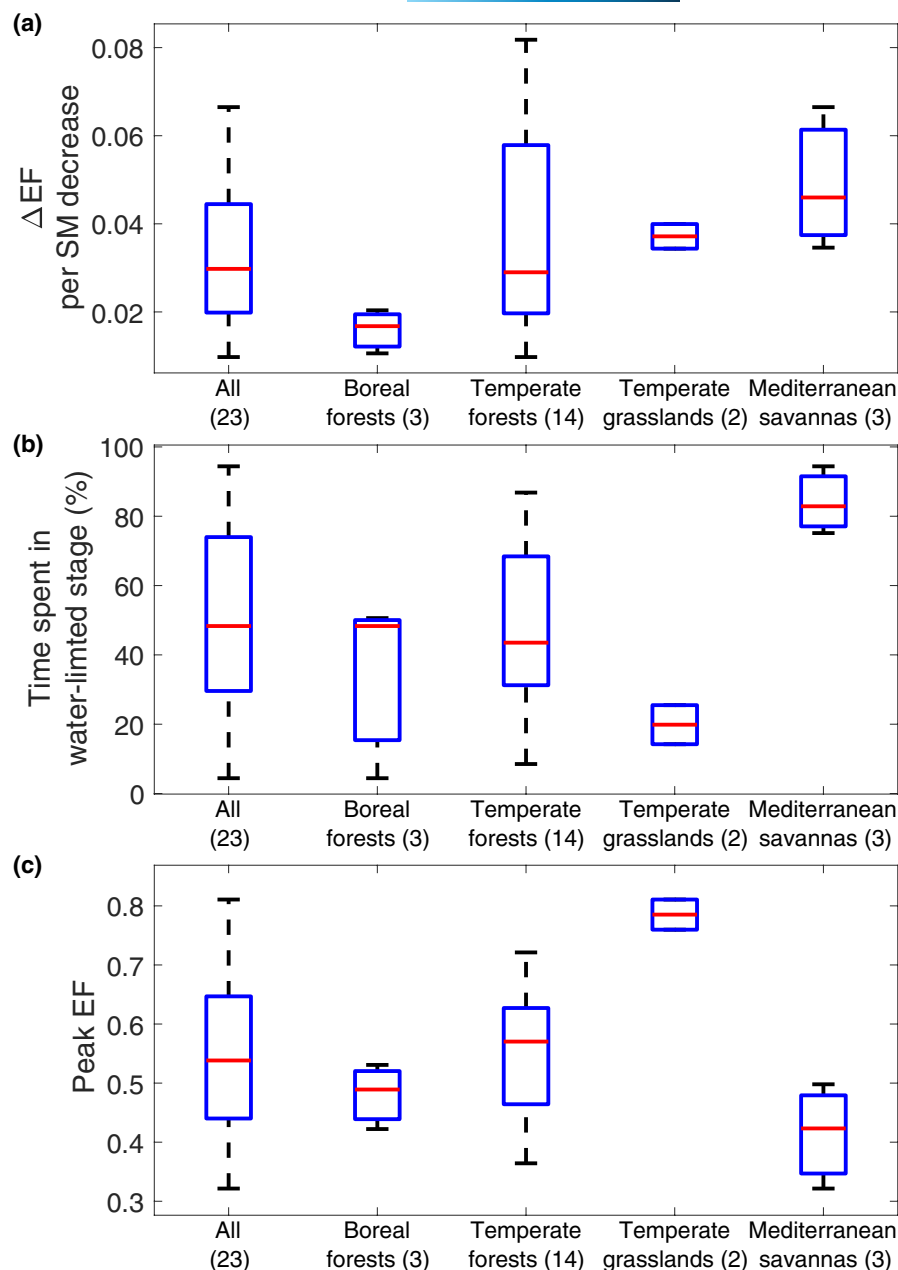


FIGURE 3 Probability density function of estimated critical soil moisture (SM) threshold (a) and soil matric potential threshold (b). Estimated SM threshold and soil matric potential threshold among different vegetation types (c). For each box plot, the middle line indicates the median; the box indicates the upper and lower quartiles, and the whiskers indicate the 5th and 95th percentiles of the data. The numbers in brackets indicate the number of sites [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16050)]

FIGURE 4 The evaporative fraction (EF) sensitivity to soil moisture (SM) (a), time fraction spent in water-limited stage (b), and the peak EF (c) among different vegetation types in Europe. For each box plot, the middle line indicates the median; the box indicates the upper and lower quartiles, and the whiskers indicate the 5th and 95th percentiles of the data. The numbers in brackets indicate the number of sites [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



covariance sign change at each site. We found that the θ_{crit} estimated from the new covariance method match well with the EF–SM method ($r = 0.86$, Figure 6i, j). Compared with the θ_{crit} estimated from the EF–SM method, our results showed that the VPD–GPP covariance method has potential to detect the critical moisture thresholds, although the absolute magnitude of SM thresholds estimated from covariance method is a bit higher than that of EF–SM methods (Figure 6i, j).

3.3 | Drivers of the spatial variability of SM thresholds and EF slopes

The multiple linear regression model showed that the five factors studied (mean annual precipitation, clay fraction, summer VPD,

incoming shortwave radiation, and wind speed) can explain 74% and 65% of the spatial variability of SM thresholds (Figure 7a) and EF sensitivities (Figure 7b), respectively. However, the dominant predictors of the spatial variability of SM thresholds and reduction rates of EF were different. For the spatial variability of SM thresholds, soil texture was the most important factor, and its RI was 76% comparing with the other four factors (Figure 7a), and clay fraction alone explained 65% of the variability across all sites. For the spatial variability of reduction rates of EF, climate factors, such as incoming shortwave radiation and VPD, were the major drivers, with RI up to 53% and 26%, respectively (Figure 7b). The same analysis using the AE (the difference between net radiation and soil heat flux) instead of the incoming shortwave radiation obtained similar results (Figure S7). AE played an important role in determining both the spatial variability of θ_{crit} (17%) and EF sensitivities (52%, Figure S7).

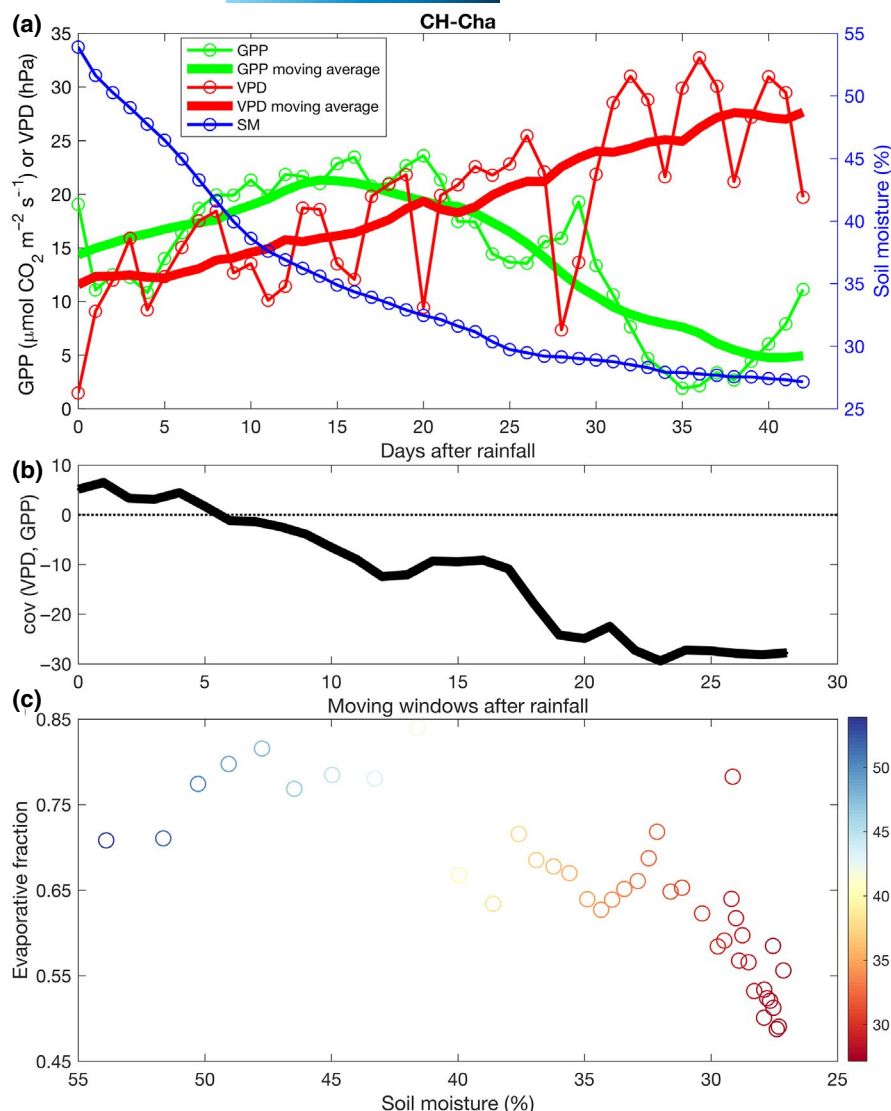


FIGURE 5 Daily soil moisture (SM), gross primary production (GPP), and vapor pressure deficit (VPD) during a soil dry-down at CH-Cha (grassland, a). Covariance between daily VPD and GPP changes with moving windows (b), and evaporative fraction (EF) changes with SM during the dry-down (c). The unit of covariance is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ hPa}$. The color coding in panel (c) indicate the soil moisture values. Please note that the soil moisture scale is from high to low [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Current water stress indicators typically hinge on the accuracy of evapotranspiration data, a flux that is very difficult to measure globally and is often estimated with assumptions, thus leading to high degrees of uncertainty (Wang & Dickinson, 2012). To our knowledge, we demonstrate for the first time that the covariance between daily VPD and GPP changes its sign from positive to negative during SM dry-downs as ecosystems transition from energy-limited regimes to water-limited regimes. Our results suggest that the sign of covariance between daily VPD and GPP can capture shifts in the surface energy partitioning characteristics and therefore has potential to be a new indicator of ecosystem water stress. For global remote sensing data products, it becomes possible to have reasonable GPP products, for example, based near-infrared reflectance of vegetation (NIR_V) (Badgley et al., 2017), normalized difference vegetation index (NDVI) (Myneni et al., 1997), enhanced vegetation index (EVI) (Huete et al., 2002), and daily FLUXCOM data (Jung et al., 2017; Tramontana et al., 2016), and VPD is computed from directly observed temperature and relative humidity, whereas global evapotranspiration products

differ between datasets and are arguably more uncertain (Badgley et al., 2015; Bai & Liu, 2018). Our covariance method provides a new option and an independent tool to quantify the critical SM threshold and detect surface energy partitioning characteristics over large regions, which we hope will be helpful to uncover the SM thresholds of plant water stress at regional and global scales. One advantage of the covariance indicator is that, from a remote sensing perspective, spatially resolved VPD and GPP products have much lower levels of uncertainty than evapotranspiration products. Another is that the type of stress is directly related to GPP, that is, carbon uptake, and not only indicative for stomatal conductance and transpiration.

Although the critical SM thresholds estimated from VPD–GPP covariance method match well with the EF–SM method, we found that the absolute magnitude of SM thresholds estimated from the VPD–GPP covariance method is a bit higher than the EF–SM method (Figure 6i, j), which may result from two reasons. First, the covariance method calculated the covariance and mean SM values using 9-day moving windows. The average values of SM across the window could lead to the difference of SM thresholds between the VPD–GPP covariance method and EF–SM method. Second, the eddy

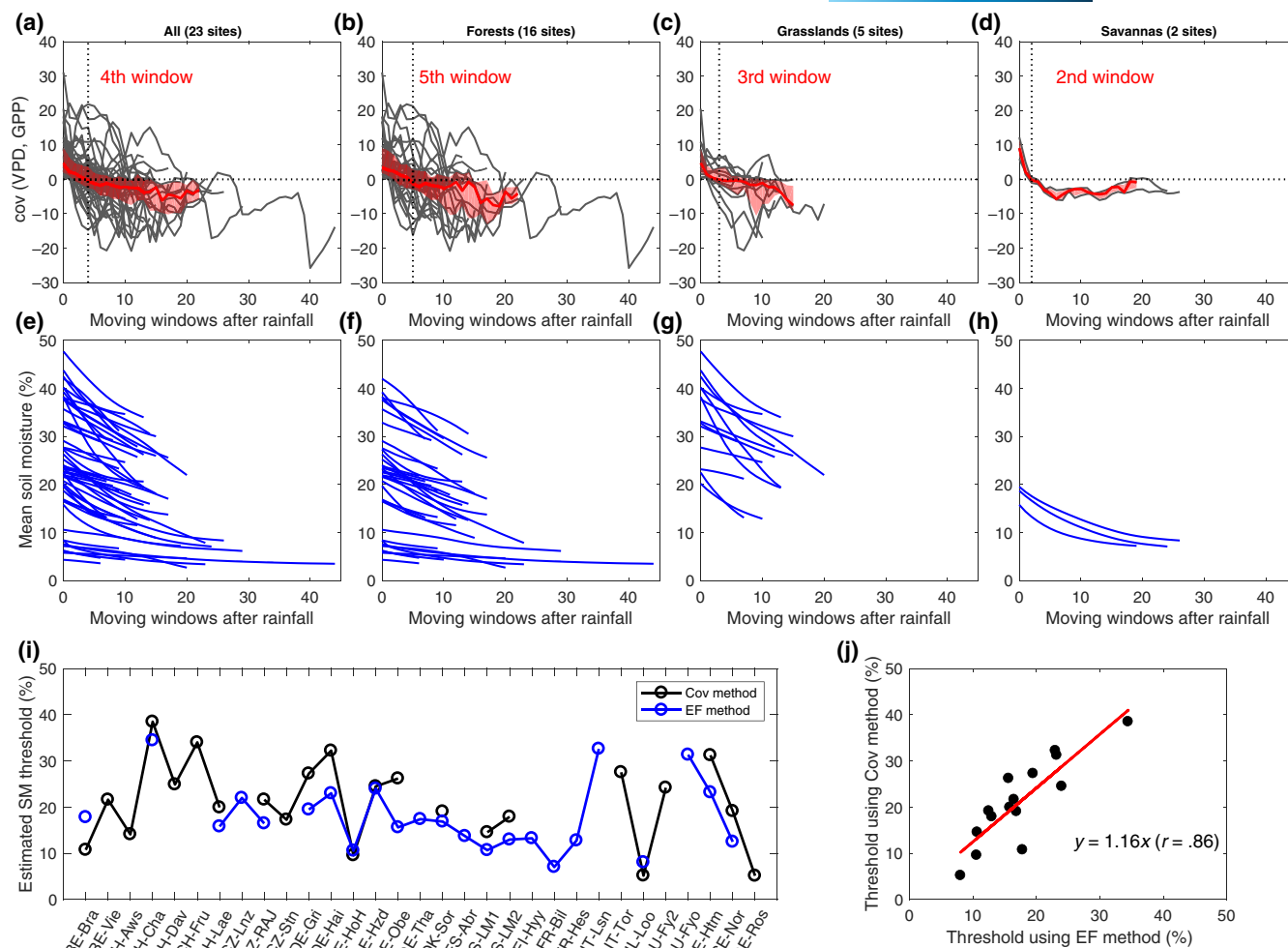
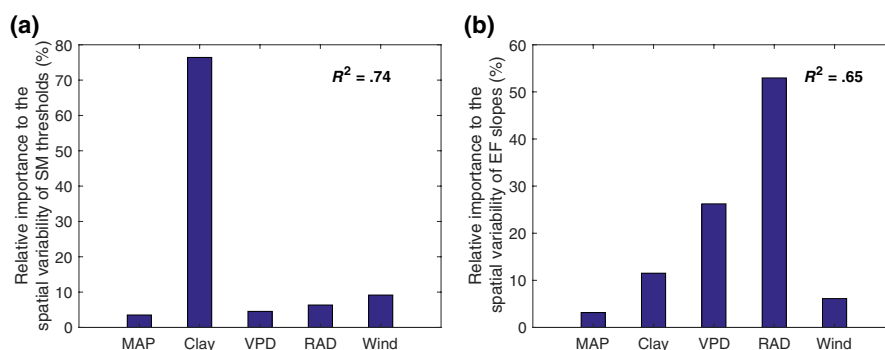


FIGURE 6 Covariance between daily vapor pressure deficit (VPD) and gross primary production (GPP) across 9-day moving window changes with moving windows after rainfall during the dry-down (a-d). Mean soil moisture (SM) during moving window for each dry-down (e-h). Comparison between the critical SM thresholds estimated from the VPD–GPP covariance method and evaporative fraction (EF) method (i-j). Covariance and mean soil moisture were calculated using 9-day moving window (e.g., 1–9 days; 2–10 days; 3–11 days...). Each black line represents the covariance change at each dry-down while the red line means the median value in equal bins of 1 day change (a-d). The shading bounds the 25th and 75th percentile of the distribution of covariance within the bin (a-d). The units of covariance is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ hPa}$ [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

FIGURE 7 Relative importance of mean annual precipitation (MAP), clay fraction, summer average vapor pressure deficit (VPD), incoming shortwave radiation (RAD), and wind speed to the spatial variability of soil moisture (SM) thresholds (a) and evaporative fraction (EF) slopes (b) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



covariance evapotranspiration analysis measures not only plant transpiration but also soil evaporation (though it is often small) (Stoy et al., 2019), which may also contribute to the differences found between approaches. To get a more plant-related estimate of the critical SM threshold, the response of plant functioning (GPP and

transpiration) with atmospheric stress (VPD) under given soil moisture conditions needs to be taken into account.

The timing when the sign of the covariance between VPD and GPP changes from positive to negative varies across vegetation types. Forests need more time for the sign of this relationship to

change after rain events than grasslands and savannas, showing that there is a longer time during which VPD-radiation coupling is stronger than VPD-SM coupling in forests compared to grasslands and savannas during SM dry-downs. The water storage in soil and plants after rainfall in forests can be larger than in grasslands because forests have deeper roots and access to moisture in deeper soils (Chapin III et al., 2011; Fan et al., 2017). Forests often have stronger resistance to drought than grasslands and savannas (Konings & Gentine, 2017; Martínez-Vilalta & García-Forner, 2017; Teuling et al., 2010), thus GPP rates are maintained for a longer time after rainfall in forests.

The surface energy partitioning-SM relationship showed that grasslands and savannas had stronger EF-SM coupling (slope) at low soil moisture values than that of forests (Figures 2 and 4a). Grasslands have shallow roots and are more sensitive to SM decrease, leading to abrupt drought, while forests have deep roots, access to deep soil water, and less sensitive to surface soil moisture changes. The high sensitivity of EF to SM in water-limited periods in grasslands and savannas will accelerate soil moisture depletion and quickly lead to large water constraints on photosynthesis (El-Madany et al., 2020; Luo et al., 2018, 2020). The low sensitivity of EF to SM in forests is in line with our findings from covariance analysis that showed it takes longer for the VPD-GPP covariance sign to change from positive to negative in forests compared to grasslands and savannas, further supported the strong resistance of forests to drought (Konings & Gentine, 2017; Teuling et al., 2010). We also found that incoming shortwave radiation and VPD are the major drivers in determining the spatial variability of EF sensitivity to SM, indicating that high radiation and VPD will increase the sensitivity of EF to SM in water-limited stage. This will likely cause EF sensitivity to increase in future because increased exposure of plants to higher VPD from warming and drier continental relative humidity is inevitable and widespread in future (Byrne & O'Gorman, 2018; Novick et al., 2016).

Consistent with previous findings from satellite observations in Africa (Feldman et al., 2019), our results showed that savannas spend more time in the water-limited regime, but we found that forests also spend almost 50% of the time in the water-limited regime, suggesting that European forest ecosystems are exposed to drought. This time fraction spent in the water-limited regime may further increase in future with anthropogenic warming (Naumann et al., 2021), leading to greater drought damages in Europe. We also found that grasslands spend more than 70% of the time in the energy-limited regime because these grassland sites are mainly located in the northern Europe, which are limited by energy due to the high latitudes or altitudes. Under energy-limited stage, the peak EF in grasslands was up to 0.79 (Figure 4c), indicating that grasslands allocate more energy for evaporative cooling, which suppresses surface heating (Teuling et al., 2010).

Across all sites in Europe, our results showed that the critical SM threshold is 16.5% (Figure 5), which is slightly higher than the value found in Africa (14%) using a different method (Feldman et al., 2019) and an annual grassland (15%) in the United States (Baldocchi et al., 2004). At the European sites, we found that soil texture is the most

important determining factor in controlling the spatial variability of SM thresholds (Figure 7a), which is in line with previous findings in Africa (Feldman et al., 2019) and the United States (Akbar et al., 2018), based on satellite data. We also converted the SM thresholds into soil matric potentials, and found that the soil matric potential threshold in Europe is about -0.71 MPa. The soil matric potential threshold in savannas is more negative than in forests and grasslands. When we focused on the forest sites in Europe, we found that the soil matric potential threshold is -0.64 MPa, which is very close from the -0.66 MPa value found by Granier et al. (2007) across six forest ecosystems. We noted that the EF-SM relationship can be affected by other factors, such as radiation and albedo (Haghighi et al., 2018). While several other factors limit evapotranspiration besides soil moisture and the linear dependency is a simple approximation, recent studies have highlighted that this EF-SM framework provides a good first-order representation of regimes of land-atmosphere coupling, both in models and observations (e.g., Koster, Dirmeyer, et al., 2004; Koster, Suarez, et al., 2004; Seneviratne et al., 2006, 2010; Teuling et al., 2006). Here we provided a comprehensive analysis across representative European ecosystems.

5 | CONCLUSIONS

Using a new database of flux tower observations across Europe, this study uncovered the critical SM threshold and surface energy partitioning characteristics by evaluating EF-SM relationships and examining the joint variability of daily VPD and GPP during SM dry-downs. We carefully studied SM dry-downs to understand how ecosystems transition from energy-limited regimes to water-limited regimes. EF-SM relationships quantified the critical SM and soil matric potential thresholds in Europe are 16.5% and -0.7 MPa, respectively. Surface energy partitioning characteristics varied among different vegetation types; EF in savannas had the highest sensitivities to SM in water-limited stage while it was the lowest in forests. We found the sign of covariance between daily VPD and GPP changed after a longer period in forests than in grasslands and savannas. The critical SM thresholds estimated from the VPD-GPP covariance method match well with that of EF-SM method, suggesting that this sign of VPD-GPP covariance can be used to detect the SM threshold. We further found that soil texture dominates the spatial variability of SM thresholds while incoming shortwave radiation and VPD are the major drivers in determining the spatial pattern of EF sensitivities. The revealed critical SM threshold and its drivers across diverse biomes and climates in Europe will be beneficial to improve climate models with parametric representations of drought stress. Our results highlighted, for the first time, the important role of the sign change of covariance between daily VPD and GPP in monitoring the surface energy partitioning characteristics and quantifying the critical SM threshold, which opens its generalized application using daily GPP estimates and VPD, for example, from remote sensing data. The new covariance method demonstrated here provides a new option and an independent tool to quantify critical SM threshold and

surface energy partitioning, which can help solve the current challenge in uncovering the SM threshold of plant water stress at regional and global scales.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ICOS at (<https://doi.org/10.18160/YVRO-4898>).

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