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Ecologically relevant moisture and temperature metrics for assessing dryland ecosystem dynamics

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Abstract

In drylands, water-limited regions that cover ~40% of the global land surface, ecosystems are primarily controlled by access to soil moisture and exposure to simultaneously hot and dry conditions. Quantifying ecologically relevant environmental metrics is difficult in drylands because the response of vegetation to moisture and temperature conditions is not easily explained solely by climate-based metrics. To address this knowledge gap, we developed and examined 27 climate and ecological drought metrics across dryland areas of the western United States. Included in the 27 metrics is a suite of 19 largely new "ecological drought metrics" that are designed to quantify multiple aspects of environmental limitation in drylands, including overall growing conditions, seasonal fluctuations, seasonal moisture timing, exposure to extreme drought and recruitment potential for perennial plants. To quantify these metrics, we simulated water balance pools and fluxes of daily soil moisture at multiple depths with historical weather from 1970 to 2010 using the SOILWAT2 ecosystem water balance model. We assessed the relationships among these metrics and their spatial and temporal patterns. We found that the inclusion of ecological drought metrics substantially increased the dimensionality of the climate metrics dataset; the number of independent variables needed to explain 90% of the variance in the dataset increased with the addition of ecological drought metrics. Spatial patterns in overall growing conditions represented well-known differences among ecoregions, for example, high temperatures and low precipitation in the southwest and cool temperatures and greater precipitation in the northeast. Seasonal fluctuation in soil water availability (SWA) was greatest in the southwest (Mojave Desert), whereas fluctuation in climatic water deficit (CWD) was greatest in the northwest (northern Great Basin and Columbia Plateau). Seasonal timing of moisture also differed among metrics; the timing of wet degree days (WDD), the timing of SWA and the timing of CWD were only weakly related to seasonal timing of precipitation. Plant recruitment metrics varied strongly across western drylands. In the Great Plains, recruitment events occurred more frequently and lasted longer than in the intermountain regions, where recruitment events were comparatively rare and short. These ecological drought metrics provide new insight into patterns of soil moisture and temperature

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that shape the structure and function of dryland ecosystems. The metrics will be useful for assessing the potential impact of climate change on dryland ecosystems and developing adaptive resource management strategies to sustain dryland ecosystem services in a changing world.

KEYWORDS
dryland vegetation, ecological drought, hot drought, plant recruitment, soil moisture

1 | INTRODUCTION

Water-limited drylands comprise approximately 40% of terrestrial ecosystems and provide ecosystem services to 38% of the global population (Prăvălie, 2016; Reynolds et al., 2007). Drylands are characterised by low and highly variable precipitation, and dryland ecosystems are strongly controlled by water availability (Noy-Meir, 1973; Wang et al., 2012). Because drylands are limited by moisture availability, even relatively subtle shifts in average moisture patterns due to climate change may have substantial consequences for dryland vegetation structure and function (Bestelmeyer et al., 2015; Reynolds et al., 2007). The strong link between ecosystems and moisture availability means that dryland ecosystems are especially prone to degradation and vulnerable to climate change. Degradation is globally common in drylands (Burrell et al., 2020), driven by combinations of human land use (Newbold et al., 2015), biological invasions (Knapp, 1996; Roundy et al., 2007), changing disturbance regimes (Davies et al., 2011; Miller & Tausch, 2001) and growing exposure to extreme conditions, including hot drought (Wang et al., 2012). As a result of this degradation, ecological conservation and restoration are important management objectives in drylands (Chambers et al., 2017; Kildisheva et al., 2016), although the success of restoration efforts has been limited (Svejcar & Kildisheva, 2017). The establishment of perennial plants in drylands is often restricted by dry conditions that induce mortality in seedlings, and so, recruitment events may occur only during rare periods with favourable conditions (Lauenroth et al., 2014; Shriver et al., 2018). Thus, understanding and managing drylands, especially in a changing world, requires insight into the specific conditions that drive ecological dynamics in dryland vegetation.

Identifying and quantifying ecologically relevant environmental metrics is challenging in drylands because the interactions and feedbacks between vegetation dynamics and patterns of soil moisture (in combination with temperature) make ecological drought conditions difficult to infer from climate or weather conditions alone (Kulmatiski, 2018; Sala et al., 1997; Silvertown et al., 2015). Drylands are defined by moisture limitation and characterised by low mean annual precipitation (MAP) relative to evaporative demand (e.g., potential evapotranspiration, PET). The ratio of MAP/PET provides an aridity index (AI), wherein lower values indicate more arid conditions and dryland regions are defined as areas with AI < 0.65 (UNEP, 1992). Similarly, bioclimatic variables (Fick & Hijmans, 2017) can be used to estimate overall conditions of water limitation and aridity. Meteorological drought indices like the Palmer Drought Severity Index (PDSI; Huang et al., 2017; Palmer, 1965) or the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) use precipitation and temperature (or PET) to estimate fluctuations of wet and dry conditions at variable temporal scales. In addition to indices of long-term aridity, other approaches have attempted to estimate soil moisture deficiencies (Hunt et al., 2009; Krueger et al., 2019; Martínez-Fernández et al., 2015; Torres et al., 2013). The generalizability and accessibility of aridity and drought indices make them useful for defining the spatial extent of drylands and for generally representing drought event severity. However, meteorological drought metrics often do not represent the biological processes (e.g., plant response to atmospheric carbon dioxide concentration) necessary to estimate water balance, drought severity and the associated ecological impacts (McColl et al., 2022). Even simple water balance approaches have a limited ability to represent the ecologically relevant dynamics that determine vegetation responses to drought, as these dynamics are influenced by plant physiology and topo-edaphic conditions (Young et al., 2021). As a result, ecologically relevant drought conditions in drylands are highly variable in space and time yet difficult to estimate.

Understanding ecological dynamics in drylands requires drought metrics that represent interactions among atmospheric conditions, temperature, soil conditions and plant activity. These interactions can unfold at short time scales yet have meaningful impacts on vegetation structure and ecological function. For example, high temperatures accompanied by low soil moisture promote hot drought conditions with strong ecological impacts (Breshears et al., 2005; Renne et al., 2019). Moisture availability patterns are controlled by overall temperature and moisture conditions but also by interactions between the precipitation regime and local soil properties, soil depth and vegetation (Lauenroth & Bradford, 2006; Noy-Meir, 1973; Renne et al., 2019; Schlaepfer et al., 2012). Seasonal and soil depth patterns of moisture availability, in particular, strongly influence the structure and function of dryland plant communities (Renne et al., 2019; Schlaepfer et al., 2012). For instance, deeply rooted shrubs might dominate at a site where cool-season precipitation results in deep soil water storage, and grasses might dominate where warm-season precipitation favours shallow-rooted grasses (Romme et al., 2009). Precipitation that occurs when evaporative demand is high (during the warm season) tends to result in shallow and intermittent soil moisture, whereas precipitation that occurs when temperatures are cool or that accumulates in a snowpack can percolate to deep soil layers where it is stored until the growing season (Germino & Reinhardt, 2014; Sala et al., 1997). Deep moisture storage sustains plant growth during the warm season—when evaporative demand far exceeds precipitation inputs—and is crucial for understanding ecological dynamics in dryland ecosystems (Schlaepfer et al., 2012; Sturges, 1993).

Dry soil event patterns are critical in drylands and may not be well represented by meteorological drought indices. The interaction of evapotranspiration and soil texture influences the fate of incoming precipitation (Sala et al., 1992, 1997) and shapes both short-term episodic drought stress and chronic drought stress (Lauenroth et al., 2014; Smith et al., 2009). Plant responses to drought stress additionally depend on plant functional type. For instance, cool-season (C3) and warm-season (C4) grasses may have different water use efficiencies and subsequently variable tolerance to drought (Munson et al., 2011). Simultaneous low soil water availability (SWA) and high atmospheric demand for moisture may reduce productivity (Smith et al., 2009) and promote plant stress, dieback, mortality and potential ecological transformation (Adams et al., 2009; Renne et al., 2019). Moreover, the size and temporal distribution of precipitation events influence soil water percolation (Harper et al., 2005; Huxman et al., 2004; Knapp, 1996). As a result, the soil moisture impacts of short-episodic and chronic droughts can vary effects at particular depths.

Plant recruitment in drylands is strongly influenced by detailed patterns of soil moisture timing and can determine ecosystem recovery from disturbances and the success of ecological restoration. Limited restoration success results in many dryland ecosystems being transformed by the combination of disturbances and invasive species (Chambers et al., 2017; Germino et al., 2016). In drylands, the prevailing dry and hot conditions inhibit germination and often result in seedling mortality (Call & Roundy, 1991; Kildisheva et al., 2016). Long-lived woody plants like sagebrush depend heavily on surface moisture during the spring for seedling recruitment and for deep soil moisture recharge, which is necessary to sustain transpiration when hot temperatures dry out the upper soil layer (Barnard et al., 2021; Germino & Reinhardt, 2014; Schlaepfer et al., 2014). Seedling establishment is typically associated with wet soils and cool temperatures in the spring. For instance, winter snowpack is a better predictor of the spring soil moisture required for seedling establishment than yearly precipitation. This is likely because of the relationship of winter snowpack to soil water storage and release (Shriver et al., 2018). Plant-centric metrics—those that consider plant response to variable soil moisture, associated temperature conditions and atmospheric CO_2 concentrations—rather than climate-derived metrics, are thus needed to describe recruitment conditions in drylands.

Metrics of SWA and ecological drought may be particularly useful for assessing the environmental conditions that influence ecological resilience to disturbance and resistance to invasive grasses in drylands. The importance of understanding the factors that control resilience or the capacity of ecosystems to reorganise and regain their fundamental structure, processes and functioning (i.e., recover) when altered by stresses like longer and more severe drought and by disturbances such as altered fire regimes (Holling, 1973) is widely recognised. Equally important in many dryland ecosystems is an understanding of the factors that limit the population growth of invasive grasses, which have altered fire regimes, displaced native species and transformed ecosystems to alternative states (Chambers et al., 2016; Germino et al., 2016). In the western United States, resilience to disturbance and resistance to invasion vary over strong environmental gradients and closely reflect the complex patterns of moisture and temperature that characterise the areas diverse ecosystems (Chambers et al., 2014, 2016). In general, areas with relatively high temperatures and low and variable SWA are characterised by low to moderately low resilience, whereas areas with relatively low temperatures and greater and more consistent SWA are characterised by moderate to high resilience. Resistance to invasive grasses is a function of both environmental conditions and species interactions and is, therefore, species-specific. The observed increase in the frequency and severity of drought in recent decades (IPCC, 2022) has already decreased the ecological resilience of dryland ecosystems (Yao et al., 2021). Developing a better understanding of the complex patterns of moisture and temperature that influence resilience and resistance in dryland ecosystems (Chambers et al., n.d.) and of the projected changes in these patterns is essential for prioritising management actions and determining the most effective adaptive strategies in drought-driven ecosystems (Crausbay et al., 2017).

Here, we attempt to address this knowledge gap by pursuing three specific objectives for drylands across the western United States. First, we define a suite of metrics that complement climate variables and quantify the environmental conditions that shape water-limited dryland ecosystems. Because of their focus on moisture limitation and drought stress, we refer to these as "ecological drought metrics." Second, we assess the relationships among climate metrics and ecological drought metrics and quantify the novel information provided by the inclusion of the ecological drought metrics. Third, we characterise and map the spatial and temporal patterns of these metrics for the recent past.

2 | METHODS

2.1 | Study extent and ecoregions

We quantified climate and ecological drought metrics across dry areas of the western United States. These metrics could be calculated from any suitable dataset, but for the purposes of this article, we used a 1/16th degree (c. 6 km) gridded dataset (Schlaepfer et al., 2022). We considered areas with AI (MAP/PET) less than 0.65; additionally, we excluded warm-moist areas with mean monthly air temperature >4 C° and April–June precipitation >75 mm. The study region is $3.1 \times 10^{\wedge}6\ km^2$ bounded by longitude −124.6° and −93.5° and latitude 25.9° and 49°. The region spans most of the western United States from Mediterranean California to the eastern edge of North and South Dakota.

We summarised spatial patterns for 12 ecoregions (Figure 1), which we derived from a combination of EPA Level II and Level III

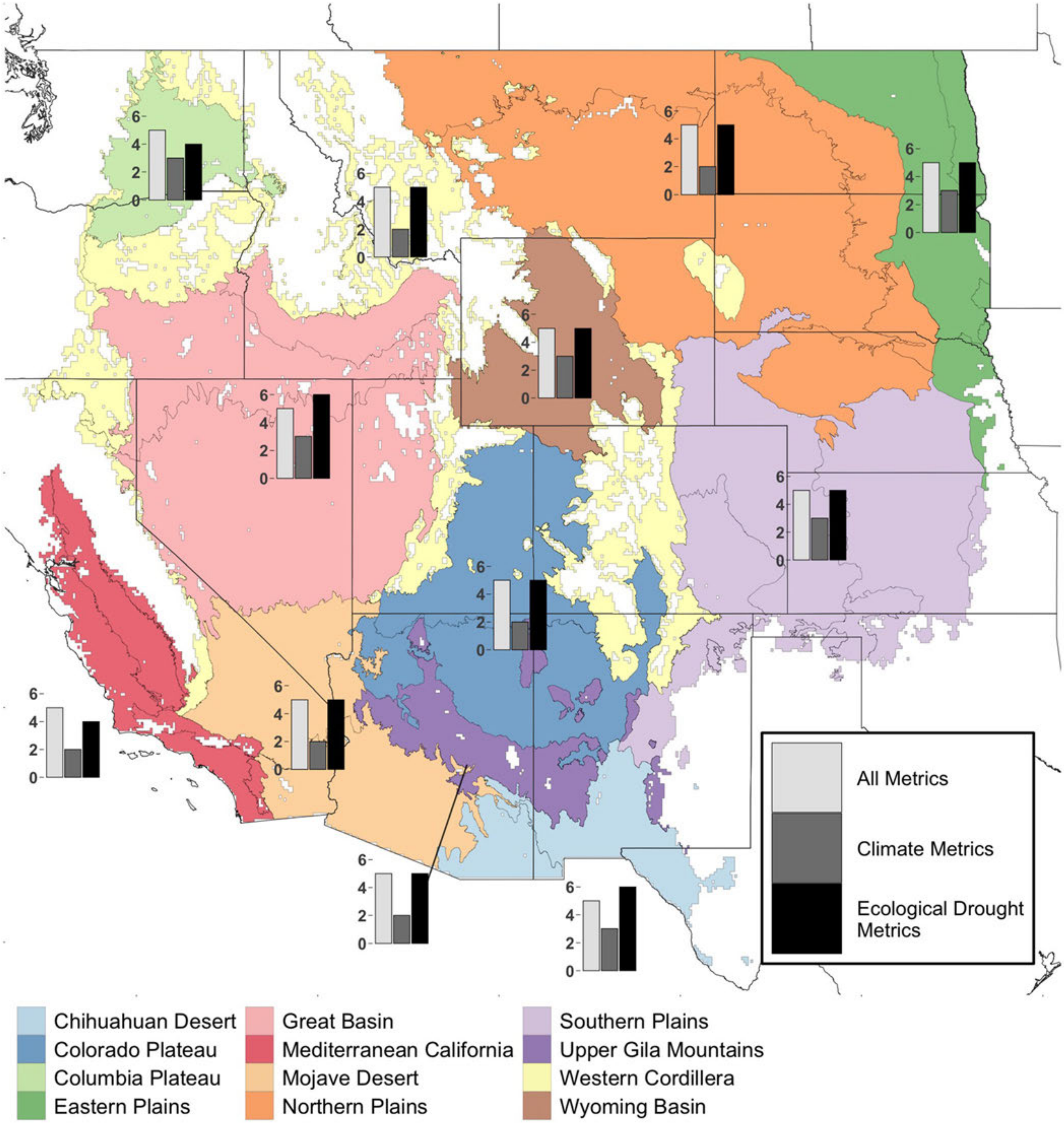


FIGURE 1 Ecoregions included in the study region and the corresponding results for the three principal component analyses (PCAs) performed on Table 1 metrics, reported as bar charts by ecoregion. Bars represent the number of principal components needed to explain 90% of the total variance of the dataset. This number is reported for a PCA using (1) all metrics, using (2) only climate metrics and using (3) only ecological drought metrics.

ecological regions (Omernik & Griffith, 2014). We separated Level II Cold Deserts into three ecoregions: the Columbia Plateau, the Great Basin and the Colorado Plateau. We defined the Colorado Plateau as the combination of Level III Arizona/New Mexico Plateau and the Colorado Plateaus, the Chihuahuan Desert as the combination of the Western Sierra Madre Piedmont and the Chihuahuan Desert and the Mojave Desert as the combined Level II Warm Deserts clipped to the study region. All other ecoregions are unaltered Level II polygons. To illustrate ecoregional differences, we examined detailed results for a single example grid cell from each ecoregion (Appendix A). Example sites were chosen from a pool of sites that were within 25% of a standard deviation of the mean for the ecoregion for mean annual temperature (MAT), MAP, and precipitation seasonality. From these sites, we chose the site with the closest MAT to the ecoregional mean. This method delivered an unusually dry site for the Eastern Plains, so instead of 25% of a standard deviation, we used 7% of a standard deviation and then chose the site with the closest MAP to the ecoregion mean.

2.2 | Ecohydrological modelling

We simulated water balance pools and fluxes on the 1/16th degree grid, including daily soil moisture at multiple depths with the SOILWAT2 ecosystem water balance model (SOILWAT2 v5.1.0; R packages rSOILWAT2 v3.1.0 and rSFSW2 v3.0.0; SOILWAT2 is open-source, details available in GitHub repositories: Schlaepfer & Andrews, 2019; Schlaepfer & Murphy, 2019). SOILWAT2 is a process-based simulation model with a daily time step, multiple soil layers, snowpack dynamics, multiple vegetation types responsive to atmospheric CO2 concentrations and hydraulic redistribution. The model has been used and validated successfully in dryland ecosystems in North American and globally (Bradford et al., 2014, 2019, 2020; Palmquist et al., 2016; Petrie et al., 2020; Schlaepfer et al., 2012; Tietjen et al., 2017).

Forcing values for the simulation runs for 1970–2010 included daily meteorological data at the 1/16th degree resolution from Livneh et al. (2013). We extracted soil properties for all grid cells for up to eight soil layers with a maximal depth of 200 cm. Each soil layer was described with content of sand, clay and silt; volume of coarse fragments; and bulk density from ISRIC-WISE30sec (Batjes, 2016). We split the shallow soil layer into two layers of 0–10 and 10–20 cm for higher resolution at shallow depths. We applied methods described in Bradford et al., 2014 to estimate relative composition of woody plants and grasses (C3 and C4 types) as well as monthly biomass, litter and root distributions from climate conditions.

We developed a new R package rSW2metrics to calculate ecological drought metrics from daily SOILWAT2 simulation output (details available in GitHub repository: Schlaepfer et al., 2022). SOILWAT2 simulations were executed on the USGS Yeti Supercomputer (Falgout & Gordon, 2022). Data generated during this study are available from the USGS ScienceBase-Catalog (Schlaepfer et al., 2022).

2.3 | Drought metrics descriptions

We defined a suite of 27 climate and ecological drought metrics (Table 1) that represent yearly conditions in five categories:

Overall conditions metrics describe the aridity and overall growth potential of a site. In these, we include MAT and MAP, total growing degree days (TDD), warm-season length, and first and last frost dates, which are all climate-driven metrics that broadly describe the suitability of growing conditions or the timing of the growing season. Wet degree days (WDD; Roundy et al., 2007), dry degree days (DDD), SWA and climatic water deficit (CWD; Stephenson, 1998) describe the general moisture conditions that are derived from soil moisture simulations. These we consider ecological drought metrics, as we do all metrics in the following categories unless otherwise noted.

Seasonal variability metrics represent the magnitude of intraannual variability and are calculated as the coefficient of variation (CV) of monthly TDD (climate metric), SWA and CWD. The seasonal variability of growing conditions can vary greatly across space and influence the functional availability of warm temperatures and moisture for plant growth.

Seasonal moisture timing metrics represent the seasonality of moisture availability and drought stress and are calculated as the monthly correlation temperature with precipitation (climate metric), WDD, SWA and CWD.

Extreme drought metrics characterise severe drought stress at a site. The 10-day maximum of CWD, maximum DDD spell and the length and number of dry soil intervals (DSIs), all describe the timing and severity of drought conditions.

Recruitment potential metrics quantify the favourability of conditions for plant recruitment during spring and fall. Recruitment potential is calculated as the sum of WDD during the most favourable continuous periods with warm conditions and wet near-surface soils in both the spring and fall. We quantified onset timing (day of year), duration and accumulated WDD for the most favourable period in the spring and fall.

2.4 | Assessment of climate and ecological drought metrics

We quantified multivariate relationships and dimensionality of metrics with principal component analysis (PCA) on scaled values. We contrasted PCAs of three groups of metrics: (i) all metrics ($n = 27$), (ii) climate-driven metrics ($n = 8$) and (iii) soil moisture-driven metrics ($n = 19$). Climate-driven metrics are MAT, MAP, precipitation seasonality, TDD and its seasonal variability, warm-season length, and the timing of first and last frosts. The remaining 19 metrics (Table 1) comprise the suite of ecological drought metrics.

We calculated the interannual mean and either the detrended standard deviation or the detrended CV for every grid cell from annual values of the 27 metrics in Table 1. Variables were detrended by subtracting trend calculated from the Theil-Sen slope of the time series. We calculated standard deviation for MAP, first and last frost days, seasonal timing of moisture metrics and the timing of recruitment and calculated CV for all other metrics. We quantified pairwise relationships among metrics, in groups by category (Table 1), as both scatterplots and maps of residuals of simple linear regression (Appendix B).

All analyses were done in R (R Core Team, 2021).

Results from the PCA on the full group of metrics (climate and ecological drought) compared to only climate metrics (Appendix D: Table D1) suggest that the ecological drought metrics provide additional information that complements the information provided by climate metrics.

TABLE 1 Climate ($n = 8$) and ecological drought metrics ($n = 19$), grouped into categories

Overall growing conditions			
Total growing degree days (TDD)	*Total growing degree days (dd), where daily mean air temperatures above 5°C accumulate on days without snow cover*		
Warm-season length	*The longest spell (days) of total growing degree days*		
Wet degree days (WDD)*	*Wet degree days (dd) where daily mean air temperature above 5°C accumulates if there is no snow cover, and if any soil layer within 0–100 has a soil water potential > −1.5 MPa*		
Dry degree days (DDD)*	*Dry degree days (dd) where daily mean air temperature above 5°C accumulate if there is no snow cover, and if all soil layers 0–100 cm have soil water potential < −3.0 MPa*		
Soil water availability (SWA)*	*Daily sum (mm) across soil layers in 0–20 cm and 20–100 cm of soil water content held at a potential > −3.9 MPa*		
Climatic water deficit (CWD)*	*Evapotranspiration (mm) subtracted from potential evapotranspiration*		
First/last frost	*The day of year during which the first/last exposure to frost occurs after the warm season/before the warm season*		
Seasonal variability		Seasonal moisture timing	
TDD seasonal variability	*Monthly CV of TDD*	Precipitation Seasonality	*Correlation of monthly precipitation and air temperature*
SWA seasonal variability*	*Monthly CV of mean daily SWA*	WDD Seasonality*	*Correlation of monthly WDD and air temperature*
CWD seasonal variability*	*Monthly CV of CWD*	SWA Seasonality*	*Correlation of monthly SWA and air temperature*
Recruitment		CWD Seasonality*	*Correlation of monthly CWD and air temperature*
Spring/fall recruitment index*	*WDD (dd) at 10–20 cm soil depth of the spring/fall recruitment period. The recruitment index has the most WDD after midsummer, where recruitment events are spells that start after 3-day periods of WDD > 0 and sum to WDD > = 15 in soil layers 0–10 cm and end either after 3-day periods of DDD > 0 that sum to DDD > = 15 in 0–20 cm OR after 3-day periods where TDD = 0.*	Extreme drought	
		CWD 10-Day maximum *	*Mean CWD (mm/day) during maximum 10-day CWD period*
		Maximum DDD spell*	*Degree days accumulated during maximum DDD spell*
Spring/fall recruitment onset and duration*	*The day of year of the onset and duration (days) of the spring/fall recruitment period*	Dry soil interval (DSI) length*	*Mean spell length (days) of dry soils where all soil layers in the 0–100 cm have soil water potential < −1.5 MPa*
Proportion of years with recruitment events*	*Proportion of years in the time series with recruitment events*	Number of DSI*	*Number of spells with dry soils*

Note: Each metric was calculated for each year at each site. Not shown are mean annual precipitation (MAP) and mean annual temperature (MAT), although they are included in the number of climate metrics (n) above.
Abbreviation: CV, coefficient of variation.
*indicates ecological drought metrics derived from water balance simulations.

3 | RESULTS

The 27 environmental metrics (see Section 2 and Table 1) include several new soil moisture metrics designed to quantify ecological drought stress and growing conditions in dryland ecosystems. Results from the PCA on the full group of metrics (climate and ecological drought) compared to only climate metrics (Appendix D: Table D1; also see Appendix D: Table D2 for PCA results including AI) suggest that the ecological drought metrics provide additional information that complements the information provided by climate metrics. Specifically, the first three principal components (i.e., the first three dimensions) explained 97% of total variance ($\sigma^2 = 5.9$) in the climate-only dataset compared to only 87% of the variance ($\sigma^2 = 13.6$) in the full dataset and 84% of variance ($\sigma^2 = 9.5$) in the ecological drought dataset (Appendix D). Likewise, five principal components were required to represent 90% of the variance for the soil moisture dataset compared to only four for the full dataset and three for the climate dataset. This increased dimensionality introduced by the ecological drought metrics was reasonably consistent within ecoregions (Figure 1; Appendix D).

These metrics may provide a more comprehensive geographic perspective on ecologically relevant temperature and moisture patterns. For example, contrasting patterns at example sites in the Great Basin (Figure 2) and in the Eastern Plains (Figure 3) illustrate how water balance and water availability are influenced by the Great Basin's winter-wet seasonality compared to the Eastern Plains' summer-wet seasonality. Mean daily SWA at the Eastern Plains example site peaks around 70 mm in May and remains above zero (~15 mm) throughout the year (Figure 3b), whereas SWA in the

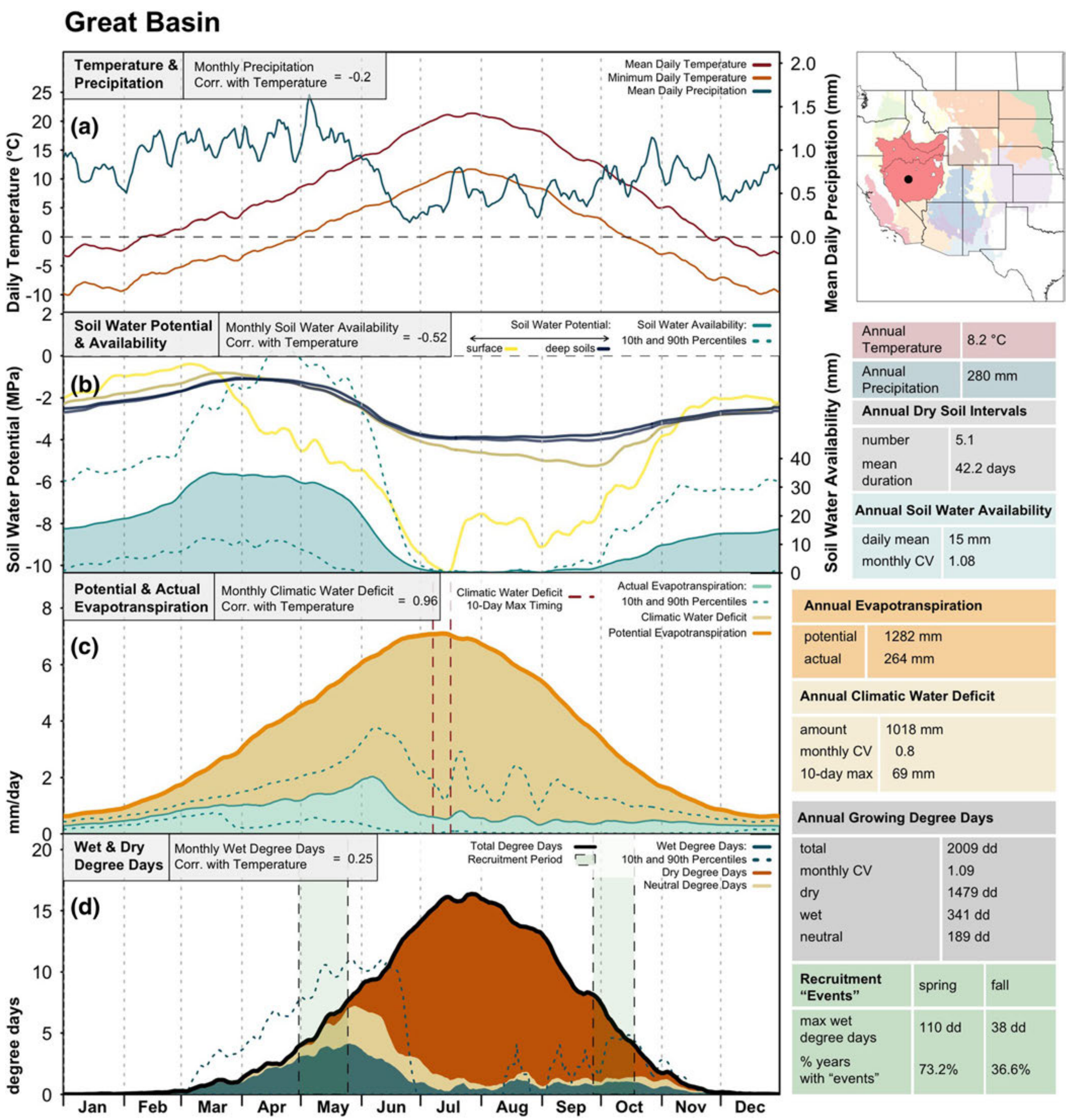


FIGURE 2 Conceptual illustration of interacting climate and ecological drought metrics at an example site in the Great Basin. Example sites are meant to show how these metrics can differ among ecoregions, not to represent variability within an ecoregion, which is described in Appendix A. (a) shows that the Great Basin has a cool-season moisture seasonality, resulting in high soil water availability (SWA) during the spring (b). Soil water potential (SWP) is shown at four depths: 0 to 10 cm (surface soils; yellow line), 10 to 20 cm (tan line), 20 to 40 cm (grey line) and 40 to 60 cm (deep soils; navy line). (c) and (d) show that unmet evaporative demand translates to high accumulation of dry degree days (DDD) by the end of the growing season. As a result, recruitment periods are short and occur in spring and infrequently in the fall. Recruitment "events" refer to the potential for recruitment during a specified season. Full definition of these variables is presented in Table 1.

Great Basin peaks around 35 mm in March and then declines to nearly zero during the hottest months (Figure 2b). Soil water potential (SWP) also illustrates the summer-wet nature of the Eastern Plains, wherein shallow soils rapidly dry in November and stay dry until March. CWD peaks during the hottest times of the year in both ecoregions, but in the Eastern Plains, actual evapotranspiration (AET) follows the same pattern as atmospheric demand, because more moisture is present and available during the warm season as

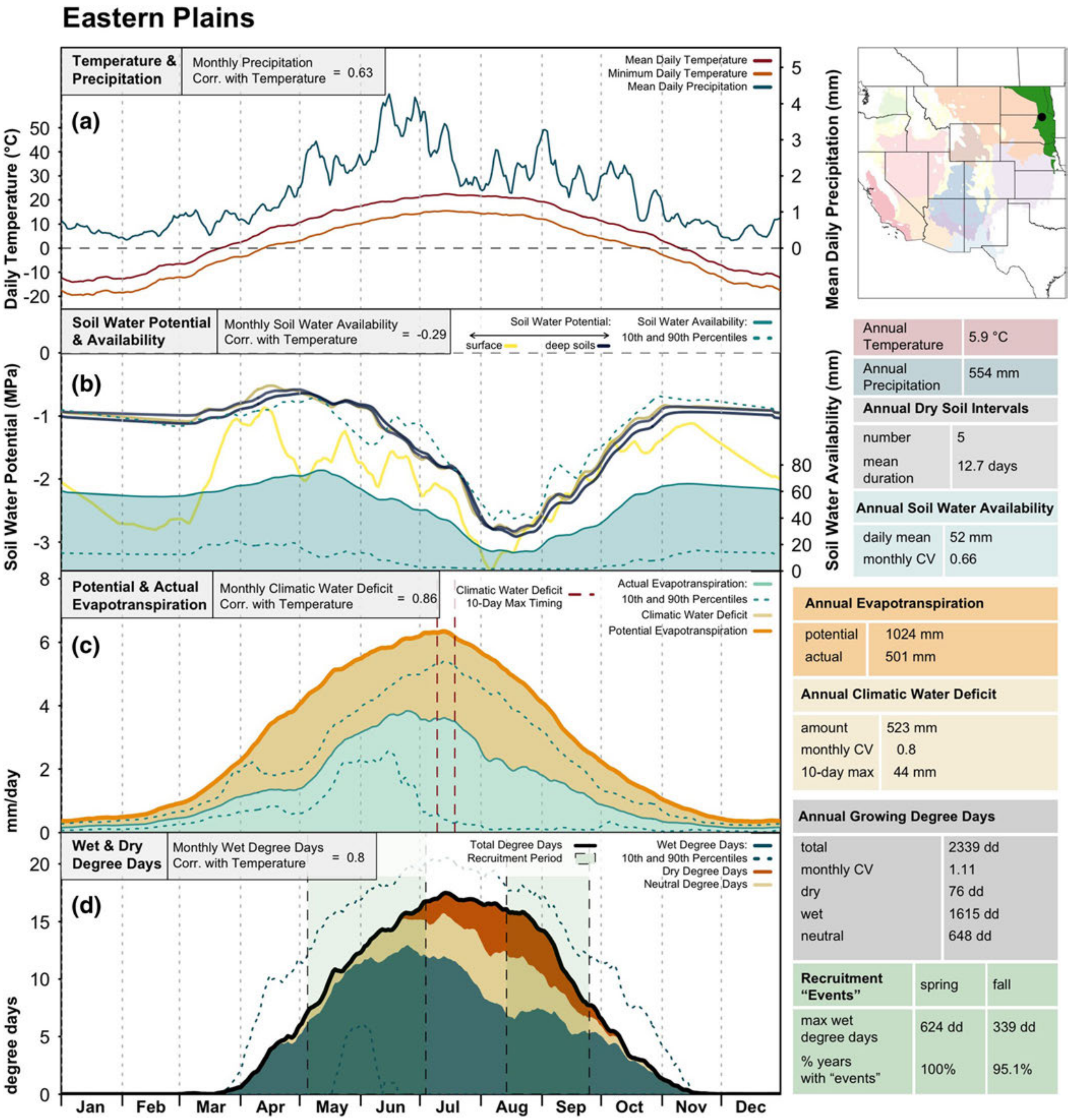


FIGURE 3 Conceptual illustration of interacting climate and ecological drought metrics at an example site in the Eastern Plains. Example sites are meant to show how these metrics can differ among ecoregions, not to represent variability within an ecoregion, which is described in Appendix A. (a) shows a warm-season moisture seasonality with soil water availability (SWA) remaining consistently above zero (a hallmark divergence from the majority of the study region; b). Soil water potential (SWP) is shown at four depths: 0 to 10 cm (surface soils; yellow line), 10 to 20 cm (tan line), 20 to 40 cm (grey line) and 40 to 60 cm (deep soils; navy line). (b) also shows the tendency of shallow soils to stay dry during the cool season. The spring recruitment period is also relatively long, lasting well into summer, and fall recruitment occurs from early August to early September (d). Recruitment "events" refer to the potential for recruitment during a specified season. Full definition of these variables is presented in Table 1.

compared to the Great Basin (Figures 2 and 3c). Recruitment periods in the Great Basin are shorter, have fewer WDD and occur less frequently than in the Eastern Plains.

Other ecoregional differences may have ecological relevance. For example, the Chihuahuan Desert is the only ecoregion with seasonal moisture availability patterns that do not rely on the winter accumulation of soil water. SWA and WDD are low at the end of winter and remain low until the onset of the monsoon in midsummer (Appendix A: Figure A1). Similarly, during midsummer, SWP declines in shallow soils in all ecoregions except the Southern Plains and the Wyoming Basin. In these regions, shallow soil moisture behaves similar to deep soils during the growing season but decreases substantially during the cool season. Additionally, maximum 10-day CWD occurs slightly after the CWD peak in the Eastern Plains, Wyoming Basin and Western Cordillera ecoregions. In other ecoregions, it coincides with the CWD peak. Water is always scarce in the Mojave Desert, where SWA is low throughout the year and mean WDD is at all times of the year (Appendix A: Figure A5). Mediterranean California, Columbia Plateau, Eastern Plains, Southern Plains and Western Cordillera also have longer spring recruitment periods than other ecoregions, with recruitment occurring much later in the season in the plains.

3.1 | Overall growing conditions

TDD, warm-season length (longest TDD spell) and the dates of first and last frost are closely related to temperature, and frost does not occur in the hot deserts (Figure 4; Appendix B: Figures B1, B2; Appendix C: Figure C1). Highest TDD occur in the Mojave Desert (long-term average of 5224 dd), the Chihuahuan Desert (4030 dd) and Mediterranean California (3940 dd), whereas the fewest TDD occur in the Western Cordillera (1543 dd) and Wyoming Basin (1631 dd; Appendix A: Table A1). Warm-season length follows the same pattern: It is longest in the Mojave Desert (312 days) and Mediterranean California (313 days) and shortest in the Western Cordillera (136 days) and the Wyoming Basin (130 days). The last spring frost occurs earliest in Mediterranean California (Day 27) and the Mojave Desert (Day 27), whereas the first autumn frost is earliest in the Wyoming Basin (Day 278) and latest in Mediterranean California (Day 347).

Moisture-driven metrics that describe overall growing conditions (WDD and DDD, SWA and CWD) display similar patterns at broad geographic scales but distinct patterns at fine scales. In general, the southwest portions of our study region have the driest conditions (high DDD and CWD and low WDD and SWA), whereas the high mountains and Eastern Plains have the wettest conditions (Figure 4). DDD and CWD are greatest in the Mojave Desert (4611 dd and 1669 mm, respectively) and lowest in the Eastern Plains (378 dd and 532 mm). WDD and SWA indicate that the greatest moisture availability is in the plains (especially the Eastern and Southern Plains; Figure 4). WDD range from 353 to 1450 dd and are highest in the Eastern Plains (1450 dd). The Southern Plains (1344 dd) and Northern Plains (915 dd) have the next highest WDD, and the Great Basin (412 dd) and the Wyoming Basin (353 dd) have the lowest WDD. SWA ranges from 4.8 to 42.4 mm across the study region and is low in ecoregions where CWD is high. SWA is highest in the Eastern Plains (42.4 mm) and decreases along a longitudinal gradient. SWA is higher with elevation; the Western Cordillera (35.2 mm) has higher SWA than the Southern (26.4 mm) and Northern Plains (20.3 mm). SWA is also lowest in the Mojave Desert (4.8 mm) and the Chihuahuan Desert (6.9 mm). Spatial correlations (Appendix C: Figure C2) indicate that WDD and SWA are strongly related to MAP ($r = 0.69$ and 0.70 respectively), whereas DDD and CWD are more clearly related to MAT ($r = 0.88$ and 0.86 respectively).

3.2 | Magnitude of seasonal and interannual variability of overall growing conditions

The within-year seasonal variability of TDD, SWA and CWD displays distinct spatial patterns in temperature and moisture conditions (Figure 5, Appendix A: Table A2). Seasonal variability (CV of monthly values) of TDD is greatest in the Wyoming Basin (1.22) and Western Cordillera (1.21) and lowest in Mediterranean California (0.55) and the Mojave Desert (0.60). Seasonal variability of SWA is greatest in the Mojave Desert (1.93) and lowest in the Eastern Plains (0.74). CWD seasonal variability ranges from 0.61 in the Chihuahuan Desert to 0.96 in the Columbia Plateau. Additionally, TDD and CWD seasonal variability are positively related ($r = 0.49$), and TDD and SWA seasonal variability have a strong negative relationship (−0.71; Appendix C: Figure C3).

These metrics also provide insight into the magnitude of interannual variability (CV of annual values) among regions. Whereas they have the highest TDD, the Mojave Desert (0.05), the Chihuahuan Desert (0.05) and Mediterranean California (0.05) are also the least variable over the course of the time series (Appendix A: Table A1). At the same time, the Western Cordillera (0.83) and Wyoming Basin (0.85) have the highest interannual TDD variation. Ecoregions with high DDD have low interannual variability, and the plains—which have the lowest DDD—also have the greatest variability. CWD is also least variable in ecoregions where it is highest—the Mojave (0.05) and the Chihuahuan Desert (0.07). WDD are least variable in the Eastern Plains (0.28), the Western Cordillera (0.30) and the Southern Plains (0.32) and most variable in the Mojave Desert (0.65). In all ecoregions, the timing of the last frost is more variable throughout the time series than the timing of the first frost, except in the plains, where the timing of the last frost is more variable.

3.3 | Seasonal moisture timing

To assess the seasonal timing of moisture, we quantified correlations between mean monthly temperature and four variables (precipitation, WDD, SWA and CWD; Figure 6, Appendix A: Table A3, Appendix B: Figure B4). Positive correlations indicate warm-season moisture, and negative correlations indicate cool-season moisture. Seasonal precipitation timing is most positive in the plains (0.54 to 0.64) and most negative in Mediterranean California (−0.57) and the Columbia Plateau (−0.46). By contrast, seasonal WDD timing is positive in all ecoregions except for Mediterranean California (−0.51) and the Mojave Desert (−0.11). Seasonal SWA timing is negative in all ecoregions (although some small areas are positive), indicating that virtually all locations have the highest SWA during cool temperatures. SWA

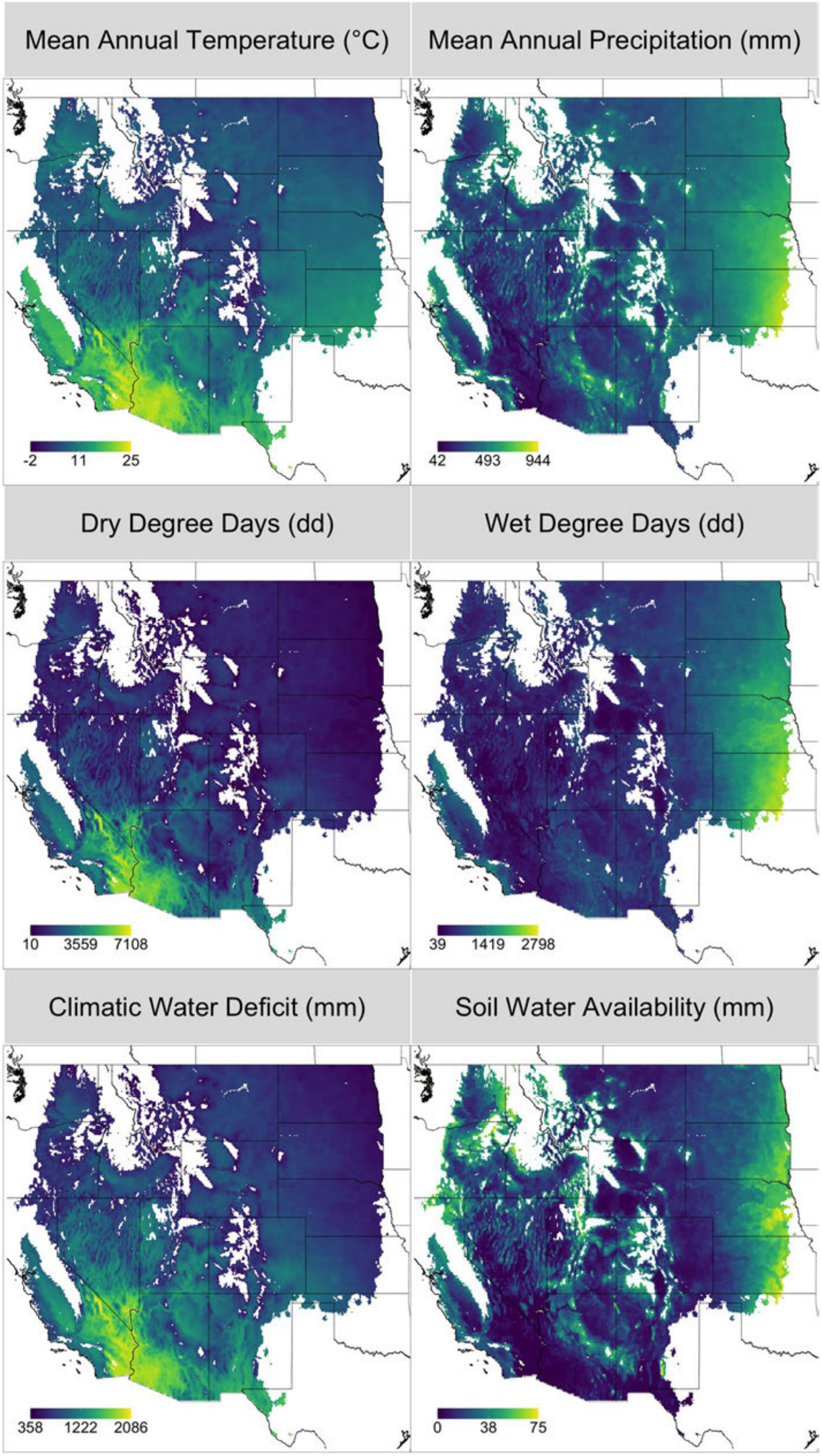


FIGURE 4 Overall moisture and temperature conditions depicting the across-year mean annual temperature (MAT) and mean annual precipitation (MAP), dry degree days (DDD), wet degree days (WDD), climatic water deficit (CWD) and soil water availability (SWA). DDD and CWD follow temperature trends, with highest values in the southwest, and WDD and SWA are similar to MAP, with the greatest moisture occurring in the plains.

seasonal timing was the most negative in Mediterranean California (−0.70) and the least negative in the Northern Plains (−0.11). CWD seasonal timing is positive in all ecoregions, meaning that high CWD occurs during the warmest temperatures. CWD seasonal timing ranges from 0.81 in the Chihuahuan Deserts (SD) to 0.95 in the Great Basin (SD).

Spatial patterns in the seasonal timing of WDD, SWA and CWD are not well explained by patterns of seasonal timing of precipitation

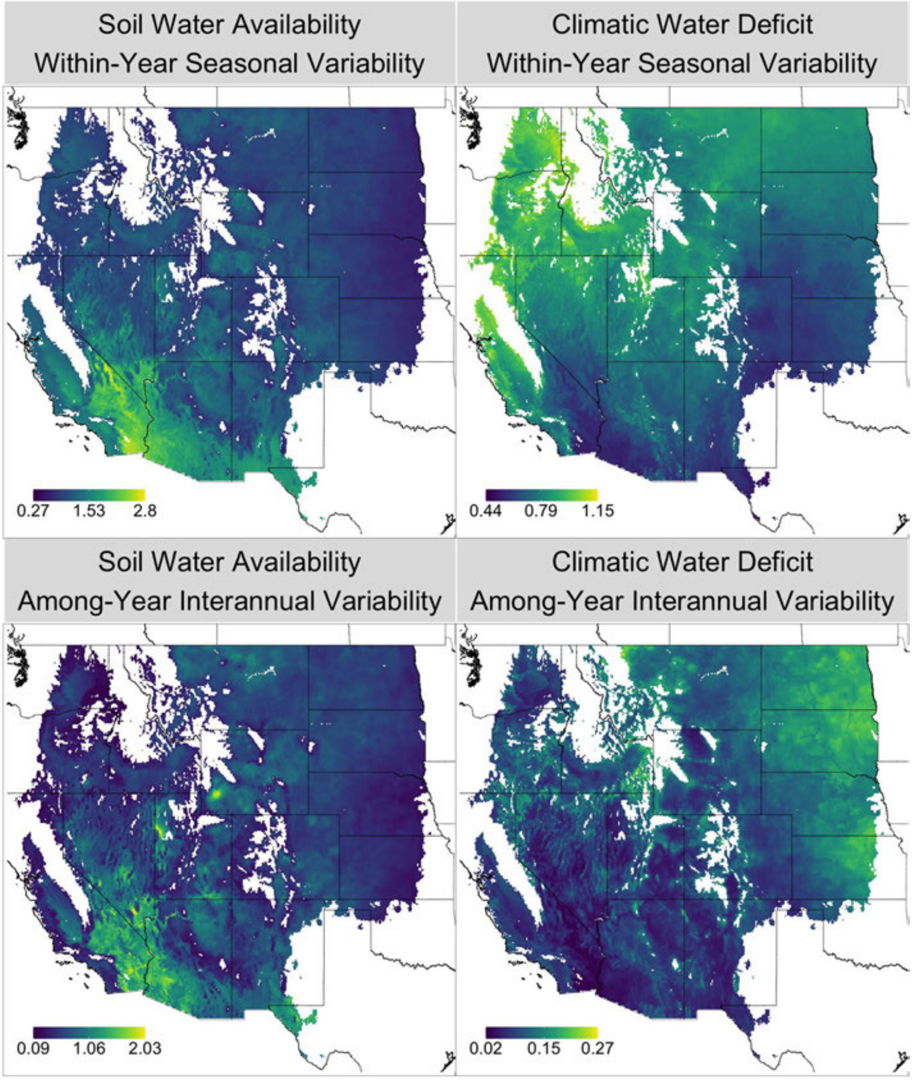


FIGURE 5 Long-term annual averages of temporal variability in soil water availability (SWA) and climatic water deficit (CWD). Seasonal variability (CV of mean monthly values; top) and year-to-year variability (CV of annual values; bottom) demonstrate that SWA is highly variable both within and among years in the southwest, whereas CWD is most variable within years in the northwest and most variable among years in the eastern great plains.

(Figure 6). The seasonal timing of precipitation explains 73% of the variability in WDD seasonal timing, 72% of the variability in SWA seasonal timing and 51% of the variability in CWD seasonal timing. Although precipitation seasonal timing changes from negative (cool-season precipitation) in the west to positive (warm-season precipitation) in the east, WDD and SWA have different geographic patterns. Areas near the eastern extent of the plains as well as portions of the Chihuahuan Desert have lower CWD seasonal timing than expected based on precipitation seasonal timing, whereas areas of the Wyoming Basin and Western Plains have higher values than expected (Figure 6, top row, second panel from the left).

3.4 | Drought events and extreme drought

To assess intraannual temporal patterns of drought conditions, we quantified the 10-day CWD maximum, maximum DDD spell, mean length and number of DSIs. CWD 10-day maximum and maximum DDD spell display similar geographic patterns, with the most extreme hot and dry conditions occurring in the southwest and less extreme hot and dry conditions in the northeastern portion of the study region (Figure 7; Appendix A: Table A4, Appendix B: Figure B5). CWD 10-day maximum ranges from 4.89 mm in the Eastern Plains to 9.04 mm in the Mojave Deserts. Interannual variability is low where CWD 10-day maximum is high (interannual CV $= 0.03$ in the Mojave Desert), and interannual variability is highest where CWD 10-day maximum is lowest (interannual CV $= 0.21$). Similarly, the maximum DDD spell is highest in the Mojave Desert and lowest in the Eastern Plains. The Eastern Plains also has the fewest degree days, 186 dd, from the maximum DDD spell compared to 423 dd in the Northern Plains and 442 dd in the Southern Plains.

Mean DSI length averages 35 days across all ecoregions and is longest in Mediterranean California (82 days) and the Mojave Desert (70 days). The Eastern Plains have the shortest and most variable DSI length (17 days). Mean annual DSI number is also the greatest and least variable in the Chihuahuan Desert (9.79). It is, however, the fewest and most variable in Mediterranean California (3.31). DSI length and DSI number are negatively related ($r = -0.46$), and MAT explains 27% of the variability of DSI length and only 1% of the variability of DSI number (Appendix C: Figure C4).

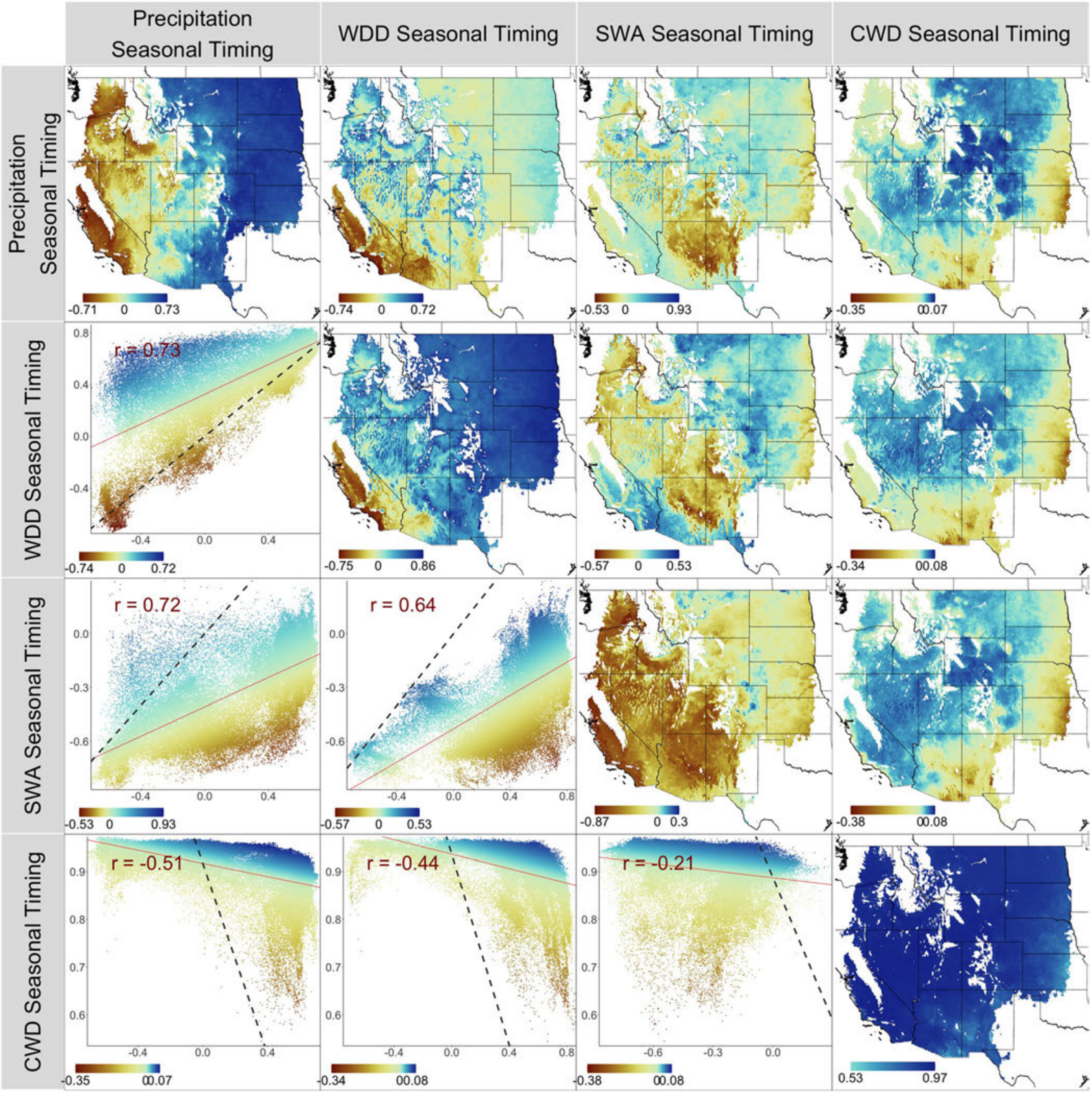


FIGURE 6 Correlation matrix displaying the relationships of metrics related to the timing of seasonal moisture. Maps along the diagonal show the mean of the metric that is labelled in both the row and the column position. The plots below the diagonal show the residuals of the regression wherein the row variables are the dependent and the column variables are the independent. The residuals are mapped for all sites in the study region based on the same regression (plots above and to the right of the diagonal). Correlations among precipitation seasonality, wet degree days (WDD) seasonality and soil water availability (SWA) seasonality were all strong and positive, whereas all three were negatively correlated with climatic water deficit (CWD) seasonality.

3.5 | Recruitment potential

We evaluated potential for plant recruitment by identifying hypothetical recruitment periods and quantifying onset, duration and WDD of the most favourable (highest WDD) periods in spring and fall for each year. We also recorded the timing and frequency of those periods in each season. Spring recruitment potential, in years when a spring recruitment period occurs, is greatest in the Eastern Plains (612 dd) and Mediterranean California (542 dd) and is generally low throughout the entire intermountain region (Figure 8, Appendix A: Table A5, Appendix B: Figure B6). Spring recruitment is earliest in Mediterranean California (Day 29) and latest in the Wyoming Basin (Day 144).

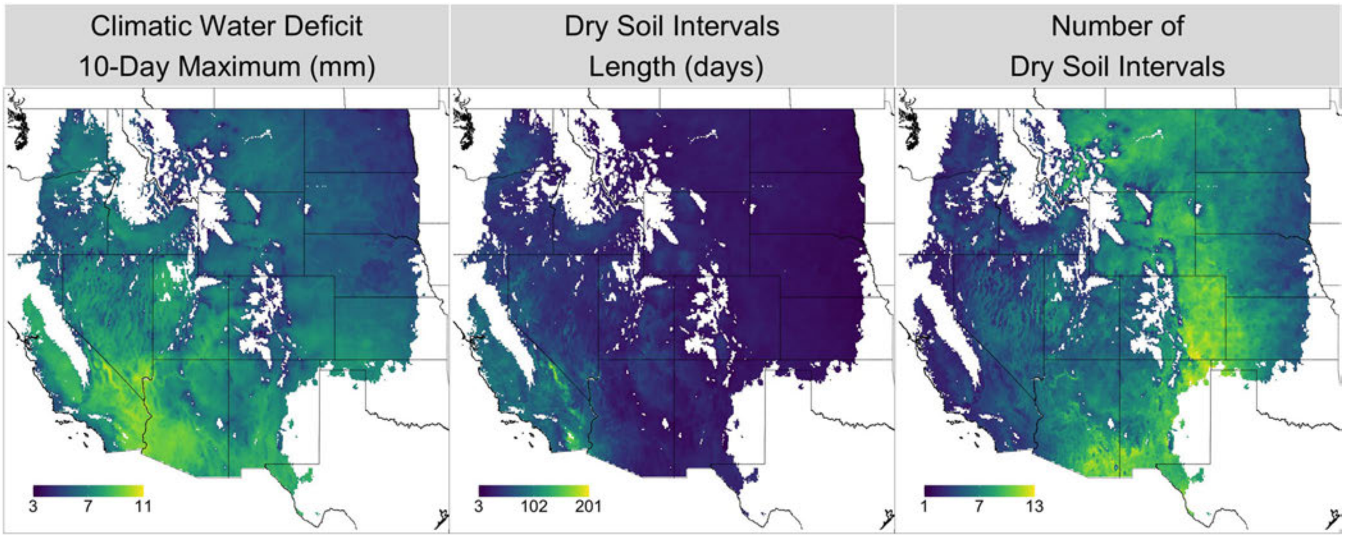
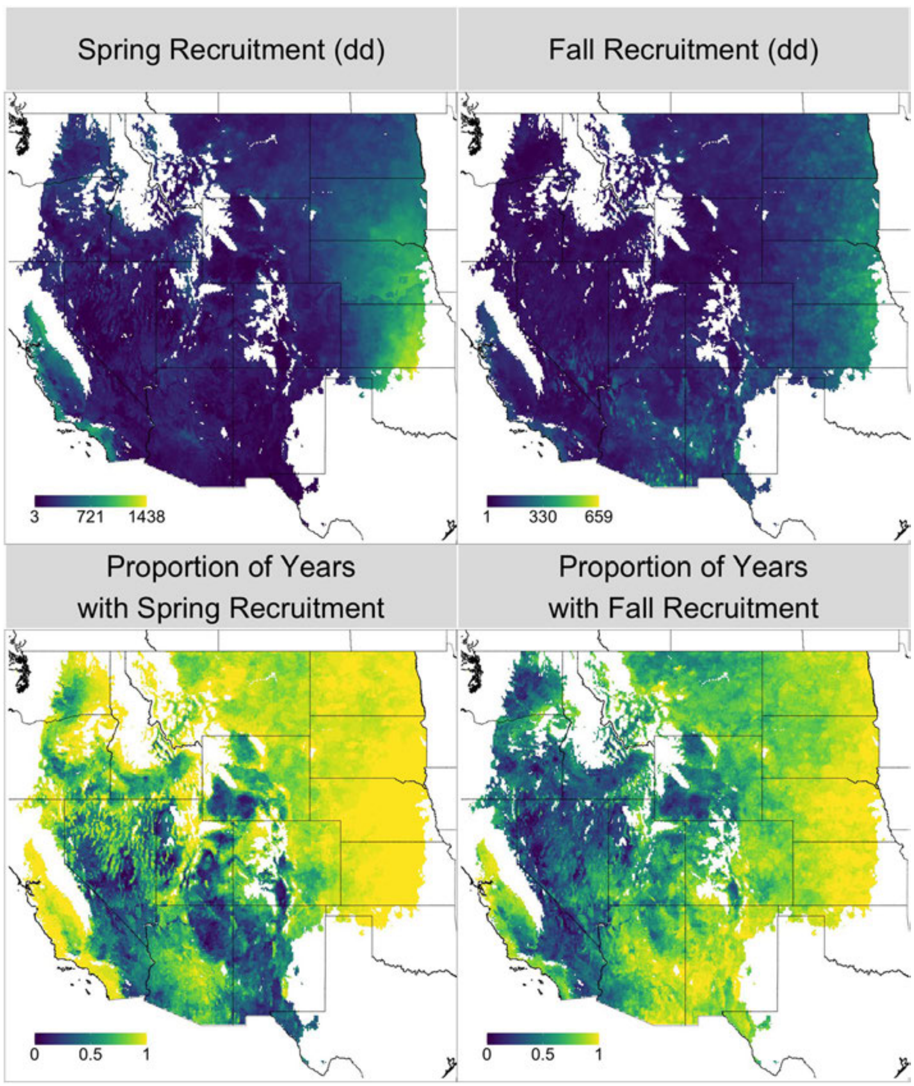


FIGURE 7 Long-term annual averages of climatic water deficit (CWD) 10-day maximum, dry soil interval (DSI) length and number across the study region. CWD 10-day maximum follows the same pattern as mean annual temperature (MAT; not shown). DSI length is greatest in the east and southeast (middle panel), but DSI is most frequent in the central/eastern portion of the study region (right panel).

FIGURE 8 Spring and fall recruitment indices (top) and proportion of years in which events occur (bottom). Spring and fall recruitment potentials are both high on the eastern extent of the study region but differ in the western half of the extent.



Spring recruitment potential has a weak negative relationship with the timing of recruitment (r = −0.19; Appendix C: Figure C5). Additionally, spring recruitment periods occur in 77% of years when averaged across all sites in the study region. The frequency of years with spring recruitment, however, was especially low in the Chihuahuan Desert (45% of years) and in the Colorado Plateau (47% of years).

Fall recruitment potential is also higher in the eastern and southern portions of the study region. It is highest in the Eastern Plains (269 dd, CV = 0.88), followed by the Upper Gila Mountains (210 dd, CV = 0.90) and the Southern Plains (209 dd, CV = 0.96). Fall recruitment timing is earliest in the Eastern Plains (Day 231, SD = 29.2 days) and latest in Mediterranean California (Day 315, SD = 22.6 days). Fall recruitment potential and timing also have a negative relationship (r = −0.39). Fall recruitment periods occur in 69% of years across the entire study region. This frequency is also lower, however, in the Great Basin (39% of years), the Wyoming Basin (47% of years) and the Columbia Plateau (47% of years). Moreover, in the Chihuahuan Desert, where the frequency of years with spring recruitment periods is low, the same frequency of fall recruitment periods is high (88% of years). At the same time, the Eastern Plains (94%), the Upper Gila Mountains (92%) and the Southern Plains (90%) have the most consistent years with fall recruitment.

4 | DISCUSSION

Drylands are highly variable water-limited ecosystems in which multifaceted moisture dynamics control vegetation. To address these dynamics, we evaluated a suite of 27 metrics that include new variables designed to represent the specific conditions that drive ecological dynamics for dryland vegetation. Compared to only climate metrics, the ecological drought metrics substantially increase data dimensionality (Figure 1; Appendix D: Table D1), illustrating that these metrics have potential to increase overall understanding of ecological responses that emerge from water limitation in drylands. This suite of metrics can be used along with other data products like land cover or species distribution models to assess patterns of spatial and temporal variation in ecological structure and function and of controls on ecological resilience and resistance in water-limited ecosystems.

4.1 | Overall patterns of dryland moisture availability

We developed metrics that have potential for quantifying overall plant growth in drylands and designed them to be more ecologically relevant than meteorologically derived indices of aridity or drought. By building on the fundamental concept of growing degree days (Wang, 1960), we partitioned TDD into WDD, which occur when soils are at least partially wet (WDD; Roundy et al., 2007), when soils are entirely dry (DDD) or intermediate "neutral" conditions. The growing degree days approach recognises that the role of moisture in an ecosystem is fundamentally mediated by temperature (Running et al., 2004). In cold conditions, moisture status is less important, whereas in warm-hot conditions, moisture status distinguishes between optimal growth conditions (e.g., hot-wet tropical rainforests with high WDD) and extreme or stressful conditions (e.g., hot-dry deserts with high DDD). Thus, regions with similar TDD can vary drastically in overall growth potential. This is evidenced by the comparison of the Great Basin (Figure 1) and the Eastern Plains (Figure 2). In water-limited drylands, WDD may, therefore, be a useful indicator of plant growth.

In addition to WDD, we quantified SWA as a measure of the amount of water available in the soil for plant transpiration (Andrews et al., 2020). Both WDD and SWA provide perspectives on dryland growth potential that complement precipitation or aridity indices, although SWA does not represent limitations imposed by low temperature. SWA accounts for the storage of accessible moisture, whereas WDD quantifies growth potential based on the presence of moisture in conjunction with suitable temperatures for growth. Unsurprisingly, WDD and SWA are both related to precipitation, but they have a weaker relationship with one another (Appendix C: Figure C2). WDD is lower than expected—based solely on its relationship to precipitation—in high-elevation areas and on the eastern extent of the study region. WDD additionally captures a bimodal pattern in ecoregions that experience monsoons, notably the Colorado Plateau and Upper Gila Mountains. Quantifying the moisture storage (SWA) and the growth potential (WDD) that arises from it is critical. Examining the daily values of these metrics over the course of a year may be especially useful for assessing rapid shifts in moisture and drought status. Moreover, WDD and SWA can be calculated at multiple depths, allowing for quantification of moisture patterns related to the specific rooting depths that vary among plant functional types and are influenced by soil conditions (Schenk & Jackson, 2002).

In addition to WDD and SWA, which are designed to assess favourable growth conditions, we examined metrics focused on potentially stressful hot-dry conditions and found that temperature has a differential ability to predict the soil moisture deficit that arises from evaporative demand. Temperature explains 86% of the spatial variability of CWD and 95% of the variability of DDD, as would be expected in dryland, water-limited regions. CWD and DDD are both higher than expected based on temperature in distinct regions. The Wyoming Basin has higher CWD than predicted by temperature relative to other cold deserts, and the Mojave Desert has greater DDD than predicted by temperature. This difference reinforces the important role that temperature plays in determining both the abundance of hot and dry conditions (DDD) that are unfavourable for growth and the magnitude of unmet atmospheric demand for moisture (CWD).

4.2 | Seasonal moisture timing

The seasonal timing of moisture is a key driver of vegetation structure and plant functional type in drylands (Sala et al., 1997). Drylands with primarily warm-season moisture tend to support herbaceous plant communities, and drylands with cool-season moisture tend to support woody plants that rely on moisture in deep soil layers that can remain wet into the warm season (Renne et al., 2019). We examined the seasonal timing of four metrics and found that they provide unique perspectives on seasonal moisture and drought patterns. Precipitation seasonality shifts from positive (summer-wet) to negative (winter-wet) along an east–west gradient. At the same time, SWA seasonality is negative throughout almost the entire region, a difference that potentially indicates the ability of SWA to capture the occurrence of stored moisture in addition to precipitation inputs. Moreover, the driest portions of the study region (Mediterranean California and the Mojave Desert) have negative WDD seasonality, meaning that temperatures are both warm enough to accumulate degree days and that moisture is suitable for plant growth during the winter months. Despite the prevalence of cool-season precipitation in other regions, like the Columbia Plateau, WDD seasonality is otherwise summer-dominated throughout the study region. Complementary timing metrics of seasonal moisture may, therefore, provide distinct information about the growing conditions that shape drylands.

4.3 | Temporal dynamics of drought

The soil moisture metrics we present here provide ecologically relevant information about temporal drought dynamics that is not described solely by meteorologically derived metrics like SPEI or PDSI (Barnard et al., 2021). Spells of dry soils act as chronic or episodic drought stresses on vegetation at distinct rooting depths (Smith et al., 2009), and infrequent or unpredictable precipitation impacts the structure and function of dryland ecosystems (Ehleringer et al., 1998; Noy-Meir, 1973). The length of dry soil spells varies across our study region, but they are as long as 200 consecutive days in the Mojave Desert. Whereas the Mojave Desert has few but long spells of dry soils, the Chihuahuan Desert and the western portions of the plains have high frequency, short spells of dry soils. Drought episodes in the Southern Plains primarily occur in shallow soils (see SWP). Pulses of moisture in shallow soils sustain transpiration in grasses (Sala et al., 1981), because grasses—which are shallow-rooted—experience strong drought stress and quick recovery (Huxman et al., 2004). In contrast, drought episodes in the Chihuahuan Desert represent periods of dry soils at all depths, affecting deep-rooted plants and shallow-rooted plants. These ecoregions exemplify that the severity of drought stress is dictated by patterns of soil moisture variability and that chronic or episodic drought stress indicates different ecological responses by plants.

4.4 | Metrics for assessing dryland plant recruitment potential

Establishment of perennial plants in many dryland regions is a pervasive problem (Kildisheva et al., 2016) that is likely to be exacerbated by climate change (Chambers et al., 2017; Germino et al., 2016). As a result, recruitment is a critical driver of ecological resilience to disturbances and resistance to invasive grasses. Although the specific conditions that enable seedling establishment can be difficult to quantify and vary among species, our WDD-based recruitment metrics provide a useful way to quantify establishment potential and how it varies among species and across environmental gradients. Metrics that quantify recruitment provide a consistent measure of warm-wet conditions in near-surface soil layers during the spring and fall. The frequency of years with events and the magnitude of recruitment potential are consistent with broad spatial trends related to challenges with restoration in drylands. Specifically, successful restoration of perennial plants is notoriously difficult in many parts of the intermountain western United States (Svejcar et al., 2017), where we found recruitment events to be both less frequent and less favourable (e.g., lower WDD during events). By contrast, ecological restoration is simpler in the great plains, where we found that recruitment events are more reliable and more favourable. The distinction between spring and fall recruitment potentials may also offer information about the challenges of seeding during spring versus fall. More detailed examination of the spatial and temporal patterns of these recruitment metrics, especially alongside observations of seedling establishment, will likely lead to improvements in the metrics.

4.5 | Ecohydrological modelling caveats and future directions

These metrics are designed to quantify ecologically meaningful variation in temperature and moisture conditions that influence dryland vegetation, although our ability to accurately quantify those conditions is limited by the specific dataset that we used and by the model we employed to derive the dataset. We did not simulate spatial subgrid variation, and each simulation represents a single site with specific vegetation and soil conditions. We considered the variability of soil structure at multiple depths because of the critical role that soil texture and coarse fragments play in defining soil moisture dynamics. An additional limitation of our results is that they do not apply to conditions when other edaphic properties, like soil organic carbon, nitrogen, phosphorus or salinity, exert the primary control over hydrologic cycling and vegetation dynamics because we did not consider those factors in our simulations. Moreover, recent extreme climate patterns such as the ongoing megadrought in southwestern North America (Williams et al., 2022) have the potential to influence our representation of temporal patterns of metrics. This recent megadrought is at least partly represented by our simulation (historical weather is taken from 1970 to 2010), and we acknowledge that any recent shifts from historical long-term norms will inevitably be represented in studies such as this one. Despite these limitations, our assessment of these metrics provides a novel perspective on broad spatial patterns in many components of dryland ecological drought. We hope that the metrics developed here may be useful for other studies, which may employ alternative hydrological models at a higher spatial resolution to capture fine-grained variability in vegetation and soils.

Understanding resilience and resistance will be increasingly important in the future. Dryland areal extent is projected to increase to approximately 50% of global land surface by the end of the 21st century (Huang et al., 2017). Drylands are projected to experience increased temperatures, aridity and shifting drought patterns (Dai, 2013; Polade et al., 2014; Schlaepfer et al., 2017). They are especially vulnerable to projected shifts in aridity because of their strong dependence on water availability (Bestelmeyer et al., 2015; Bradford et al., 2020; Noy-Meir, 1973; Reynolds et al., 2007) and, therefore, present a complex and urgent management problem (Bradford et al., 2019; Huang et al., 2017). Recognising the influence of these expected changes in coming decades, we designed metrics that would be responsive to the impact of climate change, which includes both long-term shifts in overall conditions and altered frequency and severity of extreme events. Metrics derived from degree days characterise moisture in the context of the growing season and are comparable even under temporal shifts in growing season length. Along with metrics that describe the seasonal timing and variability of moisture, climate change-induced phenological shifts are well represented.

We encourage subsequent investigations to directly assess the explanatory power of these ecological drought metrics for understanding observed dynamics in plant growth, dieback, recruitment and recovery from disturbance. We hope future studies will apply ecological drought metrics with other data products like land cover or species distribution models to study spatial and temporal variation in ecological structure and function. For example, these metrics are already being used as quantitative predictors of dryland resilience and resistance (Chambers et al., n.d.). Relating ecological drought metrics to remotely sensed estimates of productivity, species composition and vegetation dynamics may provide valuable insights into causes of recent landscape changes (Bunting et al., 2019). These types of analyses also can be used to refine these metrics to enhance understanding of environmental controls on dryland ecosystems. Analysis of temporal patterns in both metrics and ecological responses may also provide new insights into the "climate whiplash" (Swain et al., 2018) that emerges from extreme year-to-year variability and is likely increasing in severity as climate warms. More broadly, these metrics will provide useful perspectives on the ecological impacts of climate change in drylands.

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DATA AVAILABILITY STATEMENT

Data for these ecological drought metrics are available from the USGS ScienceBase-Catalog: 10.5066/P97S8RAC (Schlaepfer et al., 2022).

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