

## ARTICLE

# Precipitation versus temperature as phenology controls in drylands

Courtney M. Currier<sup>1</sup>  | Osvaldo E. Sala<sup>1,2,3</sup> 

<sup>1</sup>School of Life Sciences, Arizona State University, Tempe, Arizona, USA

<sup>2</sup>School of Sustainability, Arizona State University, Tempe, Arizona, USA

<sup>3</sup>Global Drylands Center, Arizona State University, Tempe, Arizona, USA

## Correspondence

Courtney M. Currier

Email: [courtney.currier@asu.edu](mailto:courtney.currier@asu.edu)

## Funding information

National Science Foundation, Grant/Award Number: DEB 1754106; National Science Foundation for the Jornada Basin Long-Term Ecological Research Program, Grant/Award Number: DEB 2025166

**Handling Editor:** Gordon. A Fox

## Abstract

Cycles of plant growth, termed phenology, are tightly linked to environmental controls. The length of time spent growing, bounded by the start and end of season, is an important determinant of the global carbon, water, and energy balance. Much focus has been given to global warming and consequences for shifts in growing-season length in temperate regions. In conjunction with warming temperatures, altered precipitation regimes are another facet of climate change that have potentially larger consequences than temperature in dryland phenology globally. We experimentally manipulated incoming precipitation in a semiarid grassland for over a decade and recorded plant phenology at the daily scale for 7 years. We found precipitation to have a strong relationship with the timing of grass greenup and senescence but temperature had only a modest effect size on grass greenup. Pre-season drought strongly resulted in delayed grass greenup dates and shorter growing-season lengths. Spring and summer drought corresponded with earlier grass senescence, whereas higher precipitation accumulation over these seasons corresponded with delayed grass senescence. However, extremely wet conditions diluted this effect and caused a plateaued response. Deep-rooted woody shrubs showed few effects of variable precipitation or temperature on phenology and displayed consistent annual phenological timing compared with grasses. Whereas rising temperatures have already elicited phenological consequences and extended growing-season length for mid and high-latitude ecosystems, precipitation change will be the major driver of phenological change in drylands that cover 40% of the land surface with consequences for the global carbon, water, and energy balance.

## KEYWORDS

climate change, drylands, phenology, precipitation, temperature

## INTRODUCTION

Annual cycles of plant growth, termed plant “phenology,” are sensitive to variation in their environmental cues, such as temperature or precipitation, which will be modified by

anthropogenic climate change. Phenology affects net ecosystem productivity and global carbon cycling as carbon fixation dominates over ecosystem respiration during the phase when plants are green, and respiration dominates over carbon fixation during the time

when ecosystems are bare (Goulden et al., 1996; Kikuzawa, 1995; Schlesinger, 2005). The length of the green period is one of the determinants of the carbon balance. Additionally, phenology affects the energy balance of our planet. When canopy shifts from bare to green, the albedo decreases, therefore increasing the amount of energy absorbed (Richardson et al., 2013). Duration of the phase in which ecosystems remain green affects energy partitioning with ultimate feedbacks to the global energy balance. A longer duration of the green phase will enhance the effect of increased greenhouse gas emissions on temperature. Phenology also controls ecosystem water balance. During inactive parts of the year, when more bare ground is exposed, water losses occur through soil evaporation, deep percolation, or run-off. When plants and ecosystems leaf out, transpiration then acts as an additional, major water loss from the ecosystem. Therefore, changes in the green period may affect the amount of water reaching streams, recharging water tables, and ultimately affecting precipitation patterns (Shukla et al., 1990).

Many phenological studies focus on mesic, temperate, and alpine ecosystems, demonstrating that phenology is controlled primarily by temperature in these regions (Collins et al., 2021; Goulden et al., 1996; Jackson et al., 2001; Kramer et al., 2000; Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018b; Zhang et al., 2003). Indeed, scientists have observed increased global net primary production (NPP) due to the warming temperature-driven extension of growing-season length in recent decades, mostly in mid and northern latitude regions (Nemani et al., 2003). However, the determinants and sensitivities of the timing and magnitude of greenness in relation to climate are less clear in water-limited ecosystems. Drylands are characterized by having an aridity index, the ratio of mean annual precipitation and potential evapotranspiration (MAP/PET), of  $<0.65$  (Atlas, 1992). Drylands have been relatively overlooked in phenology, yet these important ecosystems cover more than 40% of the terrestrial Earth's surface (Průvák, 2016), account for 30% of global carbon fixation (Field et al., 1998), and explain most of the interannual variability of the carbon cycle (Poulter et al., 2014). As the name suggests, these systems are biologically sensitive to water availability. Climate change in drylands is expected to decrease precipitation, probably expand the global dryland area (but please refer to Berg & McColl, 2021), and increase interannual precipitation variability (Gherardi & Sala, 2019) with more frequent and severe droughts coupled with deluges of novel magnitude and frequency (Ault, 2020; Petrie et al., 2014). Given the large terrestrial extent of drylands, phenological sensitivity of plants within these ecosystems to directional changes in precipitation amount could have large consequences from

local forage production to carbon, water, and energy balance of our planet.

Our study addressed three questions. First, we asked: Within a dryland community, how do two dominant plant species differ in their phenology patterns? Specifically, we focused on a perennial, deciduous shrub (*Prosopis glandulosa*) and a perennial grass (*Bouteloua eriopoda*). These two dominant plant species account for most (67%) of aboveground net primary production (ANPP) at our study site (Huenneke et al., 2002; Reichmann et al., 2013). The *Prosopis* and *Bouteloua* genera represent common plant-functional types found in drylands worldwide, shrubs and grasses, and therefore we refer to our study organisms as “shrub” and “grass” respectively for brevity. Second question, what are the determinants of those phenological patterns? Given the morphological and physiological differences, we expect our study species to respond differentially to changes in phenological controls, such as seasonal water availability or temperature. *P. glandulosa*, a  $C_3$ , N-fixing shrub, exhibits extensive rooting systems that can sometimes reach 5 m in depth whereas *B. eriopoda* is a  $C_4$ , shallow-rooted, stoloniferous grass (Gibbens & Lenz, 2001). Ecophysiologically, *P. glandulosa* typically outperforms *B. eriopoda* under drought stress, maintaining a more favorable leaf-water potential and higher photosynthetic rates for a longer fraction of the growing season (Throop et al., 2012). Because of the large spatial extent of our study species within North American deserts and grasslands (“Occurrence records of *Bouteloua eriopoda* (Torr.) Torr.”, 2021; “Occurrence records of *Prosopis glandulosa* Torr.”, 2021) and the ubiquity of the *Bouteloua* and *Prosopis* genera in drylands worldwide (“Occurrence records of *Bouteloua* Lag.”, 2021; “Occurrence records of *Prosopis* L.”, 2021), our third question asks: What are the consequences of a changing climate for phenology of drylands?

Our approach to understanding the effects of temperature and precipitation on dryland phenology combines long-term precipitation manipulative field experiments with temperature observations. Here, we present a multiyear experimental study at the Jornada Basin Long Term Ecological Research (LTER) (New Mexico, USA) that combines rainfall manipulation in the field and phenocameras to address our three objectives while elucidating cause–effect relationships between precipitation, temperature, and phenology patterns of two plant-functional groups, woody shrubs and grasses. The vegetation habitat types of our field site are representative of the northern Chihuahuan Desert, which covers a total spatial extent of 501,895 km<sup>2</sup> and is the largest desert of North America (Havstad et al., 2006). Mean annual rainfall of 232 mm, measured potential evaporation of

$\sim 2200$  mm year<sup>-1</sup>, and the closed-basin topography typical of the southwestern USA make this site an ideal, representative study system for understanding dryland ecosystem processes (Havstad et al., 2006; Maestre et al., 2021). Because it is impossible to detect long-term trends based on short-term observations (Collins et al., 2011), our study provides novel perspectives on precipitation–temperature–phenology interactions in drylands by synthesizing 7 years of data from a long-term rainfall manipulation experiment in a multifunctional group system. This plot-level scale provides an advantage, because community composition could amplify or offset the effects of climate change if plant groups respond differently (Ibrahim et al., 2021). Finally, one study estimates that climate change has already advanced plant greenup by 2.3–5.1 days decade<sup>-1</sup> for the Northern Hemisphere (Parmesan, 2007) and could extend growing-season length in some ecosystems by 1–2 weeks under current warming trends by the end of this century (Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018b). Our study presents a temporal resolution at the daily scale, matching the timescale of future climate-change impacts.

## METHODS

### Overview

Our objective was to investigate temperature and precipitation controls on the phenology of a dryland ecosystem co-dominated by two plant types. To address our questions, phenocameras were installed just outside a long-term rainfall manipulation experiment in which incoming precipitation was subtracted or added by 80%, located at the Jornada Basin Long Term Ecological Research site (New Mexico, USA). Daily images were analyzed for changes in greenness through time. We extracted greenup (start of season) and senescence (end of season) dates from the greenness versus time curves for each plant species and explored their relationships with temperature and precipitation using linear mixed effects models.

### Study site description

This study was conducted at the Jornada Basin LTER site, located at 32.56 latitude,  $-106.78$  longitude (Las Cruces, New Mexico, USA). The Jornada Basin receives a mean precipitation amount of 232 mm annually. In total, 76% of this mean annual precipitation comes in the form of summer monsoonal storms derived from the Gulf of Mexico (Havstad et al., 2006). During the summer, which

constitutes the main growing season for dominant vegetation, mean maximum temperature is 36°C. Dominant vegetation consists of the C<sub>3</sub> perennial shrub, *Prosopis glandulosa* (honey mesquite) and the C<sub>4</sub> perennial grass, *Bouteloua eriopoda* (black grama). Soils are classified as Cacicque loamy fine sand with weakly developed textural B (argillic) horizons overlaying semi-indurated to indurated caliche at  $\sim 30$ –60 cm in depth (Gile, 1981; Monger, 2006).

### Climate variables

Climate data were obtained from the meteorological stations nearest to the experimental plots. Gap-filled daily precipitation sums were obtained from the Jornada G-BASN long-term NPP site (32.53 latitude,  $-106.79$  longitude;  $\sim 3.3$  km southwest from experimental plots) (Yao et al., 2020). Daily temperature means were obtained from the Jornada Experimental Range Headquarters NOAA station (32.62 latitude,  $-106.74$  longitude;  $\sim 7.5$  km northeast from study plots), calculated as the mean of the daily minimum and maximum.

### Experimental design and image capture

Water treatments were achieved using rainout shelters that decreased incoming precipitation by 80% and automated irrigation systems that simultaneously applied 80% of incoming precipitation (Gherardi & Sala, 2013; Yahdjian & Sala, 2002). During precipitation events, shelters intercepted and redirected incoming rainfall to a PVC irrigation system surrounding +80% treatment plots by means of a solar-powered pump; control plots received ambient precipitation (with no shelter or irrigation system) throughout the duration of the experiment. Manipulation intensities were based on extremes of historical precipitation data for the region. Rainfall manipulation treatments were started in 2006 along with control plots that received ambient rainfall ( $n = 6$ ;  $N = 18$   $2.5 \times 2.5$  m plots) (Reichmann et al., 2013).

To address our questions, Wingscape TimeLapse Pro (WCT 00125) “phenocams” were installed just outside of nine plots ( $n = 3$  per treatment) in year 8 (2014) and an additional nine (to increase our replication to  $n = 6$  per treatment) were installed in year 12 of the experiment (2018). All cameras were installed facing west/southwest, horizontal and aimed to the center of each plot (Appendix S1: Figure S1). Images taken before 2018 were captured once during peak sunlight at noon, and images taken after 2018 were captured every 30 min between 11:00 AM and 2:00 PM.

## Image analyses

Daily images from each plot were analyzed for changes in greenness through time. Three regions of interest ( $150 \times 150$  pixels) were situated on each dominant grass patch (*B. eriopoda*) and central shrub (*P. glandulosa*) using a MATLAB-based graphical user interface, PhenoAnalyzer (patent pending), developed by the Craig Tweedie System Ecology Laboratory (University of Texas, El Paso; Ramirez et al., 2021). The regions of interest were placed on portions of each plant and plant patch that qualitatively had the most consistent leaf cover to avoid analyzing extraneous parts of the image, such as soil, sky, obstruction from other plants, or woody stems. Pixelated information was extracted and composited, resulting in output that contained date, and red, blue, and green color channel information. The green chromatic coordinate ( $g_{cc}$ ), analogous to NDVI in other phenology studies, was calculated as:

$$g_{cc} = \frac{(\text{green digital number})}{[(\text{red digital number}) + (\text{blue digital number})]} \quad (1)$$

Comparable to NDVI,  $g_{cc}$  has been found to be a suitable color index for phenology studies at the landscape and plot level (Richardson, Hufkens, Milliman, Aubrecht, Chen, et al., 2018a; Sonnentag et al., 2012). From these time series data for each plot, we followed the double logistic model curve-fitting and phenophase extraction approach using the per 90  $g_{cc}$  after Sonnentag et al. (2012) and the *phenopix* package (Filippa et al., 2016) in R version 4.0.3 (Team, 2015). Within this package, images that were below a brightness threshold of 0.2 (due to cloudy days or camera obstruction) did not pass quality control and were automatically discarded using the “night” filter within the *autoFilter()* function. A rolling window of 7 days for images taken before 2018 (one image per day) and 3 days for images taken after 2018 (multiple images per day) were applied to the 90th percentile of  $g_{cc}$  data time series. Shrub data were fitted with a Klosterman curve (Klosterman et al., 2014) using the *gu* extraction method (Gu et al., 2009), whereas grasses were best fitted with a *gu* curve (Gu et al., 2009) using the Klosterman extraction method (Klosterman et al., 2014). Some plots were missing data due to camera failure or installation of new cameras mid-season (Appendix S1: Table S1).

## Statistical analyses

The independent variables, precipitation amount (mm) and mean air temperature ( $^{\circ}\text{C}$ ), were categorized

into the following seasons: winter (1 January to 31 March), spring (1 April to 30 June), summer (1 July to 31 September, the typical monsoon season at the Jornada Basin LTER), and fall (1 October to 31 December). We selected the winter season as the independent variable for greenup analyses, as these are the months immediately preceding typical greenup events observed long-term at this site. We selected the spring and summer seasons for senescence analyses, specifically using rainfall sums across these months as the precipitation variable. For the temperature variable in senescence analyses, we used mean air temperature from the fall following the typical growing season. We used maximum likelihood to compare the fixed effects (Bolker et al., 2009) of precipitation amount and mean air temperature on plant greenup and senescence with the following linear mixed effects models:

$$Y_{si} = \beta_0 + S_{0s} + \beta_1 X_i + e_{si} \quad (2)$$

$$Y_{sj} = \beta_0 + S_{0s} + \beta_2 X_j + e_{sj} \quad (3)$$

$$Y_{sj} = \beta_0 + S_{0s} + \log(\beta_2 X_j + 2) + e_{sj} \quad (4)$$

$$Y_{sij} = \beta_0 + S_{0s} + \beta_1 X_i + \beta_2 X_j + e_{sij} \quad (5)$$

$$Y_{sij} = \beta_0 + S_{0s} + \beta_1 X_i + \log(\beta_2 X_j + 2) + e_{sij} \quad (6)$$

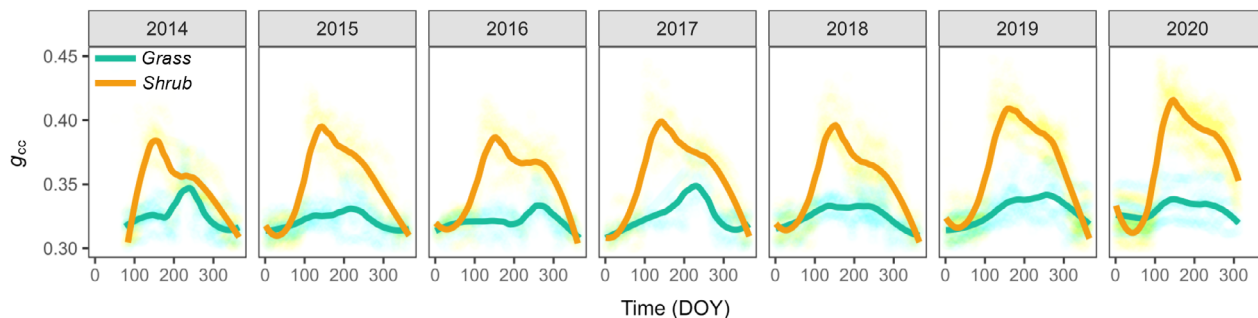
$$Y_{sij} = \beta_0 + S_{0s} + \beta_1 X_i + \beta_2 X_j + \beta_1 X_i \beta_2 X_j + e_{sij} \quad (7)$$

$$Y_{sij} = \beta_0 + S_{0s} + \beta_1 X_i + \beta_2 X_j + \beta_1 X_i \log(\beta_2 X_j + 2) + e_{sij} \quad (8)$$

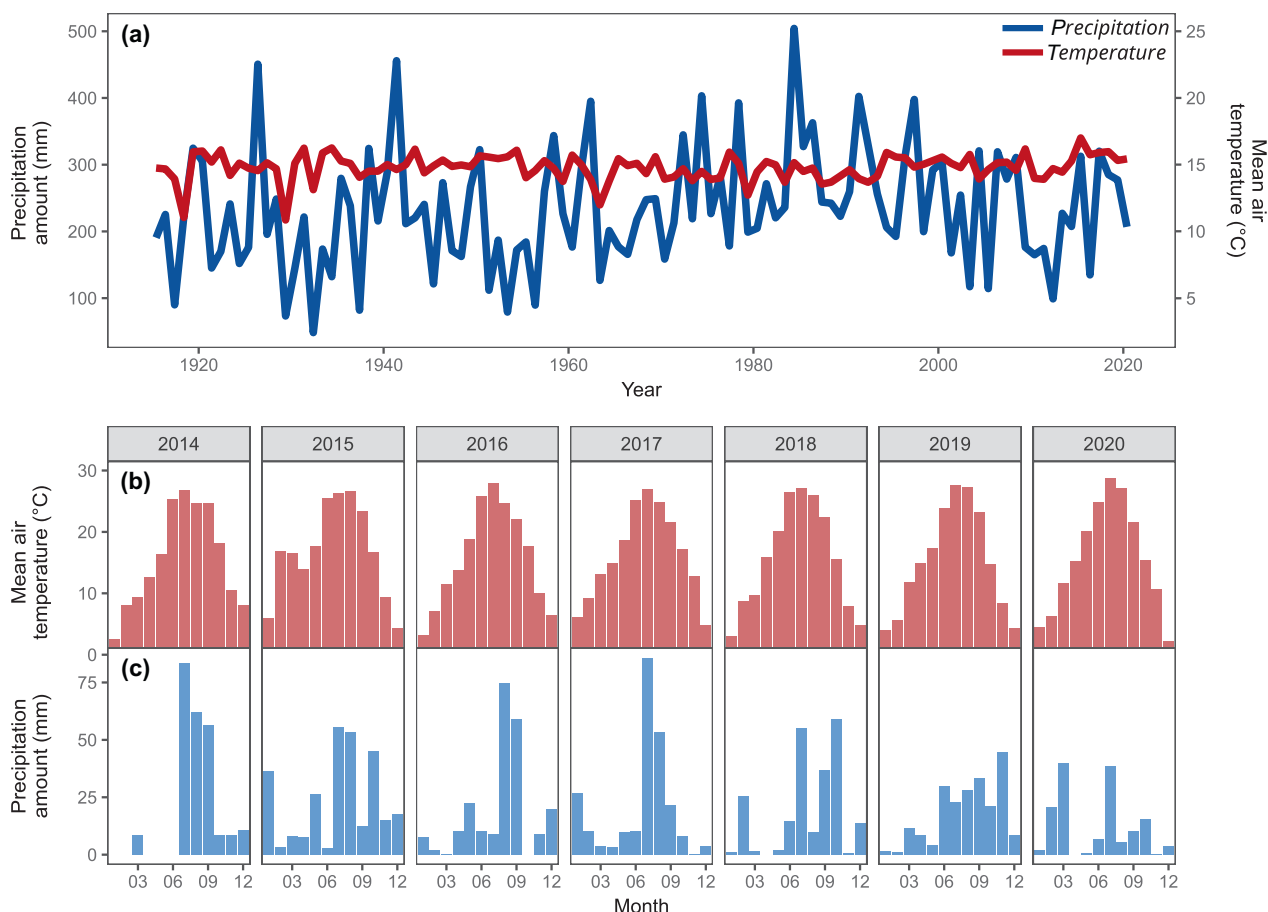
$$S_{0s} \sim N(0, \tau_{00}^2),$$

$$e_{sij} \sim N(0, \sigma^2)$$

where  $Y_{sij}$  = response (greenup or temperature),  $\beta_0$  = intercept,  $S_{0s}$  = random effect (year),  $\beta_1 X_i$  = fixed effect 1 (mean temperature),  $\beta_2 X_j$  = fixed effect 2 (precipitation amount),  $e_{sij}$  = residuals. Because some seasons may have zero or  $<1$  mm of rainfall, logarithmic models included the addition of a constant to the precipitation variable. All linear mixed effects models were analyzed using the *lmer()* function in the *lme4* package (Bates et al., 2014 p. 4). We used the Akaike Information Criterion (AIC) to select the best model (Sakamoto et al., 1986). Models that met our criteria had the lowest AIC with  $\Delta\text{AIC} > 2$ , otherwise the most parsimonious model was selected. Residuals of selected models were tested for and exhibited normality.



**FIGURE 1** Annual greenness (as green chromatic coordinate, or  $g_{cc}$ ) versus time (as Julian day of year, where DOY 1 is January 1) curves for grass (green line) and shrub (orange line) functional types at the Jornada Basin LTER.



**FIGURE 2** (a) Long-term (1915–2020) trends in annual precipitation amount and mean annual temperature at the Jornada; (b) monthly mean air temperature ( $^{\circ}\text{C}$ ) and (c) monthly precipitation sums (mm) over the study period (2014–2020) at the Jornada Basin LTER.

## RESULTS

### Overview

We found that woody shrubs greenup earlier in the summer growing season, around day of year 96 (early April), whereas grasses greenup later, with a mean greenup day of year of 157 (mid-June) (Figure 1). These results are typical of the Jornada Basin and match landscape-level observations made previously

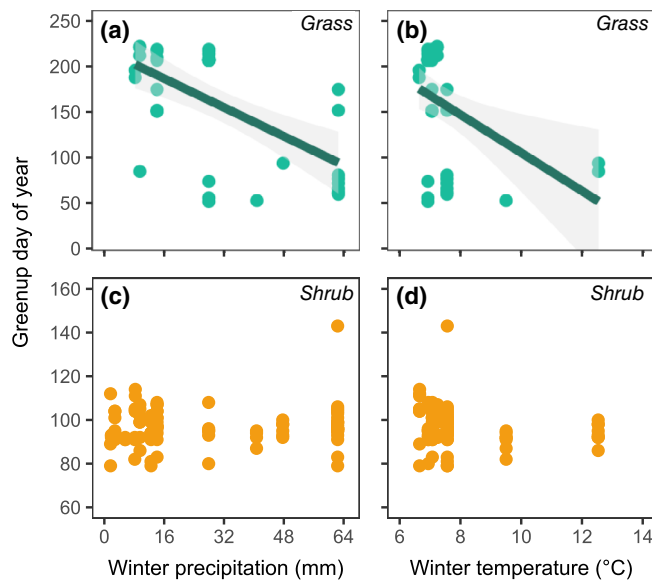
(Browning et al., 2017). In general, growing-season length for shrubs is longer than that for grasses; mean growing-season length was 187 and 97 days for shrubs and grasses, respectively.

The division of temporal niches for these two plant species may reflect the responses to the cue that varies the most at the annual scale (Okin et al., 2018). In drylands, that cue is precipitation (Gherardi & Sala, 2019; Trenberth et al., 2003), which varied the most annually at our site both over the long term (105 years; Figure 2a) and



**TABLE 1** Short-term (2014–2020) and long-term (1915–2020) climate means and coefficients of variation (CV) for temperature and precipitation at the Jornada Basin Long Term Ecological Research site, located in Las Cruces, New Mexico, United States.

Environmental cue	Study period (2014–2020)		Long term (1915–2020)	
	Mean	Coefficient of variation (%)	Mean	Coefficient of variation (%)
Temperature	289.7 K	0.26	288.9 K	0.34
Precipitation	242 mm	29	232 mm	39



**FIGURE 3** Winter temperature and winter precipitation effects on grass (a, b) and shrub (c, d) greenup, expressed as day of the year. Points represent plot-year replicates. Significant linear mixed model precipitation effects in (a) and (b) are denoted by a solid line, which represents the predicted model fit  $\pm 95\%$  confidence interval, calculated as  $\pm 2 \times$  standard error around the effect size. In (a) and (b), grass greenup =  $337.8 + (-1.8 \times \text{precipitation}) + (-16.71 \times \text{mean air temperature})$ . In (c) and (d), shrub greenup did not statistically respond to either winter precipitation or mean winter air temperature.

during our study period (7 years; Figure 2b). The long-term coefficient of variation (CV) for annual precipitation was  $\sim 39\%$ , whereas the CV for air temperature (calculated using temperature in Kelvin) was  $\sim 0.34\%$  (Table 1). At the intra-annual scale, transitions in seasonal temperature are essential triggers that plants also may use to shift between phenological stages of growth. We explored the relative effects of temperature and precipitation, two important phenological cues and components of environmental change, on grass and shrub phenology.

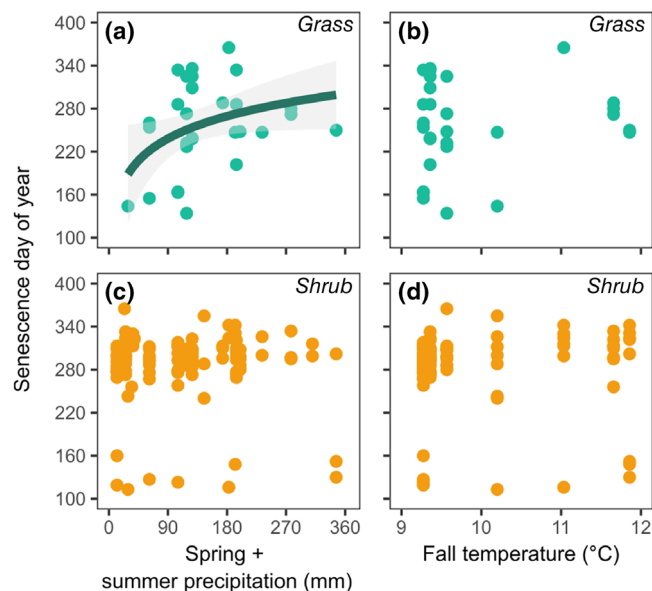
## Model selection

For grass greenup response, the additive model with both temperature and precipitation (Equation 5) met our criteria and was selected. For shrub greenup response,

the model with temperature alone (Equation 2) met our criteria and was selected. Grass senescence was best explained by the logarithmic precipitation model (Equation 4). Shrub senescence was best explained by the non-logarithmic precipitation model (Equation 3). For all selected models, except that for shrub senescence, the random effects variances were estimated as zero. Although singularity indicates a mixed model that is overfitted, we felt that it was important to retain the random effect term (year) to reflect the repeated nature of our experimental design. Bolker et al. (2009) affirmed that in cases such as these, the results remain unchanged and the random effect parameter may be retained. The Supporting Information contains statistical output for AIC comparisons (Appendix S1: Table S2) and results from each mixed model (Appendix S1: Tables S3–S6).

## Phenology responses of grasses and shrubs

Grass and shrub greenup exhibited differential responses to environmental cues. Grass greenup responded significantly to winter precipitation (Figure 3a; Appendix S1: Table S3; fixed effects estimate:  $-1.8$ ; CI:  $-2.60$  to  $-1.01$ ;  $p < 0.05$ ; marginal  $R^2 = 0.46$ ). Dry pre-season winter conditions resulted in delayed grass greenup, and wet conditions advanced grass greenup. The effect of winter precipitation on grass greenup resulted in extreme drought, delaying this important phenological transition up to 110 days, from the earliest statistically estimated day of year (DOY) 95 to the latest DOY 205 (while holding the temperature constant). The effect of winter temperature on grass greenup was also significant, indicating that warmer winter temperatures resulted in earlier grass greenup, whereas cooler temperatures delayed grass greenup up to 98 days, from the earliest estimated DOY 75 to the latest DOY 173 (while holding precipitation constant) (Figure 3b; Appendix S1: Table S3; fixed effect estimate:  $-16.71$ ; CI:  $-28.40$  to  $-5.03$ ;  $p < 0.05$ ; marginal  $R^2 = 0.46$ ). Shrub greenup, by contrast, had a relatively constant date when the standard error of greenup around a mean DOY of 97 was only 0.27. Shrub greenup was ecologically insensitive to winter precipitation (Figure 3c), and this fixed effect was not included in



**FIGURE 4** Fall temperature and spring + summer precipitation effects on grass (a, b) and shrub (c, d) senescence, expressed as day of the year. Points represent plot-year replicates. Significant linear mixed model precipitation effect in (a) is denoted by a solid line, which represents the predicted model fit  $\pm 95\%$  confidence interval, calculated as  $\pm 2 \times$  standard error around the effect size. In (a), grass senescence =  $31.24 + (45.78 \times \log[\text{precipitation} + 2])$ , whereas temperature did not statistically explain grass senescence (b). In (c) and (d), shrub senescence did not statistically respond to either spring + summer precipitation or mean fall air temperature.

the best selected explanatory model. Additionally, shrub greenup did not respond to winter temperature (Figure 3d; Appendix S1: Table S4; fixed effect estimate:  $-1.05$ ; CI:  $-2.15$  to  $0.05$ ;  $p = 0.06$ ; marginal  $R^2 = 0.036$ ).

Grass senescence was significantly linked to cumulative spring and summer precipitation (Figure 4a; Appendix S1: Table S5; fixed effects estimate:  $45.78$ ; CI:  $5.04$ – $86.51$ ;  $p < 0.05$ ; marginal  $R^2 = 0.15$ ). By contrast, grass senescence did not depend on any changes in fall temperature (Figure 4b), which was not included in the best selected explanatory model. Growing-season drought corresponded with statistically estimated senescence as early as DOY 188. Higher accumulated precipitation over these seasons resulted in delayed senescence, which extended the growing-season length. The selected logarithmic model indicates that delays in grass senescence date plateaued at approximately DOY 300. Therefore, sensitivity of grass senescence to precipitation appeared highest at low to average rainfall amount and diminished during extremely wet years. Shrub senescence was insensitive to variability in both growing-season precipitation (Figure 4c; Appendix S1: Table S6; fixed effect estimate:  $-0.05$ ; CI:  $-0.16$  to  $0.06$ ;  $p = 0.40$ ; marginal  $R^2 = 0.007$ ) and fall temperature (Figure 4d).

## DISCUSSION

### Precipitation versus temperature controls of phenology

Our study provides a unique lens to assess precipitation and temperature controls of phenology. We saw that precipitation had an effect on grass greenup and senescence, but temperature had an effect on just grass greenup. Shrubs, by contrast, were insensitive to both environmental cues. To support our conclusion, we used the selected explanatory regressions (Appendix S1: Table S2) to estimate the effects of long-term ( $>100$  years, Figure 2), historic ambient precipitation and temperature on phenology for our study species at the Jornada. The results suggest that ambient precipitation variability from historic records had a potentially larger effect on phenology relative to temperature (Table 2). Precipitation at our site over 105 years explained 27% of the variability in grass greenup, whereas historic temperature variability explained only 10% of the phenological variability. Precipitation also had a larger effect than temperature on grass senescence but the effects were smaller than those observed for greenup (Table 2). This important conclusion of our work results from both higher sensitivity of our grass species to both precipitation and temperature at the start of season (Figure 3) and higher interannual variability of precipitation relative to temperature (Table 1). Our results in conjunction with climate-change predictions suggest that, for dryland regions, changes in precipitation will be a more important driver in phenological shifts than temperature. Whereas rising temperatures have already elicited phenological consequences and extended growing-season length for mid- and high-latitude ecosystems (Cook et al., 2012; Parmesan, 2007; Richardson et al., 2018b), precipitation change will be the major driver of phenological change in drylands.

### Grasses and shrubs exhibit contrasting phenology strategies

Phenological responses to the environment are reflective of a strategy that maximizes fitness and resource acquisition while reducing competition (Jackson et al., 2001; Kikuzawa, 1991; Kraft et al., 2015; Römermann et al., 2016). Separation of phenological timing among species within a plant community reflects the stabilization strategies that facilitate coexistence (Cleland et al., 2012; Kraft et al., 2015). Grass phenology strongly depended on shifts in precipitation more than changes in seasonal temperature. Additionally, grasses were more

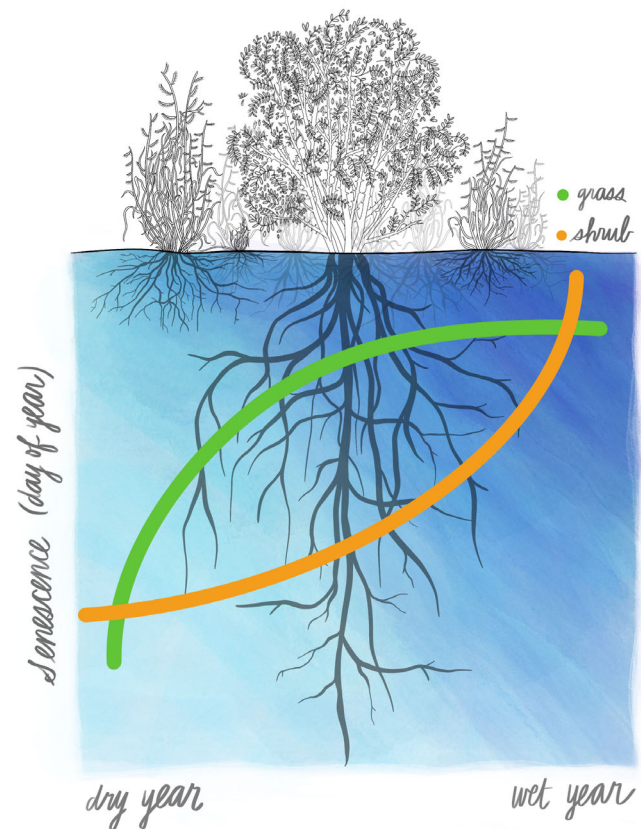
**TABLE 2** Long-term (105 years) estimates and coefficients of variation (CV) of Greenup and senescence in grasses and shrubs back-calculated from the selected explanatory models using historic, ambient precipitation and temperature as independent variables.

Environmental cue	Grass				Shrub			
	Greenup		Senescence		Greenup		Senescence	
	Range	Coefficient of variation	Range	Coefficient of variation	Range	Coefficient of variation	Range	Coefficient of variation
Winter precipitation	14–298	26%	...	...	92–105	2%	...	...
Winter temperature	DOY				DOY			
Spring + summer precipitation	...	...	153–300	9%	...	...	274–291	1%
Fall temperature			DOY				DOY	

Abbreviation: DOY, day of year.

sensitive in their phenology at lower precipitation amounts; therefore, drought has potentially higher and negative consequences for grass phenology over “deluge” by shortening the growing-season length by either delaying greenup, advancing senescence, or both. Whereas there were deluge impacts on grass senescence in our study, these effects appeared to plateau at precipitation totals over 200 mm. We interpreted the small response of senescence beyond 200 mm of precipitation to the possible water saturation of the upper layers of the soil where most of the grass roots are concentrated (Jackson et al., 1996). When precipitation exceeds 200 mm, soil water may reach layers poorly explored by grasses and then absorbed by deep-rooted shrubs or lost via deep percolation. Satellite observations of West African savanna similarly found grasslands to be more sensitive to changes in precipitation than woody-dominated landscapes, which exhibited constant greenup dates (Ibrahim et al., 2021). Studies in a Mediterranean-type ecosystem, also reported that herbaceous species were more sensitive to changes in rainfall amount, especially drought, and exhibited delayed greenup (Esch et al., 2019). Because grasses accounted for 40% of the Jornada Basin aboveground net primary productivity (Huenneke et al., 2002), and many other global drylands are grass dominated, the ecological consequence of drought on grass phenology cannot be understated.

Grass response to short-term changes in the environment represents an ecological phenomenon called phenological tracking (Cleland et al., 2012), which enables plants to adjust their growth to when favorable climatic conditions occur and maximizing growth for each year. This strategy allows grasses to maximize the use of water that otherwise would be lost via soil evaporation (Throop et al., 2012). Plants that exhibit this strategy may be more adaptive to variable precipitation predicted for future climate scenarios in drylands. The disadvantage is that coupling greenup to early precipitation pulses holds a risk



**FIGURE 5** Hypothetical relationship between senescence day of year for grasses (green line) and shrubs (orange line) and annual precipitation amount. Saturation of surface soils at higher rainfall amounts results in percolation to deeper soil depths accessible by shrubs, eliciting a senescence response.

for plants during drought years. If no subsequent rain events occur thereafter, there is the possibility of invested carbon and nitrogen resources after a rain event for root (Lauenroth et al., 1987) or shoot growth that cannot be offset during a shortened growth period.

Shrub phenology is consistent among years and may reflect a strategy associated with access to a source of



water with low interannual variance and a frost-avoidance strategy linked to predictable shifts in seasonal temperature (Medeiros & Pockman, 2014). At any given latitude, photoperiod is another stable cue at annual time scales and is often synchronous with predictable patterns in seasonal temperature (Adole et al., 2019; Jackson, 2009). Photoperiod is an indicator of very long-term adaptations over decadal/century time scales and represents a conservative phenological approach. A continental-scale study of Africa's terrestrial ecosystems found phenology to be controlled by multiple drivers that were dominated by photoperiod (Adole et al., 2019). Early theories of phenology identified the strategy of tracking photoperiod and predictable temperature cues as favoring high-light environments where resources and water were available (Jackson et al., 2001; Kikuzawa, 1995). Deep soil water has been shown to be a relatively stable source of water for shrubs (Duniway et al., 2018). If there are any precipitation effects on shrub phenology, we expect them to occur after high multiyear droughts or deluges (Figure 5). If grass senescence responses plateau at high rainfall accumulation, this water becomes available to percolate to deeper soil layers that are more accessible by shrubs. It is also possible that shrub phenology responds to multiyear precipitation cycles that result in prolonged droughts or wet years. Increased frequency of climate anomalies, such as the Pacific Decadal Oscillation (PDO) and the El Niño-Southern Oscillation (ENSO), is likely to drive these multiyear cycles (Felton et al., 2020; Petrie et al., 2014). Therefore, stable seasonal temperatures contrast the temperature- and water-insensitive shrubs at our site compared with temperature-sensitive trees in temperate systems that experience higher fluctuation of start-of-season temperatures (Zani et al., 2020).

## Implications for future climate scenarios

Although global temperature is rising and affecting temperate ecosystem phenology directly, temperature alone has a minimal effect on the phenology in drylands. Future climate simulations for the United States Southwest project a strong reduction in winter and spring precipitation under the ICPP RCP8.5 scenario (Wuebbles et al., 2014), which would drastically shorten grass growing-season length through delayed greenup and earlier senescence. Precipitation, particularly drought, affects grass phenology more than shrubs. Alteration of the length of growing season via changes to precipitation has important consequences for global carbon cycling as many drylands consist of grass-dominated systems. In terms of season length, how does this affect

C fixation? Drought is altering the cycle of grass growth by shifting greenup and senescence, and therefore shortening growing-season length. Drought impacts to phenology may result in a reduction of grass cover, and therefore grass ANPP.

Our results suggest that warming winter temperatures could have a significant impact on grass phenology by advancing greenup dates. Nonetheless, temperature is not expected to increase as much in terms of variability or directionality in our semiarid system compared with mesic or temperate counterparts (Wuebbles et al., 2014). Future climate scenarios project a temperature increase under the RCP8.5 scenario of up to 3.2°C for southern New Mexico (Scott et al., 2016). This projected temperature increase is encompassed in the observed temperature range of our study (−8.65 to 33.35°C).

A reduction in plant cover through altered phenology will subsequently have larger impacts on energy and water balance. In an example driven by this study, decreased aboveground biomass of perennial grasses will result in increased bare ground exposure, and therefore increased albedo and surface reflectance of incoming radiation. Furthermore, an increased percentage of bare ground will subsequently increase overland water flow, surface erosion, and water losses via evaporation (Okin et al., 2018), further increasing the patchiness of desert landscapes and reinforcing mechanisms for woody-plant encroachment (Huenneke et al., 2002). Decreased plant transpiration will also decrease latent heat loss during the growing season (Peñuelas et al., 2009), a mechanism that cools microclimates. Loss of herbaceous species, which have an open nutrient economy and high nutrient turnover (Sala et al., 2012), will result in decreased litterfall inputs to these oligotrophic systems, therefore further amplifying the openness of nutrient cycling under drought in these water-limited ecosystems.

This 7-year snapshot of the phenology of dominant grass and shrub species of the Chihuahuan semiarid ecosystem provides the impetus for investigating temperature–precipitation controls on phenology at larger spatial and temporal scales across global drylands. Our experimental ranges of annual precipitation over the 7-year study period were 32–372 mm, mirroring historic precipitation extremes over the last century, whereas temperature showed a mean ambient range 16.5–18.9°C that also represents long-term trends (Figure 2a). The most complete vision of phenology responses to the interactive effects of water and temperature variability will depend on complimentary approaches (Cleland et al., 2007), such as combinations of existing long-term manipulative experiments, coordinated research networks (e.g., PhenoCam Network; Seyednasrollah

et al., 2019 and the European Phenology Camera Network; Wingate et al., 2015), and satellite observations that document large-scale change through time (Adole et al., 2019). Phenological studies will benefit from a greater understanding of how water-limited systems respond to extreme precipitation. Because temperature alone does not necessarily control the phenology in all ecosystems, filling the research gap by including dryland responses to shifts in annual precipitation will be critical for our global understanding of controls on ANPP. This will ultimately be important to better understand the global carbon cycle, the energy and water balance the capacity for dryland ecosystems to sequester carbon, and how the sensitivity of these systems to shifts in precipitation and temperature may affect the services they provide.

## AUTHOR CONTRIBUTIONS

Courtney M. Currier and Osvaldo E. Sala designed the research. Courtney M. Currier carried out the field studies and data analyses. Courtney M. Currier and Osvaldo E. Sala wrote the paper.

## ACKNOWLEDGMENTS

We thank L. Gherardi, L. Reichmann, K. Duffy-McGurrin, S. Easter, S. Doucette-Riise, M. Saucedo, S. Jordan, and many REUs (A. Stettner, M. Vega, A. Hallberg, N. Oas, Z. Bergman, G. Baur, C. Yager, S. Jung, S. Smith, S. Allbee, J. Petty) for field assistance throughout the long-term experiment. This work would not be possible without further assistance from Jornada Basin LTER personnel, staff, and scientists: D. Thatcher, J. Ramirez, J. Anderson, G. Maurer, and B. Bestelmeyer. This work was supported by funding from the National Science Foundation for the Jornada Basin Long-Term Ecological Research Program Grant DEB 2025166 and National Science Foundation LTREB Grant DEB 1754106.

## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

All original and derived phenology data produced by the authors and R scripts for data processing, statistical analyses, and figure production are publicly available in the Environmental Data Initiative (EDI). EDI package knb-lter-jrn.210574001.2 (Currier & Sala, 2022a) contains daily phenocam image data and derived timeseries and associated scripts for processing and is available at <https://doi.org/10.6073/pasta/836360dce9311130383c9672e836d640>. EDI package knb-lter-jrn.210574002.2 (Currier & Sala, 2022b) contains observed phenological indicators and environmental drivers as well as associated scripts for final analyses and figure construction presented in this

manuscript and these data are available at <https://doi.org/10.6073/pasta/d327a77f6474131db8aa589011e29c29>. No novel code was generated by the authors of this manuscript. The precipitation data used in all analyses are derived from G-BASN data in EDI package knb-lter-jrn.210520001 (Yao et al., 2020) available at <https://doi.org/10.6073/pasta/cf3c45e5480551453f1f9041d664a28f>. Daily air temperature summaries from 4 June 1914 to the present for the Jornada Experimental Range Headquarters (NOAA station GHCND:USC00294426) are freely available upon request via the National Ocean and Atmospheric Administration (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00294426/detail>). Future climate scenario inferences were made using the NOAA Climate Change Web Portal (<https://psl.noaa.gov/ipcc/cmip5/>). The authors utilized the Anomaly Plot Type and input the following variables for their search query: Average of All Models (Model), RCP8.5 (Experiment), Air Temperature (Field), Mean (Statistic). The time period consisted of the entire year (Season), 2006–2100 (21st Century Period) within the Western USA (Plot Area Region).

## ORCID

Courtney M. Currier  <https://orcid.org/0000-0002-7617-239X>

Osvaldo E. Sala  <https://orcid.org/0000-0003-0142-9450>

## REFERENCES

- Adole, T., J. Dash, V. Rodriguez-Galiano, and P. M. Atkinson. 2019. "Photoperiod Controls Vegetation Phenology across Africa." *Communications Biology* 2: 391.
- Atlas, U. 1992. *World Atlas of Desertification*, Vol 80. Kent: UNEP and E. Arnold Ltd.
- Ault, T. R. 2020. "On the Essentials of Drought in a Changing Climate." *Science* 368: 256–60.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. "lme4: Linear Mixed-Effects Models Using Eigen and S4." R Package Version 1:1–23. <https://doi.org/10.48550/arXiv.1406.5823>.
- Berg, A., and K. A. McColl. 2021. "No Projected Global Drylands Expansion under Greenhouse Warming." *Nature Climate Change* 11: 1–7.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. "Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution." *Trends in Ecology & Evolution* 24: 127–35.
- Browning, D. M., J. W. Karl, D. Morin, A. D. Richardson, and C. E. Tweedie. 2017. "Phenocams Bridge the Gap between Field and Satellite Observations in an Arid Grassland Ecosystem." *Remote Sensing* 9: 1071.
- Cleland, E., I. Chuine, A. Menzel, H. Mooney, and M. Schwartz. 2007. "Shifting Plant Phenology in Response to Global Change." *Trends in Ecology & Evolution* 22: 357–65.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012.

- “Phenological Tracking Enables Positive Species Responses to Climate Change.” *Ecology* 93: 1765–71.
- Collins, C. G., S. C. Elmendorf, R. D. Hollister, G. H. R. Henry, K. Clark, A. D. Bjorkman, I. H. Myers-Smith, et al. 2021. “Experimental Warming Differentially Affects Vegetative and Reproductive Phenology of Tundra Plants.” *Nature Communications* 12: 3442.
- Collins, S. L., S. R. Carpenter, S. M. Swinton, D. E. Orenstein, D. L. Childers, T. L. Gragson, N. B. Grimm, et al. 2011. “An Integrated Conceptual Framework for Long-Term Social-Ecological Research.” *Frontiers in Ecology and the Environment* 9: 351–7.
- Cook, B. I., E. M. Wolkovich, T. J. Davies, T. R. Ault, J. L. Betancourt, J. M. Allen, K. Bolmgren, et al. 2012. “Sensitivity of Spring Phenology to Warming across Temporal and Spatial Climate Gradients in Two Independent Databases.” *Ecosystems* 15: 1283–94.
- Currier, C., and O. Sala. 2022a. “Daily Phenocam Image Data and Derived Timeseries for Global Change Experiments at the Jornada Basin LTER Site, 2014-2020 ver 2.” Environmental Data Initiative. <https://doi.org/10.6073/pasta/836360dce9311130383c9672e836d640>.
- Currier, C. M., and O. E. Sala. 2022b. “Observed Phenological Indicators and Environmental Drivers at Global Change Experiments at the Jornada Basin LTER Site, 2014-2020 ver 2.” Environmental Data Initiative. <https://doi.org/10.6073/pasta/d327a77f6474131db8aa589011e29c29>.
- Duniway, M. C., M. D. Petrie, D. P. C. Peters, J. P. Anderson, K. Crossland, and J. E. Herrick. 2018. “Soil Water Dynamics at 15 Locations Distributed across a Desert Landscape: Insights from a 27-Yr Dataset.” *Ecosphere* 9: e02335.
- Esch, E. H., D. A. Lipson, and E. E. Cleland. 2019. “Invasion and Drought Alter Phenological Sensitivity and Synergistically Lower Ecosystem Production.” *Ecology* 100: e02802.
- Felton, A. J., A. K. Knapp, and M. D. Smith. 2020. “Precipitation-Productivity Relationships and the Duration of Precipitation Anomalies: An Underappreciated Dimension of Climate Change.” *Global Change Biology* 00: 1–14.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. “Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components.” *Science* 281: 237–40.
- Filippa, G., E. Cremonese, M. Migliavacca, M. Galvagno, M. Forkel, L. Wingate, E. Tomelleri, U. Morra di Cella, and A. D. Richardson. 2016. “Phenopix: A R Package for Image-Based Vegetation Phenology.” *Agricultural and Forest Meteorology* 220: 141–50.
- Gherardi, L. A., and O. E. Sala. 2013. “Automated Rainfall Manipulation System: A Reliable and Inexpensive Tool for Ecologists.” *Ecosphere* 4: art18.
- Gherardi, L. A., and O. E. Sala. 2019. “Effect of Inter-Annual Precipitation Variability on Dryland Productivity: A Global Synthesis.” *Global Change Biology* 25: 269–76.
- Gibbens, R. P., and J. M. Lenz. 2001. “Root Systems of some Chihuahuan Desert Plants.” *Journal of Arid Environments* 49: 221–63.
- Gile, L. H. 1981. “Soils and Geomorphology in the Basin and Range Area of Southern New Mexico: Guidebook to the Desert Project, New Mexico.” *Bureau of Mines and Mineral Resources Memoir* 39: 222.
- Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy. 1996. “Exchange of Carbon Dioxide by a Deciduous Forest: Response to Interannual Climate Variability.” *Science* 271: 1576–8.
- Gu, L., W. M. Post, D. D. Baldocchi, T. A. Black, A. E. Suyker, S. B. Verma, T. Vesala, and S. C. Wofsy. 2009. “Characterizing the Seasonal Dynamics of Plant Community Photosynthesis across a Range of Vegetation Types.” In *Phenology of Ecosystem Processes*, edited by A. Noormets, 35–58. New York, NY: Springer.
- Havstad, K. M., L. F. Huenneke, and W. H. Schlesinger, eds. 2006. *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*. Oxford; New York, NY: Oxford University Press.
- Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. “Desertification Alters Patterns of Aboveground Net Primary Production in Chihuahuan Ecosystems.” *Global Change Biology* 8: 247–64.
- Ibrahim, S., J. Kaduk, K. Tansey, H. Balzter, and U. M. Lawal. 2021. “Detecting Phenological Changes in Plant Functional Types over West African Savannah Dominated Landscape.” *International Journal of Remote Sensing* 42: 567–94.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. “A Global Analysis of Root Distributions for Terrestrial Biomes.” *Oecologia* 108: 389–411.
- Jackson, R. B., M. J. Lechowicz, X. Li, and H. A. Mooney. 2001. “Phenology, Growth, and Allocation in Global Terrestrial Productivity.” In *Terrestrial Global Productivity*, edited by B. Saugier, J. Roy, and H. A. Mooney, 61–82. San Diego, CA: Academic Press.
- Jackson, S. D. 2009. “Plant Responses to Photoperiod.” *New Phytologist* 181: 517–31.
- Kikuzawa, K. 1991. “A Cost-Benefit Analysis of Leaf Habit and Leaf Longevity of Trees and their Geographical Pattern.” *The American Naturalist* 138: 1250–63.
- Kikuzawa, K. 1995. “Leaf Phenology as an Optimal Strategy for Carbon Gain in Plants.” *Canadian Journal of Botany* 73: 158–63.
- Klosterman, S. T., K. Hufkens, J. M. Gray, E. Melaas, O. Sonnentag, I. Lavine, L. Mitchell, R. Norman, M. A. Friedl, and A. D. Richardson. 2014. “Evaluating Remote Sensing of Deciduous Forest Phenology at Multiple Spatial Scales Using PhenoCam Imagery.” *Biogeosciences* 11: 4305–20.
- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. “Plant Functional Traits and the Multidimensional Nature of Species Coexistence.” *Proceedings of the National Academy of Sciences* 112: 797–802.
- Kramer, K., I. Leinonen, and D. Loustau. 2000. “The Importance of Phenology for the Evaluation of Impact of Climate Change on Growth of Boreal, Temperate and Mediterranean Forests Ecosystems: An Overview.” *International Journal of Biometeorology* 44: 67–75.
- Lauenroth, W. K., O. E. Sala, D. G. Milchunas, and R. W. Lathrop. 1987. “Root Dynamics of *Bouteloua Gracilis* during Short-Term Recovery from Drought.” *Functional Ecology* 1: 117–24.
- Maestre, F. T., B. M. Benito, M. Berdugo, L. Concostrina-Zubiri, M. Delgado-Baquerizo, D. J. Eldridge, E. Guirado, N. Gross, S. Kéfi, and Y. Le Bagousse-Pinguet. 2021. “Biogeography of Global Drylands.” *New Phytologist* 231: 540–58.
- Medeiros, J. S., and W. T. Pockman. 2014. “Freezing Regime and Trade-Offs with Water Transport Efficiency Generate Variation in Xylem Structure across Diploid Populations of

- Larrea Sp.(Zygophyllaceae)." *American Journal of Botany* 101: 598–607.
- Monger, H. C. 2006. "Soil development in the Jornada Basin." In *Structure and function of a Chihuahuan Desert ecosystem: The Jornada Basin Long Term Ecological Research site* 81–106. New York, NY: Oxford University Press.
- Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni, and S. W. Running. 2003. "Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982 to 1999." *Science* 300: 1560–3.
- Occurrence Records of Bouteloua Eriopoda (Torr.) Torr. 2021. "GBIF Secretariat." <https://www.gbif.org/species/5289847>.
- Occurrence Records of Bouteloua Lag. 2021. "GBIF Secretariat." <https://www.gbif.org/species/7557664>.
- Occurrence Records of Prosopis glandulosa Torr. 2021. "GBIF Secretariat." <https://www.gbif.org/species/5358457>.
- Occurrence Records of Prosopis L. 2021. GBIF Secretariat. <https://www.gbif.org/species/2970763>.
- Okin, G. S., O. E. Sala, E. R. Vivoni, J. Zhang, and A. Bhattachan. 2018. "The Interactive Role of Wind and Water in Functioning of Drylands: What Does the Future Hold?" *Bioscience* 68: 670–7.
- Parmesan, C. 2007. "Influences of Species, Latitudes and Methodologies on Estimates of Phenological Response to Global Warming." *Global Change Biology* 13: 1860–72.
- Peñuelas, J., T. Rutishauser, and I. Filella. 2009. "Phenology Feedbacks on Climate Change." *Science* 324: 887–8.
- Petrie, M. D., S. L. Collins, D. S. Gutzler, and D. M. Moore. 2014. "Regional Trends and Local Variability in Monsoon Precipitation in the Northern Chihuahuan Desert, USA." *Journal of Arid Environments* 103: 63–70.
- Poulter, B., D. Frank, P. Ciais, R. B. Myneni, N. Andela, J. Bi, G. Broquet, et al. 2014. "Contribution of Semi-Arid Ecosystems to Interannual Variability of the Global Carbon Cycle." *Nature* 509: 600–3.
- Právník, R. 2016. "Drylands Extent and Environmental Issues. A Global Approach." *Earth-Science Reviews* 161: 259–78.
- Ramirez, G. A., G. Ramirez, and C. Tweedie. 2021. "Phenoanalyzer." System Ecology Lab, University of Texas El Paso. <https://selutep.squarespace.com/>.
- Reichmann, L. G., O. E. Sala, and D. P. C. Peters. 2013. "Precipitation Legacies in Desert Grassland Primary Production Occur through Previous-Year Tiller Density." *Ecology* 94: 435–43.
- Richardson, A. D., K. Hufkens, T. Milliman, D. M. Aubrecht, M. Chen, J. M. Gray, M. R. Johnston, et al. 2018a. "Tracking Vegetation Phenology across Diverse North American Biomes Using PhenoCam Imagery." *Scientific Data* 5: 180028.
- Richardson, A. D., K. Hufkens, T. Milliman, D. M. Aubrecht, M. E. Furze, B. Seyednasrollah, M. B. Krassovski, et al. 2018b. "Ecosystem Warming Extends Vegetation Activity but Heightens Vulnerability to Cold Temperatures." *Nature* 560: 368–71.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. "Climate Change, Phenology, and Phenological Control of Vegetation Feedbacks to the Climate System." *Agricultural and Forest Meteorology* 169: 156–73.
- Römermann, C., S. F. Bucher, M. Hahn, and M. Bernhardt-Römermann. 2016. "Plant Functional Traits – Fixed Facts or Variable Depending on the Season?" *Folia Geobotanica* 51: 143–59.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. *Akaike Information Criterion Statistics*, Vol 81 26853. Dordrecht: D. Reidel.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and P. A. Roset. 2012. "Contrasting Nutrient-Capture Strategies in Shrubs and Grasses of a Patagonian Arid Ecosystem." *Journal of Arid Environments* 82: 130–5.
- Schlesinger, W. H., ed. 2005. *Biogeochemistry*. Amsterdam: Elsevier.
- Scott, J. D., Alexander, M. A., Murray, D. R., Swales, D., and Eischeid, J. 2016. The Climate Change Web Portal: A System to Access and Display Climate and Earth System Model Output from the CMIP5 Archive. Bulletin of the American Meteorological Society, 97(4), 523–530. <https://doi.org/10.1175/bams-d-15-00035.1>.
- Seyednasrollah, B., A. M. Young, K. Hufkens, T. Milliman, M. A. Friedl, S. Froking, and A. D. Richardson. 2019. "Tracking Vegetation Phenology across Diverse Biomes Using Version 2.0 of the PhenoCam Dataset." *Scientific Data* 6: 222.
- Shukla, J., C. Nobre, and P. Sellers. 1990. "Amazon Deforestation and Climate Change." *Science* 247: 1322–5.
- Sonnentag, O., K. Hufkens, C. Teshera-Sterne, A. M. Young, M. Friedl, B. H. Braswell, T. Milliman, J. O'Keefe, and A. D. Richardson. 2012. "Digital Repeat Photography for Phenological Research in Forest Ecosystems." *Agricultural and Forest Meteorology* 152: 159–77.
- Team Rs. 2015. *RStudio: Integrated Development for R*, Vol 42 14. Boston, MA <http://www.rstudio.com>: RStudio, Inc.
- Throop, H. L., L. G. Reichmann, O. E. Sala, and S. R. Archer. 2012. "Response of Dominant Grass and Shrub Species to Water Manipulation: An Ecophysiological Basis for Shrub Invasion in a Chihuahuan Desert Grassland." *Oecologia* 169: 373–83.
- Trenberth, K. E., A. Dai, R. M. Rasmussen, and D. B. Parsons. 2003. "The Changing Character of Precipitation." *Bulletin of the American Meteorological Society* 84: 1205–18.
- Wingate, L., J. Ogée, E. Cremonese, G. Filippa, T. Mizunuma, M. Migliavacca, C. Moisy, M. Wilkinson, C. Moureaux, and G. Wohlfahrt. 2015. "Interpreting Canopy Development and Physiology Using a European Phenology Camera Network at Flux Sites." *Biogeosciences* 12: 5995–6015.
- Wuebbles, D., G. Meehl, K. Hayhoe, T. R. Karl, K. Kunkel, B. Santer, M. Wehner, et al. 2014. "CMIP5 Climate Model Analyses: Climate Extremes in the United States." *Bulletin of the American Meteorological Society* 95: 571–83.
- Yahdjian, L., and Sala, O. E. 2002. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133(2), 95–101. <https://doi.org/10.1007/s00442-002-1024-3>.
- Yao, J., J. Anderson, H. Savoy, and D. Peters. 2020. "Gap-Filled Daily Precipitation at the 15 Long-Term NPP Sites at Jornada Basin LTER, 1980-Ongoing ver 75." Environmental Data Initiative. <https://doi.org/10.6073/pasta/cf3c45e5480551453f1f9041d664a28f>.
- Zani, D., T. W. Crowther, L. Mo, S. S. Renner, and C. M. Zohner. 2020. "Increased Growing-Season Productivity Drives Earlier Autumn Leaf Senescence in Temperate Trees." *Science* 370: 1066–71.
- Zhang, X., M. A. Friedl, C. B. Schaaf, A. H. Strahler, J. C. F. Hodges, F. Gao, B. C. Reed, and A. Huete. 2003. "Monitoring



Vegetation Phenology Using MODIS.” *Remote Sensing of Environment* 84: 471–5.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Currier, Courtney M., and Osvaldo E. Sala. 2022. “Precipitation versus Temperature as Phenology Controls in Drylands.” *Ecology* e3793. <https://doi.org/10.1002/ecy.3793>