

# Plant phenology predicts the stability of primary production in three ecosystems of the northern Chihuahuan Desert

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## Abstract

1. The temporal stability of plant productivity affects species' access to resources, exposure to stressors and strength of interactions with other species in the community, including support to the food web. The magnitude of temporal stability depends on how a species allocates resources among tissues and across phenological stages, such as vegetative growth versus reproduction. Understanding how plant phenological traits correlate with the long-term stability of plant biomass is particularly important in highly variable ecosystems, such as drylands.
2. We evaluated whether phenological traits predict the temporal stability of plant species productivity by correlating 18 years of monthly phenology observations with biannual estimates of above-ground plant biomass for 98 plant species from semi-arid drylands. We then paired these phenological traits with potential climate drivers to identify abiotic contexts that favour specific phenological strategies among plant species.
3. Phenological traits predicted the stability of plant species above-ground biomass. Plant species with longer vegetative phenophases not only had more stable biomass production over time but also failed to fruit in a greater proportion of years, indicating a growth-reproduction trade-off. Earlier leaf-out dates, longer fruiting duration and longer time lags between leaf and fruit production also predicted greater temporal stability.
4. Species with stability-promoting traits began greening in drier conditions than their unstable counterparts and experienced unexpectedly greater exposure to climate stress, indicated by the wider range of temperatures and precipitation experienced during biologically active periods.
5. Our results suggest that bet-hedging strategies that spread resource acquisition and reproduction over long time periods help to stabilize plant species productivity in variable environments, such as drylands.

**KEY WORDS**

dryland, phenological niche, plant traits, population dynamics, primary productivity

## 1 | INTRODUCTION

The temporal stability of species productivity—the constancy of population biomass production over time—can impact environmental and biotic interactions. It can affect how and when a species accesses resources, is exposed to abiotic stress or interacts with other species in the community (Elzinga et al., 2016; Harrison, 1979; Májeková et al., 2014; Tredennick et al., 2017). Temporal stability in biomass tracks other metrics of stability, such as population abundance, recruitment or growth rate (Roeder et al., 2021; Urrutia-Cordero et al., 2022), and is important to understand because it influences the timing and consistency of a species' impact on the community and ecosystem in which it is embedded (Dallas & Kramer, 2022; Mrowicki et al., 2016; Polley et al., 2013). Temporally unstable populations with 'boom or bust' dynamics can become offset with other species, creating mismatches between partners in mutualistic or antagonistic interactions (Rafferty et al., 2013; Zhang et al., 2016), and species with large temporal instability are more likely to face stochastic population extinction (Adler et al., 2006; Ma et al., 2020). However, temporal variability that creates asynchronies among individual species can also help to stabilize emergent functions, such as total ecosystem productivity (Dallas & Kramer, 2022). Therefore, the ability to predict population biomass stability can yield inferences on species interactions including coexistence, the relative sensitivity to perturbation, and emergent ecosystem properties, such as productivity.

Variation in temporal stability among species may arise from differences in life-history strategies or other species traits (e.g. Angert et al., 2007; Li et al., 2021). For example, species with acquisitive or 'fast' strategies (Wright et al., 2004) can quickly maximize productivity when resources are available and thus exhibit high temporal instability in stochastic environments with large resource fluctuations (Chesson et al., 2004). Both observational (e.g. MacGillivray et al., 1995; Sauer & Link, 2002) and experimental (Adler et al., 2006; Angert et al., 2009) studies demonstrate that life-history strategies can predict temporal patterns in biomass or population dynamics. For example, plant species with conservative strategies, such as investment in deeper roots or more fibrous leaves (higher leaf dry matter content), were more temporally stable in a mesic grassland (Májeková et al., 2014). Similarly, desert annual plants with the conservative vegetative strategy of high water use efficiency had more temporally stable populations (Angert et al., 2009). Reproductive traits may predict stability when population biomass is governed by recruitment, rather than growth or survival. For example, in masting plants, episodic fruiting years can generate large temporal instability (Kelly & Sork, 2002). In contrast, bird communities with more 'fast' species (small body size, short life span, large clutches) were more stable than communities of predominantly 'slow' species (large body size, long life span, small clutches) (Li et al., 2021). Thus, an alternative hypothesis is that species with acquisitive/fast life-history traits are less vulnerable to temporal fluctuation because they rely less on consecutive events or long periods of consistent resources to

survive and reproduce (Diaz et al., 2004). Quantifying the temporal stability of a species requires long-term observations which can be time- and labour-intensive to collect, especially for rare species. Therefore, it is valuable to identify species traits that can predict their temporal stability in the absence of long-term data.

Although prior work has focused on physiological or life-history traits, phenological traits such as the duration of the vegetative phenophase or the reproductive phenophase could also be important mediators of temporal stability in species biomass or abundance. Phenology, the timing of important life events such as leaf production or fruiting (Forrest & Miller-Rushing, 2010) can influence species' biomass by creating matches or mismatches in timing with critical abiotic events or with interacting species (e.g. pollinators, seed dispersers) (CaraDonna et al., 2017; Forrest & Miller-Rushing, 2010). For example, species with long phenophases—defined as phenological periods with discrete beginning and endpoints—may have the most temporally stable populations because they have extended time periods to accumulate resources (Moussus et al., 2011) and rely less on highly synchronized species interactions than those that leaf out, flower or fruit during short windows (Elzinga et al., 2016). Alternatively, long phenophases may destabilize species productivity through long windows of exposure to environmental extremes and biotic stressors. For example, experimental warming lengthened the growing season for several tree species but also exposed individuals to damage from late freeze events, ultimately decreasing leaf biomass in frost years (Richardson et al., 2018). Chen et al. (2023) found that experimental warming in a mesic grassland lengthened the growing season, but increased asynchrony among species. Although many studies have linked shifts in species' phenology to temporal trends (increases or declines) in *mean* biomass, abundance, or relative winner or loser species (Duveneck & Thompson, 2017; e.g. Richardson et al., 2010), these studies have not, to our knowledge, related phenological traits to the temporal *stability* of those populations.

The phenological strategies of the most temporally stable species in an ecosystem likely depend on both abiotic stability and biotic pressures. For abiotic stability, temporal patterns in climate can mechanistically link phenological traits and stability in species biomass, both of which can closely track climate (Forrest & Miller-Rushing, 2010; Parmesan & Yohe, 2003; Primack & Miller-Rushing, 2011). For example, plant species that leafed out early and had long vegetative phenophases benefited from climate warming, but species that required winter chilling instead experienced variable budburst (Morin et al., 2009). In ecosystems with highly variable climates, phenological traits that cause species to closely track climate should reduce the temporal stability of species' biomass, whereas phenological traits that buffer or decouple species' biomass from specific climate events should promote temporal stability.

The variable climates of drylands provide useful testbeds to evaluate how plant traits predict the temporal stability of species biomass. Drylands cover >40% of the Earth's land surface and are expanding in extent (Burrell et al., 2020). Unpredictable rainfall can drive large variability in phenology as well as in population stability

(Beatley, 1974; Crimmins et al., 2011), but these two responses have not yet been linked. Although some species are adapted to the low moisture and abiotic variability of drylands, dryland climates are becoming both increasingly more arid and more variable (Maurer et al., 2020; Rudgers et al., 2018). For example, in the southwestern United States, interannual variability in aridity has increased and rainfall events have become smaller and more frequent (Cook & Seager, 2013; Gutzler & Robbins, 2010; Petrie et al., 2014; Rudgers et al., 2018). The high variability of drylands enables us to leverage natural variability over time (Ibáñez et al., 2013) to detect patterns indicative of key roles for phenological traits in stabilizing plant species biomass.

Here, we asked: (1) What phenological traits best predict temporal stability in plant species above-ground biomass in drylands? Plant species with 'slow', conservative phenologies, such as long duration, may be more temporally stable because they have long windows to acquire resources. Alternatively, species with 'fast', acquisitive phenologies such as early onset and short duration may be less vulnerable to temporal fluctuation because they are less reliant on consecutive events or long periods of consistent resources to survive and reproduce. (2) How do phenological predictors of temporal stability track dryland climate? We predicted a strong role for climate in predicting phenological traits and specifically explored the average minimum, maximum and range of temperature values that each species experienced during its leafing and fruiting phenophases, as well as the average temperature and precipitation conditions immediately preceding leaf and fruit onset or offset. We predicted that species with long duration phenological strategies would be less sensitive to any single climate variable because activity occurs over a wide range of climate variation, and that short duration strategies, including early or late leaf out, would be more finely tuned to temperature and precipitation. To address these questions, we paired 18 years of monthly plant phenology observations, monthly weather data and biannual biomass measurements for 98 plant species from semi-arid grasslands and shrublands in the northern Chihuahuan Desert.

## 2 | MATERIALS AND METHODS

### 2.1 | Site description

This study took place at the northern range of the Chihuahuan Desert ecoregion at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, United States under U.S. Fish & Wildlife Special Use Permit #SEV\_Rudgers\_LTER\_24\_32 and earlier annual versions. Within the SNWR, we collected data across three sites: a typical Chihuahuan Desert grassland (34.3331, -106.736) dominated by black grama grass (*Bouteloua eriopoda*), a Chihuahuan Desert shrubland (34.3331, -106.736) dominated by creosotebush (*Larrea tridentata*) and a Plains grasslands (34.3348, -106.631) dominated by blue grama grass (*Bouteloua gracilis*), but with black grama grass and other Chihuahuan Desert species present. These sites are

located within 10 km of one another and experience the same general climate trends. During 2002–2019, mean annual precipitation across these sites was  $240 \pm 8$  mm, the majority of which falls during the monsoon season (July–October), mean annual temperature was 14.5°C and mean above-ground plant biomass was  $89 \pm 7$  g/m<sup>2</sup>. Approximately 90% of total plant biomass is produced by perennial species that are most active in late spring, summer and early fall.

### 2.2 | Plant phenology

Plant phenology was recorded monthly along four 200 m long  $\times$  2 m wide belt transects at each of the three sites ( $N=12$  transects). Here, we used 18 years of observations, from January 2002 to December 2019, for each species. Monthly observations were made within a few days of the first calendar date of each month. Along each belt transect, we recorded the phenological status of 10 individuals of each plant species. Typically, these were the first 10 individuals that we encountered, but in the case of extremely abundant species, we assessed the phenology of 10 individuals evenly spaced along the transect to best represent the phenological status over the transect. Vegetative status was classified as having green leaves, either newly grown or mature green leaves, or brown or browning leaves. Reproductive status categories were flower buds, open flowers, unripe fruit or ripe fruit.

For each species, we determined the annual onset, offset and duration of phenophases within each belt transect. For each species, we first calculated the proportion of individuals within each monthly belt transect that had green leaves and that had ripe fruit. Because our phenology observations were made only once per month, we used conservative onset and offset cut-offs rather than the absolute first/last dates when a phenophase was observed. We marked the first day when  $\geq 25\%$  of a population on a transect had green leaves or ripe fruits as the onset date for that phenophase. Similarly, offset dates were marked on the last day when  $\geq 25\%$  of a population on a transect remained in a phenophase. This method reduced the influence of rare early- or late-growing or blooming phenotypes, allowing us to quantify a single trait value that captured the typical phenology of each species. From these dates, we calculated the duration of each phenophase as the number of days between onset and offset dates. The majority of species at our sites produced fruit within 2 months of leaf onset, and the length of the spring and fall monsoon growing seasons are only 3–4 months. We therefore defined a population on a transect as being active, but failing to fruit if we observed new leaf growth for at least 2 months within a year yet made zero observations of ripe fruit. Phenological trait values for each species were averaged across 18 years of observations, with no missing data, and all 12 belt transects, representing three ecosystem types. Averaging across spatial and temporal patterns allowed us to arrive at a single value for each species that captured its phenological plasticity, variability and response to a range of climate conditions in this region (Hendry & Day, 2005; Májeková et al., 2014). Additionally, we found no significant differences among ecosystems

when we compared phenological traits to the temporal stability of biomass production within each ecosystem separately, so we combined data for analysis.

We classified each plant species by its functional group (grass, forb, shrub, tree), life-history strategy (annual, annual/biennial, perennial) and photosynthetic pathway (C3, C4, CAM) from the USDA Plants Database (USDA, NRCS, 2020). We included observations from 62 C3 species, 30 C4 species and 6 CAM species; 69 perennial species and 29 annual or annual/biennial species; and 64 forb, 21 grass and 13 shrub or tree species.

### 2.3 | Temporal stability of plant biomass

Above-ground plant biomass production is annually bimodal in our drylands. The first annual pulse of growth occurs in spring, and the second pulse, usually larger, occurs with monsoon rainfall, after a month or two of very hot and dry early summer (May–June) conditions. Spring rainfall is decoupled from fall rainfall: wet springs are rarely followed by wet fall monsoon seasons. During the past 30 years, there were only 2 years in which spring and fall were both very dry (seasonal rainfall totalling <100 mm) and no years in which spring and fall were both wet (seasonal rainfall totalling >150 mm). Because this bimodal climatic seasonality results in two distinct pulses of plant productivity, we estimated the above-ground biomass of every plant species in both the late spring (April–May) and fall (September–October) to capture both peaks of seasonal production in each year. We used non-destructive methods to measure plant productivity within 1 m<sup>2</sup> fixed-position quadrats ( $N=248$  quadrats), and with these, we estimated the above-ground productivity of each species as described by Muldavin et al. (2008). Within each fixed-position quadrat, we identified every plant to species. We recorded ground cover (m<sup>2</sup>) and maximum height (cm) of live tissue of every individual plant or clump of plants, depending on growth form. Many of the species in our study area have multiple stems, produce spreading rhizomes or grow in dense bunches, making it difficult or impossible to differentiate individual plants. In these cases, we made a single observation of plant cover and height for each unique patch of each species. From our observations of cover and height of each species, we then estimated dry above-ground biomass using species-specific allometric linear equations (Muldavin et al., 2008; Rudgers et al., 2019), all of which are publicly available (Hallmark et al., 2019). This method has been used widely for drylands for decades and was originally developed by Huenneke et al. (2001).

We tracked stability of plant productivity in units of above-ground biomass for several reasons. The first reason was functional: Chihuahuan Desert grassland and shrubland biomes are dominated by clonal or rhizomatous grasses, many-stemmed shrubs and cacti and decumbent, mat-forming forbs, making it difficult to differentiate individuals. Second, we made observations at the end of each growing season, after species had a chance to germinate, survive and grow to peak size for that season, thereby integrating both the amount of aboveground material produced each season and the

number of individual plants (or plant patches) that were present. Third, although biomass and abundance positively correlate within a species, it is difficult to compare changing counts of individuals among functional types in metrics that are maximally meaningful to ecosystems (e.g. counts of trees vs. grasses or forbs are less comparable than biomass/m<sup>2</sup>). This reason underscores why most studies of stability of plant abundance focus on a single species, species grown in lab or greenhouse settings, or ecosystems dominated by annual forbs (e.g. Angert et al., 2009; Májeková et al., 2014). In our system, above-ground biomass provides a comparable metric across time—we took the same measurements within fixed monitoring quadrats for decades, and between many species—we measured small-bodied annuals and large, clumping perennials using the same methods, resulting in a common unit of biomass—grams of dry biomass per unit area. Fourth, plant biomass is a more relevant measure of populations in our focal ecosystems when considering synchronous plant interactions with mutualists or consumers or accounting for plants' influence on ecosystem processes, particularly ecosystem productivity. For these reasons, we used above-ground biomass to compare temporal stability across the 98 plant species in our study.

We calculated temporal stability of biomass production for each species as the coefficient of variation (CV) of all biannual above-ground biomass estimates. CV of biomass production is commonly used in ecological literature as a measure of population and community stability (Caldeira et al., 2005; Song et al., 2023; Wilcox et al., 2017). The CV of above-ground biomass was calculated as the ratio of the standard deviation of above-ground biomass to the mean of above-ground biomass of each species, both of which have the same units (g/m<sup>2</sup>), and therefore, CV is standardized and unitless. The CV of maximum annual biomass (one value per year) was strongly correlated with CV of biannual biomass (two values per year) for each species ( $F_{1,92}=1893.0$ ,  $R^2=0.95$ ,  $p<0.0001$ ; Figure S1). Therefore, we chose the biannual CV metric because it captured variability over more time points.

### 2.4 | Climate

Three meteorological stations measured hourly precipitation and air temperature at each site for the duration of this study (Moore & Hall, 2022). Any missing data resulting from temporary equipment failure were gap-filled with modelled data constructed from records of nearby meteorological stations within SNWR. We aggregated daily climate data across the three stations into monthly mean air temperature and monthly total precipitation. We paired phenological observations made at the beginning of each month with the weather conditions of the preceding month. For example, we paired the phenology observations made on May 1 with the cumulative precipitation and mean temperature recorded April 1–30. Then, we calculated the average minimum, maximum and range of temperature values that each species experienced during its leafing and fruiting phenophases, as well as the average temperature and precipitation conditions preceding leaf and fruit onset or offset.

## 2.5 | Statistical analyses

To determine whether phenological traits were related to the population stability of species within our study region, we used general linear models to evaluate phenological traits as correlates of population stability. Models took the form: CV of biannual biomass ~ phenological trait, with plant population species as the unit of replication. We ranked the relative strength of each trait: stability relationship using model selection procedures with maximum likelihood estimation and the second-order Akaike information criterion (AICc) (Burnham & Anderson, 2002). These models posed no statistical issue with multicollinearity because the best predictor was the single regression model with the lowest AICc, providing the best fit to the data, following best practices for model selection procedures in Burnham and Anderson (2002).

Our models, applied across our entire plant community, could be influenced by a cluster of phylogenetically related species that share similar phenological traits or population stability values. Therefore, we assessed phylogenetic non-independence of the phenological traits and stability values we observed. We found no significant phylogenetic signal in either value and saw similar stability–trait relationships when phylogenetically independent contrasts were the unit of replication instead of species. See Supplement for more details.

We also correlated each phenological trait to the average climatic conditions species experienced during that phenophase, again using general linear models with plant species as the unit of replication. While the direction of these relationships was often easy to predict (e.g. species that leaf-out earlier in the year should experience cooler temperatures), their relative strengths revealed which climatic conditions were most consistently correlated with species' phenological strategies.

We conducted all analyses in the R programming language (R Core Team, 2020).

## 2.6 | Replication statement

We sought to understand whether the phenological traits of species predicted the temporal stability of species biomass in a semi-arid biome in the northern Chihuahuan Desert. Using 18 years of phenological observations, we calculated mean phenological trait values, stability of biomass as CV of above-ground biomass and mean monthly climate variables during various phenophases for 98 species of plants.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species biomass as g/m <sup>2</sup>	Species productivity within a plant community over 18 years	98 species

## 3 | RESULTS

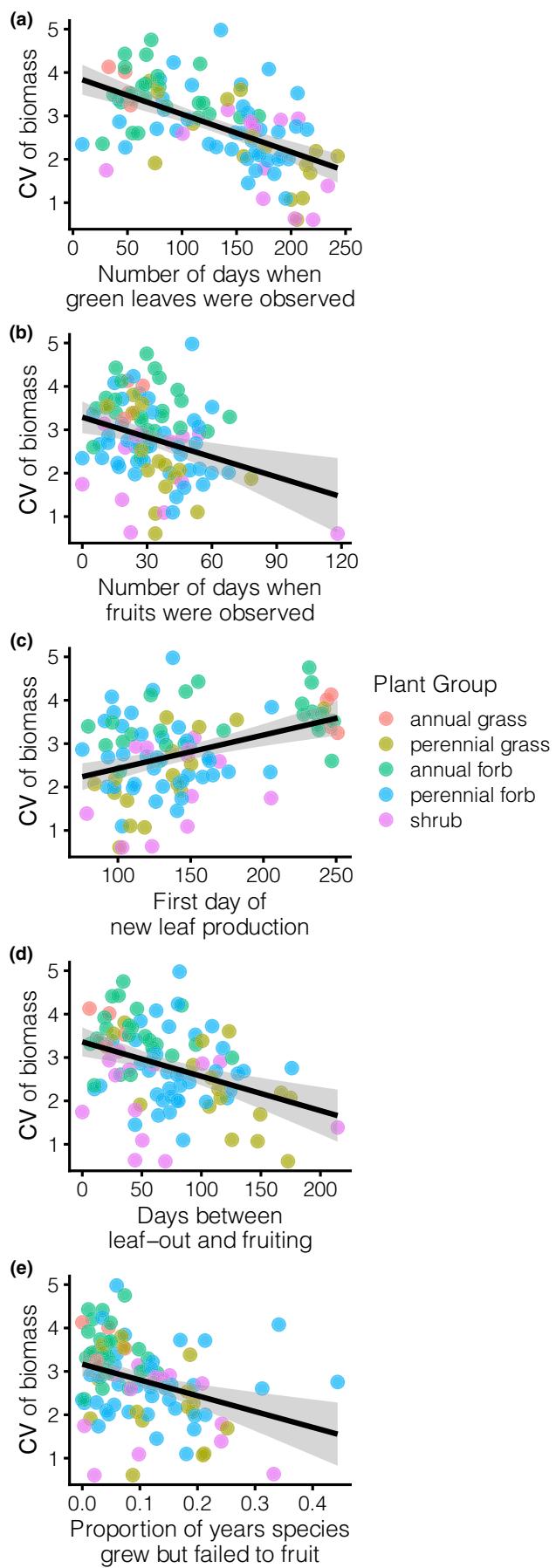
### 3.1 | Phenological traits predicted the temporal stability of species biomass production

Species with more temporally stable biomass production had longer vegetative phenophases (Figure 1a), these stable species maintained green leaves for more days each year than more variable species ( $F_{1,96}=51.9, r=-0.59, p<0.0001$ ). More temporally stable populations also had longer fruiting phenophases (Figure 1b;  $F_{1,95}=9.5, r=-0.30, p=0.003$ ). One species, the foundational plant *Larrea tridentata* (creosote bush), had an exceptionally long fruiting period (Figure 1b). When this species was excluded from analysis, the relationship between the length of fruiting phenophase and the temporal stability of biomass production remained statistically significant ( $F_{1,94}=4.7, r=-0.22, p=0.032$ ). More temporally stable populations began producing new leaves earlier in the year (Figure 1c;  $F_{1,96}=16.4, r=0.39, p=0.0001$ ) but waited longer after green-up to begin fruiting (Figure 1d;  $F_{1,96}=15.7, r=-0.37, p=0.001$ ). Species with more stable biomass also had more years in which they grew, but failed to fruit (Figure 1e;  $F_{1,95}=12.2, r=-0.33, p=0.0007$ ). Species with longer vegetative growing seasons were more likely to fail to successfully reproduce every year, suggesting growth–reproduction trade-offs because failure to fruit correlated positively with leaf duration ( $F_{1,189}=197.8, r=0.71, p<0.0001$ ).

### 3.2 | Conservative phenological traits were the best predictors of temporal stability

We compared the predictive strength of all phenological traits using model selection criteria, for which the best predictor was the single trait with the lowest AICc. Among phenological traits, leafing phenophase duration best predicted temporal stability in biomass production (Figure 1a). The next best predictor was the number of days between leaf-out and fruit onset ( $\Delta\text{AICc}=28.7$ , Figure 1d). Leafing phenophase duration and the number of days between leaf-out and fruit onset correlated positively across plant species ( $r=0.72$ ; Figure 3).

These two phenological traits, the duration of species' leafing phenophase and the number of days between leaf-out and fruit onset, were also the best predictors of mean population biomass over the 18 year time frame (Figure 2a,b), and thus are also indicators of species commonness on the commonness–rarity spectrum. Therefore, the most abundant species on the landscape—in terms of above-ground biomass—maintained green leaves throughout most of the year and also grew but failed to fruit in more years, indicating that constant investment in vegetative structures may exact a cost to reproduction, or strategies that enable plastic adjustment of fruit production could promote species competitive dominance and commonness.



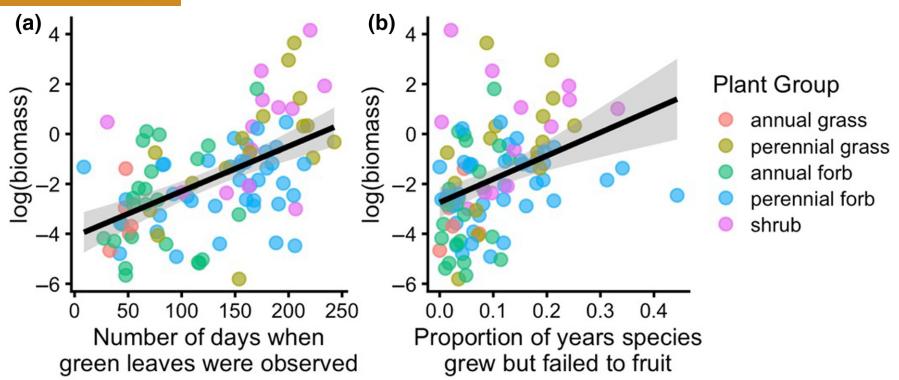
**FIGURE 1** Phenological traits predict the stability of population biomass production for 98 dryland plant species including (a) number of days annually when green leaves were observed, (b) number of days annually when fruits were observed, (c) first day of new leaf production, (d) number of days between leaf-out and fruit onset, (e) proportion of years species grew but failed to fruit. Each point represents the mean value of population stability and the mean phenological trait for a single species. Lines show significant linear fits with 95% confidence intervals (grey bands).

### 3.3 | Climate strongly predicted phenological traits for each phenophase

The phenological strategies observed in this plant community exposed species to a broad range of temperature and precipitation conditions. The onset, offset and duration of phenophases were related to both temperature and precipitation (Figure 3). Species that leafed out later in the year began this growth phase in warmer minimum temperatures than species with early leaf-out ( $F_{1,189}=57.41$ ,  $r=0.48$ ,  $p<0.0001$ ), experienced a narrower range of temperatures ( $F_{1,189}=881.8$ ,  $r=0.91$ ,  $p<0.0001$ ) and on average, wetter conditions ( $F_{1,189}=881.8$ ,  $r=0.91$ ,  $p<0.0001$ ), but their biomass was more temporally unstable than species with early leaf-out (Figure 3). These late-starting plant species also experienced wetter conditions as they started to produce ripe fruit ( $F_{1,189}=881.8$ ,  $r=0.91$ ,  $p<0.0001$ ). In addition, the temperature range during the vegetative phenophase best predicted both the duration of active leaf production ( $F_{1,189}=881.8$ ,  $r=0.91$ ,  $p<0.0001$ ) and failure-to-fruit ( $F_{1,191}=122.4$ ,  $r=0.62$ ,  $p<0.0001$ ). Species that maintained green leaves longer, waited longer to fruit after leaf-out, or failed to fruit more frequently were all associated with similar climatic variables: a broader range of temperatures ( $r=0.91$ ,  $0.69$  and  $0.62$ , respectively; all  $p<0.0001$ ), lower minimum temperatures ( $r=0.44$ ,  $0.50$  and  $0.32$ , respectively; all  $p<0.0001$ ), higher maximum temperatures ( $r=0.53$ ,  $0.28$  and  $0.35$ ; all  $p<0.0001$ ) and leaf production initiated during drier conditions ( $r=0.41$ ,  $0.48$  and  $0.30$ ; all  $p<0.0001$ ).

## 4 | DISCUSSION

Our work demonstrated that plant phenological traits can predict the temporal stability of species biomass production. The relationships revealed phenological trait syndromes that predicted stability over variable climatic conditions across three semi-arid biomes. The single best predictor of the temporal stability of species productivity was long leaf duration, estimated by the average number of days per year when green leaves were produced, which explained 35% of the variation among species in their temporal stability. This result supported the hypothesis that plant species with 'slow', conservative phenologies, such as long phenophase duration, are more temporally stable because they have long windows to acquire resources, rather than the alternative that species



**FIGURE 2** Phenological traits predict population size for 98 dryland plant species including (a) number of days annually when green leaves were observed and (b) the proportion of years in which species grew but failed to produce fruit. Each point represents the mean value of population stability and phenological trait for a single species. Lines are linear fits and grey bands are 95% confidence intervals around the parameter estimate for the slope. A nonlinear fit (e.g. quadratic) did not improve model fit (results not shown).

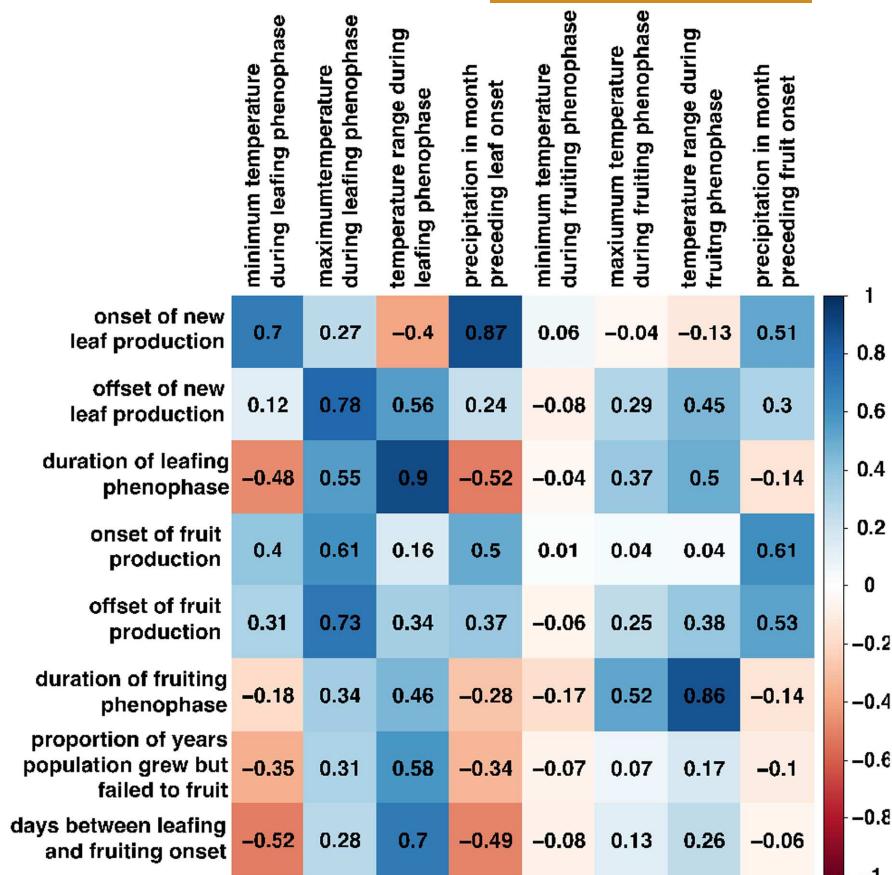
with 'fast', acquisitive phenologies are less vulnerable to temporal fluctuation because they rely less on consecutive events or long periods of consistent resources. In semi-arid grassland and shrubland sites in the northern Chihuahuan Desert, conservative phenological traits were positively related to the temporal stability of species above-ground biomass as well as population mean biomass. Species with longer vegetative and reproductive phenophases had more stable biomass and produced more biomass than species with shorter phenophases. The explanatory power of these phenological traits to predict stability ( $R^2$  up to 0.35) was comparable to previous studies in which leaf economic spectrum traits explained up to 31% of the variation in stability of species abundance in a mesic grassland in the Czech Republic (Májeková et al., 2014). Similarly, physiological traits (specific leaf area, foliar nitrogen and water use efficiency) explained 'booms' in fecundity for Sonoran Desert annual plant species (Angert et al., 2009). Thus, our analyses reinforced previous findings in which traits associated with conservative growth strategies were most positively associated with species abundance or stability (Angert et al., 2007; Diaz et al., 2004; Májeková et al., 2014).

Phenological traits were tightly coupled to climatic conditions experienced during species growing seasons in our variable dryland ecosystems. Acquisitive species that only leaf-out late in the year during the monsoon rainy season when resources are most abundant, produced leaves during warmer, wetter conditions than conservative species. Plants with acquisitive strategies typically have faster germination and growth rates, allowing rapid responses to rainfall that can increase fitness by avoiding costs of reproduction during years with scant resources (Angert et al., 2007; Shriver, 2017; Venable, 2007). In our system, this strategy was associated with more flashy temporal dynamics and lower biomass relative to other species in the community. In contrast, species with more conservative strategies started growing earlier in the year, maintained green leaves longer, waited longer to fruit after leaf-out and failed to fruit more frequently. These conservative strategy species were more temporally stable than the acquisitive species, experienced a broader range of temperature conditions, including lower minimums

and higher maximums, and initiated leaf production under drier conditions. Our results support the general pattern that plant species with conservative traits typically have slower growth rates but greater water use efficiency—they can better withstand drought conditions (Lasky et al., 2016)—but here we add new phenological traits to the acquisitive-conservative trait economic spectrum (Wright et al., 2004).

While trade-offs between allocation to growth versus reproduction occur commonly across the tree of life (Silvertown et al., 2015; Stearns, 1992), we found mixed support for this trade-off. In our set of 98 plant species, those that maintained green leaves for more days of the year failed to fruit in a given year more frequently; however, these species also fruited over longer periods because of their longer total activity periods. Of the 45 species that rarely (<5% of years) or never failed to fruit, 56% ( $n=25$ ) were annuals, and only one was a shrub (*Larrea tridentata*). All seven species that failed to fruit in >20% of years were perennial. *Ephedra torreyana*, a common, succulent shrub, failed to produce ripe cones in 32% of study years and is known to adopt a masting reproductive strategy, one method of maintaining a stable population while not reproducing sexually in every growing season (Hollander & Vander Wall, 2009). Plants that invest substantially in growth and maintenance may face both physiological and ecological trade-offs with reproduction, and climate conditions could exacerbate these costs of reproduction, making plastic reproductive strategies, such as failure to fruit, beneficial to fitness. For example, in a prior experimental study at our site, suppression of flowering with the application of gibberellic acid to tree cholla cactus (*Cylindropuntia imbricata*) reduced the cost of reproduction indirectly, via reduced herbivory by cactus bugs, which prefer plants with flowers (Miller et al., 2006). Although reproductive adjustments in response to climate were not investigated in that study, plant species that plastically adjust whether or not to fruit in a given year may be advantaged in years with limited resources because they can reduce the costs of reproduction. For example, larger salamanders better survived drought, but had slower reproductive maturation and reduced reproduction; small, fast-maturation strategies were

**FIGURE 3** Correlogram of phenological traits related to climate variables. Values represent correlation coefficients (R). Darker colours correspond to stronger relationships, with warmer tones indicating negative correlations and cooler tones indicating positive relationships.



projected to outcompete large, slow-maturation strategies in non-drought conditions (Luhring & Holdo, 2015). Similarly, beech trees had a growth-reproduction trade-off that intensified in years of summer drought (Hacket-Pain et al., 2017). Our results suggest that plant species with long phenophases may have greater capacity to reduce the costs of reproduction in response to environmental stress than taxa with short-activity periods.

Phenological strategies may underlie the vulnerability of species to different aspects of climate change. Previous meta-analyses revealed that early-growing species were most sensitive to warming (Pau et al., 2011; Wolkovich et al., 2012). However, growing earlier in spring also increases risk of frost damage (Inouye, 2008), and many dryland species are cold-intolerant (Pockman & Sperry, 1997) with dramatic responses to extreme freezes (Ladwig et al., 2019). In addition to warming temperature, water availability is decreasing in drylands (Williams et al., 2022). In the south-western United States, where many plant species track monsoon rains, the monsoon season is predicted to shift later in the year, increasing the length of the hyperarid period between spring and summer rains (Cook & Seager, 2013). We found that the propensity for plants to abandon fruiting increased with the range of temperatures a species endured during its growth phase. Plant species with strategies to reduce costs of reproduction—those that waited longer to fruit after leaf-out or failed to fruit more frequently—were more likely to initiate leaf production during dry conditions, although the climate correlates of these strategies were primarily temperature-based, including

greater temperature ranges and higher temperature maxima than species that had short activity periods and less conservative fruiting strategies. Hot temperatures exacerbate water stress in drylands by driving increased evapotranspiration (Williams et al., 2013) and may signal plants to adjust fruiting strategies to reduce costs of reproduction. Therefore, we predict that, under future climate conditions, species with the most stable productivity (Figure 1) and highest productivity (Figure 2) will be those that grow over a long window and fruit irregularly.

Sustaining vegetative and reproductive structures can result in large, stable populations, but at the cost of exposure to environmental extremes. Similar to prior work and *a priori* expectations, we found that species with earlier leaf-out dates experienced colder temperatures (Polgar & Primack, 2011), and species with longer vegetative phenophases grew during a broader range of temperatures. Longer growing seasons in drylands require maintenance of vegetative structures through hot, dry conditions, limiting growth in some species but allowing others to capitalize on growth opportunities when rain does occur, including during cooler shoulder seasons of early spring and late fall (Barber et al., 2000; Petrie et al., 2015). Broad reproductive windows allow some dryland species to make multiple flowering attempts before successfully fruiting (Crimmins et al., 2013). However, even though these strategies were not without risk, the phenological traits of early onset and longer phenophases were both associated with higher temporal stability in population biomass production.

Although we captured a large range of phenological trait variation, our study was limited by some practical factors. First, we recorded monthly phenology for up to 10 individuals per species per transect. This method could be biased towards larger, more phenologically advanced individuals and could discount cryptic, intraspecific phenological variation (Albert et al., 2019). Second, our method assigned only qualitative phenological stages to each individual plant, limiting precision of our estimates of phenophase (e.g. we did not estimate percentage of buds in flower). Lastly, we used traditional phenophase transition dates rather than process-based metrics that capture within-year population variability (Inouye et al., 2019). These methods simplified complex variation in plant phenology but facilitated comparisons across a wide range of species.

Long-term monitoring programmes are uniquely poised to capture population dynamics and ecologically meaningful trait data that can be difficult and time consuming to measure (Kominoski et al., 2018). We leveraged decades of data across ecosystems and climate conditions to link the stability of plant species' above-ground biomass, phenological traits and climate, inferences that are not easily replaced by space-for-time substitutions (Gerst et al., 2016; Harris et al., 2018; Kazenel et al., 2019; Lasky et al., 2016). Alternative vegetative and reproductive investment strategies among species influenced their exposure to climatic extremes. We revealed the potential for phenological traits to predict differences in the temporal stability of population biomass among species in highly variable, dryland environments.

## AUTHOR CONTRIBUTIONS

Alesia J. Hallmark completed this work as part of their Ph.D. in Biology. Alesia J. Hallmark generated the original question driving the work, led the data analysis and led the writing of this manuscript. Scott L. Collins is currently a co-investigator and former lead PI of the Sevilleta LTER program through which he led work to collect, curate and maintain the long-term data sets used in this study. Scott L. Collins contributed to writing and editing. Marcy E. Litvak is co-PI of the Sevilleta LTER program and assists with ongoing work to curate, manage and maintain the long-term data sets used in this study. Marcy E. Litvak contributed to writing and editing. Jennifer A. Rudgers currently directs the Sevilleta LTER program to collect, curate and maintain the long-term data sets used in this study. Jennifer A. Rudgers contributed to conducting data analysis, researching the background literature, writing and editing.

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## CONFLICTS OF INTERESTS STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All data packages and R scripts used in this study are available through the Environmental Data Initiative: <https://doi.org/10.6073/pasta/3aa17817f28596b2823d492474a8a409> (Hallmark, 2024).

## STATEMENT ON INCLUSION

Our study was conducted as part of the Sevilleta Long-Term Ecological Research program. Over the past 30 years, the leadership, staff and associated researchers of this program has been comprised of an international, diverse group of people. The authors represent a range of professional stages, genders and backgrounds, a reflection of the diversity seen in the Sevilleta LTER program overall.

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## SUPPORTING INFORMATION

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

**Figure S1:** CV of maximum annual biomass compared to the CV of biannual biomass.

**Figure S2:** Correlogram of all phenological traits included in our analyses.

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